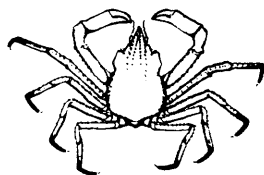




SHRIMPS, LOBSTERS, AND CRABS
OF THE ATLANTIC COAST
OF THE EASTERN UNITED STATES,
MAINE TO FLORIDA



AUSTIN B. WILLIAMS



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Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida

Austin B. Williams

Introduction

This book is an illustrated compilation of information on identification, description, distribution, life history and ecology for species of decapod crustaceans that occur over the continental shelf of the temperate eastern United States. It is a critical review of published biological information on an animal group that includes species of shrimps, lobsters and crabs which are the direct basis for some of our most valuable fisheries, as well as many other species which are either known to have ecologically conspicuous roles in their biological communities or are subjects for research. Understanding of these animals depends first on identity and then on assessment of relationships.

The presentation includes general brief treatments on the history of decapod crustacean studies in the region, classification of the group, its zoogeographic relationships, details concerning study materials, and a set of species accounts to which the reader is led by indexes and keys for identification.

History

Literature concerning shrimps, lobsters, and crabs found in temperate coastal waters of the eastern United States dates from the beginning explorations of Europeans in the western Atlantic in the

Austin B. Williams, National Oceanic and Atmospheric Administration, National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

16th century. Accounts regarding these animals, from the first quaint tales to the comprehensive technical and popular works of our own time, have been reviewed from historical perspectives in a few general works, but the facts mostly rest in synonyms or brief remarks in species accounts. I attempt no full historical treatment of this subject here, for it contributes little to the main purpose of the work. The major monographs are apparent in the species accounts that follow.

The book is a revised and extended "Marine Decapod Crustaceans of the Carolinas" (Williams 1965), originally Hay and Shore's (1918) "The Decapod Crustaceans of Beaufort, N. C., and the Surrounding Region."

Clarence A. Shore (1873–1933) planned a handbook on decapod crustaceans of the Beaufort, N. C., region while he was teaching in the medical school of the University of North Carolina at Chapel Hill. He entered the University in 1897, majored in biology, earned the M. S. degree in 1902, and spent several summers at the U. S. Bureau of Fisheries Marine Laboratory at Beaufort, N. C., where he developed an interest in taxonomy and ecology of crustaceans, and in 1904 began three years of study, extending and embellishing with descriptions and photographs a list of most of the decapod crustaceans known to occur in that region which was compiled between 1880 and 1903 by Professor W. K. Brooks and his students from Johns Hopkins University, but the work was incomplete when he left the project to enter a career in medicine (Cooper 1933, 1940; Wilson 1933). Shore's manuscript included 87 species.

William Perry Hay (1871–1947), graduate of Butler University in 1891 and teacher in the Washington, D. C., area from 1892 to 1934, had a great interest in natural history, especially herpetology and carcinology (Needham 1947). He took up Shore's uncompleted project in 1912, incorporated much new data, and finally published it 14 years after initiation of the effort. The paper treated 153 species, including three freshwater crayfishes.

By 1965, the marine fauna of the Beaufort area had become much better known through efforts of a large number of biologists in the cluster of university and government laboratories located there and in neighboring states. In updating the manual, I retained Hay and Shore's dual objective of providing aids to identification and a condensed review of what was known concerning the life history-ecology of each species, treating 220 species plus notes on 14 others doubtfully represented in the region. Now it seems appropriate to extend similar coverage to the coastal area north of Cape Hatteras where faunal studies antedate those mentioned above.

Studies for the New England-Middle Atlantic region that parallel those mentioned for the Carolinas are the monumental works on Brachyura by M. J. Rathbun (1918b, 1925, 1929, 1930a, 1935, 1937) which were preceded by her (1905) list of the Crustacea of New England, and H. W. Fowler's (1912) "Crustacea of New Jersey." Later versions of these reviews are the chapter edited by R. I. Smith (1964) in keys to marine invertebrates of the Woods Hole region, a treatment of the group by Gosner (1971) for the Cape Hatteras to Bay of Fundy region, and a key and list of species in the New England area with mapped distributions by Williams (1974c) and Williams and Wigley (1977). Other popular handbooks such as Miner (1956) swell this list of references.

Recent exploratory work has contributed many extensions of range as well as a few newly described species. The new total for the entire region is 342, plus a few extralimital species.

The most time-consuming part of rewriting has been researching and condensing the life history-ecological literature whose recent geometric rise in quantity has made that part of the task almost unmanageable. There has been no attempt to abstract strictly physiological papers or the proliferating studies on environmental alteration; therefore the coverage is selective, but the reader will find reference to much of the critical literature through about 1979, including scattered papers from 1980–81 for nomenclatural purposes.

Abundant intertidal or littoral species and a few species belonging to the genera *Penaeus*, *Homarus*,

and *Callinectes* that have great commercial value are still the most thoroughly studied decapod crustaceans in the region. Integrated community analyses seldom treat other than "well known" species, and it remains fair to say that ecological studies involving this fauna, though well started, are far from completed.

Classification

What arrangement of families should be followed in classifying decapod crustaceans? When identification of taxa is the chief objective, this question is perhaps of little concern, but in setting up a framework for families some attention must be directed to it. The task would be routine if a single system were the accepted standard, but there are alternate systems suggested for the order Decapoda. Thus, the question regarding arrangement of families is unanswerable conclusively.

Most recent classifications of the Decapoda have followed that summarized by Borradaile (1907) which is based on adult morphology of living species. It is a system which lends itself well to construction of keys to the hierarchy, but it has some weaknesses that result from parallelism. Moreover, paleontologists have pointed out difficulties in attempts to harmonize this system with evidence from the fossil record (Glaessner 1969). A third indirect line of evidence involves the relationships implied by larval development, if larval characters are admitted as indicators of relationship (Rice 1980, for a recent analysis of brachyuran larvae).

Balss (1957) reviewed the various classifications employed up to that time, and Glaessner (1969) introduced further modifications necessitated in part by a definition of the term "tribe" as subordinate to subfamily (*International Code of Zoological Nomenclature* 1961), allowing that term to be superseded by the terms "infraorder" and "section" between the rank of suborder and superfamily. These classifications, including another from Bouvier (1940), are outlined below for comparative purposes.

Borradaile's (1907) system.—

Suborder Natantia

Tribe Penaeidea

Caridea

Stenopodidea

Suborder Reptantia

Tribe Palinura

Astacura

Anomura

Brachyura

Bouvier's (1940) system.—
 Suborder Macrura Natantia
 Suborder Reptantia
 Section Macrura Reptantia
 Tribe Homaridea
 Palinura
 Thalassinidea
 Section Anomura
 Brachyura

Balss' (1957) system.—
 Suborder Natantia
 Tribe Penaeidea
 Eucyphidea (Caridea)
 Stenopodidea
 Suborder Reptantia
 Division Palinura (subdivision into Tribes)
 Astacura " " "
 Anomura " " "
 Brachyura " " "

Glaessner's (1969) system.—
 Suborder Dendrobranchiata
 Infraorder Penaeidea
 Suborder Pleocyemata
 Infraorder Stenopodidea } ["Macrura"]
 Caridea
 Astacidea
 Palinura
 Anomura
 Brachyura

It is obvious that there is basic unity among the systems, but branching at the infraordinal level among shrimps, lobsters and certain anomurans has been a matter of debate. Divergence in opinion has centered on the relation of the Penaeidea to the remaining shrimps, and to some degree on the possible connection of the Penaeidea to other groups such as the Astacidea (*Homarus* and relatives, all with first three pairs of legs chelate). Paleontologists and some neozoologists point out that the Penaeidea have a suite of characters which separate them from other Decapoda (first three pairs of legs chelate, hatch from eggs broadcast in the water, develop through numerous larval stages beginning with a nauplius; whereas the remaining decapods usually lack chelae in this combination, having first three pairs of legs variously chelate or not, hatch from eggs retained on pleopods of females as larvae advanced beyond the naupliar stage). Glaessner (1969) building on the proposals of Burkenroad (1963), devised what he conceived to be a conservative classification, accommodating the paleontological view of the Penaeidea as primitive to the classification acceptable as standard by most neozoologists. Since that time, Chace and Manning

(1972) described a new superfamily of caridean shrimps, Procaridoidea, to receive *Procaris ascensionis* which possesses a suite of characters otherwise represented only in the Penaeidea, including the absence of chelae on most (all) legs, seven-segmented third maxillipeds and massive epipods. Lack of chelae in this seemingly primitive species, together with evidence from another caridean, *Pseudosquilla enigma*, from the Great Barrier Reef having all five pairs of legs chelate (Chace and Brown 1978), and other groups, seems to indicate that chela formation is variable, a specialization which has evolved independently in several lines. Such adaptations leave the penaeid line perhaps less isolated than Glaessner's system would have it.

There are further differences of opinion as to arrangement of superfamilies within infraorders. Every classification is a compromise. In Williams and Wigley (1977), I accepted Glaessner's classification in toto, but here I have adopted his superfamily arrangement modified slightly on the basis of later studies.

Recently, the Brachyura have been a focus of interest among several students of decapod crustacean phylogeny. New evidence from adult morphology, fossil record, and larval development is leading to reinterpretation of classical views of relationships within the group and of it to its antecedents (Guinot 1978, 1979; Rice 1980; de Saint-Laurent 1980a, 1980b). The merits of these ideas have yet to be evaluated, and therefore they are not elaborated here.

Zoogeographic Considerations

The fauna treated ranges in marine waters along parts of the eastern and southern United States considered by Hedgpeth (1953) to lie in the Boreal (north of Cape Cod), Virginian (between Cape Cod and Cape Hatteras), and Carolinian provinces (between Cape Hatteras and a region just north of Cape Canaveral but extending in modified form through the northern Gulf of Mexico from about Sanibel I., Fla., to the Rio Grande River). These are faunal provinces or marine climatic zones resulting from seasonal temperature regimes. Hazel (1970) reviewed concepts applied to marine climatic zones of this region by workers during the last hundred years, showing that perhaps a less cumbersome terminology groups the provinces as subdivisions of a temperate region: cold temperate, mild temperate, and warm temperate respectively, although references to Carolinian, Virginian, or Boreal are retained here.

Watling (1979) referred to faunal assemblages of northeastern North American amphipods as con-

forming most closely to a pattern summarized (in preparation) by Franz and Merrill as (1) "Arctic-Boreal," containing a few species endemic to the northwestern Atlantic, a large number of species which range from south of Newfoundland into Arctic waters, and a few extending into the Pacific; (2) "Boreal," containing both endemic and amphiatlantic species ranging from Cape Hatteras to Labrador or over shorter distances within these ranges; and (3) "Transatlantic," comprised of shallow nearshore and estuarine species endemic to American Atlantic waters which range extensively north and south of Cape Hatteras (although this category fits few decapod crustaceans). Whatever system of names is chosen, it is clear that prominent coastal features serve to mark more or less distinct latitudinal ranges or marine zoogeographic provinces in eastern shelf waters of the continent (Table 1).

Species which occur from the heads of estuaries to the 190-m (100-fathom) contour are included. Strictly freshwater decapods have been excluded because they never occur in the marine environment. Species that occur only beyond 100-fathom depths more properly belong to a deep-sea fauna that ranges far beyond the coastal provinces, and are not included. Judgments undoubtedly will differ as to which species are extralimital and which are not. A few species with marginal relationships to this regime are listed below.

A summary distribution of basically arctic-boreal and tropical-subtropical groups of decapod crustaceans occurring in marine waters of the eastern United States is given in Table 1. Here, limits in geographic range are interpreted broadly, especially in their reaches beyond the primary center of interest, eastern North America, and the natural boundaries or barriers along this stretch of coast.

It is apparent that a small number (7.9%) of the species are northern in affinity, 1.2% ranging from circumarctic centers southward, 3.2% from the North Pacific to western Atlantic or beyond, and 3.5% through the eastern and western North Atlantic.

A transitional group (7.0%) ranges from the Canadian maritime provinces for variable distances southward. By comparison, Herbst, et al. (1979) listed 17.6% of Carolinian species ranging north of Cape Cod, a figure that included some species from the preceding northern group.

A much larger element is southern in affinity. At its greatest extension northward, 14% of the species reach to Cape Cod, that landmark representing a thermal barrier in shelf waters beyond which these animals do not thrive (15.5% in Herbst, et al. 1978). Totals are also given for species extending

northward to the Middle Atlantic States (9.4%) (10.3% in Herbst, et al. 1979). Many of these records are for accidental or seasonal occurrences, i.e., species whose northern limits of range might well be set at Cape Hatteras, but there are other species in the group which must be permanent residents in those latitudes and are not dependent on annual repopulation from breeding stock to the south.

At Cape Hatteras, warm water of the Gulf Stream meets the cold Labrador Current, to be deflected seaward (Hutchins 1947), and there 18.4% of the southern decapods are apparently unable to bridge the varying but relatively narrow transition zone to colder water. Herbst, et al. (1979) listed this fraction as 28.2%.

Cape Lookout, surprisingly, seems to represent a greater barrier to northward extension of range among Antillean species (34.2%) than Cape Hatteras. Herbst, et al. (1979), in reviewing distributions of decapod crustaceans along the east coast of the United States, found a value for northern limits of southern species there almost identical to that reported by Williams (1965), 32.6% and 31.4% respectively, and postulated that substrate diversity and stability in the warm waters of the region provide suitable environments which are absent from the sandier, less stable substrates and more variable temperatures around Cape Hatteras. The region around these two capes together is a major barrier to northward extension of approximately 50% of the east coast decapod fauna.

Records of southern species showing distributions reaching northward to the ill-defined Cape Fear-Charleston-Georgia region (9.1%) seem to represent accidental or casual occurrences, for there is no apparent barrier to northward dispersal beyond that latitude.

A very few of the species are cosmopolitan in tropical and warm temperate waters of the world, and endemic forms are even less numerous.

Aside from the above patterns of distribution, a number of species ranging along the Atlantic coast (especially south of Cape Hatteras) and the Gulf of Mexico coast to Texas have a disjunct distribution in peninsular Florida. The number of these species is conservatively estimated, from published records, at 10% of the total. This type of distribution, discussed at length by Hedgpeth (1953), shows a fairly recent separation of Gulf elements from the Atlantic portion of the species range by emergence of peninsular Florida, but with the two areas being climatically similar (Hutchins 1947). In a few cases, geminate species have apparently evolved from this separation. It is also clear, from families represented in this group, that many are relatively sedentary, at least as adults.



Fig. 1. Area of western North Atlantic Ocean, including parts of eastern North America, Middle America, and northern South America, covering centers of distribution for most species treated in this handbook.

Species Accounts

A great deal of recent spadework by specialists has made abbreviation of synonymies desirable and practical; therefore, most synonymies are re-

stricted to citation of original description, important systematic or faunistic papers which include synonymies and/or descriptions, and the most recent published revision. Inclusion of species treated in the thorough and well-illustrated papers by Chace

TABLE 1.—Geographic ranges of marine decapod crustacean species occurring on continental shelf of temperate eastern United States, arranged by family. Coverage: Temperate-tropical species—western Atlantic exclusive of Bermuda; arctic-boreal species—northern Pacific, Arctic Ocean, west and east Atlantic. Lower portion of table shows combined total

Family	Number of Species	Circum-arctic to N. Pac. and Japan; E and W N. Atl. to Cape Cod and mid Atl. states	Eastern N. Pac.; N. Atl. E thru Kara Sea	N. Pac. to New England or N. C.	Japan thru arctic Canada to Cape Cod or Florida	E and W N. Atl.	Canadian Maritime Provinces and G. of Maine to—	G. Bank and Cape Cod thru G. Mex. and Carib. to S. Am.	Cape Cod thru G. Mex. and Carib.	Cape Cod to E. Fla., E G. Mex. and Carib.
Solenoceridae	4									
Penaeidae	8								1	
Sicyoniidae	7									
Sergestidae	2							1		
Stenopidae	2									
Pasiphaeidae	4					1		1	1	
Bresiliidae	1									
Palaemonidae	18					1	2WM			
Gnathophyllidae	1									
Alpheidae	11									
Ogyrididae	2									
Hippolytidae	23	4	2	1	1	1WA	1SA	2	1	2(1NC)
Processidae	7									
Pandalidae	5			1	1	2				
Crangonidae	8		2	1	1	2	1M			
Nephropidae	1						1NC			
Palinuridae	1									
Scyllaridae	4									
Callinassidae	3								1	
Axiidae	3						1L 1EM 2NC			
Laomedidae	1									1NC
Upogebiidae	1							1		
Paguridae	31					1	2V 2WM			2F
Lithodidae	1					1				
Galatheididae	6							1	1	
Porcellanidae	8							1		1
Abuneidae	3									
Hippidae	2								1	
Dromiidae	4									
Tymolidae	2									
Homolidae	1							1		
Latreillidae	1							1		
Raninidae	4									
Dorippidae	3								1	
Calappidae	10								1	1
Leucosiidae	9							1		
Majidae	44				1M	2	1NC 1WM	3	2(1GM)	1FS
Parthenopidae	9							1	1	
Cancriidae	2						2F			
Portunidae	20					1	2SA 1G	1		
Xanthidae	29						1FS 1WM	2	1	
Goneplacidae	7									
Pinnotheridae	15						1SA	3	2(1GM)	1E
Grapsidae	7						1C		1	
Ocypodidae	4							1	2	1F
Palicidae	3									
Total	342	4	4	3	4	12	10 14	21	17	10
		Circum-arctic—South	North Pacific to W Atlantic		E and W North Atlantic		Canada—South	Cape Cod—South		
Combined total		4	11		12		24	48		
Percent total	100	1.2	3.2		3.5		7.0	14.0		

of species with ranges limited by natural barriers. (C = Caribbean; EM = eastern Gulf of Mexico; F = Florida; FS = Florida Straits; G = Georgia; GM = Gulf of Mexico; L = Long Island Sound; M = Gulf of Maine; NC = North Carolina; SA = South America; V = Virginia Capes; WA = western North Atlantic; WM = western Gulf of Mexico.)

			Cape Hatteras thru G. Mex. and Carib. to S. Am.	Cape Hatteras thru E G. Mex., Carib. to S. Am.	Cape Hatteras thru G. Mex. and Carib.	Cape Hatteras thru G. Mex.	Cape Lookout thru G. Mex., Carib. to S. Am.	Cape Lookout thru E G. Mex. Carib. to S. Am.	Cape Lookout thru G. Mex. and Carib.	Cape Lookout thru G. Mex., some to Carib.	Cape Fear, Charleston, S. C.—Ga., to G. Mex., Carib. and S. Am.
1 1 2 1 1 3 1 1 4 1 15	1 1 1 1 1 1 7	2 1 1 1 IFS 2 1 10	3 1 2 1 1 2 1 3 4 2 1 33	1 2 2 1 3(2C) 16	1 1 2 1 6	8	1 3 1 6 1 2 1 1 2(1C) 1 2 2 5(2C) 1 5 1 3 41	1 2 1 2 5 2 1 34.2	1 1 1 4 1 1 3 1 1 2 1 2(1NC) 14	1 2 1 2 1 5(1G—FS, 1GM) 1EM 2 1 1 3(1GM) 1 3 3 1C 3(1G, 1GM, 1C) 1C 31	
Middle Atlantic—South			Cape Hatteras—South				Cape Lookout—South				Cape Fear, Georgia— South
32			63				117				31
9.4			18.4				34.2				9.1

(especially West Indian elements, 1972, 1976) is in a sense redundant, except for convenience. Not only have I depended heavily on his work but also on Coelho and Ramos (1972), Holthuis (1951a, 1952, 1959), Rathbun (1918b, 1925, 1930a, 1937), and Schmitt (1935a) for key characters, color notes, or depth and latitudinal ranges. For these works, specific citations in the text have often been excluded for the sake of brevity.

Still a tremendous source of information is Holthuis's (1955) key to Recent genera of Caridea and Stenopodidea, though the more modern key of Burukovsky (1974) includes lobsters as well, but that work is entirely in Russian and hence of diminished utility to most readers of English. Moreover, Manning and Holthuis (1981) have given an exhaustive review of brachyuran family names in their treatment of West African crabs.

For convenience, the arrangements of genera within families and species within genera are alphabetical except where such arrangement would obscure natural clusters in groups such as the Xanthidae that are not yet well subdivided. Important diagnostic characters of families are given in brief paragraphs as well as in the keys. Important characters of genera containing two or more species are sometimes given in short diagnoses as well as in the generic keys, but often in the generic keys alone, and in the case of monotypic genera may be included in recognition characters for the species. Such treatment leads to some repetition but gives more complete accounts under each heading.

The general key to suborders, infraorders, sections, superfamilies and families serves as a rough index. Other keys to subfamilies, genera and species are either combined or separate, depending on number of groups involved, and scattered throughout the text.

Materials Studied

Materials studied include the rich collections in the Smithsonian Institution, National Museum of Natural History, many valuable acquisitions in recent years having come from explorations carried out on vessels of the National Marine Fisheries Service (NMFS). Specimens listed by Springer and Bullis (1956) from the M/V *Oregon*, actually identified by F. A. Chace, Jr., and later collections from the vessels *Oregon*, *Silver Bay*, *Combat*, and *Pelican*, listed by Bullis and Thompson (1965), are housed in the crustacean collection of the National Museum and are designated in text as (USNM) when they represent known range limits for species. A large collection at the National Marine Fisheries

Service Northeast Fisheries Center, Woods Hole, Mass., taken during benthic sampling by the M/V *Albatross III*, *Albatross IV*, *Delaware I*, and *Delaware II* was also studied (Williams and Wigley 1977). Crustacean collections at the University of North Carolina Institute of Marine Sciences (UNC-IMS), Morehead City, and Duke University Marine Laboratory (DUML), Beaufort, N. C., documenting the Carolinian fauna are derived in part from various sampling programs by the DUML-sponsored R/V *Eastward*, and other material from that region was provided by the South Carolina Marine Resources Research Institute (SCMRRI), Charleston. Additional materials or records confirmed came from the Charleston Museum, Charleston, and the former Bears Bluff Laboratories, Wadmalaw Island, S. C., the NMFS Laboratory, Beaufort, N. C., and fishing vessels and private individuals too numerous to mention individually. Remnants of Hay and Shore's collections were also examined and are now housed at the UNC-IMS.

Measurements

Measurements for individuals considered adult are either from the literature or from specimens examined. Sizes recorded usually represent the maximum. Width of the brachyuran carapace is the width including lateral spines. Length of shrimps includes the rostrum unless stated otherwise.

Glossary

There is a tendency in carcinology to assume that most readers have a specialized background, and beginners, therefore, may find themselves troubled with terms. A number of monographs have included introductory glossaries and figures with detailed labeling as aids, but these are not always adequate because terminologies in various categories of the hierarchy lack consistency.

An illustration of inconsistency follows: Among shrimps, the pereopods are often called the first, second, third, fourth, and fifth walking legs. Among crabs, the tendency is to call the first pereopods "chelipeds," because they are almost invariably larger than the remaining legs and are the only chelate pair (except in anomuran and some dromiid crabs). The remaining pereopods are then termed the first, second, third, and fourth walking legs. This inconsistency seems firmly entrenched and is based on functional morphology, the shrimps tending to have five pairs of legs that may be used in walking, but most crabs only four. Because many shrimps actually do not walk, legs in this group

herein have been called "legs," the term "walking legs" being reserved for crabs. The use of explanatory figures adapted from existing works, together with the glossary, should resolve most of such difficulties.

Many of the structures listed alphabetically and defined are shown schematically on Figs. 2, 3, and 4. Other terms not listed are shown on these figures.

Acicle.—Antennal scale reduced to a spine.

Afferent channels.—Openings through which water passes to gills. In brachyuran crabs, usually opening behind pterygostomian regions and in front of chelipeds except in certain Oxystomata in which they open at anterolateral angles of palate or endostome.

Antennal spine.—Spine on anterior edge of carapace immediately below orbit adjacent to base of antenna (Fig. 2).

Anterolateral teeth.—Teeth on anterolateral border of crabs between orbit including lateral spine, exclusive of outer orbital tooth.

Apodeme.—Any cuticular ingrowth of body wall.

Appendix interna.—Small separate branch on

mesial side of pleopodal endopodite, usually tipped with hooks which interlock with opposite member in swimming.

Appendix masculina.—Accessory male organ located mesially on second pair of pleopods between endopodite and appendix interna.

Arthrobranchiae.—Gills attached to articular membrane between coxa of an appendage and body wall.

Basis (basipodite).—Second article (from body) of leg or maxilliped. Sixth segment from distal end of limb.

Basicerite.—Spine on dorsal side of basis of antenna; sometimes more lateral than dorsal.

Branchiocardiac groove.—Groove separating branchial and cardiac regions.

Branchiostegal spine.—Spine on anterior edge of carapace, or near it, immediately below branchiostegal groove (Fig. 2).

Branchiostegite.—Part of carapace not coalesced ventrally with thoracic somites, but overhanging on each side as covering for gill chamber.

Buccal cavity.—Cavity on ventral surface of body

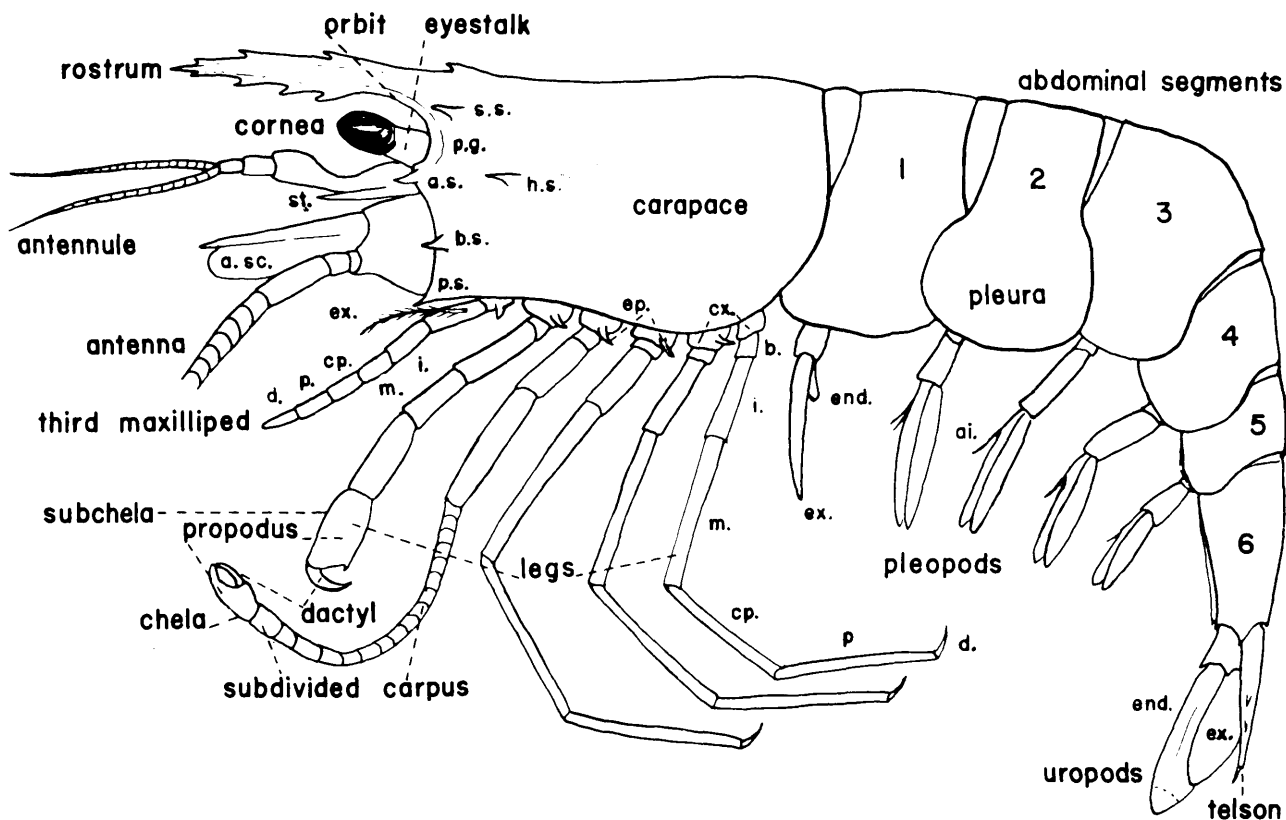


Fig. 2. Schematic drawing of shrimp in lateral view: ai, appendix interna; as, antennal spine; asc, antennal scale; b, basis; bs, branchiostegal spine; cp, carpus; cx, coxa; d, dactyl; end, endopod; ep, epipod; ex, exopod; hs, hepatic spine; i, ischium; m, merus; p, propodus; pg, postorbital groove; ps, pterygostomian spine; ss, supraorbital spine; st, stylocerite. (Modified from Holthuis 1955; Schmitt 1921.)

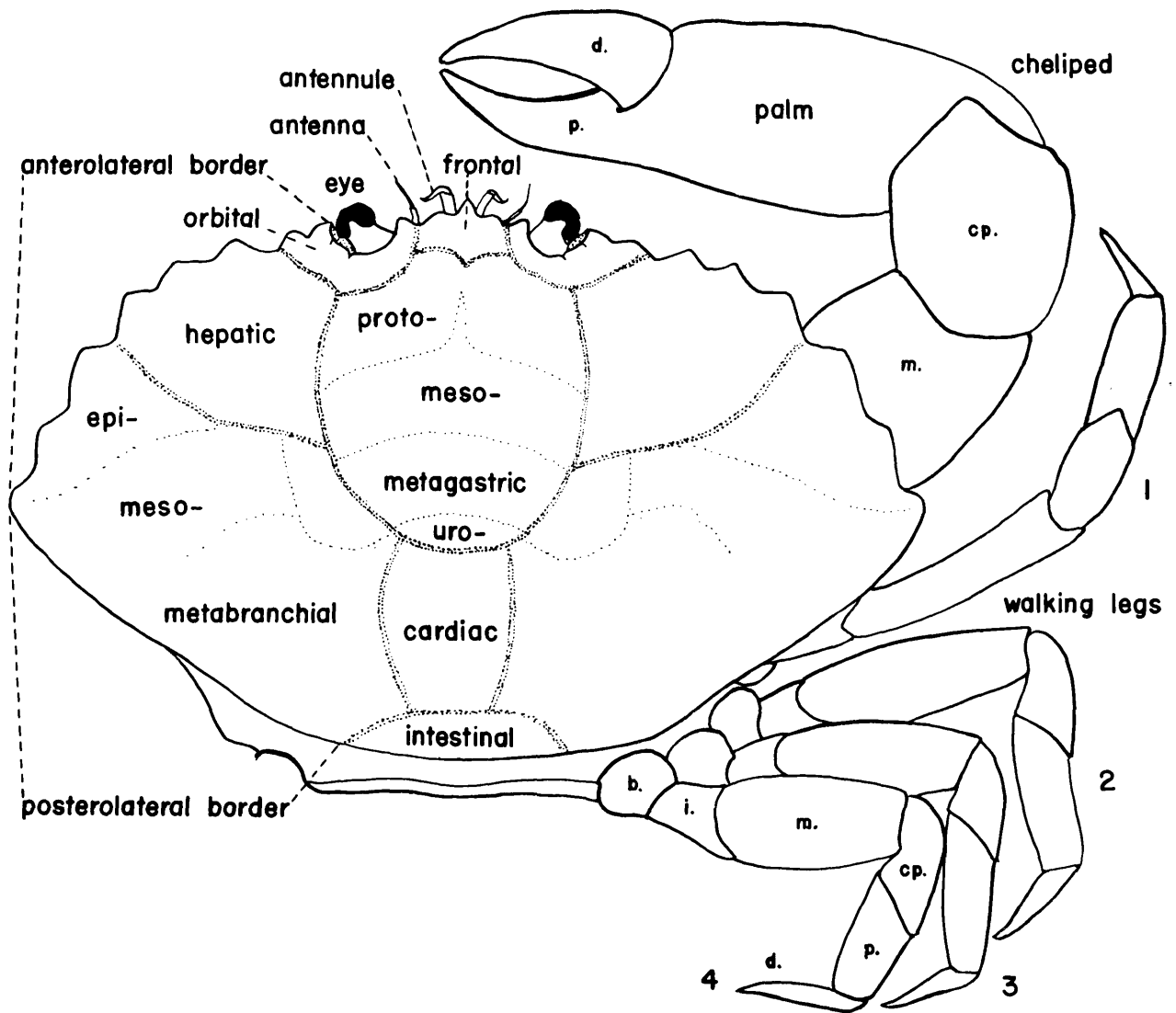


Fig. 3. Schematic drawing of brachyuran crab in dorsal view; areas of carapace indicated; legs of right side only shown; b, basis; cp, carpus; d, dactyl; i, ischium; m, merus; p, propodus.

in which mouthparts are situated; bounded anteriorly by epistome, laterally by free edges of carapace. Within this "frame" lie the mouthparts, which in most Brachyura are covered by operculiform third maxillipeds.

Carina.—Keel-like ridge or prominence.

Carpus (*carpopodite*).—Third article from distal end of leg.

Cervical groove.—Complex groove running across carapace. Transverse at middle, then turning obliquely forward (and outward in brachyurans) to anterolateral margin.

Chela.—Arrangement of distal 2 articles of crustacean limb in which terminal article is opposed to article preceding it in an adaptation for grasping.

In true chela, terminal 2 articles shaped as fingers, one closing against other.

In subchela, terminal article (dactyl) usually closes against distal surface of penultimate article (propodus).

Chelipeds.—Pair or pairs of thoracic legs behind maxillipeds; bearing chelae, or pincer-claws, and often stouter, sometimes much stouter, than other legs.

Coxa (*coxopodite*).—First or proximal article of leg or maxilliped.

Dactyl (*dactylus* or *dactylopodite*).—Terminal or distal article of leg; movable finger of cheliped.

Efferent channels.—Channels through which water passes from gills. Opening at sides of endostome, except in Section Oxystomata in which they open at middle of endostome.

Endognath.—Inner or principal branch of a maxilliped.

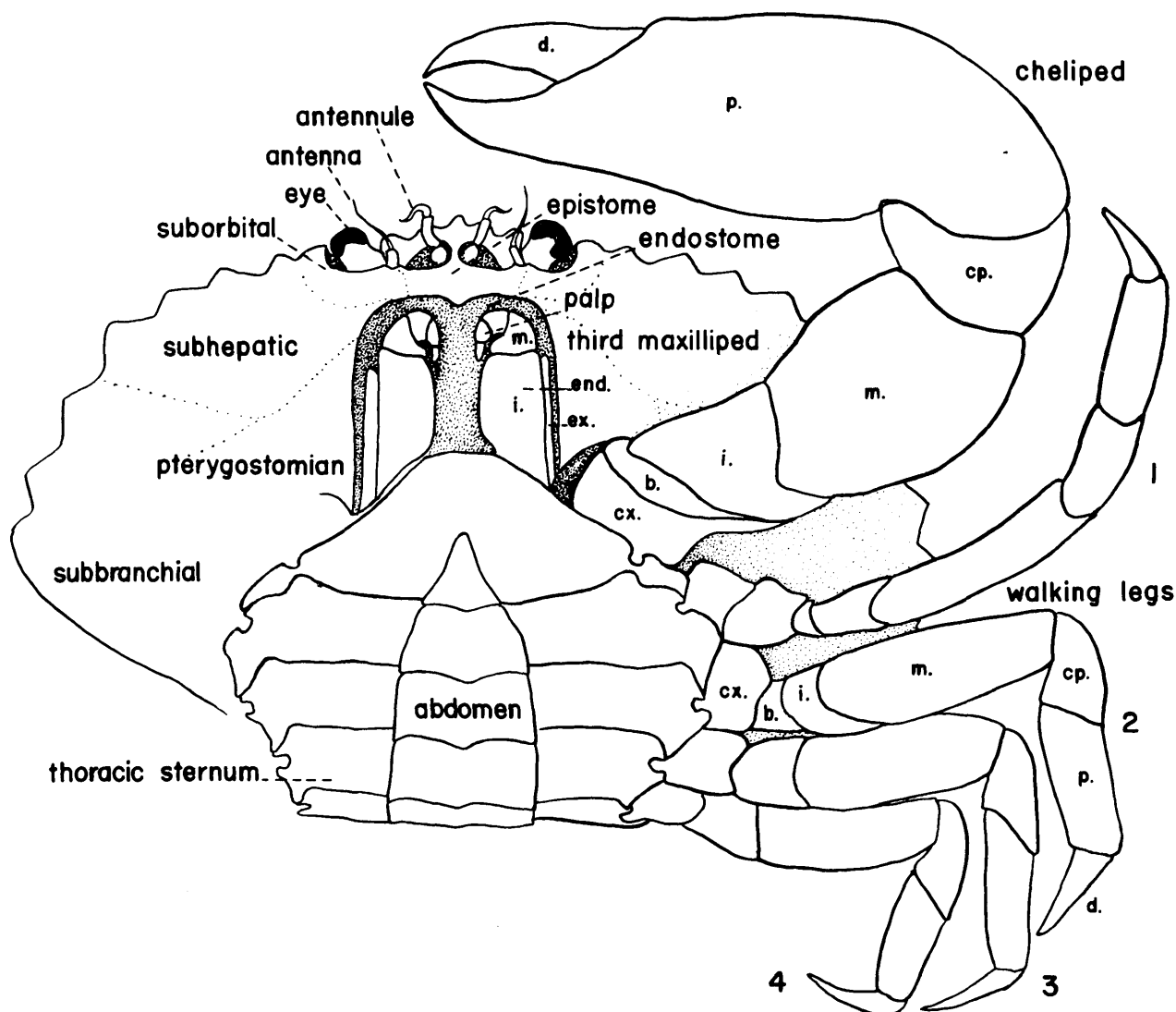


Fig. 4. Schematic drawing of brachyuran crab in ventral view; areas of carapace indicated; legs of left side only shown; b, basis; cp, carpus; cx, coxa; d, dactyl; end, endognath; ex, exognath; i, ischium; m, merus; p, propodus.

Endopodite.—Mesial ramus of biramous appendage.

Endostome.—Part of epistome forming palate in brachyurans and usually separated from epistome proper by transverse ridge.

Epibranchial (epibranchial region).—Part of porcellanid (crab) carapace situated behind orbit and above metabranchial region. Region situated between cervical groove and *linea anomurica*. Often a strong spine on region, referred to as epibranchial spine.

Epigastric lobes.—Anterior lobes or subregions of gastric regions.

Epimere.—Lateral part of wall of body somites situated between tergum and insertion of appendages.

Epipodite.—Outgrowth of first 7 thoracic coxae.

Epistome.—Antennal sternum mainly represented by epistome, a plate of varying shape lying between labrum and bases of antennae. In shrimps, comparatively narrow and separated on each side from lateral portions of carapace by exhalant branchial channels. In Astacidea and Anomura, broad and in contact with carapace on each side; in Brachyura, becoming firmly united with carapace. The epistome forms the anterior part of the buccal frame.

Exognath.—Lateral or secondary branch of maxilliped.

Exopodite.—Lateral ramus of biramous appendage.

Fingers (digits).—Narrow scissorlike blades of pincer end of cheliped, movable finger being dactyl, and fixed finger the terminal part of propodus.

Front.—Frontal portion of carapace; that portion of crab carapace lying between orbits.

Frontal teeth.—True frontal teeth; those teeth originating on front but exclusive of inner orbital teeth.

Gastric region.—Large median area, in crab carapace, bounded behind by cervical suture, laterally by hepatic regions, and anteriorly by frontoorbital regions. Divisible into following subregions or lobes: epigastric, protogastric, mesogastric, metagastric, and urogastric.

Genital region.—See urogastric lobe.

Hand (chela).—Propodus and dactyl of cheliped.

Hepatic region.—Small (paired) subtriangular, anterolateral region, wedged between branchial and gastric regions, and either margin of carapace or margin of orbit in Brachyura.

Hepatic spine.—Spine on hepatic region in shrimps (Fig. 2).

Ischium (ischiopodite).—Fifth article from distal end of leg; usually first large article of maxilliped.

Linea anomurica, L. thalassinica.—Longitudinal groove or uncalcified line on carapace which may form a hinge; such lines found in various groups, from which come the names.

Merus (meropodite).—Fourth article from distal end of leg; sometimes called arm of cheliped.

Mesogastric lobe.—Median lobe or subregion of gastric region; pentagonal in form, and with long, narrow, anterior prolongation.

Metabranial (metabranial region).—That region of porcellanid (crab) carapace situated below *linea anomurica* and, therefore, not completely united with main part of carapace.

Metagastric lobe.—Posterolateral lobe or subregion of gastric region; often not defined.

Ocellus.—Little eye, distinct from main organ of vision.

Ocular peduncle.—Eyestalk.

Orbit.—Cavity in carapace containing eye.

Orbital region.—Narrow space bordering upper margin of orbit; not always distinguishable.

Palate.—Roof of buccal cavity in crabs.

Palm.—Proximal part of propodus of chela.

Petasma.—Endopodite of first pleopods in male Penaeidea; a complicated membranous plate bearing coupling hooks mesially which interlock with those on member of opposite side; may terminate distally in various complex-shaped lobes.

Pleurobranchia.—Gills attached to lateral wall of body dorsal to articulation of appendage.

Podobranchia.—Gills attached to coxa of appendage.

Postorbital groove.—Groove on carapace behind

orbit and more or less parallel to margin of orbit (Fig. 2).

Propodus (protopodite).—Second article from distal end of leg. Propodus of cheliped consists of palm and narrower fixed finger.

Prosartema (dorsal eye brush).—Long, thin, ciliated lobe arising dorsally from proximomesial border of first antennular segment and extending anteriorly; found in Penaeidea.

Protogastric lobe.—Anterolateral lobe or subregion of gastric region.

Protopodite.—Peduncle of an appendage; in unmodified form, consisting of 1 coxal and 1 basal article.

Pterygostomian region.—Triangular space on ventral surface of carapace, on either side of buccal cavity in Brachyura. Region at anterolateral corner of carapace in shrimps.

Pterygostomian spine.—Spine at anterolateral (anteroventral) corner or border of carapace in shrimps (Fig. 2).

Scaphocerite.—Antennal scale (Fig. 2).

Stylocerite.—Spine or rounded lobe on lateral aspect of basal article of antennule.

Subhepatic region.—Area below hepatic region and anterolateral border of carapace.

Suborbital spine.—Spine on lower rim of orbit (Fig. 2).

Supraorbital spine.—Spine above and behind orbit (Fig. 2).

Telson.—Terminal somite of abdomen.

Tergite.—Dorsal plate of segment.

Thelycum.—External seminal receptacle, variously developed, lying on sternum of thorax and formed by outgrowths from last and next to last thoracic somites.

Urogastric lobe.—Posteromedian lobe or subregion of gastric region; sometimes called genital region.

Systematic and Ecological Discussion

Order Decapoda

Caridoid facies either retained or greatly modified. Exopodite of maxilla (scaphognathite or bailer) large. First 3 pairs of thoracic limbs specialized as maxillipeds. Gills typically in several series, attached to coxae of thoracic limbs, to their articular membranes, and to lateral walls of thoracic somites (podo-, arthro-, and pleurobranchia); rarely absent. Young rarely hatched in nauplius stage (Calman 1909).

Key to Suborders, Infraorders, Sections, Superfamilies and Families

Characters used in this and all following keys apply primarily to Decapoda along the east coast of the United States, not to areas outside that region.

1. General form shrimplike, usually compressed; pleura of second segment never overlapping those of first segment; first 3 pairs of legs usually chelate (except in some Sergestoidea), third pair never unusually robust [Suborder Dendrobranchiata; Infraorder Penaeidea] 2
- General form shrimplike, lobsterlike or crablike; if shrimplike with pleura of second abdominal segment overlapping those of first segment and third pair of legs not chelate or unusually enlarged (except *Stenopus*) with pleura of first abdominal segment overlapping those of second segment and third legs chelate and massive. [Suborder Pleocyemata] 6
2. All 5 pairs of legs well developed [Superfamily Penaeoidea] 3
- Last 2 pairs of legs small or wanting [Superfamily Sergestoidea] 5
3. Postorbital spine present Family **Solenoceridae**
- Postorbital spine absent 4
4. Integument more or less flexible, not stony and rigid in appearance, cervical groove present and easily discerned Family **Penaeidae**
- Integument rigid, of stony appearance; cervical groove very faint or absent. Family **Sicyoniidae**
5. Anterior region of cephalothorax not greatly elongated; gills present Family **Sergestidae**
- Anterior region of cephalothorax greatly elongated; gills absent Family **Luciferidae**
6. Form shrimplike; usually with body compressed 7
- Form lobsterlike or crablike 17
7. Pleura of second abdominal segment not overlapping those of first segment; third leg chelate, stronger than preceding [Infraorder Stenopodidea] Family **Stenopodidae**
- Pleura of second abdominal segment overlapping those of first segment; third pair of legs never chelate [Infraorder Caridea] 8
8. First pair of legs chelate or simple 9
- First pair of legs subchelate [Superfamily Crangonoidea] Family **Crangonidae**
9. Fingers of chelae on first and second legs slender, opposable edges all comblike [Superfamily Pasiphaeoidea] Family **Pasiphaeidae**
- Fingers of chelae on first or second legs variable in thickness, opposable edges not all comblike 10
10. Carpus of second legs entire; first legs always with well-developed chelae 11
- Carpus of second legs usually subdivided into 2 or more joints; first pair of legs with chelae asymmetrical or sometimes obscure. 13
11. First pair of legs stronger and heavier, though often shorter, than second [Superfamily Bresilioidea] Family **Bresiliidae**
- First pair of legs usually more slender than, rarely subequal to, second [Superfamily Palaemonoidea] 12
12. Third maxillipeds leglike; body slender in most species Family **Palaemonidae**
- Third maxillipeds broad, leaflike; body short and thick Family **Gnathophyllidae**
13. Chelae of first legs distinct, at least on one side [Superfamily Alpheoidea] 14

- Chelae of first legs microscopically small or absent [Superfamily Pandaloidae] Family **Pandalidae**
14. First pair of legs chelate; rostrum dentate or unarmed, not with single subdistal dorsal tooth 15
 Usually right first leg chelate, left ending in simple claw-like dactyl; if both chelate, rostrum with distal setose notch formed by subdistal dorsal tooth Family **Processidae**
15. Eyestalks short, usually covered by carapace; first legs stronger than second Family **Alpheidae**
 Eyestalks medium length or long, not covered by carapace; first legs not stronger than second 16
16. Rostrum small or wanting; eyestalks long, slender; first 2 pairs of legs subequal. Family **Ogyrididae**
 Rostrum well developed; eyestalks not unusually lengthened; second legs usually longer than first Family **Hippolytidae**
17. Body lobsterlike and strongly calcified; abdomen with pleura well developed; first 3 pairs of legs either all chelate or none chelate 18
 Body crablike or lobsterlike, sometimes weakly calcified in part, pleura often reduced or absent; first 3 pairs of legs never alike, first, second, or first and second legs chelate or subchelate. 20
18. First 3 pairs of legs chelate, first largest; uropods well developed, lateral ramus transversely divided. [Infraorder Astacidea; Superfamily Nephropoidea] Family **Nephropidae**
 First 3 pairs of legs never chelate, approximately equal in size; uropods well developed, lateral ramus without transverse division [Infraorder Palinura; Superfamily Palinuroidea] 19
19. Carapace subcylindrical; antennal flagella long, strong, and spiny Family **Palinuridae**
 Carapace more or less flattened dorsoventrally, lateral margins sharp; antennae short, flagella replaced by plates with dentate or lobulate margins Family **Scyllaridae**
20. Either lobsterlike or crablike; abdomen extended, bent upon itself, or flexed beneath thorax; last thoracic sternite free; uropods present; carapace not fused with epistome; first, second, or first 2 pairs of legs chelate or subchelate [Infraorder Anomura] 21
 Crablike; abdomen permanently flexed beneath carapace; last thoracic sternite fused with preceding; uropods rarely present, never biramous; carapace fused with epistome; first pair of legs chelate or subchelate [Infraorder Brachyura] 31
21. Second to fourth legs with dactyls conspicuously curved and flattened; abdomen much reduced in size and flexed beneath thorax [Section Hippidea; Superfamily Hippoidea] 22
 Second to fourth legs with dactyls not conspicuously curved and flattened; abdomen well developed but may be flexed beneath thorax 23
22. First pair of legs subchelate; carapace depressed Family **Albuneidae**
 First pair of legs simple; carapace subcylindrical. Family **Hippidae**
23. Abdomen usually asymmetrical (rarely secondarily straightened), usually membranous and with uropods adapted for holding body in hollow objects; rarely leathery, unprotected and bent under thorax [Section Paguridea] 24
 Abdomen symmetrical and obviously segmented; uropods well developed for swimming, never for holding body in hollow objects 26
24. Third maxillipeds approximated at base; chelipeds subequal, or left much larger than right, rarely with right slightly larger than left. [Superfamily Coenobitoidea] Family **Diogenidae**
 Third maxillipeds widely separated at base by sternum; right cheliped usually

- much larger than left, left never larger than right, occasionally subequal. [Superfamily Paguroidea] 25
25. Carapace firm anteriorly, more or less membranous posteriorly; rostrum obsolete or nearly so; fourth legs unlike third Family **Paguridae**
Carapace firm all over, spiny; rostrum spiniform; fourth legs like third. Family **Lithodidae**
26. Body subcylindrical; first 2 pairs of legs chelate or subchelate; abdomen extended [Section Thalassinidea; Superfamily Thalassinoidea] 27
Body depressed; only first legs chelate; abdomen bent under thorax [Section Galatheidea; Superfamily Galatheoidea] 30
27. No *linea thalassinica*; both movable and fixed antennal thorns present; first legs strongly chelate and conspicuously hairy Family **Axiidae**
Linea thalassinica present; fixed antennal thorn absent; first legs chelate or subchelate but not conspicuously hairy 28
28. Sutures on both rami of uropods; dactyls or subchelate first legs folding to reflexed position when closed Family **Laomediidae**
Sutures on uropods absent; dactyls of first legs never as above. 29
29. First legs chelate; rostrum inconspicuous or absent Family **Callianassidae**
First legs subchelate; rostrum well developed, dorsally flattened, spiny, and hairy Family **Upogebiidae**
30. Form somewhat lobsterlike; rostrum extended, well developed Family **Galatheidae**
Form crablike (*Euceramus* elongate) with abdomen folded under thorax; rostrum short and broad or wanting. Family **Porcellanidae**
31. Female openings on coxae of third legs (second walking legs); last pair of legs dorsal to others, tending to adaptation for grasping [Section Dromiacea] 32
Female openings on sixth sternite adjacent to third legs (apparent fifth sternite adjacent to second legs in Palicidae); last pair of legs almost never dorsal to others, or, if so, markedly reduced [Superfamily uncertain] Family **Palicidae**
and
[Superfamily Homoloidea] 36
32. Body compact and adapted for housing under pelecypod valve or epizootic growth; eyestalks short, orbits never ventrolateral [Superfamily Dromioidea] 33
Body rectangular, pyriform or elongate, not adapted for protective housing as above; eyestalks long, orbits hidden ventrolaterally if present 34
33. Sixth segment of abdomen with rudimentary uropods present; legs short and stout Family **Dromiidae**
Sixth segment of abdomen lacking rudimentary uropods; legs long and slender (small species) Family **Tymolidae**
34. Body rectangular or pyriform in dorsal view; legs not adapted for burrowing; eyes never sheltered in orbits; *linea homolica* (lateral on carapace) present [Superfamily Homoloidea] 35
Body elongate in dorsal view, subcylindrical; legs adapted for burrowing; orbits hidden ventrolaterally if present; *linea homolica* absent [Superfamily Raninoidea] Family **Raninidae**
35. Body rectangular; basal article of eyestalk not much longer than terminal article Family **Homolidae**
Body pyriform; basal article of eyestalk much longer than terminal article Family **Latreilliidae**
36. Mouth field prolonged forward and roughly triangular [Section Oxystomata] 37
Mouth field usually almost parallel sided, sometimes transversely ellipsoid

- or kidney shaped (in commensal Pinnotheridae) 39
37. Body more or less abnormal in shape; abdomen not hidden from dorsal view; antennae large; last 2 pairs of legs subprehensile with hooklike terminal articles [Superfamily Dorippoidea] Family **Dorippidae**
Body of normal crablike shape; abdomen hidden from dorsal view; antennae small; last 2 pairs of legs neither subprehensile nor with hooklike terminal articles [Superfamily Calappoidea] 38
38. Afferent opening to each gill chamber in front of base of cheliped Family **Calappidae**
Afferent opening to each gill chamber at base of third (external) maxilliped Family **Leucosiidae**
39. Body usually conspicuously narrowed in front (except Ophthalmiinae); rostrum usually distinct and often forked; orbits often incomplete [Section Oxyrhyncha] 40
Body moderately to quite broadened in front; rostrum absent or greatly reduced; orbits usually complete 41
40. Chelipeds not much larger than other legs; hooked hairs almost always present; second article of antenna well developed, usually fused with epistome and front [Superfamily Majoidea] Family **Majidae**
Chelipeds very much larger than other legs; hooked hairs almost always absent; second article of antenna small, short, and not fused with epistome or front [Superfamily Parthenopoidea] Family **Parthenopidae**
41. Front of carapace with 3 teeth, one of these median; antennules folding longitudinally [Section Cancridea; Superfamily Cancroidea] Family **Cancridae**
Front of carapace notched medially or entire but never with median tooth; antennules folding obliquely or transversely [Section Brachyrhyncha] 42
42. Last legs modified, distal articles flattened and often broadened to form swimming paddles; carapace usually flattened, anterolateral margins dentate, often terminating in strong lateral spine; small "portunid lobe" present on inner angle of endopod of first maxilliped [Superfamily Portunoidea] Family **Portunidae**
Last legs essentially unmodified, used as preceding 3 pairs in walking; carapace not usually flattened, anterolateral margins dentate or smoothly arched, parallel, or convergent to posterolateral corner; no "portunid lobe" on inner angle of endopod of first maxilliped 43
43. Carapace transversely oval or rectangular; front wide, notched medially; antennules in fossae 44
Carapace rectangular, wider than long, front narrow, unnotched medially; antennules without fossae [Superfamily Ocypodoidea] Family **Ocypodidae**
44. Carpus of third maxillipeds articulating at or near anterointernal angle of merus; lateral margins of mouth frame parallel or divergent [Superfamily Xanthoidea] 45
Carpus of third maxillipeds not articulating at or near anterointernal angle of merus; lateral margins of mouth frame parallel or extremely convergent, becoming transversely ellipsoid or kidney shaped 46
45. The next two families overlap:
Carapace usually transversely oval or transversely hexagonal (xanthoid); male openings coxal; male abdomen greatly narrowed in segments 4-7; tending to occur in shallow water Family **Xanthidae**
Carapace subquadrate to xanthoid; male openings coxal with genital duct lying in groove between sternites 7 and 8, or sternal; male abdomen

- somewhat more triangular than above; part of sternite 8 visible from above at level of second abdominal segment but variable in size (some species in above family share this character); tending to occur in deeper water near edge of continental shelf Family **Goneplacidae**
46. Small, usually commensal crabs with reduced eyes and orbits; adult females sometimes with carapace somewhat membranous; mouth field transversely elliptical [Superfamily Pinnotheroidea] Family **Pinnotheridae**
- Free living crabs with eyes not strikingly reduced; body usually quadrate, adult females with carapace normally calcified; mouth field parallel sided [Superfamily Grapsoidea] Family **Grapsoidea**

Suborder Dendrobranchiata

Decapods with dendrobranchiate gills (biserial primary branches themselves ramified); first 3 pairs of legs chelate; eggs hatched as nauplii. (Adapted from Glaessner 1969.)

Infraorder Penaeidea

Carapace laterally compressed; antennular stalk strong; antennal scale large, oval. Abdomen long; first segment not shortened, not overlapped by pleura of second segment. Male with petasma on first pleopods, female with thelycum on posterior thoracic somites. (Adapted from Glaessner 1969.)

Superfamily Penaeoidea

Family Solenoceridae

Integument flexible, not rigid in appearance. Carapace with postorbital spine; cervical groove extending nearly or quite to dorsal midline. Basal article of ocular peduncle bearing mesial scale, ocular plate lacking styliform projections. Prosartema well developed. Exopodites on all maxillipeds and pereopods. Podobranchs on second maxilliped, rarely posteriorly, never on fourth and fifth pair of pereopods. Two large arthrobranchs on somites VIII (second maxillipeds) through XIII (fourth pereopods). Pleurobranchs on somites XI (third maxillipeds) to XIV (fifth pereopods). Epipodites from second maxillipeds to fourth pereopods. Third and fourth pair of pleopods biramous. Second pair of pleopods in males bearing appendix maxculina, appendix interna and lateral spur.

Key to Genera and Species

(Adapted from Pérez Farfante 1977)

1. Lateral ramus of uropod with distolateral spine; dorsal antennular flagella subcylindrical, somewhat thickened proximally but abruptly narrowed and whiplike distally with small setae along edges distinct only proximally, broader and flattened ventral pair with long setae along edges ***Mesopenaeus tropicalis***
- Lateral ramus of uropod spineless; antennular flagella flattened, broad ventral pair concave mesially and heavily setose along edges, covered by more slender dorsal pair with narrowed distal part to form respiratory siphon [Solenocera] 2
2. Rostral + epigastric teeth 8–11; postrostral carina high and sharp, extending almost to posterior margin of carapace ***S. vioscai***
- Rostral + epigastric teeth 4–8; postrostral carina low or absent posterior to cervical sulcus 3
3. Anterior part of carapace glossy; scaphocerite exceeding antennular peduncle by > 10% of its own length ***S. necopina***
- Anterior part of carapace setose; scaphocerite never exceeding antennular peduncle by > 10% of its own length, usually less. ***S. atlantidis***

Genus *Mesopenaeus* Pérez Farfante 1977

Pérez Farfante 1977:331.

***Mesopenaeus tropicalis* (Bouvier)**

Fig. 5

Parartemesia tropicalis Bouvier 1905:748.

Haliporus tropicalis.—Bouvier 1906:4.—A. Milne Edwards and Bouvier 1909:217, pl. 3, figs. 1–9, text-figs. 45–54.

Hymenopenaeus tropicalis.—Burkenroad 1936:103.—Williams 1965:15, figs. 6–7.

Solenocera weymouthi Lindner and Anderson 1941:181, fig. 1.

Mesopenaeus tropicalis.—Pérez Farfante 1977:332, figs. 56–58, 60–63.

Recognition characters.—Body robust, laterally compressed; integument thin, polished, except finely setose at sides of rostrum; carapace deeper than broad with antennal, hepatic, and postorbital spines well developed, small stout spine on orbital margin; cervical groove extending nearly to mid-dorsal line; hepatic carina extending from near

anterolateral corner to level of base of third maxillipeds. Rostral crest not extending beyond level of cervical groove, armed above with 7 to 10 teeth excluding rostral tip, posterior tooth slightly remote from others; rostrum reaching base of second antennular article, straight or slightly upturned at tip, lower edge convex, unarmed, ciliated. Eye with cornea rather broad. Prosartema long, hairy, extending to or beyond middle of second article of antennular peduncle.

Dorsal antennular flagella subcylindrical, broader and flattened ventral pair setose along thin edges, dorsal pair about $\frac{1}{3}$ diameter of ventral pair at base and setose there, but rather abruptly narrowed and cleanly long and whiplike distally. Antennal flagella about 3 times body length. Exopods on all maxillipeds and legs. Spine on basis and ischium of first leg slender and strong; second legs with sharp, slender spine on basis (sometimes absent on third).

Female with projections on coxae of last 3 pairs of legs, anterior pair posteromedial and blunt pointed; second pair medial, bladelike, with thin, styliform posterior projection; third pair medial, broad, bladelike, partially covering posteriormost

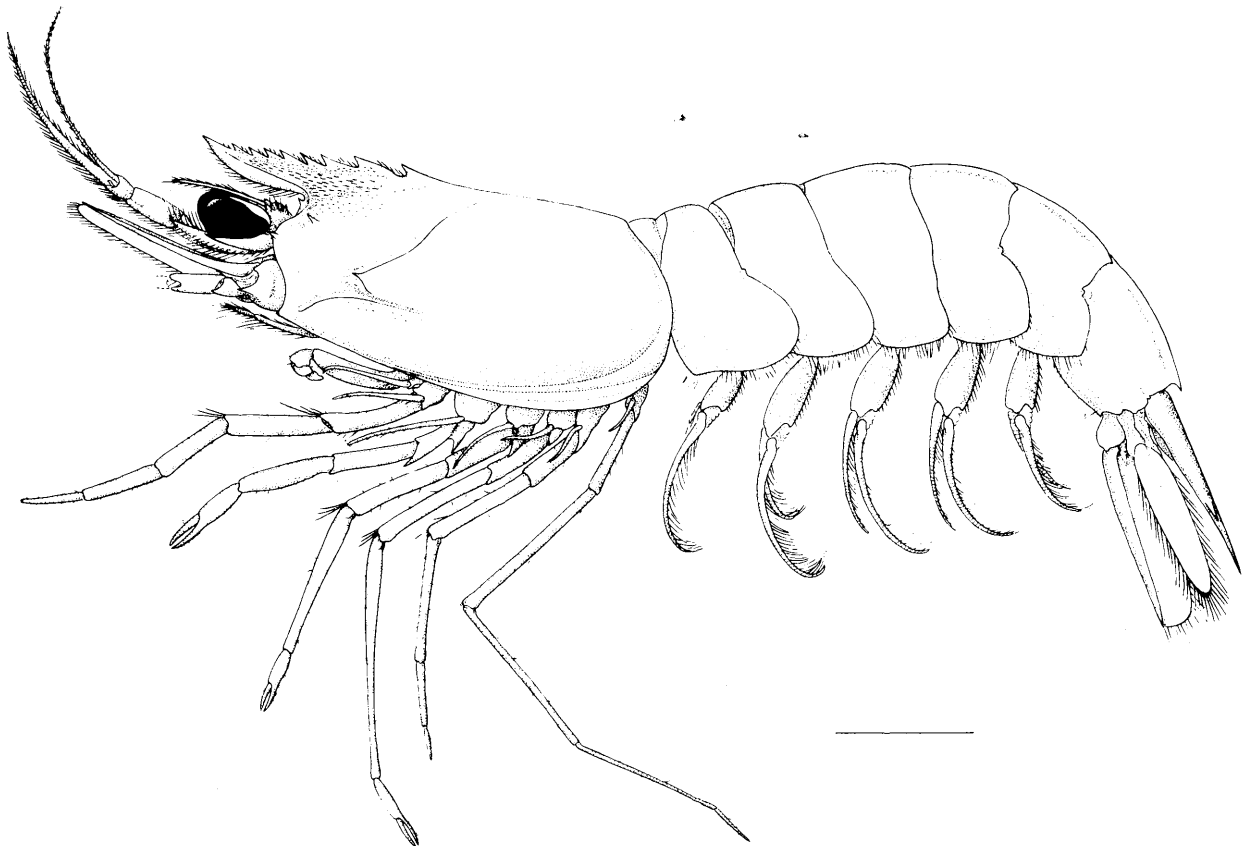


Fig. 5. *Mesopenaeus tropicalis* (Bouvier). Female in lateral view, 10 mm indicated (from Pérez Farfante 1977).

part of thelycum. Thelycum setose, bearing single posterior blade or shield; middle lobes rounded, discrete; anterior lobes closely approximated at midline, partially covered by coxal projections of fourth legs.

Abdomen with middorsal carina low and faint on third segment, progressively more prominent posteriorly; segments 3 to 5 variably cleft posterodorsally; segment 6 with small middorsal posterior spine, spine at posterolateral corners, and tooth-like projection at middle of posterolateral edge. Telson tapering to strong slender point flanked on each side by strong, fixed, subterminal spine; middorsal groove bifurcated at midlength, forks ending medial to base of fixed spines. Lateral rami of uropods with small spine at distolateral corner. Male with large, membranous, complexly folded petasma; tips of petasma reaching base of second legs.

Measurements in mm.—Length of carapace: male 20.5, female 28 (Pérez Farfante 1977).

Color.—Body translucent salmon, vertical deep yellow stripes, and milky white patches on carapace. Three anterior stripes on carapace resembling chevron; additional posterior stripe narrow on middorsum, broadening rapidly anteroventrally, then narrowing again to form band along dorsal part of branchiostegite. Three white lateral patches on carapace conspicuous, progressively larger from below hepatic spine to branchiostegite. First abdominal segment with yellow spot anterior to posterolateral hinge, remaining 5 with uniformly broad yellow stripe extending from anterior half of middorsum posteroventrally to lateral hinge, except that on 6 to extremity of pleuron as well as yellow stripe from dorsum to lateral base of telson. Pleura with salmon spot. Telson salmon, median sulcus yellow. Antennules and antennae deep salmon. Thoracic sternites and bases of maxillipeds, legs and pleopods deep salmon except for white in longitudinal band on articles and laterally on pleopods, with orange tints on endo- and exopods. Transverse orange band at posterior margin of sternites interrupting overall translucent salmon. (Selected from Pérez Farfante 1977.)

Habitat.—Continental shelf to shelf edge, being infrequent in shallow water and more abundant off the shelf edge in Antillean and southern parts of the range; 11 to 915 m (Pérez Farfante 1977; Wenner and Read 1982).

Type-locality.—*Mer des Antilles* (Pérez Farfante 1977).

Known range.—Northeast of Cape Lookout, N. C., 34°43'N, 76°40'W, through Florida Straits to Alabama; off Cape Catoche and Bahamas through Caribbean Sea and along coast of South America to Rio Grande do Sul, Brazil.

Remarks.—In a revision of American solenocerid shrimps, Pérez Farfante (1977) erected a new genus to receive *M. tropicalis*, pointed out differences between the antennular flagella of it and those of other solenocerids, confirming variations already observed in their relative lengths (Lindner and Anderson 1941), and showed how this feature in northern populations differs proportionately (longer) from that in southern (shorter) populations. She also discussed variations in the thelycum of females and summarized a great deal of distributional data.

Genus *Solenocera* Lucas 1849

Pérez Farfante and Bullis 1973:2.

Rostrum relatively short, strongly compressed and armed only dorsally. Postorbital, antennal and hepatic spines present; pterygostomian or branchiostegal spines present or absent. Hepatic sulcus well developed. Abdomen carinate dorsally; lateral ramus of uropods usually lacking distolateral spine.

Prosartema present. Antennular flagella longer than carapace, lamellate, broad ventral pair forming trough covered by narrower dorsal pair, 4 together constituting respiratory siphon. First leg with spine on basis and ischium, second usually with spine on basis. (Abridged from Pérez Farfante and Bullis 1973.)

Solenocera atlantidis Burkenroad

Fig. 6

Solenocera atlantidis Burkenroad 1939:10, figs. 5–10.—Holthuis 1959:54, fig. 3.—Williams 1965:14, fig. 5.—Pérez Farfante and Bullis 1973:20, figs. 11, 13–14.

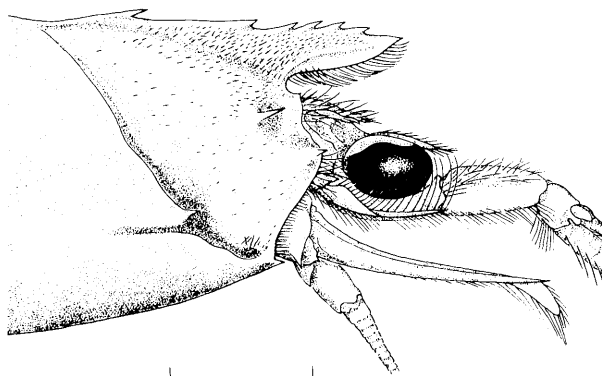


Fig. 6. *Solenocera atlantidis* Burkenroad. Female, anterior region of body in lateral view, 5 mm indicated (from Pérez Farfante and Bullis 1973).

Recognition characters.—Body compressed, carapace deeper than broad. Rostrum not reaching distal edge of eye; upper margin straight, lower margin convex; rostral + epigastric teeth 5 to 7, usually 6, not counting dagger-shaped tip, 2 behind, 1 above orbital margin, posterior tooth slightly remote from others. Postrostral carina not continued beyond cervical groove. Sides of rostrum and area near its base covered with short setae; carapace with small pterygostomian spine, sometimes doubled; postorbital and hepatic spines well developed; antennal spine well defined; orbital angle with distinct spine on apex; cervical groove reaching to middorsal line; hepatic groove prominent. Prosartema almost reaching distal end of first antennular article. Antennular flagella about 1.5 to 2 times carapace length. Antennal scale usually reaching distal end of antennular peduncle or extending no more than 0.1 its length beyond peduncle. Coxa of fifth legs with strong tooth on anteromesial margin in female, on anterolateral margin in male.

Abdomen with last 3 segments carinate; third to fifth segments cleft posterodorsally at midline; sixth with spine at middorsal posterior and posterolateral corners and toothlike projection at middle of distolateral edge. Telson short, broad, lateral spines large.

Measurements in mm.—Length of carapace: male 8.9; female 18.5.

Variation.—The antennular flagella are moderately long in the North American population but short in the West Indian to South American population (e.g., ratio length of dorsal flagellum to carapace length: northern 2.1–1.9 to 1.5, Antillean to southern 1.9–1.5 to 1.4–1.1, diminishing in each case with increasing body size). The epipodites are usually mitten-shaped, but sometimes more distinctly forked, the thumb or inferior branch never exceeding the proximal or palmar portion of the blade, exclusive of the peduncle.

Color.—Orange red, color most concentrated as bands across posterior parts of abdominal tergites (Burkenroad 1939).

Habitat.—A variety of substrates including muds, mud and fine shells, fine white sand and black specks, sand-shell, broken shell, coral, *Lithothamnion* (Cain 1972), sponges, and dark slate; 16–18 m to 198 to 232 m, usually less than 75 m (Pérez Farfante and Bullis 1973; Wenner and Read 1982).

Type-locality.—Gulf of Mexico off Alabama, 29°45'N, 88°11'W, 37 m *Atlantis* Stn. 281).

Known range.—Off Oregon Inlet, N. C., around Gulf of Mexico and Caribbean Sea to Cananeia, São Paulo, Brazil (Pérez Farfante and Bullis 1973).

Remarks.—Burkenroad (1939) reported females of *S. atlantidis* with well-ripened ovaries off Ala-

bama in March. Cook (1966) included the genus *Solenocera* in his key to protozoan, mysis and post-larval developmental stages, and Subrahmanyam (1971a) figured the developmental stages. Moreover, he (1971b) found larval stages in the Gulf of Mexico off Mississippi more or less year round but most abundantly in pulses beyond 54 m during warmer months and 18–36 m during cooler months. He did not distinguish the larvae of *S. atlantidis*, *necopina* and *vioscai*, all of which range through the Gulf of Mexico.

Solenocera necopina Burkenroad

Fig. 7

Solenocera necopina Burkenroad 1939:7, figs. 1–4.

—Pérez Farfante and Bullis 1973:14, figs. 7, 9–10.

Recognition characters.—Body compressed, glabrous except for elongate patch of setae covering sides of rostral area above adrostral carina anterior to epigastric tooth. Rostrum horizontal or uplifted, dorsal margin straight, bearing 5 to 8, usually 6, teeth (including epigastric); acute tip reaching distal edge of eye and almost to distal level of first antennular article; ventral margin convex. Postrostral carina low, rounded, extending almost to posterior margin of carapace, but sometimes (mainly in young) only to cervical sulcus. Orbital angle not spined; postorbital spine slender and long; antennal and hepatic spines shorter; pterygostomian spine acute with broad base. Cervical sulcus rather broad; hepatic sulcus almost horizontal posteriorly, merging with depressed area below hepatic spine; then turning anteroventrally to end at pterygostomian pit. Prosartema extending almost to distal end of first antennular article. Antennular flagella relatively short, dorsal slightly longer than ventral, short terminal filaments present. Antennal scale elongate, exceeding antennular peduncle by as much as 0.2 of its own length, distolateral spine long. Spine on basis and ischium of first leg long and slender but strong; second leg with sharp, slender spine on basis. Females with median ridge on anterior part of sternite XIII (between 4th legs).

Abdomen with sharp middorsal carina on segments 4–6; low rounded carina on posterior $\frac{2}{3}$ of segment 3 of large individuals; posterior margin of 3–5 cleft middorsally, 6 with sharp spine posteriorly on carina and small spines posteroventrally. Telson with median sulcus obsolete distally, rather broad, fixed lateral spines relatively small but strong.

Measurements in mm.—Length of carapace: male 17; female 27 (Pérez Farfante and Bullis 1973).

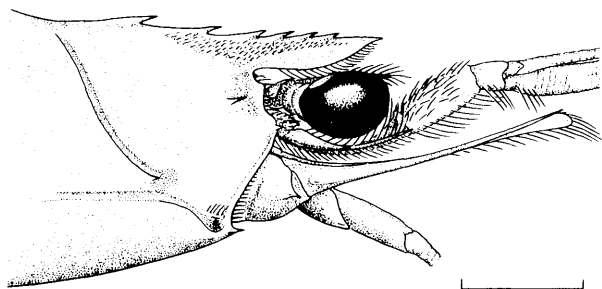


Fig. 7. *Solenocera necopina* Burkenroad. Female, anterior region of body in lateral view, 5 mm indicated (from Pérez Farfante and Bullis 1973).

Color.—Body translucent with pale salmon suffusion; second to fifth abdominal terga with transverse white band parallel to posterior margin; same color on posterior of sixth segment, base of telson, and on uropods as spot on proximal article, triangular distal spot on lateral ramus, and broad marginal band on mesial ramus; antennular peduncle and gnathal appendages dark pinkish orange; legs and pleopods pinkish orange (Pérez Farfante and Bullis 1973).

Habitat.—Gray or green mud, same with shells, green clay with mud, sand and shells, broken shells, dead coral and urchin shells; 90 (Wenner and Boesch 1979) to 550 m, usually below 180 m (Pérez Farfante and Bullis 1973).

Type-locality.—Off Mobile Bay, Alabama, 29°16'N, 87°54'W, 229 m, Atlantis Stn. 2377.

Known range.—SE of Cape Lookout, N. C., through Gulf of Mexico and Caribbean Sea to Rio Grande do Sul, Brazil (Iwai 1973), and Uruguay.

Solenocera vioscai Burkenroad

Fig. 8

Solenocera vioscai Burkenroad 1934a (part):65, figs. 1–4.—1939:13, figs. 12–15.—Pérez Farfante and Bullis 1973:3, figs. 1A–B, 3.

Recognition characters.—Body glabrous except for elongate patch of setae covering sides of rostral area above adrostral carina anterior to epigastric tooth. Rostrum horizontal or slightly uplifted; dorsal margin straight and bearing 8–11, usually 9 teeth (including epigastric), progressively smaller and more crowded from posterior to anterior tooth placed near tip; ventral margin tapered, straight (or with slight convexity) from short basal portion of uniform height to acute tip reaching distal level of first antennular article. Postrostral carina high, extending almost to posterior margin of carapace, notched at level of cervical sulcus. Orbital angle

spined; postorbital spine long; antennal spine relatively small; hepatic spine prominent; pterygostomian spine acute with broad base, often slightly inclined ventrally. Cervical sulcus deep, broad and sinuous, carina sharp; hepatic sulcus almost horizontal posteriorly, merging with depressed area below hepatic spine, then turning anteroventrally to end at pterygostomian pit. Prosartema extending to distal margin of first antennular article. Antennular flagella abruptly tapered distally, each bearing short terminal filament, that of dorsal ramus longer. Antennal scale usually reaching distal end of antennular peduncle or exceeding it by 0.1 its own length, distolateral spine strong. Spine on basis and ischium of first leg long and slender but strong; second leg with sharp, slender spine on basis.

Abdomen with sharp middorsal carina on segments 3–6; low rounded carina on posterior half of 2 on some large individuals; posterior margin of 3–5; cleft middorsally, 6 with sharp spine posteriorly on carina and small spines posterolaterally. Telson with median sulcus obsolete distally, rather broad fixed lateral spines relatively small but strong.

Measurements in mm.—Length of carapace: male 23.5; female 31 (Pérez Farfante and Bullis 1973); tip of rostrum to tip of telson, female 130.

Color.—In general, pale orange interspersed with many translucent areas; pigment concentrated on rostrum and antennules and as bands across posterior parts of abdominal terga; patches of opaque

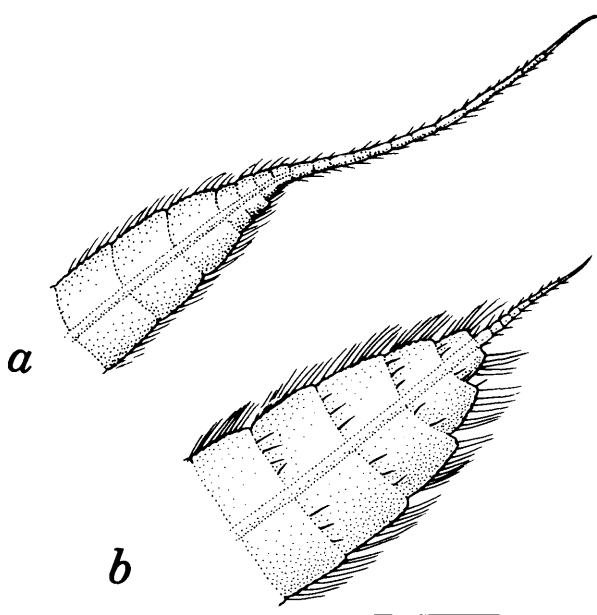


Fig. 8. *Solenocera vioscai* Burkenroad. Distalmost portion of antennular flagella: a, dorsal flagellum; b, ventral flagellum, 1 mm indicated (from Pérez Farfante and Bullis 1973).

white on outer sides of legs and pleopods, on uropods and fifth abdominal segment (Burkenroad 1939).

Habitat.—Gray, gray-green, blue and blue-black mud, mud and sand, shells; 37 to 239 m, mostly 50 to 80 m (Pérez Farfante and Bullis 1973).

Type-locality.—About 5 miles (8 km) off Pass a L'outre, Louisiana, 27 m.

Known range.—Southeast of Cape Lookout, N. C., to Dry Tortugas, Fla., but rare off Florida; northern and western Gulf of Mexico to Tabasco.

Remarks.—Brusher, et al. (1972) found males in the northwestern Gulf of Mexico to measure 45–75 mm in total length, and females to measure 70–110 mm; both were most prevalent at 46–64 m depth and a few occurred to 110 m. Females with ripe eggs were present year round but most abundant during July–September.

Sprague (1970) listed *Nosema* sp., a microsporidian parasite, from *S. vioscai* in Louisiana.

Family Penaeidae

Integument more or less flexible, not stony in appearance. Carapace without postorbital spine; cervical groove not extending to or nearly to dorsal midline. Basal article of ocular peduncle bearing mesial scale (sometimes considerably reduced);

ocular plate lacking styliform projections. Prosartema well developed. Thoracic exopodites present at least on 1 pair of appendages behind first maxillipeds. Podobranchs absent behind second maxilliped. Only 1 large arthrobranch (posterodorsal) on somite XIII (fourth pereopods), a rudimentary anteroventral one sometimes present. Pleurobranchs on at least 3 somites behind somite IX (third maxillipeds). No epipodites behind third pereopods. Third and fourth pair of pereopods biramous. Second pair of pleopods in males bearing only appendix masculina.

This group has been studied intensively during the past 50 years and the literature bearing on various aspects of its biology has become so voluminous that a number of authors have compiled summaries of appropriate subjects. To be contained within reasonable limits, the species accounts must necessarily be selective from this literature.

Studies on parasites in *Penaeus*, as well as diseases and responses to toxic substances, have been reviewed in a compendium by Couch (1978) and will not be treated in the remarks that follow.

Spelling of the name *Penaeus* and related compounds was not uniform in the past, but the “-penaeus” spelling was adopted as standard in 1969 (Opinion 864) by the International Commission on Zoological Nomenclature.

Key to Genera and Species Except Those of *Penaeus*

1. Rostrum usually with ventral teeth *Penaeus*
Rostrum without ventral teeth 2
2. Telson with subterminal pair of fixed spines 3
Telson without subterminal pair of fixed spines 4
3. Carapace with longitudinal and transverse sutures; body nearly smooth . .
. *Parapenaeus politus*
Carapace without longitudinal or transverse sutures; body pubescent . . .
. *Metapenaeopsis goodei*
4. Rostrum about half length of carapace, straight, dorsal teeth evenly spaced
except for remote epigastric tooth *Trachypenaeus constrictus*
Rostrum as long as or longer than carapace, sinuous, basal thin high crest
armed with 5 teeth plus an isolated epigastric tooth
. *Xiphopenaeus kroyeri*

Genus *Penaeus* Fabricius 1798

Pérez Farfante 1969:462.

Rostrum usually with ventral teeth. Carapace without longitudinal or transverse sutures; cervical and orbito-antennal sulci and antennal carinae always present. Hepatic and antennal spines pronounced, pterygostomian angle rounded. Telson with median sulcus; with or without lateral mova-

ble spines. Antennular flagella usually shorter than carapace. First and second legs with spine on basis; first 4 legs with exopods, usually also on 5. Petasma symmetrical, with or without distomedian projections, lateral lobes usually with long ventral costae. Thelycum often with median protuberance at posterior margin of sternite XIII (fourth legs), usually with 2 lateral plates covering or almost covering sternite XIV (fifth legs). (Abridged from Pérez Farfante 1969).

Keys to Species

Key to Adults and Subadults

(Adapted from Pérez Farfante 1969)

1. Lateral rostral grooves reaching only slightly beyond posterior tooth of rostral series (non-grooved shrimp) [Subgenus *Litopenaeus*] ***P. (L.) setiferus***
Lateral rostral grooves reaching nearly to posterior margin of carapace (grooved shrimps) [Subgenus *Farfantepenaeus*] 2
2. Petasma of male with distomesial projection long; distal fold expanded mesially to form large spined lobe; ventral costa with apex free. Thelycum of female with anteromesial corners of lateral plates extended to cover posterior process of median protuberance ***P. (F.) brasiliensis***
Petasma of male with distomesial projection relatively short; distal fold not forming lobe; ventral costa with apex attached to adjacent membranous part. Thelycum of female with anteromesial corners not extended, exposing posterior process of median protuberance 3
3. Petasma armed with minute spines on ventral costa along terminal part of free border. Thelycum with anteromesial corners of lateral plates slightly divergent, posterior process of median protuberance with undivided median carina ***P. (F.) duorarum***
Petasma unarmed on ventral costa along terminal part of free border. Thelycum with anteromesial corners of lateral plates widely divergent, posterior process of median carina bifurcate anteriorly ***P. (F.) aztecus***

Key to Juveniles between 17 and 47 mm Total Length

(Key adapted from Williams 1953 and Pérez Farfante 1970)

Juveniles of three species of *Penaeus* that commonly occur in coastal waters from northeastern Florida northward can be distinguished fairly easily in living or freshly preserved condition with the aid of the following key. A fourth species, *P. (F.) brasiliensis*, whose juveniles may occasionally occur in that region can perhaps be distinguished on the basis of rostral characters. Juveniles of the three species of grooved *Penaeus* can be distinguished by means of characters well illustrated by Pérez Farfante (1970). Zamora and Trent (1968) showed that almost all postlarval *P. (L.) setiferus* lack carinal spines on the sixth abdominal segment whereas postlarval *P. (F.) aztecus* have them [also present in *P. (F.) duorarum*].

1. Lateral rostral grooves reaching only slightly beyond posterior tooth of rostral series; rostrum long and slightly upturned at tip in individuals exceeding 22 mm total length. Ground color light gray, sometimes with greenish cast in shrimp taken from beds of vegetation; chromatophores (widely spaced except on spines, ridges, and uropods) colored slate-blue and brown; uropods with reddish-brown to brown areas distally ***P. (L.) setiferus***
Lateral rostral grooves reaching almost to posterior margin of carapace (shallow in 17-mm individuals); rostrum relatively short. Color gray to light brown; sometimes with greenish cast in shrimp taken from beds of vegetation; chromatophores numerous and closely spaced, often in bands or patches. 2
2. Rostrum with toothed dorsal margin straight; tip attenuate and straight ***P. (F.) brasiliensis***
Rostrum with toothed dorsal margin slightly arched over eye; tip short or attenuate and slightly upturned. 3

3. Rostrum usually not upturned at tip and not extremely attenuate. Chromatophores slate-blue and brown; usually with conspicuously pigmented lateral spot at juncture of third and fourth abdominal segments; uropods with uniform sprinkling of chromatophores, degree of transparency uniform throughout (color more dense in older individuals)

. *P. (F.) duorarum*

Rostrum usually slightly upturned and attenuate at tip. Chromatophores brown and olive-green; uropods with reddish-brown to brown areas distally. *P. (F.) aztecus*

***Penaeus (Farfantepenaeus) aztecus* Ives**

(Brown shrimp)

Figs. 9–10

Penaeus brasiliensis var. *aztecus* Ives 1891:190.

Penaeus brasiliensis.—Hay and Shore 1918:377, fig. 6 (part ?).

Penaeus aztecus.—Burkenroad 1939:34 (part, "Form A"), figs. 20–21, 24, 30–31.—Williams 1965:22, fig. 12.

Penaeus (Melicertus) aztecus aztecus.—Pérez Farfante 1969:527, figs. 39–43, 46–48, 50.

Penaeus aztecus aztecus.—Cook and Lindner 1970:1476.

Penaeus (Farfantepenaeus) aztecus.—Burukovskii 1972:10.

Recognition characters.—Integument thin, polished, translucent. Carapace with median carina continuous anteriorly with rostrum and extending nearly to posterior border, flanked on each side by

broad, rounded groove; posterior part of carina with median longitudinal groove; anterior part arcuate, highest above rear portion of orbit and with 5–10 sharp teeth (mode 8); posterior epigastric tooth remote from others, anterior 6 or 7 on rostrum proper. Lower margin of rostrum with 0–3, usually 2, teeth, tip slender, horizontal, or directed slightly upward, unarmed. Anterior margin of carapace with strong antennal spine on carina extending backward nearly to well-developed hepatic spine. Cervical groove extending halfway from hepatic spine to dorsal carina. Sharp hepatic carina below hepatic spine, and orbito-antennal sulcus extending from near hepatic spine to near orbital margin; gastrofrontal carina behind orbit.

Female with thelycum composed of 2 broad lateral plates and median protuberance. Posteromedian part of median protuberance variably ovate-acuminate in outline with tip raised into short posterior carina diverging anteriorly into raised margins. Ventral surface concave; broad anterior end of posterior part merging into concave, trian-

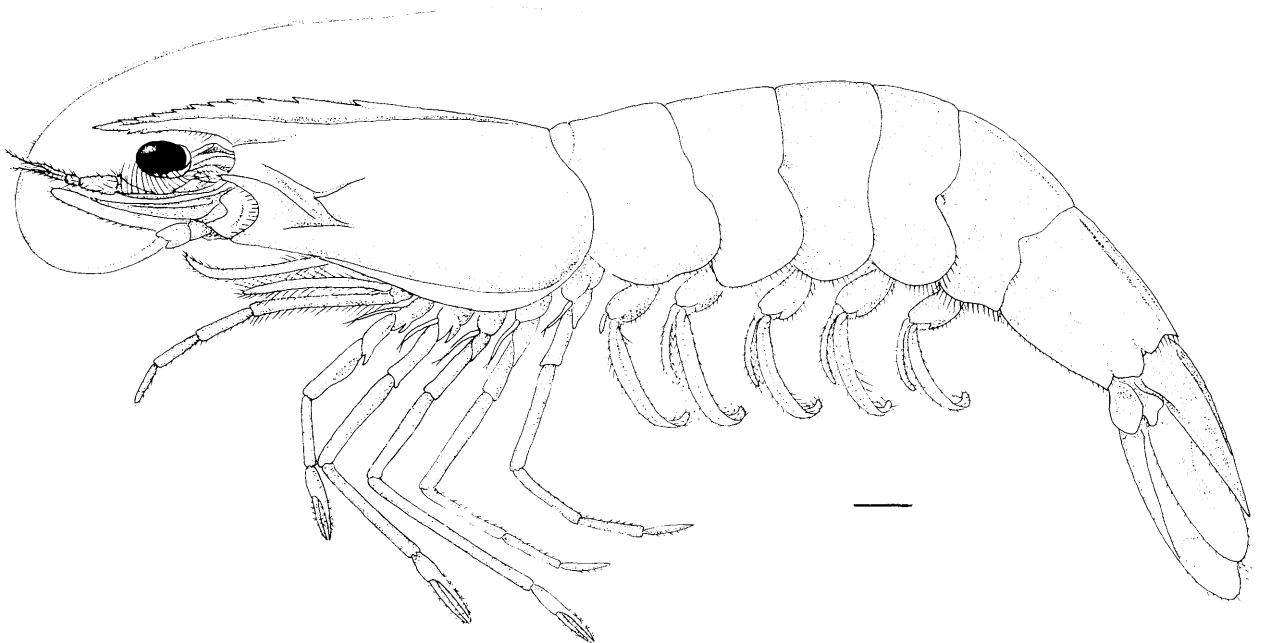


Fig. 9. *Penaeus (Farfantepenaeus) aztecus* Ives. Female in lateral view, 1 cm indicated (from Pérez Farfante 1978).

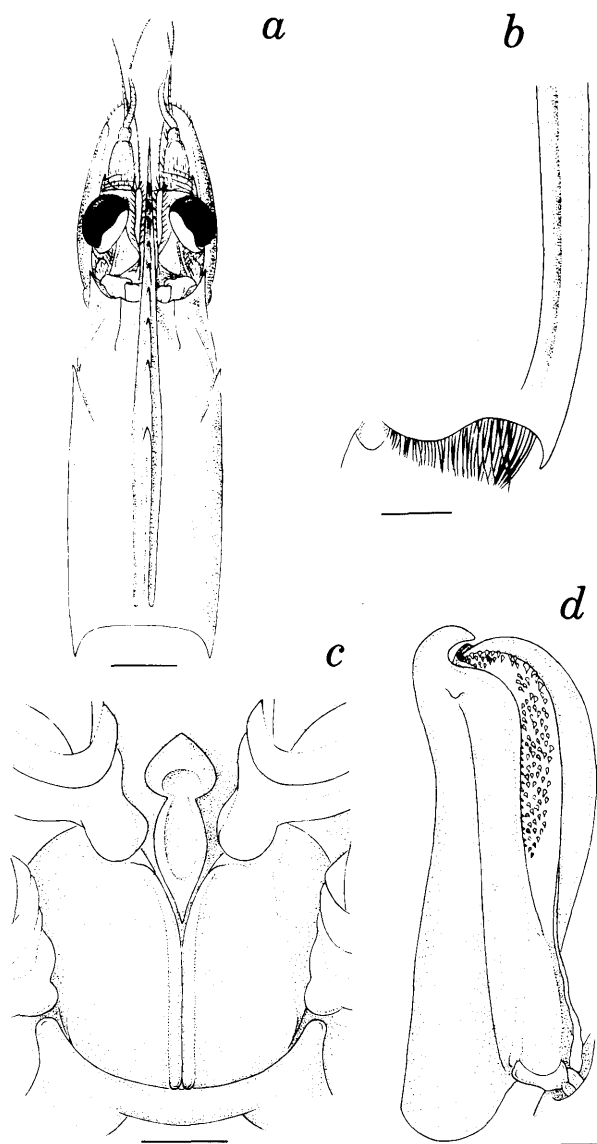


Fig. 10. *Penaeus* (*Farfantepenaeus*) *aztecus* Ives. *a*, Carapace in dorsal view; *b*, sixth abdominal segment in lateral view; *c*, thelycum of female; *d*, petasma of male; *a*, 10 mm; *b-d*, 2 mm indicated (from Pérez Farfante 1978).

gular or semicircular anterior process. Lateral plates meeting in midline except diverging to expose median protuberance.

Abdomen with segments 4 to 6 carinate, carina of 6 flanked on each side by broad groove. Telson with deep median groove and acuminate tip. Petasma of male with distomedian projections not projecting free of ventral costae; several compact series of short, crowded spines near distal end of ventral costa, its attached border with elongated narrow patch of 14–25 small closely set teeth arranged in 2 or 3 series.

Measurements in mm.—Length of body: large male 195; large female 236. The size difference between

males and females is statistically significant at about 100 mm total length (Williams 1955, and other authors).

Variation.—The species as restricted by Pérez Farfante (1969) shows little morphological variation within its range.

Color.—Juveniles and young adults from estuaries or oceanic water near shore are usually brown or grayish brown, occasionally with darker spots or faint concentrations of chromatophores at the pleural articulations; red and green specimens also occur. Large individuals from offshore often have an orange or lemon coloration, deeper on the legs and around the tail fan which often has a darker edge that may be purple or reddish purple; occasionally there is a lateral spot at the juncture of abdominal segments 3 and 4 (Williams 1953; Pérez Farfante 1969).

Habitat.—Estuarine and oceanic littoral, predominantly on mud bottom from water's edge to 110 m; highest adult density 27–55 m, rarely to 165 m.

Type-locality.—Veracruz, Mexico.

Known range.—Martha's Vineyard, Mass., around peninsular Florida to Sanibel grounds; Appalachicola Bay, Fla., around Gulf of Mexico to northwestern Yucatan.

Remarks.—Pérez Farfante (1969) recognized two subspecies of *P. aztecus*, the nominate form and *P. a. subtilis* Pérez Farfante which ranges from Cuba and Honduras to Rio de Janeiro, Brazil. The latter is not discussed here, but is now recognized as a full species.

Penaeus aztecus, extensively used for food, is caught commercially throughout its range, but in greatest quantities along the Texas coast and in the southwestern Bay of Campeche. The total catch for this species exceeds that of other penaeids taken in the United States.

Maturation of gonads in *P. aztecus* parallels the process as understood in *P. setiferus*. Broad (1950) described maturing ovaries found in August as opaque white, yellow, tan, or gray in color. The color changes were illustrated by Brown and Patlan (1974). Burkenroad (1939), working in Louisiana, noted that whereas the proportion of males to females in *P. aztecus* near shore was about 1:1, this ratio progressively changed in samples farther from shore, in deeper water, to a ratio of 1:2 in water 90–130 m deep. Knowledge that impregnated females occurred only beyond 18 m, together with the fact that mature (and possibly spent) ovaries were found only in individuals beyond these depths at various times of year, led him to propose that the females spawned a number of times during an ill-defined spawning season. Evidence indicates that

P. aztecus has an extended spawning season which probably varies in different parts of the range. The spawning site is probably deeper and farther from shore than in *P. setiferus* and *P. duorarum*. According to Renfro (1964), brown shrimp spawn off Texas at a total length as short as 140 mm.

Cook and Murphy (1969, 1971) reared and described five naupliar, three protozoal, three mysis and several postlarval stages from eggs spawned by mature females in the laboratory, and Cook (1966) gave a generic key to larval stages found in waters off Texas. Temple and Fischer (1965) gave a summary analysis of penaeid planktonic larval stages off Galveston, Tex., in 36.5-m water, finding *Penaeus* most abundant below mid-depth, protozoae most abundant near bottom and postlarval stages at or above mid-depth, but each stage extending into surface layers just prior to or after darkness, although there was no evidence of movement into surface layers at night by any planktonic stage. In the unstable temperatures of November there was homogeneous distribution. In 1967, these authors also summarized seasonal distribution and relative abundance of *Penaeus* spp. in that area. Sick (1970) found a pattern of penaeid larval distribution off North Carolina that suggested seaward transport in which nauplii and protozoae were near shore but progressively later stages were found seaward. Postlarvae, although distributed over the entire sampling range, were found in greatest concentration 50 mi. (80 km) southeast of Beaufort Inlet. Sandifer (1973d) found an early postlarva of *Penaeus* off Chesapeake Bay in September.

Williams (1959) favorably assessed Pearson's (1939) determination of *P. brasiliensis* as most probably *P. aztecus*, and proceeding on the basis of Pearson's distinguishing characters was able to separate *P. duorarum* and *P. aztecus* postlarvae in the plankton in North Carolina. Later, Zamora and Trent (1968) gave better distinguishing characters for grooved and non-grooved shrimp postlarvae. Postlarvae of *P. aztecus* were found entering the sounds from October to May, with peak recruitment from late March to early April. Bearden (1961) found peak recruitment to occur in February and March in South Carolina. These patterns agreed well with collection of juveniles (Williams 1955) in which recruitment began in mid-April and continued through the summer. A long winter spawning season supplies postlarvae to the Carolina sounds, but fall and midwinter recruits are apparently killed by cold weather, for they never progress beyond postlarvae in the samples taken. Pearson found postlarvae in Louisiana in all months of the year,

but in no more than 11 months of any calendar year. The usual recruitment period seemed to run from late January to late summer.

Copeland and Truitt (1966) found *P. aztecus* postlarvae contributing to a spring peak of recruitment in Texas bays, with catches greatest during flood tide at night. Williams and Deubler (1968) and Williams (1969) found the correlation of recruitment of postlarvae in surface layers with new moon periods at night to be high in North Carolina (see account for *P. duorarum*). King (1971), while finding that postlarvae were concentrated near the surface or in mid channel at the entrance to Texas bays, especially against north and northwest winds, found no correlation with time of day, lunar phase, salinity, pH, tide duration, cloud cover, incident light or levels of light at depth. Simultaneous sampling at two multiple depth stations in the entrance to Galveston Bay showed postlarvae to occur at all depths sampled; catches were greater at middle depths in daytime in the less turbulent of the two, and at the surface at night (Duronslet, et al. 1972). Christmas, et al. (1966) found good correlation of postlarval numbers with succeeding commercial catch in Mississippi in a preliminary assessment.

Young *P. aztecus* which enter the estuaries as postlarvae migrate to shallow, often low-salinity water, and undergo a remarkably rapid growth in warmer months. As they grow, they gradually move to deeper, saltier water and eventually return to sea. Gunter, et al. (1964) summarized evidence that brown shrimp are most abundant in estuarine waters of between 10‰ and 20‰ salinity. Parker (1970) showed distinct patterns of juvenile brown shrimp distribution in Texas; smallest shrimp concentrated in peripheral and shore zones. The short time elapsed during mass emigration to the passes leading to the Gulf indicated a direct path, not random search, and was most evident in the segment of the population measuring about 70–100 mm total length. He concluded that salinity per se had no detectable effect on distribution. McCoy and Brown (1967) and McCoy (1972) indicated a similar emigration pattern in mark-recapture experiments in North Carolina; departure from estuaries lead directly to the nearest inlets, although residence time in estuaries varied with size of the body of water.

In North Carolina, the juveniles increase in mean length by an estimated 46 mm per month (1.5 mm per day, Williams 1955); Wilson (1969) estimated 45–50 mm per month in Louisiana. As they grow, they gradually move to deeper, saltier water and eventually return to sea. In North Carolina, and perhaps elsewhere, *P. duorarum* and *P. aztecus* use

essentially the same nursery grounds over large areas of the sounds; however, the season of recruitment to and occupation of these areas is staggered in such a manner that the two species are rarely on common ground (Williams 1955a).

McCoy (1972) estimated growth of slightly older to adult shrimp with the aid of mark-recapture data, constructing a series of growth curves, and Parack (1979) studied growth with the aid of models utilizing mark-recapture data. Growth is not the same in all areas. The linear function is the poorest estimate, although this size-age relationship does appear to hold for juveniles. The rate of increase decreases with age. Males apparently grow to about $\frac{3}{5}$ the weight and $\frac{5}{6}$ the length of females; however the coefficients of growth are nearly equal. Increase in size tends to fall off at an earlier age in males, and it is not unreasonable to assume that males mature at an earlier age than females. Growth of populations is probably positively correlated with temperatures. As a corollary, Williams (1969a) showed an apparent association of good commercial catches with warm years and poor catches with cold years in the waters along the southeastern and southern United States. The effect was most pronounced at the most northern localities examined, and he proposed that annual winter temperatures might be used as predictors for catch in the succeeding seasons. Fontaine and Neal (1968) demonstrated a linear relationship between abdomen length and total length in this species.

McCoy and Brown (1967) and McCoy (1972) showed that tagged adult brown shrimp moved southward along the Carolina coast, the record being 150 mi. (241 km) in five weeks.

Distribution of *P. aztecus* is correlated with substrates. Hildebrand (1954, 1955) and Springer and Bullis (1954) stated that the commercial fishery for this species in the Gulf of Mexico is confined largely to bottoms of terrigenous silt. Like *P. duorarum*, *P. aztecus* is a burrower, and in many areas is more active in open water at night than in daytime. In experimental tanks, when given a choice of sand, shell-sand, loose peat, muddy sand and sandy mud, *P. aztecus* was found to favor loose peat, sandy mud and muddy sand, closely paralleling *P. setiferus* in choice of bottom type (Williams 1958). The experiments confirm field observations on habitat along the coast of North Carolina and in the Gulf of Mexico.

Penaeus aztecus has been found to have a less efficient osmoregulatory mechanism at low temperatures in low salinities than *P. duorarum* (Williams 1960). For this reason, it is probably not so resistant to wintertime conditions in estuaries as *P. duor-*

arum. McFarland and Lee (1973) showed that *P. aztecus* and *P. setiferus* have osmoregulatory powers that coincide with their different salinity distributions in nature.

The food of commercially harvested penaeid shrimps in estuaries was studied by Williams (1955). Stomachs of adult and young shrimp were full or half filled in autumn, nearly always empty in winter, and usually full in summer. Contents were macerated and hard to identify, but the most abundant material was "usually a mass of unrecognizable debris, probably a mixture of digesting tissue and organic deposit from the bottom . . . Most of the material, except the muscle fibers and unrecognizable debris, are hard. Although they indicate types of food that shrimp eat, they are too hard to be triturated easily and, because large fragments will not pass through the straining apparatus in the pyloric stomach, hard parts may accumulate in quantity in the stomach. Whether most of these hard materials are further broken down for alimentation or are regurgitated is not known, but unrecognized softer and more easily digested materials could easily form the bulk of the diet." Meiss and Norman (1977a, b) studied the stomatogastric musculature and skeleton of *P. aztecus*.

Penaeus aztecus has been used as an experimental animal for many laboratory studies on larval development and pond culture of juveniles and adults. That literature also has become too comprehensive to review here, but some of the early studies (Zein-Eldin 1963) showed that growth rate of postlarvae did not differ significantly among shrimp held at 5, 10, 25, or 40‰ salinity. In temperatures of 7° to 35°C there were varied responses at these salinities (Zein-Eldin and Aldrich 1965): survival but almost no growth for 1 month at 11°C in salinity of 15‰ or above; significant growth beginning at some temperatures above 11°C but below 18°C; most marked increases in growth occurring in the 11° to 25°C temperature range. At temperatures below 15°C the postlarvae showed decreased tolerance to low salinity. Such reduced tolerance may influence natural distribution and survival of postlarvae which do not ordinarily enter estuaries in abundance until spring when temperatures are rising. A later laboratory study (Zein-Eldin and Griffith 1966) showed that maximal increases of postlarval growth rate per unit of temperature occurred in the 17.5° to 25°C range, gross production being optimal at temperatures of 22.5° to 30°C.

Parasites and/or diseases of *P. aztecus* were reviewed by Couch (1978), Overstreet (1973), Sinderman and Rosenfield (1967), and Sprague (1970).

Penaeus (Farfantepenaeus) brasiliensis Latreille

Figs. 11–12

Penaeus brasiliensis Latreille 1817:156.*Penaeus (Melicertus) brasiliensis*.—Pérez Farfante 1969:562, figs. 68, 75–76.—Chace 1972:9.*Penaeus (Farfantepenaeus) brasiliensis*.—Burukovskii 1972:10.

Recognition characters.—Much like *P. aztecus* with which it has been confused in North America.

Dorsal margin of rostrum slightly arched. Median carina on carapace with deep median groove, sometimes widened in anterior or posterior half.

Thelycum of female with broad lateral plates contiguous mesially or overlapping anteromesially, covering rather small posterior projection or median protuberance; anterior process with subtriangular ridge bounding central concavity.

Petasma of male with rather long distomedian projections extending free over ventral costae; latter unarmed along distal border but with 6 to 12 pointed teeth in 2 irregular rows on attached border; distal fold forming large rounded auricle armed with numerous spines in half-moon formation on inner surface; ventrolateral lobule armed externally with spines increasing in number proximally.

Measurements in mm.—Length of body: large male 191; large female 250.

Type-locality.—Brazil.

Known range.—Off Cape Hatteras, to Florida Keys, off Campeche and Yucatan; through Caribbean Sea to Rio Grande do Sul, Brazil; Bermuda; to 275 m. The species is absent from the Gulf of Mexico from north of Tortugas-Florida Bay to Bay of Campeche (Pérez Farfante 1969; 1971a; 1980).

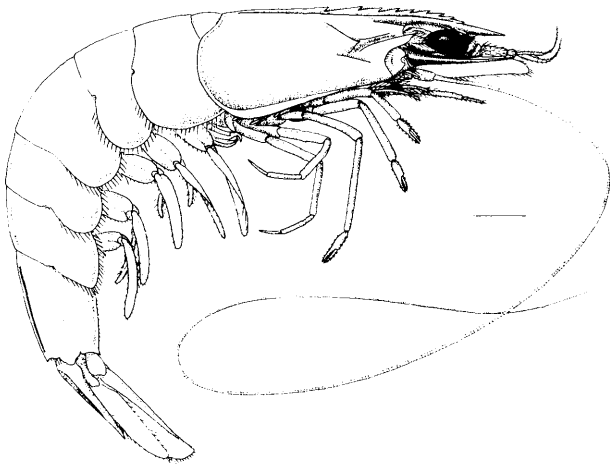


Fig. 11. *Penaeus (Farfantepenaeus) brasiliensis* Latreille. Male in lateral view, 1 cm indicated (adapted from Pérez Farfante 1978).

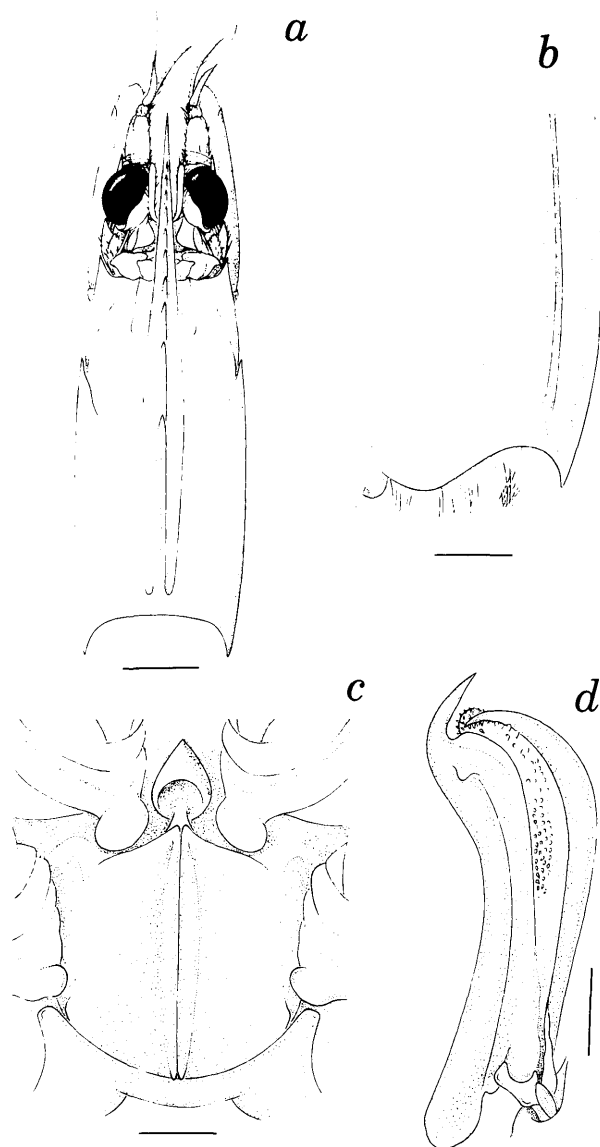


Fig. 12. *Penaeus (Farfantepenaeus) brasiliensis* Latreille. *a*, Carapace in dorsal view; *b*, sixth abdominal segment in lateral view; *c*, thelycum of female; *d*, petasma of male; *a*, 10 mm; *b-d*, 2 mm indicated (from Pérez Farfante 1978).

Remarks.—This species is rare in the northernmost part of its range, although variably abundant in Florida, mainly south of the range covered by this account (Pérez Farfante 1969; 1971a). For a discussion of variation, color, habitat, and biology see this author.

Penaeus (Farfantepenaeus) duorarum Burkenroad

(Pink, spotted, pink spotted, pink night shrimp)

Figs. 13–14

Penaeus brasiliensis.—Hay and Shore 1918:377 (part), pl. 25, fig. 6.

Penaeus duorarum Burkenroad 1939:31 (part, Form "A"), figs. 23, 25.—Williams 1965:21, figs. 10–11.

Penaeus (Melicertus) duorarum duorarum.—Pérez Farfante 1969:499, figs. 20–22, 25–27, 30–31.

Penaeus duorarum duorarum.—Costello and Allen 1970:1504, figs. 1, 3–4.

Penaeus (Farfantepenaeus) duorarum.—Burukovskii 1972:10.

Recognition characters.—Integument thin, polished, translucent. Carapace with median carina continuous anteriorly with rostrum and extending nearly to posterior border of carapace, flanked on each side by broad, rounded groove; posterior part of carina with median longitudinal groove; anterior part arcuate, highest above rear margin of orbit and with 7–10 sharp teeth; posterior epigastric tooth remote from others, anterior 6 or 7 on rostrum proper. Lower margin of rostrum with 2–3 teeth (occasionally 1); tip slender, horizontal or directed slightly downward, unarmed. Anterior margin of carapace with strong antennal spine on carina extending backward nearly to well-developed hepatic spine. Cervical groove extending halfway from hepatic spine to dorsal carina. Sharp hepatic carina below hepatic spine, and orbito-antennal sulcus extending from near hepatic spine to near orbital margin; gastrofrontal carina behind orbit.

Female with thelycum composed of 2 broad lateral plates, and median protuberance. Posteromedian part of median protuberance of adult with well-developed, short, longitudinal carina extending anteriorly toward roughly semicircular, concave anterior process. Lateral plates meeting in midline, except variably divergent at anteromesial corners, thus exposing carina of median protuberance.

Abdomen with segments 4 to 6 carinate, carina of 6 ending posteriorly in spine and flanked on each side by narrow groove. Telson with deep median groove and acuminate tip. Petasma of male with

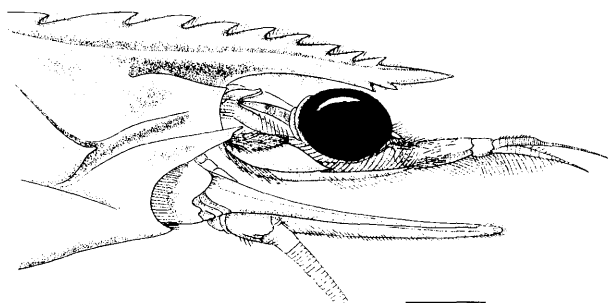


Fig. 13. *Penaeus (Farfantepenaeus) duorarum* Burkenroad. Female, anterior region of body in lateral view, 5 mm indicated (from Pérez Farfante 1978).

distal ends of distomedian projections curved mesially, not projecting free of distolateral lobes; external edge of distoventral costa with series of 1 to 12, usually 4 to 7, small distomarginal spinules; mesial or attached edge of distoventral costa with compact group of 6 to 16 large, long, sharp, curved spines; fold of distolateral lobe rather small and armed inconspicuously if at all.

Measurements in mm.—Length of body: large male 169; large female 280. The size difference between males and females is statistically significant at about 100 mm total length (Williams 1955, and other authors).

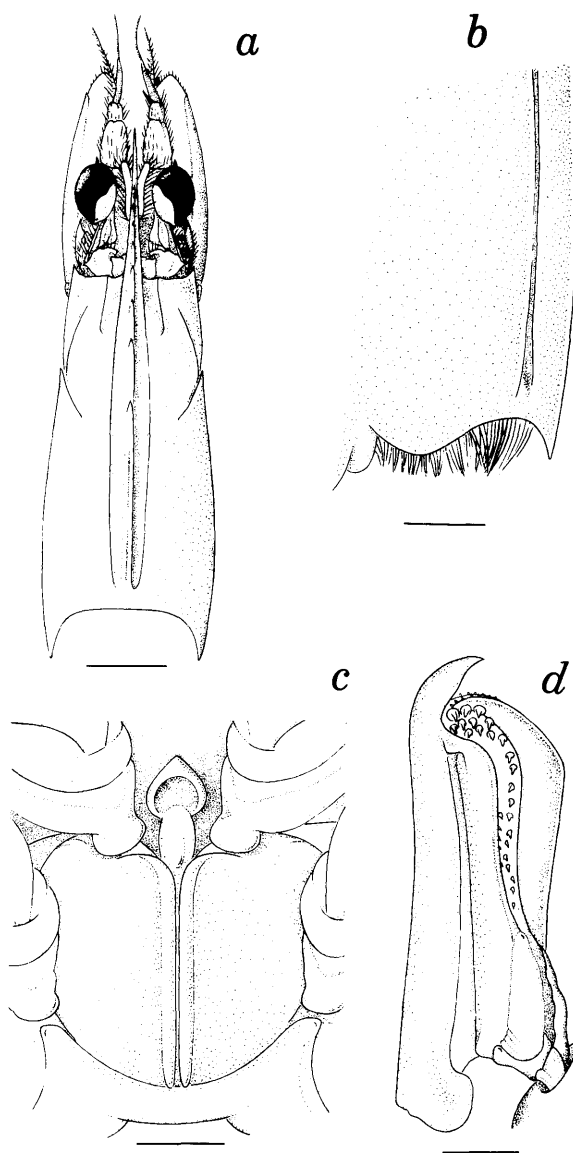


Fig. 14. *Penaeus (Farfantepenaeus) duorarum* Burkenroad. a, Carapace in dorsal view; b, sixth abdominal segment in lateral view; c, thelycum of female; d, petasma of male; a, 10 mm; b–d, 2 mm indicated (from Pérez Farfante 1978).

Variation.—Throughout the range there is variation in the width of the median carina of the carapace and its groove, in width of the lateral rostral grooves, in number of external spines at the distal end of the ventral costa of the petasma of males, and presence or absence of submarginal spinules on the distal fold of the petasma.

The rostrum is relatively shorter and deeper in old individuals than in young ones. It extends to the end of the basal antennular article in average sized adults. The rostrum in *P. duorarum* is less sinuous and slender than in *P. aztecus*.

Color.—The color is variable. Juveniles and young adults from estuaries or oceanic water near shore in North Carolina are usually gray, reddish brown, or bluish gray of various shades, with a more or less distinct spot of darker color at the pleural juncture of the third and fourth abdominal segments. In juveniles or young adults, this spot and other bandings may be gray, blue gray, blue, or purplish. The tail fan is nearly transparent and edged with blue. In older individuals, especially from deeper oceanic water, the colors tend to be red, pinkish, blue gray, or nearly white. The abdominal spots are reddish, purplish brown, or lacking entirely (Pérez Farfante 1969). Detailed coloration of the young was given by Williams (1953).

Habitat.—Estuaries and inner oceanic littoral, predominantly on sand, shell-sand, or coral-mud bottom from water's edge to 35 m but in some areas to 64 m, occasionally to 330 m, and perhaps as much as 365 m (Pérez Farfante 1969).

Type-locality.—Off Mobile Bay, Ala., 29°15'N, 88°11'W, 36.5 m, *Atlantis* Stn. 2813.

Known range.—Lower Chesapeake Bay through Florida Straits, around Mexico to Cape Catoche and Isla Mujeres at the tip of Yucatan Peninsula. Major centers of abundance are off southwestern to northwestern Florida and in the southeastern Bay of Campeche; there is a minor center of abundance in the Beaufort area of North Carolina.

Remarks.—Pérez Farfante (1969) recognized two subspecies of *P. duorarum*, the nominate form and *P. d. notialis* Pérez Farfante which ranges from Cuba and Quintana Roo on the southern Yucatan Peninsula, with some skips, to Cabo Frio, Brazil, and along the coast of Africa from Cap Blanc to Angola. The latter is not discussed here, but is now recognized as a full species (Pérez Farfante 1978).

Penaeus duorarum, extensively used for food, is caught in commercial quantities mainly in the centers of concentration. At other points in the range, the species is not abundant enough to support a fishery worthy of note.

A number of recent studies, especially in Flor-

ida, have greatly enhanced knowledge of this species but only a brief summary is appropriate here.

In North Carolina, roe-bearing females and mature males appear in commercial catches from the ocean near Beaufort Inlet in May (Broad, 1950; Burkenroad, 1949; Williams, 1955), and they continue to occur into July. Mature ovaries are blue-green in color. One spawning season a year is indicated for this, the northernmost breeding population of the species.

In Florida, Cummings (1961) found stages of maturation in the ovaries of *P. duorarum* females similar to those in *P. setiferus*; i.e., the ovary passing through a flaccid undeveloped stage, a developing stage containing larger ova, a nearly ripe stage in which the ovary is large, visible from the outside and glaucous in color, and a ripe stage in which the ova contain characteristic rodlike refractive bodies, and finally a difficult-to-determine, spent stage. The highest rate of spawning was judged to extend from April through July, a period comparable to that in North Carolina, but ripe and nearly ripe females were found at other times of year as well (see also Eldred, et al. 1961). Cummings indicated that multiple spawning probably occurs. Location of year-round spawning grounds on the Tortugas, Fla., shelf (15–48 m) was outlined by Jones, et al. (1970) as coinciding roughly with that of the commercial fishery, shifting to deeper water as winter approaches (Munro, et al. 1968), and occurring in temperatures of 19.6°–30.6°C with greatest activity when temperature is highest, although Eldred, et al. (1965) found some spawning in temperatures as low as 16.1°C and thought that rising temperatures trigger the process. The latter authors reported that location of intensive spawning off Tampa Bay, Fla., varies from year to year. Munro, et al. (1968) found most spawning during the waning moon. Martosubroto (1974) estimated that shrimp weighing 10.1–66.8 g contain 44,000–534,000 developing ova.

The egg and larval stages of *P. duorarum* were described in detail by Dobkin (1961) from material taken from the Dry Tortugas fishing grounds. Viable, yellow brown, opaque eggs, 0.31–0.33 mm in diameter, were obtained from mature females spawning in the laboratory. The act of hatching required two to three minutes. Dobkin described five naupliar, three protozoal, three mysis, and a number of postlarval stages. The naupliar and first protozoal stages were reared in aquaria, but remaining stages were taken from plankton. Ewald (1965) also reared the larvae from captive females spawned in early morning hours through non-feeding naupliar stages, protozoae fed on algae and yeast, to mysis and postlarval stages fed on brine

shrimp nauplii in addition to the plant cultures. The larvae were reared at 21°, 26°, and 31° ± 1.5°C, with best results at 26°C, metamorphosis occurring in 15 days. There was some variation in staging in various temperatures, protozoal stages being the most critical. All stages were positively phototropic. Cook (1966) provided keys to larval stages of *Penaeus*, and Sick (1970) commented on off-shore distribution of these stages off North Carolina, saying that progressively older stages are progressively farther from land but that postlarvae are widespread.

Postlarvae of *P. duorarum* were distinguished from those of *P. aztecus* by Williams (1959), and more fully described by Dobkin (1961), and Ringo and Zamora (1968). In North Carolina, the recruitment period extends from June to November, but stragglers are occasionally found in April, or more often in May, and December (Williams 1969). Peak influx of the late postlarvae into estuaries is from July to September. Similar occurrences of postlarval stages were reported by Bearden (1961), Copeland and Truitt (1966), Lunz (1965), St. Amant, et al. (1963), Tabb, et al. (1962), and Christmas, et al. (1966), although movement occurs at different times in other localities. There is some evidence that *P. duorarum* postlarvae entering estuaries are more abundant at night than in daytime, more abundant in surface than bottom samples (Williams 1969), and that more occur in surface samples on dark of the moon than at full moon (Williams and Deubler 1968). Other studies generally confirmed the diel and lunar abundance patterns but found bottom samples largest (Roessler and Rehner 1971).

Once on the nursery grounds in estuaries, the young undergo rapid growth. Williams (1955) estimated an average increase in length of young shrimp at 52 mm per month (about 1.8 mm per day) for warmer months. More recent work shows that this estimate may be too high. Eldred, et al. (1961) found that pink shrimp spawned in late March or April could reach lengths of 45–65 mm by July, while those spawned in May could reach lengths of 25–35 mm by July. Iversen and Jones (1961) showed that a 103-mm shrimp will grow 7 mm, a 130-mm shrimp will grow 5 mm, and a 153-mm shrimp will grow little or none in a month in either summer or winter. Eldred, et al. (1961) estimated that a 140-mm shrimp is about 1 year old and that on such basis shrimp measuring 200 mm in length are approximately 2 years old. Most individuals that grow to maturity may live a year or longer. Growth curves were computed for length and weight by Kutkuhn (1966) and McCoy (1971) as part of analyses of dynamics for Gulf of Mexico and selected North Carolina populations respec-

tively. Fontaine and Neal (1968) computed linear regressions for abdomen and total body length of this species, *P. setiferus*, and *P. aztecus*.

The young shrimp tend to seek shallower, often somewhat fresher, portions of the estuaries in the early part of their benthonic existence, and with increasing size move gradually into deeper, saltier water as they grow; finally, with approaching maturity they return to sea. This general pattern of movement may best be taken as a model which is variously modified in different parts of the range. In North Carolina, and perhaps elsewhere (Iversen and Idyll 1960; Eldred, et al. 1961), many of the juveniles present in the sounds in fall do not return immediately to sea but linger in the estuaries over winter. Here they are often subjected to quite low temperatures (about 3°C) (McCoy 1971), and in severe winters nearly all of this overwintering population may be killed. Normally they survive the winter, but because they are relatively inactive in the cold, they grow little, at least in North Carolina (November–April estimated average increase in length, 7.5 mm per month). Rising springtime temperatures induce increased activity and feeding, resulting in resumption of rapid growth and an ensuing spring migration to sea in May and June. In North Carolina, this migrating population is large enough to create a sizable late spring fishery.

There is strong evidence that the North Carolina population is endemic, although McCoy and Brown (1967) and McCoy (1972) demonstrated by mark-recapture techniques that juveniles released in the sounds off Carteret and Pender counties migrated generally southward, the record being 120 mi. (193 km) in five weeks from Core Sound to Long Beach, Brunswick County. Iversen and Idyll (1960) and Iversen and Jones (1961) demonstrated a general northwestward movement for shrimp tagged on the fishing grounds west of Key West and suggested that small shrimp move from shallow water at the end of the Florida peninsula to the Tortugas fishing grounds.

Hildebrand (1954, 1955) and Springer and Bullis (1954) emphasized that *P. duorarum* fisheries are located in areas where the bottom is composed of calcareous muds and sands or mixture of mud and sand. Laboratory experiments have shown that subadult *P. duorarum*, when allowed a free choice of sand, shell-sand, loose peat, muddy sand or sandy mud, tend to choose shell-sand with a somewhat lower preference for loose peat (Williams 1958). In shell-sand the animals were often completely buried, and could be observed only after being dug out. The experiments confirmed observations on the correlation of location of fisheries with bottom

type in the Gulf of Mexico and in North Carolina.

Penaeus duorarum beyond the early juvenile stages exhibits a marked diel activity, usually burrowed in the substrate during daylight, but active in the water column at night (or during daylight in very turbid water), a fact which governs the usual nighttime fishery for this form. Emergence from the substrate is markedly synchronized in all members of a population. Hughes (1968) experimentally demonstrated persistence of the pattern of nocturnal activity for several days under low light intensity, confirming that emergence and subsequent activity are under rhythmic control. Resynchronization of rhythmic phase controlling emergence to a shifted light-dark cycle indicated that light-dark itself, or some component of it, is responsible for maintaining the relation between emergence and the day-night regime. Light-dark transition seems to be the important component or Zeitgeber responsible for control of the time of emergence. Maximum response occurred when a light-dark transition was imposed at a time (1800 h) to which shrimp had previously been trained to receive it. Shrimp fed 24 h previously emerged from substrate and sought food despite high-intensity illumination and absence of food. Phases of feeding and emergence rhythms probably supplement each other because they are almost identical. Shrimp smaller than 4 cm length emerged significantly earlier than larger ones, possibly reflecting the lesser dependence of early juveniles on inherent rhythms and greater receptivity to exogenous stimuli. Fuss (1964) observed burrowing behavior with the aid of SCUBA and described it in some detail. Size of animal correlated positively with burrow depth, shrimp of 130–140 mm length burrowing as deep as 50 mm, usually less. Usually there is an inhalent hole near the tip of the rostrum and often another to the side, but flow of water is reversible. Often there is a cavity below the animal. Fuss and Ogren (1966) observed circadian rhythms of activity under constant light and found solar light to be the most important inhibiting factor in diel activity. Greatest activity was associated with temperature of 26°–27°C, but there was a general inverse relationship between nocturnal activity and water temperature below about 26°C; activity diminished greatly below 14°–16°C and ceased below about 10°C, but they observed that emergence may occur above 33°C followed by quiescence. Conservation of energy by burrowing probably extends the ability of the shrimp to undergo periods of starvation (i.e., winter hibernation). They observed this species to penetrate very coarse bottom including hard sand, sand-shell, and substrates overlaid with heavy plant growth.

Distribution of *P. duorarum* may be limited by

factors that influence *P. setiferus*; i.e., salinity and temperature.

In Texas (Hildebrand 1955) and Florida (Higman 1952) young of *P. duorarum* are especially abundant in grassy areas of estuaries where salinities are 20‰ or more. This is true of some areas in North Carolina, and the young are also concentrated most heavily in areas where there is a possibility of tidal transport (Williams 1955a). Gunter, et al. (1964) pointed out that *P. duorarum* is generally found in higher salinity than its congeners.

That *P. duorarum* alone of the three commercially abundant species of *Penaeus* treated here is able to overwinter in estuaries in the northern part of its breeding range has suggested that it is better able to withstand a combination of low salinity and temperatures because of superior osmoregulatory abilities at low temperature. Studies have shown that *P. duorarum* is better able to regulate its internal fluids at low temperatures than its close relative *P. aztecus*, but regulatory ability of both species is impaired when temperatures are lowered to about 8°C, and survival of both species is better in moderate to high salinities at low temperatures (Williams 1960).

Odum and Heald (1972) studied food habits of *P. duorarum* in a mangrove ecosystem, finding it to be an opportunistic omnivore. In a volumetric analysis of contents in the buccal cavity of 18 shrimp, they found: unidentified fine particles 25%; inorganic particles 44%; unidentified animals, harpacticoid copepods, small molluscs, and ostracods, each 3%; benthic diatoms 2%; filamentous green and blue-green algae 4%; and vascular plant detritus 15%. Dall (1968) reported penaeids to capture animals and consume algal cells and filaments and sediment particles, all obtained from browsing on the surface of estuarine muds. Idyll, et al. (1967) mentioned the dietary importance of bacterial films, yeast and slime molds which exist on mud particles. Meiss and Norman (1977a, b) studied both the stomatogastric skeleton and musculature of this shrimp. Many authors have recorded the role of this species as prey of fishes.

Parasites and/or diseases of *P. duorarum* were reviewed by Couch (1978), Sinderman and Rosenfield (1967), and Sprague (1970).

Penaeus (Litopenaeus) setiferus (Linnaeus)

(White shrimp)

Figs. 15–16

Cancer setiferus Linnaeus (in part) 1767:1054.

Penaeus setiferus.—Hay and Shore 1918:378, pl. 25, fig. 5.—Burkenroad 1939:17.—Holthuis

1962:115–118.—Williams 1965:18, figs. 8–9.—Lindner and Cook 1970:1444.

Penaeus fluviatilis.—Gunter 1962a:107–114.—1962b:118–121.

Penaeus (Litopenaeus) setiferus.—Pérez Farfante 1969:468, figs. 4–11.

Recognition characters.—Integument thin, polished, translucent. Carapace with high median carina continuous anteriorly with rostrum and extending back about $\frac{2}{3}$ length of carapace; not grooved posteriorly, lateral rostral grooves terminating near posterior tooth in rostral series; armed with 5–11, usually 9, sharp teeth dorsally, anterior 6 teeth on rostrum proper; gastrofrontal carina absent. Rostrum with tip long, slender, unarmed, up-curved distally (apex sometimes depressed), first dorsal tooth near distal edge of eye, ventral edge usually armed with 2 teeth. Antennal spine extending upward short distance from hepatic spine. Mesial antennular flagellum of adult male dorso-ventrally flattened and armed dorsally with 2 sizes of teeth. Antennal flagellum very long.

Anterolateral marginal ridges of last thoracic sternite of female extending conspicuously mesad near middle of segment making an interrupted crescentic transverse ridge with concavity directed forward; posterior portion of sternite with conspicuous pair of fleshy protuberances. Tonguelike lamella on anterior part of sternite VIII (fourth legs).

Abdomen with segments 4–6 carinate; carina of segment 6 with narrow, shallow groove on each side. Telson with deep median groove and acuminate tip. Ventral margin of pleura of segment 1 almost straight. Petasma of male with diagonal ridge across face of dorsolateral lobe.

Measurements in mm.—Length of body: large male, 182; large female, 200. Females beyond the juvenile phase are consistently larger than males.

Color.—Body translucent, bluish white with dusky bands and patches composed of scattered black specks; rostrum and sides tinged with pink; blades of pleopods marked with dark red; antennae dark brown; uropods with tips of blades dark brownish purple with narrow stripe of yellowish green along margin.

Habitat.—Estuaries and inner oceanic littoral, predominantly on mud bottom from water's edge to 30 m off Atlantic coast; rarely to 82 m in Gulf off Mexico (Bullis and Thompson 1965). Most abundant in areas characterized by extensive inland, brackish marshes connected by passes to shallow, offshore areas of relatively high salinity (Anderson, et al. 1949).

Type-locality.—Off Matanzas Inlet, Fla.

Known range.—Fire Island, N. Y., to Saint Lucie Inlet, Fla.; near Dry Tortugas, Fla. (rarely); Gulf of Mexico from Ochlocknee River, Fla., to Campeche, Mexico. Centers of abundance are: Georgia and northeast Florida; Louisiana; Tabasco and Campeche.

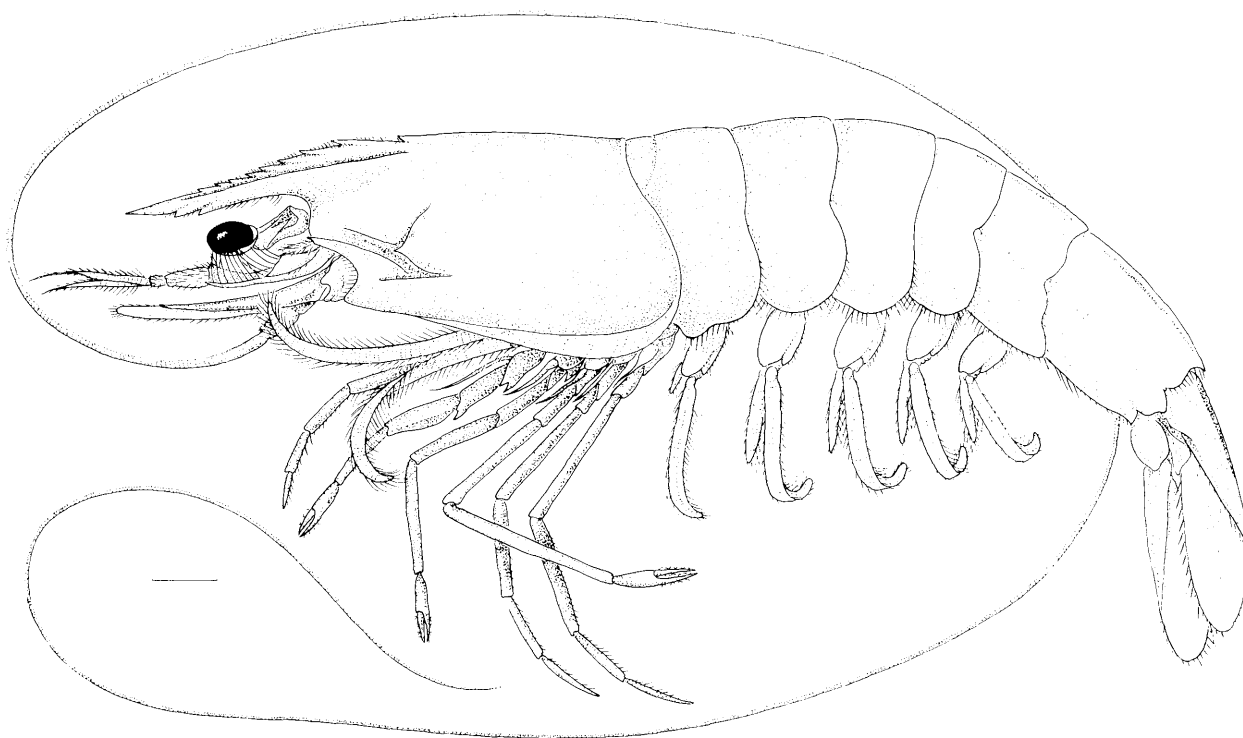


Fig. 15. *Penaeus (Litopenaeus) setiferus* (Linnaeus). Female in lateral view, 1 cm indicated (from Pérez Farfante 1978).

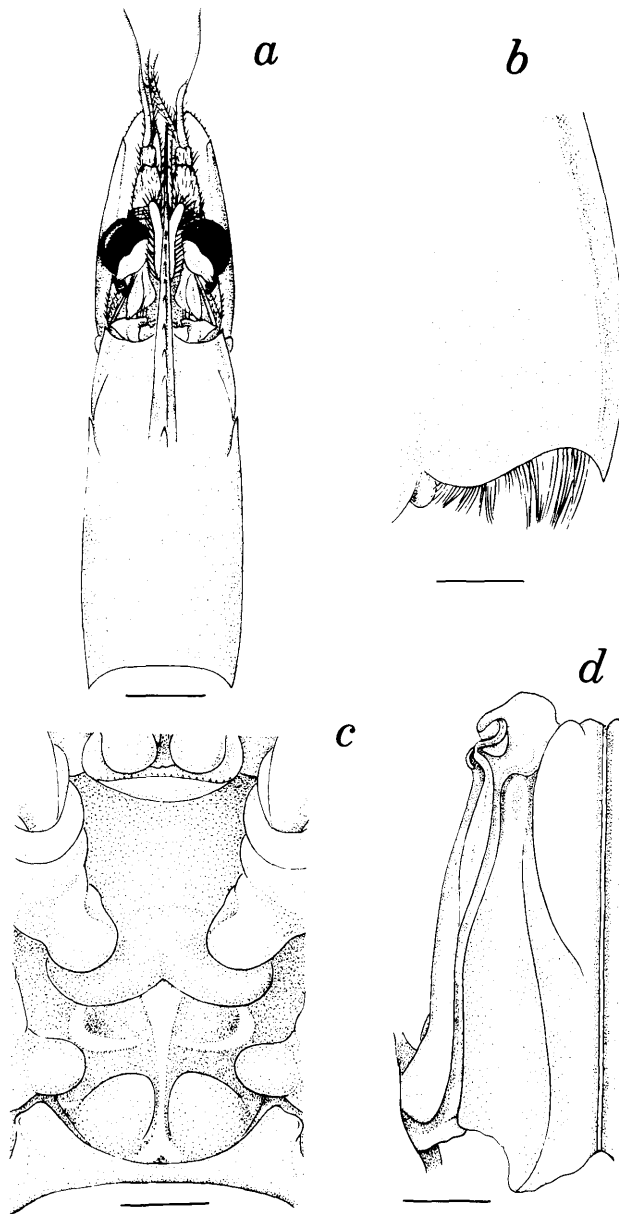


Fig. 16. *Penaeus (Litopenaeus) setiferus* (Linnaeus). *a*, Carapace in dorsal view; *b*, sixth abdominal segment in lateral view; *c*, thelycum of female; *d*, petasma of male; *a*, 10 mm; *b-d*, 2 mm indicated (from Pérez Farfante 1978).

Remarks.—Of the shrimps occurring in the Carolinian Province, *P. setiferus* was the first to be studied extensively. This was because the species has great commercial value, and was the first of the American penaeids to be extensively marketed for food. In the early 1930's, when popular demand caused shrimp fishing effort to expand greatly, concern over the possibility of depleting the resource led the Bureau of Commercial Fisheries to initiate a research program on various aspects of the biology of this species. At that time, *P. setiferus* composed over 95% of the commercial catch

(Lindner and Anderson 1956). A voluminous literature, scholarly and popular, has accumulated in the ensuing 50 years, and though it would be presumptuous to attempt a complete review of this work here, the chief results of studies can be outlined. (Exhaustive bibliographies or reviews have been compiled by Chin and Allen 1959; Pérez Farfante 1969; and Lindner and Cook 1970.)

The species is caught commercially throughout most of its geographic range (from North Carolina to Mexico); however, by far the greatest concentration occurs in Louisiana, in and near the Mississippi River Delta, and it was here that Viosca (1920) first worked on some aspects of the species' natural history, anticipating in many respects later, more detailed studies.

Young (1959), in an exhaustive morphological study of *P. setiferus*, reiterated the generalized structure of the Penaeidae. This work is profusely illustrated and the text illuminates details which were often obscurely presented in older works. Complexes such as the branchial apparatus and associated structures are clearly delineated, as are the skeletal, muscular, nervous, circulatory, and respiratory systems in general.

In 1956, Lindner and Anderson summarized work of the U.S. Bureau of Commercial Fisheries and the Fish and Wildlife Service in the 1930's and 1940's that had been presented in a series of shorter articles. Reference to this paper will lead the reader to earlier detailed studies.

Structure of the thelycum and spermatophore of *P. setiferus* and its related species in the subgenus *Litopenaeus* was described, profusely illustrated, and discussed by Pérez Farfante (1975).

Spawning of the white shrimp in the Carolinian Province probably begins in May and extends into September (Lindner and Anderson 1956; Williams 1955); farther south in the Gulf of Mexico the season probably extends from March to September or October, or spring to late fall (Franks, et al. 1972). Gunter (1950) suggested two periods of spawning (spring and fall) for Texas waters, but in the Carolinas there is probably only one, as is the case in Florida (Joyce 1965).

Maturation of gonads has been studied in detail (King 1948) in both males and females. In females, the stages of maturity can be judged macroscopically by color of the ovary. The earliest or undeveloped stage may last for an indeterminate time (Lindner and Anderson 1956); the developing stage was judged to last a month or less, the succeeding yellow stage for 1 to 2 months, and the ripe, olive-drab colored ovaries to become spent in less than a month. Spent ovaries were found to revert to the yellow stage in a period of a few days and then to

develop toward a ripened stage again in 2 or 3 months. The color changes were illustrated by Brown and Patlan (1974). A large female is estimated to produce a half million to a million eggs at a single spawning (Anderson, et al. 1949).

It was thought that studies of the ovary would lead not only to discovery of spawning grounds but also to knowledge of how many times a female shrimp might spawn, and to the approximate age and length of life of the shrimp. Such hopes were incompletely realized. The likelihood of multiple spawning and absence of permanent scars or walled-off areas in the ovary precluded age determination by this method. Occurrence of ripe females suggests that spawning in Louisiana takes place offshore in depths greater than 8.2 m, probably between 9 and 31 m. Heegaard (1953) reported occurrence of spawning 6 or more mi. (9.7 km) from shore in from 8- to 27-m water in Texas. The exact location of spawning grounds off the Carolinas remains unknown.

Developmental stages of the white shrimp were studied in detail by Pearson (1939), based on plankton tows off the Mississippi River Delta and the coasts of South Carolina, Georgia, and Florida, and on rearing experiments with material taken from plankton catches at St. Augustine Inlet, Fla. (The eggs of penaeids are not carried on the pleopods of the females as in other decapods, but are broadcast.) In this study, few eggs were found, but this circumstance was attributed to the fact that the eggs are demersal, hence, hard to capture, and perhaps deposited chiefly beyond the area sampled. Of the material available for rearing, 5 of 15 eggs hatched within 24 hours after capture. Developmental stages prior to hatching were described, and, following hatching, five naupliar (non-feeding), three protozoal (fed on algae and *Artemia* nauplii in laboratory), two mysis, and a series of postlarval stages were described. Lindner and Cook (1970) reported three mysis stages in laboratory reared stock. Pearson thought it likely that though the larvae are more or less at the mercy of currents, they still are capable of considerable independent movement. From the spawning place at sea, a great number of the larvae move inshore and enter estuaries at about the second postlarval stage (7 mm total length), and it is at this stage that they abandon planktonic for a benthonic existence. The length of larval existence from time of hatching to entrance into estuaries was judged to be about two or three weeks. When reared in the laboratory at 30°C, larvae grew to first postlarva in 9–13 days, or 15–24 days at 22°C, (Lindner and Cook 1970).

Heegaard (1953), studying wild populations of larval white shrimp, and Johnson and Fielding

(1956), studying animals reared in captivity, gave somewhat different interpretations of this portion of development. Heegaard suggested that the number of molts in certain portions of the larval sequence may vary individually; Johnson and Fielding, while agreeing with Pearson's descriptions of stages, gave evidence for shorter time of development from hatching to first postlarva (about 2 weeks). They also gave evidence for very rapid growth of the young, 2.1 mm and 1.7 mm per day in different experiments under conditions of full feed. The same authors secured good growth in both high and medium salinities.

Bearden (1961) demonstrated that postlarval *P. setiferus* enter South Carolina sounds from June through September, a period similar to the supposed recruitment period in North Carolina (Williams 1959), although the season is longer in the Gulf of Mexico. There King (1971) found *P. setiferus* postlarvae in small numbers from July to December in samples from the Aransas-Copano Bay system. Wilson (1969) found peak recruitment in the canal-lake area southwest of New Orleans during June-July, the same period in which *P. aztecus* juveniles return from Galveston Bay, Tex. Duronlet, et al. (1972) took *P. setiferus* postlarvae at all depths in daytime but significantly more abundantly near the surface at night. Christmas, et al. (1966) demonstrated that the abundance of *P. setiferus* postlarvae entering estuaries may be used as an index for prediction of adult catch, an idea held by numerous authors but never successfully put into standard practice as a measurement.

Once in estuaries on so-called "nursery grounds" the young grow rapidly. Williams (1955) estimated an average increase in length of 36 mm per month (1.2 mm per day), and other similar (Gunter 1956; Loesch 1957) or higher estimates (Loesch 1965) of 65 mm per month or 2.2 mm per day have been made. The young, which in the early part of their benthonic existence tend to seek the fresher, shallower portions of estuaries, move gradually into deeper, saltier water as they grow, and with approaching maturity return to sea. Hoese (1960) suggested that migration to estuarine nursery grounds may not be essential to development in this species, but Gunter (1961) gave much evidence to the contrary. Most of the individuals that grow to maturity appear to live a year or a little longer. Some exceptional individuals in the deeper part of the range may live to be about two years old. Lindner and Anderson (1956) estimated that mature *P. setiferus* grow at a rate of about 20 mm per month during the period March to October.

In addition to annual cyclic movements of larvae into estuaries, and subsequent movement of sub-

adults back to sea, tagging experiments have indicated that *P. setiferus* may make coastwise migrations of considerable length. In their analysis of these experiments, Lindner and Anderson (1956) showed that in fall and winter, shrimp tend to move south along the Atlantic coast; in late winter and early spring, there is a return movement; and during late spring and summer, position of the population is relatively static. Large individuals are prone to move longer distances than small shrimp. The longest recorded southward movement was by a shrimp tagged at Beaufort, N. C., in October, and recovered 95 days later off Florida, 360 mi. (579 km) from the point of release; McCoy and Brown (1967) and Schwartz (1977) reported comparable results, 345 mi. (555 km) and 357 mi. (524 km) respectively from point of release. The greatest counter movement was from Cape Canaveral, Fla., in January, to South Carolina 168 days later, a distance of 260 mi. (270 km).

Distribution of *P. setiferus* is not uniform, and this may be conditioned by a number of factors. These are usually thought to be salinity, temperature, and substrate. The young may utilize waters of somewhat lower salinity than the young of related penaeids (Burkenroad 1934b; Williams 1955). Body fluids are hyperosmotic in brackish water and hypotonic in full marine salinities, regulation of ions and osmotic concentrations being more effective in low salinity water (McFarland and Lee 1963). Hildebrand and Gunter (1953) and Gunter and Hildebrand (1954) demonstrated a strong positive correlation between the white shrimp catch for a given year and total rainfall for that year and the two preceding years in Texas, high rainfall being

followed by good catches. In colder portions of the year no young are found in inside waters, at least in the Carolinas (Williams 1955a). *Penaeus setiferus* is usually found on a muddy substrate on trawling and nursery grounds (Springer and Bullis 1954; Hildebrand 1954, 1955), and in experimental tanks it has been shown to choose muddy substrates in preference to sandy or rocky bottoms even though it burrows to a lesser extent than its near relatives (Williams 1958).

Subadult populations of white and other penaeid shrimp in estuaries have been exploited for fish bait. Studies of such fisheries have given more detail on migrations and density of population (Loesch 1957) and on individual length-weight relationships (Chin 1960).

Genus *Metapenaeopsis* Bouvier 1905

Bouvier 1905a:981.—Pérez Farfante 1971:7.

Metapenaeopsis goodei (Smith)

Figs. 17–18

Parapenaeus goodei Smith 1885:176.

Penaeopsis goodei.—Verrill 1922:44, pl. 15, figs. 1A–1Aiv; pl. 16, fig. 3.—Williams 1965:29, figs. 16, 17A, B.

Metapenaeopsis goodei.—Pérez Farfante 1971:9, figs. 4–8.—Coelho and Ramos 1972:140.—Chace 1972:7.

Recognition characters.—Carapace and abdomen covered with rather stiff, plumose hairs. Carapace

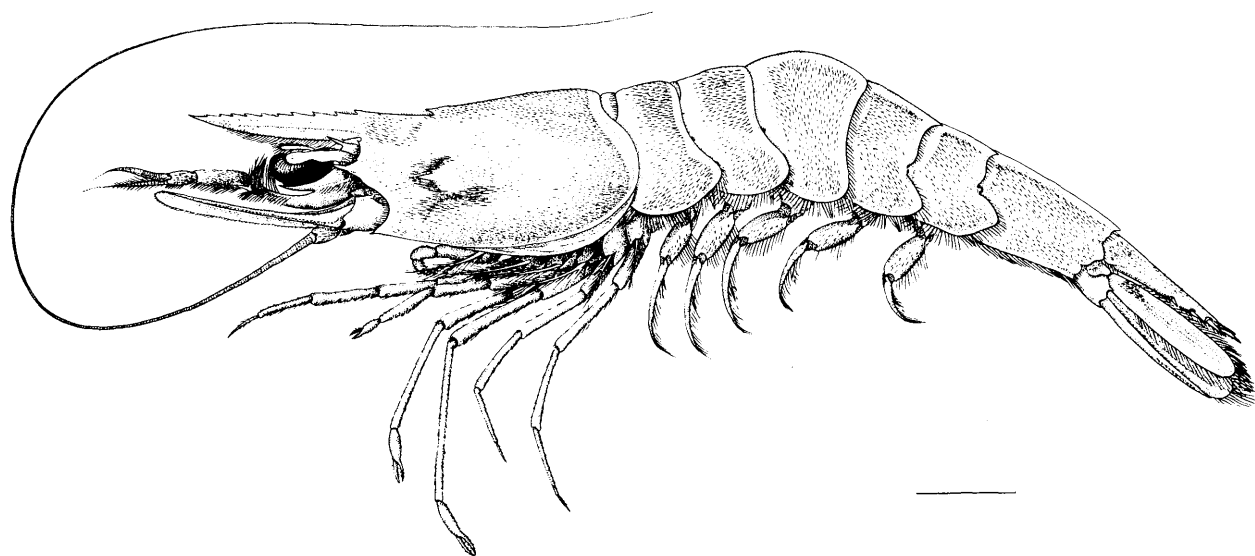


Fig. 17. *Metapenaeopsis goodei* (Smith). Female in lateral view, 5 mm indicated (from Pérez Farfante 1971).

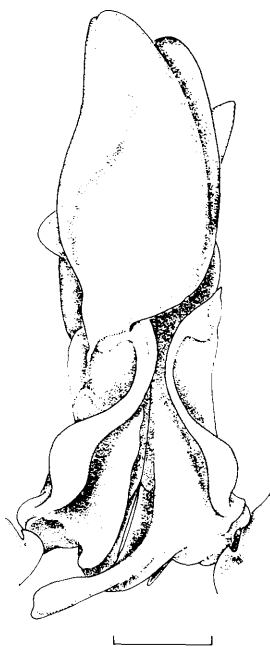


Fig. 18. *Metapenaeopsis goodei* (Smith). Petasma of male, ventral view, 1 mm indicated (from Pérez Farfante 1971).

about as wide as deep and very little compressed anteriorly. Rostrum rising obliquely above level of dorsum, shorter than carapace proper and armed above with 9 to 13 teeth in front of orbital margin; sharp epigastric tooth behind rostral carina. Antennal, hepatic, and pterygostomial spines well developed; rectangular toothlike eminence at orbital angle; grooves, except hepatic, inconspicuous. Eyes large, reniform, flattened above. Antennular flagella subequal in length and about as long as second article of peduncle. Antennal scale overreaching tip of antennular peduncle; distal portion of thickened outer margin armed above with series of minute spines directed obliquely forward and outward.

Third maxilliped, first and second legs armed with basal spines. Small distal spine on ventral side of ischium of first leg. Pair of long, slender spines arising from sternum between second legs.

Thelycum of female composed of anterior concave oval portion with slender anterior median spine on somite XIII (between fourth legs), and short broad, posterior portion on somite XIV connected to preceding structure by less elevated median prominence flanked by an irregular bulbous enlargement on each side.

Abdomen with segments 3–6 carinate dorsally; carina of 4 and 5 narrowly cleft at posterior margin. Telson considerably longer than sixth segment; rounded and obscurely grooved above; regularly tapered; armed with long fixed spines at each

side of acute tip, and 3 pairs of movably articulated spines in front of lateral spines, posterior ones largest.

Petasma of male exceedingly complicated and asymmetrical; left side irregularly folded longitudinally, projecting proximally in curved process beyond right half and to right of median line, and extending distally in a foliaceous process; right side enlarged distally and divided into several irregularly curved processes projecting beyond left appendage, and partially covered posteriorly by spoon-shaped lamella, distoventral projection arising at their bases.

Measurements in mm.—Length of body: male 61; female 75 (Smith 1885; Pérez Farfante 1971).

Color.—Body mottled with spidery pinkish-red chromatophores overall on white to cream background; legs similar but 1–3 flushed with yellow and speckled alternately with white chromatophores, 4–5 and pleopods speckled with white chromatophores; eyes bronze-green; antennules and antennae banded orange and white (R. H. Gore, personal communication).

Habitat.—Mud, sand, gravel, broken shell, rock, coral reefs, sometimes in algae; surface to 329 m (Pérez Farfante 1971; Coelho and Ramos 1972; Chace 1972).

Type-locality.—Bermuda.

Known range.—Bermuda; between Capes Hatteras and Lookout, N. C., through Florida Straits and along west Florida to Pensacola; Isla de Lobos reef, Veracruz (Ray 1974), around Yucatan, through Caribbean Sea, and along South American coast to Espírito Santo, Brazil (Coelho and Ramos 1972).

Remarks.—Larval stages from Bermuda that probably belong to this species were described by Gurney (1943b). From observations at Bermuda, Wheeler (1937) described characteristic swarming of this species at about an hour after sunset, with monthly maxima on the 2nd and 26th days of the lunar month.

Randall (1967) recorded *P. goodei* as food of the spotted scorpionfish, *Scorpaena plumieri* Bloch.

Genus *Parapenaeus* Smith 1886

Burkenroad 1934b:107.—China 1966:227.

Parapenaeus politus Smith

Fig. 19

Parapenaeus politus Smith 1881:444.—1885:172.—

Hay and Shore 1918:379, pl. 25, fig. 7.—Pérez Farfante 1982.

Parapenaeus longirostris.—Burkenroad 1934b:108.—

1939:53.—Williams 1965:27, fig. 27 (part, the western Atlantic population).—Roberts and Pequegnat 1970:48 (part, the western Atlantic population).

Recognition characters.—Integument smooth, not setose. Carapace with low carina extending almost to posterior margin and bearing epigastric spine some distance behind rostrum. Rostrum arched; distal half deflexed, tip somewhat upturned, extending to or beyond distal edge of eye; dorsal margin with usually 7 teeth diminishing in size anteriorly; ventral margin heavily ciliated. Hepatic, antennal, and branchiostegal spines well developed, latter placed a little behind margin of carapace. Rectangular toothlike eminence at orbital angle. Narrow shallow groove extending from behind eye almost to posterior edge of carapace, and another, extremely faint, running upward from inferior margin at base of second pair of legs. Basal antennular article with spine on ventromedian margin distally.

Thelycum of female composed of triangular plate with obtuse apex on somite XIII (base of fourth leg); sternite XIV raised anteriorly, with low relief posteriorly; lateral ridges with nearly straight but divergent mesial borders separated by nearly plane, broad medial groove; lateral border of ridges ornately curved to fit contour of adjacent coxae and sternite XIII.

Abdomen with segments 4, 5, and 6 carinate, carina ending on each segment in small tooth. Segment 6 a little more than twice length of 5. Telson tapering to sharp point, furrowed above, with slender spine on each side near tip.

Petasma of male with each half terminating in dorsomesial spinelike projection with fleshy distomesial lobe at base; broad lateral spine proximal to latter with fleshy distolateral lobe at base continuous with distomesial lobe but not projected laterally as a spoutlike horn as in *Xiphopenaeus*; finally, still farther proximally, a spinelike distoventral projection partially covered by mesial distoventral flap.

Measurements in mm.—Western Atlantic population: length of body, 104.

Variation.—The length of the rostrum increases with age, becoming relatively longer with variable development of an unarmed tip in large individuals. The sixth abdominal segment is relatively shorter in large than in small individuals.

Color.—Eyes green; body and appendages mottled with red and pale translucent areas; uropods with lateral ramus and distal half of mesial ramus deep red (Burkenroad 1934b).

Habitat.—Soft mud or muddy sand bottom; 27



Fig. 19. *Parapenaeus politus* Smith. Anterior part of animal in lateral view, 5 mm indicated (from Williams 1965).

to 330 m or more (Burkenroad 1934b, 1939).

Type-locality.—39°55'N, 70°54'W, 260.6 m, mud (Fish Hawk Stn. 878, S Block Island, R. I.).

Known range.—Martha's Vineyard, Mass., through Gulf of Mexico; Gulf of Paria off Venezuela.

Remarks.—Pérez Farfante (1982) has analyzed eastern and western Atlantic populations of *Parapenaeus longirostris* s.l., and concluded on the basis of morphology and color that the two are specifically distinct.

Parapenaeus politus is quite abundant in the northern Gulf of Mexico. Brusher, et al. (1972) found it infrequently at stations near east Texas and Louisiana from 64 to 110 m depths, almost exclusively at night. Females were generally larger than males. Some developmental stages from off South West Pass, La., found by Pearson (1939) were protozoal, mysis, and postlarval stages, principally during July when a complete set of larval stages was usually taken in a single plankton collection. A single mysis was taken south of Barataria Pass, La., in May and a single first protozoa at Fort Pierce, Fla., in January. Cook (1966) gave a key to larval stages of members of the genus. Subrahmanyam (1971a, b) described and figured protozoal and mysis stages from plankton and outlined larval abundance and distribution off Mississippi, showing that larval maxima were positively correlated with depth at the lower end of his station transect (36–90 m), that spawning was judged to occur mainly in fall-winter-spring, and that spawning in winter was in shallower water than the minimal amount of spawning in summer.

Genus *Trachypenaeus* Alcock 1901

Burkenroad 1934b:94.

Trachypenaeus constrictus (Stimpson)

(Roughneck shrimp)

Figs. 20–21

Penaeus constrictus Stimpson 1871b:135.

Trachypenaeus constrictus.—Hay and Shore 1918:378, pl. 25, fig. 9.—Schmitt 1935a:131.—Williams 1965:31, fig. 21.

Trachypenaeus constrictus.—A. Milne Edwards and

Bouvier 1909:232, figs. 60–63; pl. 5, figs 7–10; pl. 6, figs. 1–2.—Chace 1972:9.

Recognition characters.—Dorsal region of carapace with fine, short, appressed setae; branchial region of carapace and last 2 abdominal segments variably pubescent; abdomen smooth. Carapace carinate except for short stretch near posterior border; spine behind base of rostrum; antennal and hepatic spines well developed; rectangular tooth-like eminence at orbital angle; lateral groove extending about $\frac{3}{5}$ length of carapace; anterolateral angle truncate. Rostrum reaching to about middle of second segment of antennal peduncle, directed slightly upward; upper margin usually slightly arched and usually bearing 7 to 9 equidistant teeth diminishing in size toward tip. Eyes large, reniform. Antennular peduncle pubescent above, extending slightly beyond antennal scale; flagella shorter than carapace. Third maxilliped, first and second legs with basal spines.

Thelycum of female with anterior margin of median plate and lips of transverse groove evenly rounded, notched in middle; lateral plates of last thoracic somite overlapping median plate; rib supporting expanded median plate extending anteriorly and sharply set off from anterior ventral margin of plate; ventral surface pubescent. Sternal elevation between coxae of fifth leg of male with lateral margins indented setting off posterior part

from broad anterior basal part; petasma with distolateral corners greatly produced as hornlike projections.

Abdomen carinate from fourth to sixth segment. Telson with 2 rounded carinae above; tapering to short acuminate tip, armed on either side with short spine.

Measurements in mm.—Length of body: female 93 (smallest with ripe ovaries 63), male 63 (Anderson 1970).

Color.—Translucent with purplish-gray blotches; appendages pink.

Habitat.—Primarily sand or mud and shell bottom in high-salinity water; shallow water to 84 m (Brusher, Renfro, and Neal 1972).

Type-locality.—Beaufort, N. C.

Known range.—Tangier Sound, Chesapeake Bay, to Veracruz, Mexico (Ray 1974); Bermuda; Puerto Rico and Sombbrero Island; Surinam; off Ceará, São Paulo, and Santa Catarina, Brazil (Mistakidis and Neiva 1964, 1966; Fausto-Filho 1966b, 1967a; Iwai 1973).

Remarks.—*Trachypenaues constrictus* is of minor importance in commercial fisheries. Eldred (1959) reported it as common in the Tortugas area of Florida where, along with its congener, *T. similis*, it made up about 7% of the annual catch. She thought it probably contributed more to catches in deeper water than to catches in the area sampled. Joyce (1965) found 14.8% of offshore try-net samples in

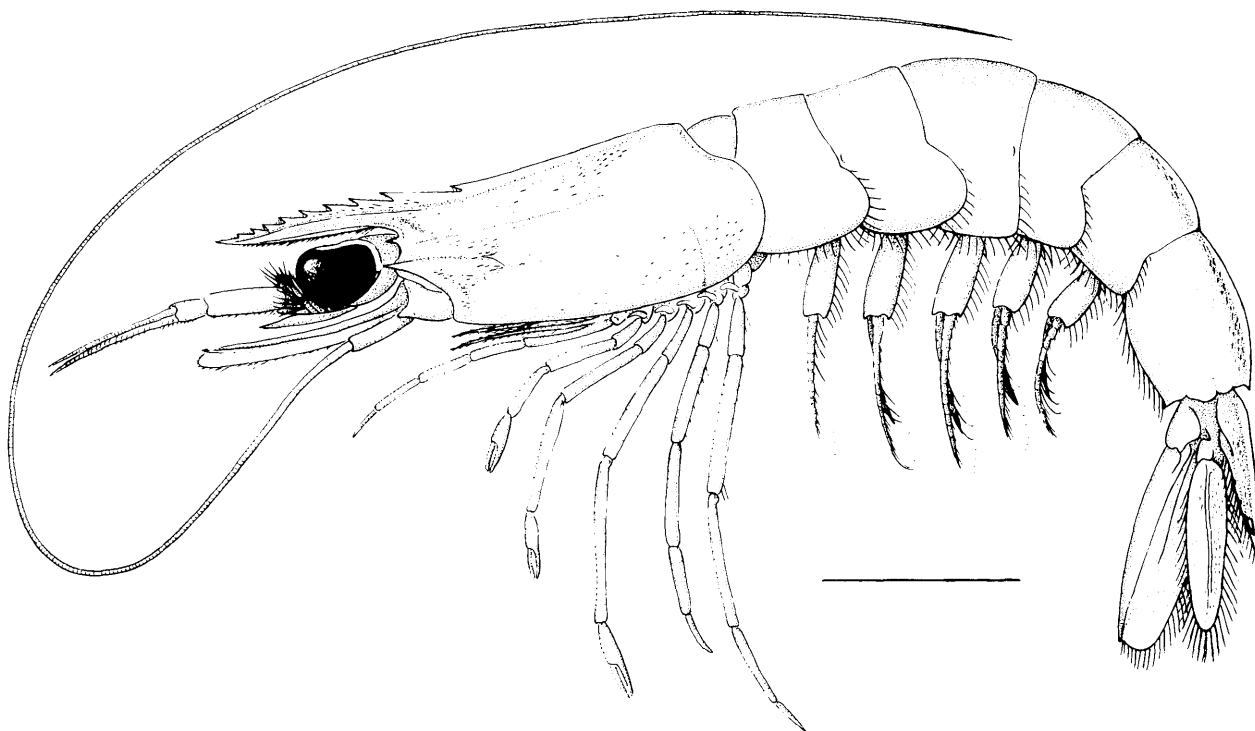


Fig. 20. *Trachypenaues constrictus* (Stimpson). Female in lateral view, 2 cm indicated (from Pérez Farfante 1978).

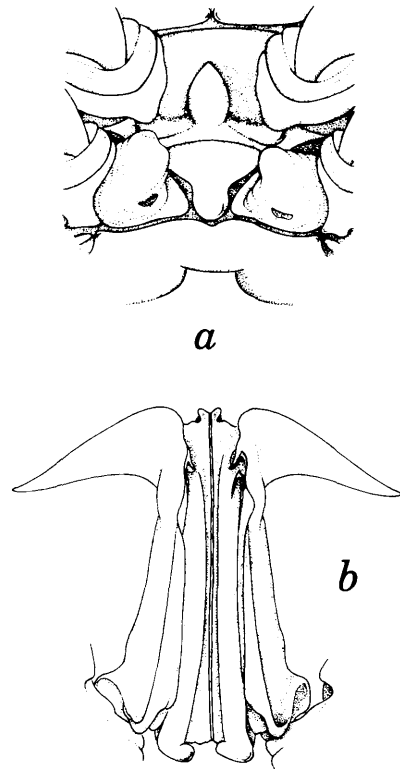


Fig. 21. *Trachypenaeus constrictus* (Stimpson). a, Thelycum of female; b, petasma of male (from Pérez Farfante 1978).

northeast Florida made up of this species. Inshore it made up almost 100% of the minor penaeid species in his samples. Gunter (1950) reported it as rare in coastal bays of Texas, being largely confined to waters above 30‰ salinity. The South American occurrences reported above were minor in commercial catches. Burkenroad (1939) remarked that *T. constrictus* might be restricted largely to sandy bottom, and Hildebrand (1955) suggested a distribution possibly correlated with bottom type, but did not specify the type.

Joyce (1965) found largest females to be 70–79 mm in length whereas males were 30–39 mm long. Anderson (1970) reported similar lengths, and both authors found a preponderance of females, their samples from South Carolina to northeastern Florida, as well as those of Subrahmanyam (1971b) from Mississippi, indicating spawning peaks in spring-early summer and again in October-November. Gunter (1950) found ripe females in September in Texas.

Early developmental stages were treated by Pearson (1939), larval and postlarval stages being pieced together by successful rearing techniques coupled with plankton catches at St. Augustine Inlet, Fla. Descriptions were given of the egg (from the 2-cell stage onward), five naupliar, three pro-

tozeal, two mysis, and early postlarval stages. He thought spawning was year-round because eggs were taken at St. Augustine, Fla., from April to August, and at Fort Pierce, Fla., in summer and from December to February. Nauplii were found from April to August, and the remaining stages from May to August, with a few protozoaea also in winter. Developmental stages of this species were more abundant than those of related species in shallow oceanic water, although in estuarine water the postlarvae were rare, and Pearson attributed both this rarity and the comparative scarcity of adults in commercial catches to the burrowing habits of postlarvae and adults, as observed in the laboratory. Subrahmanyam (1971a) reported thousands of embryonated eggs and larvae (the dominant penaeid) in samples from Mississippi, and described and illustrated protozoaea, mysis and postlarval stages. He (1971b) found larval maxima in 18–36 m depths, the shallower occurring in summer, but spawning continued from April through November. Cook (1966) gave a key to protozoecal through postlarval stages.

Juvenile stages of this species have been caught commonly in surface plankton tows made with a coarse-mesh net on nightly flood tides in North Carolina estuaries (Williams 1969). These collections also indicated spawning during summer. Although there was some penetration into mesohaline Neuse River, by far the largest samples came from near inlets south of Cape Lookout. Sykes (1966) reported occurrence of juveniles in Tampa Bay, Fla.

The food of hakes, *Urophycis regius* and *U. floridanus*, includes *T. constrictus* (see Sikora, et al. 1972). Helminth and cestode parasites of the shrimp were discussed by Sinderman and Rosenfield (1967).

Genus *Xiphopenaeus* Smith 1869

Burkenroad 1934b:102.

Xiphopenaeus kroyeri (Heller)

(Seabob; camarão sete barbas)

Figs. 22–23

Peneus kroyeri Heller 1862:425, fig. 51.

Xiphopenaeus kroyeri.—Burkenroad 1934b:103, fig.

12.—Schmitt 1935a:132, fig. 5.—Holthuis

1959:70, fig. 7.—Williams 1965:30, figs. 18–20.—

Chace and Hobbs 1969:55, figs. 6, 7e.

Xiphopenaeus kroyeri.—Boschi 1963:32, fig. 10.

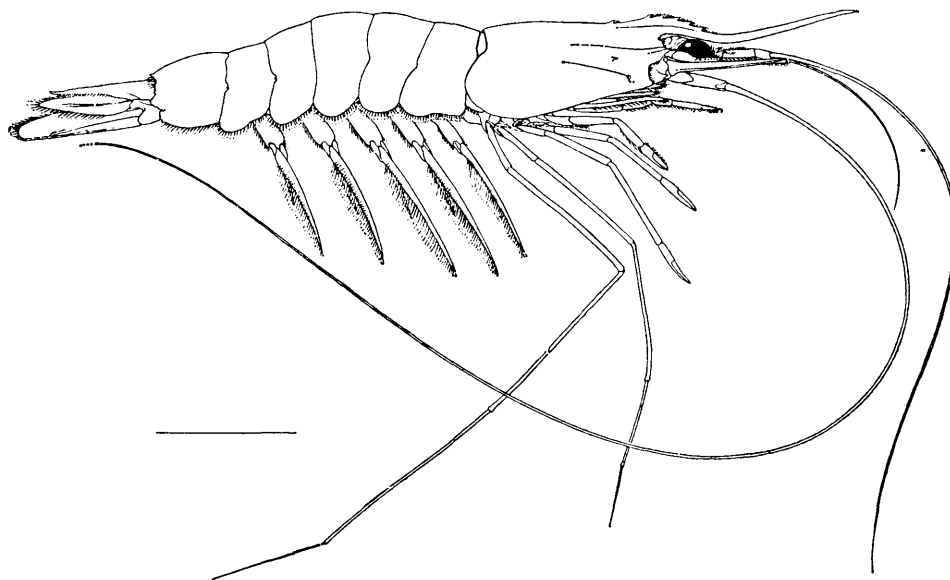


Fig. 22. *Xiphopenaeus kroyeri* (Heller). Female in lateral view, 2 cm indicated (from Chace and Hobbs 1969).

Recognition characters.—Carapace and abdomen smooth. Rostrum laterally compressed, sinuous, armed with usually 5 dorsal teeth at base, styliform tip greatly elongated beyond antennal scales and varyingly elevated. Carapace with epigastric tooth behind rostral series on rounded postrostral carina extending from base of rostrum to near posterior border; no transverse suture in adults; hepatic groove reaching anterior margin and contiguous with branchiocardiac groove reaching almost to posterior border; hepatic and antennal spines present. Antennal flagella much longer than body; antennal scale extending beyond tip of antennular peduncle. Inferior antennular flagellum up to half length of antenna. Exopodites of second and third maxillipeds slender.

Last 2 pairs of legs elongate, flagelliform, with dactyls many jointed.

Thelycum of female externally appearing as an unpaired plate extending forward from last thoracic somite.

Fourth to sixth abdominal segments carinate, with small dorsal tooth at posterior end of carina on each segment; sixth segment with carina high and deep. Telson tapering to acute tip.

Petasma of male with distolateral corners greatly produced as hornlike projections, open along distal margins on thoracic face.

Measurements in mm.—Maximum length of body 129 (Juneau 1977).

Variations.—The rostrum is somewhat longer in

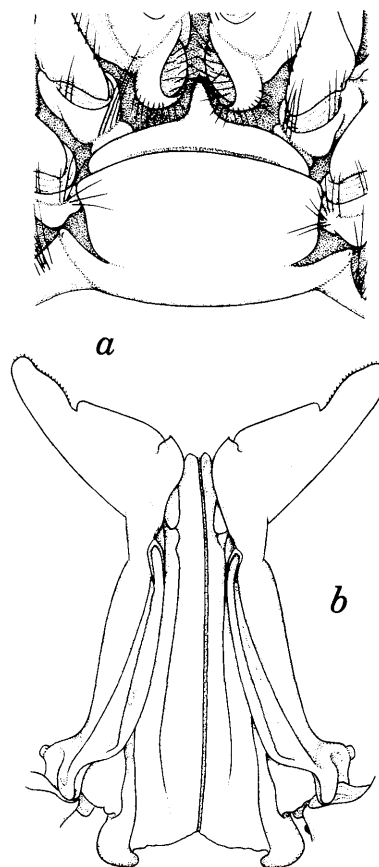


Fig. 23. *Xiphopenaeus kroyeri* (Heller). a, Thelycum of female; b, petasma of male (from Pérez Farfante 1978).

females than in males, and varies with age. In individuals with carapace length under 9 mm, the rostrum is shorter than the carapace, but beyond this size it is usually longer than the carapace.

Color.—Whitish, ventral part yellowish, occasionally with yellow over whole body but most distinct ventrally; dark chromatophores scattered throughout and when expanded giving animal a grayish cast; tips of rostrum and flagella reddish; legs pinkish or yellowish orange; pleopods and uropods yellowish at base, pink distally; telson and sixth abdominal segment sometimes pink (Holthuis 1959).

Habitat.—This species lives in a narrow zone along shore, and at times in the lower part of estuaries (Gunter 1950; Holthuis 1959), from 4.5 to 36.5 m, rarely to 44 m (Burkenroad 1939; Gunter 1950) or 70 m (Young 1978).

Type-locality.—Rio de Janeiro, Brazil.

Known range.—Between Capes Hatteras and Lookout, N. C., through Gulf of Mexico and Caribbean Sea to Ponta do Zimbro, Santa Catarina, Brazil (Pérez Farfante 1978). Pacific Coast variety (*X. riveti*, see Burkenroad 1934b) from Mexico to northern Peru.

Remarks.—*Xiphopenaeus kroyeri* is of limited commercial importance in the southern United States (Weymouth, et al. 1933; Hildebrand 1954; Kutkuhn 1962; Brusher, Renfro, and Neal 1972; Juneau 1977) but of greater importance in South America (Lindner 1957; Higman 1959; Tremel and Mistakidis 1965; Neiva 1967), especially along the northeast coast where it is prominent in the near-shore fishery and the young dominate the coastal nursery areas, perhaps offering serious competition to other penaeids, and off Santa Catarina, Brazil. In the early 1930's the species was abundant along the coast of Georgia and adjoining states, but has since declined drastically (Anderson 1970). There and in Texas it seemed most abundant in fall, occurring deeper in summer than in winter (Gunter 1950; Gunter, et al. 1964). Gunter pointed out that the species does not customarily live in bays, even though it lives in shallow water close to shore. The young may enter the lower end of Texas bays (salinity 21.2–30.7‰), but most individuals were found in the Gulf of Mexico in salinities of 29.7 to 35.2‰. Similar salinity tolerances were implied by Lindner (1957) and noted by Holthuis (1959). Though the South American shrimp are caught in estuaries and rivers, penetration into these areas is greatest in dry seasons. Both Lindner and Holthuis gave data on the fisheries and processing methods.

Renfro and Cook (1963) observed gravid females from spring to fall in Texas, and Burken-

road (1949) observed ripe or nearly ripe females off North Carolina in May. Viera (1947), in a study on maturation, found mature females off São Paulo, Brazil, from November to January, and Mota Alves, et al. (1977) found them from April to December along the coast of Ceará. From gravid females spawned in the laboratory, Renfro and Cook (1963) cultured viable eggs that hatched and developed through five naupliar stages and a protozoal stage in seawater of 29.5‰ salinity at 19.6°–25.0°C. Detailed, illustrated descriptions were given, and Cook (1966) provided a key to certain larval stages. Subrahmanyam (1971a, b) found mysis stages and later stages off Mississippi nearly year round, but most abundant in depths near 10 m in late spring-summer and deeper (to 72 m) in late fall. He judged spawning sites to coincide with those where larvae were found.

Nosema nelsoni Sprague, a microsporidian parasite of *X. kroyeri*, occurs in shrimp from the southern United States (Sprague 1970; Couch 1978).

Family Sicyoniidae

Integument rigid, of stony appearance. Carapace without postorbital spine; cervical groove very faint or absent. Basal article of ocular peduncle lacking mesial scale; ocular plate bearing styliform projections. Prosartema absent. No thoracic exopodites behind first maxillipeds. Podobranchs absent behind second maxillipeds. Only 1 large arthrobranch (posterodorsal) on somite XIII (fourth pereopods), a rudimentary anteroventral one present. Pleurobranchs absent behind somite IX (third maxillipeds). No epipodites behind third pereopods. Third and fourth pair of pleopods unir-

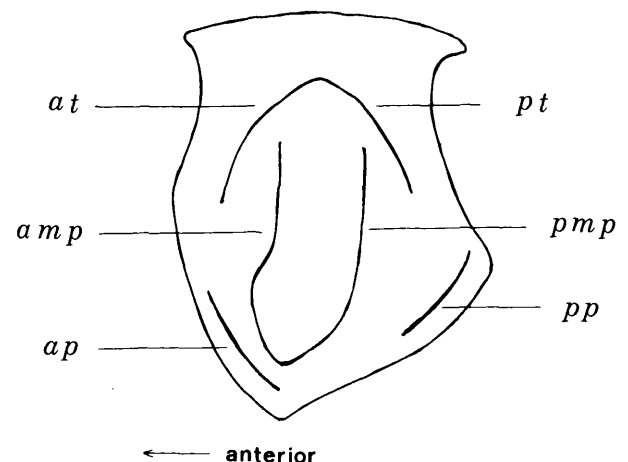


Fig. 24. Schematic lateral view of *Sicyonia* abdominal segment showing grooves: *at*, anterior tergal; *amp*, anteromedian pleural; *ap*, anterior pleural; *pt*, posterior tergal; *pmp*, posteromedian pleural; *pp*, posterior pleural (from Cobb, et al. 1973).

mous, lacking endopodites. Second pair of pleopods in males bearing only appendix masculina.

Burkenroad (1934a) pointed out that the family Sicyoniidae (his Eusicyoninae) is an extremely uniform group. Unlike other penaeoids, sexual maturity may be attained at quite small size. "Differences between small and large individuals of any species are slight and chiefly affect the rostral length, elevation and distal armature, these features in general becoming respectively shorter, more horizontal, and with more numerous distal teeth as size increases; and the armature of the pleonic [abdominal] pleura, which generally increase in strength and extent with growth." The thelycum, and corresponding male genital sternites, are less diversified than among other penaeoid groups, and, consequently, are not so serviceable in distinguishing species. The serious student is referred to Bur-

kenroad (1934b:70–76) for full discussion of these characters.

Genus *Sicyonia* H. Milne Edwards 1830

Burkenroad 1934a:70.—1945:1.—Hall 1956:87.—Hemming 1958b:126.

The generic name *Sicyonia* H. Milne Edwards was validated under Plenary Powers of the International Commission on Zoological Nomenclature (Opinion 382, Hemming 1958b).

Integument firm, whole body with covering of short, fine hairs. Rostrum toothed dorsally, tip bifurcate or compound, conspicuous ridge parallel to ventral margin. Abdomen often irregularly tuberculate, segments sculptured with some variant of pattern shown in Fig. 24.

Key to Species

1. First leg with basis and ischium armed with a spine; abdominal segment 2 with dorsal carina notched at junction of transverse sulci . . [Division I] 2
First leg with basis and ischium unarmed; abdominal segment 2 with dorsal carina unnotched [Division II] 3
2. Rostrum (excluding tip) with 2 dorsal teeth anterior to posterior orbital margin; carina of carapace with 3 teeth, first tooth smallest *S. laevigata*
Rostrum (excluding tip) with 3 dorsal teeth; carina of carapace with 3 evenly spaced, subequal teeth. *S. parri*
3. Carapace with 3 large dorsal teeth behind hepatic spine. . . *S. brevirostris*
Carapace with 1 or 2 large dorsal teeth behind hepatic spine. 4
4. Two teeth on dorsal carina behind hepatic spine *S. typica*
One tooth on dorsal carina behind hepatic spine 5
5. Pleura of abdominal segment 4 with both antero- and posteroventral margins spined or angular. *S. dorsalis*
Pleura of abdominal segment 4 with posteroventral margin rounded . . . 6
6. Antennal spine long, acute, buttressed; pleura of abdominal segments 1–4 with ventral spines laterally recurved *S. burkenroadi*
Antennal spine short, often minute, not buttressed; pleura of abdominal segment 1 rounded, 2–4 angulate, but without laterally recurved marginal spines *S. stimpsoni*

Sicyonia brevirostris Stimpson

(Rock shrimp, Japanese shrimp, red shrimp, coral shrimp, ridgeback)

Figs. 25–26

Sicyonia brevirostris Stimpson 1871b:132.—Hay and Shore 1918: 380, pl. 25, figs. 2, 4.—Williams 1965:35, figs. 25–26.—Cobb, Futch, and Camp 1973:7, figs. 3, 4A–C.

Eusicyonia brevirostris.—Burkenroad 1934a:84.—Lunz 1945:6, fig. 3.

Recognition characters.—Rostrum variously curved dorsally, slender, narrowing considerably to tip, shorter or longer than cornea; armed dorsally with 2, occasionally 3, subequal teeth not counting bifid or trifid tip with ventral tooth projecting anteriorly farther than dorsal tooth, small node often present between terminal teeth in bifid condition. High postrostral carina with 4, occasionally 3, teeth behind orbital margin; 3 large teeth behind hepatic spine, usually small tooth anterior to it. Antennal angle armed with small buttressed spine. Hepatic spine well developed. Ocular stylets long.

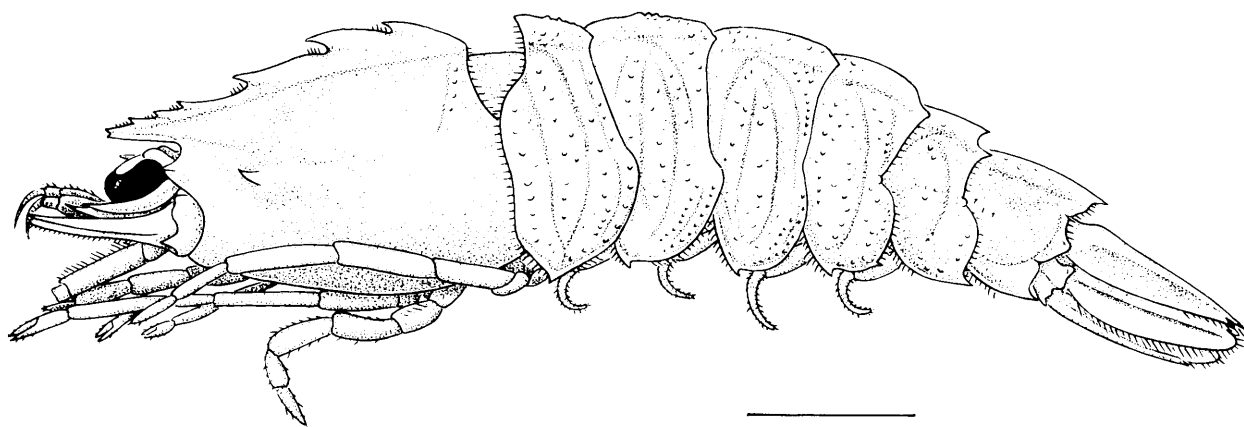


Fig. 25. *Sicyonia brevirostris* Stimpson. Male in lateral view, 10 mm indicated (from Cobb, et al. 1973).

Abdomen with prominent tergal carina deeply notched posteriorly on first 5 segments. Segment 1 with carina produced into elevated tooth directed anteriorly; conspicuous tooth on posterior margin of segments 5 and 6. Ventral margins of pleura bordered by smooth, narrow ridge; those of first 3 segments broadly rounded posteriorly but segment 4 rectangular or spined; anteroventral angle of segments 1–4 armed with spine, progressively more developed and curved laterally or lateroposteriorly and dorsally in series. Segments 5 and 6 broadly rounded anteriorly, posterolateral angle with acute tooth. Anterior margin of first segment and posterior margin of 1–3 slightly concave; deep V-shaped indentation near midpoint of posterior pleural margin on 4 and 5; 6 with pronounced angular projection on posterior margin near midpoint. Sulci on segments as follows: 1 with deep anteromedian pleural dorsally terminating at concavity of tergal margin; long, well-defined posteromedian continued to dorsal side of tergum; posterior tergal shallow, often obscure; posterior pleural shallow. Segments 2 and 3 each marked with deep anteromedian and posteromedian pleural extending far dorsally on tergum; anterior and posterior tergal well defined; posterior pleural shallow. Segments 4 and 5 traversed by anterior tergal terminating near midpoint; posterior tergal long, continuing to curve anteriorly near ventral margin of pleuron on 4 only. Six with shallow, short posterior and broad longitudinal sulcus.

Petasma of male with distolateral lobes curved mesially, distoventral lobes curved laterally.

Measurements in mm.—Length of body: males to approximately 116, females to approximately 118 (Kennedy, et al. 1977); both sexes rarely to 153.

Variation.—This species exhibits considerable variation in degree of elevation of the rostrum (5°–45°). The rostral length also varies, and length and

angle of elevation tend to decrease with increasing age, but this tendency is highly irregular.

Considerable variation in placement of teeth on the carapace occurs. The anterior tooth of the dorsal carina usually is located behind the orbital margin and appears as part of the carapace series, in which case there are 4 teeth on the carapace and 2 on the rostrum (exclusive of tip); or occasionally this tooth may be located anterior to the orbital margin and appear as part of the rostral series, in which case there are 3 teeth on the rostrum and 3 on the carapace (see Cobb, et al. 1973).

Color.—Ground color off white to light pink, pubescence grayish to grayish yellow; dorsal carina barred with white; appendages reddish purple, thoracic appendages barred with white; ventral side of abdomen and uropods reddish, sternal ridges white with purple median spines. Burkenroad (1939) gave a somewhat different and more detailed color description.

Habitat.—Most frequent on sand and shell-sand bottoms of the continental shelf; shallow water to 329 m, densest populations between 18 and 73 m (details in Cobb, et al. 1973).

Type-locality.—Cuba.

Known range.—Off Norfolk, Va., through Bahamas to southern Cuba; around Gulf of Mexico to southern Texas; Yucatan and Campeche Banks; one occurrence on Pacific coast of southern Mexico. Centers of abundance are known off Cape Lookout, N. C., north of Palm Beach, and off Cape San Blas, Fla., off Louisiana, Campeche Banks, and Cabo Catoche (Cobb, et al. 1973).

Remarks.—During the past 15 years the rock shrimp has grown in market volume and value from incidental catch to annual landings in 1976–77 of 2.2 to 2.4 million pounds worth approximately \$2 million (Anonymous 1979), and an increase to 3.7 million pounds in 1979 (I. Pérez Farfante, per-

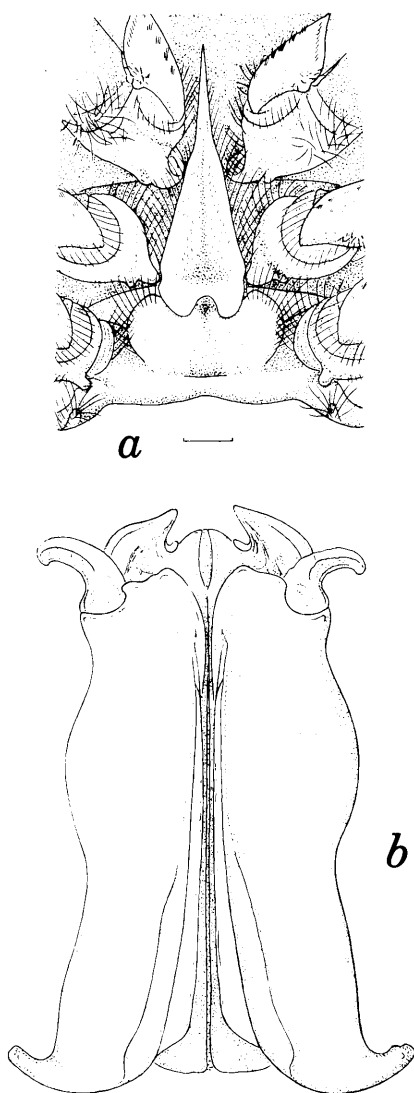


Fig. 26. *Sicyonia brevirostris* Stimpson. *a*, Thelycum of female (from Pérez Farfante 1978); *b*, petasma of male (from Williams 1965); *a*, 2 mm, *b*, 1 mm indicated.

sonal communication). Catches from both U.S. and Mexican waters contributed to this total. Tremendous schools of *S. brevirostris* were reported off Contoy, Yucatan, in 1973 that yielded some single boat catches of 6,400 lbs. per night, according to one report; annual landings that year first exceeded 1 million lbs. (NOAA News, Vol. 5, No. 3, p. 1, 1973).

Kennedy, et al. (1977), in a major population analysis of *S. brevirostris* off northeastern Florida that extends the findings of earlier authors, showed that ovarian development of females followed that observed in other penaeoid shrimps, i.e., undeveloped, developing, nearly ripe, ripe, and advanced ripe, a stage not previously recorded for this group. In addition, three stages of spent ovaries were de-

scribed, the first two capable of regeneration, but the last (terminally spent), without viable oogonia or oocytes, was judged incapable of further spawning. The smallest mature female had a carapace length of 17 mm; those of 34 mm length were 79% mature. At this and larger sizes, variations in ovarian development in alternating size groups suggested multiple spawning of the same individuals in two or more lifetime spawns. Petasma fusion was first observed in 14% of males in the 10-mm carapace length size class; all males 14 mm or larger showed fusion. Spermatozoa first appeared in 18% of the 11-mm group, but were in all of the 18-mm group or larger and there was no seasonal variation.

Approximate peak spawning off northeastern Florida occurred in November, December, or January (October through February off west Florida [Cobb, et al. 1973]), ovarian development apparently being triggered by increasing temperatures (or decreasing photoperiod [Cobb, et al. 1973]) and spawning itself seeming to be stimulated by lunar light. Larvae were present year round. Cook and Murphy (1965) reared, described and illustrated the early development from eggs spawned in the laboratory (5 naupliar, 3 protozoal, 4 mysis, and the first postlarval stages). In temperatures of 21°–24.6°C at 24.5–27.4‰ salinity, the postlarva was reached in 29 days in first experiments. Survival of nauplii was best at 24°C, but that of later stages improved with increase in temperature. Larvae did not survive salinities above 35‰ or below 27‰. Cook (1966) provided a key for identification of these stages, and, building on that, Subrahmanyam (1971a, b) recorded presence of *Sicyonia* larvae off Mississippi throughout the year, though abundance varied from station to station; these larvae were third in abundance among penaeoids, reaching a peak in late summer and fall.

Females off northeastern Florida grew faster than males, varying to some degree among generations on the ground at the same time (Kennedy, et al. 1977). Males increased roughly 2.3–3.2 mm in carapace length per month and females 2.9–3.3 mm per month, but a maximum of 5 mm for both sexes was calculated for June–July. The life span was judged to be 20–22 months and the overall sex ratio was nearly 1:1.

Diet, based on examination of 412 stomachs, was mainly mollusks, crustaceans and polychaetes, in that order (Kennedy, et al. 1977), and feeding, on the basis of nearly 100% empty stomachs in daytime catches, was judged to be mainly nocturnal (Cobb, et al. 1973).

Zyznar (1970) showed that both distal and proximal dark eye pigments migrate in *S. brevirostris*.

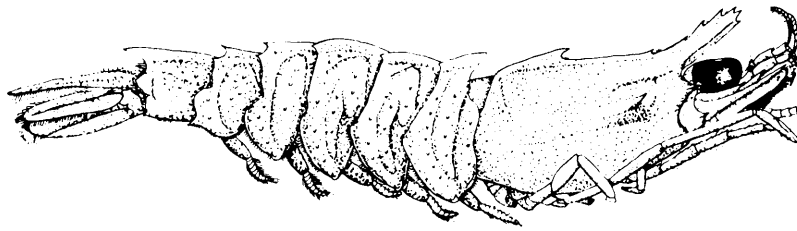


Fig. 27. *Sicyonia burkenroadi* Cobb. Female in lateral view, 5 mm indicated (from Cobb 1971).

***Sicyonia burkenroadi* Cobb**

Fig. 27

Sicyonia dorsalis.—Rathbun 1901:103 (part).

Eusicyonia stimpsoni.—Burkenroad 1934b:123 (part).—1939:57.—Lunz 1945:10 (part).

Sicyonia stimpsoni.—Holthuis 1959:75.—Williams 1965:38 (part).

Sicyonia burkenroadi Cobb 1971:104, figs. 1, 2A–E.—Coelho and Ramos 1972:141.

Recognition characters.—Rostrum not overreaching antennular peduncle; in males horizontal, slightly elevated or deflexed; in females elevated as much as 45°, rarely horizontal; dorsal margin straight or arcuate, armed with 3, rarely 4, subequal teeth excluding tip, proximal tooth distinctly anterior to level of posterior orbital margin; tip usually bifid, dorsal tooth occasionally displaced proximally, obscuring bifurcation; ventral border often concave, sometimes with small node, subapical tooth occasionally becoming ventral tooth of bifurcation. Postrostral carina low; small tooth anterior to level of hepatic spine; larger tooth, anteriorly directed, posterior to level of hepatic spine, arising at posterior margin of carapace. Antennal spine long, acute, buttressed. Ischium of first legs unarmed.

Abdomen irregularly tuberculate; high median dorsal carina produced into large anterior tooth on segment 1 and conspicuous tooth on posterior margin of last 3 segments. Ventral margin of first 4 pleura each broadly rounded posteriorly but anteroventrally produced into laterodorsally curved spine; 5 and 6 armed with small posteroventral spine. Segment 1 traversed by shallow, often obscure anteromedian pleural groove terminating dorsally at concavity of tergal margin, and single long posterior groove formed by confluence of posterior tergal and posteromedian pleural grooves. Segments 2 and 3 with anterior tergal groove ending slightly below midlateral level; posterior tergal groove shorter; deep posteromedian pleural groove sometimes turning abruptly anteriorly near midpoint, anteromedian pleural groove with ventral $\frac{3}{4}$ expanded to anterior margin of pleuron as broad

furrow. Segments 4 and 5 each with anterior tergal and long posterior groove formed by confluence of posteromedian pleural and posterior tergal grooves. Segment 6 with broad longitudinal sulcus and short posterior pleural groove.

Measurements in mm.—Carapace length: male to 12.7, female to 14.3 (Cobb 1971).

Habitat.—Predominantly on mud, mud-shell, or mud-sand bottoms, less common on sand; 33 to 118 m, occasionally as deep as 585 m (Pérez Farfante 1980).

Color.—Branchial region of carapace with orange, or brownish and yellowish-white ring in posterior half (Holthuis 1959). North Carolina specimens show a purple spot with surrounding vermilion ring in this region.

Type-locality.—Gulf of Mexico off Port Isabel, Texas, 26°13'N, 96°45'W, 42 m.

Known range.—Off Cape Lookout, N. C., 34°12'N, 76°11'W, through Gulf of Mexico to Bahia, Brazil (Pérez Farfante 1980).

Remarks.—From eggs and planktonic larvae attributed to *Eusicyonia stimpsoni* (probably = *S. burkenroadi* according to Cobb 1971), Pearson (1939) reconstructed an ontogeny proceeding through five naupliar, three protozoal, and two mysis stages. Eggs were taken abundantly at St. Augustine Inlet, Fla., in plankton, from March 30 to August 8; they were taken in lesser abundance from January to March, and August to September at Fort Pierce, Fla., and off Stono Inlet, S. C., in September. Naupliar and protozoal stages were found from April to August, and mysis stages were found in January and August–September. Thus, the breeding season along that stretch of coast lasts at least from January to September.

Holthuis (1959) noted that males in Surinam material outnumbered females about 3 to 1.

***Sicyonia dorsalis* Kingsley**

Fig. 28

Sicyonia dorsalis Kingsley 1878b:97.—Hay and Shore 1918:380, pl. 25, fig. 3.—Williams 1965:37, fig. 28.—Coelho and Ramos 1972:141.

Eusicyonia dorsalis.—Burkenroad 1934b:121, figs. 13, 14.—Lunz 1945:8, fig. 5.

Recognition characters.—Body slightly compressed. Carapace minutely punctate, less deep and inflated than *S. stimpsoni*. Rostrum extending horizontally or decurved variable distance beyond eye; ridge on lateral surface confluent with dorsal tooth of tip; armed dorsally with 3 teeth not counting tip, posterior tooth anterior to level of orbital margin and variable distance from anterior carinal tooth of carapace; tip appearing bifurcate, dorsal tooth enlarged, ventral tooth reduced to blunt angle. Postrostral carina with 2 teeth, anterior tooth anterior to level of hepatic spine, posterior tooth near midlength of postrostral carapace.

Abdomen with conspicuous tergal carina; segment 1 with tergal carina produced into elevated anterior tooth; margins of notches at posterior ends of carinae on segments 3 to 5 sometimes produced into long slender spines; carina of 6 always extended into strong posterior spine. Pleura of segments 1–4 with antero- and posteroventral margins angulate, sometimes dentiform, and often strongly spiniform except for rounded posteroventral angles of 1 and 2; segment 1 with anterior pleural margin broadly rounded anteroventrally but drawn to strong, curved, acute posteroventral spine. Segment 2 with tergal and pleural grooves connected as uninterrupted sulci.

Measurements in mm.—Length of body: male 63; female 71.

Variation.—Angles and spines on the pleura become better defined with increasing age.

Color.—Two specimens collected in Beaufort Inlet, N. C., 22 July 1972 by C. A. Johnson III. Dorsum of carapace and first 3 abdominal segments tannish olive followed ventrally by lighter almost iridescent band running laterally along pleura of all abdominal segments and with diagonal extension crossing segment 3 to dorsum of anterior part of segment 4. This portion followed posteriorly by diagonal dark maroon stripe on lateral part of segment 3 and posterior part of 4, followed posteriorly by same color as carapace on terga of segments 5 and 6, telson and inner uropod. Portion of distal half of inner half of uropodal exopod

purplish blue; proximal half of this member flesh colored and entire lateral half as well as terminal portion of ramus light flesh colored to almost iridescent. The striping seems a camouflage for the animal when burrowed in substrate.

Habitat.—Common on mud bottom (Hildebrand 1954), or mud and shells (Holthuis 1959); from mouths of bays to 60 m, rarely to 420 m.

Type-locality.—Fort Jefferson, Dry Tortugas, Fla.

Known range.—Cape Hatteras, N. C., to Texas; Colombia to French Guiana; Ceará to Santos and Santa Catarina, Brazil (Mistakidis and Neiva 1964, 1966; Iwai 1973).

Remarks.—Hildebrand (1954, 1955) listed this species as third in abundance on the brown shrimp grounds in Texas but less common on Campeche Bank. It is most common in 27–46 m but ranges shoreward to depths of 12 m, and small specimens are occasionally taken in the mouths of bays. Brusher, Renfro, and Neal (1972) found the species mainly at 27-m stations off Texas, more abundantly at night than in daytime and seasonally most numerous in July and August. Most male–female lengths in their samples were in the 60–75 mm range. Ripe females were present year round but more numerous during May through September. Eldred (1959) listed this species as the most common among *Sicyonia* species taken in the Tortugas controlled area in Florida.

Adults of this species fouled with the barnacle *Balanus amphitrite niveus* Darwin, and *Polydora* sp., were reported from the Gulf of Mexico off Marquesas Key by Eldred (1962). Such specimens, ranging in size from 58 to 70 mm total length, were judged to be near maximum size for the species.

Serum of *S. dorsalis* is slightly hyposmotic to sea water (about 97%–98%), serum ions accounting for 95% of osmotic concentration (McFarland and Lee 1963). High Mg levels occur in *S. dorsalis* but not in other penaeoids tested (*Penaeus aztecus*, *setiferus*, *Trachypenaeus similis*), and this relates to its more sluggish activity. Muscle K concentrations are highest in the euryhaline penaeoids, intermediate in *T. similis*, and lowest in *S. dorsalis*.

Sicyonia laevigata Stimpson

Fig. 29

Sicyonia laevigata Stimpson 1871b:131.—Hay and Shore 1918:379, pl. 25, fig. 1.—Williams 1965:33, figs. 22–23.—Coelho and Ramos 1972:142.

Eusicyonia laevigata.—Burkenroad 1934a:76, figs. 21, 26, 32.—Lunz, 1945:4, fig. 1.

Recognition characters.—Rostrum about half as long as carapace, elevated at angle of about 20°; armed

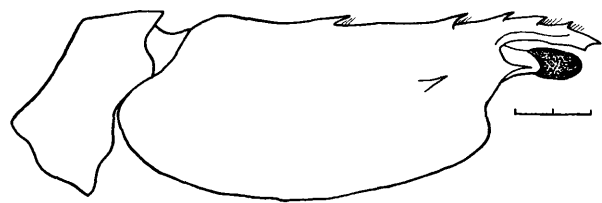


Fig. 28. *Sicyonia dorsalis* Kingsley. Carapace and first abdominal segment in lateral view, 2 mm indicated (from Lunz 1945).

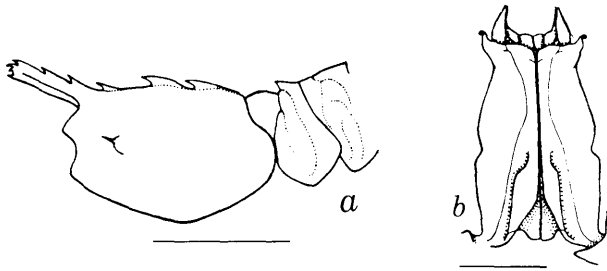


Fig. 29. *Sicyonia laevigata* Stimpson. a, Carapace and first two abdominal segments in lateral view, 5 mm indicated; b, petasma of male in ventral view, 0.5 mm indicated (from Burkenroad 1934a).

dorsally with 2 teeth not counting tip; terminal part divided into 4 teeth; notch between median pair shallower than dorsal and ventral notches; often 2 short, stout, asymmetrically placed, mobile spines distally above ventral margin. Postrostral carina with 3 teeth behind orbital margin; anterior one slightly advanced beyond level of hepatic spine and about same size as rostral teeth, often appearing as part of rostral series; posterior 3 teeth closer together; carina sometimes nearly obliterated anterior to each tooth. Antennal angle unarmed. Stylets of ocular plate short.

Abdominal carina deeply notched posteriorly on segments 1–5; segment 1 with carina produced into elevated anterior tooth; segment 2 with carina narrowly and deeply cleft above juncture of tergal grooves; smaller posterior tooth on 6. Segment 1 marked laterally by 2 grooves, a long posteromedian and short anteromedian groove obliterated a short distance ventral to juncture with anterior margin of pleura but with short resumption below juncture. Second and third segments with anterior and short posterior tergal grooves; short, shallow anteromedian pleural, and posteromedian pleural groove turning sharply anteriorly somewhat above middle of lateral surface. Segments 4–5 with posterior tergal groove, and an anterior groove, obliterated for interval below short dorsal section, reappearing farther ventrad. Segment 6 with a posteromedian pleural, anterior tergal and a longitudinal groove. Ventral pleural margins rounded except for posterior tooth on segments 5 and 6. Telson ending in strong “point” flanked by pair of shorter blunt spines; sometimes with pair of mobile lateral spines posterior to basal shoulders.

Petasma of male with distolateral projections extending straight distally. Thelycum most conspicuously marked by elongate plate arising on somite XIII (between fourth legs), with slender tip extending to level of somite XI (second legs).

Measurements in mm.—Length of body: males 14; females 50.

Variation.—The angle of rostral elevation varies with age. Nearly horizontal among the young, it rises to as much as 35° in older individuals. The usual angle is somewhat in excess of 20°. The number of carinal teeth on the carapace may be reduced to 2 (Lunz 1945).

Color.—Yellowish brown; carapace darker than abdomen and sometimes bluish or greenish.

Habitat.—A littoral species fairly common in the Carolinas, especially on shelly bottoms of harbors; shallow water to 100 m.

Type-locality.—Charleston, S. C.

Known range.—Cape Hatteras, N. C., to north-west Florida; through West Indies to Colombia, and Santa Catarina, Brazil (Fausto-Filho and Neto 1976; Pérez Farfante 1980). Pacific coast of Panama.

Remarks.—This small species becomes sexually mature at quite a small size (length of 18 mm).

Randall (1967) reported *S. laevigata* in the stomach contents of the yellowtail snapper.

Sicyonia parri (Burkenroad)

Fig. 30

Eusicyonia parri Burkenroad 1934a:80, fig. 22.—Lunz 1945:5, fig. 2.

Sicyonia parri.—Williams 1965:34, fig. 24.—Chace 1972:11.—Coelho and Ramos 1972:141.

Recognition characters.—Resembling *S. laevigata*; integument rather firm, lacking setae and more or less sculptured. Rostrum elevated at angle of approximately 15°, armed dorsally with 3 teeth not counting tip; terminal portion bearing 3 teeth with rudiment of another between lower ones. Postrostral carina armed with 3 large, subequal, almost equidistant teeth, anterior one approximately at level of hepatic spine. Antennal spine absent.

Abdominal segments with tergal carina notched posteriorly on segments 1–5; segment 1 with carina produced into elevated anterior tooth; segment 2 with carina cleft above juncture of tergal grooves; carina on 6 produced into posterior tooth. Pleura rounded ventrally except for posteroventral spine on segments 5 and 6. Segment 1 marked

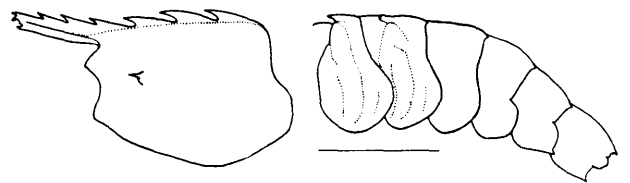


Fig. 30. *Sicyonia parri* (Burkenroad). Carapace and abdomen in lateral view, 5 mm indicated (from Burkenroad 1934a).

laterally with short anteromedian groove as in *S. laevigata*, but reappearing below obliteration and continuing conspicuously to ventral margin, not connected to posteromedian pleural groove ventrally; segments 1–4 each with shallow but perceptible posterior pleural groove; fourth with dorsal and ventral parts of anterior tergal groove separated by narrow area of obliteration.

Petasma of male with distolateral projections curved mesially at tips; distoventral lobes constricted abruptly near tip.

Measurements in mm.—Length of body: male 24, female 42.

Habitat.—Sand and calcareous algae; shallow littoral (in seine) to 83 m (Coelho and Ramos 1972).

Type-locality.—Crooked Island, Bahamas.

Known range.—Beaufort, N. C.; through Gulf of Mexico (Ray 1974) and West Indies to Bahia, Brazil.

Sicyonia stimpsoni Bouvier

Fig. 31

Sicyonia stimpsoni Bouvier 1905:748.—Holthuis 1959:75.—Williams 1965:38 (part), fig. 29.—Cobb 1971:110.

Sicyonia dorsalis.—A. Milne Edwards and Bouvier 1909:253, text figs. 86–88, pl. 8, figs. 4–13.

Eusicyonia stimpsoni.—Burkenroad 1934b:121.—Lunz 1945:10 (part), fig. 6.

Recognition characters.—Rostrum not overreaching antennular peduncle; elevated above level of carapace; dorsal margin with 3 teeth behind bifid tip; posterior tooth distinctly anterior to level of posterior orbital margin; ventral margin with or without subapical tooth. Postrostral carina low; small tooth anterior to level of hepatic spine; larger tooth, anteriorly directed, posterior to level of hepatic spine. Antennal spine small, often minute, but-tressed. Ischium of first legs unarmed.

Abdomen with low median dorsal carina produced into large, acute, anteriorly directed tooth on first segment and into smaller posteriorly directed tooth at posterior margin of segments 5 and 6. Pleuron of segment 1 with ventral margin rounded; that of segments 2 through 4 with posteroventral margins angulate, and of 5 and 6 armed with small posteroventral tooth. Segment 1 traversed by shallow, often obscure anteromedian pleural groove terminating dorsally at concavity of tergal margin; formed by confluence of posterior tergal and posteromedian pleural grooves and single long posterior groove. Segments 2 and 3 with anterior tergal groove ending slightly below midla-



Fig. 31. *Sicyonia stimpsoni* Bouvier. Carapace and part of first abdominal segment in lateral view, 2 mm indicated (from Lunz 1945).

teral level; posterior tergal groove shorter; deep posteromedian pleural groove curved abruptly anteriorly near dorsal end; anteromedian pleural groove with ventral $\frac{3}{4}$ expanded to anterior margin of pleuron as broad furrow. Segments 4 and 5 each with anterior tergal and long posterior groove formed by confluence of posteromedian pleural and posterior tergal grooves. Segment 6 with broad longitudinal sulcus and short posterior pleural groove.

Measurements in mm.—Carapace length: male to 10.4, female to 12.4.

Habitat.—Predominantly mud bottoms; 20 to 420 m, usually < 100 m (Pérez Farfante 1980).

Type-locality.—Off Barbados, 13°03'05"N, 59°-36'18"W, 185 m.

Known range.—Near Cape Hatteras (6.8 mi. off) through Florida Straits, and including west Florida, to Barbados and Colombia to Surinam.

Remarks.—The above account is paraphrased from Cobb (1971) who distinguished *S. stimpsoni* from *S. burkenroadi*, pointing out morphological differences as well as the generally deeper habitat of the former, although the geographic ranges are partly parallel. Cobb also discussed the tangled synonymy.

Sicyonia typica (Boeck)

Fig. 32

Sicyonia carinata H. Milne Edwards 1830:344, pl. 9, fig. 9.—Bate 1888:294, pl. 43, figs. 2–3.

Synhimantites typica Boeck 1864:189.—Danielssen and Boeck 1872:192, figs. 1–14.—Sars 1882:8, 49.

Sicyonia edwardsii Miers 1881:367.—Hay and Shore 1918:380.—Schmitt 1935a:133 (not fig. 6).

Sicyonia edwardsi.—A. Milne Edwards and Bouvier 1909:251, pl. 8, figs. 1–3.

Eusicyonia edwardsi.—Lunz 1945:7, fig. 4.

Sicyonia typica.—Burkenroad 1945:2.—Holthuis 1959:77.—Williams 1965:36, fig. 27.—Coelho and Ramos 1972:142.

Recognition characters.—Integument with short, thick pubescence more evident dorsally than ventrally, especially on abdomen. Rostrum extending halfway along eye, directed obliquely upward, armed dorsally with 1 or 2 small teeth not counting tip. Postrostral carina with 2 or 3 teeth, last 2 posterior to level of hepatic spine (third tooth, if present, may look like part of rostral series). Antennal angle armed with short, often blunt buttressed spine.

Abdomen with tergal carina deeply notched posteriorly on segments 1–5; segment 1 with carina produced into elevated anterior tooth; segment 5 with carina ending posteriorly in low tooth; segment 6 with carina produced into posteriorly directed tooth. Pleura of first 4 segments with lateroventrally directed acute tooth on anteroventral margin (progressively prominent posteriorly). Segments 5 and 6 with tooth at posteroventral corner of pleura, that of 5 often small and rectangular. Abdominal grooves deep and well defined. Segment 1 with posteromedian and anteromedian grooves connected ventrally; segment 2 with anterior and posterior tergal grooves connected dorsally and ventrally, a thin and more or less interrupted posterior pleural groove connected with posterior tergal. Telson usually lacking subterminal spines.

Measurements in mm.—Length of body: male 77, female 73.

Variation.—Position of the posterior rostral tooth is variable. In some individuals this tooth is located behind the orbital margin, thus appearing as one of the carinal series on the carapace (Lunz 1945).

Color.—Blue spots on tail prominent in life; bright red blotch surrounding rostrum (note by W. L. Schmitt, USNM records).



Fig. 32. *Sicyonia typica* (Boeck). Carapace and first abdominal segment in lateral view, 1 mm indicated (from Lunz 1945).

Habitat.—Between tide marks to 101 m (Pérez Farfante 1980).

Type-locality.—Molde Fjord, west coast of Norway [erroneous locality, evidently incorrectly labeled].

Known range.—Off Wrightsville Beach, N. C., through Gulf of Mexico; Cuba through West Indies to near Ilha de Santa Catarina, Brazil (Mistakidis and Neiva 1964, 1966; Iwai 1973).

Remarks.—Hildebrand (1954) stated that this species is taken in commercial quantities in the Gulf of Batabanó off southwest Cuba, and occurs in commercial but unexploited quantities in parts of Campeche Bay.

Superfamily Sergestoidea

Carapace moderately to extremely compressed. Rostrum shorter than eyestalks. Antennule with small lower flagellum modified or absent. Antennal flagellum with bend. Chelae (sometimes very obscure) on at least third legs; legs 4 and 5 and gills reduced or absent. (Modified after Glaessner 1969.)

Family Sergestidae

Carapace moderately compressed. Inferior antennular flagella present; with prehensile organ in male. Second and third pair of legs, at least, terminated by a pincer. Gills present. Sixth abdominal segment and telson without sexual differences; without protuberances or ventral processes in males. Petasma with short base. No protuberance on peduncle of first pleopod. (After Hansen 1922; Opinion 864:141.)

Genus *Acetes* H. Milne Edwards 1830

Burkenroad 1934a:99.—1934b:126.—Opinion 864:138.—Omori 1975:5.

Acetes americanus carolinae Hansen

Fig. 33

Acetes americanus Ortmann 1893:39, pl. 2, fig. 2.—Chace 1972:12.

Acetes carolinae Hansen 1933:31, figs. 1–8.

Acetes americanus carolinae.—Holthuis 1959:49, fig. 1 a-c.—Williams 1965:39, figs. 30–31.—Omori 1975:24, fig. 7a-g.

Recognition characters.—Body small. Integument thin, smooth, polished. Carapace with rostrum ele-

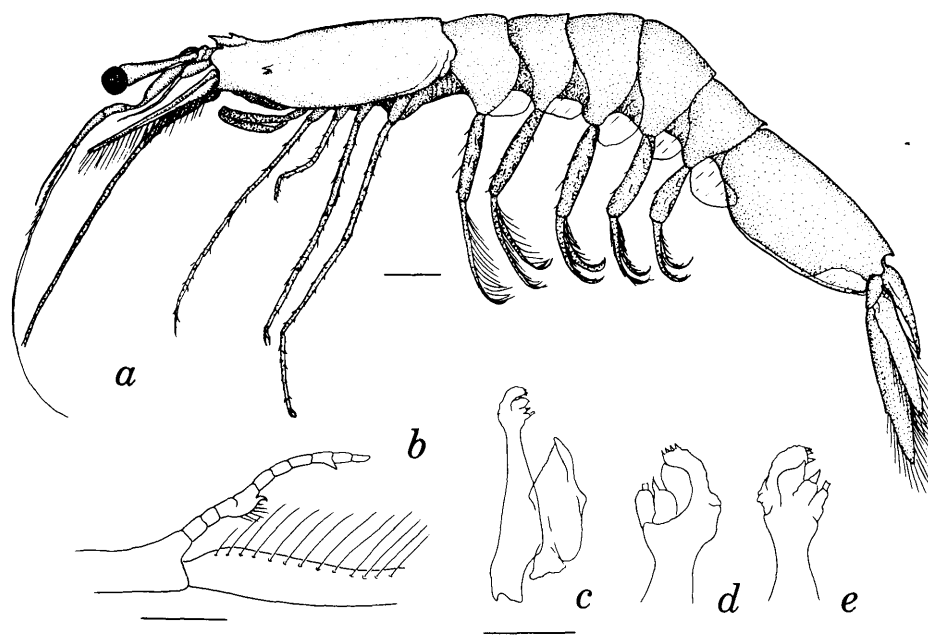


Fig. 33. *Acetes americanus carolinae* Hansen. *a*, Female in lateral view; *b*, clasping organ on antennule of male (from Williams 1965); *c*, petasma of male; *d-e*, capitulum of same (from Omori 1975); *a*, 1 mm; *b*, 0.1 mm; *c*, 0.5 mm; *d-e*, 0.2 mm indicated.

vated, short, single tooth behind acute tip; prominent spine on rounded ridge behind eye; hepatic spine small. Eyes prominent, stalk conical, cornea large. Antennules with peduncle long, third article more than twice length of second; upper flagellum hairy ventrally near base, lower much shorter and more slender; in males, curved lower flagellum forming clasping organ, basal 4 annuli thicker than distal annuli, third and fourth armed dorsally with short row of spines, distal one strongest. Antennal scale reaching end of second article of antennular peduncle in males, beyond end of second article in females. Lobes behind base of last pair of legs greatly enlarged in males forming genital coxae broader than long. Coxae of third legs in females with posteromedian corner produced into protuberance; sternite immediately behind third legs bearing 2 curved projections forming U-shaped thelycum.

Sixth segment of abdomen with convex ventral margin bifurcated caudally. Lateral ramus of uropod about 4.5 times longer than broad; proximal $\frac{3}{5}$ of outer margin smooth, ending in minute tooth, remainder of margin hairy.

Petasma of male with membranous, triangular tipped external portion exceeded by slender median part; median portion ending in complicated capitulum, a distomedian crooked lobe tipped with

4 thick, short spines, and 3 other shorter lateral lobes each produced into an acute point.

Measurements in mm.—Length of body: 15 to 26.

Variation.—Omori (1975) followed Burkenroad (1934a) and Holthuis (1948, 1959) in considering *A. americanus* to be subdivided into subspecies or clinal variants, but he was the first to define range limits for a northern and southern subspecies with an apparent zone of overlap in the southern Caribbean Sea and along the northern coast of South America.

Color.—Nearly transparent with faint red flecks. It is probable that *Acetes* species produce steady emission of greenish-blue light, for fishermen in the Indo-Pacific locate the position of large swarms by their luminescence at night (Omori 1975).

Habitat.—Littoral oceanic and estuarine waters to 42 m.

Type-locality.—Beaufort Inlet (about 34°47'N), North Carolina.

Known range.—Lower Chesapeake Bay (Mobjack Bay and York River) (Van Engel and Sandifer 1972) through Gulf of Mexico to Panama, Surinam and French Guiana (Omori 1975). *Acetes a. americanus* ranges from the Caribbean Sea to São Paulo, Brazil (Iwai 1973).

Remarks.—Burkenroad (1934b) found larval stages of *A. americanus carolinae* at the surface of

the outer littoral of Louisiana in spring. He described the spermatophore as gourd-shaped, much as the spermatophore of *Lucifer*, and gave other structural details of the reproductive system.

In Bogue Sound, near Beaufort Inlet, N. C., specimens have been taken in every month of the year in a large plankton net fished from a pier at the surface on flood tides at night. Gutsell (*in* Hansen 1933) reported that this species can sometimes be taken near Beaufort Inlet, N. C., "in gallons at a time," especially in late summer and early fall. Joyce (1966) reported that the animal is abundant off northeast Florida in spring, often becoming enmeshed in the nets of commercial shrimp trawlers. Wilson (1969) likewise found it only in spring in bayous of Louisiana, near the shoreline and in "current" canals, but Franks, et al. (1972) found it at surface, midwater, and bottom stations off Mississippi at temperatures of 13.9° to 30.1°C in salinities of 21.3 to 37.4‰. Williams (1969) found the subspecies year round in estuarine plankton near inlets in North Carolina, in greatest densities from April to November, but in decreasing abundance upstream as salinities lowered. When surface and bottom samples were taken simultaneously in an essentially non-tidal body of water, the animals seemed to be slightly more abundant on bottom.

Acetes is one of six genera in the family Sergestidae. According to Omori (1975), the 14 species in the genus fall into two groups; ten of these occur in the Indo-West Pacific, particularly in the Indo-Malay Archipelago. Abundant in estuaries and backwaters, tons of the shrimp are caught from aggregations near shore in certain seasons of the year from southeast Asia to as far north as Korea and Japan, mostly to be dried, pickled, or fermented for food.

Family Luciferidae

Carapace extremely compressed. Antennules without inferior flagella in both sexes. Third legs with microscopic dactyl but no fixed finger, forming at most a subchela. Gills absent. Sixth abdominal segment of male with 2 ventral processes, second far behind first. Telson of male with strong protuberance on internal face. Petasma sessile, proximal part fixed like large disc on peduncle of first pleopod; each peduncle, near disc, possessing protuberance with distal spines. (After Hansen 1922; Burkenroad 1934b; Opinion 864:141.)

Genus *Lucifer* Thompson 1829

Hansen 1919:48.—Opinion 864:138.

Lucifer faxoni Borradaile

Fig. 34

Lucifer faxoni Borradaile 1915:227.—Hay and Shore 1918:381, text-fig. 4, pl. 26, fig. 10.—Holthuis 1959:52.—Williams 1965:40, fig. 2.—Bowman 1967, figs. 2c-k, 3d, e.—Bowman and McCain 1967:660–670, figs. 1c-d.—Chace 1972:12.

Recognition characters.—Body small, thin; integument smooth, thin, transparent. Anterior portion of cephalothorax cylindrical, greatly lengthened (about 1.5–2.5 times longer than posterior portion), bearing eyes, antennules, and antennae far in front of mouthparts and legs. Rostrum small, spine on each side behind eye and at anterolateral corner. Posterior portion of cephalothorax with spine on each side in front. Eyes large, prominent, on stout conical stalks about $\frac{1}{4}$ to $\frac{1}{3}$ length of anterior part of cephalothorax. Peduncles and flagella of antennules long, slender. Peduncle of antennae about half as long as first article of antennular peduncle; flagellum longer than that of antennule; antennal scale almost linear, fringed on inner margin with long hairs.

Third maxilliped long, pediform. Three pairs of legs; first pair short; last 2 pairs of equal length extending almost to end of cephalothorax.

Abdomen much compressed; segments deepest and produced into spiniform angle where pleopods originate. Sixth segment as long as preceding 2 segments, posterolateral angles spiniform near base of uropods; small median spine above base of telson; male with 2 strong ventral spines, posterior spine curved and about twice length of anterior spine. Telson slender, about half length of uropods; truncate distally with strong spine at each corner; 2 pairs of intermediate spines on distal border, and 2 pairs of lateral spines about equidistant; males with prominent ventral projection on distal half. Outer ramus of uropod long and broader than inner ramus.

Petasma of male membranous, folded, foliaceous; ventral process needlelike, curved, tapering to acute end directed ventrolaterally.

Measurements in mm.—Length of body 10–12.

Color.—Almost perfectly transparent in life.

Habitat.—Oceanic and estuarine waters from surface to 91 m.

Type-locality.—Hampton Roads, Virginia (Chace 1972).

Known range.—"Coastal waters of North and South America from Long Island Sound to Rio de Janeiro," around Gulf of Mexico and throughout Caribbean Sea (probably widespread); Bermuda and scattered mid-Atlantic occurrences in path of

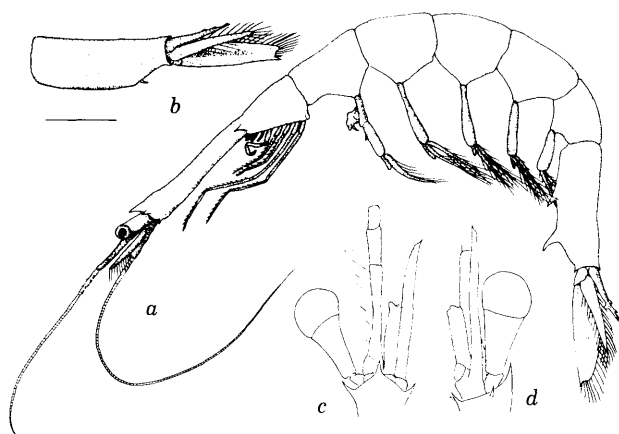


Fig. 34. *Lucifer faxoni* Borradaile. a, Male in lateral view; b, sixth abdominal segment and tail fan of female in lateral view (from Williams 1965); a-b, 1 mm indicated; c, anterior end of male head; d, same, lateral (from Bowman 1967).

Gulf Stream; Bay of Dakar, Senegal (Bowman and McCain 1967).

Remarks.—This interesting little shrimp occurs throughout the year in North Carolina, often in swarms.

Brooks (1882) worked out the larval development of a species of *Lucifer* in the Beaufort, N. C., area, and from his figures and present knowledge of distribution, it is almost certain that he was dealing with *L. faxoni*. Brooks found egg-bearing females only in April, but larvae as late as September. Since then, egg-bearing females have been found from April to November but not all stations were equally productive of egg-bearing females; none were found in mesohaline tidal rivers. Ripe males were found in all months except January and March, and they probably occur the year around, often far up tidal rivers. Where surface and bottom samples were taken simultaneously in essentially non-tidal water, the species seemed to be slightly more abundant on bottom (Williams 1969). Brooks illustrated the eggs, a number of larval stages (two nauplii, three protozoeae, one zoea, one schizopod, one mastigopus, one lucifer), and a final adult stage in males. Woodmansee (1966a), from nearshore stations in the Gulf of Mexico off Mississippi, essentially confirmed Brooks's work, recognizing five ovarian developmental stages and finding that egg maturation occurs in the diel cycle at about 1700 h, that oviposition follows about five hours later, and that hatching occurs after about 26 h at 2400 h. Presence of spermatophores indicated that copulation occurs at about 0200 h when eggs in the female ovary are first beginning to mature. Females swim upward just prior to hatching of eggs to release nauplii near the surface.

Burkenroad (1934b) reported a female with large ova from the outer littoral of Louisiana. He gave a detailed account of the reproductive systems of males and females showing that they are fully bilateral and not asymmetrical as stated by Brooks (1882), Bate (1888), and Hansen (1922). The males, however, carry but one spermatophore at a time, possibly because the body is so strongly compressed. Hartnoll (1968), from whole mounts (also Woodmansee 1966a) and sections, showed that the oviducts descend, from paired ovaries that lie parallel to the gut on each side, to open in the normal position in shrimps at the bases of the third legs. There "are paired spermathecae, but they open by a single median aperture and have no internal connections with the oviducts. The spermathecae and their canal have a complex structure, and are homologous with the 'thelycum' found in the rest of the Penaeidea."

As various authors have pointed out, Brooks mistakenly thought that the species was primarily estuarine, the adults leaving the marshes on ebb tides to spawn in the ocean, because he found the species most concentrated in the estuary near Beaufort on ebb tides. He failed to find specimens on flood tide. The species can be found in estuaries on both flood and ebb tide, but its primary home is oceanic coastal water, as adequately shown from results of cruises by R/V *T. N. Gill* (Bowman and McCain 1967). Kelly and Dragovich (1967) reported larval and postlarval *L. faxoni* as dominant zooplankters in Tampa Bay during fall, winter and summer, and Swingle (1971) found the species in Mobile and Perdido bays, Ala. Franks, et al. (1972) found it to be more abundant than *Acetes* in surface, mid-water, and bottom levels in a transect off Mississippi in waters of 14.5° to 30.4°C at 15.7 to 37.9‰ salinity. Harper (1968) found distribution off Texas to be seasonal, the population inshore increasing during August-September and declining in October-November, but widely dispersed during the remainder of the year. Large numbers of larvae in the peak population suggested that August-November is the period of maximum reproduction there, and decrease in larvae seaward off the 14-m station indicated that reproduction is confined primarily to nearshore waters, perhaps concentrated there by water movements and autumnal plankton blooms. Although never abundant in the Chesapeake Bay area, Sandifer (1973d) found late larvae in the lower bay, and postlarvae occasionally in the York River, from September to November, indicating that hatching occurs offshore. Most samples were taken in salinities >25‰ and at temperatures of 13° to 24°C, in greatest abundance near the bottom. Woodmansee (1966b)

seemed to corroborate the observation that the species chooses currents as a dispersal agent landward, but found individuals more abundant at the surface during flood than ebb tides and more abundant at night than during the day. Calef and Grice (1967) found extensive populations in large lenses of low-salinity water located several hundred miles north of the mouth of the Amazon River.

Finally, from samples taken fortnightly for over a year at three fixed stations off Cananéia, São Paulo, Brazil, Lopez (1966) found that juveniles occurred year round but in two peaks, the largest from December to April, and a smaller one during September and October. Sexual maturity was reached at a neck length of 1.18 mm in males and 1.19 mm in females (linearly correlated with total length), with peaks in summer and autumn. The largest males (neck length 1.7–1.92 mm) were present in July, September–November, and January.

Suborder Pleocyemata

Infraorder Stenopodidea

Family Stenopodidae

Carapace cylindrical, with cervical and branchio-cardiac grooves. Abdomen with pleura of second segment not overlapping first. First 3 legs chelate, 1 or both third legs considerably longer than first 2, no exopodites on legs. Gills numerous, tricho-

branchiate. First pleopods reduced, others long, carrying eggs in females. Females without spermatheca. (From Glaessner 1969.)

Genus *Stenopus* Latreille 1819

Holthuis 1946:5.—1959:143.—China 1966:204.

Body slender, compressed, conspicuously spinulate overall. Carapace densely covered with forward curving spinules; cervical groove distinct. Abdomen with distinct bend between third and fourth segments; spinules on first 3 similar to those on carapace but on last 3 directed posteriorly and pressed against body; pleura of first segment slightly overlapping second, in turn overlapping third; pleura of first ending in 2 teeth, second to fifth broadly truncate and bearing 3–4 lateral spines; sixth without pleura.

Antennal scale long, slender, concave laterally near base. First leg reaching end of antennal scale, carpus and propodus with ventral setiferous organ, small tufts of hair at tip of fingers. Second leg similar to first but longer and stronger. Third leg largest and strongest, carpus and hand extending beyond antennal scale; merus, carpus and propodus with many longitudinal rows of spinules; dactyl with 1 large ventral tooth fitting between 2 teeth on fixed finger; all teeth triangular. Fourth and fifth legs long and slender, dactyls small, biunguiculate. (From Holthuis 1946.)

Key to Species

(Adapted from Chace 1972)

1. Rostrum unarmed ventrally; third abdominal segment without shield-shaped boss; spines on terga of 3 posterior abdominal segments not arranged in transverse rows *S. hispidus*
- Rostrum armed ventrally with 6–8 spines; third abdominal tergum bearing lobate, shield-shaped boss on posteromesial part; spines on 3 posterior abdominal terga arranged in transverse rows *S. scutellatus*

Stenopus hispidus (Olivier)

(Banded coral shrimp, bandanna shrimp; banded shrimp; barber-shop shrimp; barber-pole shrimp; cleaner shrimp; porcelain shrimp; spiny shrimp)

Fig. 35

Palaemon hispidus Olivier 1811:666.

Stenopus hispidus.—Holthuis 1946:12, pl. 1, figs. a–g.—Limbaugh, Pederson, and Chace 1961:251, fig. 8.—Chace 1972:144.—Coelho and Ramos 1972:157.

Recognition characters.—Carapace densely covered with spinules arranged in more or less distinct rows, dorsal double row of 4–6 extending from rostrum to cervical groove. Rostrum slender, straight, triangular at base, compressed near tip, not overreaching articulation between last 2 articles of antennular peduncle; armed dorsally with 6–8 strong spines, last reaching beyond apex, and laterally with row of 2–8 spines (some minute) directed obliquely upward; ornamented below with feathered setae. Eyestalks spinulose dorsally, those at base of cornea sometimes curving beyond it. An-

tennular peduncle with third article shortest; first with dorsodistal marginal row of spinules, second with scattered spinules often in rows, and last with dorsal and ventral forward pointed spinules. Antennal peduncle spinulose; scale reaching far beyond tip of rostrum, serrate proximally and distally, slight ridges spinulose dorsally and rows of minute spinules ventrally.

Third legs very strong, usually symmetrical, articles variably armed with compressed spinules seeming to form carinae; ischium with row of 9–26 dorsal and ventral weak spinules; merus with 2, seldom 1, dorsal rows of 10–18 spinules, ventral row of 7–16, and scattered laterals, all increasing in size distally; carpus narrowed abruptly near base, dorsally with 3 diverging rows of 9–18 spinules, ventrally with 2 diverging rows of 8–12 spinules; propodus with row of 16–25 dorsal spinules, ventrally 21–32 spinules, lateral surfaces with rows of spinules and some others scattered; dactyl with dorsal row of spinules.

Abdomen with ventral surface of sixth segment spinulose, and male with 1 ventral median spine on each preceding segment. Pleura of first segment ending in 2 pointed teeth; those of 2–5 truncate, their lateral margin bearing 3 spines; third segment produced into spineless triangular area overlapping spineless anteromesial part of fourth. Uropodal exopod with 10–16 marginal teeth and longitudinal rows of spinules to each side of dorsal ridges; endopod with 4–10 lateral teeth. Telson ending in 2 blunt spines.

Measurements in mm.—Length of body: to 62 (Holthuis 1946).

Color.—Body and legs white with bands of red;

blotch of red on anterior part of carapace; bases of legs blue in large adults; antennae and antennules white; eyes brown; cluster of eggs carried by female turquoise or green. Color brilliance usually contrasts sharply with dull background of gray coral rock. In shade, red dulled by white remains conspicuous; the antennae, which are usually displayed in sunlight, are clearly visible (Limbaugh, et al. 1961; Johnson 1969).

Habitat.—Mostly from water near shore associated with coral reefs, rocks, shipwrecks, etc., usually beyond the turbulent zone, occasionally to 210 m (Holthuis 1946; Limbaugh, et al. 1961).

Type-locality.—“Australasiatic seas.”

Known range.—Western Atlantic from North Carolina (Kruczynski and Jenner 1969) and Bermuda, southern Florida through Gulf of Mexico (Ray 1974), to Fernando de Noronha and Espírito Santo, Brazil (Coelho and Ramos 1972). Indo-Pacific from Durban, South Africa, and Red Sea, to Japan, Hawaii, western Australia south to ~24°S and eastern Australia as far south as Shellharbour, N.S.W., through New Caledonia, New Hebrides, Lord Howe Island, northern New Zealand, to Tuamotu Archipelago (Yaldwyn 1968). Bruce (1974) regarded the distribution as truly circumtropical, but there are no eastern Atlantic or Pacific records.

Remarks.—In addition to the above records, *S. hispidus* has been taken from rocks near the Coast Guard station at Bogue Inlet, N. C., 24 August 1978, and maintained on display at the Marine Resources Center, Bogue Banks, N. C. Yaldwyn (1968) gave an excellent summary of distribution, names, and habits.

Records indicate that *S. hispidus* breeds nearly year round (Johnson 1969; USNM). Gurney (1936c) and Gurney and Lebour (1941) described nine larval stages for this species from plankton rearing studies at Bermuda, remarking that the later stages tend to be multiple if suitable conditions for metamorphosis to postlarva are not present. Williamson (1976) added notes on structures not previously described in stage II and variations in stage III. He noted that adults are apparently confined to relatively shallow water, often on coral reefs, but that the teleplanic larvae can be taken in open ocean over very deep water and may be able to delay metamorphosis, continuing to molt and grow until they reach coastal water.

Pair formation was studied and discussed by Yaldwyn (1964; 1966; 1968) and Johnson (1969). *Stenopus hispidus* is found in pairs, each pair consisting of a male and female, the male sometimes being much smaller than the female. One female in a rock crevice at the mouth of Botany Bay, near Sydney, Australia, was observed in situ at intervals

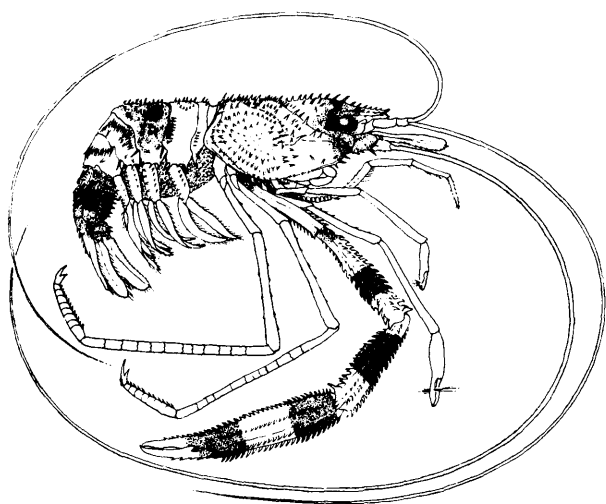


Fig. 35. *Stenopus hispidus* (Olivier). Female in lateral view (from Limbaugh, et al. 1961).

for eight months before removal to an aquarium for further observation. At time of capture a small male was found in association, the latter often riding on the back of the female; another pair was observed over a period of 18 months (Yaldwyn 1966; 1968). The above authors described this and other behavior (agonistic; courtship when male is equal to or larger than female; visual, olfactory, and tactile responses; but pheromones eliciting these behaviors were not demonstrated). Pairs often appear to be formed as juveniles and remain in an area of less than a m² for a long time, perhaps years (Limbaugh, et al. 1961).

In addition, *S. hispidus* has been observed to clean fishes, apparently attracting them with the displayed white antennae and then reaching out with appendages, without leaving the station, to clean their surfaces (Limbaugh, et al. 1961). However, the shrimp has been found in stomachs of the Coney (*Cephalopholis fulva* (Linn.)), and the Red hind (*Epinephelus guttatus* (Linn.)), indicating that it is not entirely immune to predation (Randall 1967).

Stenopus scutellatus Rankin

(Cleaner shrimp)

Fig. 36

Stenopus scutellatus Rankin 1898:242, pl. 29, fig. 3.—Holthuis 1946:28, pl. 3, figs. *a-b*.—Limbaugh, Pederson, and Chace 1961:253, fig. 9.—Chace 1972:145.—Coelho and Ramos 1972:157.

Recognition characters.—Carapace densely covered with slender spinules arranged in more or less longitudinal rows; double row extending from base

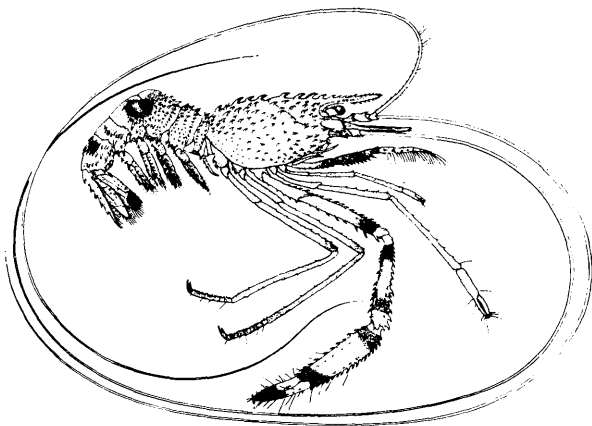


Fig. 36. *Stenopus scutellatus* Rankin. Animal in lateral view (from Limbaugh, et al. 1961).

of rostrum to cervical groove. Rostrum slightly triangular at base, compressed near apex, slender, straight, almost as long as carapace, reaching beyond antennular peduncle; 10–11 strong dorsal, 0–3 lateral, and 6–8 ventral spines. Eyestalks minutely spined. Antennular peduncle with third article shortest; stylocerite small but more conspicuous than in *S. hispidus*; anterolateral corner of basal article with small spined scale, second with some dorsal spinules, and third with forward pointed spine. Antennal peduncle multispinose; scale reaching $\frac{1}{3}$ or more of its length beyond tip of rostrum, margin serrate.

First and second legs with carpus often spined dorsally, remainder smooth. Third legs very strong, usually symmetrical; ischium with row of 3–5 spinules dorsally and ventrally; merus with similar rows of 9–15 spinules and scattered ones laterally; carpus narrowing gradually toward base, dorsally with 3 diverging rows of 7–11 spinules, ventrally 2 rows of 4–6 spinules; propodus with dorsal row of 11–14 spinules, a few spinules in rows laterally; and dactyl with dorsal spinules.

Abdomen similar to *S. hispidus*; third segment with posterodorsal shield-shaped area bearing about 4 lobes at each side. Spinules on last 3 segments aligned in distinct transverse rows; 4 and 5 with 1 row, 6 with 3 rows. Uropodal exopod with 8–10 lateral marginal teeth; endopod with 5 lateral teeth near base; upper surface with row of spinules near median ridge.

Measurements in mm.—Length of body: 35, perhaps 40 (Holthuis 1946).

Color.—General color pattern similar to *S. hispidus* but with back lemon yellow (Limbaugh, et al. 1961).

Habitat.—Sponges, coral reefs, waterlogged stump, grass flats with conchs and *Porites* clumps, rocky bottom; to 113 m (Holthuis 1946; Limbaugh, et al. 1961).

Type-locality.—Silver Cay, New Providence, Bahamas.

Known range.—Bermuda; South Carolina (Wenner and Read 1982); Gulf of Mexico to Fernando de Noronha and Rio Grande do Norte, Brazil.

Remarks.—Limbaugh, et al. (1961) observed the species in small holes on solid substrates in protected quiet water, always in pairs. It is believed that the pairs remain nearly in the same spot for continued (undetermined) lengths of time. The shrimp whip their light-colored antennae in the sun in front of the hole in which they live in order to attract fishes (usually small); they reach out to pick at the skin of hosts thus attracted, rarely leaving the hole, and never climbing onto the fish.

Infraorder Caridea

Superfamily Pasiphaeoidea

Family Pasiphaeidae

Pleura of second abdominal segment overlapping those of first and third segments. Third legs never with chelae. Gills phyllobranchiate (Holthuis 1955).

Rostrum small or obsolete. Legs with exopods; first 2 pairs of legs chelate, chelae slender, cutting edges pectinate; legs 3–5 smaller than chelipeds, 4 generally smallest (Rathbun 1901; Holthuis 1955).

Key to Genera and One Species

(Adapted from Holthuis 1955)

1. Rostrum formed by erect, postfrontal spine, fourth leg shorter than fifth
 *Pasiphaea multidentata*
- Rostrum normal, projecting forward from carapace, fourth leg longer than
 fifth *Leptochela*

Genus *Leptochela* Stimpson 1860

Chace 1976:2.

Carapace and rostrum unarmed dorsally. Branchiostegal tooth and branchiostegal sinus absent. Sixth abdominal segment with transverse carinate ridge near anterior end of dorsal surface and long, fixed, posteriorly directed spine near posterior end of ventrolateral margin. Telson with mesial pair of movable spines anteriorly, 1 or 2 pairs of dorsolat-

eral movable spines, and 5 pairs of prominent posterior movable spines, all but lateral pair of latter minutely serrate on one or both lateral and mesial margins. Legs 4 shorter than 3, longer than 5. Both branches of uropod with series of movable lateral spines. (Abridged but largely quoted from Chace 1976.)

Chace's excellent recent review of the genus makes the following accounts almost superfluous. They are abstracted from his paper and included only for convenience.

Key to Species

1. Sixth abdominal segment bearing movable lappet near anterior end of dorsal surface; third leg with exopod reaching nearly or quite to end of ischium [Subgenus *Proboloura*] *L. (P.) carinata*
- Sixth abdominal segment lacking dorsal lappet; third leg with exopod not nearly reaching distal end of ischium [Subgenus *Leptochela*] 2
2. Suborbital angle dentate; orbital margin serrate dorsolaterally *L. (L.) serratorbita*
- Suborbital angle rounded, unarmed; orbital margin usually entire dorsolaterally 3
3. Fifth abdominal segment with 1–3 low prominences on dorsal margin. *L. (L.) papulata*
- Fifth abdominal segment regularly convex or nearly straight in lateral view *L. (L.) bermudensis*

Leptochela (Leptochela) bermudensis Gurney

Leptochela bermudensis Gurney 1939:427, figs. 1–10.
Leptochela (Leptochela) bermudensis.—Chace 1976:7, figs. 5–7.

Remarks.—This species has not been recorded from the region covered by this survey but eventually may be found there.

Leptochela (Leptochela) papulata Chace

Fig. 37

Leptochela (Leptochela) papulata Chace 1976:26, figs. 22–24.

Recognition characters.—Rostrum usually not reaching distal edge of eye; usually with dorsal

margin regularly convex, rarely slight convexity in anterior half. Carapace with median dorsal carina on anterior $\frac{1}{5}$ – $\frac{1}{2}$ in males and nonbreeding females, 3 longitudinal dorsal ridges in breeding females only. Orbital margin entire, rarely minutely serrate, without tooth on ventral portion; suborbital angle rounded. Cornea slightly wider than eyestalk, papilla on mesial surface of stalk. Antennular peduncle with stylocerite reaching nearly as far as distolateral margin of basal article, middle article longer than distal article in mesial view but distinctly shorter in dorsal view. Antennal scale barely half as long as carapace, lateral margin sinuous, blade forming rather distinct shoulder at base of distal tooth; distal articles of peduncle about $\frac{2}{3}$ as wide as, and nearly reaching, midlength of scale.

When extended forward: First leg usually overreaching antennal scale by little more than length of fingers; fingers with comblike spines on opposed margins (16–28 on dactyl). Second leg similar, sometimes overreaching antennal scale by more than length of fingers (22–36 prehensile spines on dactyl). Third leg overreaching anterior margin of carapace by length of dactyl. Fourth overreaching ischium of second by length of dactyl; fifth slightly shorter than fourth.

Abdomen regularly rounded dorsally on first 4

segments; 5 bluntly carinate dorsally and usually surmounted in posterior half by 1–3 pimplelike elevations (rarely obsolescent); segment 6 usually with minute blunt tooth on posterodorsal margin of posterolateral lobe. Telson with pair of dorsolateral spines at about midlength in addition to anterior mesial pair.

Measurements in mm.—Length of carapace: male 3.9; female, nonbreeding 3.6, nonovigerous breeding 3.6, ovigerous 4.4.

Variation.—Most specimens have one to (usually) three elevations on the dorsal midline of the fifth abdominal segment; occasionally, these elevations are obscure but the dorsal margin of the segment is always faintly sinuous in lateral view. The dorsolateral margin of the orbit may be minutely serrate, but much less so than in *L. (L.) serratorbita*.

Habitat.—White or gray sand with black specks, sand, terrigenous sand, coarse sand, mud, coral and sand, gravel, shell debris, rock; 20 to 202 m.

Type-locality.—East of Cape Lookout, N. C., 34°35'30"N, 75°45'30"W, 59 m.

Known range.—Georges Bank off Cape Cod, Mass. (Fontaine 1977b); North Carolina to Georgia; eastern Gulf of Mexico.

Remarks.—This species is slightly larger than *L. (L.) bermudensis* and apparently closely related to it. Ovigerous females are known from the eastern Gulf of Mexico in March, and North Carolina in October–November (Chace 1976).

From six specimens, Fontaine (1977b) described a postlarva, identified as *L. serratorbita*, and illustrated some adult characters. His figures seem referable to *L. papulata* which was described at about the same time as this paper appeared.

Leptochela (Leptochela) serratorbita Bate

Fig. 38

Leptochela serratorbita Bate 1888:859, pl. 139, fig. 1.—Rathbun 1901:127.—Schmitt 1935a:134, fig. 7.—Williams 1965: 41, figs. 33–34.—Chace 1972:16.
Leptochela (Leptochela) serratorbita.—Chace 1976:36, figs. 29–31.

Recognition characters.—Rostrum reaching about level of articulation between first and second articles of antennular peduncle; dorsal margin straight, concave, sinuous, or rarely convex. Carapace without longitudinal dorsal ridge. Orbital margin minutely spinulose dorsolaterally and with mesially directed rectangular or obtuse tooth on ventral portion; suborbital angle dentate. Cornea slightly wider than eyestalk, papilla on dorsomesial surface of stalk at base of cornea. Antennular pe-

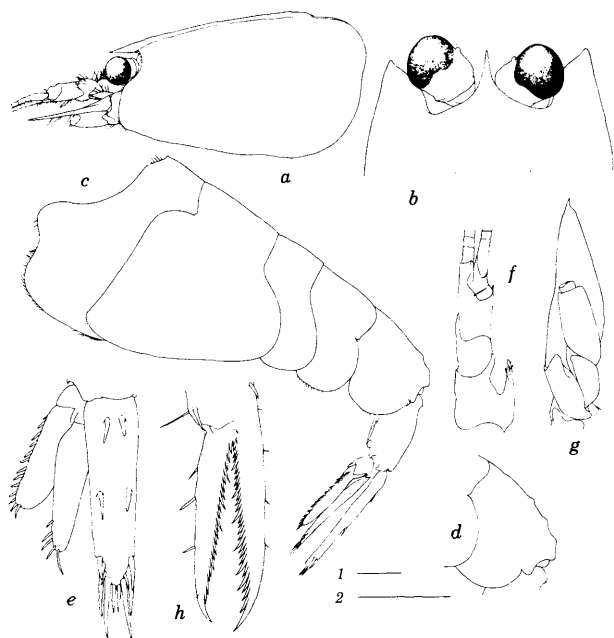


Fig. 37. *Leptochela (Leptochela) papulata* Chace. a, Carapace and anterior appendages, lateral view; b, anterior part of carapace and eyes, dorsal view; c, abdomen, lateral view; d, fifth abdominal segment; e, telson and left uropod; f, right antennule, dorsal view; g, right antenna, ventral view; h, fingers of right first leg. Scales: 1(a, c, d) = 1 mm; 2(b, e, f, g) = 1 mm, 3(h) = 1 mm (from Chace 1976).

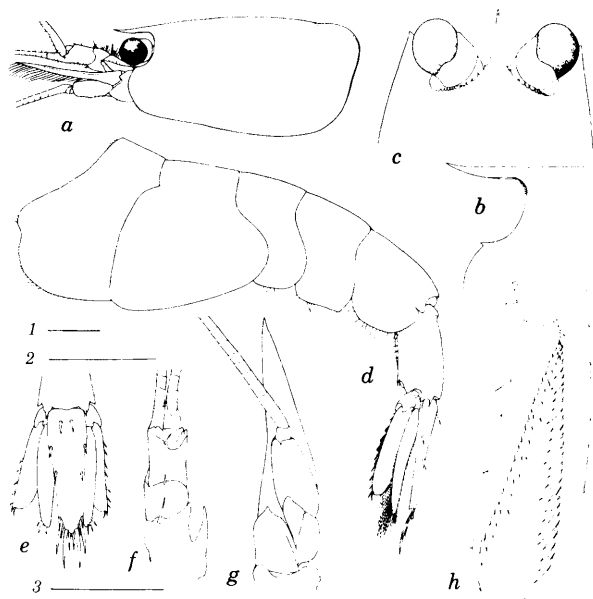


Fig. 38. *Leptochela (Leptochela) serratorbita* Bate. a, Carapace and anterior appendages, lateral view; b, orbital region; c, anterior part of carapace and eyes, dorsal view; d, abdomen, lateral view; e, telson and uropods; f, right antennule, dorsal view; g, right antenna, ventral view; h, fingers of right first leg. Scales: 1(a, d-e) = 1 mm; 2(b-c, f-g) = 1 mm; 3(h) = 1 mm (from Chace 1976).

duncle with stylocerite reaching about as far as distolateral margin of basal article, middle article about as long as distal article in ventromesial view, shorter in dorsal view. Antennal scale as long as carapace, lateral margin noticeably concave at about midlength, distal tooth usually continuous with mesial margin, latter rarely with subdistal shoulder; distal articles of peduncle about $\frac{3}{4}$ as wide as scale, not reaching its midlength, ventral tooth on basal article neither prominent nor sharp.

When extended forward: First leg usually overreaching antennal scale by less than length of fingers; fingers with comblike spines on opposed margins (9–29 on dactyl). Second leg similar, reaching same level (13–37 prehensile spines on dactyl). Third leg overreaching anterior margin of carapace by length of propodus and dactyl. Fourth reaching nearly to midlength of ischium of second; fifth a little shorter.

Abdomen rounded dorsally on 3 anterior segments, usually bluntly carinate on at least posterior part of 4 and all of 5, latter without dorsal prominences or posterior tooth; 6 with rather strong acute tooth on posterodorsal margin of posterolateral lobe. Telson with 2 pairs of dorsolateral spines, posterior pair near midlength, in addition to anterior mesial pair.

Measurements in mm.—Length of carapace: male 3.7; female without eggs 4.1, ovigerous 3.9.

Habitat.—Most specimens studied have been taken under light at the surface at night; coral, shells, and compact sand; 5.5 to 40 m (Young 1978).

Type-locality.—Saint Thomas, Virgin Islands.

Known range.—Beaufort, N. C.; South Carolina; western Gulf of Mexico and Florida Keys to Leeward Islands.

Remarks.—Chace (1976) remarked that *L. (L.) serratorbita* may have a more restricted depth and areal range than *L. (L.) bermudensis*, but is far the commonest species of *Leptochela* within its range. This small shrimp has been taken in May, July, October, and November in surface plankton tows in Bogue Sound, near Beaufort Inlet, N. C., on flood tides at night. Ovigerous females are known from Puerto Rico and Vieques in February, Leeward Islands in April, and North Carolina in May.

Leptochela (Proboloura) carinata Ortmann

Fig. 39

Leptochela carinata Ortmann 1893:41 (part), pl. 4, fig. 1.—Chace 1972:16.

Leptochela (Proboloura) carinata.—Chace 1976:45, figs. 35–37.

Recognition characters.—Rostrum short, not overreaching basal article of antennular peduncle; dorsal margin usually somewhat convex, occasionally straight or concave. Carapace with median dorsal carina on anterior $\frac{1}{3}$ to $\frac{1}{2}$ of length, dorsally tricarinate over most of length in breeding females. Orbital margin entire, mesially directed tooth on ventral portion; suborbital angle rounded. Cornea wider than eyestalk, papilla on mesial surface of stalk proximal to cornea. Antennular peduncle with stylocerite considerably overreaching basal article, middle article subequal to distal article in mesial view but distinctly shorter in dorsal view. Antennal scale 0.7 to 0.9 times length of carapace; lateral and mesial margins straight, tapering to distal spine with no indication of mesial shoulder; distal articles of peduncle little more than half width of scale and reaching middle $\frac{1}{3}$ of scale, basal article with prominent ventral spine.

When extended forward: First leg overreaching antennal scale by about length of fingers; fingers with comblike spines on opposed margins (41–58 on dactyl). Second leg similar, rarely overreaching antennal scale by length of fingers (43–66 spines on dactyl). Third leg overreaching anterior margin of carapace by length of dactyl and about $\frac{1}{2}$ of propodus. Fourth reaching to middle $\frac{1}{3}$ of ischium of second; spines on ischium and flexor margins of merus, carpus, and propodus; fifth leg

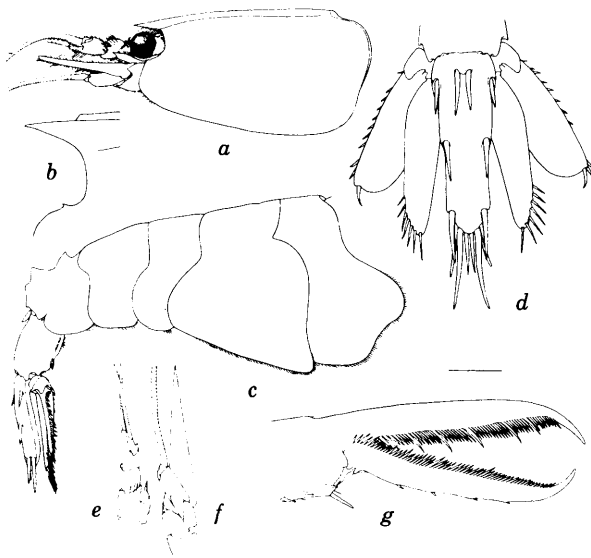


Fig. 39. *Leptochela (Proboloura) carinata* Ortmann. a, Carapace and anterior appendages, lateral view; b, orbital region; c, abdomen, lateral view; d, telson and uropods; e, right antennule, dorsal view; f, right antenna, ventral view; g, fingers of right first leg. Scales: a, c, e-f=2 mm; b, d=1 mm, g=?mm (from Chace 1976).

not much over $\frac{2}{3}$ length of fourth, spined as latter.

Abdomen regularly rounded dorsally on 3 anterior segments and anterior $\frac{2}{3}$ of 4; carina on 5 produced into 2 prominent acute anterior teeth and 2 low blunt teeth; 6 with movable lappet subtriangular, acute but sometimes obscure spine on posterodorsal margin of posterolateral lobe. Telson with 1 pair of anteromesial, and 2 pairs of dorsolateral long spines.

Measurements in mm.—Length of carapace: male 5.7; female, non breeding 7.7, ovigerous 6.7.

Habitat.—Rock, coral, coralline rubble, coralline algae, shells, sand; 11 to 66 m (Wenner and Read 1982); specimens have been taken in plankton.

Type-locality.—Off Baia de Marajó, Pará, Brazil, 50–100 m.

Known range.—Georges Bank; South Carolina; Gulf of Mexico through Bahamas to Pará, Brazil.

Remarks.—Chace (1976) found the species to be relatively rare in collections, suggesting that it either is not attracted to light as are some species in the genus, or it does not swarm as do *L. (L.) bermudensis* or *serratorbita*. Ovigerous females are known from Puerto Rico in February and the eastern Gulf of Mexico in March (Chace 1976).

Genus *Pasiphaea* Savigny 1816

Holthuis 1955:33.—Hemming 1958b:1959.—Zariquiey Alvarez 1968:70.

Pasiphaea multidentata Esmark

(Pink glass shrimp)

Fig. 40

Pasiphaea multidentata Esmark 1866:259, 314–316.—Sund 1913:4.—Sivertsen and Holthuis 1956:27, figs. 19–21.—Zariquiey Alvarez 1968:73, fig. 31.—Holthuis 1980:78.

Recognition characters.—Body greatly compressed. Carapace with maximum height near posterior margin nearly double anterior height. Rostrum small, dorsoventrally flattened, anteriorly convex; straight, elevated or bent downward in lateral view; smooth. Much more prominent postrostral tooth usually directed anteriorly above rostrum and base on eyestalk; variably shaped in lateral view, erect in some specimens, or curved downward at tip. Carapace with rounded suborbital angle, antennal angle less prominent and rounded; small branchiostegal spine sharp and sometimes overreaching anterior margin; pterygostomial angle almost rectangular, somewhat rounded. Eyes well developed, cornea globular, stalk short. Antennular peduncle extending well beyond that of antenna; basal article slightly longer than second and third together, stylocerite ending in acute tip reaching about distal margin of article; flagella long. Antennal scale definitely exceeding antennular peduncle, nearly $\frac{1}{4}$ as wide as long, narrowing gradually from base to somewhat rounded anterior margin, distolateral spine long and slender; basal article with prominent ventral spine distolaterally. Third maxilliped with prominent exopod tapering from slightly broadened base to tip overreaching base of penultimate article.

Legs with exopods. First 2 pairs of legs most robust; chelate; long, slender fingers finely pectinate on opposed margins, tips crossed. First legs with about 9–15 strong teeth on ventral surface of merus; second with 28–32 such teeth, but less than 20 such in small individuals; spine row continued on proximal articles of limb; spine numbers tending to be unequal on 2 legs of pair. Legs 3–5 smaller; third slender; fourth shortest; fifth stoutest, with spatulate dactyls.

Abdomen with dorsal carina extending from posterior half of first segment through anterior $\frac{3}{4}$ of sixth. Pleura more or less rounded on segments 1–4, posteroventral corner of 5 somewhat rectangular, that of 6 sharply so. Telson strongly grooved dorsally; forked distally, spine at extremity of each ramus finely serrate mesially, mesial aspect of each ramus with 6–10 distal spines finely serrated lat-

erally and mesially. Uropods exceeding telson, lateral ramus half again as long as telson, lateral margin ending in distal tooth.

Measurements in mm.—Length of body: to 105 (Zariquiey Alvarez 1968); smallest ovigerous female, carapace length 19.1 (Appolonio 1969).

Variation.—Both Sivertsen and Holthuis (1956) and Zariquiey Alvarez (1968) discussed variation in this species. The latter had earlier recognized, and rediscussed here, a Mediterranean population with rostrum longer, higher, and projecting farther forward than that observed in Atlantic material. Sivertsen and Holthuis showed that great variability in this character, as well as in shape of the postrostral tooth and eye size among Atlantic specimens, seemed to preclude establishment of subspecies. They felt that more material should be studied.

Color.—Cephalothorax milk white, translucent; with delicate reddish coloration in hepatic region more or less extensive or intense. Chromatophores orange, red, and violet on pterygostomian and branchial region. Abdomen white, with similar chromatophores along dorsal line and posterior border of first segment; posterior and lower parts of sixth segment orange. Telson with numerous red dots, latter larger on internal ramus of uropods. Peduncles of antennules and antennae with tiny red dots. Legs likewise with red and sometimes violet dots (Zariquiey Alvarez 1968).

Habitat.—Pelagic; in waters of 3.5°–8°C off eastern Canada (Williams and Wigley 1977, summary), –1.07° to 8.07°C off Norway (Grieg 1927); 10 (rarely) to 2000 m (Sivertsen and Holthuis 1956).

Type-locality.—Bjorumsfjord, about ⅓ mile from Namsos, Norway.

Known range.—North Atlantic Ocean; St. Lawrence estuary, Trois Pistoles, Quebec (USNM); Strait of Belle Isle to Cape Cod; off S Greenland to N Norway, southward along west coast of Europe and

through Mediterranean Sea (Sivertsen and Holthuis 1956; Squires 1966).

Remarks.—Sivertsen and Holthuis (1956) discussed the complex nomenclatural history of this species.

In the Gulf of Maine, Appolonio (1969) found two clutches of eggs for each mature female per year. The first is spawned from March through May, larvae hatching by early or mid-August. During later stages of development in these eggs, renewed ovarian development in the brooding females leads to production of another clutch in late August to early September, and these eggs may hatch in December-January. The eggs are rather large, 1.5–1.6 × 2.0–2.2 mm in diameter, and swell somewhat during development. Grieg (1927) found ovigerous females from January to September along the coast of Norway and also thought that there are two breeding seasons. Zariquiey Alvarez (1968) found ovigerous females during January and September-October in the Mediterranean Sea.

Pasiphaeid larvae collected in the Korsfjord, western Norway, occur in two groups based on size and number of telson spines (Elofsson 1961). The small larvae, 8–10 mm with fewer telson spines, were referred to *P. tarda*. Four zoeal stages were briefly described for each species. Larvae of the genus discussed in scattered literature, especially that of Williamson (1960, 1961), were referred to *P. multidentata*.

Lagardere (1976) investigated feeding habits of *Pasiphaea multidentata*, *P. sivado*, *Sergestes arcticus*, *S. robustus*, and *Psathyrocaris infirma* on the continental slope of the Bay of Biscay. These species apparently use the resources available in a similar way, but spatial distribution in different layers prevents any trophic competition among them. Nature of the prey is broadly determined by size, efficiency of catching technique, and possibly special detection (eyes in *P. sivado*?); *P. multidentata* (cl 16–29 mm) fed nocturnally in open water on young fishes, young cephalopods, natantian, and euphausiid shrimps. Absorption of sediment during rest hours is supposed to help these shrimps to stay immobile and could result in decrease of sonic detection by predators feeding on them.

Superfamily Bresilioidea

Family Bresiliidae

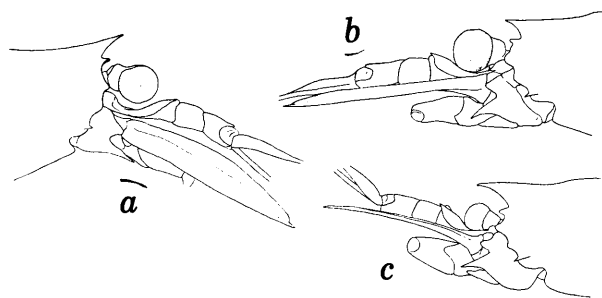


Fig. 40. *Pasiphaea multidentata* Esmark. Anterior part of body in lateral view, ovigerous females. *a*, *b* from Norway; *c* from Mediterranean coast of Spain (from Sivertsen and Holthuis 1956).

Mandible with palp; second maxilliped normal (2 distal articles in series, not parallel); first legs chelate with only 1 finger movable, more robust

than second; second legs with undivided carpus (modified after Chace and Brown 1978).

Scope of the small and relatively poorly known family Bresiliidae has been a matter of debate, most authors splitting the group into the families Bresiliidae and Disciadidae, but Chace and Brown (1978) concluded that characters of the two merge.

Genus *Discias* Rathbun 1902

Rathbun 1902a:290.

Discias atlanticus Gurney

Fig. 41

Discias atlanticus Gurney 1939a:388, figs. 1–13.—Holthuis 1951b:35, fig. 4.—Bruce 1975:301, figs. 1–3.—Gore and Wilson 1979:109, fig. 1.

Recognition characters.—Rostrum not extending beyond eyes, depressed, narrow, with slight median ridge. Carapace smooth, rounded orbital angle flanked by antennal spine; anteroventral angle rounded. Eyes large and globular. Antennules with

peduncle not reaching tip of antennal scale; stylocerite pointed and reaching beyond middle of basal article; latter bearing small ventral spine; second and third articles short and stout, about 10 basal joints of upper flagellar ramus broadened. Antennal scale slightly convex laterally, tiny distolateral spine exceeded by rounded lamella.

Chelate first leg with basis distinct but ischium-merus fused, merus cupped distally to receive minute (hidden) carpus, palm more than twice as long as wide, not narrowed proximally, and with deep hollow in posterior (mesial) face bearing transverse row of small spines; dactyl a round flat plate with small distal outer spine. Second leg also with ischium and merus fused; carpus short; palm nearly twice as long as wide; fingers tapering, curved and clawlike; dactyl with series of small teeth on prehensile edge, about $\frac{2}{3}$ length of palm. Legs 3–5 decreasing in length; third and fourth with 2 inner spines on ischium and 5 on merus; carpus with 1 spine; propodi with 5 spines (sometimes 3 on fourth); dactyls spiny, that of third leg with about 5 slender spines near middle of flexor margin and 5 smaller ones on upper margin close to tip; fourth with smaller and fewer ventral spines, and fifth with 1 ventral and 3–4 dorsal spinules.

Abdomen with pleura of fourth and fifth segments rounded; sixth segment about twice length of fifth, small posterior spine present. Telson tapered to subtruncate distal margin bearing short median point and 3 pairs of spines, mesial pair longest; 2 pairs of lateral spines on distal half.

Measurements in mm.—Length of body: male 10.8, female 13.1 (Wilson and Gore 1978).

Variation.—Specimens from west Africa have the rostrum more narrowed than that originally described by Gurney, slightly concave laterally, and with minutely serrate edges (Holthuis 1951b). There is also minor variation in spination of the dactyls on the third to fifth legs that is illustrated by authors who have described the species (synonymy).

Habitat.—Adults of the genus are known from sponges and soft corals, usually in shallow water (Bruce 1975; Wilson and Gore 1978); from shallow depths to 66 m, rarely to 201 m (Bruce 1975).

Type-locality.—The Reach, Bermuda.

Known range.—Bermuda; off Savannah, Ga., (B. B. Boothe, Jr., personal communication); off Fort Pierce, Fla.; Guadeloupe; Cape Verde Islands and Gabon; off northern Kenya (Bruce 1975; Gore and Wilson 1979).

Remarks.—The above authors have worked with very small numbers of specimens. Bruce (1975) regarded his three specimens as a last larval stage and postlarvae, all of more or less adult size that were caught in an offshore current from which they

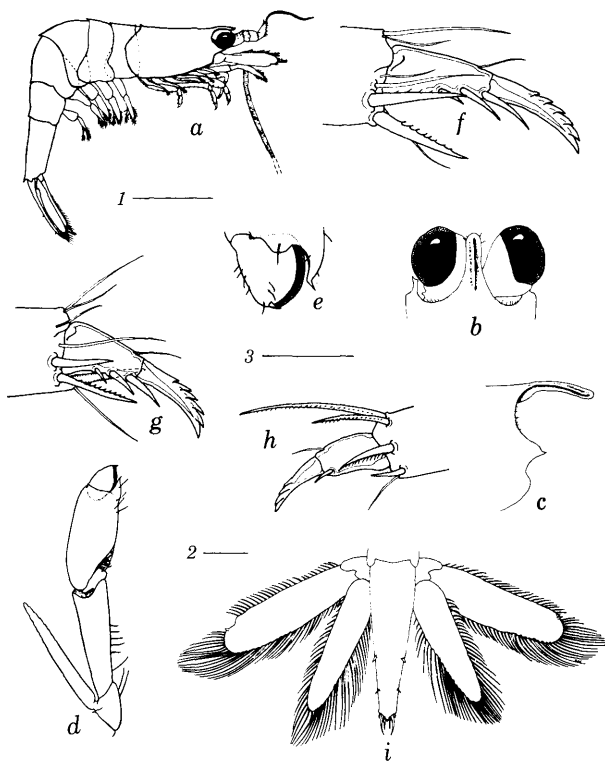


Fig. 41. *Discias atlanticus* Gurney. Female: a, lateral view; b, eyes and anterior carapace, dorsal; c, anterior carapace, lateral; d, tail fan (from Gore and Wilson 1979); e, cheliped, first leg; f, distal end, scale not given (from Gurney 1939); g–h, dactyl of third–fifth legs (from Bruce 1975). Scales: 1(a) = 2 mm; 2(b–c, i) = 0.4 mm; 3(f–h) = 0.4 mm.

were unlikely to reach a suitable habitat for settlement.

Another species of *Discias* from off South Carolina is presently being described (B. B. Boothe, Jr., personal communication), and still another, *D. serratirostris*, is known from off Vero Beach, Fla. (Wilson and Gore 1979).

Both Gurney (1942) and Bruce (1975) described the last larval stage of *D. atlanticus*.

Superfamily Palaemonoidea

Family Palaemonidae

Caridea having first 2 pairs of legs chelate, second pair usually larger than first, carpus of second pair not subdivided. Rostrum usually armed with teeth and not movable. Mandibles usually with an incisor process (Holthuis 1951a).

Key to Subfamilies

1. Posterior margin of telson with 2 pairs of spines and 2 or more setae **Palaemoninae**
- Posterior margin of telson with 3 pairs of spines (except *Anchistioides* with 1 or 2 pairs). **Pontoniinae**

Subfamily Palaemoninae

Upper antennular flagellum with both rami fused in basal part. Appendix masculina generally present on second pleopod of male, appendix interna

on second pleopod of female. Pleurobranch present on third maxilliped segment (IX). Posterior margin of telson with 2 pairs of spines and 1 or more pairs of setae (Holthuis 1952).

Key to Genera and Some Species

(Adapted from Holthuis 1952; Chace 1972)

1. Hepatic spine present, branchiostegal spine absent; chelate second legs enlarged and greatly elongated. 2
- Hepatic spine absent, branchiostegal spine present; chelate second legs not greatly enlarged. 3
2. Dactyls of last 3 legs bifurcate; marine **Brachycarpus biunguiculatus**
- Dactyls of last 3 legs simple; fresh or brackish water **Macrobrachium**
3. Carapace without branchiostegal groove ventral to antennal spine; endopod of first pleopod of male with accessory appendix; mandible with palp. **Leander tenuicornis**
- Carapace with branchiostegal groove; endopod of first pleopod of male entire, without accessory appendix; mandible without palp **Palaemonetes**

Genus *Brachycarpus* Bate 1888

Holthuis 1952:2.—Hemming 1958b:154.

Brachycarpus biunguiculatus (Lucas)

Fig. 42

Palaemon biunguiculatus Lucas 1849:45, pl. 4, fig. 4.
Brachycarpus biunguiculatus.—Holthuis 1952:3, pl. 1, figs. a-q.—Williams 1965:51, fig. 42.—Chace 1972:18.—Pequegnat and Ray 1974:251, figs. 61–62.

Recognition characters.—Rostrum well developed, rather high, directed straight forward, reaching

about to end of antennal scale; upper margin with 7 (seldom 8) teeth, first 2 placed behind orbit with first tooth at about midlength of carapace; lower margin with 3 (seldom 2 or 4) teeth. Carapace smooth; antennal and hepatic spines present; strong postorbital ridge paralleling orbit. Eyes well developed. Basal article of antennular peduncle with anterolateral spine strong, reaching beyond second article of peduncle; stylocerite small, acute, closely appressed to article; rami of inner antennular flagellum fused for 8 to 23 joints; free part of shorter ramus about as long as fused part. Antennal scale about 3 times longer than broad, outer margin concave, terminal spine overreaching lamella.

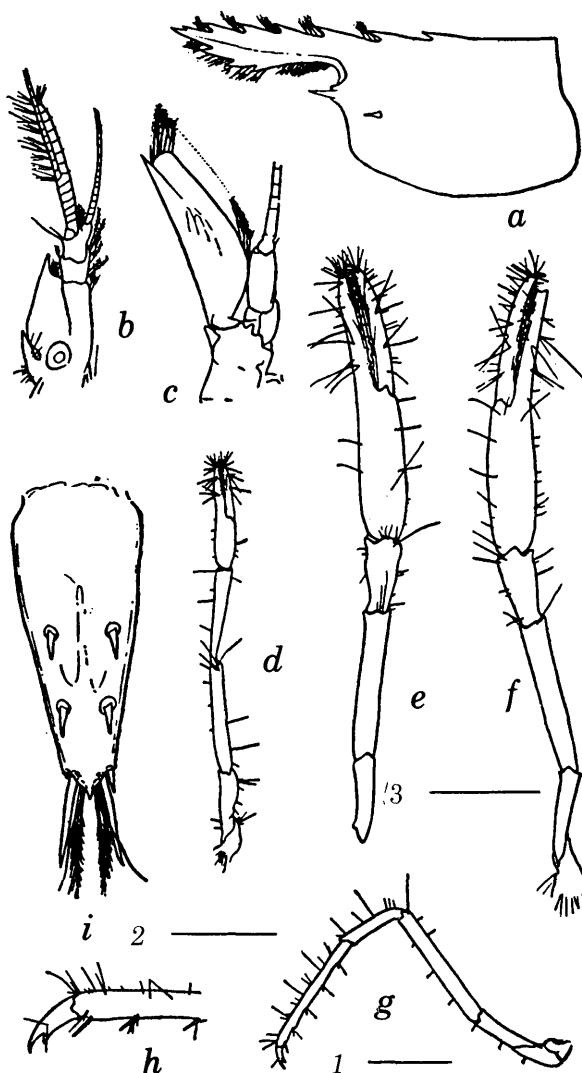


Fig. 42. *Brachycarpus biunguiculatus* (Lucas). a, Carapace in lateral view; b, antennule; c, antenna; d, first leg; e, left second leg; f, right second leg; g, third leg; h, dactyl of third leg; i, telson. Scales: 1(a, d-g)=2 mm; 2(b-c)=2 mm; 3(h-i)=1 mm (from Schmitt 1939).

First legs slender; fingers of chela longer than palm; carpus longer than chela. Second legs much stronger than first, smooth, part of carpus extending beyond antennal scale; fingers slightly shorter than palm, but in adult males sometimes only half length of palm, cutting edge of dactyl with 2 to 4, fixed finger with 2 small teeth in proximal part, adult males with fingers widely agape, opening hairy; carpus short, cup shaped, half length of merus. Last 3 legs slender, dactyls bifurcate, propodi with spines present on posterior margin.

Abdomen smooth, pleura of fourth and fifth segments pointed. Telson with 2 pairs of dorsal and 2 pairs of posterior spines; numerous setae between inner posterior spines. Appendix interna present on first pleopods in males, missing in females.

Measurements in mm.—Length of body: 65 (Holthuis 1952).

Variation.—Dorsal spines on the telson are sometimes not placed in symmetrical pairs and may be asymmetrically doubled.

Color.—Living individuals: body dark blue green mottled with white; palm of chela uniform blue green, fingers barred; fringes of antennules, antennae, antennal scale and tail fan orange; some individuals colorless, with tawny-tinged spots. Preserved specimens: pale brownish yellow, tips of fingers brownish red preceded by colorless band, then a fainter band of brownish red; antennular flagella red with white rings at articulations between joints (Holthuis 1952).

Habitat.—Found near shore among corals or rocks, on reefs (Corredor 1978), and on sea buoys; surface to 45.7 m (Pequegnat and Ray 1974).

Type-localities.—Oran and Bône, Algeria.

Known range.—Virtually pantropical (Bruce 1974); east and west American coasts, Mediterranean; West Africa; and Indo-Pacific region. Western Atlantic distribution: Cape Fear, N. C., western Gulf of Mexico (Ray 1974; Pequegnat and Ray 1974) through West Indies to Curaçao and Old Providence Island; Bermuda.

Remarks.—Gurney and Lebour (1941) described a complete series of 11 larval stages and a postlarval stage of this species from Bermuda. They pointed out that the larval life may be indefinite in length and number of developmental stages, and that this feature of development may account for the wide distribution of the species. Gurney (1943a) noted proportional changes in growth of the articles of the second legs in the last larval stage, first postlarval stage, and adult female.

The species is known to be a cleaning shrimp (Corredor 1978), having the long antennae, one pair of large chelipeds used as pruners, and smaller chelipeds used as sorters that are characteristic of these specialists. From observations on the reefs off Saint Vincent Island (West Indies), it was learned that the species is nocturnal, living as male-female pairs in smaller protected recesses than *Stenopus*, and ranging over areas about 2 m in diameter. The animals are timid, searching for sea urchins under which to hide when moving about. Although members of a pair live in the same recess, they have different though defined cleaning stations. Unlike diurnal cleaners which mount the host and concentrate on its mouth and gills, these cleaners concentrate on the surface of small fishes which present one side and then the other to the shrimp while it remains standing on the substrate, but large morays or fishes of lengths up to 100 cm are mounted for surface cleaning.

Ovigerous females were found from January to June at Saint Vincent and during the rest of the year at Santa Marta Bay, Colombia. Ray (1974) found ovigerous females in October, January, and March off Texas, and in April off Veracruz, Mexico, indicating year-round breeding.

Genus *Leander* Desmarest 1849

Holthuis 1952:167.—China 1966:213.—Carvacho 1977:100.

Leander tenuicornis (Say)

Fig. 43

Palaemon tenuicornis Say 1818:249.—Hay and Shore, 1918:392, pl. 27, fig. 6.

Leander tenuicornis.—Holthuis 1952:155, pl. 41, figs. a-g; pl. 42, figs. a-f.—Williams 1965:55, fig. 46.—Chace 1972: 19.—Pequegnat and Ray 1974:252, fig. 63.

Recognition characters.—Rostrum well developed; high in female, more slender in male, reaching about to end of antennal scale; upper margin with 8 to 14 regularly spaced teeth, first 2 behind orbit; lower margin with 5 to 7 teeth partially concealed by double row of setae. Carapace smooth; antennal spine present, branchiostegal spine

placed some distance behind anterior margin; branchiostegal groove absent. Eyes well developed, rounded; 2 dark-colored bands visible on cornea, especially in fresh material. Basal article of antennule with stylocerite large and pointed, reaching beyond middle of article, and with anterolateral spine reaching almost to end of second article of peduncle, anterior margin of basal article between spine and second article straight or only slightly convex; second and third antennular articles shorter and narrower than first; upper flagellum with fused part of rami shorter than free part of shorter ramus. Antennal scale 3 to 5 times longer than broad; outer margin about straight; terminal tooth strong, as long as lamella; antennal peduncle not reaching middle of scale; strong external spine near base of scale. Mandible with 2–3 jointed palp.

First pair of legs slender; reaching about to end of scale; fingers longer than palm. Second legs more robust than first, equal in size and shape; chelae reaching beyond scale; fingers longer than slightly swollen palm, cutting edges of fingers entire except for small basal tooth in males; carpus shorter than chela and about as long as merus. Last 3 legs slender, dactyls simple, slender; propodi armed with posterior spinules; fifth leg more slender than third.

Abdomen smooth; first 3 pleura broadly rounded; pleura of fourth and fifth segments narrower, ending in minute, acute tooth. Sixth segment lightly longer than fifth and about $\frac{2}{3}$ length of telson. Telson with 2 pairs of dorsal spines, first pair at midlength, second at $\frac{3}{4}$ length; inner 2 pairs of posterior spines overreaching acute tip of telson, pair of strong feathered setae between inner pair of spines.

Measurements in mm.—Length of body: 47; males generally smaller than females; ovigerous females 26 (Holthuis 1952).

Variation.—Length of the second legs is variable, and the palm of the chela is more swollen in some specimens than in others. Length of the terminal tooth of the antennal scale is variable.

Color.—Green or olive, with opaque spots (Schmitt in Holthuis 1952, for specimens from Tortugas); color plate (Sivertsen and Holthuis 1956). Brown in varying shades; mature females with ocelli on pleura of first and third abdominal segments (Manning 1961a).

Habitat.—Found in floating sargassum, on wharf pilings, and among submerged vegetation.

Type-locality.—Newfoundland Banks.

Known range.—Tropical and subtropical waters all over world except for west coast of Americas; Newfoundland Banks (occasionally mouth of Bay

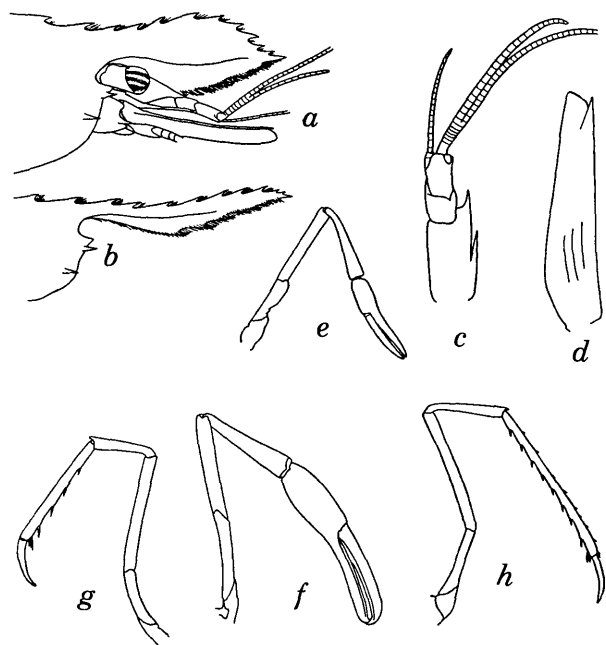


Fig. 43. *Leander tenuicornis* (Say). a, Female, anterior part of body in lateral view; b, male, anterior part of carapace in lateral view; c, antennule; d, antennal scale; e, first leg; f, second leg; g, third leg; h, fifth leg (from Holthuis 1952).

of Fundy and New England, Wigley 1970; Williams and Wigley 1977) to Falkland Islands in western Atlantic (Holthuis 1952; Bruce 1974).

Remarks.—Wigley (1970) considered the New England and Canadian occurrences to represent tropical vagrants that soon perish when temperatures drop in autumn. Ovigerous females have been observed from July to October in the Carolinas, in August in the Bay of Fundy, in June in the middle and western Atlantic (Sivertsen and Hol-

thuis 1956), and in August at Old Providence Island (Schmitt 1939). Gurney (1939) described the fifth(?) larval and first postlarval stages and compared them to related forms, with remarks on the statocyst in adults.

Genus *Macrobrachium* Bate 1888

Holthuis 1952:45.—Chace and Hobbs 1969:89.

Key to Species

(Adapted from Holthuis 1952)

1. Carpus of second legs with maximum length as great or greater than merus 2
 Carpus of second legs distinctly shorter than merus *M. carcinus*
2. Palms of chelae on second pair of legs cylindrical, not greatly swollen; fingers not noticeably gaping but may be hairy 3
 Palms of chelae on second pair of legs greatly swollen; prehensile surfaces of noticeably gaping fingers thickly set with long, stiff setae *M. olfersii*
3. Fingers of chelae on second pair of legs thickly pubescent throughout length; rostrum with teeth extending to tip *M. acanthurus*
 Fingers of chelae on second pair of legs with scattered hairs, except thicker on fingers along cutting edges; rostrum with toothless daggerlike tip *M. ohione*

Macrobrachium acanthurus (Wiegmann)

Figs. 44–45

Palaemon acanthurus Wiegmann 1836:150.

Macrobrachium acanthurus.—Holthuis 1952:45, pl. 9, figs. a-b.—Williams 1965:52, figs. 43–44.—Chace and Hobbs 1969:89, figs. 20, 25a, g.—Bonnely de Calventi 1974:44, fig. 13.

Recognition characters.—Rostrum almost straight, reaching slightly beyond antennal scale; upper margin slightly arched basally, with 9–11 teeth, proximals closer together than distals, first 2 teeth on carapace behind orbit, second tooth sometimes partly over posterior margin of orbit and separated from first tooth by distance greater than that between other proximal teeth; lower margin with 4 to 7 (generally 6) teeth, proximals closer together than distals. Carapace smooth, with short hairs especially on anterolateral region; antennal spine a little below orbit and slightly removed from margin; hepatic spine behind and a little below antennal spine. Antennal scale about 3 times longer than broad; outer margin straight or convex.

First legs with chela and sometimes part of carpus reaching beyond scale; fingers as long as palm; carpus $\frac{1}{3}$ longer than merus. Second legs equal,

with carpus and sometimes part of merus reaching beyond scale; fingers slender, thickly pubescent throughout length, slightly shorter than palm, cutting edges with tooth on each finger in proximal $\frac{1}{4}$ (that of dactyl more advanced) preceded by row of about 4 denticles; palm elongate, cylindrical, with several longitudinal rows of spinules, largest and farthest apart on inner and lower regions; carpus and merus spinulose like palm. Articles of last 3 walking legs with numerous densely placed small spinules.

Abdomen smooth; pleura of fifth segment ending in acute point. Telson 1.5 times length of sixth segment, with pairs of dorsal spines at middle and $\frac{3}{4}$ of length; posterior margin ending in sharp median point flanked by 2 pairs of spinules, inner pair overreaching median point.

Measurements in mm.—Length of body: male 179; ovigerous females 36 to 110.

Variation.—The rostrum may vary in length and shape. Adult females and young males have second legs shorter, more slender, and less spinulose and pubescent than adult males.

Color.—Green or pale yellow with red speckles; carapace with middorsal stripe of red or brownish orange and occasionally with irregular red bands laterally; chelipeds greenish becoming blue dis-

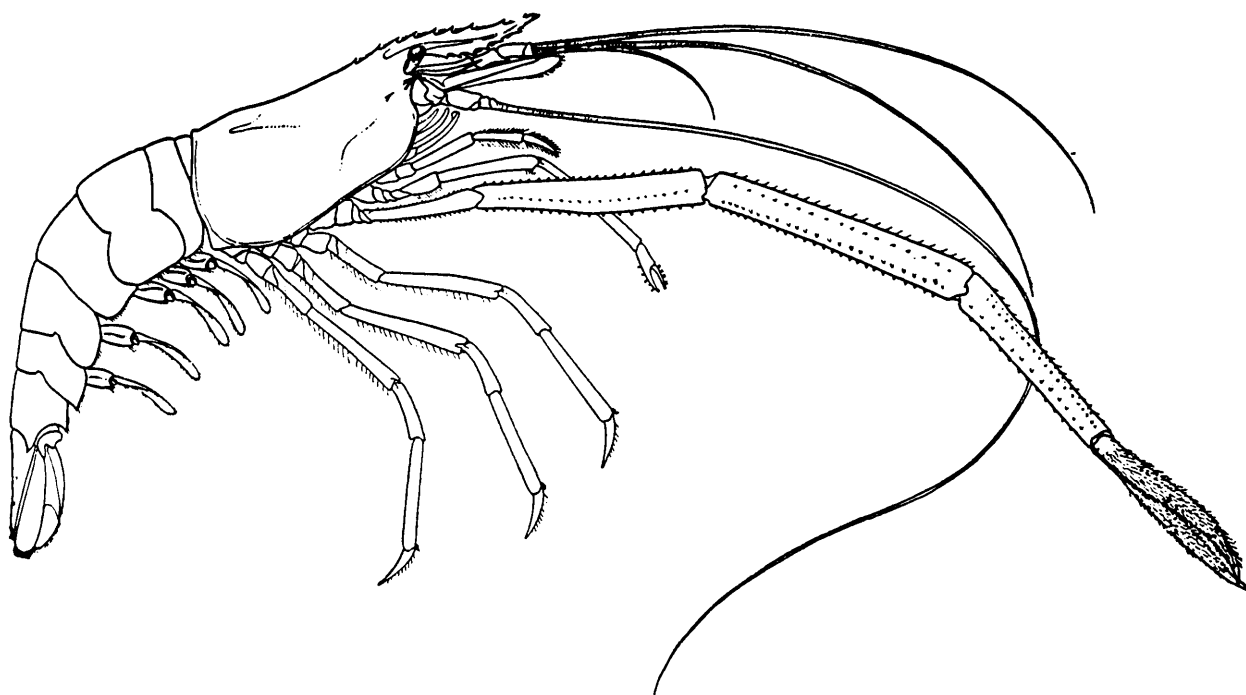


Fig. 44. *Macrobrachium acanthurus* (Wiegmann). Animal in lateral view (from Hedgpeth 1949).

tally, articulation orange; abdomen with middorsal stripe similar to carapace, pleura green with blue edges and striped with red; eggs green (Hedgpeth 1949; Schmitt *in* Holthuis 1952).

Habitat.—The species lives in coastal rivers and bays, usually near brackish water, but sometimes quite far upstream; 97 mi. (156 km) from mouth of Rio Grande River in Texas (Hedgpeth 1949).

Type-locality.—Brazilian coast.

Known range.—Neuse River estuary, N. C., to Rio Grande do Sul, Brazil.

Remarks.—North American records from the Carolinas are more numerous than in 1965. Two females, 44 and 48 mm total length, have been taken from intake screens of the Brunswick Nuclear Power Plant near Southport, N. C. (USNM), as well as other individuals from South Carolina localities.

Chace and Hobbs (1969) gave an excellent description and short ecological summary, pointing out that in Dominica the species frequents comparatively quiet waters near the mouths of streams that enter the Caribbean over a bed below sea level or lacking riffles. During the day the animals lie hidden among debris and roots of shoreline plants, but after dark they move by the thousands into open water on to the tops of debris accumulations. Carrillo (1968) discussed morphological variation in populations from Veracruz which fall within the normal range for the species.

In Colombia, females spawn throughout the year, bearing eggs 25%–45% of the time, although an

intense reproductive period lasts from August to October, with a massive spawning in September when most females at ages of 6 to 12 months have a body length of about 90 mm (Martinez 1975). Ovigerous females were reported to bear 150,000 to 250,000 eggs, although Paiva and da Costa (1962) found only ca. 4500 eggs on females 64 mm long; larvae hatch at a length of 2 mm; postlarval development lasts two months, development progressing best in 20‰ salinity. Martinez found that males in El Totumo swamp were larger than females, some reaching lengths of 179 mm (an unspecified individual reached 213 mm) and a weight of 89 g. Weight of individuals in his samples increased geometrically, 2.96 g for each mm increase in total length, the latter increasing at a mean of 1.87 mm; and for individuals between 12 and 130 mm long, increase in total weight was 2.33 g for each g weight of abdomen. Beyond 130 mm total length, total weight made a major increase to 3.86 g for each g increase in weight of abdomen. Martinez discussed other details on growth of adults and larvae.

Both Martinez and Choudhury (1971) observed mating in captivity, the latter remarking that it is always preceded by a premating molt of the female and prolonged courtship display in which the strongest males dominate other males. Egg-laying occurs 4–12 h after mating, the female bringing the abdomen near the genital opening on the coxae of the third legs to extrude eggs at the bases of pleopods 1–4, to which they become attached. Un-

mated females will also deposit unfertilized eggs, but they drop off the pleopods within 5 days. Incubation lasts 16–18 days.

Choudhury (1970) described and selectively illustrated 10 larval stages, first and second juveniles, and a 1-month-old juvenile hatched from ovigerous females collected in the Cabarita River, Jamaica, and transported to Kingston in aerated containers. The larvae, reared in 60% seawater in mass culture on a diet of brine shrimp nauplii, developed to Stage VIII in 22–29 days, and to Stage X in 32–42 days. In other experiments Choudhury (1971) transferred newly hatched larvae by slow acclimation to an array of salinities (fresh, 5, 10, 15, 20, 25, and 34‰) and reared them at ambient temperatures on a variety of diets. Though adults live and breed in freshwater, salinity of 15–20‰ was best for larval development; those in waters outside this range died during development. Starved larvae, living on stored yolk, died in two days; those fed detritus died in 14 days at Stage III; those fed boiled rice and a combination of vegetables died in 13 days at Stage III; of those fed fish, shrimp and crustacean muscle, five Stage IV larvae were alive on day 16 at termination of the experiment; larvae fed brine shrimp nauplii lived 18 days through Stage V when the experiment was terminated. Dobkin (1971), from ovigerous females trapped in canals near Boca Raton, Fla., and maintained in 1:1 seawater and canal water, hatched larvae and reared them in plastic boxes at 12, 23.5, and 35‰ salinity at 26° and 30°C on a diet of *Artemia* nauplii. He found molting frequent, survival best in the higher two salinities, mortality before metamorphosis in the lower salinity, and illustrated zoal stages 1–4.

Current chamber experiments have indicated that gravid females of *M. acanthurus* tend to swim consistently downstream whereas nongravid females tend to swim consistently upstream (Hughes and Richard 1973). This behavior suggests a mecha-

nism for insuring that larvae will hatch where they can survive. A similar experiment showed that larvae held in brackish water will drop to a position low in the water column when salinity is reduced (simulating ebb tide) and revert to swimming higher in the water column when salinity is increased (simulating flood tide). These responses are interpreted as a mechanism helping to prevent larvae from being carried out to sea, thus facilitating their eventual migration upstream to a freshwater environment where adults spend most of their lives.

Macrobrachium carcinus (Linnaeus)

Cancer Carcinus Linnaeus 1758:631.

Macrobrachium carcinus.—Holthuis 1952:114, pl. 30; pl. 31, figs. a-c.—Chace and Hobbs 1969:93, fig. 21.—Chace 1972:20.

Remarks.—Distribution of this species lies largely beyond the temperate east coast of the United States. The range extends from St. Augustine, St. Johns County, and Silver Glen Springs, Marion County, Fla., southward around the Gulf of Mexico and Caribbean Sea to Santa Catarina, Brazil. Hedgpeth (1949) gave a good short account of its occurrence in Texas rivers and bays, and Chace and Hobbs (1969) provided additional and more detailed observations from Dominica.

Macrobrachium ohione (Smith)

Fig. 46

Palaemon Ohionis Smith 1874:640.

Macrobrachium ohione.—Holthuis 1952:62, pl. 14, fig. b.—Williams 1965:54, fig. 45.

Recognition characters.—Rostrum high and straight, tip curving somewhat upward and reaching to between end of antennular peduncle and end of antennal scale; upper margin with 9 to 13 teeth, 3 or 4 teeth behind orbit, first 3 more widely separated than remainder; lower margin with 1 to 3 teeth; distal 2/5 of rostrum unarmed. Carapace smooth; antennal spine slightly remote from anterior margin; hepatic spine below antennal spine. Antennal scale about 2.5 times longer than broad; outer margin straight or slightly concave.

First legs with chelae reaching beyond scale; chelae slender; fingers about as long as palm; carpus twice length of chela. Second legs in adult female stronger than in male, with carpus and chela reaching beyond scale; fingers somewhat shorter than palm, cutting edges pubescent and with 4 to 8 small denticles of equal size on proximal half, remainder of surface with scattered hairs; palm

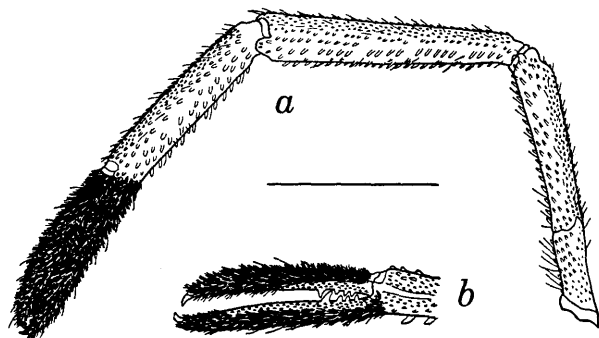


Fig. 45. *Macrobrachium acanthurus* (Wiegmann). Adult male: a, second leg; b, fingers of second leg (part of hairs removed); 3 cm indicated (from Holthuis 1952).

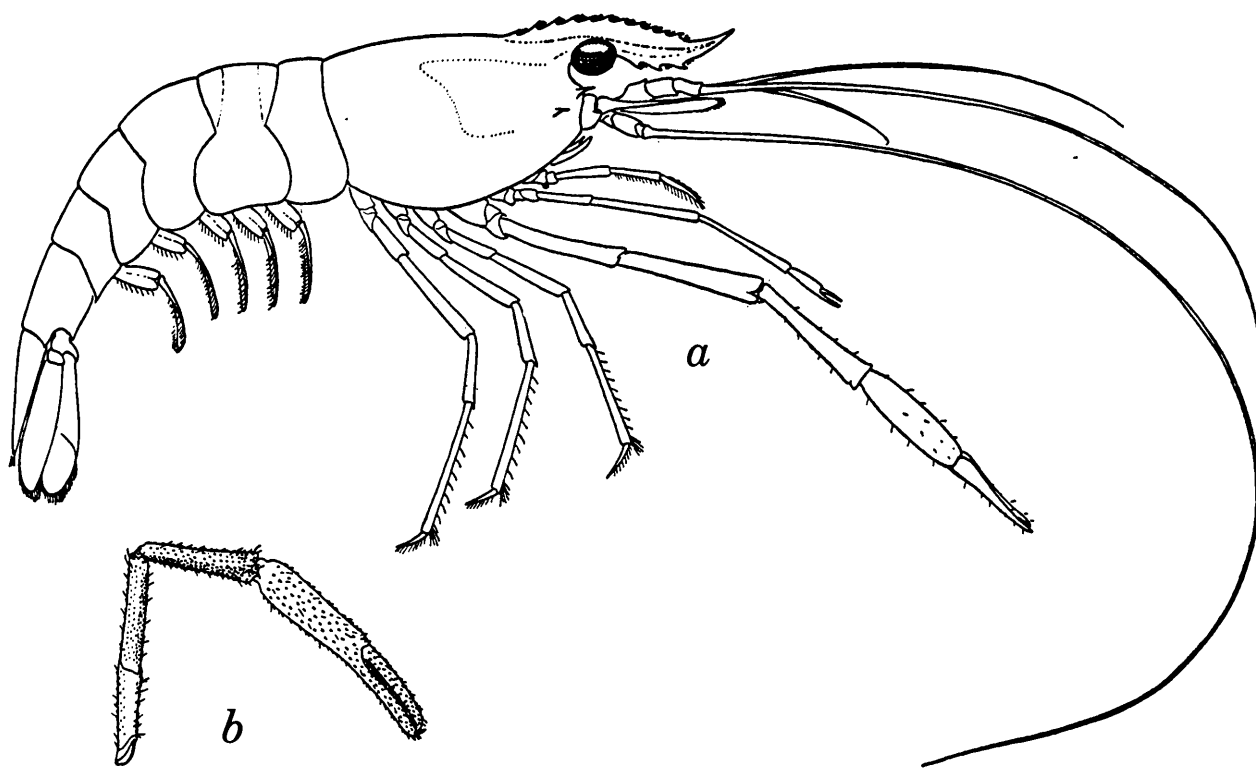


Fig. 46. *Macrobrachium ohione* (Smith). a, Animal in lateral view (from Hedgpeth 1949); b, second leg of adult male (from Holthuis 1952).

elongate, cylindrical, entirely pubescent, most conspicuous pubescence along lower surface; carpus, merus, and palm of equal length, these articles and fingers with longitudinal rows of small spinules, carpus most pubescent anteroventrally; merus somewhat pubescent anteroventrally.

Abdomen smooth; pleura of fifth segment ending in acute point. Telson about 1.5 times length of sixth segment; pairs of dorsal spines at middle and $\frac{3}{4}$ length; posterior margin ending in an acute tip overreached by inner pair of posterior spines.

Measurements in mm.—Length of body: male 68; female 102.

Variation.—Juveniles (10 mm and larger) have the same number of rostral spines as adults but fewer spines behind the orbit. In such juveniles, the hepatic spine is very close to the anterior margin of the carapace, similar in position to a branchiostegal spine.

Color.—Pale gray flecked with small blue spots; uropods pale blue (Hedgpeth 1949).

Habitat.—Rivers and estuaries.

Type-locality.—Ohio River at Cannelton, Ind.

Known range.—A narrow zone along Atlantic seaboard from James River, Hopewell, Va. (Hobbs and Massmann 1952), to southern Georgia; widespread from coastal Alabama to Aransas Bay, Tex.; Mississippi River and tributaries upstream to

McCurtain County, Okla.; Fort Smith, Ark.; St. Louis, Mo.; Washington County, Ohio (Hedgpeth 1949).

Remarks.—This species is distributed chiefly in brackish and fresh water, ranging far inland in the Mississippi River drainage. It is abundant enough to provide a fishery, especially in Louisiana, though the exact magnitude is not known. Gunter (1937) described the Louisiana fishery and gave information on ecology of the species. Commercially, the shrimp are taken in traps made of wooden slats, similar to lobster traps, baited with meat scraps or cotton seed cake. The shrimp are sometimes captured by lifting submerged willow branches from the water and catching the animals as they drop off. Such catches are best made at night. Commercial shrimping is done in the warmer months, as the animals are scarce in winter. The shrimp will attack fish kept in live boxes in the river, and, though feeding habits of the species are not known completely, stomachs of animals examined have contained 50% finely ground detritus and bits of organic matter, 20% sand, and 30% clams (*Rangia*), miscellaneous plant, invertebrate, and vertebrate remains (Darnell 1958).

During a period of study from November to early July, Gunter found that ovigerous females first appeared in mid-April, and were still present when

the work was terminated in July. Ovigerous females have been found in April and May in North Carolina. McCormick (1934) stated that eggs in various stages of development were found in females at the same time that they were in berry, which indicates a long egg-laying season. Gunter (1937) found females to outnumber males by more than 3 to 1. However, this ratio varied. When females were carrying eggs, males made up only 9% of the captured individuals, but prior to the egg-laying season males made up 31.8% of the total. He concluded that this indicated a change in sex ratio at the egg-bearing period.

Thirteen percent of the females caught were ovigerous, and these ranged in length from 38 to 76 mm. Eggless females ranged from 23 to 93 mm in length. From November to December, the population was made up of individuals 60–80 mm long. In January, shrimp below 30 mm average length predominated, but from then until April the average length increased to about 50 mm, and thereafter the range of variation widened as smaller animals came into the catch.

Gunter found ovigerous females in bay water with salinities ranging from 1.38 to 14.24‰. He noted that when the river was on the rise, with turbidity high, few shrimp were taken in water over 6 m deep, and these were sometimes dead. He conjectured that because these shrimp were not buried in mud, high turbidity in deep water during flood may have an adverse effect on respiration. Hedgpeth (1949) suggested that silt causing interference with respiration may drive the shrimp from rivers to estuaries during such seasons, but he also suggested that in regions such as the Atlantic seaboard, where the species is apparently a comparatively recent immigrant, it may still depend on bay waters to complete its breeding cycle. In any case, it is thought

that these shrimp and other species of the genus move from river to river through the estuaries at the river mouths (Gunter 1937).

This species and *M. acanthurus* are forms which may be advanced in the process of moving from the sea to fresh water. Few such examples exist.

Bridgeman (1969) found *M. ohione* to be the second intermediate host for the trematode, *Carneophallus choanophallus*, whose natural definitive hosts are the raccoon and black rat, and first intermediate host is the snail, *Lyrodes parvula*.

Macrobrachium olfersii (Wiegmann)

Figs. 47–48

Palaemon Olfersii Wiegmann 1836:150.

Macrobrachium olfersi.—Holthuis 1952:95, pl. 24; pl. 25, figs. a, b.

Recognition characters.—Rostrum straight or bent slightly downward, reaching about to end of antennular peduncle; upper margin bearing 12–15 evenly spaced teeth, 4 or 5 on carapace behind orbit; distance between first tooth and orbit somewhat less than $\frac{1}{3}$ total length of carapace excluding rostrum; lower margin with 3 (rarely 4) teeth. Carapace smooth; hepatic spine smaller than antennal spine. Antennal scale less than 3 times as long as broad; outer margin nearly straight.

First legs with $\frac{1}{3}$ or less of carpus reaching beyond antennal scale; fingers about as long as palm; carpus twice length of chela; merus $\frac{1}{2}$ length of carpus. Second legs very unequal. Larger leg reaching with all of carpus and small part of merus beyond antennal scale; palm and fingers bearing longitudinal row of spines or spinules, as do carpus and merus, longitudinal row of strong spines

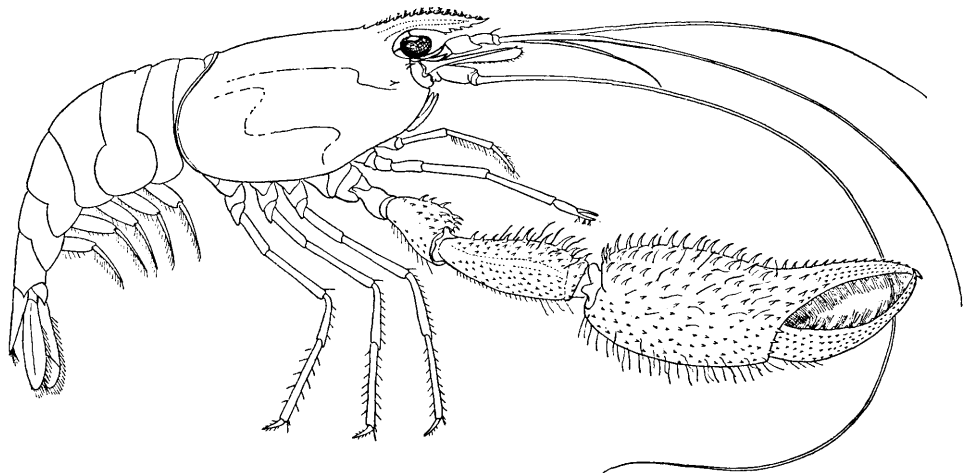


Fig. 47. *Macrobrachium olfersii* (Wiegmann). Animal in lateral view (from Hedgpeth 1949).

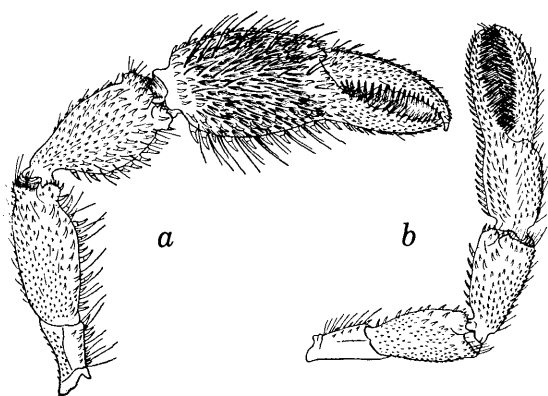


Fig. 48. *Macrobrachium olfersii* (Wiegmann). a, Larger, b, smaller second leg of adult male (from Holthuis 1952).

along lower margin; fingers (especially dactyl) curved and gaping, cutting edges with rather large proximal tooth succeeded by 2–4 smaller ones followed in turn by a number of denticles, stiff inwardly directed long hairs along cutting edges; palm slightly compressed, both upper and lower margin convex, about as long as fingers, dense pubescence on inner, outer, and lower surfaces plus scattered stiff hairs; carpus shorter than palm, about as long as merus, swollen distally but constricted near base. Smaller second leg with part of carpus reaching beyond antennal scale; fingers with 1 proximal tooth on cutting edge; ornamentation as in larger leg. Articles of last 3 legs much smaller and smoother; row of posterior short spinules on merus of third leg; otherwise with scattered spinules.

Abdomen smooth; pleura of fifth segment rectangular or slightly acute distally. Telson 1.5 times length of sixth segment, with pairs of dorsal spines at middle and $\frac{3}{4}$ length; posterior margin ending in acute median point flanked by 2 pairs of spinules, inner pair overreaching median point.

Measurements in mm.—Length of body: male 90; ovigerous female 30 to 65 (Holthuis 1952).

Color.—Male dark brown, some individuals overlain with bister or olive, others speckled muddy brown; hazy lines of cream buff on carapace, especially laterally, and on first and third abdominal segments, extending down almost to top line of epimera. Large cheliped of bister individuals bluish dark green, of muddy speckled individuals blackish brown, with remainder of limb black. Smaller chela dark brown. Walking legs more or less transparent; first type having faint bands of blue spots, but second type speckled with moderate brown.

Females more russet in color, marked like male; larger chela faint pea green mottled with rather large patches of light marine blue on inner and outer margins and fingers; walking legs almost white with few dark mottlings on anterior side; abdomen with dark, blackish area posteriorly on segments 1

and 3. (Abridged from notes by Schmitt in Holthuis 1952.)

Habitat.—Fresh and low salinity waters.

Type-locality.—“Brazilian Coast.”

Known range.—Lower Cape Fear River near Southport, N. C.; Florida; Louisiana; Texas; Veracruz, Mexico, to Santa Catarina, Brazil. Villalobos F. (1969) gave a distributional map for this and related species.

Remarks.—Holthuis and Provenzano (1970) acknowledged long-standing records of the species from St. Augustine, St. Johns County, and Silver Glen Springs, Marion County, Fla., and added a record from Dade County, Fla. They attributed these occurrences to introduction from South America, probably with water plants or fishes. Since then, J. O. Lee (personal communication and USNM) found *M. olfersii* (a 31-mm male) on intake screens of the Brunswick Nuclear Power Plant, Southport, N. C., in 1975. Horne and Beisser (1977) documented its occurrence in Texas in the Guadeloupe River and Rio Grande River at Brownsville, suggesting that larval drift might account for its spread. White (1977) found a male at the confluence of Little Pecan Bayou and the Mermentau River, Cameron Parish, La., in 2.4‰ salinity water influenced by tide.

Dugger and Dobkin (1975) collected ovigerous females with males in a Lake Worth, Palm Beach County, Fla., drainage canal. Maintained in an environmental chamber on a 12 h light-dark cycle at 30°C in an aerated jar in which salinity was gradually raised during two weeks to 21‰, the eggs of one female hatched 17 days after capture, releasing 150–200 larvae. These were reared in 21 and 35‰ salinity in partial isolation and mass culture. Stages and development were described (similar to *M. acanthurus*), the largest larvae undergoing 12 molts without metamorphosing, but developing pleopod buds. Larvae in 35‰ salinity were 85% dead in seven days, and all dead by day 50, whereas those in 21‰ showed gradual mortality over 27 days. The authors thought that the species may be present throughout the east coast drainage of Florida.

Genus *Palaemonetes* Heller 1869

Holthuis 1952:199.—Hemming 1958b:158.—Chace 1972a:12.—Bray 1976:66.

Diagnosis.—Carapace with branchiostegal spine and groove but lacking supraorbital spine. Without appendix interna on first pleopod of males.

Subgenus *Palaemonetes* Heller

Holthuis 1952:207.

TABLE 2.—Determination of *Palaemonetes* species in marine waters of eastern United States (from Holthuis 1952 and Fleming 1969).

Structure	<i>P. vulgaris</i>	<i>P. intermedius</i>	<i>P. pugio</i>
Rostrum:			
dorsal teeth	up to tip	usually up to tip	tip unarmed
ventral teeth	generally 4 or 5	generally 4 or 5	generally 2 or 3 (but up to 5)
teeth behind orbit	2	1	1
Shape upper margin	often concave	often concave	usually straight (directed up-ward)
Second legs:			
carpus of male	1.1 × palm; 0.8 × merus	almost = chela; = to merus	almost = chela; = to merus
carpus of female	shorter than palm; 0.7 × merus	longer than palm; = to merus	longer than palm; = to merus
Teeth of chela (usual):			
dactyl	2	1	0
fixed finger	1	0	0
Male second pleopod, appendix masculina:			
shape	straight	straight	somewhat curved distally
apical setae	4	4	5
subapical setae	2	2	1–2
exceeds appendix interna	0.25	0.33	0.33

Key to Species

1. Rostrum with 2 teeth of dorsal series behind posterior margin of orbit, teeth reaching to tip, 3 to 5 ventral teeth; carpus of second leg in adult female shorter than palm, in male slightly longer or shorter (1.1 times); dactyl of second leg with 2 teeth, fixed finger with 1 on cutting edge *P. (P.) vulgaris*
Rostrum with only 1 tooth of dorsal series behind posterior margin of orbit; carpus of second leg in adult female much longer than palm (1.3–1.5 times), in male almost as long as whole chela; dactyl of second leg with or without single tooth, fixed finger without tooth on cutting edge 2
2. Rostrum with dorsal teeth reaching to often bifurcate tip, 4 or 5, seldom 3, ventral teeth; dactyl of second leg with tiny and sometimes blunt tooth *P. (P.) intermedius*
Both margins of rostrum with unarmed stretch before dagger-shaped tip, 2 to 5, generally 3, ventral teeth; fingers of second leg without teeth on cutting edge *P. (P.) pugio*

Palaemonetes (Palaemonetes) vulgaris Say

Fig. 49

Palaemon vulgaris Say 1818:248.*Palaemonetes carolinus*.—Hay and Shore 1918:393, pl. 27, fig. 4.*Palaemonetes (Palaemonetes) vulgaris*.—Holthuis 1952:231, pl. 54, figs. f–l.—Williams 1965:56, fig. 47.—Fleming 1969:445 ff., figs. 4, 10.

Recognition characters.—Rostrum reaching to or slightly beyond end of antennal scale; tip directed upward making upper margin more or less concave; dorsal margin with 8 to 11 teeth, first 2 behind posterior orbital margin and separated more widely than other proximal teeth, all teeth rather regularly distributed along rostrum but proximals generally closer together than distals, no unarmed space behind often bifurcate tip; ventral margin with 3 to 5 teeth (usually 4, rarely 2). Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle with slender stylocerite reaching slightly beyond middle of basal article, anterolateral spine of basal article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 7 to 9 joints; free part of shorter ramus with 10 to 17 joints, at least 1.5 times as long as fused part. Antennal scale 3 times longer than broad; terminal tooth strong, reaching almost to end of lamella.

First leg usually not reaching to end of antennal scale; fingers about as long as palm; carpus 1.3 to 1.7 times as long as chela and slightly longer than merus. Second leg longer and stronger than first,

stronger in adult females than in males, fingers and sometimes entire palm reaching beyond scale; fingers a little over half length of palm, cutting edge of dactyl with 2 small proximal teeth, fixed finger with 1 similar tooth fitting between those of dactyl; carpus shorter than palm and about $\frac{3}{4}$ length merus. Second leg of male not so large as in female; teeth on fingers indistinct. Third leg with propodus less than twice length of carpus. Fifth leg with propodus about 3 times length of dactyl, twice length of carpus.

Abdomen smooth; fifth segment with tip of pleura rectangular or slightly acute. Sixth segment 1.5 times length of fifth, shorter than telson. Male with appendix masculina on endopod of second pleopod straight, bearing 4 apical and 2 subapical setae and exceeding length of appendix interna by $\frac{1}{4}$ its length. Telson with 2 pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by 2 pairs of spines, inner pair longest, and between them 2 feathered setae. Outer margin of uropodal exopod with strong terminal tooth flanked mesially by slender movable spine.

Measurements in mm.—Length of body: male 30; ovigerous females 22 to 42.

Variation.—Every character given in the key and table of comparisons for this species is subject to some variation, but most specimens fit the standard described.

Color.—Transparent in life.

Habitat.—Estuarine waters, especially in beds of submerged vegetation; water's edge to (rarely) 15 m. In North Carolina, *P. vulgaris* is usually found in waters of 15 to 35‰ salinity; Wilson (1969) found that it preferred saltier areas of the Louisiana canal-lake area, especially flowing canals. Bowler and Seidenberg (1971) showed that extremely low salinity is not tolerated well and may be fatal, confirming the findings of Nagabhushanam (1961), but in salinities of 36–40‰ this species is much more tolerant than *P. pugio*, indicating that this tolerance may help to separate niches of these species which otherwise are apparently similar. Thorp and Hoss (1975) confirmed these findings but thought predator-prey interactions, competition, or behavioral differences rather than physiological tolerances may help to explain coexistence of the species.

Type-locality.—Atlantic coast of United States.

Known range.—Southern Gulf of St. Lawrence from northern Cape Breton Island (Bousfield 1956) through Northumberland Strait (Bousfield, personal communication) to St. Simons Inlet and Miscou Harbor near Portage Bay (Bousfield and Laubitz 1972), southward to Cameron County,

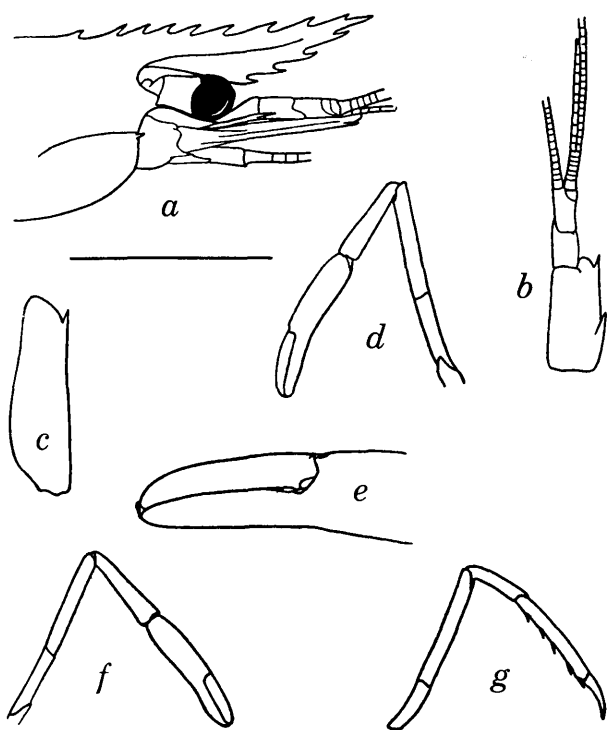


Fig. 49. *Palaemonetes (Palaemonetes) vulgaris* (Say). a, anterior part of body in lateral view; b, antennule; c, antennal scale; d, second leg of female; e, fingers of second leg of female; f, second leg of male; g, third leg; 5 mm indicated (from Holthuis 1952).

Texas. Published records also from Rio Champoton and near Progreso, Yucatan, Mexico (Holthuis 1952).

Remarks.—Correct identification of the species of *Palaemonetes* occurring on the east coast of the United States was not possible until Holthuis (1949) introduced his key. Two closely related species, *P. intermedius* and *P. pugio*, occupy much the same habitat and geographic range as *P. vulgaris*. An unfortunate but natural result of such confusion is that the voluminous older literature on *P. "vulgaris"* undoubtedly concerns all three species in unknown ways, hence must be viewed with reserve. Breeding experiments have shown that there is no natural hybridization among these species (Boston and Provenzano 1978).

Jenner (1955) showed that both *P. vulgaris* and *P. pugio* occur in the Woods Hole, Mass., region where much of the experimental work on *Palaemonetes* has been done. His useful field character for differentiating the two species is color of the eyestalks, those of *P. pugio* being generally much more yellow than the more red-brown *P. vulgaris*. The source of *Palaemonetes* for the Marine Biological Laboratory is thought to have been principally the dock, where only *P. vulgaris* has been found; Jenner suggested that most of the experimental work at Woods Hole was correctly referred to *P. vulgaris*.

In southern North Carolina, overt development of ovaries in largest females of *P. vulgaris* begins in February, egg deposition in early April. These events occur later in progressively smaller females. Zoeae begin to appear in plankton around the first of May. Peak egg production occurs in May when virtually all females are ovigerous. Breeding is continuous through summer; new eggs are deposited within 1 to 2 days after hatching of a previous brood. Larval development is rapid, juveniles appearing in early June. Sexual maturity is attained in animals having about a 5-mm carapace length. Females of the spring-hatched generation spawn in later summer and at a smaller size than overwintering 1-year-olds (in spring) which disappear from inshore areas by August. Reproductive activity wanes during September and hatching ceases by mid-October. Larvae are common in plankton throughout the breeding season, up to late November. Growth of adults largely stops during winter, resuming in spring (Knowlton and Williams 1970).

Larvae occur in much the same pattern in Chesapeake Bay (Sandifer 1973d), and a similar breeding season is inferred for other parts of the range, with allowance for latitudinal differences in temperature. Near northern extremes, ovigerous females are reported from southern Nova Scotia in early July (Bousfield 1958).

Burkenroad (1947a) showed that male *P. vulgaris* respond only to females which have molted to breeding form recently. After mating, the female resists further courtship. Males recognize such females only upon contact of the antennae with any surface of the female. The spermatophore will adhere to any part of the integument of either sex, but becomes non-adhesive almost immediately after exposure. Burkenroad stated that the sperm-bearing matrix of the spermatophore dissolves about a half-hour or less before spawning, and he thought that some substances freeing the sperm cells must be released by the female at the approach of spawning.

Eggs are released simultaneously from both oviducts in a continuous stream. Fertilization is external and, because sperm cells of decapod crustaceans in general are non-motile, Burkenroad suggested that entry of the sperm cell precedes development of the egg membranes in all decapods. All parts of the eggshell are produced by the ovum or the embryo. The first membrane is developed upon contact with water, the second about half an hour after spawning, and the third about 12 hours after spawning in fertile eggs only. The fourth and last membrane is an embryonic molt skin.

In *Palaemonetes*, the eggs are not adhesive when laid and first adhere to each other about half an hour after spawning. No attachment surface other than the first membrane of the egg develops. The eggs become fused, apparently by their own membranes, to the special setae in the brood pouch of the female. Egg stalks are drawn out by stretching movements of the pleopods. It is possible that the membrane is activated to become adhesive by the secretion of an enzyme-like material released among the eggs by the female from the pleopodal glands during attachment. Only near sources of this secretion would such attachment occur; therefore, the eggs usually do not stick to each other but rather to the setae.

Under experimental conditions *P. vulgaris* larvae tolerate a wide range of temperature and salinity, provided sufficient food is available. Salinity alone at five levels from 15 to 35‰ was found to have no effect on development of larvae but temperature profoundly affected both molting frequency and rate of growth. As temperature increased, growth and molting frequency increased, but the former decreased with respect to the latter. Thus, the average amount of growth per molt varied inversely with temperature, resulting in an increasing number of instars. Increased amounts of *Artemia* nauplii accelerated growth. Temperature and amount of food are important factors affecting rate of larval development, and growth and molting are semi-independent processes (Knowlton 1965).

Knowlton (1974) amplified this idea hypothesizing that food energy is utilized for maintenance activities at the expense of molting processes, which in turn have priority over growth and morphogenesis, considered to be roughly at the same level of demand. In a factorial experiment Sandifer (1973a) examined larval development of the species at 20°, 25° and 30°C in a different range of salinities (5–30‰). Lowest survival was in 5‰ at all temperatures. Time of development was twice as long at 20°C as at 25° and 30°C in most salinities, but a general retarding influence was noted at 5 to 10‰. Sandifer found metamorphosis as early as the 5th and late as the 12th molt. Salinity and temperature-salinity interaction had no detectable influence on number of instars, but the effect of temperature on number of instars was statistically significant at the 1% level. He concluded that optimal conditions for survival, rate of development and number of instars are at 25°C over a salinity range of 10 to 30‰.

For adults, McFarland and Pickens (1965) found no changes in rate of oxygen consumption related to salinity. They did, however, find moderate seasonal acclimation to temperature such that although metabolic rates did not change markedly, warm-adapted shrimp swam faster per unit of oxygen consumed when exposed to warm temperature than did intermediate or cold-acclimated shrimp. The reverse condition prevailed for cold-acclimated shrimp.

Since the early 1930s, much experimental work has been done on the endocrine system in relation to color control in *Palaemonetes*, mostly assumed to be *P. vulgaris*. The shrimp has been found to have four kinds of pigment under independent hormonal control—red, yellow, white, and blue. These pigments are mediated through the eyes by the background on which the animal is found. The source of the hormones is principally the sinus gland complex in the eyestalk and the central nervous system. Literature on this subject is beyond the scope of this paper. Kleinholz (1961) and Fingerman (1968) gave comprehensive reviews.

Palaemonetes vulgaris and *P. pugio* are both eaten by hakes, *Urophycis regius* and *U. floridanus* (Sikora, et al. 1972), and probably by many other predatory fishes.

Palaemonetes (Palaemonetes) intermedius Holthuis

Fig. 50

Palaemonetes (Palaemonetes) intermedius Holthuis 1949:94, fig. 2 j-l.—1952:241, pl. 55, figs. a-f.—Williams 1965:58, fig. 48.—Fleming 1969:445 ff., figs. 3, 11.—Chace 1972:22.

Recognition characters.—Rostrum reaching to or somewhat beyond end of antennal scale, tip directed upward making upper margin more or less concave; dorsal margin with 7 to 10 (usually 8 or 9) teeth, first tooth placed behind posterior orbital margin, second before or just over posterior orbital margin, proximal teeth more closely spaced than distal ones leading to often bifurcate tip; ventral margin with 4 or 5 (occasionally 3) teeth. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle with slender stylocerite reaching about to middle of basal article; anterolateral spine of basal article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 7 to 10 joints; free part of shorter ramus with 7 to 12 joints, longer than fused part. Antennal scale slender, 3 to nearly 4 times longer than broad in females, even more slender in males; outer margin straight or slightly concave; terminal tooth not overreaching end of lamella.

First leg almost reaching tip of antennal scale; fingers as long as palm; carpus twice length of chela and slightly longer than merus. Second leg in adult female with fingers or almost entire chela reaching beyond antennal scale; fingers a little over half length of palm, cutting edge of dactyl with 1 proximal tooth, remainder of cutting edges of both fingers entire; carpus 1.2 to 1.5 times length of palm and as long as merus. Second leg of male somewhat more slender than in female; only fingers reaching beyond scale; carpus as long as merus. Third leg with propodus about 3 times as long as dactyl, twice as long as carpus.

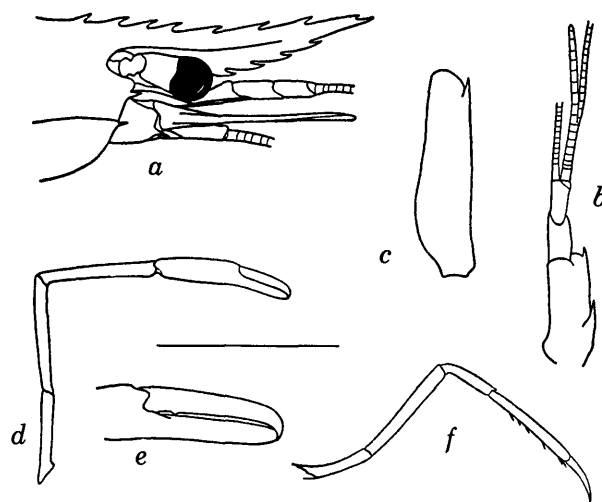


Fig. 50. *Palaemonetes (Palaemonetes) intermedius* Holthuis. a, Anterior part of body in lateral view; b, antennule; c, antennal scale; d, second leg of female; e, fingers of second leg of female; f, third leg; 5 mm indicated (from Holthuis 1952).

Abdomen smooth; pleura of fifth segment with tip rectangular or slightly acute; sixth segment 1.5 times length of fifth, somewhat shorter than telson. Male with appendix masculina on endopod of second pleopod straight, bearing 4 apical and subapical setae and exceeding length of appendix interna by $\frac{1}{3}$ its length. Telson with 2 pairs of dorsal spines; anterior pair somewhat behind middle, second pair halfway between these and tip; posterior margin with strong median point flanked by 2 pairs of spines, inner pair longest, and between these 2 feathered setae. Outer margin of uropodal exopod with strong terminal tooth flanked mesially by slender movable spine.

Measurements in mm.—Length of body: male 30; ovigerous females 20–42.

Variation.—Other than variations indicated in the description, the legs reach less far forward in males and juveniles than in ovigerous females (Holthuis 1952), and the second chelae of some females have one tooth on the cutting edge of each finger.

Color.—Transparent in life.

Habitat.—Estuarine waters, especially in beds of submerged vegetation.

Type-locality.—Iron Box Bay, Chincoteague Bay, Va.

Known range.—Vineyard Sound, Mass., to Port Aransas, Tex. (Holthuis 1952); Bahía de la Ascension, Quintana Roo, Mexico (Chace 1972).

Remarks.—The taxonomic status of this species is discussed in the account for *P. vulgaris*, in which a table of comparisons with closely allied species is given, and dealt with in more detail by Holthuis (1952).

Palaemonetes intermedius is variably abundant in south and southwestern Florida where it is more abundant than *P. pugio* and found in higher salinities (Tabb and Manning 1961; Rouse 1970). In studies of osmotic concentration of body fluids determined by freezing point depression, Dobkin and Manning (1964) found that *P. intermedius* is able to regulate over a wide range of salinities whereas regulation in *P. paludosus* (Gibbes) breaks down in salinities above 20‰. Odum and Heald (1972) found food habits of the latter two species similar in mangrove ecosystems except for the salinity range occupied. Both were considered opportunistic omnivores whose guts contained 22% unrecognized fine particles, 41% fine inorganic particles, 8% microalgae, 7% animal (invertebrate) remains, and 22% vascular plant detritus from which important food source bacteria, protozoa and fungi are removed.

Ovigerous females are reported in southern Florida from January to April and August to November (Tabb and Manning 1961; Rouse 1970). They are known from February to April in

(Hedgpeth 1950) and May to September in the Carolinas and Virginia. Hubschman and Broad (1974) described six larval forms and a postlarva in experimental rearings from females taken near Beaufort, N. C. Development closely resembles that of related species, size and number of molts being intermediate between marine and freshwater species (fewer molts) in the genus.

Palaemonetes (Palaemonetes) pugio Holthuis

Fig. 51

Palaemonetes (Palaemonetes) pugio Holthuis 1949:95, figs. 2 m-o.—1952:244, pl. 55, figs. g-l.—Williams 1965:59, fig. 49.—Fleming 1969:445, ff., figs. 7, 9.

Recognition characters.—Rostrum reaching to or slightly beyond end of antennal scale; straight, sometimes slightly upturned at tip; dorsal margin with 7 to 10 teeth (usually 8 or 9), first tooth placed behind posterior orbital margin, distal tooth placed at distance from tip leaving space before tip unarmed, distal teeth more widely spaced than proximal ones; ventral margin with 2 to 4 teeth (rarely 5 and usually 3), distal tooth also placed at distance from dagger-shaped tip. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle with slender stylocerite reaching slightly beyond middle of basal article, anterolateral spine of article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 10 to 14 joints; free part of shorter ramus with 12 to 18 joints, longer than fused part. Antennal scale 2.5 to 3 times longer than broad (3 times breadth in males); lateral margin convex; terminal tooth strong, almost reaching end of lamella.

First leg not quite reaching tip of antennal scale; fingers as long as palm; carpus nearly twice length of chela and slightly longer than merus. Second leg of adult female stronger than first; fingers more than half length of palm, reaching beyond scale, cutting edges of both fingers with no teeth, often gaping proximally; carpus 1.3 to 1.5 times length of palm but shorter than entire chela; merus as long as carpus. Male with second leg more slender and shorter than in female; fingers shorter than palm; carpus nearly as long as whole chela and as long as merus. Third leg with propodus twice length of carpus.

Abdomen smooth; fifth abdominal segment with occurring in fresh water (Beeston 1971; Bowler and pleura ending in acute tooth, sometimes extremely

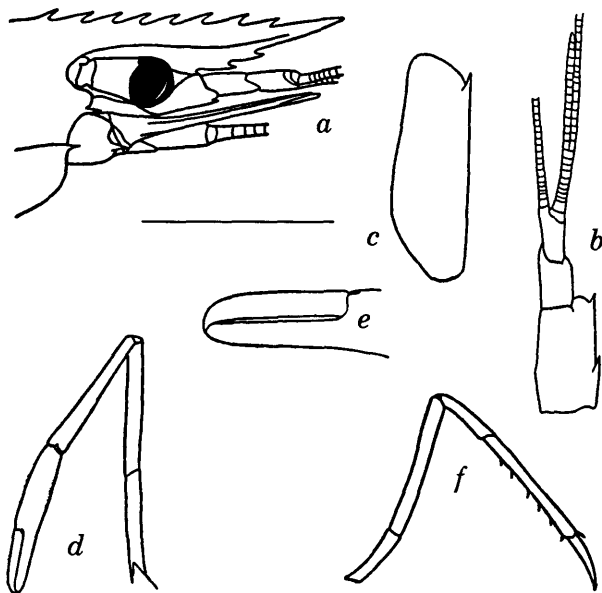


Fig. 51. *Palaemonetes (Palaemonetes) pugio* Holthuis. a, Anterior part of body in lateral view; b, antennule; c, antennal scale; d, second leg of female; e, fingers of second leg of female; f, third leg; 5 mm indicated (from Holthuis 1952).

small; sixth segment half again as long as fifth, somewhat shorter than telson. Male with appendix masculina on endopod of second pleopod somewhat curved laterad distally, bearing 5 apical and 1–2 subapical setae and exceeding appendix interna by $\frac{1}{3}$ its length. Telson with 2 pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by 2 pairs of spines, inner pair longest, and between them 2 feathered setae. Outer margin of uropodal exopod with strong terminal tooth flanked mesially by slender movable spine.

Measurements in mm.—Length of body: male 33; ovigerous females 30 to 50.

Variation.—Males further differ from females as follows: smaller size, more slender rostrum, free part of shorter ramus of upper antennular flagellum longer in relation to fused part, somewhat shorter legs, and carpus of second leg longer in relation to chela. Juveniles resemble males (Holthuis 1952). The second chelae of a few females have one small tooth on the cutting edge of the dactyl.

Color.—Transparent in life.

Habitat.—Estuaries, especially in beds of submerged vegetation (Marsh 1973). *Palaemonetes pugio* seems more tolerant of low salinity than *P. vulgaris*, being most abundant in the 10 to 20‰ range but Seidenberg 1971; Thorp and Hoss 1975; Wilson 1969; Wood 1967) as well as higher salinities. Welsh (1975) linked its abundance in estuaries to toler-

ance of poor flushing rather than to low salinity.

Type-locality.—Lagoon near Cove Point Light, Chesapeake Bay.

Known range.—Probably intermittent from Verte R., 3 mi. W St. Modeste (47°51'N, 69°26'W) Quebec, to near Yarmouth, Nova Scotia, Newcastle and East Brunswick, Maine (Bousfield, personal communication; Bousfield and Laubitz 1972; Knowlton 1973a; Williams 1974c), southward to Corpus Christi, Tex. (Holthuis 1952).

Remarks.—The taxonomic status of this species is discussed in the account for *P. vulgaris* where a table of comparisons with closely allied species is given, and dealt with in more detail by Holthuis (1952).

Breeding in *P. pugio* is comparable to that in *P. vulgaris*, varying with latitude. Rouse (1970) reported ovigerous females all year round in southwestern Florida in salinities varying from 0 to 43‰, but usually 10 to 15‰, at temperatures of 15° to 32°C; Hoese (1972) reported them from the Chandeleur Islands, La., in June in what must be high salinity for the species; and Knowlton (1973a) found them in Maine in mid-September.

Broad (1957) first worked out the larval development of *P. pugio* and *P. vulgaris*. He found that mature individuals of both species were abundant in the Beaufort, N. C., area from April until mid-October. Larval development is similar, 10 zoeal stages and a postlarval stage being described for both. The chief difference between larvae of the two is the presence of a pair of chromatophores on the second abdominal sternite of *P. pugio*, but absence in *P. vulgaris*. The number of larval stages and length of developmental period may vary, and one apparent cause of such variation is availability of suitable food. In rearing *Palaemonetes* with artificial diets, Broad (1957a) found that algae alone were not sufficient to promote survival; mixtures of plant and animal food were better, but best survival was obtained by feeding living *Artemia* nauplii. This was one of the pioneer experiments with this food in the rearing of decapod crustacean larvae. Frequency of molting and rate of development were directly correlated with amount of suitable food available.

Little (1968) showed that *P. pugio* could be induced to breed in winter. In November, two groups of animals whose water temperature was raised from 10° to 25°C over a period of 20 days and then held constant, one group being maintained at day lengths of 10.5 h and the other group at day lengths increased from 10.5 to 14.5 h in a month, spawned after two months, producing eggs which hatched into viable larvae. Animals in a similar experiment initiated in February spawned in five weeks. Eggs from the latter, maintained in 33‰ seawater and

22°–23°C, hatched in 15–19 days and larvae were reared to metamorphosis in 25–47 days. Both normal and abnormal larvae were produced.

Aspects of the physioecology of *P. pugio* have been studied in both field and laboratory. Wood (1967) found shrimp active throughout the year in Texas, with greatest abundance in July and October, mainly in salinities of 10–20‰. Growth to maturity there takes two to three months in summer and four to six months during the rest of the year. He found no appreciable variation in the length or weight associated with differences in salinity or temperature, but the most rapid increases occurred in temperatures over 30°C and the lowest ones at 11°–14°C. Welsh (1975), in Rhode Island, found an annual cycle with spawning in May–July, most rapid growth in late summer–fall, and over wintering in deep holes. Adams and Angelovic (1970) experimentally demonstrated what Odum and Heald (1972) found in the field, i.e., that *P. pugio* ingests and assimilates detritus with associated bacteria and that this material is perhaps one of their main sources of energy. Welsh (1975) amplified these findings, elaborating on the energetics of the species in the tidal marsh ecosystem. The shrimp macerate detritus into a heterogeneous assortment of uneaten particles by plucking away cellular matrix from surfaces of large detrital fragments. Resulting cavities in the detrital mass become heavily invaded by pennate diatoms, particles suspended in the water column and bacteria. Nutrient analyses indicate that the shrimp excrete large quantities of ammonia and phosphate which together with release of dissolved organic matter is presumably responsible for the heavy microfloral growth and in-

creased protein fraction in both feces and large and small uneaten detrital fragments. The shrimp while supporting their own trophic requirements accelerate breakdown of detritus. Welsh extended the finding of Johannes and Satomi (1966) that feces of these shrimp are rich in assimilable organic matter, particularly protein, and that a considerable fraction of energy in marine communities is channeled into feces to be consumed by the shrimp themselves and other organisms. Fecal pellets are thus a component of marine ecosystems, contributing to energy flow and nutrient cycles in a quantitatively significant way.

A number of parasites have been reported from *P. pugio*. Pearse (1952b) reported *Probopyrus pandicola* from the gill chamber of specimens from Texas, and Bousfield (personal communication) found bopyrids associated with it in Nova Scotia. Bridgeman (1969) described a microphallid trematode, *Carneophilus choanophallus*, whose definitive hosts in southern Louisiana are the raccoon and black rat (as well as other mammals in experiments) and second intermediate host is *P. pugio*. Sprague (1970) reported microsporidians in metacercariae from *P. pugio* in Georgia as well as from muscles of the shrimp.

Subfamily Pontoniinae

Upper antennular flagellum with both rami fused in basal part. Appendix masculina generally present on second pleopod of male; appendix interna on second pleopod of female. Pleurobranch absent from third maxilliped. Posterior margin of telson with 3 pairs of spines (Holthuis 1951a).

Key to Genera and Some Species

(Adapted from Holthuis 1951a; Chace 1972a)

1. Third maxilliped with well-developed exopod 2
 Third maxilliped without exopod 4
2. Hepatic spine present. *Periclimenes*
 Hepatic spine absent 3
3. Rostrum compressed, with distinct teeth. *Periclimenaeus*
 Rostrum depressed, with at most 2 small teeth near tip *Pontonia*
4. Second maxilliped with exopod *Anchistioides antiguensis*
 Second and third maxilliped without exopods
 *Neopontonides beaufortensis*

Genus *Anchistioides* Paulson 1875

Holthuis 1951a:175.

Anchistioides antiguensis (Schmitt)

Fig. 52

Periclimenes antiguensis Schmitt 1924a:84.

Periclimenes barbadensis Schmitt 1924a, pls. 3–4.

Anchistioides antiguensis.—Holthuis 1951a:175, pl. 57, legend on p. 310 facing pl. 55.—Coelho and Ramos 1972:148.

Recognition characters.—Rostrum large, toothed part nearly triangular in lateral view, reaching

somewhat beyond antennal scale; upper margin bearing 8–10 teeth on anterior $\frac{2}{3}$ of margin; lower margin bearing 5–8 teeth. Carapace smooth; large and conical postorbital tubercle slightly behind orbital margin; antennal spine below rounded lower orbital angle sharp and slender; anterolateral angle rounded and not produced. Eyes well developed, cornea as broad as short stalk and rounded. Basal article of antennular peduncle broad, stylocerite closely appressed, extending about to midlength of article, distolateral spine strong; second and third articles together half length of first; upper antennular flagellum thick and hairy, indistinctly jointed, fused with longer ramus for half its own length. Antennal scale 3 times as long as broad, far overreaching antennular peduncle; slightly sinuous outer margin ending in strong, laterally divergent tooth exceeding lamella; latter narrowed anteriorly and subrectangular mesiodistally; antennal peduncle not reaching midlength of scale.

First leg slightly overreaching antennal scale,

fingers about as long as palm, carpus slightly longer than chela. Second legs very strong and equal, fingers or part of palm reaching beyond antennal scale; fingers long, slender, tips curved and crossing, cutting edges entire, fitting closely; palm somewhat inflated and cylindrical; carpus somewhat conical, $\frac{1}{2}$ length of palm, $\frac{1}{3}$ length of merus. Third leg not reaching tip of antennal scale, dactyl narrow and indistinctly bifid; fourth and fifth similar but fourth both more slender and shorter than third or fifth.

Abdomen smooth, pleura of first 5 segments broadly rounded, those of sixth pointed. Fifth and sixth segments of about same length, posterior margin of latter with minute median tooth. Telson twice length of sixth segment; 2 pairs of dorsal spines in anterior half; 2 pairs of spines on posterior border, outer pair minute. Uropods elongate oval; outer margin of exopod ending in tooth flanked mesially by movable spine.

Measurements in mm.—Length of body: 25; ovigerous female 18 (Holthuis 1951a).

Habitat.—Coral rock, white rocks and coral, coarse sand and coral, coarse gray sand and broken shells, calcareous algae, fine white sand and black specks, enclosed in cavities in sponges (USNM); surface to 118 m.

Type-locality.—English Harbor, Antigua.

Known range.—Off Charleston, S. C. (Wenner and Read 1982); off west Florida through West Indies to Maranhão, Pernambuco, and Alagoas, Brazil (Coelho and Ramos 1972); Bermuda.

Remarks.—Samples of *A. antiguensis* taken throughout the year at or near the Biological Station in Bermuda in The Reach have shown regular nocturnal periodicity in occurrence at the surface, sometimes of sufficient intensity to indicate swarming (Wheeler and Brown 1936; Wheeler 1937). The peaks of abundance appear to coincide with two phases of the lunar month from last quarter to first quarter of the new cycle. The animals appear to come up from the bottom directly below, not to be drifting in with the tide. Swarming is thought to be inhibited by light. Sex and reproductive period, surface temperature, wind and weather, and stage of tide were shown to have no connection with swarming, but feeding on annelids (identified as epitokes of *Perinereis melanocephala* and *Leptonereis* sp. near *L. glauca*) may account for the behavior; stomachs of the shrimp were filled with setae of these species.

Ovigerous females of the shrimp were observed in June and early July. The double maximum of swarming was thought to represent two stages of growth. The species was less frequent in July–August and again in December–March. The summer reduction is due to dying out of a generation in

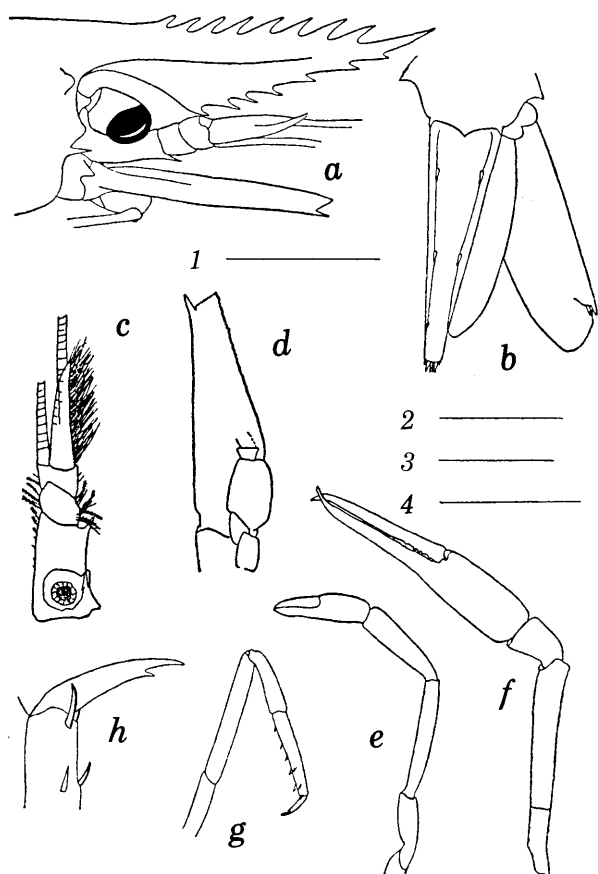


Fig. 52. *Anchistioides antiguensis* (Schmitt). a, Anterior part of body in lateral view; b, telson and right uropod in dorsal view; c, antennule; d, antenna; e, first leg; f, second leg; g, third leg; h, dactyl of third leg. Scales: 1(a-c, e, g) = 2 mm; 2(d) = 2 mm; 3(f) = 2 mm; 4(h) = 1 mm (from Holthuis 1951a).

July, but the winter scarcity was attributed to seasonal conditions.

Genus *Neopontonides* Holthuis 1951

Holthuis 1951a:189.

***Neopontonides beaufortensis* (Borradaile)**

Fig. 53

Periclimenes beaufortensis Borradaile 1920:132.

Neopontonides beaufortensis.—Holthuis, 1951a:190, pl. 59, figs. g-k; pl. 60, figs. a-k.—Williams 1965:49, fig. 41.—Chace 1972:25.

Recognition characters.—Rostrum slender, straight; a little shorter than antennular peduncle; laterally compressed but broadened at base, covering eye-stalks, lateral margin of widened base not merging with orbital margin; upper margin with 0–5 teeth, most proximal teeth, when present, in front of posterior margin of orbit on a crest, crest remaining visible in absence of teeth; lower margin unarmed. Carapace smooth or somewhat areolated; anterior margin of carapace with lower angle of orbit produced in rounded lobe; antennal spine strong, located considerably below orbit; rounded lobe slightly below antennal spine followed by an emargination ending in produced anterolateral angle; hepatic and supraorbital spines absent. Eyes large, reaching almost to end of rostrum. Basal article of antennular peduncle with stylocerite rather broad, ending in slender point reaching almost to middle of article; outer margin of article slightly concave ending in strong anterolateral spine reaching end of second article; upper antennular flagellum with rami fused for 2–4 joints; short ramus with 2–4 free joints. Antennal scale reaching beyond antennular peduncle; concave outer margin ending in strong tooth; lamella exceeding tooth; small lateral tooth at base; antennal peduncle reaching about to middle of scale.

First leg reaching beyond end of antennal scale; fingers slightly shorter than palm, unarmed, slightly agape; carpus about as long as merus. Second legs unequal. Part of palm of larger leg exceeding antennal scale; fingers half or less length of palm, dactyl with 2, fixed finger with 1 tooth on cutting edge; palm slightly swollen; carpus short, conical; merus about twice as long as palm, slender, unarmed; carpus nearly as long as palm. Third leg with heavy, simple dactyl.

Abdomen smooth, all pleura broadly rounded. Sixth segment as long as telson. Telson with 2 pairs of dorsolateral spines; posterior pair midway between anterior pair and tip; 3 pairs of spines on

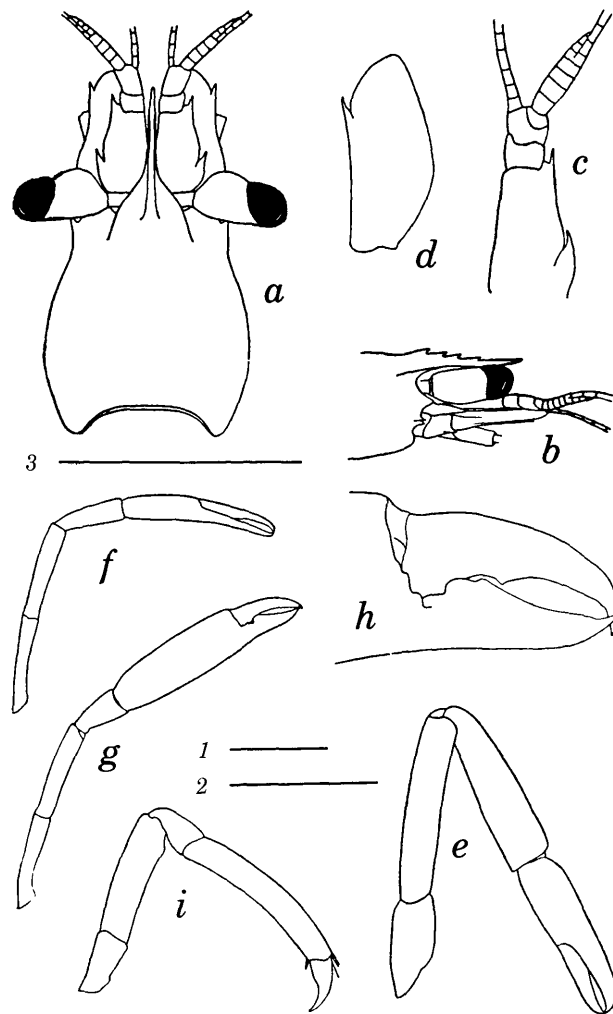


Fig. 53. *Neopontonides beaufortensis* (Borradaile). Anterior part of body in a, dorsal view, b, lateral view; c, antennule; d, antennal scale; e, first leg; f, smaller second leg; g, larger second leg; h, fingers of larger second leg; i, third leg. Scales: 1(b) = 1 mm, (c-d, f-g, i) = 0.5 mm, (e) = 0.33 mm; 2(a) = 1 mm; 3(h) = 0.5 mm (from Holthuis 1951a).

posterior border, intermediate pair less than twice length of inner pair. Uropods elongate; outer margin of exopod ending in tooth flanked mesially by movable spine.

Measurements in mm.—Length of body: male 9; ovigerous females 7 to 10.

Variation.—In young specimens, the legs are relatively shorter than in adults, and the larger second leg resembles the smaller second leg of adults.

Color.—At Beaufort, N. C., Patton (1972) observed females bearing yellow and red chromatophores located in ventral half of main portion of body; by differential expansion of pigments, animals match yellow or orange color of host *Leptogorgia*. Males basically transparent, although containing some of same pigments.

Habitat.—This species is found in coastal waters

where it lives in association with gorgonian coral, *Leptogorgia virgulata*; surface to a few meters. It also has been noted on the octocoral, *Eunicea tourneforti*, in the Dutch West Indies (Criales 1980).

Type-locality.—Beaufort, N. C.

Known range.—Beaufort, N. C., to Grand Isle, La. (Dawson 1963); Caledonia Bay, Panama; Antigua.

Remarks.—*Neopontonides beaufortensis* is one of the commensals living on *L. virgulata*. The shrimp usually rests motionless on the coral with walking legs wrapped around a branch, the propodus of each leg somewhat bowed outward to facilitate grasp (Patten 1972), but it is capable of rapid movement. Scavengers feeding mainly on material on the surface of the host or from inside extended polyps,

starved individuals placed on a piece of the coral soon fill the stomach with spicules, mucus, and other surface material in a flurry of activity; occasionally they will stretch out to pick at sediment or briefly leave the host to feed. They feed with the first legs, and to some degree with the fourth legs; the large second legs rarely go to mouthparts, and seem to be used mainly in aggressive behavior.

Ovigerous females have been taken in Bogue Sound near Beaufort Inlet, N. C., in August and November; in Panama in April, and in Antigua in May.

Genus *Periclimenaeus* Borradaile 1915

Holthuis 1951a:76.—Hemming 1958b:159.

Key to Species

1. Antennal scale with no terminal tooth *P. schmitti*
- Antennal scale with terminal tooth *P. wilsoni*

Periclimenaeus schmitti Holthuis

Fig. 54

Periclimenaeus schmitti Holthuis 1951a:90, pl. 27, figs. a-m.—Williams 1965:45, fig. 37.—Chace 1972:29.

Recognition characters.—Rostrum short, straight, or somewhat decurved, not reaching to end of basal article of antennular peduncle; upper margin bearing 1 or 2 teeth, exclusive of upturned tip; lower margin convex, unarmed. Carapace smooth; post-orbital ridge paralleling orbit, extending from strong antennal spine dorsally and becoming gradually obsolete; anterolateral angle broadly rounded, produced forward. Eyes well developed, cornea globular, shorter and narrower than eyestalks. Basal article of antennular peduncle with short, broad, blunt-tipped stylocerite reaching about to middle of article; outer margin with blunt angle at level of stylocerite tip, concave beyond angle, anterolateral angle of article with rather large tooth; second and third articles short; upper antennular flagellum with 3 fused joints, free part of short ramus with 1 short joint. Antennal scale broadly ovate; outer margin nearly straight, with no terminal tooth.

First leg with carpus and chela extending beyond antennal scale; chela slender, fingers $\frac{2}{3}$ length of palm, unarmed, carpus about as long as chela, slightly shorter than merus. Second legs unequal, both reaching with chela and part of carpus beyond antennal scale. Larger second leg heavy, fingers slightly less than half as long as palm, inwardly curved; upper margin of dactyl broadly

rounded, cutting edge finely denticulate distally, with large rectangular-shaped tooth fitting into pit on fixed finger when closed; fixed finger with strong, narrow tooth at inner margin of pit; palm

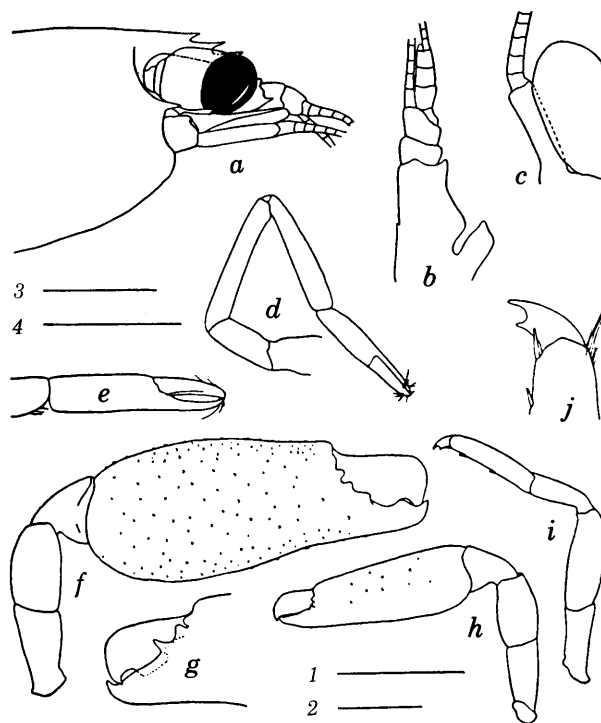


Fig. 54. *Periclimenaeus schmitti* Holthuis. a, Anterior part of body in lateral view; b, antennule; c, antenna; d, first leg; e, chela of first leg; f, larger second leg, outside; g, fingers of larger second leg, inside; h, smaller second leg; i, third leg; j, dactyl of third leg. Scales: 1(a)=1 mm, (e)=0.5 mm; 2(b-d)=0.5 mm; 3(f-i)=1 mm; 4(j)=0.33 mm (from Holthuis 1951a).

swollen, covered with number of small scalelike tubercles; carpus conical, about $\frac{1}{4}$ length of palm; merus about $\frac{1}{3}$ length of palm, sometimes with small tubercles at lower edge. Smaller second leg with fingers straight, slightly shorter than $\frac{1}{3}$ length of palm; cutting edge of dactyl denticulate throughout, that of fixed finger straight; tubercles on palm fewer than on opposite member. Third leg with propodus and part of carpus reaching beyond antennal scale, dactyl short, distinctly bifurcate.

Abdomen smooth; pleura of first 5 segments rounded; sixth segment about as long as fifth and about $\frac{2}{3}$ length of telson. Telson with 2 pairs of small dorsal spines somewhat removed from lateral margin, placed at $\frac{1}{3}$ and $\frac{2}{3}$ length; 6 spines on posterior margin placed in row, intermediate spines longest. Uropods broadly ovate, exopod with outer margin ending in tooth flanked mesially by movable spine.

Measurements in mm.—Length of body: ovigerous females 8–10 (erroneously 20 in Williams 1965).

Variation.—Specimens with a single rostral tooth are young.

Color.—Specimens preserved a few days in 10% formalin and one day in 40% isopropanol: scattered small reddish chromatophores on body and limbs, background yellowish white.

Habitat.—Shallow water.

Type-locality.—Tortugas, Fla.

Known range.—Bogue Sound, Black Rocks off New River, and Lockwoods Folly River, N. C.; Tortugas, Fla.

Remarks.—Two specimens from North Carolina were taken August 16, 1957, in a nighttime surface plankton tow on flood tide near Beaufort Inlet. Though these have intermediate spines on the telson longer than the other terminal pairs, they agree well with specimens of *P. schmitti* from Tortugas. A third specimen (color notes above) was taken in nocturnal plankton from Lockwoods Folly River on flood tide in December.

Ovigerous females are known in July and August from North Carolina, and August at Tortugas.

Periclimenaeus wilsoni (Hay)

Fig. 55

Coralliocaris wilsoni Hay 1917:71.—Hay and Shore 1918:394, text-fig. 13; pl. 27, fig. 8.

Periclimenaeus wilsoni.—Holthuis 1951a:103, pl. 31, figs. a-m; pl. 32, figs. b-c.—Williams 1965:46, fig. 38.—Chace 1972:29.

Recognition characters.—Rostrum nearly straight

or somewhat decurved, almost reaching end of antennular peduncle; upper margin somewhat convex, bearing 10–12 regularly spaced teeth, first tooth directly over or immediately behind orbital margin; lower margin straight or concave, unarmed. Carapace smooth with only an antennal spine placed close to acute lower orbital angle; postorbital ridge paralleling orbit indistinct; anterolateral angle somewhat anteriorly produced, broadly rounded. Eyes well developed. Stylocerite of antennular peduncle broad, short, and pointed, almost reaching middle of basal article; outer margin of basal article with blunt angle near tip of stylocerite, concave beyond angle, ending in strong tooth; second and third antennular articles about same size; upper antennular flagellum with 6 to 9 fused joints; free part of short ramus with 2 joints. Antennal scale a little longer than antennal peduncle; outer margin straight, ending in small spine; lamella broadest proximally.

First legs with carpus and chela extending be-

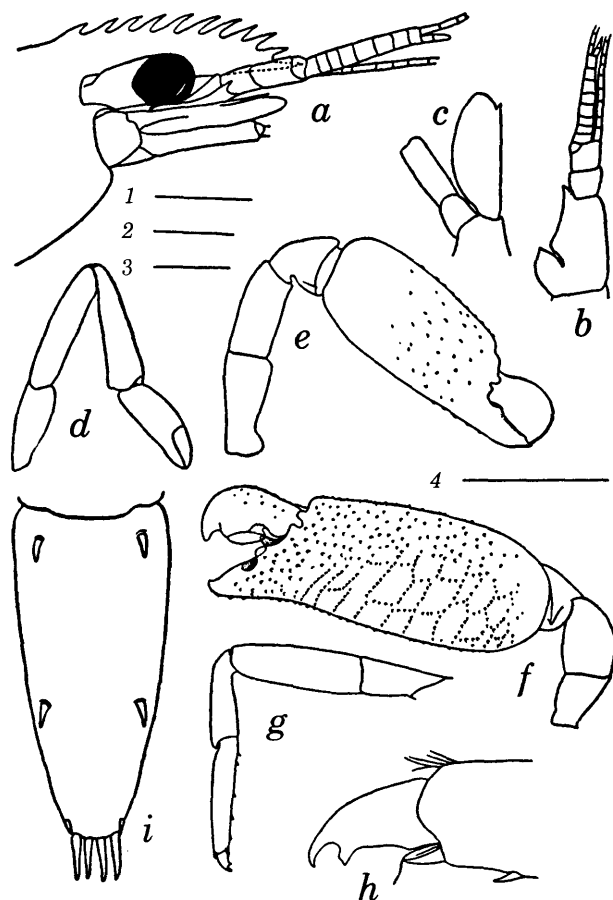


Fig. 55. *Periclimenaeus wilsoni* (Hay). a, Anterior part of body in lateral view; b, antennule; c, antenna; d, first leg; e, smaller second leg; f, larger second leg; g, third leg; h, dactyl of third leg; i, telson in dorsal view. Scales: 1(a) = 1 mm, (h) = 0.2 mm; 2(b-e, g) = 1 mm; 3(f) = 2 mm; 4(i) = 1 mm (from Holthuis 1951a).

yond tip of antennal scale; chela rather thickset; fingers shorter than palm, unarmed; carpus about as long as merus. Second legs strong, unequal, with part of carpus and chela extending beyond tip of antennal scale. Larger second legs with chela almost equal to bulk of body; fingers inwardly curved, somewhat less than half length of palm; dactyl with upper margin convex, cutting edge with large rectangular tooth fitting into pit on fixed finger when closed; fixed finger with distinct tooth at inner margin of pit; palm swollen, tuberculate at base and on base of fingers, tubercles on proximal lower part of palm arranged in rows or honeycomb pattern; carpus smooth, short, cup-shaped; merus about $\frac{1}{3}$ length of palm. Smaller second leg much as larger one in general shape; palm somewhat swollen, with scattered tubercles anteriorly. Third leg with greater part of propodus reaching beyond tip of antennal scale; dactyl short, broad, bifurcate.

Abdomen smooth; pleura of first 5 segments broadly rounded; sixth segment half length of telson. Telson with 2 pairs of dorsal spines somewhat removed from lateral margin; anterior pair close to anterior margin; posterior pair slightly behind midlength; posterior margin with 3 pairs of spines, outer pair short and located in advance of larger intermediate and inner pairs. Uropods broadly ovate, outer margin of exopod ending in tooth flanked mesially by movable spine.

Measurements in mm.—Length of body: male 20;

ovigerous females 16 to 20.

Variation.—Juveniles may have a shorter rostrum with fewer dorsal teeth, and in some specimens the second chelae may be smooth.

Color.—Clear, milky white; integument so transparent that color of internal organs is plainly visible; egg masses light bluish green.

Habitat.—This species is known to live in sponges in coastal waters in company with *Synalpheus longicarpus* and *S. townsendi*; 18 to 73 m.

Type-locality.—Fishing grounds, 20 miles off Beaufort Inlet, N. C.

Known range.—Off Beaufort, N. C.; off Sapelo Island, Ga.; off Loggerhead Key, near Tortugas, and Franklin County, Fla.

Remarks.—Ovigerous females have been reported from Florida in July and North Carolina in August, and are known from Georgia in August. Gurney and Lebour (1941) described the last larval stage of a shrimp doubtfully referred to *P. wilsoni*.

When disturbed, the animals are able to make a snapping sound with the large chela that is quite as loud as that made by one of the true snapping shrimps.

Genus *Periclimenes* Costa 1844

Holthuis 1951a:23.—Hemming 1958b:159.—Chace 1972:29.

Key to Species

(Adapted from Chace 1972)

1. Carapace without antennal spine below suborbital lobe *P. longicaudatus*
Carapace with antennal spine below suborbital lobe 2
2. Pleuron of fifth abdominal segment with posteroventral angle pointed *P. americanus*
Pleuron of fifth abdominal segment with posteroventral angle rounded. 3
3. Third abdominal segment sometimes moderately produced posteromesially but never into laterally compressed hump; rostrum proper with dorsal teeth noticeably raised into an arch *P. iridescens*
Third abdominal segment strongly produced posteromesially into laterally compressed hump; rostrum proper with dorsal teeth not raised into an arch, slender and attenuated in female *P. pedersoni*

Periclimenes americanus (Kingsley)

Fig. 56

Anchistia americana Kingsley 1878b:96.

Periclimenes (Harpilius) americanus.—Holthuis 1951a:60, pl. 18, figs. a-j; pl. 19, figs. a-e.—Williams 1965:43, fig. 36.

Periclimenes americanus.—Chace 1972:31.—Coelho and Ramos 1972:147.—Pequegnat and Ray 1974:253, fig. 65.

Recognition characters.—Rostrum rather high and straight; tip directed upward, reaching about to end of antennular peduncle; upper margin nearly straight, with 7–10 teeth, first 2 behind orbit and

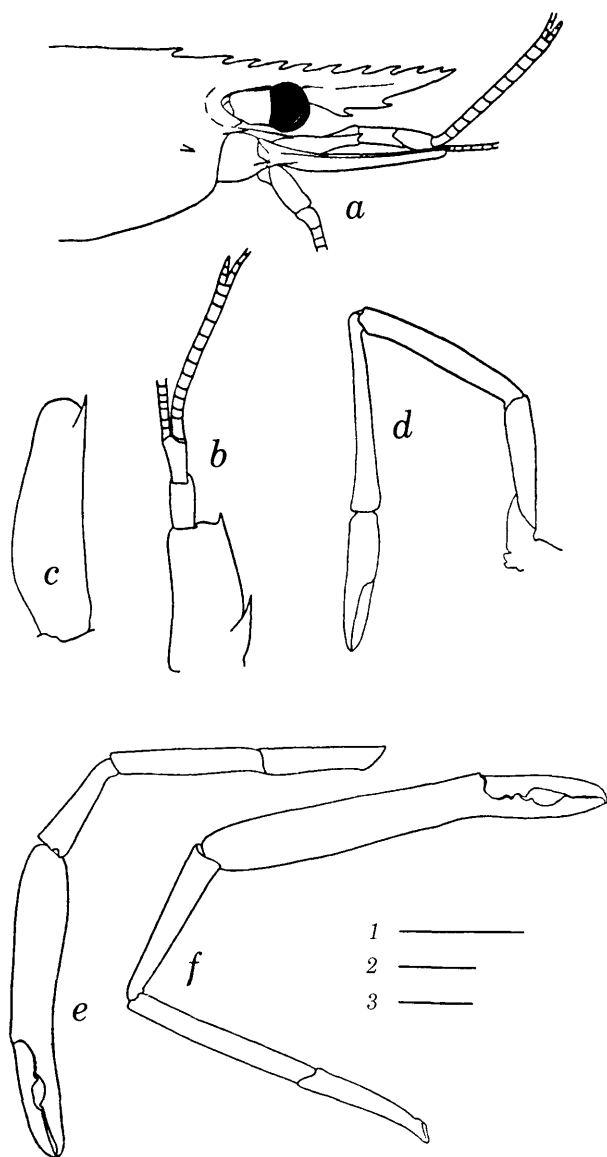


Fig. 56. *Periclimenes americanus* (Kingsley). a, Anterior part of body in lateral view; b, antennule; c, antennal scale; d, first leg; e-f, second leg (different specimens). Scales: 1(a)=1 mm; 2(b-c)=1 mm, (d)=1.3 mm; 3(e-f)=2 mm (from Holthuis 1951a).

considerably separated; lower margin with 2, sometimes 3 teeth, but unarmed stretch before tip. Carapace with only antennal and hepatic spines; lower orbital angle acute; postorbital ridge paralleling orbit; anterolateral angle broadly rounded. Eyes well developed; cornea globular, 2 dark-colored bands visible on cornea in fresh material; ocellus present. Stylocerite rather strong, sharply pointed, almost reaching middle of basal antennular article; outer margin of basal antennular article convex, ending in well-developed anterolateral tooth; second and third articles elongate, second slightly shorter than third; upper antennular fla-

gellum with 2 rami fused for 8–12 joints (often 6 in younger specimens), free part of shorter ramus with 3 or 4 joints, length less than $\frac{1}{4}$ that of fused part. Antennal scale slightly exceeding antennular peduncle, outer margin straight or slightly concave and ending in strong tooth slightly exceeding distally narrowed lamella; scale with distinct spine near base; antennal peduncle not reaching to middle of scale. All maxillipeds with well-developed exopods.

First legs slender; chela and sometimes small portion of carpus extending beyond antennal scale; fingers smooth, as long as palm. Second legs equal in size and shape, very strong and longer than first; adult males with fingers less than half as long as palm, 3 or 4 teeth on cutting edges leaving gape at midlength when closed; second legs shorter and fingers not agape in juveniles and adult females.

Abdomen with pleura of first 4 segments rounded, of fifth ending in small tooth; median posterior margin of third only slightly produced posteriorly. Sixth segment about 1.5 times as long as fifth and about $\frac{3}{4}$ length of telson. Telson with 2 dorsal pairs of spines at $\frac{1}{3}$ and $\frac{2}{3}$ length; posterior margin with 3 pairs of spines, intermediate pair less than twice length of inner spines.

Measurements in mm.—Length of body: male 22; ovigerous females 13 to 20.

Variation.—The carpus of the second pair of legs varies in length as do the dactyls of the last three pairs of legs.

Color.—Ground color translucent grayish white; carapace with three oblique orange-brown lateral lines and pair of dorsal lines running back from base of rostrum; each abdominal segment crossed by narrow brown band and row of small dark spots on posterior margin; tail fan with two larger lateral and median spots and an orange-brown tip (Verrill 1922).

Habitat.—This species lives in coastal waters, preferring sandy or rocky bottom, often between algae or coral, or among turtle grass or debris. Verrill (1922) found large schools near the surface in Bermuda, and Gurney (1943a) found it to swim singly or in small numbers at the surface at night in certain periods of the lunar cycle (see Holthuis 1951a). Shallow water to 73 m.

Type-locality.—Key West, Fla.

Known range.—Beaufort, N. C.; to western Gulf of Mexico (Felder and Chaney 1979), and through West Indies to Aruba; Pará to São Paulo, Brazil (Coelho and Ramos 1972).

Remarks.—Gurney (1943a) listed this species as one of the commonest decapod crustaceans in the littoral region of Bermuda. Females outnumbered males two to one; however, ovigerous females were

never collected there. From plankton, Gurney (1936c, 1943a) described the first and fifth larval, and the first postlarval stages, and gave remarks on allometric growth of the second legs. These legs are stronger and longer in males than in females, with fingers agape in old males. The center of greatest growth is in the palm.

Ovigerous females have been found virtually year round in southwestern Florida (Rouse 1970) where the species endures a temperature range of 12° to 34°C and salinities of 15 to 61‰; a long breeding season is indicated for other parts of the range.

Holthuis (1951a) listed *P. americanus* as common in North Carolina, but it has seldom been taken in surface plankton tows in Bogue Sound that have produced hundreds of *P. longicaudatus*.

Periclimenes iridescens Lebour

Fig. 57

Periclimenes iridescens Lebour 1949:1112, figs. 4–5.—Chace 1972:37.

Periclimenes (*Periclimenes*) *iridescens*.—Holthuis 1951a:43, pl. 12; pl. 20, figs. i–j.

Recognition characters.—Rostrum straight, short, rather high, reaching along length of second article of antennular peduncle; upper margin somewhat convex and bearing 5 to 7 teeth, 1 or 2 of these placed behind orbit on carapace and wider apart than others; tip of rostrum often unarmed; lower margin with 0–3 teeth, extremely small if present; lateral carina near lower margin. Carapace lacking postorbital ridge; lower orbital angle produced into blunt lobe somewhat constricted at base; antennal and hepatic spines about same size, no supraorbital spine present; anterolateral angle broadly rounded. Eyes well developed, cornea globular, ocellus present. Stylocerite not reaching to midlength of basal antennular article, slender and sharply pointed; lateral margin of article slightly sinuous, ending in strong tooth extending about as far forward as sinuous distal margin; second and third articles about equal in length; upper flagellum with 2 rami fused for 6 or 7 joints. Antennal scale with outer margin somewhat concave, ending in distal tooth overreached by lamella; antennal peduncle reaching almost to middle of scale, distinct outer spine near base of scale. All maxillipeds with well-developed exopods.

First legs slender, not reaching end of antennal scale; second legs unequal, part of palm reaching beyond antennal scale; fingers of larger chela 0.5 to 0.8 times length of palm and armed with 2 teeth on cutting edge, those of smaller chela slightly

longer or shorter than palm, slender and unarmed. Dactyls of last 3 legs simple or bifid.

Abdomen smooth; all pleura rounded. Third segment slightly produced posteromesially but not forming hump. Sixth segment about twice length of fifth and slightly longer than telson. Telson with 2 pairs of minute dorsal spinules at mid and $\frac{3}{4}$ length; posterior margin with 3 pairs of spines, intermediate pair longer than inner pair.

Measurements in mm.—Length of body: ovigerous females 14–15 (Holthuis 1951b).

Habitat.—Sand and algae; reported on both octocorals and antipatharians in Curaçao and Bonaire (Criales 1980); 3.6 to 183 m.

Type-locality.—Off Castle Roads, Bermuda.

Known range.—Northeast off Cape Hatteras, 35°32.9'N, 75°11.9'W (Herbst, et al. 1979); southern and northwestern Florida; Tobago; Cubagua Island, Venezuela; Bermuda (Chace 1972).

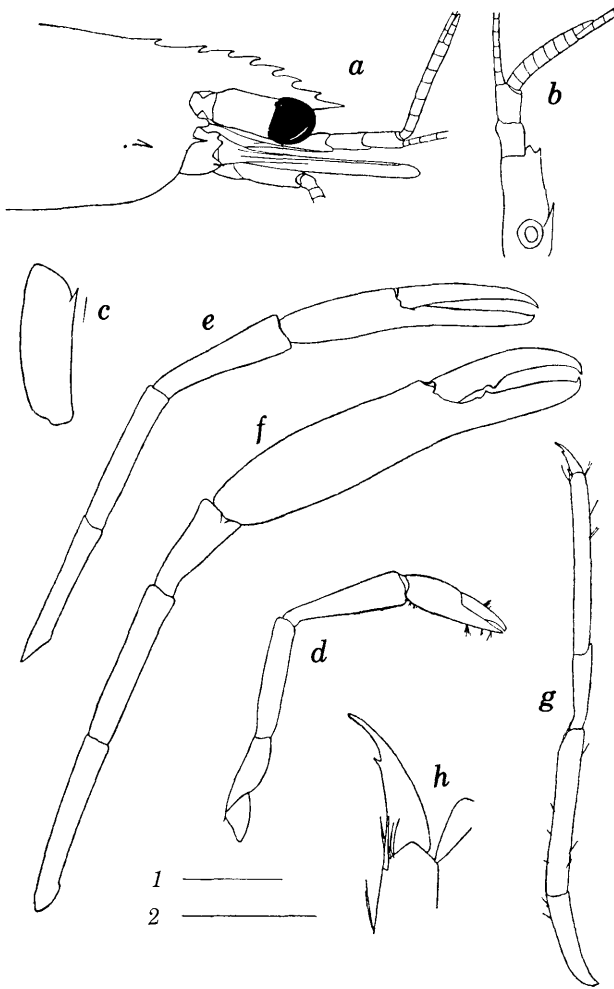


Fig. 57. *Periclimenes iridescens* Lebour. a, Anterior part of body in lateral view; b, antennule; c, antennal scale; d, first leg; e, smaller second leg; f, larger second leg; g, third leg; h, dactyl of third leg. Scales: 1(a) = 1 mm, (b–c) = 1.2 mm, (h) = 0.2 mm; 2(d–g) = 1 mm (from Holthuis 1951a).

Remarks.—The distribution of this tiny shrimp is questionable in some details. Herbst, et al. (1979) cited a record off Panama City, Fla., that was erroneously attributed to Chace (1972), but specimens in two lots from there questionably referred to this species by him are in the USNM along with others from Key West. Some of the Panama City specimens seem to have more slender posterior abdominal segments than the remainder of specimens in four lots, but with such meager material, range of variation cannot be assessed.

From an ovigerous female taken at the type-locality, Lebour (1949) maintained eggs until hatching and described the first larval stage.

***Periclimenes longicaudatus* (Stimpson)**

Fig. 58

Urocaris longicaudata Stimpson 1860:39.—Hay and Shore 1918:394, pl. 27, fig. 7.

Periclimenes (*Periclimenes*) *longicaudatus*.—Holthuis 1951a:26, pl. 6, figs. a-m; pl. 8, fig. m.—Williams 1965:42, fig. 35.

Periclimenes longicaudatus.—Chace 1972:37.—Coelho and Ramos 1972:147.

Recognition characters.—Rostrum straight, short, reaching to end of second or third article of antennular peduncle; upper margin raised into high arcuate crest with 7 to 9 teeth, first 2 teeth behind orbit more widely spaced than distal teeth; lower margin with 1 or 2 small spines near tip. Carapace with lower angle of orbit produced into lobe con-

stricted at base; supraorbital and antennal spines absent; anterolateral angle rounded. Eyes well developed and elongate. Stylocerite well developed but not reaching to middle of basal antennular article; basal antennular article convex and ending in strong spine; upper antennular flagella with 2 rami fused for 4 to 8 joints. Antennal scale with outer margin slightly concave, ending in strong tooth exceeded distally by lamella; antennal peduncle reaching almost to middle of scale, with distinct outer spine near base of scale. All maxillipeds with well-developed exopods.

First legs slender, reaching almost to end of antennal scale; second legs equal in size and shape, stronger and longer than first legs.

Abdomen smooth; all pleura rounded. Third segment somewhat produced in middle of posterior margin. Sixth segment twice length of fifth and longer than telson. Telson with 2 pairs of dorsal spines both lying behind middle; posterior margin with 3 pairs of spinules.

Measurements in mm.—Length of body: male 17; ovigerous females 15 to 22.

Color.—Body transparent in life.

Habitat.—This species is found in abundance on submerged vegetation along with *Hippolyte* species and *Tozeuma carolinense*, on *Leptogorgia*, algae and *Sargassum*, among turtle grass and *Porites* (Chace 1972), or from sponges (Schmitt 1924b); however, it is hard to detect because of its almost perfect transparency. Surface to 27 m.

Type-locality.—Coast of Carolina.

Known range.—Cape Hatteras, N. C., to southwestern Florida; West Indies to São Paulo, Brazil. There are doubtful records from the Indian Ocean and deeper waters of the Gulf of Mexico (Holthuis 1951a).

Remarks.—This species is abundant in the Beaufort, N. C., area, and has been collected there throughout the year. Ovigerous females have been found from May through October. Rouse (1970) found this to be the most common caridean in southwestern Florida, next to *Tozeuma carolinense*; it occurred in a temperature range of 12° to 34°C, and salinities of 15 to 55‰. He found ovigerous females from September to April, but they were never common (see also Tabb and Manning 1961). They occur in Cuba in January and March (Schmitt 1924b) and in Texas in May. Pearse and Williams (1951) found the form on reefs off the North Carolina coast along with an unidentified *Periclimenes*. Last larval, postlarval, and early juvenile stages doubtfully assigned to this species were described by Gurney and Lebour (1941) from Bermuda.

Periclimenes longicaudatus is one of the decapods eaten by the spotted and southern hakes, *Urophycis*

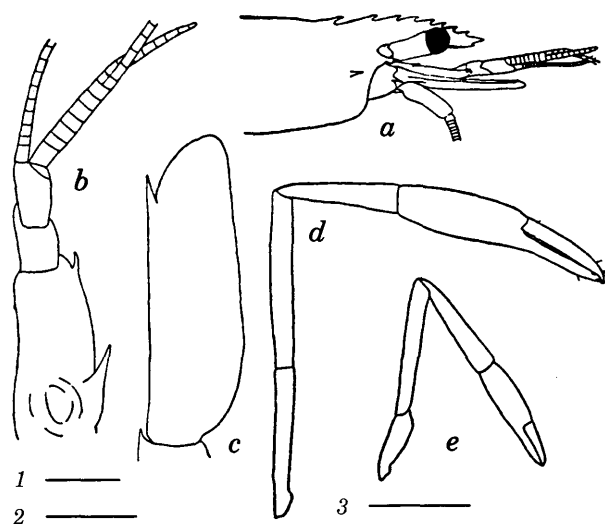


Fig. 58. *Periclimenes longicaudatus* (Stimpson). a, Anterior part of body in lateral view; b, antennule; c, antennal scale; d, first leg; e, second leg. Scales: 1(a) = 2 mm; 2(b-c) = 1 mm; 3(d-e) = 1 mm (from Holthuis 1951a).

regius and *floridanus*, in Georgia estuaries (Sikora, et al. 1972).

***Periclimenes pedersoni* Chace**

Fig. 59

Periclimenes (*Periclimenes*) *pedersoni* Chace 1958:125, figs. 1–17.—Limbaugh, Pederson, and Chace 1961:242, figs. 3–4.

Periclimenes pedersoni.—Chace 1972:38.

Recognition characters.—Carapace of male narrowed and bent upward in anterior $\frac{2}{3}$; rostrum directed obliquely upward, scarcely reaching base of cornea in adult; dorsal margin with 3–5 teeth, posterior tooth somewhat anterior to level of hepatic spine, next anterior tooth at about level of orbital margin; unarmed ventrally. Carapace of adult female not bent upward anteriorly; rostrum attenuate, nearly horizontal, reaching to or beyond second article of antennular peduncle; dorsal margin with 5–6 teeth, posterior tooth about at level of hepatic spine, next anterior tooth just behind orbital margin, remainder at decreasing intervals; 2–4 ventral teeth. Antennal spine small; lower antennal angle blunt and strongly produced. Eyes well developed, cornea subglobular. Stylocerite divergent, not reaching beyond middle of eyestalk; basal article of antennular peduncle slightly concave laterally, distolateral tooth not exceeding acutely produced anterior margin (except in juveniles); second article slightly shorter and broader than third; upper antennular flagellum with 2 rami fused for 12–18 joints, free part of shorter ramus $\frac{1}{4}$ – $\frac{1}{3}$ length of fused part. Antennal scale about as long as antennular peduncle; length over 2.5 times width in males, slightly broader in females, outer margin nearly straight and ending in spine far exceeded by variably subtruncate lamella; antennal peduncle reaching to or beyond middle of scale.

First legs slender, reaching beyond antennal scale by length of finger or entire hand in males, and by at least $\frac{1}{3}$ of carpus in females; fingers as long as palm, carpus longer than chela. Second legs unequal, especially in males. Larger overreaching antennal scale by chela and from $\frac{1}{3}$ to more than $\frac{2}{3}$ carpus, fingers about $\frac{2}{3}$ length of palm; dactyl triangular in cross section, cutting edge with 2–5, of fixed finger with 1–4 denticles in proximal half. Smaller overreaching antennal scale by chela or $\frac{1}{3}$ of carpus; fingers more than $\frac{3}{4}$ length of palm, cutting edges with fewer denticles.

Abdomen with pleura rounded; third segment strongly produced posteromesially into laterally compressed hump. Sixth segment of male nearly

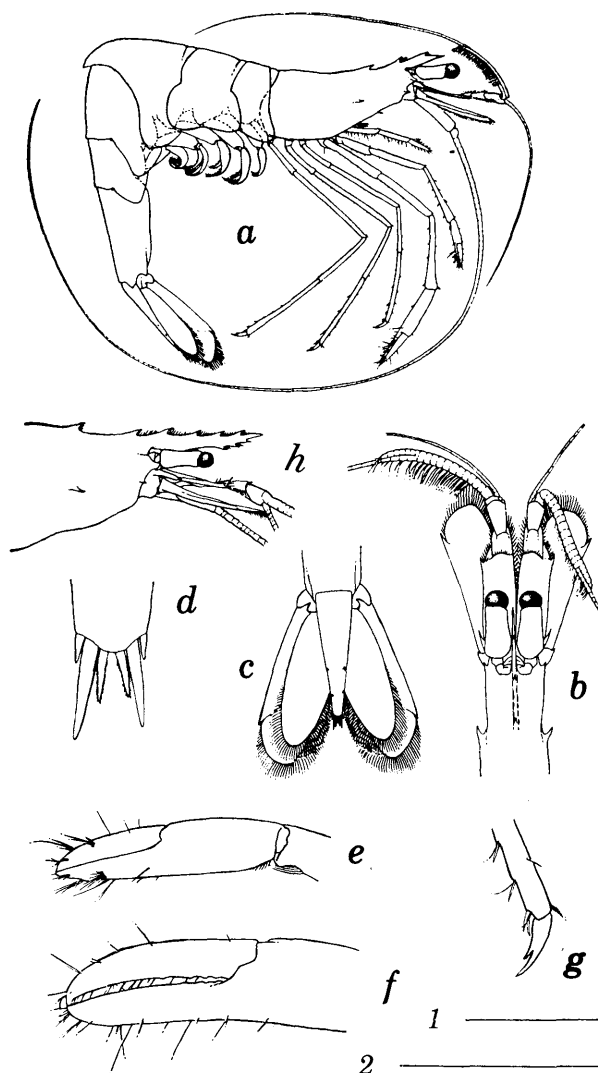


Fig. 59. *Periclimenes pedersoni* Chace. Male: a, lateral view; b, anterior part of body, dorsal; c, tail fan; d, tip of telson; e, chela of right first leg; f, fingers of right second leg; g, dactyl of right third leg. Female: h, anterior part of body in lateral view. Scales: 1(a, h) = 5 mm, (d) = 0.5 mm, (e–g) = 1 mm; 2(b–c) = 5 mm (from Chace 1958).

twice length of fifth and longer than telson; that of female usually less than twice length of fifth and shorter than telson. Telson with 2 dorsal and 3 posterior pairs of spinules, both dorsal pairs posterior to midlength.

Measurements in mm.—Length of carapace: male 4.6; female 6.5, may be ovigerous at 3.8 (Chace 1958).

Color.—Variable. Body transparent; longitudinal white line at each side running posteriorly from bases of third maxillipeds to converge dorsally near posterior margin of third abdominal segment. Back of abdomen between lines crowded with irregularly sized violet spots. Outside white lines on each side of posterior half of third segment, two or three

similar small spots of violet followed by large, triangular violet patch edged with white. Fourth and fifth segments each with usually two median spots, others laterally, and about four or five spots diverging posteriorly on either side of midline of sixth. Sometimes a white stripe in dorsal midline of sixth segment as well as near posterior part of preceding two segments. Telson with about three median spots, a transverse bar of violet and a white tip. Uropods tipped with blue violet outlined proximally and laterally with white, and few violet spots near bases. White line on ventral surface of body from base of walking legs to telson. Eyestalks transparent with purple and sometimes a white line below. Two small white dots on either side of rostrum. Outer antennular flagella white from base, inner transparent; antennal flagella mostly opaque white, transparent basally. Third maxillipeds and first and second legs banded with purple and white, brown saddle on inner surface at base of palm and on basal half of carpus. Walking legs translucent pale violet. A color variety off west Florida differs somewhat from Caribbean and Bahamian specimens. (Paraphrased from Chace 1958; Limbaugh, et al. 1961.)

Habitat.—Usually associated with the sea anemone *Bartholomea annulata*; North Carolina specimens taken in a trawl were entangled in an algal mat; seen walking about on coral reef, away from anemones in Belize (B. Kensley, personal communication); 1.5 to 35 m.

Type-locality.—Simms (Lyford) Cay, New Providence Island, Bahamas.

Known range.—East of Cape Lookout, N. C., 34°35.5'N, 75°05.5'W (Herbst, et al. 1979); off northwest Florida (?), Bahamas, through West Indies to Bonaire; Belize.

Remarks.—Limbaugh, et al. (1961) found this

species to be usually hanging from or occupying the same hole as the anemone *Bartholomea annulata*, frequently occurring singly, in pairs, or groups of up to five. The associations may last for a period of weeks. The Pederson shrimp is one of the cleaner shrimps, attracting its fish hosts by whipping its antennae and swaying back and forth. Limbaugh, et al. (1961) observed cleaning of 10 species of fishes. The shrimp crawls onto a fish as soon as it comes near and becomes quiet, picking at parasites, removing tissue around parasites, and picking at injured flesh around wounds; it enters the fish's gill cavity as well as the mouth, probably feeding there on bits of food clinging to the gills, but when it reaches satiety it ceases feeding and retires from the fish even though other fishes may remain to be cleaned. Juvenile arrow crabs, *Stenorhynchus seticornis*, a snapping shrimp and other commensals also are associated with this anemone.

Periclimenes pedersoni is very similar to *P. anthophilus* from Bermuda (Chace 1972) which is associated with other anemones. The North Carolina specimens seem closer to *P. pedersoni* although as Chace pointed out, the range of variation in the Bermuda species is not known. Limbaugh, et al. (1961) found *P. pedersoni* off west Florida that were not associated with anemones and that did not clean fishes; these were morphologically similar to West Indian material but slightly different in color.

Ovigerous females of the species are known in March-April from the Virgin Islands, May in Bonaire, and July to September off northwestern Florida.

Genus *Pontonia* Latreille 1829

Holthuis, 1951a:115.—Hemming 1958b:124.

Key to Species

1. Dorsal spines of telson small and rather inconspicuous *P. domestica*
Dorsal spines of telson well developed *P. margarita*

Pontonia domestica Gibbes

Fig. 60

Pontonia domestica Gibbes 1850:196.—Holthuis 1951a:122, pl. 38, figs. a-j.—Williams 1965:47, fig. 39.—Chace 1972:39.

Recognition characters.—Rostrum depressed, rather narrowly triangular, decurved; reaching to second article of antennular peduncle; tip acute in dorsal and lateral view, flat dorsally; inconspicuous lon-

gitudinal carina ventrally; inconspicuous dorsal and ventral tooth near tip with tuft of long hairs between upper tooth and apex. Carapace with lower orbital angle bluntly triangular, strong antennal spine below angle; anterolateral angle broadly rounded and anteriorly produced. Eyes well developed, not reaching laterally to antennal spine. Antennular peduncle with stylocerite broad, bluntly pointed; anterolateral angle of basal article produced forward, rounded; third article longer than second; upper antennular flagellum with 7–10 fused

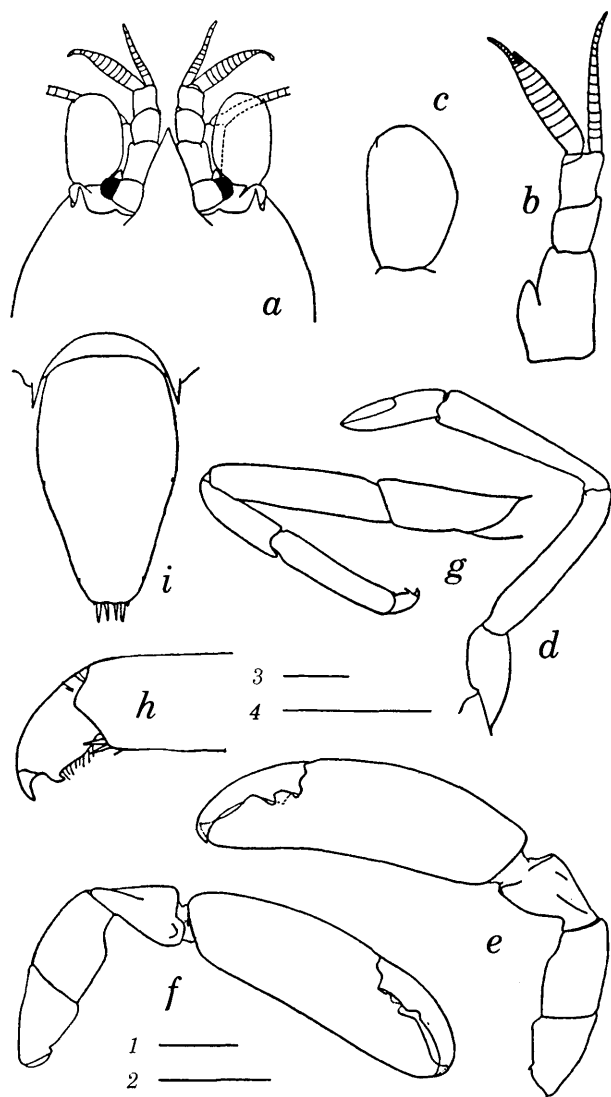


Fig. 60. *Pontonia domestica* Gibbes. a, Anterior part of body in dorsal view; b, antennule; c, antennal scale; d, first leg; e, larger second leg; f, smaller second leg; g, third leg; h, dactyl of third leg; i, telson in dorsal view. Scales: 1(a, d, g)=2 mm, (e-f)=4 mm; 2(b-c)=2 mm; 3(i)=1 mm; 4(h)=1 mm (from Holthuis 1951a).

joints; short ramus with 2–3 joints. Antennal scale broadly oval, outer margin a little convex, terminal tooth small, exceeded by lamella; antennal peduncle reaching beyond middle of scale.

First leg with carpus and chela reaching beyond antennal scale; fingers of chela somewhat longer than palm; carpus as long as merus. Second legs strong, unequal in size and shape; carpus and chela reaching beyond antennal scale. On one leg, fingers about half length of palm; fixed finger somewhat higher than dactyl and bearing 2 large teeth on cutting edge, posterior tooth truncate with crenulate margin; dactyl with 1 tooth, palm with upper and lower margin somewhat compressed,

surface appearing minutely roughened under magnification; carpus short, conical, with depression above and knob below; merus a little longer than carpus. Other second leg much as above but with relatively longer fingers; fixed finger higher in comparison to dactyl; teeth smaller and carpus more slender. Remaining legs with bifurcate dactyls.

Abdomen with first 5 pleura broadly rounded. Sixth segment with pleura and posterolateral angle ending in slender, sharp spines; slightly longer than fifth segment. Telson half again as long as fifth segment; 2 dorsal pairs of spines on lateral margin of telson small, almost invisible; anterior pair about in middle; posterior pair closer to posterior border than to anterior pair; posterior border with 3 pairs of spines in row; inner 2 pairs equal in length, outer pair smaller; uropods broadly ovate, outer margin of exopod ending in blunt angle with small movable spine at tip.

Measurements in mm.—Length of body: male 32; female 33.

Color.—Translucent white.

Habitat.—The species lives commensally in lamellibranch molluscs in coastal waters and has been recorded from *Atrina seminuda*, *A. serrata*, and *Pecten* sp. (Holthuis 1951a), and on 12 April 1971 was taken from the giant Atlantic cockle, *Dinocardium robustum*, off Carteret County, N. C.; shallow water to 42 m.

Type-locality.—South Carolina.

Known range.—Atlantic Beach near Beaufort Inlet, N. C., to Gulf of Mexico S of Houma, Terrebonne Parish, La. (USNM); Bahamas; Madeira.

Remarks.—Brooks and Herrick (1892) illustrated a section through the segmenting egg of *Pontonia domestica* on plate 28.

Pontonia margarita Smith

Fig. 61

Pontonia margarita Smith 1869c:245.—Holthuis 1951a:137, pl. 43, figs. a-i; pl. 44, figs. a-h.—Williams 1965:48, fig. 40.—Chace 1972:39.

Recognition characters—Rostrum depressed and decurved, dorsally flat and triangular; tip reaching to end of basal article of antennular peduncle or slightly beyond; inconspicuous dorsal and ventral tooth near tip with small tuft of hairs between upper tooth and apex; longitudinal median carina ventrally. Carapace smooth; with strong antennal spine located well below narrowly rounded lower orbital angle; anterolateral angle broadly rounded and anteriorly produced. Eyes somewhat larger than in *P. domestica*, reaching laterally beyond antennal

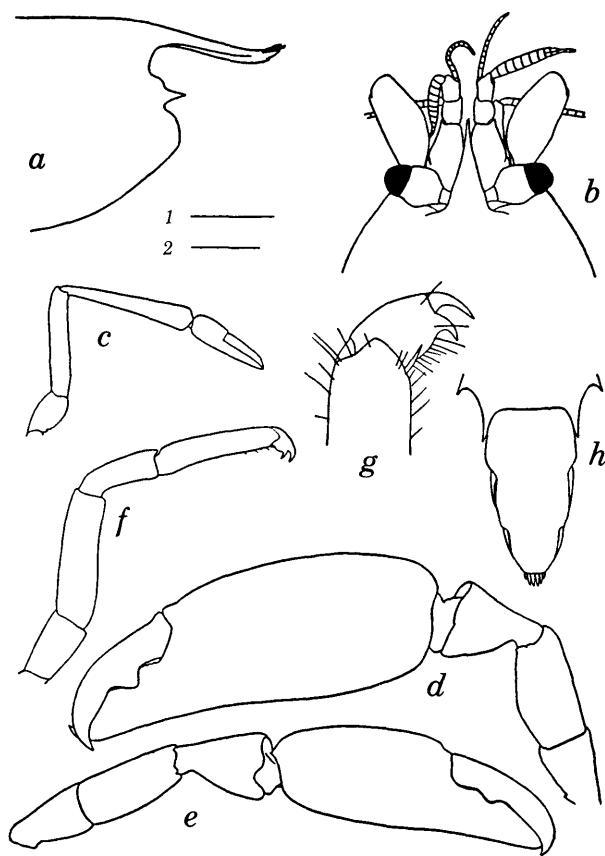


Fig. 61. *Pontonia margarita* Smith. a, Anterior part of carapace in lateral view; b, anterior part of body in dorsal view; c, first leg; d, larger second leg; e, smaller second leg; f, third leg; g, dactyl of third leg; h, telson in dorsal view. Scales: 1(a-b, h)=1 mm, (c-e)=2 mm, (g)=0.17 mm; 2(f)=1 mm (from Holthuis 1951a).

spine. Basal article of antennular peduncle with blunt-pointed stylocerite more or less pressed against outer border; anterolateral angle of article produced forward, rounded; upper antennular flagellum short, thick, curved backward; fused part with 6-7 joints; short ramus with 2 joints. Antennal scale with convex outer margin ending in small inwardly curved distal tooth, lamella far exceeding tooth.

First leg with half or more than half of carpus reaching beyond antennal scale; fingers longer than palm, unarmed carpus longer than merus. Second legs unequal in size but similar in shape. Larger leg with fingers a little over half length of palm; palm twice as long as deep, somewhat inflated; dactyl narrower than fixed finger and bearing large tooth slightly behind middle; cutting edge of fixed finger with 2 large teeth fitting on each side of opposed dactylar tooth and separated by hole on inner side of edge, posterior tooth with denticles at apex; carpus shorter than merus, conical. Smaller second leg resembling larger except for relatively

longer fingers. Dactyls of last 3 walking legs bifurcate.

Abdomen with pleura of first 5 segments broadly rounded, of sixth ending in strong spine overlapping base of uropods. Sixth segment a little more than half length of telson. Telson with pair of large dorsal spines placed laterally at $\frac{1}{3}$ and $\frac{2}{3}$ of length; posterior border with 3 pairs of spines in row, inner 2 pairs equal, outer pair smaller. Uropods broadly ovate, exopods ending in minute movable spine on outer margin.

Measurements in mm.—Length of body: male 19; ovigerous females 17 to 27.

Color.—Glassy, translucent; internal organs clearly visible; ovigerous females with two colors of eggs, one with light, muddy green eggs and ovarian ova of same color, another with pale orange eggs (from specimens taken in *Argopecten gibbus* and *Pteria colymbus* in North Carolina), and in the pearl oyster *Pinctada fimbriata* on the west American coast; tidal flats to 60 m.

Type-locality.—Bay of Panama.

Known range.—Atlantic coast: Drum Inlet to Beaufort Inlet, N. C.; east and west Florida. Pacific coast: Gulf of California to Colombia; Galapagos Islands.

Remarks.—Ovigerous females have been taken in North Carolina in January and April.

Family Gnathophyllidae

Caridea with first 2 pairs of legs chelate, first pair smaller than second; carpus of second pair not subdivided. Rostrum short and toothed. Third article of third maxillipeds very broad. Mandibles simple. Second maxillipeds with short seventh article.

Genus *Gnathophyllum* Latreille 1819

Armstrong 1940:6.—Hemming 1958b:156.

Gnathophyllum modestum Hay

Fig. 62

Gnathophyllum modestum Hay 1917:72.—Hay and Shore 1918:395, pl. 28, fig. 1.—Manning 1963:48, figs. 1-2.—Williams 1965:61, fig. 50.—Chace 1972:53.

Recognition characters.—Body short and thick; carapace with moderate carina continuous in front with rostrum and extending about $\frac{2}{3}$ distance to posterior margin. Rostrum obliquely truncate dorsally and armed with 5-6 dorsal teeth; 1-2 small

ventral teeth near tip; tip reaching to distal end of basal article of antennule. Suborbital angle prominent; antennal spine present; anterolateral angle strongly produced. Eyes rather large and with prominent, conical, black protuberance on cornea. Antennular peduncles with basal article large, stylocerite reaching beyond middle of article, spine at anterolateral corner of article; second article with similar but smaller and blunter anterolateral spine; second and third articles of about equal length; outer antennular flagellum bifurcate, upper ramus longer and thinner than lower ramus. Antennal scale reaching beyond antennular peduncles, lateral margin almost straight, terminating in spine; lamella of scale rounded distally, slightly exceeding spine.

Third maxillipeds with merus and carpus broad, closing whole front of buccal region; 2 terminal articles flattened, much more slender, and extended straight forward. Second pair of legs much stronger than first, exceeding rostrum by length of chela; fingers more than half length of palm. Last 3 pairs of legs with dactyls bifurcate.

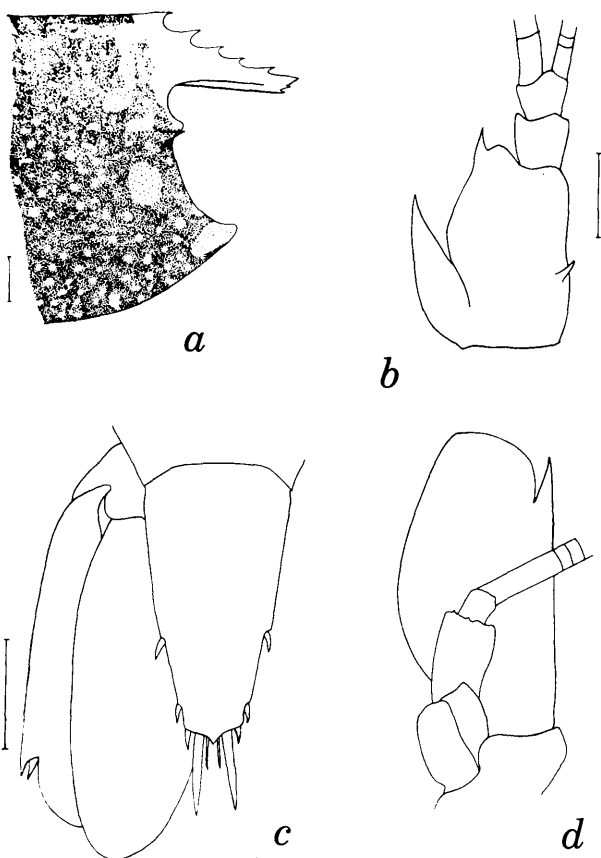


Fig. 62. *Gnathophyllum modestum* Hay. a, Anterior part of carapace in lateral view; b, antennular peduncle in ventral view; c, telson and left uropod; d, antennal scale; 1 mm indicated; b, d to same scale (from Manning 1963).

Abdomen with last 3 segments abruptly smaller than preceding segments and strongly flexed. Telson with pair of marginal spines at about distal third and minute pair near tip, tip with median point and with 3 pairs of spines, intermediate pair longest.

Measurements in mm.—Length of ovigerous holotype female 21.

Color.—Body deep brown with many scattered small yellow and a few larger orange spots; antennal scale, distal portions of rostrum and tail fan clear; orbital margins and eyestalks white; legs grading from brown proximally through purple to white distally but barred with purple on distal portion of some elements; markings of yellow below and on some articles of appendages (Manning 1963).

Habitat.—Found around clumps of coral and sponges in shallow water; to 27 m.

Type-locality.—20 miles SW Beaufort, N. C.

Known range.—Off Beaufort, N. C.; Biscayne Bay, Fla.

Remarks.—This species, long known only from Hay's ovigerous female type-specimen, was reported from Florida by Manning (1963). Manning reviewed the east American species of *Gnathophyllum*, pointing out the close similarity of *G. modestum* to the eastern Atlantic species *G. elegans*, and giving detail on the importance of color patterns in living material as diagnostic characters in the genus. Excellent figures accompany Manning's discussion.

Ovigerous females are known from Florida in June, and North Carolina in August.

Superfamily Alpheoidea

Family Alpheidae

Carapace smooth, with cardiac grooves; rostrum reduced; antennal and branchiostegal spines always absent; carapace almost always projecting over eyes (*Automate* excepted). Antennular base cylindrical, basal article not longer than sum of other 2 articles. Antennal scale rarely longer than antennal peduncle. Mandible bipartite with palp of 2 points. Chela of first leg predominant, always large (usually asymmetrical); carpus short. Second legs weakly developed; carpus multiarticulate. Third to fifth leg with spinous propodi and simple or bifurcate dactyls; propodus of fifth leg with more or less well-developed brush of bristles in transverse to oblique rows. Abdomen usually with gradual curve, no pronounced bend at third segment; sixth segment short, broad, sexually dimorphic. (Adapted from Banner 1953.)

Key to Genera and One Species

1. Movable plate at posterolateral angle of sixth abdominal segment; carapace extended to cover eyes but rostrum absent *Leptalpheus forceps*
No movable plate at posterolateral angle of sixth abdominal segment . . . 2
2. Eyestalks completely exposed *Automate*
Eyestalks covered by carapace 3
3. Epipods present on at least first 2 pairs of legs *Alpheus*
Legs without epipods *Synalpheus*

Genus *Alpheus* Fabricius 1798

Banner 1953:46.—Hemming 1958b:108.

The status of the name *Alpheus* has been stabilized by the International Commission on Zoolog-

ical Nomenclature (Opinion 334). The suppressed generic names *Alpheus* Weber 1795, and *Crangon* Weber 1795 were placed on the Official Index of Rejected and Invalid Generic Names in Zoology (Hemming 1958a).

Key to Species

1. Orbital hoods of carapace with small supramarginal spine in front *A. formosus*
Orbital hoods of carapace without distinct spine 2
2. Orbital hoods forming anterior toothlike marginal projection; large chela with groove above and below along outer margin, between these grooves a thick tooth *A. normanni*
Orbital hoods rounded anteriorly; large chela broad, notched on both margins 3
3. Base of rostrum passing gradually into dorsolateral surface of carapace; merus of first legs unarmed distoventrally *A. heterochaelis*
Base of rostrum usually with borders sharply defined; merus of first legs armed with distoventral spine *A. armillatus*

Alpheus armillatus H. Milne Edwards

(Banded snapping shrimp)

Fig. 63

Alpheus armillatus H. Milne Edwards 1837:354.—Verrill 1922:73, text-figs. 5a, 6b; pl. 20, fig. 4b; pl. 21, figs. 4, 4a; pl. 26, figs. 1–1d; pl. 23, fig. 4; pl. 27, figs. 1–1s.—Williams 1965:67, fig. 55.—Chace 1972:63.

Crangon armillatus.—Hay and Shore 1918:386, text-fig. 9; pl. 27, fig. 1.—Schmitt 1935a:142.

Recognition characters.—Rostrum in form of narrow raised crest from base to tip, projecting beyond orbital hoods, widening abruptly just behind eyes into triangular area with borders slightly concave and distinctly limiting rostro-orbital depressions, slightly overhanging depressions in adults. Carapace compressed; orbital hoods prominent in front, with slight obtuse anterior lobe but without spine or denticle, and with strong emargination below eyes. Eyes entirely covered by carapace. An-

tennules with stylocerite large, scalelike, not very acute, and not reaching to end of basal antennular article; second article longer than third; inner flagellum filiform; outer flagellum thickened in about proximal half. Antennal scale with strong terminal spine equal to or extending beyond antennal peduncle, scale distinctly curved outward in distal $\frac{2}{3}$; a small spine (basicerite) near base of scale. Third maxilliped covered with long hairs distally, reaching about to end of antennal peduncle.

First legs strongly chelate, hairy, unequal; merus armed distoventrally. Larger chela thick; outer and inner margin deeply notched near base of finger; upper and lower surfaces with irregular shallow grooves; dactyl broad, heavy, curved, with large basal tooth. Small chela slender; cutting edges of fingers closely fitting, dactyl with small tooth at base, dactyl in males lacking setose crests and expanded external surface characteristic of *A. heterochaelis*. Second legs long, slender, weakly chelate, with part of merus reaching beyond rostrum; carpus subdivided with joints diminishing in length as follows (numbered from proximal end): 1, 2, 5, 3–4. Third to fifth legs with simple dactyls, not subspatulate.

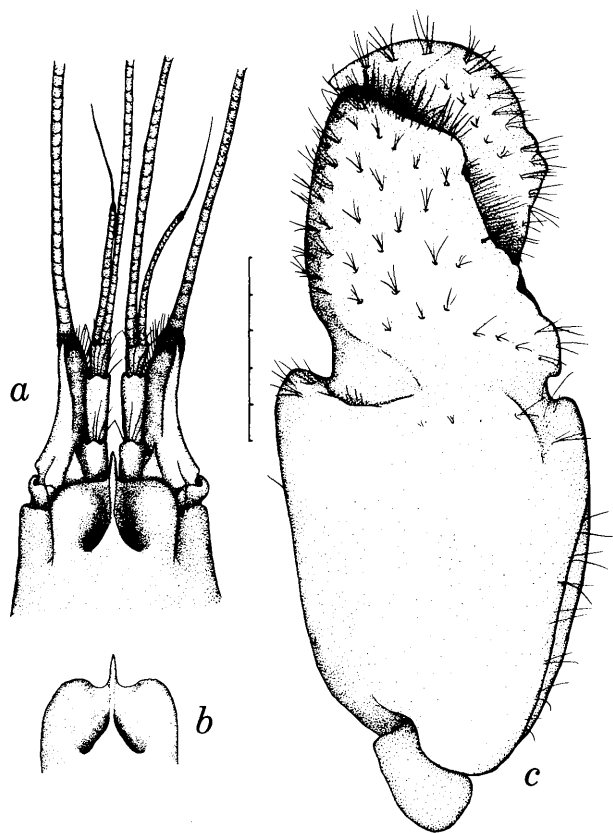


Fig. 63. *Alpheus armillatus* H. Milne Edwards. *a*, Anterior region in dorsal view; *b*, rostral region in dorsal view; *c*, large chela in dorsal view; 5 mm indicated (from Williams 1965).

Abdomen smooth, compressed. Telson with 2 pairs of dorsal spines, first pair at $\frac{1}{3}$, second at $\frac{2}{3}$ length; sides somewhat convergent distally, tip rounded, with pair of spines at each posterolateral corner, mesial spine twice length of outer spine. Uropodal exopod with outer margin ending in small spine flanked mesially by larger spine.

Measurements in mm.—Length of body: male 43; female 45 (Hazlett and Winn 1962).

Color.—Body with dark gray or brown ground color, crossed by 9 conspicuous lunate or elliptical spots or bands of translucent white equal in width to intervening dark bands; carapace with 3 white bands, third one at posterior margin; abdomen with 6 bands, first blending with last on carapace; abdomen often dark green with spots bordered by line of orange; uropods and telson usually with broad crossband and sometimes tipped with orange; chelae thickly speckled with dark gray, whitish bands above, tipped with pale pink or white; antennal peduncles grayish, flagella and walking legs orange yellow banded with white (Verrill 1922).

Hendrix (1971) stated that two other color phases have been recorded from Florida, a blue-gray color similar to that of *A. heterochaelis*, and a straw-yellow

pattern. Male and female pairs in the same burrow are always of matched color, suggesting that sympatric species may be involved.

Habitat.—Under rocks and shells or in holes in rocks; turtle grass; shallow water to 14 m (Felder and Chaney 1979).

Known range.—North Carolina, through Gulf of Mexico and West Indies to Cananéia, São Paulo, Brazil; Bermuda (Holthuis 1956).

Remarks.—This species closely resembles *A. heterochaelis*, its similar-sized and (in the Carolinas) much more abundant congener. *Alpheus armillatus* is named for its conspicuously banded body, but in preserved material it can usually be distinguished from similar species by the distinctive form of the rostrum, and from *A. heterochaelis* males by the lack of a specialized dactyl on the small first chela and by presence of a distoventral spine on the merus of the first legs.

The species is rarely taken in the Beaufort region of North Carolina. Hay and Shore (1918) found males and females living in pairs under rocks at Fort Macon. Ovigerous females are known more or less year round in Florida and Caribbean parts of the range; June in Brazil, and August in Bermuda (USNM).

Coonfield (1940) observed the chromatophore system of this shrimp in one of the early studies of this kind, showing that it reacts to different backgrounds under varying light conditions.

Hess (1940, 1941) demonstrated that *A. armillatus* is sensitive to light in many regions of the body, regardless of the amount of time elapsed since the preceding molt. At Tortugas, he found diurnal molting apparently controlled by daily temperature changes, molting occurring when the temperature rises to or above 29°C. Animals in constant temperature failed to exhibit diurnal molting as did ovigerous females.

Darby (1934) studied regeneration of chelae in *A. armillatus* and *Synalpheus longicarpus*, together with determination of right or left handedness. He found that in development of chelae a stage was reached that permitted determination of which side would have a large chela. Equal chelae were produced experimentally and were of three varieties: (1) both small (pinch claws); (2) both large (snap claws); and (3) both intermediate.

Darby offered a hypothesis, involving two substances and a metabolic condition, which could explain the regenerative phenomena in these and allied crustaceans. In such animals, a substance A is produced which controls production of pinch claws; but at certain stages in the intermolt cycle a substance B is produced, for a limited time, and concentrated in whichever claw is regenerating or al-

ready modified as a snap claw. This circumstance will produce or reinforce production of a snap claw. Chance alone is responsible for whether a snap claw will be on one side or the other, or whether the animal will be symmetrical. Also, time at which regeneration occurs depends on chance.

Identity of the experimental animals reported by Darby is open to some question because Armstrong (1949) ascribed some of Darby's specimens to his newly described *A. viridari*. Presently, there are four lots of Darby's material in the USNM collection identified as *A. armillatus*; two contain adults (28 in all); one lot of larvae is unidentifiable; and one lot of three specimens could not be found in 1980. Therefore, at least some of Darby's material was correctly identified. *Alpheus armillatus* and *A. viridari* occur together in hollowed decayed roots among old mangroves in Belize (B. Kensley, personal communication).

Hazlett and Winn (1962) found that no single part of the major chela fingers is involved in sound production. Whole fingers produced loud sound, but ablation of various parts weakened sound. They considered sound to be used in territorial behavior, as have students of behavior in other alpheids. Actual fighting occurred only when the home of a shrimp was invaded. A male 35 mm long took possession of a glass tube from a 30-mm male after a short fight. Then a 43-mm female was introduced and after some movement and snaps, the two occupied the glass tube together. When a second female 45 mm long was introduced, the first female came out of the tube and after an intense fight retained possession of the tube. The male took no part in this combat and showed no behavior when the 43-mm female returned to the tube. When a *Synalpheus* was introduced to an *Alpheus*, aggression-retreat behavior resulted in *Synalpheus* often backing down the *Alpheus* which was larger.

Sikora, et al. (1972) recorded *A. armillatus* as food of two species of hake in Georgia estuaries.

Pearse (1932b) reported encysted larvae of *Rhyncobothrius* in viscera of *A. armillatus*.

Alpheus formosus Gibbs

(Striped snapping shrimp)

Fig. 64

Alpheus formosus Gibbs 1850:196.—Verrill 1922:84, text-figs. 5d, 6a; pl. 20, fig. 3; pl. 23, figs. 5a, b; pl. 29, figs. 4, a-u; pl. 25, figs. 6–6a.—Williams 1965:64, fig. 52.—Chace 1972:67.—Christoffersen 1979:314.

Crangon formosus.—Hay and Shore 1918:384, pl. 26, fig. 5.—Schmitt 1935a:144.

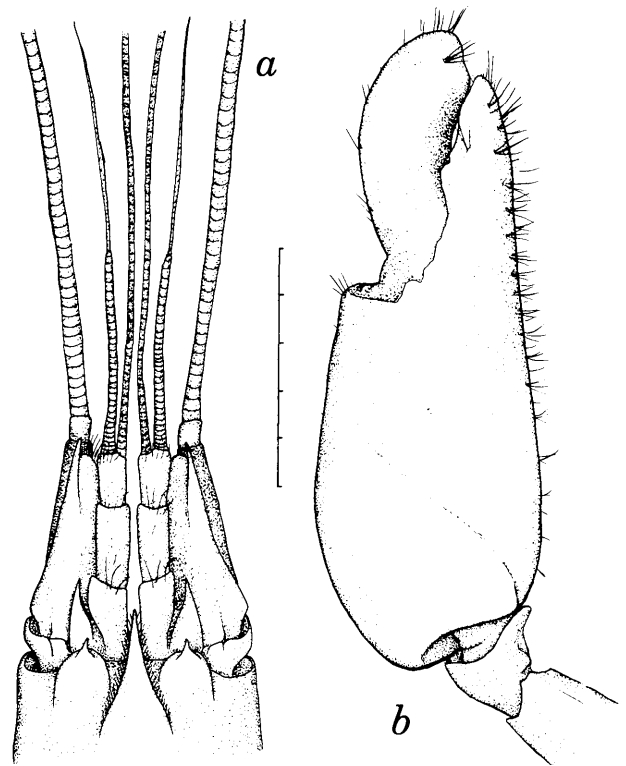


Fig. 64. *Alpheus formosus* Gibbs. a, Anterior region in dorsal view; b, outer surface of large chela; 5 mm indicated (from Williams 1965).

Recognition characters.—Rostrum beginning at posterior line of eyes and reaching about to second article of antennular peduncle; flat above; margins concave at base but regularly convergent anteriorly and with scattered stiff hairs; tip rounded, often bearing 2 or 3 minute spines. Carapace half length of abdomen, compressed, not grooved; orbital hoods each with acute, anteriorly directed spine much shorter than rostrum. Eyes completely covered by carapace. Antennular peduncles with scalelike stylocerite, slender tip reaching slightly beyond basal article; second article twice length of third; inner flagellum filiform, outer flagellum thick proximally, filiform distally. Antenna longer than body; antennal scale with strong apical spine reaching to or beyond tip of antennular peduncle; spine separated from and exceeding lamella; weak spine (basicerite) below near base of scale. Third maxillipeds with terminal article hairy; slightly exceeding antennal peduncle.

First legs strongly chelate, very unequal. Larger leg compressed, smooth above and unnotched along margins; fixed finger acute, incurved at tip, shorter than stout, gradually arched, blunt dactyl; carpus short, convex above, with distal tooth; merus with acute distal spine. Smaller chela much more slender, long and smooth, inner surface with stout spine

overhanging base of dactyl; fixed finger nearly straight, slender, somewhat turned up near tip; dactyl about half length of hand, nearly straight to about middle, then gently arched to tip, hairs arising from nearly straight groove below ridge on both sides; inner surfaces of fingers with slender groove and carina; fingers meeting closely. Second pair of legs slender; weakly chelate; carpus subdivided, with joints diminishing in length as follows (numbered from proximal end): 1, 5, 2, 3–4. Third to fifth legs with simple dactyls.

Telson with 2 pairs of dorsal spines at about $\frac{1}{3}$ and $\frac{2}{3}$ length; posterolateral corners with pair of spines, mesial spine much longer than lateral, distal margin with long hairs. Uropodal exopods with lateral margin ending in black movable spine between 2 fixed spines; black spine remaining amber colored after long preservation.

Measurements in mm.—Length of body: male 40; ovigerous females 17 to 35.

Color.—Color pattern conspicuous and characteristic; ground color yellowish or greenish brown finely speckled with orange; narrow light stripe along middorsal line extending from distal end of antennular peduncle to base of telson, line light orange anteriorly merging into yellowish green and finally gray posteriorly; brown stripe on each side dorsolaterally and below this another stripe of white, or colors similar to dorsal stripe, along each side followed by stripe of light reddish brown and still another stripe of blue bordering abdomen; chelae greenish brown with orange red fingers; antennules, antennae, and walking legs blue; telson and uropods white at base blotched and bordered with yellow.

Habitat.—Chace (1972) recorded the species from "sand, mud flats with and without *Pocillopora* and *Porites*, rock-studded beaches, seawalls, wrecks, and exposed and submerged reefs from above low-tide" to 42 m.

Type-locality.—Key West, Fla.

Known range.—Near Beaufort, N. C., through Gulf of Mexico (Ray 1974; Felder and Chaney 1979) and West Indies to São Paulo, Brazil; Bermuda.

Remarks.—Ovigerous females are documented from January through July in the Bermuda-Venezuela region, and Gore, et al. (1978) stated that the breeding season on sabellariid reefs along east Florida is January-July. They are known from June to January from São Paulo to Bahia, Brazil (Christoffersen 1979), and Bimini in October; Hendrix (1972) stated that they have been collected in all months of the year.

Manter (1933) found metacercariae of *Helicometrina nimia* encysted in muscles of *A. formosus* at Tortugas.

Alpheus heterochaelis Say

(Big-clawed snapping shrimp)

Fig. 65

Alpheus heterochaelis Say 1818:243.—Verrill 1922:76, pl. 22, figs. 1, 2, 4a-c; pl. 24, figs. 7, 7a; pl. 30, figs. 1–1a, lt, 2a–2e; pl. 33, figs. 1, 2.—Holthuis 1959:102.—Williams 1965:66, fig. 54.—Chace 1972:67.—Coelho and Ramos 1972:148.

Crangon heterochaelis.—Hay and Shore 1918:386, text-fig. 8, pl. 26, fig. 6.—Schmitt 1935a:144.

Recognition characters.—Rostrum carinate, extending back about as far as base of eyestalks; tip not reaching to base of second article of antennular peduncle. Carapace more than half length of abdomen, somewhat compressed; without grooves; front produced into rounded ocular hood over each eye; rostro-orbital depressions passing gradually into dorsal surface; emarginate below eye on anterior border. Eyes relatively small, covered by carapace. Antennular peduncles with scalelike stylocerite, minute spine at tip not reaching end of basal article; second article twice length of third; inner flagellum filiform, about half length of antenna; outer flagellum with proximal $\frac{2}{3}$ thickened. Antennae a little longer than body; antennal scale with strong apical spine reaching slightly beyond antennular peduncle, spine separated from and slightly

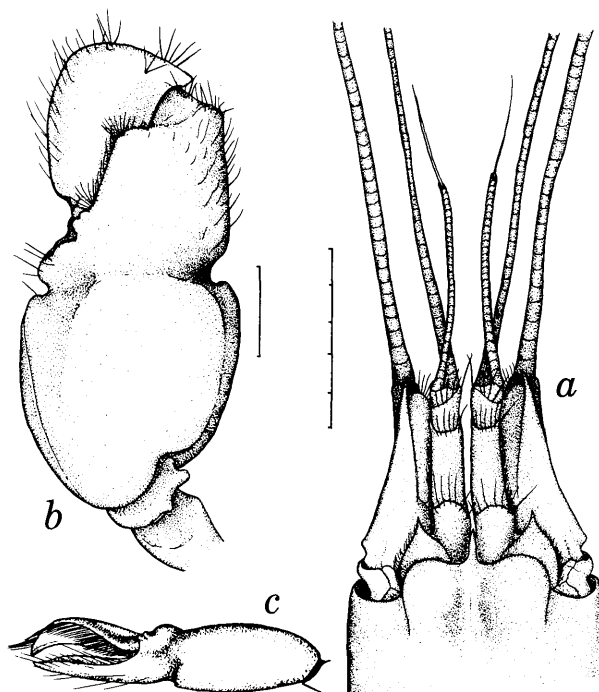


Fig. 65. *Alpheus heterochaelis* Say. a, Anterior region in dorsal view; b, large chela in dorsal view; c, small chela of male (after Verrill 1922); a-b, 5 mm indicated (from Williams 1965).

exceeding lamella; weak spine (basicerite) below near base of scale. Third maxillipeds with terminal article hairy; slightly exceeding antennal peduncle.

First legs strongly chelate, very unequal; merus unarmed distoventrally. Larger chela thick; outer and inner margins deeply notched near base of fingers; upper and lower surfaces with irregular shallow grooves; dactyl broad, heavy, strongly curved, with large basal tooth. Small chela sexually dimorphic; in male broad, elongate; proximal dorsal area of palm bounded by an impressed line, upper margin notched distally; dactyl flattened and expanded on outer surface; opposed edges of fingers keeled, closely fitting, fringed by dense hairs. Fingers of small chela in both sexes weaker, less curved, and more hairy than in large chela; carpus short; merus smooth. Second legs slender, weakly chelate; carpus subdivided with joints diminishing in length as follows (numbered from proximal end): 1, 2, 5, 4, 3. Third to fifth legs with lateral movable spine on ischium, dactyls usually subspatulate.

Abdomen compressed, smooth, tapering. Telson with subparallel sides and rounded tip; dorsal surface with 2 pairs of movable spines, first pair at about midlength, second at a little less than $\frac{3}{4}$ length; pair of spines at each posterolateral corner, mesial spine longest; distal margin heavily setose; pair of anal tubercles beneath with accompanying cups on uropods forming locking devices. Uropodal exopods with lateral border ending in fixed spine flanked mesially by longer movable spine.

Measurements in mm.—Length of body: male 40; ovigerous female 54.

Color.—Dark translucent green, slightly flushed with purple on sides of carapace; white markings on chelipeds; walking legs pale red; tips of uropods blue with narrow border of orange on distal margin; outer blade with patch of red just above blue, and a narrow white border; articular surfaces and joints of abdominal segments, and a small streak along cervical groove, white.

Habitat.—Lives among broken shells and stones or in burrows in mud, often among shells; water's edge to 30 m; common in lakes and canals of Everglades National Park, Fla., in salinity of 2‰ (Hendrix 1971).

Type-locality.—Amelia Island, Nassau County, Fla.

Known range.—Lower Chesapeake Bay (Van Engel and Sandifer 1972) to Aransas County, Tex.; Cuba; Curaçao; Surinam (Chace 1972); Bermuda. Other authors have listed the range as extending to São Paulo, Brazil.

Remarks.—This is the largest snapping shrimp found in the Carolinas. It is nearly as abundant as *A. normanni*. Brooks and Herrick (1892) gave a good

colored figure of *A. heterochaelis* (plate 2), as well as a series of figures of segmenting eggs and developing larval stages, but the latter are confusing because the authors skipped or overlooked larval stages and confused these with early postlarvae (Knowlton 1973b).

Ovigerous females have been taken through much of the annual cycle in various localities: February and April in Surinam (Holthuis 1959); March to October in the Gulf of Mexico; at least June to November in North Carolina; October to January in Cuba, Puerto Rico, and Bonaire; also March, July and August, if Brazilian specimens are included (Ramos 1971).

Knowlton reared the larvae of *A. heterochaelis* in laboratory cultures maintained at 24.6°–27.6°C in salinities of 31–36‰, describing an abbreviated development through three stages, postlarvae, and juveniles. Eggs of females from near Beaufort, N. C., hatched in 27 days at 25°C, usually between 8:00 p. m. and 2:00 a. m. Larvae passed through Stage I usually within 6 h, but sometimes skipped this stage, hatching at Stage II. Stage II was almost always completed in a day, and Stage III lasted 2.5–3 days at 25°C. Postlarvae usually molted to juveniles 3–3.5 days following metamorphosis, usually between 5:00 and 9:00 a. m. Two-week-old young are 5 mm long; Brooks (1892) illustrated this stage (pl. 17, fig. 3). At one month the first walking legs are stouter than the second pair, and asymmetry of the first legs is first noticeable at two months (~7 mm length). Sandifer (1973d) found Stage II and III larvae attributed to this species in lower Chesapeake Bay rarely during July and August.

Larvae swim dorsal side down, horizontally or at an angle, and are positively phototropic. Postlarvae and juveniles are nearly always benthonic. The larvae apparently feed somewhat on detritus despite their containing an amount of yolk sufficient to sustain them through metamorphosis. Postlarvae and juveniles fed actively on *Artemia* in experiments (Knowlton 1973b).

The full geographic range of this species is in doubt because identity has not been fixed with certainty (Chace 1972). Knowlton, in his comprehensive review, pointed out that specimens from North Carolina with large eggs produce larvae with abbreviated development (rare in the Alpheidae), whereas some specimens from Florida identified as *A. heterochaelis* had smaller eggs and normal extended larval development. He noted that there were minute differences between these forms in adult morphology, indicating that two or more species were being treated as one.

Abundant in a Florida mangrove-*Juncus* system (salinities 1–27.5‰) (Odum and Heald 1972), *A.*

heterochaelis is preyed upon by several species of fishes (see also Heard 1970, white catfish; Sikora, et al. 1972, hakes). Shrimp stomachs contained particles ranging up to 400 μm in diameter; contents of vascular plant detritus, inorganic particles, harpacticoid copepods, amphipods, and unrecognizable material, indicating omnivorous feeding which was observed mainly at night.

Snapping sounds produced by the large chela in shrimps of the genera *Alpheus* and *Synalpheus* have been the subject of a number of papers reviewed by Knowlton and Moulton (1963). Snap audibility is positively correlated with body size (Schein 1975), and is relatively louder in *Alpheus* than in *Synalpheus*; moreover, a large population of snapping shrimp in water 1–6 m deep can produce a continuous crackling sound resembling the fine sizzle of sparks drawn from an electrostatic generator, a sound clearly audible through the bottom of an anchored skiff (see also Knowlton and Moulton 1963:311). Each snap is caused by the sudden impact of the hardened major finger tips coming rapidly together. Structural detail of fingers differs among alpheid genera. Cocking devices that hold the dactyl open until overcome by great muscular contraction of its adductor would seem to increase the sound produced, and Ritzmann (1973) showed by experiment with *A. californiensis* that a pair of smooth discs at the base of the dactyl and adjacent distal margin of palm are temporarily held together by cohesive forces of water until overcome by this contraction. Matched protuberances on propodus and dactyl of *Synalpheus* may serve the same function (Knowlton and Moulton 1963).

Male *A. heterochaelis* collected near Beaufort, N. C., have proportionately larger major chelae than females, although females tend to have longer bodies than males (Schein 1975). In Y-maze tests, males tend to seek females by chemical clues. Stimulus intensity offers potential clues to size of another individual. The snaps signal presence of an alpheid, identify the genus, and indicate size and location of the snapping animal (Schein 1977). Initial contacts between wandering males and unpaired females in burrows elicit snap-threats and possibly other behavior related to "fight winability"; in the case of heterosexual contact, the encounter leads to suppressed aggression with possibility of burrow sharing and mating. Schein discussed other behavioral aspects as did Nolan and Salmon (1970) in great detail.

Laboratory experiments show that after removal of the large chela or immobilization of its dactyl, *A. heterochaelis* can not compete successfully with normal shrimp in acquiring or holding a shelter (Conover and Miller 1978); evidently action of the

dactyl plays a primary role in successful defense of a shelter. Shrimp lacking the large chela often were allowed to encroach beneath shelters by their like-sexed competitors, suggesting that structure of the chela itself and not its movements elicit aggressive behavior by competitors.

Alpheus normanni Kingsley

(Green snapping shrimp)

Fig. 66

Alpheus affinis Kingsley 1878a:195 (not *A. affinis* Guise 1854: 275–280).

Alpheus normanni Kingsley 1878b:93.—Williams 1965:65, fig. 53.—Chace 1972:68.—Christoffersen 1979:322.

Alpheus packardii Kingsley 1880:417.—Verrill 1922:80, pl. 20, figs. 2, 5; pl. 21, fig. 5; pl. 22, fig. 7; pl. 23, figs. 6, c-d; pl. 25, figs. 4, 4a; pl. 31, figs. 1, b-l, 2, b-u, 3, u, t.

Crangon packardii.—Hay and Shore 1918:385, pl. 26, fig. 4.—Schmitt 1935a:144.

Crangon normanni.—Chace 1937:122.

Recognition characters.—Rostrum with carina extending as far back as base of eyestalks, spiniform tip not reaching to base of second peduncular article of antennule. Carapace about $\frac{2}{3}$ length of abdomen, somewhat compressed; cervical groove hardly evident; front with ocular hoods produced into blunt angle above each eye; anterior border emarginate below ocular hoods. Covered eyes well developed. Antennules with third article of peduncle much shorter than second; stylocerite scalelike with spiniform tip reaching about to end of basal article; inner flagellum slender, outer one shorter with proximal $\frac{1}{2}$ enlarged. Antennae a little longer than body, slender; antennal scale reaching a little beyond end of antennular peduncle, lateral margin slightly sinuous with strong terminal spine separated from and exceeding lamella; strong ventral spine (basicerite) near base of scale. Third maxillipeds slender, not reaching tip of antennal scale; terminal article with long hairs.

First legs strongly developed with chelae unequal. Larger leg broad and flattened; slightly sinuate along inner margin; outer margin with longitudinal groove above and below, ridge between grooves ending in strong tooth behind base of dactyl; dactyl heavy, curved, toothed at base. Smaller chela about half as wide and $\frac{3}{4}$ as long as larger one; similarly formed but with sharp spine above (and small one below in males) at base of dactyl; no basal tooth on dactyl; sexually dimorphic fingers in males broad externally but with keeled, closely fit-

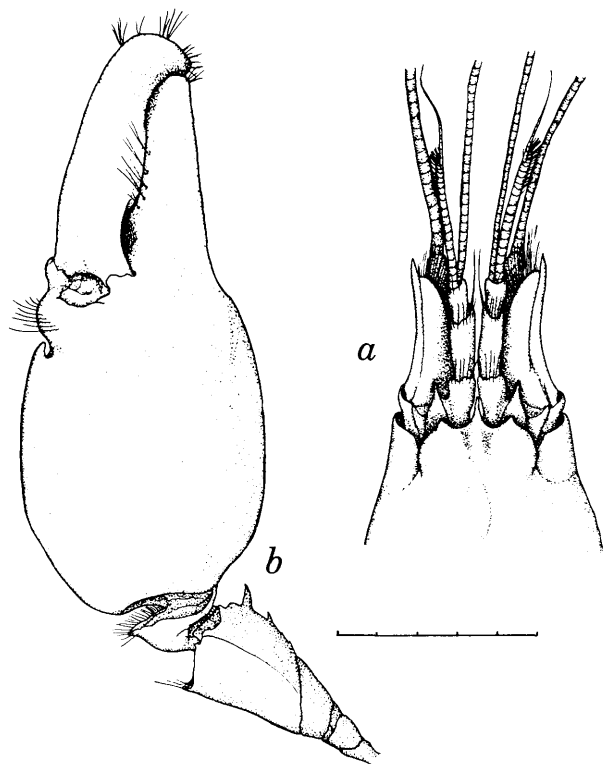


Fig. 66. *Alpheus normanni* Kingsley. *a*, Anterior region in dorsal view; *b*, large chela in ventrolateral view; 5 mm indicated (from Williams 1965).

ting opposed edges fringed by dense hairs; females with hand a bit hairy but fingers unornamented; carpus of both legs short, broad, irregularly cup shaped, merus with spiniform tooth near distal end and 1 or 2 spines below, distal end cupped to receive carpus with leg extended. Second legs very slender, weakly chelate; with carpus subdivided, joints diminishing in length as follows (numbered from proximal end): 2, 1, 5, 3–4. Third to fifth legs with dactyls simple.

Abdomen somewhat compressed. Telson with sides slightly convergent distally; 2 pairs of dorsal spines, first pair at $\frac{1}{3}$, second at $\frac{2}{3}$ length; tip broadly rounded, pair of spines at each posterolateral corner, distal margin heavily setose; pair of anal tubercles beneath with accompanying cups on uropods forming locking devices. Uropods oval; exopod with lateral margin ending in small spine flanked mesially by strong movable tooth.

Measurements in mm.—Length of body: male 26; ovigerous female 30; carapace length ovigerous females 4.5–10 (Hendrix 1971; Christoffersen 1979).

Color.—Gray or dull green, sometimes with median and lateral stripe of whitish often clouded or mottled with dark green or brown, a paler spot behind each eye; large chela dark green usually banded with yellowish brown or yellow on inner

surface; smaller chela and other legs paler, often banded with dull gray or reddish; occasionally body banded with red and pale yellow, large chela with 2 pale bands, fixed finger blackish, dactyl reddish (various authors).

Habitat.—Shelly or rocky bottoms, in burrows in sand or on pilings in shallow water, common in saltier parts of estuaries in Carolinas. Nolan and Salmon (1970) found the species in 10-m water offshore in March near Beaufort, N. C., but mainly in eel grass beds or in small-sized rubble during summer. Van Engel and Sandifer (1972) found the species occasionally in oyster trays on the eastern shore of Virginia. Chace (1972) found it most frequent on sand and mud flats covered with turtle grass and *Porites*, occasionally on mud bottom under rocks and oysters, and among reef corals in the Lesser Antilles. Hendrix (1971) reported it most abundant among blades and rhizomes of *Thalassia testudinum* from spring through late fall, noting that it does not build permanent burrows or shelters but is often found in sabellariid polychaete tubes, on mats of *Halimeda* sp., and in some sponges. Water's edge to 73 m.

Type-locality.—Key West, Fla.

Known range.—Bermuda; around Cape Charles, Va., and lower Chesapeake Bay through Gulf of Mexico (Ray 1974) and West Indies to São Paulo, Brazil (Christoffersen 1979); Gulf of California and Panama (Chace 1972).

Remarks.—This is one of the commonest snapping shrimps in the Carolinian region. As Hay and Shore (1918) pointed out, this was probably the species called *Alpheus minor* in early lists for the area. The epithet *minor* is correctly referred to *Synalpheus minus* (Say) found only in offshore waters, a different habitat from that frequented by *Alpheus normanni*. Brooks and Herrick (1892) followed the older lists adopting the name *Alpheus minor (minus)* and illustrated the adult in color on plate 1 and larval stages on plates 16 and 17. They illustrated the first three larval stages, as well as stages in segmentation of the embryo, but their specific identifications are somewhat unreliable.

Knowlton (1973b) considered *A. normanni* to have an extended larval development, i.e., small eggs and 5 larval stages. Sandifer (1973d) found larvae of the species uncommon in surface samples from lower Chesapeake Bay in a salinity range of 21.35 to 25.77‰ in temperatures of 25.3°–26.9°C during August and September.

Ovigerous females have been recorded throughout the year in various parts of the range, the season being most extended in lower latitudes (Tabb and Manning 1961; Rouse 1970; Hendrix 1971; Christoffersen 1979; USNM). Knowlton (*in* Nolan

and Salmon 1970) found ovigerous females from April 26 to September 20 at Beaufort, N. C.

In a compendious paper, Nolan and Salmon (1970) discussed behavior of *A. heterochaelis* and *normanni*, finding many traits to be similar. Though their discussion cannot be covered completely here, they found that animals in the laboratory tend to hide under or alongside hard objects or the sides of containers. Shelters or burrows may be constructed by digging with legs, pleopods and body, burrow maintenance being a more or less continuous process. If a unisexual pair of a species has a single available shelter, one animal will become dominant by action of a suite of aggressive acts: moving forward, lunging, fanning, spread stance, cocked claw, chela snap, touching or overlapping head and thoraci appendages, prowling and chasing. Retreat and avoidance are submissive acts. Moreover, when individuals from each of these two species are paired, the larger animal, usually *A.*

heterochaelis, almost always dominates. Other behavioral aspects are reviewed in the account for *A. heterochaelis*.

Sikora, et al. (1972) found *A. normanni*, *armillatus*, and *heterochaelis* in stomach contents of hakes, *Urophycis regius* and *U. floridanus*, in Georgia estuaries.

Genus *Automate* de Man 1888

de Man 1888:529.—Rathbun 1901:112.—Banner and Banner 1966b:36.

Carapace compressed. Eyes not covered by carapace, cornea reduced. Antennular peduncles extremely long; stylocerite reduced. Third maxillipeds longer than antennular peduncles. Chelate first legs asymmetrical and sexually dimorphic; surface smooth; fingers without cylinder and plunger as in *Alpheus*.

Key to Species

(Adapted from Chace 1972)

1. Rostrum reduced to acute, short tooth; propodus of legs 3 and 4 setose, not spinulose; dactyl of legs 3 and 4 subspatulate *A. evermanni*
 Rostrum broadly rounded or subtriangular; propodus of legs 3 and 4 armed with series of stout, movable spines on flexor margin; dactyl of legs 3 and 4 slender, not subspatulate *A. gardineri*

Automate evermanni Rathbun

Fig. 67

Automate evermanni Rathbun 1901:112, fig. 22.—Holthuis 1951b:115, fig. 24.—Crosnier and Forest 1966:306, fig. 33.—Chace 1972:74.
Automate kingsleyi.—Williams 1965, fig. 51.

Recognition characters.—Carapace compressed, deeply emarginate behind eyestalks, slightly produced over base of antenna, anteroventral corner receding and very broadly rounded, deeper at level of first leg. Rostrum a small acute tooth. Eyestalks exposed and flattened dorsally, contiguous, base broadened, small cornea subterminal. Antennular and antennal peduncles long and nearly equal; stylocerite scalelike, reaching to $\frac{2}{3}$ length of basal antennular article; second article reaching $\frac{1}{2}$ – $\frac{2}{3}$ length of penultimate article, outer margin straight, ending in tooth equal to or exceeded by lamella. Third maxilliped exceeding antennal peduncle by length of terminal article.

First pair of legs chelate, very unequal. Major hand of male granulate along lower side near middle; not so in female; fingers gaping, pointed

tips crossing; fixed finger in line with hand and broad at base, lower edge in female slightly sinuous, cutting edge with complex blunt tooth near base, finely serrate and slightly concave near tip; dactyl tapering, small tooth near base, remainder of cutting edge sinuous. Carpus with lateral tooth on anterior margin projecting distoventrally, smaller tooth on mesiodistal corner. Second legs slender, overreaching antennal peduncle by full length of carpus, weakly chelate, carpus divided into 5 joints with proportions of 1:2.8:1.3:0.9:1.2. Third to fifth legs with dactyls subspatulate, merus of 3 and 4 with setae along flexor margin.

Abdomen well developed, compressed, pleopods strong. Telson tapering, margins laterally constricted near base but convexly curved to converge toward narrow posterior margin bearing 2 pairs of spines, outer stout, inner longer and more slender; dorsally armed with 2 pairs of very small spines, anterior pair distinctly anterior to mid-length.

Measurements in mm.—Length of body: male 14.2 (Rathbun 1901); female 27.4.

Color.—Practically colorless except eggs of ovigerous female color of red lead (W. L. Schmitt notes).

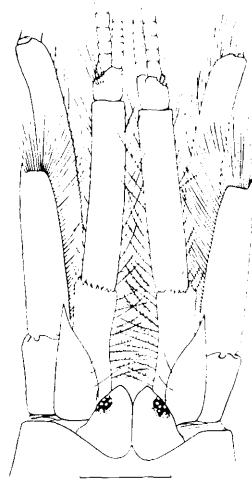


Fig. 67. *Automate evermanni* Rathbun. Anterior region of body in dorsal view, 25 mm indicated (from Crosnier and Forest 1966).

Habitat.—Sand, mud, shells; to 250m (Rathbun 1901).

Known range.—North Carolina (?); Georgia to Texas and Puerto Rico; eastern Atlantic from Cape Verde Islands and Liberia to Nigeria (Chace 1972).

Remarks.—Hay and Shore (1918) confused the description of *A. kingsleyi* by including illustrations of *A. evermanni*, and Williams (1965) continued the error by copying their figure (Chace 1972). Specimens of *Automate* formerly in the UNC-IMS collection were inadvertently discarded, therefore the old collections cannot be redetermined. Several speci-

mens from the S. Gray collection from off Sapelo Island, Ga., now in the USNM, include the largest female measured. The Georgia occurrence suggests that the species ranges into the Carolinas.

Automate gardineri Coutière

Fig. 68

Automate Gardineri Coutière 1902:337.

Automate kingsleyi Hay 1917:72.—Hay and Shore 1918:387, text-fig. 10; pl. 26, fig. 7.—Williams 1965:62.

Automate johnsoni Chace 1955:13, fig. 7.

Automate gardineri.—Banner and Banner 1966a: 150.—1966b:37, fig. 8.—Chace 1972:74, fig. 23.

Recognition characters.—Carapace about half length of abdomen; deeply emarginate dorsally behind eyestalks with rostrum a broadly rounded projection; anterior margin entire, produced farthest forward at base of antennular and antennal peduncles. Eyestalks contiguous, broad at base; cornea well developed with minute point on anterior surface in lateral view. Antennular and antennal peduncles long; stylocerite scalelike, reaching to end of basal antennular article; second antennular article nearly equal in length to first; third very short. Antennal scale extending to middle of penultimate article of antennal peduncle; lateral border ending in small spine; lamella broadly rounded distally, equaling spine. Third maxilliped exceeding anten-

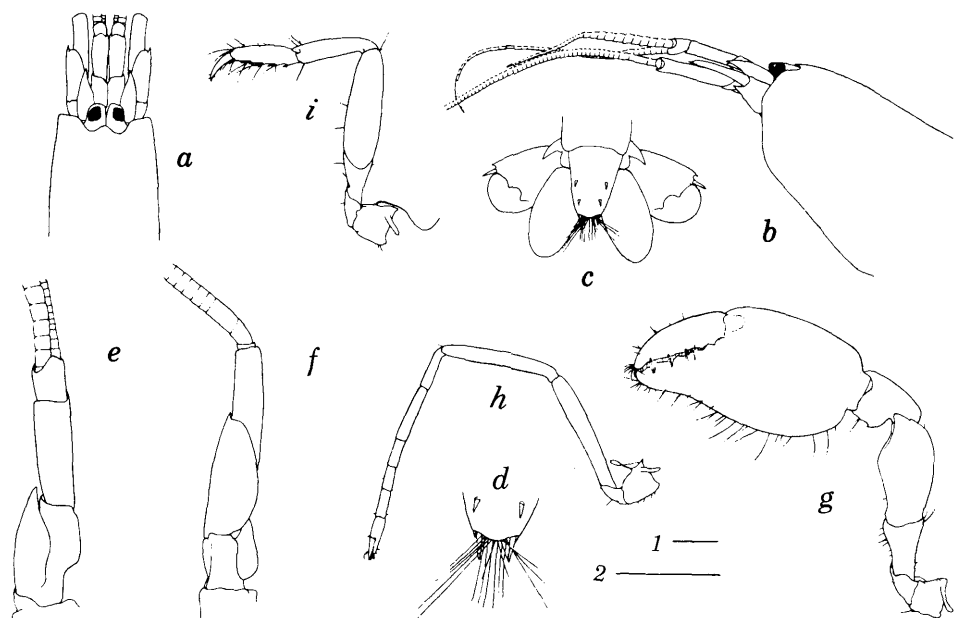


Fig. 68. *Automate gardineri* Coutière. Female: a, anterior region in dorsal view; b, same, lateral view; c, telson and uropods; d, end of telson; e, left antennule; f, left antenna; g, left first leg; h, left second leg; i, left third leg. Scales: 1(a-c, g, i), 2(d-f, h) = 1 mm (from Chace 1972).

nal peduncle by less than length of terminal article.

First legs chelate, prismatic, unequal; larger appearing somewhat rougher and stouter than smaller; fingers slightly gaping, fixed finger in line with hand and broad at base; dactyl narrower and moderately curved; carpus short; merus nearly as long as dactyl. Second legs nearly as long as first but slender, weakly chelate, and with carpus divided into 5 joints with proportions of 1:1.25:0.80:0.66:0.80. Third to fifth legs with dactyls slender, simple; merus of 3 and 4 with movable spines along flexor margin.

Abdomen well developed; compressed pleopods strong. Telson tapering; truncate terminally, ending in 2 short lateral spines flanked mesially by 2 longer spines and median pair of feathered setae; dorsally armed with 2 pairs of spines, first pair at midlength, second at $\frac{3}{4}$ length. Uropods with oval blades; lateral border of exopod deeply notched distally, border ending in small tooth flanked mesially by strong movable spine.

Measurements in mm.—Length of body: ovigerous females 7 to 16.

Color.—Almost transparent except for a small amount of red pigment on appendages and telson.

Habitat.—Under rocks at low tide; shallow grass flats to 50 m (USNM).

Type-locality.—Maldivé and Laccadive Islands.

Known range.—Beaufort Inlet, N. C.; Yucatan; Virgin Islands, Barbados; Indo-Pacific region from Red Sea to Samoa.

Remarks.—Chace (1972) stated that *A. kingsleyi* is a synonym of *A. gardineri*, that the latter is probably a pantropical species, including two other species named from the eastern Atlantic and eastern Pacific, and that all of these may be synonyms of *A. dolichognatha* de Man (1888).

Ovigerous females are known from North Carolina in July and September.

Genus *Leptalpheus* Williams 1965

Williams 1965a:193.

Leptalpheus forceps Williams

Fig. 69

Leptalpheus forceps Williams 1965a:194, figs. 1–2.—Chace 1972:77.

Recognition characters.—Body compressed. Carapace smooth, produced into hood projecting over eyes, nearly flat dorsally, extremely shallow excavation between eyes, anterior margin bent slightly downward in front of eyes; anterolateral angle obtuse; cardiac notch on posterior border well devel-

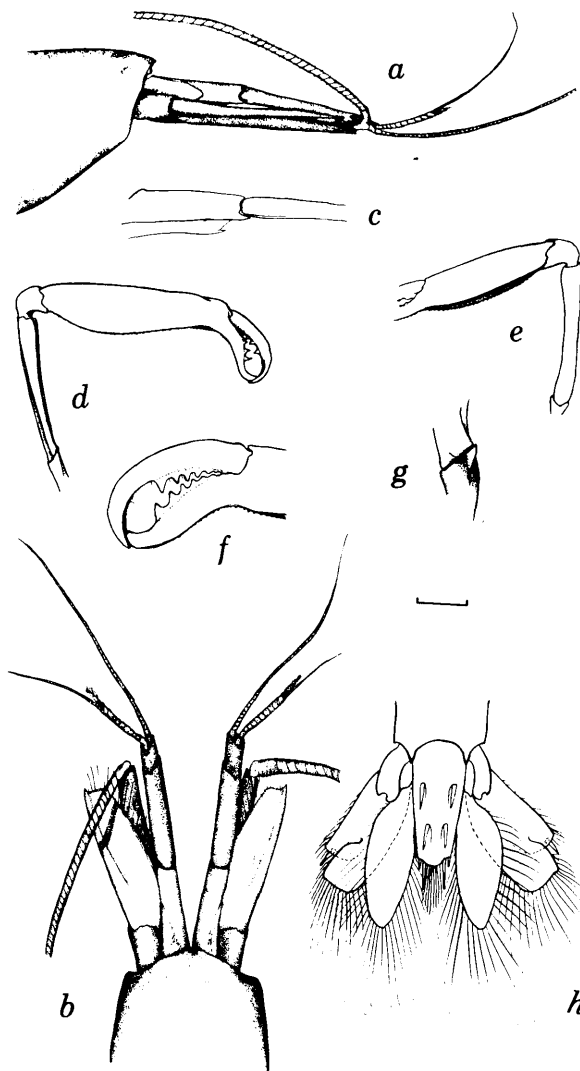


Fig. 69. *Leptalpheus forceps* Williams. Female: a, anterior region in lateral view; b, same, dorsal view; c, lateral view of antennular peduncle showing mesioventral keel; d, large cheliped in lateral view; e, part of large cheliped in mesioventral view; f, fingers of large chela; g, ischio-meral articulation of large cheliped; h, tail fan in dorsal view. Scales: a-b, d-e, h, 1 mm; c, f-g, 0.5 mm indicated (from Williams 1965a).

oped. Eyes concealed from dorsal view but visible from anterior, cornea well developed. Antennular peduncle slightly longer than antennal peduncle, a little broadened proximally, first and second articles of about equal length, each with prominent but appressed anterolateral spine, third shorter; stylocerite small, appressed, with thin mesioventral keel terminating in small anterior spine, outer flagellum shorter than inner, fused part with 10 segments. Antennal peduncle slightly convex, ending in spine exceeding lamella.

Chelipeds very asymmetrical, chelae carried folded back completely on merus; major with propodus longer than merus, slender, excavated along flexor surface, finely tuberculate ventrally, fingers thin, not inverted, conspicuously curved,

gaping, with meshing teeth proximally, tips crossing; merus long irregularly triangular in cross section, excavate somewhat internally, twisted and smooth; ischium triangular in cross section, blade-like spine on mesiodistal border. Minor cheliped with propodus somewhat longer than merus, flexor side of each excavated; fingers and palm of nearly equal length, fingers with single tooth at mid-length and thin shearing edge distally, tips crossing. Second legs weak, carpus divided into 3 segments, proximal longest, distal intermediate, middle 3 equally short. Third and fourth legs strong, merus well developed, carpus with distoventral movable spine; fifth legs weaker.

Abdomen smooth; pleura of first 5 segments broadly rounded, of sixth ending in acute, triangular, movable plate. Telson rounded distally, 2 pairs of movable dorsal spines at $\frac{1}{3}$ and $\frac{2}{3}$ length, movable outer short spine and adjacent long spine mesial to it at each corner. Uropods with exopod more or less truncate distally, lateral edge broken by overlapping rectangular cleft armed with strong subterminal spine, mesial margin with overlapping pointed lamina; no well-defined transverse suture present; endopod ovate and longer.

Measurements in mm.—Length of carapace: male 5.2; ovigerous female 7.8.

Variation.—Fingers of the major chela are slightly less gaping in females than in males, and the number of teeth on fingers of the major chela vary as do the fused segments on the outer antennular flagellum.

Color.—Translucent, colorless in life; eggs light green in formalin.

Habitat.—The species is a commensal in *Upogebia affinis* burrows (Williams 1965a; Saloman 1971; Simon and Dauer 1977), and may occur in *Callinassa* burrows as well (Dawson 1967). Specimens have often been taken at night in surface plankton inside inlets and in tidal currents in the sounds of North Carolina.

Type-locality.—Gallants Point, Newport River, Carteret County, N. C.

Known range.—Drum Inlet, Beaufort, Banks Channel near Wrightsville Beach, and Lockwoods Folly Inlet, N. C.; Old Tampa Bay, Fla. (Saloman 1971; Simon and Dauer 1977); Davis Bayou, Miss. (Dawson 1967).

Remarks.—Ovigerous females have been taken in June and August in North Carolina.

Genus *Synalpheus* Bate 1888

Banner 1953:26.—Hemming 1958b:161.

Key to Species

1. Dactyls of third to fifth legs with 2 very unequal hooks, ventral strongest (broadest); an inconspicuous, obtuse supernumerary process proximal to ventral hook *S. fritzmuelleri*
Dactyls of third to fifth legs with 2 hooks approximately equal in width at base 2
2. Dactyls long and slender, hooks continuing general direction of axis of dactyl; stylocerite longer than basal article of antennular peduncle; lamella of antennal scale present 3
Dactyls short, hooks strongly curved, ventral one usually bent at considerable angle to axis of dactyl; stylocerite not exceeding first article of antennular peduncle; antennal scale lacking lamella in male, small in female *S. longicarpus*
3. Frontal teeth more or less equilaterally triangular, at times with an inferior vertical prolongation to rostrum; basicerite strongly spinous above *S. minus*
Frontal teeth always longer than wide, spinous; rostrum armed with ventral prolongation which embraces ocellary beak; basicerite unarmed above *S. townsendi*

Synalpheus fritzmuelleri Coutière

Fig. 70

Synalpheus fritzmuelleri Coutière 1909:35, fig. 18.—Verrill 1922:97; Schmitt, 1935a:148.—Williams

1965:69, fig. 56.—Chace 1972:92.—Coelho and Ramos 1972:150.—Christoffersen 1979:341.

Recognition characters.—Rostrum slender, compressed, acute from dorsal view, a little longer than

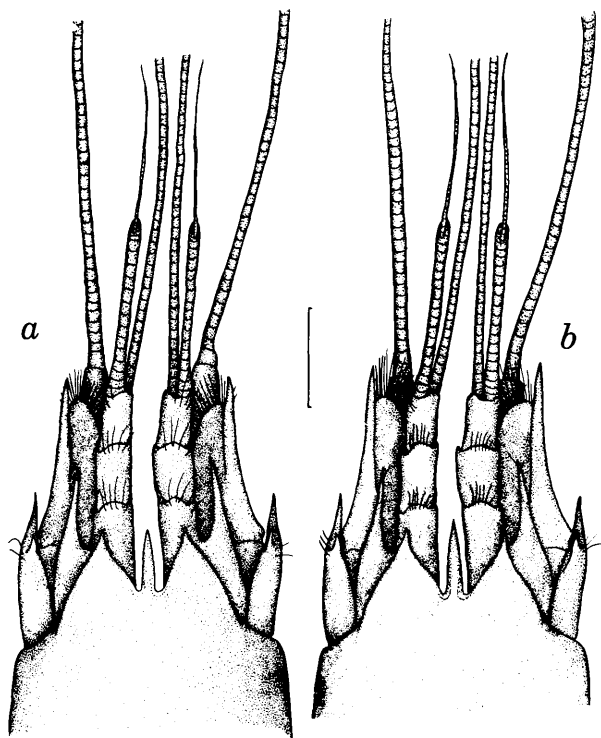


Fig. 70. *a*, *Synalpheus fritzmuelleri* Coutière, anterior region in dorsal view; *b*, *S. f. elongatus* Coutière, anterior region in dorsal view; 1 mm indicated (from Williams 1965).

orbital spines, reaching to midlength of visible portion of basal antennular article. Orbital spines wide at base, acuminate; margins incurved. Eyes completely covered by carapace. Antennular peduncle with stylocerite of basal article reaching to middle of second article; third article slightly shorter than second; inner flagellum filiform, outer bifurcate beyond about eighth joint, thickened proximally. Spine of antennal scale equaling terminal article of antennal peduncle, both reaching a little beyond antennular peduncle, spine separated from and exceeding narrow lamella distally; basal article (basicerite) with short, sharp lateral spine nearly as long as stylocerite; above it a smaller, acute, secondary spine.

First pair of legs chelate, unequal. Large chela ellipsoidal, only a little swollen in middle; small obtuse tubercle on distal dorsal margin; width of palm about $\frac{1}{3}$ total length of chela; dactyl heavy, strongly arched above; fixed finger narrow at tip; carpus short and wide, prolonged downward and inward; merus stout, superior margin ending distally in sharp angular point. Smaller chela similar in form; fingers pointed; carpus short, cup shaped; merus like that of larger chela. Second legs slender, weakly chelate; carpus subdivided, first joint about equal to remaining 4. Third to fifth legs with bifurcate

dactyls, hooks unequal; outer one thinner and a little longer, regularly curved, sharp; inner one wider at base, strongly divergent, curved inward; slight obtuse protuberance or rudimentary spur proximal to inner hook.

Telson broad, tapering, obtusely rounded distally; each posterior angle with pair of unequal spines; 2 pairs of small dorsal spines, first pair at midlength, second at $\frac{3}{4}$ length. Uropodal exopods with lateral margin ending in notch with fixed spine on each side, longer movable spine between them.

Measurements in mm.—Length of body: ovigerous female 22.

Variation.—In the subspecies *S. f. elongatus* Coutière (1909:37, fig. 19) the lateral spine of the antennal scale greatly exceeds the terminal article of the antennal peduncle, and the rostrum is decidedly longer than the ocular spines. In the subspecies *S. f. carolinensis* Verrill (1922:99, pl. 22, fig. 6; pl. 39, figs. 1–1d) and *S. f. caribaea* Verrill (1922:98, text-fig. 8; pl. 39, figs. 3a–3c) the basicerite is shorter than in typical specimens.

Color.—*Synalpheus fritzmuelleri*: chela varying shades of green, darker toward extremities of fingers; body more or less colorless, specked with quite numerous tiny red chromatophores. *Synalpheus fritzmuelleri elongatus*: similar to preceding; chelipeds and second legs blue, except anterior part of chela light green (Schmitt 1930).

Habitat.—Often living in sponges; variety of niches on reefs and jetties such as loose boulders, crevices, fouling mat, and nearby bottom (Gore, et al. 1978; Christoffersen 1979; Felder and Chaney 1979); low tide mark to 51 m.

Type-locality.—*Synalpheus fritzmuelleri*, Marco, Fla.; *S. f. elongatus*, mouth of Bull Creek, S. C.

Known range.—Off Beaufort, N. C., to Santa Catarina, Brazil; Bermuda; St. Helena Island, South Atlantic; Baja California (Chace 1972).

Remarks.—Distribution of the named subspecies and varieties of *Synalpheus fritzmuelleri* shows that local populations parallel each other at widely separated locations. As Banner (1953) pointed out, earlier workers, with only a few specimens from these widely separated localities, naturally tended to name the variants, the range of variation being then unknown. Varietal names, therefore, must be regarded as conditional. Verrill (1922:89) may have concurred for he quoted Stebbing's dim view of naming infinite variations but proceeded to name varieties anyway.

In the Carolinas, this species lives on offshore reefs (Pearse and Williams 1951) in large sponges. Specimens may be found in beach drift after severe storms. Ovigerous females of typical *S. fritzmuelleri* are known from the Carolinas in February,

and June to October, indicating a long breeding season. Gore, et al. (1978) found breeding populations year round along central eastern Florida; they are known from January to April at St. Helena Island (USNM), and year round in Brazil (Christoffersen 1979).

Three recent studies have treated association of *S. fritzmuelleri* with reef substrates. McCloskey (1970) found it breeding within the *Oculina arbuscula* community off the Carolinas. Gore, et al. (1976; 1978) found it fourth in abundance among decapod crustaceans associated with subtropical sabelariid worm reefs, *Phragmatopoma lapidosa*, off eastern Florida, and Felder and Chaney (1979) in a reef off south Texas found the species in every month of the year at mean densities $> 100/\text{m}^2$.

***Synalpheus longicarpus* (Herrick)**

Fig. 71

Alpheus saulcyi var. *longicarpus* Herrick 1892 (part): 383.

Synalpheus longicarpus, Coutière 1909:53, fig. 31.—Hay and Shore 1918:383, text-fig. 6; pl. 26, fig. 2.—Verrill 1922:113, pl. 25, figs. 1a–1h.—Williams 1965:73, fig. 59.—Chace 1972:93.—Christoffersen 1979:344, figs. 23–27.

Recognition characters.—Rostrum carinate, slender and slightly longer than triangular, obtuse orbital hoods, reaching about to middle of basal antennular article; space between rostrum and hoods U-shaped, broadest in females. Eyes small, completely covered. Basal article of antennular peduncle with short stylocerite reaching to distal $\frac{1}{3}$ of article; second article $\frac{1}{3}$ longer than third article; inner flagellum filiform, outer branching at seventh joint, thickened proximally. Terminal article of antennal peduncle exceeding antennular peduncle; antennal scale with strong terminal spine separated from and exceeding rudimentary lamella distally; spine variable in length, often exceeding antennular peduncle by $\frac{1}{2}$ length of distal article; lamella of scale rudimentary in males, small and variable in females; basal article (basicerite) slender, acute, with angle but no accessory spine above, tip reaching to end of second article of antennular peduncle.

First legs chelate, very unequal. Larger chela elongate, somewhat ovate, about 2.75 times longer than broad; margins somewhat convex; posterior end swelled and produced backward beyond articulation with small, short carpus inserted below central axis of palm; anterior dorsal margin of palm with small, acute spine near base of dactyl; dactyl somewhat oblique at end, toothed at base, about $\frac{1}{4}$

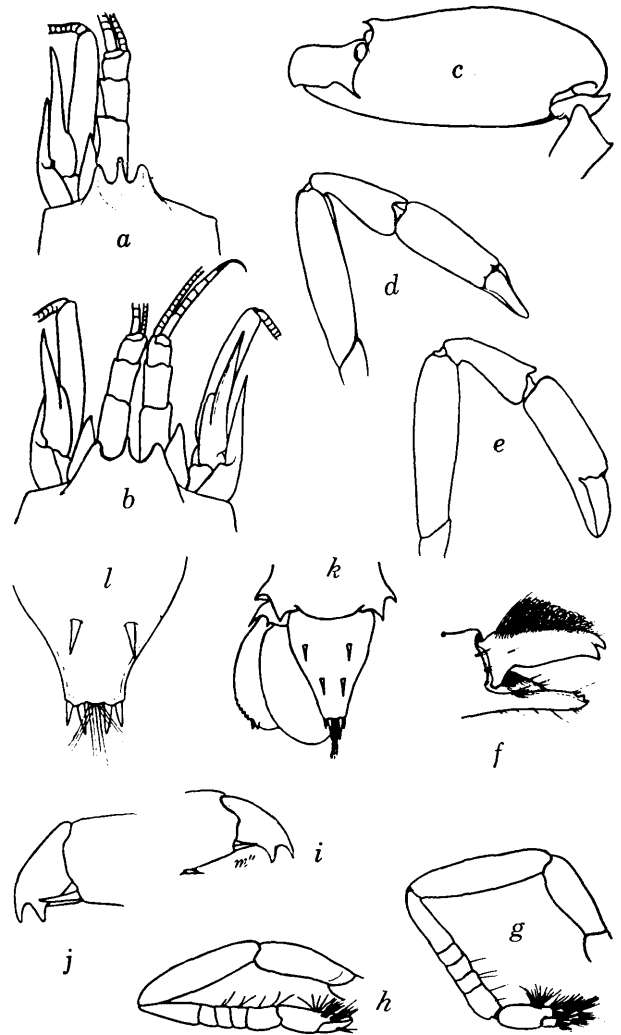


Fig. 71. *Synalpheus longicarpus* (Herrick). Anterior region in dorsal view, a, male, b, female; c, large chela; d, small first cheliped, male; e, same, female; f, fingers of small first cheliped; g, second leg of male showing subdivided carpus; h, same, female; i, dactyl of third leg; j, same in large adult; k, telson and left uropod in dorsal view, female; l, tip of telson (from Coutiere 1909).

to $\frac{1}{5}$ length of chela. Small chela elongate, gently arched dorsally, dense tuft of erect hairs on dorsal surface along most of length, cutting edge bearing 2 apical teeth, nearly straight; fixed finger with 3 teeth, apical stronger. Second pair of legs slender, weakly chelate; stronger in male than in female; carpus subdivided, first joint shorter than sum of remaining 4. Third to fifth legs with dactyls bifurcate.

Sixth abdominal segment with strong triangular tooth on each posterior angle. Telson with sinuous sides tapering to subtruncate tip; dorsal spines strong, first at $\frac{1}{3}$, second at $\frac{2}{3}$ length; tip with 2 pairs of strong spines, inner pair slightly longer. Uropodal exopod broadly oval; lateral border spined with 7 or 8 denticles, movable spine at distal end of series.

Measurements in mm.—Length of body: male 18.5 (Christoffersen (1979); ovigerous females 16 to 22.

Variation.—Length of the carpus of the small cheliped varies with age. The rostrum and projections on the orbital hoods may be entirely lacking or their relative lengths may vary (Wass 1955).

Color.—Translucent white; fingers brown.

Habitat.—To depths of 60 m in and under shells, rubble, coral, rock, or in interior of sponges; especially abundant in *Sphaciospongia* (= *Spirastrella*) (Wells, et al. 1960). Sometimes found in sponges cast on beach during storms at Beaufort, N. C.

Type-locality.—Bahamas [probably Nassau, New Providence Island].

Known range.—Beaufort, N. C., to west Flower Garden Reef, SSE Galveston, Tex.; Yucatan, Mexico, through West Indies to Rio de Janeiro, Brazil.

Remarks.—Christoffersen (1979) synonymized *S. pandionis* Coutière and its subspecies with *S. longicarpus*, discussing variations in these groups as well as similarities to still other species that he implied may fall into large and variable species. Presumably, further work needs to be done before the relationships within this complex are understood, but the variability probably poses no obstacle to identification in the Carolinian region.

Synalpheus longicarpus is common in the Carolinas and often occurs in enormous numbers in the canals of large sponges. Infestation by parasitic isopods is common, *Phryxus subcaudalis* occurring on the surface of the abdomen and *Synsynella deformans* in the branchial chambers.

Ovigerous females have been taken off North Carolina in August and December; they are also known from the Windward Islands, West Indies in March and April, in Florida during October-November (USNM), and Rio de Janeiro, Brazil, in February (Christoffersen 1979). Herrick (1892) stated that the species hatches in essentially the adult form, but Coutière (1909) noted that it hatches as a zoea. Coutière (1909) and Wass (1955) remarked that a number of ovigerous females occur among crowded populations in sponges.

Synalpheus minus (Say)

Fig. 72

Alpheus minus Say 1818:245.

Synalpheus minus.—Hay and Shore 1918:382, text-fig. 5; pl. 26, fig. 3.—Verrill 1922:102, pl. 21, fig. 1; pl. 23, fig. 3; pl. 25, fig. 3; pl. 31, fig. 4; pl. 33, figs. 4, 4a; pl. 36, figs 1–1d, 2; pl. 47, figs. 1–1c, 2; pl. 48, figs. 3–3c.—Schmitt 1935a:149.—Williams 1965:70, fig. 57.—Chace 1972:95, figs. 35–36 (not *S. brevicarpus*).—Coelho and Ramos

1972:150.—Christoffersen 1979:350, fig. 28.

Recognition characters.—Front of carapace with 3 teeth each in form of equilateral triangle; rostrum usually a little wider at base, compressed and sometimes slightly longer than orbital teeth. Eyes completely covered by large orbital hoods. Basal article of antennular peduncle with stylocerite reaching to distal $\frac{1}{3}$ of second article; third article $\frac{1}{2}$ length of second; second of intermediate length; inner flagellum filiform, outer flagellum thickened proximally. Antennal scale narrow, inner edge regularly curved; lateral spine a little longer than antennular peduncle, separated from and exceeding lamella; basal article (basicerite) reaching to distal end of basal antennular article, above it a prominent secondary spine (subject to great variation (Chace 1972)).

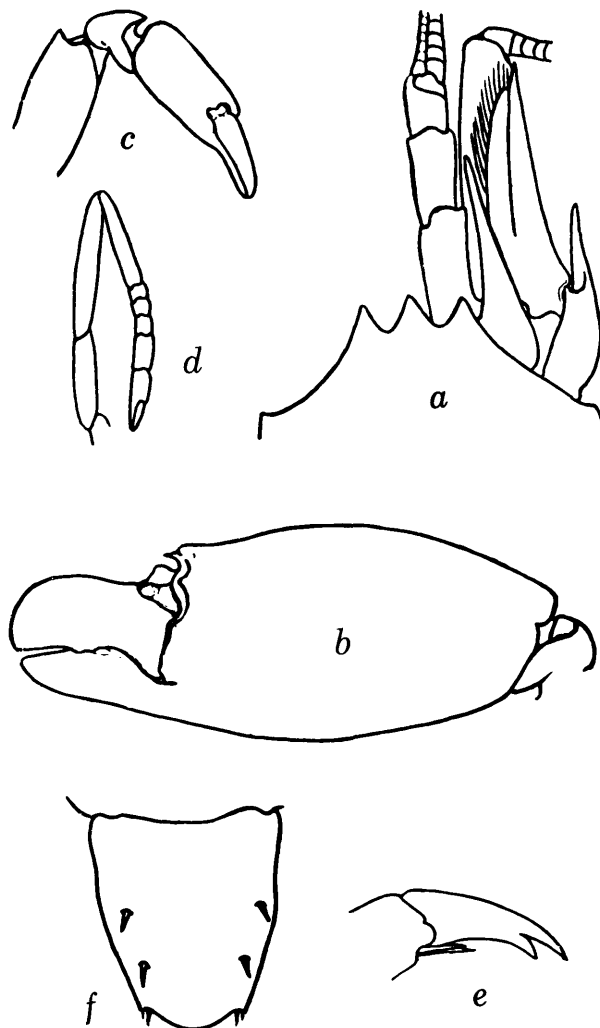


Fig. 72. *Synalpheus minus* (Say). a, Anterior region in dorsal view with right antennule and antenna; b, large chela; c, small first cheliped; d, second leg showing subdivided carpus; e, dactyl of third leg; f, telson in dorsal view (from Coutière 1909).

First legs chelate, unequal, thicker in male than in female. Large chela ovoid; palm about 2.5 times length of fingers, anterior dorsal margin with strong, sharp tooth at inner side and blunter tooth on lateral and ventral side near base of dactyl; dactyl broad, larger than fixed finger, tip obtuse, cutting edge a little sinuous, large tooth at base, dorsal edge curved distally; fixed finger with tip nearly straight, inner edge a little sinuous. Smaller chela elongate, slender, about $\frac{1}{3}$ length of larger; fingers a little shorter than palm, with tufts of hair, acute at tips and curved a little downward; palm narrowly elliptical, surface plain. Second legs slender, weakly chelate; carpus subdivided with joints diminishing as follows (numbered from proximal end): 1, 5, 2–3–4.

Telson with sides slightly sinuous, tip broadly rounded; 2 pairs of dorsal spines, first pair at about midlength, second pair at about $\frac{3}{4}$ length; distal margin with pair of spines at each posterolateral corner. Uropodal exopods with lateral margin ending in notch armed with 2 spines separated by longer movable spine.

Measurements in mm.—Length of body: maximum 38 (Chace 1972).

Color.—Body translucent, yellowish white; large chela white or translucent gray, fingers orange, tips red; banded near base of fingers with white in female, white tipped with green in male. Body sparsely dotted by green chromatophores, tips of third maxillipeds and distal $\frac{1}{3}$ of first pair of chelae bright pink; eggs green (Christoffersen 1979).

Habitat.—Any place that provides hiding; sponges, dead coral, coral rock, abandoned gastropod shells; beneath stones, *Porites*, and *Pocillopora* on grass flats in West Indies (Chace 1972; Christoffersen 1972); intertidal to 85 m.

Type-locality.—"Coasts of the southern states, and off East Florida."

Known range.—Near Cape Hatteras, N. C., to São Paulo, Brazil (Christoffersen 1979); Bermuda.

Remarks.—A number of authors, among them Hay and Shore (1918) and Verrill (1922), pointed out that Brooks and Herrick (1892) identified *Alpheus normanni* (= *packardii*) as *A. minus*. *Synalpheus minus*, not treated by them, was not available for study in the Beaufort, N. C., harbor area. Christoffersen (1979) gave a detailed synonymy.

A long breeding season is indicated for this species. Ovigerous females have been taken from February to November in various localities from North Carolina to the Gulf Coast; spring in the Windward Islands, West Indies; April in Bermuda; September in Venezuela; January and February in Rio de Janeiro. Adults usually occur in pairs (Wass 1955).

Synalpheus townsendi Coutière

(Small snapping shrimp)

Fig. 73

Synalpheus townsendi Coutière 1909:32, figs. 14–17 (16–17 as subspecies).—Hay and Shore 1918:384, pl. 26, fig. 1.—Verrill 1922:100.—Williams 1965:72, fig. 58.—Chace 1972:104.—Pequegnat and Ray 1974:249, figs. 53d, 55.—Christoffersen 1979:352.

Recognition characters.—Rostrum slender, 1.5 times as long as lateral teeth and reaching usually to end of proximal $\frac{1}{3}$ of second article of antennular pe-



Fig. 73. *Synalpheus townsendi* Coutière. a, Anterior region in dorsal view with left antennule and antenna; b, tip of large chela; c, large cheliped, merus, carpus and proximal end of propodus; d, small first cheliped; e, second leg showing subdivided carpus; f, dactyl of third leg; g, telson in dorsal view (from Coutière 1909).

duncle, armed with ventral prolongation embracing ocellary beak. Teeth on orbital hoods slender; eyes completely covered by hoods. Basal antennular article overreached by stylocerite; third article about $\frac{1}{2}$ length of second; inner flagellum filiform, outer flagellum thickened proximally, bifurcate beyond fourth joint. Antennal scale with strong, slender lateral spine separated from and exceeding lamella distally, spine reaching about to or beyond end of antennal peduncle; basal article (basicerite) well developed, angled above but lacking dorsal spine, extremity reaching to distal $\frac{1}{3}$ of basal antennular article.

First pair of legs chelate, very unequal. Large chela with small, acute dorsal spine at distal margin of palm; upper margin of dactyl elevated into thick crest; carpus small, irregularly shortened; merus with dorsolateral margin convex, ending in hooked spine. Small chela $\frac{1}{3}$ length of large one; no brush of hairs on dactyl. Second pair of legs slender, weakly chelate; carpus subdivided, first joint longer than others combined. Third to fifth legs with bifurcate dactyls, both hooks nearly parallel, ventral one narrower and much shorter than dorsal.

Abdomen compressed. Telson with sides somewhat convergent; posterior angles sharp and each provided with pair of spines, inner spine longer than outer; 2 pairs of strong dorsal spines, first pair at $\frac{1}{3}$, second at $\frac{2}{3}$ length. Uropods ovate, exopod with lateral margin ending in notch with strong fixed spine at its outer and inner angles, between these spines a longer movable spine.

Measurements in mm.—Length of body: ovigerous females 13.

Variation.—The rostrum is variable in length, often shorter than as described above.

Color.—Body and legs translucent pinkish red; large chela pink, changing to green on fingers.

Habitat.—Often found in large sponges or on reefs; low tide mark to 102 m.

Type-locality.—Gulf of Mexico south of Cape San Blas, Fla., 29°14'00"N, 85°29'15"W, 46 m.

Known range.—Off Beaufort, N. C., to Rio de Janeiro, Brazil; Bermuda; Gulf of California.

Remarks.—Ray (1974) discussed variants seen in the western Gulf of Mexico that are similar to the Pacific *S. t. brevispinis*; he concluded, as have other authors, that great variation in *Synalpheus* renders such named subspecies invalid, although Christoffersen (1979) thought that this material might represent a distinct species.

Wass (1955) remarked that the species seems less dependent on sponges than other members of the genus taken in the Alligator Harbor area of Florida. Pearse and Williams (1951) found it on offshore reefs and in sponges off North Carolina at 13–15 and 29–37 m respectively. Gore, et al. (1978) found breeding from January to August on sabel-lariid worm reefs, *Phragmotopoma lapidosa*, along eastern Florida; elsewhere ovigerous females have been found virtually the year round in Florida and in Texas, in February, June, August, and September in the Carolinas, July and August at Obregon, Mexico, September in Venezuela, and November in Brazil (Christoffersen 1979).

Family Ogyrididae

Caridea with first 2 pairs of legs chelate, nearly equal in size and not much if any larger than other legs. Carpus of second legs subdivided. Rostrum small or wanting. Eyestalks long, slender, fully exposed but with corneal surface reduced. Telson thick, obtusely pointed. Blades of uropods curved outward. Thelycum present in females (Hay and Shore 1918).

Genus *Ogyrides* Stebbing 1914

Stebbing 1914:31.—Hemming 1958b:158.

Key to Species

1. Single movable spine behind rostrum on middorsal line *O. alphaerostris*

 Postrostral crest with 3 to 14 small, fixed spines *O. hayi*

Ogyrides alphaerostris (Kingsley)

Fig. 74

Ogyris alphaerostris Kingsley 1880:420, pl. 14, fig. 7.

Ogyris occidentalis Ortmann 1893:46, pl. 3, fig. 4.

Ogyrides yaquiensis Armstrong 1949:3, fig. 1.

Ogyrides limicola Williams 1955b:56, fig. 1.—1965:74, fig. 60.

Ogyrides occidentalis.—Christoffersen 1979:356, fig. 31a-i.

Ogyrides alphaerostris.—Williams 1981:144.

Recognition characters.—Rostrum short, depressed, equilaterally triangular. Postrostral carina with 8 to 14 teeth, flanked on each side by row of setae extending to tip of rostrum. Pterygostomian

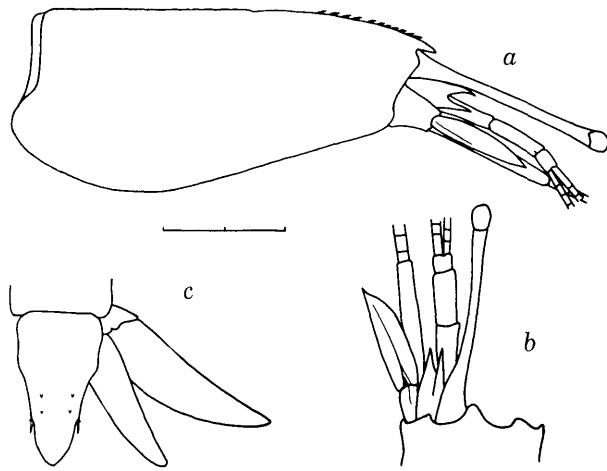


Fig. 74. *Ogyrides alphaerostris* (Kingsley). a, Carapace and anterior appendages in lateral view; b, anterior region in dorsal view showing left eyestalk, antennule and antenna; c, telson and uropods of right side, approximately 2 mm indicated (from Williams 1955c).

area broadly obtuse. Eyestalks long, lightly setiferous dorsally and dorsomesially, narrowest in middle, exceeding antennular peduncles by up to 2.5 times corneal length. Antennal and antennular peduncles nearly equal in length; second antennular article almost 2 times as long as third article; styllocerite of basal article terminating in 2 strong acuminate spines of nearly equal length, never exceeding basal antennular article. Antennal scale and second article of antennular peduncle reaching nearly same level distally; scale evenly rounded mesially, 3 times longer than greatest width, greatest width in basal half; basal article with lateral and ventral spine inconspicuous or absent. Third maxilliped, when extended, exceeding eyestalks.

First legs exceeding midlength of antennal peduncle by full length of chelae; fingers of chelae pointed, agape when closed. Carpus of second legs 4-segmented; third leg with single spine on ischium and merus.

Telson with anterior pair of spines placed well behind lateral prominences. Uropods with exopods slightly falciform, lateral borders nearly straight. Telson with 3 horny ridges at proximolateral corners ventrally, and uropods with an interlocking horny eminence on basal article dorsally.

Measurements in mm.—Length of body: ovigerous holotypic female 16.

Variation.—Individual variations are shown in number of spines on the postrostral crest, in length of eyestalks, and in lengths of spines of the styllocerite.

Color.—Females with general body structure colorless, clear; internal organs visible; gut dark; he-

patopancreas light brown; eyestalks, antennal and antennular peduncles, and distal portions of anterior appendages with red and yellow spots; uropods and sixth segment of abdomen with scattered red spots. Ovigerous females with yellow green (chartreuse) colored eggs on swimmerets (Williams 1955a).

Habitat.—On (or in) the bottom of muddy estuaries, or in plankton; inshore ocean on very fine sand (Frankenberg and Leiper 1977); surface to 52 m. Collections have been made in an observed bottom salinity range of 9 to over 31‰. Felder and Chaney (1979) reported one occurrence in a fish stomach from a nearshore reef off Texas.

Type-locality.—Northampton County, Va., eastern shore, Atlantic side.

Known range.—Eastern shore of Accomack County, and lower James River, Va., through Gulf of Mexico to Rio Grande do Sul, Brazil (Christoffersen 1979).

Remarks.—The systematic confusion surrounding the two species *O. alphaerostris* and *O. hayi* was discussed by Williams (1981). The two species are quite distinct morphologically and differ in total size, *O. alphaerostris* being the smaller. The latter occurs most frequently in collections from estuaries. Young specimens have frequently been taken in plankton tows made at night in Bogue Sound, N. C., but adults are seldom taken by this method of collection. Occurrence of adults in samples taken with a beam trawl suggests burrowing habits similar to those described for *O. hayi*, but in muddier situations or very fine sand (Frankenberg and Leiper 1977), and often in low salinities.

In North Carolina, collections of *O. alphaerostris* have been made in all seasons of the year. Ovigerous females have been taken from May to September there, and in April and October in Florida. From ovigerous females taken July 9 in black mud in a Petersen grab at 6–7 m depth in lower York River, Va., and maintained at 23.9°–28.9°C in 19.6‰ salinity, eggs hatched and developed through 8–9 zoeal stages and a postlarva, molting every two days during the first half of development but less often thereafter (Sandifer 1974b). Lengthened eyestalks and shortened first legs do not assume adult proportions until the postlarval stage. Unlike alpheid larvae which show precocious development of the fifth legs along with the first legs, the legs of *O. alphaerostris* develop in sequence from first to last. In plankton studies, Sandifer (1973d; 1974b) commonly collected larvae of this species in the York River and once in lower Chesapeake Bay, concentrations ranging to 37.5/kL. Nearly all were in a salinity range of 15 to 25‰, mostly in temperatures between 23° and 27°C. Eight zoeal stages were re-

covered and these were generally larger than comparable reared stages. Peak occurrences were during July and September, but presence ranged from May to November. All zoeal stages were more abundant in bottom than in surface samples.

Ogyrides hayi Williams

Fig. 75

Ogyris alphaerostris.—Hay and Shore 1918:388, fig. 11, pl. 26, fig. 9.—Pearse, Humm, and Wharton 1942:148, 185, figs. 1, 12.

Ogyrides alphaerostris.—Williams 1955b:56–57.—1965:75, fig. 61.—Van Engel and Sandifer 1972:156.—Chace 1972:106.—Saloman 1979:151.

Ogyrides hayi Williams 1981:145.

Recognition characters.—Rostrum depressed, equilaterally triangular, tipped with setae. A single, postrostral, movable spine. Pterygostomian area obtuse. Eyestalks long, setiferous mesially, narrowest in middle, exceeding antennular peduncle by approximately twice corneal length. Antennal and antennular peduncle nearly equal in length; second article of antennular peduncle about 3 times

as long as third article; stylocerite terminating in 2 acuminate spines; lateral spine longer. Antennal scale and second article of antennular peduncle reaching same level distally; scale evenly rounded mesially, approximately 3 times longer than greatest width near base; basal article with lateral and ventral spine. Third maxilliped, when extended, exceeding eyestalks.

First legs scarcely extending to tip of antennal scale. Second legs exceeding antennal scale by full length of chelae; fingers of chelae pointed, agape when closed. Carpus of second legs 4-segmented; third leg with single spine on ischium and merus.

Telson with anterior pair of spines placed a little behind level of lateral prominences. Uropods with exopods somewhat falciform, curvature greatest distally. Telson with 3 horny ridges at proximolateral corners ventrally, and uropods with an interlocking horny eminence on basal article dorsally.

Measurements in mm.—Length of body: ovigerous female 27.

Color.—Body nearly transparent; red and green spots or flecks on eyestalks, antennules, and antennae; green only on distal joints of third maxillipeds; red only on basal articles of legs on first pleopods, at bases of all pleopods, and on abdominal pleura and sterna; a conspicuous red area on sixth abdominal segment distoventrally and another around mouth.

Habitat.—Often found on firm bars of sand just offshore along open ocean in water 1–3 m deep (Pearse, et al. 1942; Saloman 1979); surface to 9 m.

Type-locality.—Off Bogue Bank W of Ft. Macon, North Carolina, ~3.5 m.

Known range.—Beaufort, N. C., to Sebastian Inlet, Fla.; northwestern Florida to Mississippi; Puerto Rico.

Remarks.—Hay and Shore (1918), lacking comparative material, referred their species with a single postrostral spine to the then only known ogyridid from the western Atlantic, but it remained unrecognized in synonymy until Williams (1981) clarified the taxonomic status of postrostrally multi-spined *O. alphaerostris* and supplied a name for the single spined species.

Ogyrides hayi apparently is more restricted to high-salinity water than *O. alphaerostris*, for it has seldom been collected in the sounds of North Carolina and then only near inlets. Pearse, et al. (1942) described burrowing habits of the species on sandy bars and commented that members of the genus are unusual in that they have long eyestalks like *Uca*, yet are burrowers. *Ogyrides hayi* burrows forward (head first), using the third maxillipeds and legs for digging and propulsion. Sand is pushed upward and over the head, the abdomen often

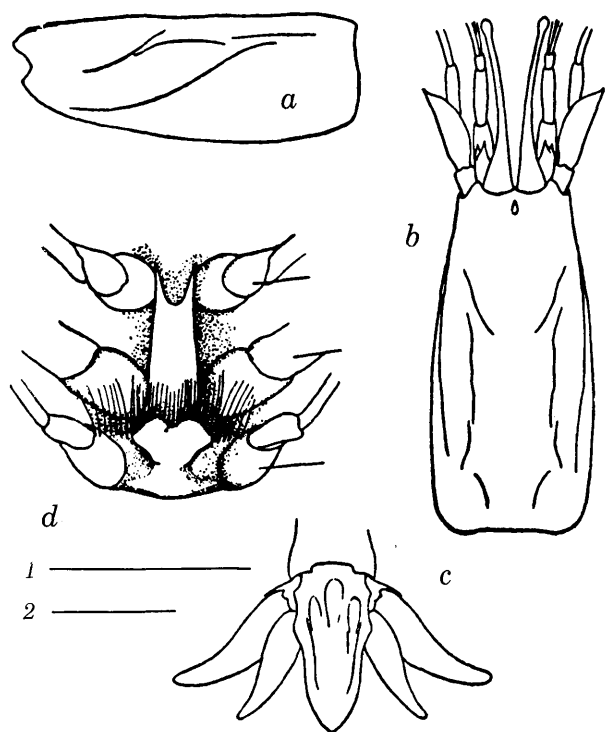


Fig. 75. *Ogyrides hayi* Williams. a, Carapace in lateral view; b, carapace and anterior appendages in dorsal view; c, uropods and telson in dorsal view; d, sterna of last three thoracic segments showing thelycum of female. Scales: 1(a-c)=5 mm; 2(d)=2 mm (from Hay and Shore 1918).

being left above sand for a time, especially in ovigerous females. The fifth leg is held high on the sides and stroked dorsally and posteriorly, legs 1 to 4 are stroked laterally and posteriorly, and the third maxillipeds moved anteriorly and dorsally. The animals scrape food from the antennae with setose mouth parts.

Ovigerous females have been taken in July and August in Florida and North Carolina, July in Puerto Rico, and August in Mississippi (USNM).

Various authors cited imply that the breeding season extends through the summer months.

Family Hippolytidae

Caridea with first 2 pairs of legs chelate, first pair not much stronger than rest; carpus of second pair of legs subdivided. Eyes well developed and not covered by carapace. Mandibles usually deeply cleft.

Key to Genera and One Species

1. Rostrum shorter or longer than carapace, but clearly less than 1.3 times its length 3
 Rostrum noticeably longer than carapace, 1.4 times to nearly twice its length 2
2. Rostrum horizontal, lacking basal crest of crowded teeth *Tozeuma*
 Rostrum upturned, with basal crest of crowded teeth *Exhippolyasmata oplophoroides*
3. Carpus of second leg subdivided into 7 or fewer joints 4
 Carpus of second leg subdivided into more than 7 joints, multiarticulate *Lysmata*
4. Carpus of second leg subdivided into 3 or 5 joints 5
 Carpus of second leg subdivided into 7 joints 7
5. Carpus of second leg divided into 3 joints 6
 Carpus of second leg divided into 5 joints *Thor*
6. Rostrum with deep ventral blade; series of small spines (5- 9) along anterior margin of carapace below eye *Latreutes*
 Rostrum lacking deep ventral blade but may be somewhat deepened distally; no small spines on edge of carapace below eye *Hippolyte*
7. Supraorbital spines absent. *Eualus*
 Supraorbital spines present 8
8. One supraorbital spine on each side; third maxilliped without exopod *Lebbeus*
 Two or more supraorbital spines on each side; third maxilliped with exopod *Spirontocaris*

Genus *Eualus* Thallwitz 1892

Holthuis 1947:10.—1950:46.—1955:100.—China 1966:243.—Noël 1978:22.

Rostrum short or long. Supraorbital spine ab-

sent. Stylocerite long, ending in sharp point. Antennal spine present. Mandible with incisor process and palp of 2 articles. Third maxilliped with exopod. Carpus of second leg divided into 7 joints, third from proximal end longest. Telson with 2–7 pairs of dorsal spines.

Key to Species

(From Williams 1974c; Noël 1978)

1. Tip of rostrum usually not reaching distal edge of eye (rarely exceeding eye). *E. pusiolus*
 Tip of rostrum greatly exceeding distal edge of eye 2
2. Rostrum slender, toothed dorsally throughout length; second leg often with epipod *E. gaimardii*
 Rostrum noticeably deepened at midlength, lacking dorsal teeth on distal part beyond eye; second leg usually without epipod *E. fabricii*

Eualus fabricii (Krøyer)

Fig. 76

Hippolyte fabricii Krøyer 1841:571.

Spirontocaris fabricii.—Leim 1921:138, pl. 4, fig. 10.

Eualus fabricii.—Holthuis 1947:10 (synonymy).—

Couture and Trudel 1968:873, fig. 13.

Recognition characters.—Rostrum slender but variable in depth; thicker above but lamellate below distally; horizontal or trending slightly upward distally to end in acute tip; about twice length of antennular peduncle; dorsal margin without teeth anterior to distal edge of eye but 1–7 teeth on posterior half (usually 2–3 of these postorbital), and 1–5 ventral teeth. Carapace with strong antennal spine below suborbital lobe and smaller pterygostomian spine at distoventral angle. Eyes well developed. Stylocerite with acutely pointed tip reaching to or beyond distal margin of basal antennular article; second article shorter, with dorsolateral spine; third article about $\frac{1}{2}$ length of second and with dorsal spine on distal margin, slender flagellum extending well beyond antennal scale in male, less far beyond in female. Antennal scale overreaching antennular peduncle by half its length, outer border straight; strong distolateral spine exceeded by lamella. Third maxilliped not reaching to tip of antennal scale; epipod and exopod present.

First leg with epipod; moderately stout, reaching about tip of antennal peduncle; carpus about as long as palm; fingers with darkened and hooked corneous tips. Second leg much longer and more slender, carpus divided into 7 joints, generally without epipod. Legs 3–5 well developed, each with row of spines laterally on merus; dactyls with strong curved spines on flexor surface progressively longer distally, tip biunguiculate.

Abdomen with pleura of first 3 segments broadly rounded; acute posteroventral spine on segments 4 and 5; less prominent on 6, but strong acute spine with ventral shoulder projecting beyond base of telson. Telson with (3)4–8 pairs of dorsal lateral spines.

Measurements in mm.—Length of body: males to 36 (Leim 1921); females to 58.

Color.—White ground spotted with deep bright red: area of fine red dots and larger spots to either side of dorsal carapace spines; larger scattered spots ventrally and posteriorly on cephalothorax; still other spots just posterior to orbit and at end of rostrum. Antennules and antennae with bands near end; edge of each antennal joint with faint red line. Basis and coxa of legs 3–5 purple; merus of first leg with red ring, that of 2–5 with 2; propodus of 3–5 with ring. Abdominal segments with scattered spots, small dots posteriorly on third segment (Leim

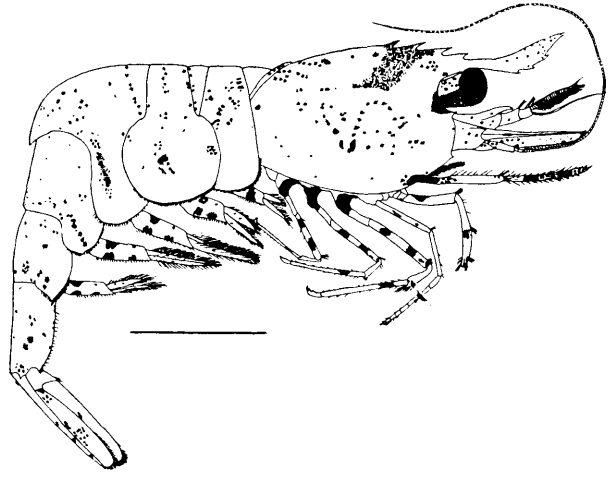


Fig. 76. *Eualus fabricii* (Krøyer). Animal in lateral view, 2 mm indicated (from Leim 1921).

1921). Fairly transparent with reddish orange in hepatic region; ovigerous females translucent white with red markings (MacGinitie 1955).

Habitat.—Variety of bottoms; 4–200 m.

Type-locality.—Greenland.

Known range.—Northwestern Greenland to Cape Cod; arctic Alaska to Cook Inlet; Siberian seacoast; Sea of Japan (Holthuis 1947; Squires 1965a).

Remarks.—Almost all females examined from Newfoundland and Labrador are ovigerous in spring (May–June) and autumn (October–November) (Squires 1965a). In Foxe Basin, Squires (1962) found only 64% of mature females potentially ovigerous in autumn, which may indicate that females in this population spawn only every two years, although those from Hudson Bay may spawn annually (Squires 1967). Ovigerous females in the USNM collection are represented from northwestern Greenland in June and July, Cape Sabine, Alaska, in August, and Point Barrow, Alaska, and Plover Bay, Siberia, in September. MacGinitie (1955) reported them at Point Barrow in mid-October. Stephensen (1916) considered this to be the most widely distributed species of *Eualus* (= *Spirontocaris*) in southern Greenland, and Frost (1936) reported its larvae to be the most common of the genus *Eualus* in plankton; although never numerous, the greatest numbers of larvae were reported off the coast of Labrador in spring and off the southeast coast of Newfoundland in fall. Pike and Williamson (1961) reviewed the work of previous authors on larvae, pointing out that Stephensen described and figured stages III, and V or VI, and that Frost figured the last zoeal stage, probably stage VI or VIII.

Food of the shrimp in the Hudson Bay–Foxe Basin region contains phyto-benthos, crustaceans (including ostracods), hydroids, foraminiferans,

polychaete worm fragments, and sponge spicules, in descending order of quantity (Squires 1967). The species is preyed upon by cod, ringed, bearded, and harbor seals (Squires 1965a), and beluga whales (Squires 1967).

***Eualus gaimardii* (H. Milne Edwards)**

Fig. 77

Hippolyte Gaimardii H. Milne Edwards 1837:378.

Eualus gaimardii.—Heegaard 1941:36.—Holthuis 1947:10 (synonymy).—1950:46, fig. 15.

Eualus gaimardi.—Christiansen and Christiansen 1962:18.—Couture and Trudel 1968:875, fig. 14b.

Eualus belcheri.—Couture and Trudel 1968:875, fig. 14a.

Recognition characters.—Rostrum slender, curving slightly upward distally to end in acute tip, slightly carinate laterally, twice length of antennular peduncle; armed usually with 5–7 dorsal teeth (including postrostral crest) progressively more remote distally, and usually 3–5 ventral teeth. Carapace with antennal spine below suborbital lobe and pterygostomial spine at distoventral angle. Eyes well developed. Distal margin of basal antennular article exceeded by acutely pointed stylocerite; second article shorter, with distolateral spine; third article about $\frac{1}{2}$ length of second and with erect dorsal spine on distal margin. Antennal scale overreaching antennular peduncle by half its length, outer border slightly concave; distolateral spine exceeded by lamella. Third maxilliped reaching to or slightly short of tip of antennal scale; epipod and exopod present.

First and second legs with epipods; first leg

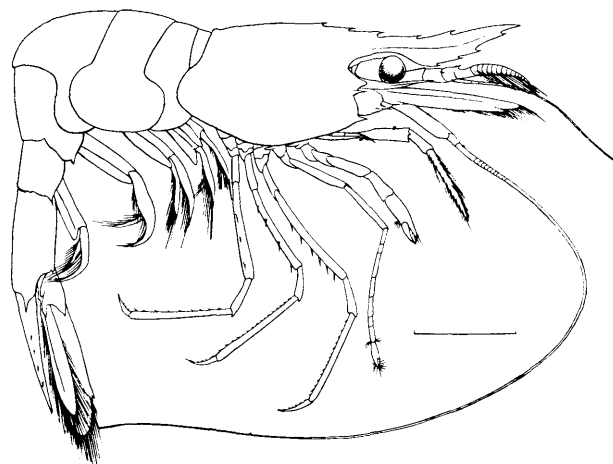


Fig. 77. *Eualus gaimardii* (H. Milne Edwards). Animal in lateral view, 5 mm indicated (from Holthuis 1950).

moderately stout, reaching about to end of antennal peduncle; carpus about as long as palm; fingers with darkened and hooked, corneous tips. Second leg much longer and more slender, carpus divided into 7 joints. Legs 3–5 well developed, dactyls with strong, curved spines on flexor surface progressively longer distally.

Abdomen with pleura of first 3 segments broadly rounded, posterior margin of third segment with mesiodorsal eminence variously developed; acute posteroventral spine on segments 4 and 5, less prominent on 6, but strong, acute spine with ventral shoulder projecting beyond base of telson. Telson with 3–5 pairs of dorsolateral spines.

Measurements in mm.—Length of body: to 100 mm (Smaldon 1979).

Variation.—This species shows great variation over its broad range. The rostrum proper varies considerably in shape and armature (dorsal teeth 3–7, ventral 2–6) (Dons 1915, fig. 5). Holthuis (1947) summarized the status of the named varieties of *E. gaimardii* as viewed by a number of authors. He concurred with the opinion that the species is composed of local forms which cannot be sharply distinguished because they gradually merge over their range: in the southern part of the range, both sexes have the third abdominal segment smooth and rounded (typical *gaimardii*); in the far northern and northwestern Atlantic, Arctic Ocean and North Pacific part of the range, males bear a strong tubercle ending in a curved hook on the posteromedian part of this segment and females have a distinct blunt tubercle (var. *belcheri*); in the area between these range extremes, males have a blunt tubercle on the third abdominal segment and females are smooth (var. *gibba*). Some authors continue to at least mention these varieties, for example, Greve (1963) included them in discussion, and Noël (1978) included them in his key to species of the genus; Couture and Trudel (1968) accorded var. *belcheri* full species rank, and Squires (1965a) recognized it as a subspecies, although in his other papers he did not always make a distinction and in one instance (1968) considered representatives of all these variants from the far northern Queen Elizabeth Islands area as *E. gaimardii*. I follow Holthuis here.

Color.—Translucent, “slightly tinged with greenish brown” (Smith 1879); transparent pale green with markings of red, eggs green (MacGinitie 1955); “pale translucent, with brownish-red markings on carapace on pleon” (Smaldon 1979).

Habitat.—On variety of bottoms such as stones, gravel, sand and shells, or mud bottom with algae, often off glaciers in North, -1.67° to 5.46°C , scarce above 3°C (Christiansen and Christiansen 1962); usually 20 to 150 m, but intertidal (Smith 1879) to 900 m (Smaldon 1979).

Type-locality.—"Habits les mers d'Islande" (off Iceland).

Known range.—Circumarctic southward to Cape Cod; North Sea (Kiel and Yarmouth); White Sea; Sitka, Alaska; Siberia (Holthuis 1947; Squires 1965a). Heegaard (1941) mapped the distribution.

Remarks.—Stomach content of this species in Hudson Bay was found to consist of phytobenthos, ostracods, amphipods, foraminiferans, hydroids, polychaetes, pelecypod shells, and sponge spicules, in descending order (Squires 1967).

Information on occurrence and life history is spotty and undoubtedly reflects discontinuous and seasonal collecting, especially in higher latitudes. For example, Squires (1967) found a few specimens in 33% of hauls taken in Hudson Bay, mostly in Richmond Gulf (east of Belcher Islands). The species was also present in stomachs of beluga whales taken along the northwestern coast of the Bay. Males were judged to be mature at a carapace length of 6 mm, females at 9 mm, but only 41% of females in this bay were assessed as potentially ovigerous per year. Squires postulated biennial spawning in these females (also in Foxe Basin, Squires 1965a), which perhaps are a stressed population. The USNM collection contains ovigerous females from Bering Strait in June to Point Barrow, Alaska, in September, as well as off Newfoundland, Labrador, and northeastern Greenland in July-August. MacGinitie (1955) reported eggs on females in August, September and October in progressive states of development. Smaldon (1979), referring to British coastal species, reported ovigerous females from January to April. Christiansen and Christiansen (1962) found ovigerous females in Spitsbergen during July-August.

From *E. gaimardii* eggs hatched in March at Millport, Scotland, Pike and Williamson (1961) reared and described five zoeal stages and a megalopa. Only stages I and II were found there in plankton. These authors reviewed published accounts of the larvae of this species, remarking on difference in size of eggs and larvae over the geographic range which they thought were most likely features of the named varieties.

Hansen (1897) reported the parasitic copepods *Choniostoma hansenii* and *C. mirabile* from the branchial cavity of *E. gaimardii*, and MacGinitie (1955) added the isopod *Phryxus abdominalis*.

Eualus pusiolus Krøyer

Fig. 78

Hippolyte pusiola Krøyer 1841:576.

Spirontocaris pusiola.—Kemp 1910:107, pl. 15, figs. 6–8.

Eualus pusiolus.—Holthuis 1947:11 (synonymy).—Couture and Trudel 1968:877, fig. 16.

Recognition characters.—Body small. Rostrum small, not exceeding eye; directed slightly downward; dorsal margin with 1–4, rarely 5, teeth, 1–2 of these behind orbital margin; tip acute, rarely 1 ventral tooth near tip making it bidentate. Carapace with antennal spine below suborbital lobe and small pterygostomian spine at distoventral angle. Eyes well developed. Stylocerite broad and not widely separated from basal antennular article for most of its length but narrowed abruptly to acute distolateral tip reaching from $\frac{2}{3}$ length to distal margin of basal antennular article; basal article with strong dorsolateral, distal spine, and mesioventral spine; second article shorter, with prominent, analogous distolateral spine; third article somewhat shorter than second and with small dorsal spine on distal margin. Antennal scale exceeding antennular peduncle by $\frac{1}{3}$ – $\frac{1}{2}$ its length, outer border straight, distolateral spine about equal to lamella; basal article of peduncle bearing distal acute ventrolateral spine and obtuse dorsolateral projection. Third maxilliped reaching to or beyond tip of antennal scale; epipod and exopod present.

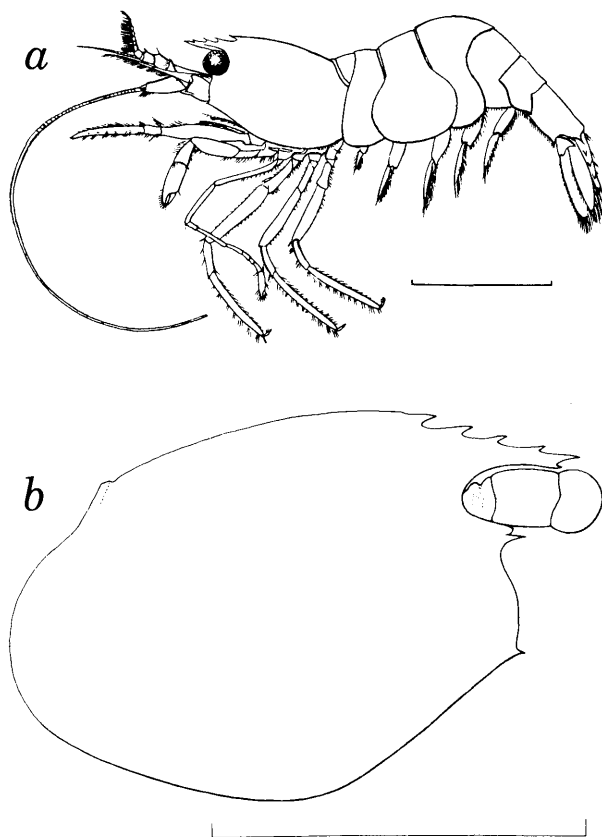


Fig. 78. *Eualus pusiolus* (Krøyer). a, Animal in lateral view, 5 mm indicated (from Kemp 1910); b, carapace in lateral view, 5 mm indicated (from Williams 1974c).

Legs 1–3 with epipods. First leg stout, reaching about as far as tip of antennular peduncle or length of fingers beyond it; carpus as long as palm; fingers with darkened and hooked, corneous tips. Second leg much longer and more slender, carpus divided into 7 joints. Legs 3–5 well developed, dactyls with a few spines on flexor surface, penultimate one stronger and more curved, forming with terminal spine, a biunguiculate tip.

Abdomen with pleura of first 3 segments broadly rounded; acute posteroventral spine on segments 4 and 5; less prominent on 6, but broad, acute spine with slight ventral shoulder projecting beyond base of telson. Telson with 4 or 5 pairs of dorsal spines.

Measurements in mm.—Length of body: to 30 mm (Couture and Trudel 1968).

Variation.—There is some variation in strength of spines on the antennular and antennal peduncles and in separation of the stylocerite from the basal antennal article. Dons (1915) figured some rostral variants; dorsal teeth on the rostrum tend to increase with age (Greve 1963).

Color.—Few deep red to orange-red spots scattered over whitish translucent background; spots evenly spread over cephalothorax and first two abdominal segments, 5 or 6 spots on third abdominal segment, and fourth to sixth segments with 2 or 3 ventral spots and posteroventral edges defined by red line; edges of uropods red. Scattered spots on peduncles of antennules and antennae, third maxillipeds and legs; joints of antennal flagellum and lateral edge of antennal scale red (Leim 1921). Pink, green, and cobalt forms are known (Smaldon 1979). Dark brownish green like color of *Laminaria* among which it occurs; stripes of red brown on body and extremities; eggs green (Greve 1963).

Habitat.—Sandy bottom with algae preferred (Greve 1963); inshore rock and offshore gravel (Allen 1966); intertidal among algae or under rocks low on shore to over 500 m (Smaldon 1979), in a recorded temperature range of -1.3° to 10.5°C (Williams and Wigley 1977).

Type-locality.—Norway's west coast.

Known range.—Gulf of St. Lawrence to off Cape Henry, Va.; Bering Island, Alaska Peninsula, and Aleutian Islands; San Juan Islands, Wash.; Iceland; Murman coast to Channel Islands; southward along Bay of Biscay to Spain (Holthuis 1947; Squires 1965a; Smaldon 1979).

Remarks.—Northeast of the British Isles breeding occurs year round, but is at its greatest intensity from January to September–October (Smaldon 1979). There are two broods of 8–10 weeks each there, a female bearing 100–300 eggs (Allen 1966). In Norway, ovigerous females are present from January to August (Greve 1963). Elsewhere, ovig-

erous females in the USNM collection are known from Massachusetts in July and August, Gulf of Maine in August and September, British Columbia and Bering Sea in June, and San Juan Islands, Wash., in July and August. The latter records are undoubtedly spotty and seasonally biased.

Pike and Williamson (1961) reared stage I larvae from a laboratory hatching at Millport, Scotland, in March, and reported all stages from the Irish Sea and Firth of Clyde from February to August–September. Six zoeal stages and some intermediates were described and figured; the variants probably are attributable to variations in diet. The postlarva was reared from the last larval stage at Millport and Port Erin, Isle of Man. The authors thought "*Spirontocaris* C" of Frost (1936) is almost certainly *E. pusiolus*.

Genus *Exhippolysmata* Stebbing 1915

Stebbing 1915:94.—Chace 1972:110.

Exhippolysmata oplophoroides (Holthuis)

Fig. 79

Hippolysmata (*Exhippolysmata*) *oplophoroides* Holthuis 1948:1106.—1959:112, fig. 17.—Williams 1965: 85, fig. 69.

Exhippolysmata oplophoroides.—Chace 1972:110.—Christoffersen 1979:360.

Recognition characters.—Rostrum long, slender, directed somewhat upward, reaching beyond antennal scale by nearly half of length; basal portion elevated into crest bearing 9 to 10 closely placed teeth, 1 tooth some distance behind crest, remainder of upper margin with 1 to 6 widely separated teeth; ventral margin with 10 to 14 teeth. Carapace coarsely pitted; anterior margin produced into slight lobe below eye closely followed ventrally by antennal spine; pterygostomian spine at anterolateral angle. Eyes well developed. Basal article of antennular peduncle with stylocerite rather broad and pointed, reaching beyond middle of article; second article somewhat longer than third; upper flagellum simple with about 20 to 25 basal joints thickened, hairy below. Antennal scale almost 3 times as long as broad; outer margin slightly concave, ending in strong tooth; lamella of scale exceeding spine; outer spine near base of scale directed ventrally.

Epipods on first 4 pairs of legs small but distinct. First legs equal, reaching somewhat beyond end of antennal peduncle; fingers short and blunt, fixed finger ending in dark colored, sharp point fitting between 2 dark points on end of dactyl, outer surface of fingers convex, inner surface concave, fin-

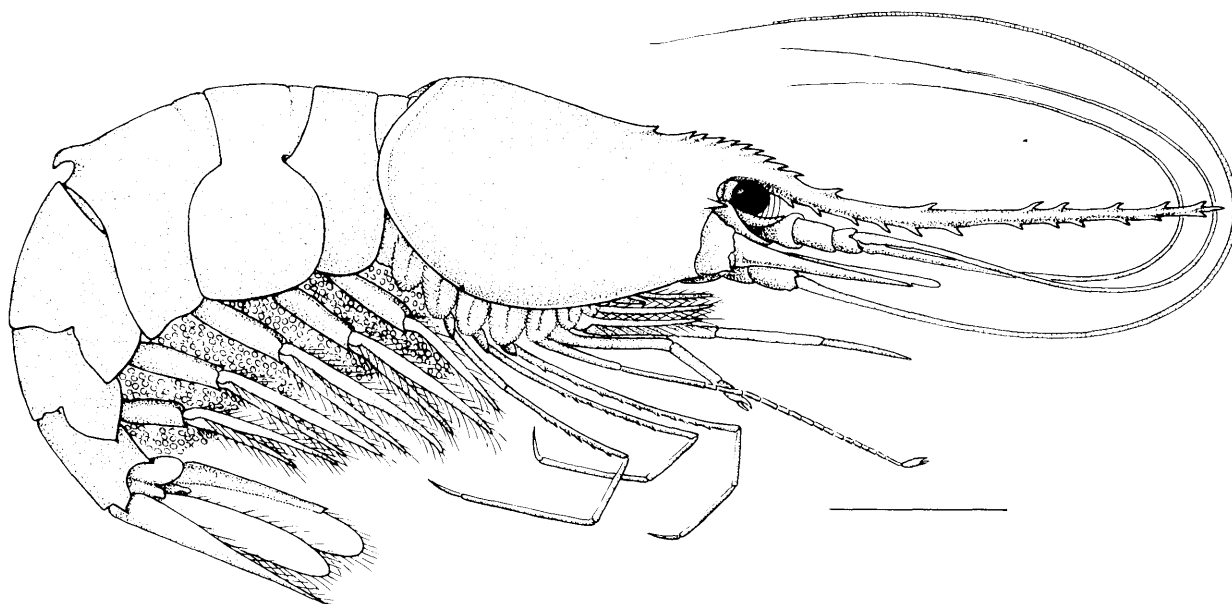


Fig. 79. *Exhippolysmata oplophoroides* (Holthuis). Ovigerous female in lateral view, 1 cm indicated (from Pérez Farfante 1978).

gers about 0.63 length of palm; carpus slightly shorter than chela and $\frac{3}{4}$ length of merus. Second legs slender; slightly unequal in size, reaching almost to end of third maxilliped; chela small and slender; carpus 5 times length of chela and divided into 13 to 15 joints, first and last joints longest. Third to fifth legs slender; dactyls simple.

Abdomen coarsely and shallowly pitted; third segment with dorsal carina ending in strong, posteriorly directed spine; pleura of second to fourth segment produced posteroventrally in narrowly rounded tip, pleura of fifth and sixth ending in distinct sharp tooth; posterolateral angle of sixth spiniform. Telson tapering gradually to slender point; dorsal surface with 2 pairs of spines, anterior pair at $\frac{1}{3}$ length, second pair closer to first pair than to tip. Uropods elongate; outer margin of exopod ending in 2 distinct teeth, between these a slender movable spine.

Measurements in mm.—Length of body: male 77; ovigerous females 47 to 85 (Christoffersen 1979).

Variation.—In the case of a rostrum with one distal tooth dorsally, there were suggestions of three other small, malformed teeth.

Color.—General color pink; rostrum and anterior part of carapace pink, posterior part of carapace white and yellowish; abdomen white with pink most pronounced along posterior margins of first to fourth segments, spine on third segment almost red, fifth and sixth segments entirely pink; tail fan red, pink at base; antennular and antennal flagella pink; legs red, sometimes purplish distally; pleopods red; eggs yellow or greenish (Holthuis 1959).

Habitat.—The species has been taken near shore,

often in estuaries (salinity 15.89‰) over mud bottom (Holthuis 1959); 0-6 to 27 m (Christoffersen 1979).

Type-locality.—Mouth of Suriname River near Resolutie, Surinam.

Known range.—Off Cape Fear River, N. C., to Port Aransas, Tex.; Guyana to the north of Uruguay.

Remarks.—Most information on this species is summarized by Holthuis (1959) and Christoffersen (1979). The species is more abundant than *Xiphopenaeus kroyeri* in Guyana but apparently less abundant to the eastward in nearby countries. Records from the United States are sporadic. Ovigerous females have been reported virtually the year round in Brazil, from Uruguay in April (Christoffersen 1979), April-June in Surinam (Holthuis 1959), and from August to October in the Carolinas.

Genus *Hippolyte* Leach [1814]

Verrill 1922:124.—Holthuis 1947:53.—Barnard 1950:701.—Hemming 1958b:157.

Rostrum long. Supraorbital spine present. Stylocerite acute. Mandible with incisor process and molar, without palp. Third maxilliped with exopod, lacking epipod; epipods present on first and second maxilliped. Chela of first leg rather short and stout. Carpus of second leg 3 jointed. Legs 3–5 subprehensile in male, propodus expanded in middle. Second abdominal segment very large. Telson with 2 pairs of dorsolateral spinules. (Barnard 1950.)

Key to Species

(Adapted from Chace 1972)

1. Lateral (branchiostegal) spine on carapace overreaching anterior margin; tergum of fifth abdominal segment armed with pair of strong posterior spines; antennal scale with blade and distolateral spine about equally advanced. *H. coerulescens*
 Lateral (hepatic) spine on carapace not overreaching anterior margin; tergum of fifth abdominal segment unarmed; antennal scale with blade reaching far beyond distolateral spine. 2
2. Rostrum usually with 3 or 4 strong teeth on dorsal margin and distinct lateral carina in proximal $\frac{1}{3}$ of length; basal article of antennular peduncle armed with 1–3 distolateral spines. *H. curacaoensis*
 Rostrum usually with 2 (rarely 1 or 3) strong teeth in proximal half of dorsal margin and no lateral carina; basal article of antennular peduncle unarmed distally. 3
3. Rostrum not overreaching antennular peduncle in adult females, barely overreaching its basal article in males *H. pleuracanthus*
 Rostrum distinctly overreaching antennular peduncle in adult females, extending nearly to distal margin of its second article in males *H. zostericola*

Hippolyte coerulescens (Fabricius)

Fig. 80

Astacus coerulescens Fabricius 1775:414.*Hippolyte acuminata*.—Gurney 1936b:27, 31, pl. 2, figs. 28–31; pl. 3, figs. 32–33; pl. 4, figs. 48–49; pl. 5.*Hippolyte coerulescens*.—Holthuis 1947:15, 53.—1952a:60, fig. 13.—Chace 1972:111, figs. 42–43.

Recognition characters.—As *H. pleuracanthus* except as follows: Rostrum rather stout at base, thinning distally, a little shorter than carapace, slightly decurved, armed with single dorsal and ventral tooth and tapering to acute tip reaching about to tip of antennal scale (somewhat shorter in male). Supraorbital spine strong. Branchiostegal spine overreaching anterior margin. Antennal scale broadest in proximal third, narrowing somewhat distally, lamella rather acutely angled anteromedially and about on level with distolateral spine.

Pleura of abdominal segment 2 very large, bending mesad in female to form broad pouch; segments 5 and 6 with large downturned spinous process on either side. Telson with tip truncate, bearing 3 pairs of small spines; lateral pair tiny; 2 pairs of tiny dorsolateral spines on margins of distal $\frac{1}{4}$.

Measurements in mm.—Length of body: male 13; female 12.8 (Gurney 1936b).

Color.—Body “banded with brownish yellow in such a way that it seems to be broken up into two parts [cephalothorax-abdomen], each of which looks very like a vesicle of *Sargassum* (Pl. V)” (Gurney 1936b).

Habitat.—Usually associated with floating *Sargassum* (Chace 1972).

Type-locality.—“Pelago inter Tropicos.”

Known range.—Widespread in tropical and subtropical Atlantic Ocean (Chace 1972).

Remarks.—Chace (1972) thought the distinction between this and other species of *Hippolyte* might eventually warrant reestablishment of the genus *Virbius* Stimpson (1857–60, pars VIII).

Gurney (1936b) described the first larval stage of this species.

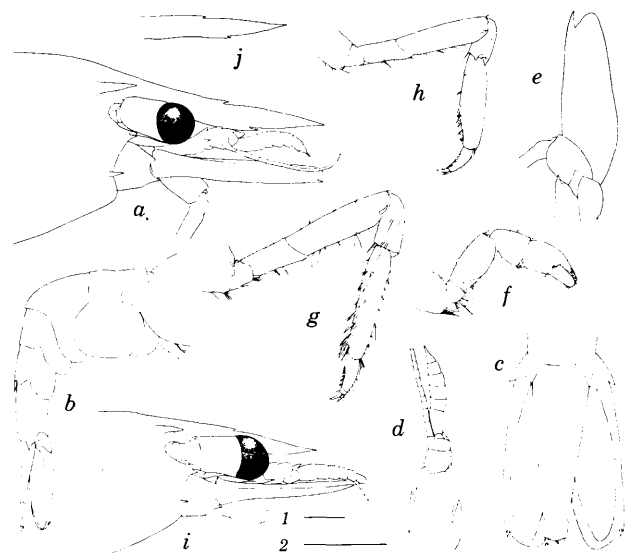


Fig. 80. *Hippolyte coerulescens* (Fabricius). Female: a, anterior region; b, abdomen; c, telson and uropods; d, right antennule; e, right antenna; f, right first leg; g, right third leg. Male: h, right third leg; i, anterior region; j, rostrum. Scales = 1 mm: 1 = b; 2 = all others (from Chace 1972).

Hippolyte curacaoensis Schmitt

Fig. 81

Hippolyte curacaoensis Schmitt 1924c:68, fig. 4.—Chace 1972:111, figs. 44–45.

Hippolyte zostericola.—Williams 1965:82, fig. 66. [Not *Virbius zostericola* Smith 1873c.]

Recognition characters.—Body smooth. Rostrum rather stout at base, thin distally, slightly decurved, armed dorsally with 3–4 and ventrally with 1–3 teeth; tip reaching beyond antennular peduncle in males. Anterior margin of carapace produced into prominent narrow lobe below eye followed ventrally by antennal spine; shallow emargination at base of antenna, anterolateral angle broadly rounded; hepatic spine well developed. Antennular peduncle with basal article long and broad, styllocerite slender, divergent at tip and well separated from article; basal article terminating in 1–3 spines on anterolateral corner; second and third articles much shorter than first; antennular flagella of about equal length, outer ramus stout basally, tapering to slender distal portion, hairy on ventral border. Antennal scale large, slightly exceeding rostrum and reaching nearly to end of antennular flagella, length a little over 3 times width; outer margin slightly concave, terminating in small spine exceeded by lamella; spine near base of scale.

First legs short, nearly equal, reaching base of distal article of antennal peduncle; chelae lightly setose, palm inflated, fingers about half length of palm, cutting edges finely serrate; carpus irregularly conical in shape, about $\frac{3}{4}$ length of chela, lower outer border with spiniform setae. Second legs slender, reaching to distal end of basal article of antennular peduncle; carpus longer than merus, divided into 3 joints; fingers about $\frac{2}{5}$ length of chelae, tips of cutting edges with spines; chelae hairy. Third to fifth legs long; third reaching to tip of antennal scale; dactyls with series of spines in comblike arrangement on inner border; propodi spined on flexor margin.

Abdomen strongly bent at third segment; posterior portion of third segment raised with hook-like projection overhanging fourth segment. Telson tip truncate, bearing 3 pairs of spines, inner 2 pairs about equal, outer pair much shorter. Uropodal exopods with lateral border ending in small spine flanked mesially by movable spine.

Measurements in mm.—Length of body: male about 7.5 (Schmitt 1924c); ovigerous females 10 to 12.

Habitat.—Sand and mud flats; associated with marine grasses.

Type-locality.—West Punt, Curaçao.

Known range.—Beaufort and Sneads Ferry, N. C.; West Indies from Cuba to Curaçao.

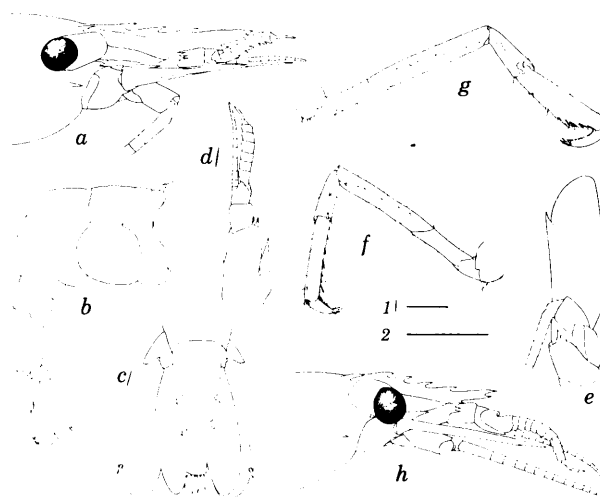


Fig. 81. *Hippolyte curacaoensis* Schmitt. Female: a, anterior region; b, abdomen; c, telson and uropods; d, right antennule; e, right antenna; f, left third leg. Male: g, right third leg; h, anterior region. Scales = 1 mm: 1 = b; 2 = all others (from Chace 1972).

Remarks.—This species, confused with *H. zostericola* by Williams (1965), is the only species of *Hippolyte* in the region possessing a lateral carina on the basal region of the rostrum and terminal spines on the first peduncular article of the antennule (Chace 1972).

Ovigerous females are known from July to September in North Carolina, and November to April in the West Indies (USNM).

Hippolyte pleuracanthus Stimpson

Fig. 82

Virbius pleuracanthus Stimpson 1871b:127.

Hippolyte pleuracantha.—Williams 1965:80, fig. 65.

Hippolyte pleuracanthus.—Chace 1972:118, fig. 48.

Recognition characters.—Body smooth, with tufts of plumose hairs on dorsal surface of carapace and abdomen, tips of abdominal pleura, and distal portion of eyestalks. Rostrum rather stout at base, thin distally, slightly decurved, armed dorsally with 2 (rarely 1 or 3) teeth and ventrally with 1–3 teeth; tip in adult female reaching about to end of antennular peduncle, barely overreaching basal article in male. Anterior margin of carapace produced into lobe below eye followed ventrally by antennal spine, an emargination at base of antenna followed by slightly produced, broadly rounded anterolateral angle; hepatic spine strong. Eyes well developed. Antennular peduncle with basal article long and broad, styllocerite slender, lanceolate, reaching about to middle of article and separated from lateral border of article by about width of styllocerite, article ending in short, broad, elevated, bladelike projec-

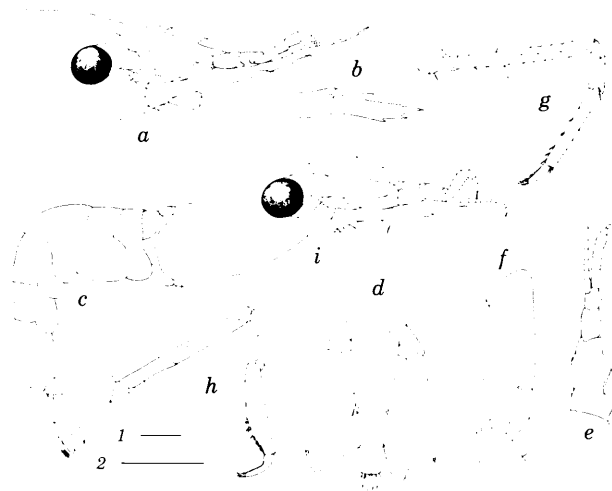


Fig. 82. *Hippolyte pleuracanthus* (Stimpson). Female: *a*, anterior region; *b*, rostrum; *c*, abdomen; *d*, telson and uropods; *e*, right antennule; *f*, right antenna; *g*, right third leg. Male: *h*, right third leg; *i*, anterior region. Scales = 1 mm; 1 = *c*, 2 = all others (from Chace 1972).

tion, a short spine at anterolateral corner under blade; second and third articles much shorter than first; antennular flagella of about equal length; outer ramus stout, broadest in middle; tapering to slender distal portion, hairy on ventral border. Antennal scale large, exceeding rostrum and reaching nearly to end of antennular flagella, length a little over three times width; outer margin slightly concave, terminating in small spine exceeded by lamella; spine near base of scale.

First legs short, nearly equal, reaching a little beyond base of distal article of antennal peduncle; chelae setose, palm inflated, fingers about half length of palm, cutting edges finely serrate; carpus irregularly conical in shape, about $\frac{3}{4}$ length of chela, lower outer border with spiniform setae. Second legs slender, reaching to tip of antennular peduncle; carpus longer than merus, divided into 3 joints; fingers $\frac{2}{5}$ length of chelae, tips of cutting edges with spines; chelae hairy. Third to fifth legs long; third reaching to tip of antennal scale; dactyls with series of spines in comblike arrangement on inner border; propodi spined on flexor margin.

Abdomen strongly bent at third segment; posterior portion of third segment raised with hood-like projection overhanging fourth segment. Telson with tip truncate, bearing 3 pairs of spines, inner 2 pairs nearly equal, outer pair much shorter. Uropodal exopods with lateral border ending in small spine flanked mesially by movable spine.

Measurements in mm.—Length of body: ovigerous females 12 to 18; males somewhat smaller.

Variation.—The rostrum of some females exceeds the antennular peduncle, but is shorter than

that of *H. zostericola*; the rostrum of some males exceeds the second peduncular article (Shield 1978).

Color.—Usually mottled brown or red, often a bright green.

Habitat.—Extremely abundant in beds of vegetation (*Zostera* and *Diplanthera*) in sounds and bays. Also found among rocks of jetties.

Type-localities.—Norfolk Harbor, Va., and Somers Point, Great Egg Harbor, N. J.

Known range.—Connecticut to North Carolina.

Remarks.—*Hippolyte pleuracanthus* and *H. zostericola* have been much confused over the years. Chace's (1972) concept of the former removes from active consideration published observations on its biology made outside the recorded geographic range. Little is lost because virtually the only information concerns breeding time. Provenzano and Dobkin (1962) reared larvae attributed to *H. pleuracanthus* (= *zostericola*?), but Shield (1978) gave results of a more complete study. From ovigerous females collected between June and September in Bogue Sound, N. C., eggs were hatched in the laboratory and larvae reared on a diet of *Artemia salina* nauplii in average water temperature and salinity of 25.2°C and 33.9‰. Eight larval stages were described and figured. Stages occurred in regular sequence until the fifth molt, but varied after that, postlarvae appearing after stages VII and VIII, others passing through intermediate stages, and metamorphosis of survivors occurring during the ninth or tenth molt. Shield summarized studies on larvae of the genus showing that, for two western North Atlantic species, Gurney (1936b) had described stage I of *H. coerulescens* and six zoeae and a postlarva of *H. zostericola* from hatched eggs or plankton, and she outlined developmental variation in a number of forms. *Hippolyte coerulescens* larvae are transparent with a few green-brown chromatophores; *H. pleuracanthus* larvae have twice as many red pigmented spots; *H. zostericola* larvae are dark olive-brown with chromatophores.

Hippolyte zostericola (Smith)

Fig. 83

Virbius zostericola Smith 1873c:550, pl. 3, fig. 11.

Hippolyte zostericola.—Chace 1972:118, figs. 49–50.

Recognition characters.—As *H. pleuracanthus* except as follows: Rostrum somewhat upturned distally in females, more nearly straight or slightly decurved in males; armed dorsally with 2 (rarely 1 or 3) teeth and ventrally with 1–4 teeth; tip reaching beyond antennular peduncle in adult females, nearly to distal margin of second article in males.

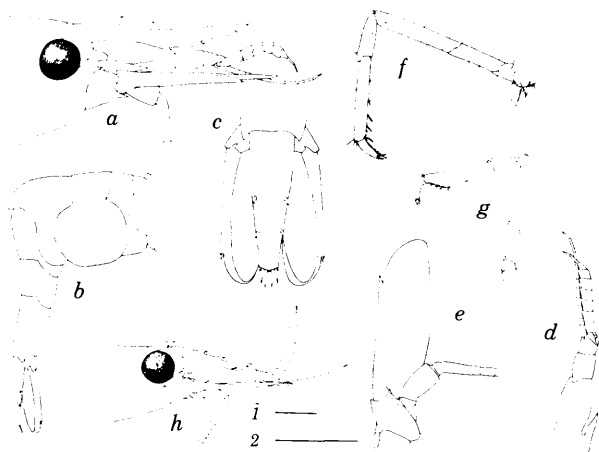


Fig. 83. *Hippolyte zostericola* (Smith). Ovigerous female: a, anterior region; b, abdomen; c, telson and uropods; d, right antennule; e, right antenna; f, third left leg. Male: g, third left leg; h, anterior region. Scales = 1 mm: 1 = b; 2 = all others (from Chace 1972).

Measurements in mm.—Length of body: male 14 (carapace 4.75); female 15.5 (carapace 6).

Variation.—Chace (1972) observed that *H. zostericola* and *H. pleuracanthus* may not prove to be distinct but that the problem may be resolved by study of large series of specimens. His discussion will not be repeated here except to observe that relative

rostral length of the two species overlaps, that of *H. zostericola* females from south of Woods Hole, Mass., to North Carolina being no longer than the antennular peduncle, as in *H. pleuracanthus*, but at Woods Hole many females have the rostrum considerably overreaching the antennular peduncle, as do specimens from east Florida, and especially from the northern and eastern Gulf of Mexico where the tendency is most pronounced.

Color.—Bright green, pale or translucent tinged with green; sometimes specked with reddish brown and with a broad median band of dark brown extending whole length of body (Smith 1873c).

Habitat.—Beds of vegetation such as eelgrass.

Type-locality.—Vineyard Sound, Mass.

Known range.—Southern Massachusetts; North Carolina to Yucatan; Trinidad and Curaçao; Ceará, Brazil (Fausto-Filho (1975); Bermuda.

Remarks.—Ovigerous females are known throughout the year in Florida and the Caribbean region, and from June to October in Massachusetts (USNM). Life history comparisons in which Shield (1978) found differences from *H. pleuracanthus* are given in the account for *H. pleuracanthus*.

Genus *Latreutes* Stimpson 1860

Stimpson 1860:27[96].—Hemming 1958b:157.

Key to Species

1. Carapace and rostrum unarmed dorsally except for single, small, median spine on gastric region; rostrum an elongate blade nearly as long as carapace *L. fucorum*
- Carapace strongly humped and armed dorsally with 5 or 6 spiniform teeth; rostrum a deep ovoid blade, shorter than carapace *L. parvulus*

Latreutes fucorum (Fabricius)

Fig. 84

Palaemon fucorum Fabricius 1798:404.

Latreutes ensiferus.—Hay and Shore 1918:390, pl. 26, fig. 13.

Latreutes fucorum.—Verrill 1922:131, pl. 16, figs. 5–5b; pl. 42, figs. 2–2t; pl. 44, figs. 1–1m, 2a–2n, 3.—Sivertsen and Holthuis 1956:31, pl. 1, figs. 1–2 (color).—Williams 1965:78, fig. 63.—Chace 1972:121.—Pequegnat and Ray 1974:251, fig. 60.

Recognition characters.—Rostrum thin, nearly as long as carapace, smooth edged, broadest at base and deepest near base, slightly concave dorsally and upturned at tip, convex ventrally; tip subtruncate and armed with about 5 to 7 small, acute spinules. Carapace smooth; small middorsal spine on gastric

region; anterior margin produced into acute lobe below eye followed ventrally by wide, nearly rectangular emargination and series of 4 to 9 small denticles at anterolateral angle; spine removed from margin near suborbital lobe. Eyes well developed, with tuberculate swelling anteromesially near cornea. Antennular peduncle with basal article excavate laterally; stylocerite broad, thin, cupped dorsally; distal spine on lateral border of basal article reaching about to base of third article; second and third articles short; distal border of third obscurely denticulate, outer flagellum thick at base. Antennal peduncle stout; antennal scale wide at base, tapering to acute terminal spine, scale about as long as rostrum. Third maxilliped elongated, leglike; distal article long, with 8 or 9 acute marginal spines.

First legs incurved, short, relatively stout, unequal; larger chela thick, proximally broad, ovate,

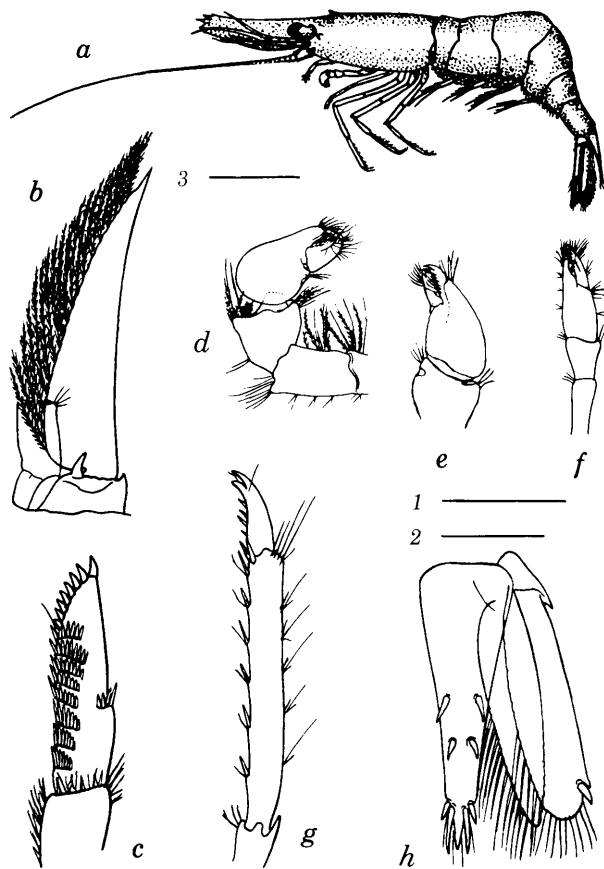


Fig. 84. *Latreutes fucorum* (Fabricius). a, Animal in lateral view (from Bate 1888); b, antennal scale; c, distal article of third maxilliped; d, right first cheliped; e, left first cheliped; f, second cheliped; g, distal articles of third leg; h, telson and uropods (from Verrill 1922). Scales: 1(a-b, d, f-h) = 1 mm; 2(c) = 0.3 mm; 3(e) = 0.5 mm.

tapering distally; dactyl wide, longer than fixed finger, with broad lateral lobe and about 3 denticles at tip; fixed finger bent slightly inward and arched, tip subacute or slightly bidentate; fingers hairy; carpus large, cup shaped, broader than long; merus and carpus excavate beneath. Second legs slender; chelae slender, somewhat unequal; fingers about as long as palm, hairy at tip; carpus with 3 unequal joints, middle one longest. Third to fifth legs long, slender, subequal; propodi and dactyls with row of spines on lower edge.

Abdomen smooth. Telson long, narrow, tapering to narrow tip with spiniform median process flanked by 2 pairs of unequal spines, inner pair longer than median process; pair of dorsal spines at half and $\frac{3}{4}$ of length. Uropodal exopods with outer edge terminating in small spine flanked mesially by movable spine.

Measurements in mm.—Length of body: adults 12 to 20, males smaller than females.

Variation.—The rostrum varies greatly in length, depth, and number of spines (Wass 1955).

Color.—Often nearly colorless and transparent; sometimes with body pale yellow, yellowish green, greenish brown, brown, red, black, black with white spots and bars; bright blue patches on dorsal and lateral surfaces; often mottled, striped or barred, and corresponding in pattern to irregularly colored bits of weed (various authors).

Habitat.—Common in floating masses of *Sargassum*; surface waters; also common on grass flats in tropical Atlantic (Rouse 1970; Chace 1972).

Known range.—Western North Atlantic between 10° and 50°N; Azores and Cape Verde Islands (Chace 1972).

Remarks.—Ovigerous females have been found virtually year round in various parts of the range. Gurney (1936a) described the first stage larva.

Brown (1939) found four kinds of pigment in this shrimp (white, red, yellow, and blue) similar to pigments found in *Hippolyte*, *Leander*, and *Palaeomonetes* species. The red and yellow pigments respond to white background by concentration into the chromatophore centers and to black background by dispersion into the chromatophore branches. *Latreutes* has a great abundance of white pigment which may vary in color from yellowish white to clear white. Darkness produces concentration, and darkness or black background with low intensity of incident light calls forth concentration of the reflecting white chromatophores. Direct sunlight of a bright sky produces dispersion of white pigment in spite of black background. Blue patches on the animals apparently consists of blue pigment accumulated in particular white chromatophores. Brown concluded that the different color patterns in this species are not solely results of responses to particular situations, but are at least partly genetic patterns repressed or encouraged by light intensity in color of the background. The response is similar to responses in crustaceans having far less ability to change color.

Markham (1977) annotated the description of the bopyrid parasite *Probopyrinella latreuticola*, reviewing its taxonomic status and geographic distribution. This branchial parasite is the only known parasite of *L. fucorum*. It is found equally in right or left gill chambers of the host.

Latreutes parvulus (Stimpson)

Fig. 85

Rhynchocyclus parvulus Stimpson 1866:48.—1871b: 124.

Concordia gibberosus.—Hay and Shore 1918:391, pl. 26, fig. 11.

Latreutes parvulus.—Holthuis 1947:59.—1951b:131, fig. 28.—Williams 1965:79, fig. 64.—Chace 1972:124.—Coelho and Ramos 1972:153.

Recognition characters.—Rostrum laterally compressed, almost circular in outline in female, more elongate in male; upper margin with 6–8 teeth in female, 2–4 in male; few small teeth on tip; lower margin unarmed or with up to 5 shallow teeth; ventral part of rostrum produced somewhat backward. Carapace with middorsal row of 5–7 small, erect teeth, row starting somewhat anterior to middle of carapace, extending to base of rostrum; carapace somewhat swollen in female, making an angle at base of middorsal row of teeth; upper margin nearly straight in males; anterior margin with narrow, anteriorly directed lobe forming lower angle of orbit, slender spine on lobe; anterolateral angle serrate with 2–4 teeth; row of 3 or 4 slender

spines a bit removed from and parallel to margin between anterolateral angle and lower margin of orbit. Eyes well developed; cornea globular; eye-stalks with truncated process at upper inner margin overlapping line separating cornea from stalk. Antennular peduncle with stylocerite broad and rounded, hollowed above and together with basal article of peduncle forming concavity for reception of eye; second article of peduncle much shorter than third; upper flagellum shorter than lower, with 7 or 8 broad and 1 or 2 narrow joints. Antennal scale about twice as long as broad, overreaching end of rostrum; outer margin nearly straight, ending in small tooth reaching about as far as lamella; small spine on outer surface of peduncle near base of scale.

First legs equal, short, thickset, slightly overreaching base of antennal scale; fingers somewhat shorter and narrower than palm, tips of fingers ending in dark-colored nails; palm broadened posteriorly; carpus somewhat conical, about as long as palm. Second legs more slender, reaching about to end of antennal peduncle; chelae with fingers shorter than palm; carpus almost twice length of chela, 3-jointed, median joint longest; merus $\frac{2}{3}$ as long as carpus. Third to fifth legs with dactyls ending in sharp tooth, posterior margin with 4 comb-like teeth progressively smaller proximally.

Abdomen smooth. Telson triangular; with pairs of dorsal spines at $\frac{1}{2}$ and $\frac{3}{4}$ length; tapering to narrow tip with spiniform median process flanked by 2 pairs of spines, inner pair longest; terminal portion with feathered setae. Uropodal exopods with outer margin ending in small spine flanked mesially by movable spine.

Measurements in mm.—Length of body: 7 to 12; males smaller than females.

Variation.—Shape of the rostrum, as well as its spination, is subject to some variation.

Habitat.—Littoral waters from (in?) sponges among shells, dead coral, hydroids, and on sea-grass flats; surface to 44 m.

Type-locality.—St. Joseph Island, Texas.

Known range.—Beaufort, N. C., to Rio de Janeiro, Brazil; West Africa.

Remarks.—*Latreutes parvulus* is not known to be common anywhere in its range. It has been taken throughout the year in the Carolinas. Ovigerous females have been taken throughout the year in various part of the range north of the equator and in February in Brazil.

Genus *Lebbeus* White 1847

Holthuis 1947:9 (synonymy).—China 1966:243.

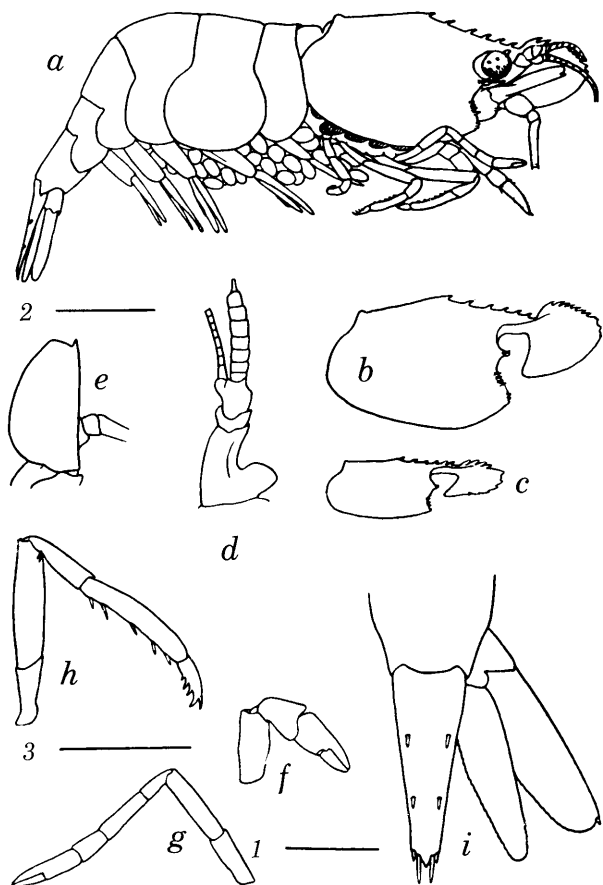


Fig. 85. *Latreutes parvulus* (Stimpson). a, Ovigerous female in lateral view; b, carapace of ovigerous female in lateral view; c, carapace of male in lateral view; d, antennule; e, antennal scale; f, first leg; g, second leg; h, third leg; i, telson and right uropod in dorsal view (from Holthuis 1951b). Scales: 1(a-c) = 2 mm; 2(d-e), 3(f-i) = 1 mm.

Key to Species

(From Williams 1974c; Couture and Trudel 1968)

1. Four (sometimes 3) prominent spines along middorsal line of carapace; pleura of all abdominal segments toothed ventrally or posteroventrally *L. groenlandicus*
No more than 2 spines along dorsal line of carapace; pleura of first 3 abdominal segments rounded 2
2. Rostrum long, tip exceeding basal antennular article in juveniles and entire peduncle in adults; ventral margin of rostrum variable but not horizontal *L. polaris*
Rostrum short, tip not exceeding basal article of antennular peduncle; ventral margin of rostrum horizontal *L. zebra*

Lebbeus groenlandicus (Fabricius)

Fig. 86

Astacus groenlandicus Fabricius 1775:416.*Lebbeus groenlandicus*.—Holthuis 1947:9 (synonymy).—Couture and Trudel 1968:870, fig. 10.

Recognition characters.—Rostrum rather slender in lateral view, inclined slightly upward to acute tip reaching beyond second article of antennular peduncle in adults; usually 2–3 dorsal spines on rostrum proper, and 2–3 ventral spines near tip, but 0/0 in juveniles and sometimes 2/5 in adults. Carapace surmounted with carina extending from rostrum to posterior margin and bearing usually 4 (sometimes 3) strong, forward pointing spines or teeth; single supraorbital spine very strong and acute; suborbital lobe closely flanked by very long,

buttressed, slender, acute antennal spine; concave anteroventral margin ending in smaller pterygostomian spine. Eyes well developed. Antennules with basal article bearing spine on distodorsal margin, strong distolateral spine, and mesioventral spine; stylocerite slender, ending in acute point reaching to beyond third peduncular article; latter with elongate, acute lateral spine; third article about half length of second and bearing slender distal spine directed obliquely dorsad. Antenna with peduncle reaching to about midlength of antennal scale; basal article with acute dorsolateral spine, and longer, stronger ventrolateral spine; antennal scale with lateral margin slightly concave or straight, distolateral spine strong, slightly short of or exceeding convex tipped lamella. Third maxilliped with epipod, extending beyond antennal scale.

First 3 legs with epipods. First legs stout, reaching beyond antennal peduncle; fingers shorter than palm, tips dark, dactyl cleft distally to receive tip of fixed finger; palm a little shorter than merus, latter with lateral spine proximally. Second legs longer and more slender, carpus 7-jointed. Third to fifth legs with stout dactyls bearing curved spines on flexor margin, penultimate spine stout at base, shorter than terminal spine but making tip biunguiculate; meri of third leg with up to 9, fourth with about 5–7 lateral spines, fifth with about 5–7, distalmost of each distinctly strongest.

Abdomen with pleura of all segments toothed or spined ventrally; that of first segment ending in 2 nearly equal points, posterior somewhat stronger; of second ending in single point; of third to fifth each ending in strong posterior point but secondary smaller point anterior to it, both progressively stronger posteriorly; sixth with long posteroventral spine with shoulder at base and above it a posterior spine with variable shoulder overlapping base of telson. Telson broadly sulcate dorsally, median boss proximally; rather obtusely pointed tip bearing 2 pairs of stout spines, outer pair short, mesial

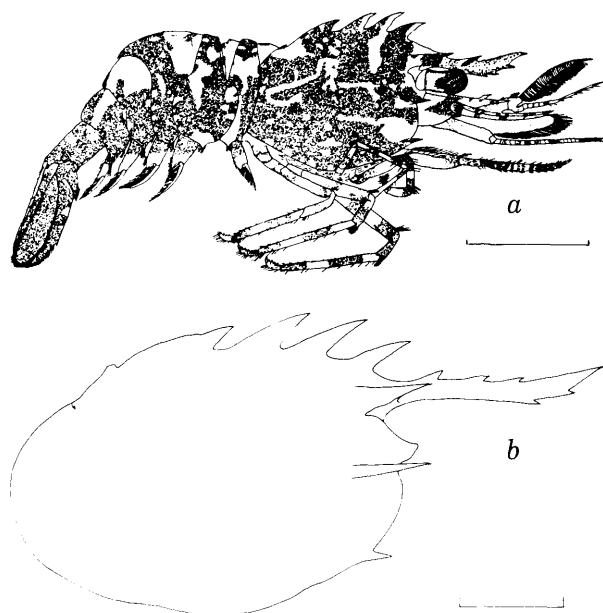


Fig. 86. *Lebbeus groenlandicus* (Fabricius). a, Female in lateral view, 10 mm indicated (from Leim 1921); b, carapace in lateral view, 5 mm indicated (from Williams 1974c).

pair long and setae mesial to these; 4–5 pairs of dorsolateral setae, often asymmetrical in number and arrangement.

Measurements in mm.—Length of body: male 74, female 97.

Variation.—The rostrum varies considerably from stout to rather slender, the latter usually in males (Leim 1921). Moreover, its relative length changes with growth, being shorter than the eyes in juveniles; tooth number increases with age. Number of pleural spines is usually two on segments 1, 3, 4, 5, and one on 2 and 6. About 25% of individuals seen by Leim (1921) had only one pleural spine on segment 3, and a few had this number on 4 and 5; conversely, there were sometimes three on 4 and 5, or an asymmetrical number.

Color.—Shades of color and pattern variable; usually brownish red, sometimes brownish green; greater part of animal colored but carapace uncolored in small areas, just posterior to eye, dorsal to pterygostomian spine, running ventrally from second dorsal spine, posterior to fourth dorsal spine, and scattered smaller areas variable in position except for 5 along posterior half of ventral edge. Abdomen with principal non-colored areas across segment 1 dorsolaterally, anterodorsally on segment 4, narrowing and continuing diagonally across 5 and extending slightly onto segment 6. Ventral edges of abdominal segments red. Rostrum, antennules and antennae with scattered dots, flagella banded; distal article of third maxilliped and legs variously banded (Leim 1921).

Habitat.—Rock and gravel bottom (Proctor 1933); 2 to 314 m in a recorded temperature range of -1.3° to 9.4°C (Holthuis 1947; Squires 1965a; Williams and Wigley 1977).

Type-locality.—"Habitat in mari groenlandico."

Known range.—Greenland southward to Rhode Island; arctic Canada and Alaska; southern Chuckchi Sea through Bering Sea to Puget Sound, and Sea of Okhotsk southward to Vladivostok (Holthuis 1947; Nesis 1963; Squires 1965a). Heegaard (1941) mapped and summarized the distribution, characterizing it as that of a "boreo-arctic-pacific species which on its way eastwards has reached Greenland," and Nesis (1963) characterized it as "arctic-boreal or lower arctic-boreal."

Remarks.—Squires (1965a) reported one ovigerous female in May, but many in August and September from which embryonated eggs probably hatch in late autumn or early winter. A single spawning per year was indicated by his samples from southern to middle parts of the northwestern Atlantic range, but farther north in Hudson and Frobisher bays where animals first mature at carapace lengths of 11 (δ), 15 (ϕ), and 10 (δ), 14 (ϕ)

mm respectively, ovigerous females found in August were judged to spawn only every two years. Samples in the USNM collection contain ovigerous females from Kamchatka in June and September, southeastern Alaska and Aleutian Islands in July to November, Murchison Sound, Greenland, in August, and Puget Sound, Washington, in September; these samples are spotty and seasonally biased.

From eggs of known parentage held until hatching in a refrigerated recirculating aquarium system maintained between 6° and 8°C at 32–34‰ salinity, Haynes (1978b) reared larval stages of *L. groenlandicus* in flasks suspended at 6-m depths in the sea. Development from the rather large eggs passed through two zoeal stages and a megalopa which were described and illustrated from the reared larvae and plankton. Haynes reviewed the status of larvae previously attributed to this species. Ivanov (1971) also described and illustrated some developmental features of this species from laboratory rearings.

In 35 stomachs examined, phyto-benthos, crustacean fragments including euphausiids and ostracods, foraminifera, and hydroids were found in decreasing order (Squires 1967). Cod is a predator on *L. groenlandicus* (Squires 1965a); most specimens taken in the southern part of the northwestern Atlantic were in stomachs of this fish. In Ungava Bay, Squires (1957) found the bearded seal to be a common predator, as is the beluga whale in northwestern Hudson Bay (Squires 1967).

Lebbeus polaris (Sabine)

Fig. 87

Alpheus polaris Sabine 1824:ccxxviii, pl. 2, figs. 5–8.

Lebbeus polaris.—Holthuis 1947:9 (synonymy).—Christiansen and Christiansen 1962:15.—Greve 1963:35, fig. 1E.—Couture and Trudel 1968:871, fig. 11.—Smaldon 1979:62, fig. 23.

Recognition characters.—Rostrum rather long in adults, extending forward to often daggerlike tip reaching beyond antennular peduncle, shorter in juveniles; 0–8 spines in rostral series (2–3 behind orbital margin) and 1–5 ventral spines (see variation); low lateral carina thinning distally toward tip, lamellate portion below it deepest anterior to eye. Carapace with single strong supraorbital spine; suborbital lobe closely flanked by antennal spine; slightly convex anteroventral margin ending in smaller pterygostomian spine (rarely obsolescent). Eyes well developed. Antennules with basal article bearing dorsolateral spine on distal margin, lateral

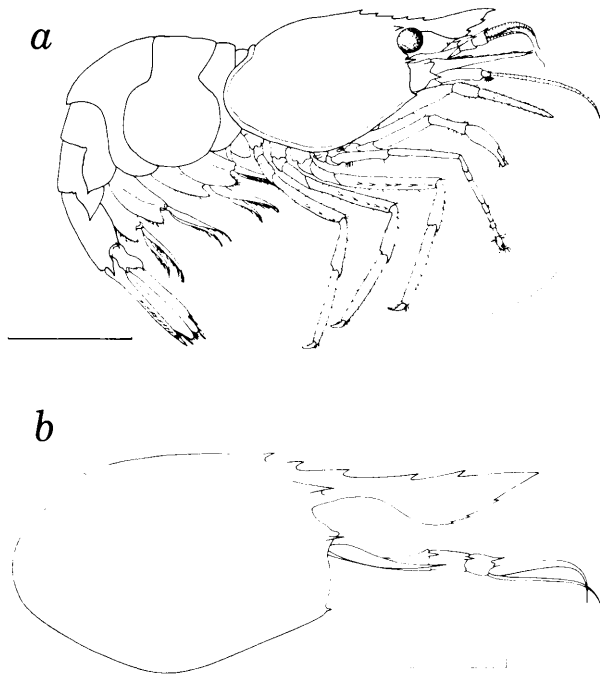


Fig. 87. *Lebbeus polaris* (Sabine). *a*, Animal in lateral view, 10 mm indicated (from Smaldon 1979); *b*, carapace and antennule in lateral view, 5 mm indicated (from Williams 1974c).

spine or lobe below it, and mesioventral spine; stylocerite slender, ending in acute point reaching about to end of basal article or beyond it nearly to distal end of second article bearing lateral spine; third article about $\frac{1}{2}$ length of second and bearing distal spine directed obliquely dorsad; mesial thickened ramus bearing short terminal flagellum, slender lateral ramus longer. Antenna with peduncle reaching about half length of antennal scale; basal article with ventrolateral spine and dorsolateral lobe; antennal scale with lateral margin straight, distolateral spine exceeded by rounded tip of lamella. Third maxilliped with epipod, extending well beyond antennal scale.

First 2 legs with epipods. First legs stout, reaching from about length of fingers to $\frac{1}{2}$ length of chela beyond antennal peduncle; fingers shorter than palm, tips dark, dactyl cleft distally to receive tip of fixed finger; palm about $\frac{1}{3}$ – $\frac{1}{2}$ length of merus, latter with tiny lateral spine proximally. Second legs longer and more slender, carpus 7-jointed. Third to fifth legs with stout dactyls bearing curved spines on flexor margin, penultimate spine stout at base, shorter than terminal spine but making tip biunguiculate; merus of third leg with usually 7–8 (range 5–10) lateral spines, distalmost longest; fourth leg similarly with 6–7 (range 1–9) lateral spines, and fifth with 3–4 (range 1–7) lateral spines.

Abdomen with pleura of first 3 segments

rounded; fourth segment with small posteroventral spine; fifth similar though with spine directed more posteriorly; sixth with even less prominent posteroventral spine and above it an acute lateral spine with ventral shoulder overhanging base of telson. Telson with 3 pairs of terminal spines, outermost shortest, and 4–5 pairs of dorsolateral spines.

Measurements in mm.—Length of body: male 82, female 90.

Variation.—Sexual dimorphism becomes pronounced with increasing age. Females have both dorsal and ventral rostral spines, but older males lack rostral spines. Younger males (up to 43 mm) have an intermediate spinous pattern on the rostrum (Greve 1963; Squires 1965a). Dons (1915) illustrated several tooth patterns. Variations in number of spines on legs 3–5 (as above) were recorded by Leim (1921).

Color.—Scattered orange red areas of minute dots over carapace and abdomen, mainly dorsally; larger dots behind and below posterior carapace spine and below these some small areas of dots with sulfur yellow tinge. Rostrum orange spotted, ventral edge bright red. Head appendages and first 2 legs with scattered spots; legs 3–5 dark orange. Posterior border of abdominal segments 5 and 6 red (Leim 1921). Butler (1964) found two specimens in British Columbia to have body milkish white with 6 main red and yellow transverse bands extending over dorsal and lateral carapace and abdomen, with 15 lighter bands of blue and yellow between these; most appendages yellow.

Habitat.—Variety of soft to hard bottoms; < 1 to 930 m (Holthuis 1947; Greve 1963; Christiansen and Christiansen 1962; Squires 1965a).

Type-locality.—Coast of Melville Island, 50 fm (91.45 m).

Known range.—Circumarctic southward to off Chesapeake Bay; Bering Sea; British Columbia; Sea of Okhotsk; Skagerrak and Hebrides (Holthuis 1947; Butler 1964; Squires 1965a). Heegaard (1941) mapped the distribution.

Remarks.—Ovigerous females in the USNM collection are from eastern Georges Bank in January, off Woods Hole, Nantucket, Cape Cod, Nova Scotia, Newfoundland and Labrador from July to September, and off Delaware in October; Foxe Basin in August; off northern Greenland in July and August; Aleutian Islands in July and in September, along with Pribilof Islands and Point Barrow; and Franz Joseph Land in July. Heegaard (1941) reported ovigerous females from Greenland throughout the year, and Christiansen and Christiansen (1962) found them during July–August in Spitsbergen. MacGinitie (1955) found females with

new eggs at Point Barrow in September. Greve (1963), in a review, reported ovigerous females from western Norway in November, March, May and July, and northern Norway in summer. She thought that females either carry eggs all year or that there is a difference in time of spawning between southern and northern Norway. Squires (1965a; 1967) found larvae hatched in autumn as well as spring in the northern Atlantic, suggesting that a majority of females reach maturity at an early age and spawn annually more than once, although in the far northern Queen Elizabeth Islands (1968) spawning may be biennial. He presented evidence that there are three age groups representing at least that number of years. Several authors have commented on variation in size in different areas.

Pike and Williamson (1961) commented on knowledge of the larvae, the only described examples being one which Krøyer (1842) dissected from a ripe egg, and specimens described by Stephensen (1916; 1935), some of which probably belong to another species.

Observed stomach contents (Squires 1967) consisted of phytobenthos, detritus, crustacean fragments of shrimps, mysids, amphipods and ostracods, hydroids, sponge spicules, polychaete worms, foraminiferans, and gastropod and pelecypod shells in decreasing order of abundance. Predators are cod, seals, and mures (Squires 1965a).

Hansen (1897) found the parasitic copepod, *Choniostoma hansenii*, in the branchial cavity of *L. polaris* from the Kara Sea and west coast of Greenland.

Lebbeus zebra (Leim)

Fig. 88

Spirontocaris zebra Leim 1921:133, pls. 2–3.

Lebbeus zebra.—Holthuis 1947:10 (synonymy).—

Couture and Trudel 1968:873, fig. 12.

Recognition characters.—Rostrum short, inclined slightly downward; with 2–5 spines in dorsal series, 1 (–2?) behind orbital margin; small acute tip not exceeding basal article of antennular peduncle, slightly overhanging small subterminal spine at end of horizontal ventral margin. Carapace highest at level of posterior spine in rostral series; single supraorbital spine strong, acute; suborbital lobe closely flanked by strong antennal spine; somewhat angled anteroventral margin ending in smaller pterygostomial spine. Eyes well developed. Antennules with basal article bearing 2–4 spines on distodorsal margin (sometimes asymmetrical in number), and appressed mesioventral spine; sty-

locerite ending in acute, slightly divergent point falling slightly short of prominent distolateral spine on short second article; third article much shorter than second, with strong and less acute distodorsal spine; lateral ramus with slender distal whip about as long as thickened proximal portion, mesial ramus slender and longer. Antenna with peduncle reaching beyond distal margin of basal article of antennular peduncle; basal article with acute ventrolateral spine and dorsal lobe; antennal scale exceeding antennular peduncle, lateral margin straight, distolateral spine equaling lamella with convex tip. Third maxilliped with epipod but no exopod, extending well beyond antennal scale.

First 3 legs with epipods. First legs rather stout, reaching about length of fingers beyond antennal peduncle; fingers shorter than palm, tips dark, dactyl cleft distally to receive tip of fixed finger; palm $\frac{3}{4}$ length of merus, carpus $\frac{2}{5}$ length of merus; merus with proximolateral spine. Second legs longer and more slender, carpus 7-jointed. Third to fifth legs with stout dactyls bearing curved spines on flexor margin, penultimate spine stout at base, shorter than terminal spine but making tip biunguiculate; merus of third leg with 3–5 lateral spines, distalmost longest; fourth leg with 2–6 lateral spines; fifth leg with 0–2 lateral spines.

Abdomen with pleura of first 3 segments rounded; fourth segment with small posteroventral spine; fifth similar though with spine directed more posteriorly; sixth with even less prominent

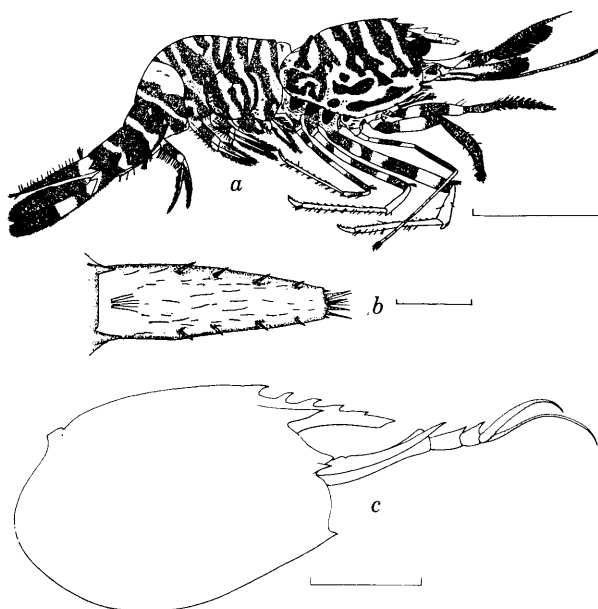


Fig. 88. *Lebbeus zebra* (Leim). a, Female in lateral view; b, telson; a, approx. 10 mm; b, approx. 2 mm indicated (from Leim 1921); c, carapace and antennule in lateral view, 5 mm indicated (from Williams 1974c).

posteroventral spine and above it an acute lateral spine with ventral shoulder overhanging base of telson. Telson with 3 pairs of terminal spines, outermost shortest, and 4–5 pairs of dorsolateral spines.

Measurements in mm.—Length of body: female 49 (Leim 1921).

Color.—Banded with bright brownish red to orange stripes generally running dorsoventrally, those of cephalothorax and 3 anterior abdominal segments somewhat oblique; areas between stripes bluish on cephalothorax, white elsewhere. Appendages alternately banded white and orange, but bands purplish on coxa, basis and ischium of legs. Sharp red line defining edges of all abdominal segments (except anterior edge of second), lateral edge of stylocerite, antennal scale, and antennal peduncle (Leim 1921).

Habitat.—On rock (Proctor 1933); 10 to 91 m in a temperature range of 8.2° to 9.7°C (Williams and Wigley 1977).

Type-localities.—Head Harbor, Campobello Island, N. B. (ROM 5143); Passamoquoddy Bay, Joe's Point, St. Andrews, N. B. (ROM 5144); Stn. 4, Passamoquoddy Bay, 30 m (ROM 5145).

Known range.—Port Burwell, Ungava; Gulf of St. Lawrence to southeast of Isles of Shoals, 42°52'N, 70°20'W (Proctor 1933; Holthuis 1947; Squires 1965a; Couture and Trudel 1968); Checleset Bay, Vancouver Island (Butler 1964).

Remarks.—Holthuis (1947) pointed out that in 1935 Makarov described *Hetairus zebra* from the Bering Sea and Kamchatka which may be the same as Leim's species, having similar color and general body structure but differing in shape of rostrum (longer, more dorsal and ventral teeth, and deeper distal to eyes). Butler (1964) compared a female from Vancouver Island with paratypes of *L. zebra*, deciding that they agreed closely in color pattern and morphology, but he thought that Makarov's species differed, as pointed out above. Couture and Trudel (1968) noted the great resemblance of *L. zebra* to *L. microceros* (Krøyer 1841), which may be synonymous, but rarity of specimens has prevented an evaluation of differences or similarities between them.

Genus *Lysmata* Risso 1816

Chace 1972:124.

Key to Species

(Adapted from Chace 1972)

1. Rostrum usually reaching as far as, or beyond, end of antennular peduncle; antennal scale 5 times as long as wide *L. rathbunae*
 Rostrum reaching not much, if at all, beyond second article of antennular peduncle; antennal scale less than 4 times as long as wide
 *L. wurdemanni*

Lysmata rathbunae Chace

Fig. 89

Lysmata rathbunae Chace 1970:59, figs. 1–4.

Recognition characters.—Rostrum straight or slightly concave dorsally, reaching as far as or beyond antennular peduncle; armed dorsally with 5 or 6 teeth, posteriormost widely separated from second tooth, and ventrally with 3–5 teeth. Carapace smooth; not dorsally carinate behind teeth or rostral series; anterior margin with large, sharp antennal spine overlying and concealing bluntly triangular ventral angle of orbit; anterolateral angle rounded. Eyes well developed, short and stout. Basal article of antennular peduncle large, small ventral tooth near midlength of mesial margin; stylocerite tapering to sharp point reaching about to end of proximal 1/3 of article; second and third articles

progressively shorter; each article of peduncle with 2–4 dorsolateral spinules near distal margin; inner flagellum slender; outer flagellum with about 14–35 thickened basal joints. Antennal scale 5 times as long as wide; lateral margin slightly concave, terminating in sharp distal tooth distinctly overreaching subtruncate distal margin of blade.

Epipods on first 4 pairs of legs. First legs stout, reaching to end of antennal scale; fingers slightly more than 1/2 length of palm; carpus slightly shorter than chela. Second legs subequal in length but much longer and more slender than first legs; chela small; carpus nearly twice as long as merus and divided into 30–35 joints, merus into 16–24 joints; ischium with 3–5 joints in distal half. Third to fifth legs not so slender as second, dactyls with few coarse spines on flexor surface.

Abdomen smooth, posterolateral angle of fifth segment acute, sixth with buttressed posteroventral

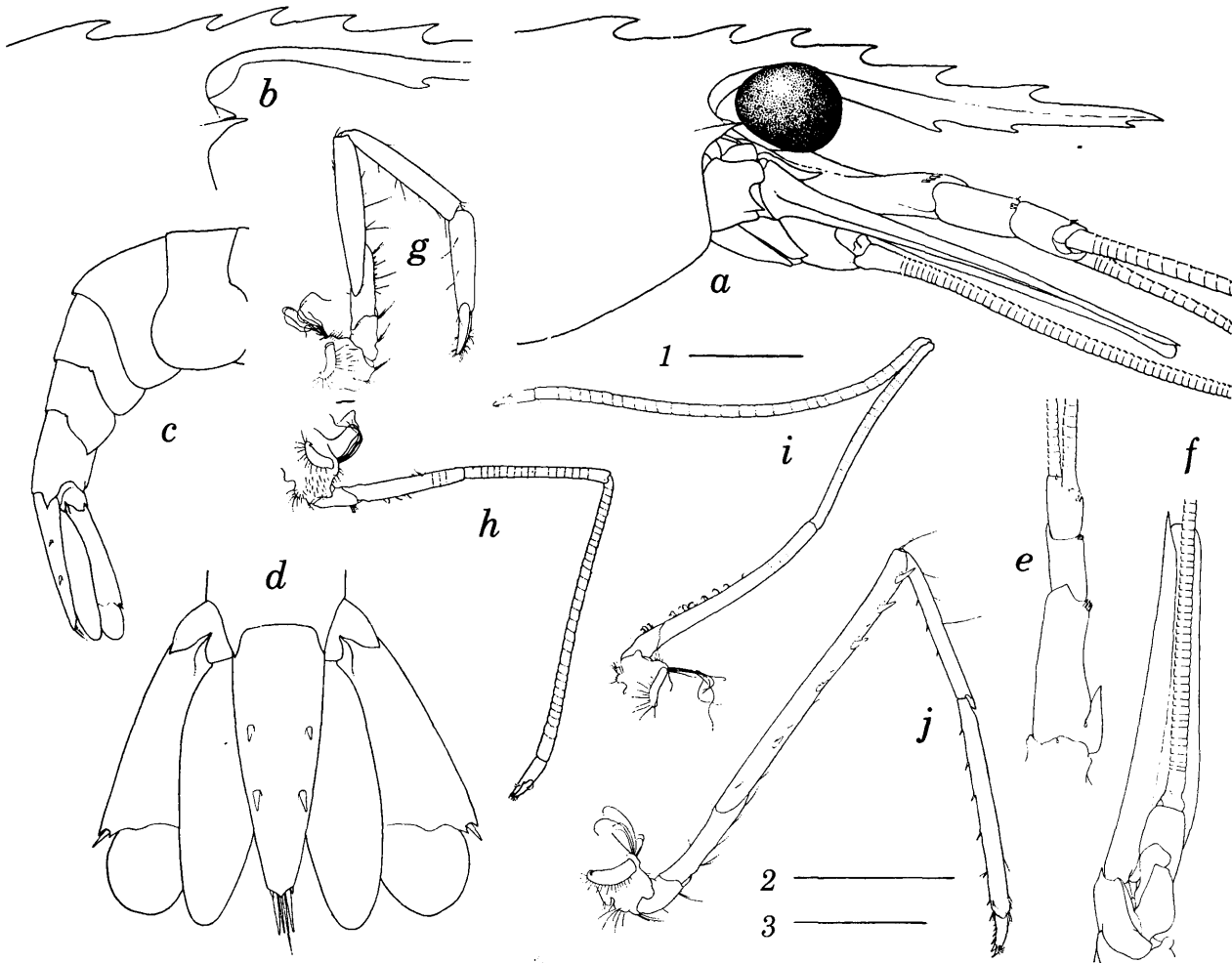


Fig. 89. *Lysmata rathbunae* Chace. Male: a, anterior region in lateral view; b, orbital region; c, abdomen; d, telson and uropods; e, right antennule; f, right antenna; g, right first leg; h, right second leg; i, left second leg; j, right third leg (from Chace 1970). Scales: 1(c); 2(a-b, d); 3(e-j) = 5 mm.

tral tooth. Telson tapering to tip with tiny median projection flanked by 2 long, slender spines, short spine outside these on each side; armed dorsally with pair of prominent spines at $\frac{1}{3}$ and $\frac{2}{3}$ length. Uropodal exopods with outer margin ending in 2 teeth, slender movable spine between these.

Measurements in mm.—Length of carapace: male 6.7; ovigerous females 6.3–9.6 (Chace 1970).

Variation.—Chace (1970) pointed out that there are two varieties of this species, the typical form with the penultimate proximal tooth of the rostral series in line with the rear edge of the orbit, and another form having more numerous rostral teeth with the posterior two teeth of this series placed distinctly posterior to the rear of the orbit, and having 38–43 joints in the carpus of the second leg. The latter may prove to be a distinct species if more material confirms this dichotomy.

Habitat.—Sometimes from sponges; typical form 13 to 119 m; many-spined form 9 m and less.

Type-locality.—Off Boynton Beach, Fla., 26°31'N, 80°01'W, 55–64 m.

Known range.—Typical form: SE Cape Fear, N. C., 33°30'24"N, 77°24'30"W, 25 m; east coast of Florida to Yucatan. Variety with more numerous rostral teeth: Bermuda; Miami, Fla.; Venezuela.

Remarks.—Ovigerous females are reported from Florida in March, and July–September.

Lysmata wurdemanni (Gibbes)

(Red cleaning shrimp)

Fig. 90

Hippolyte Wurdemanni Gibbes 1850:197.

Hippolysmata wurdemanni.—Hay and Shore 1918: 392, pl. 26, fig. 12.

Hippolysmata (Hippolysmata) wurdemanni.—Williams 1965:84, fig. 68.—Coelho and Ramos 1972:153.

Lysmata wurdemanni.—Chace 1972:129.

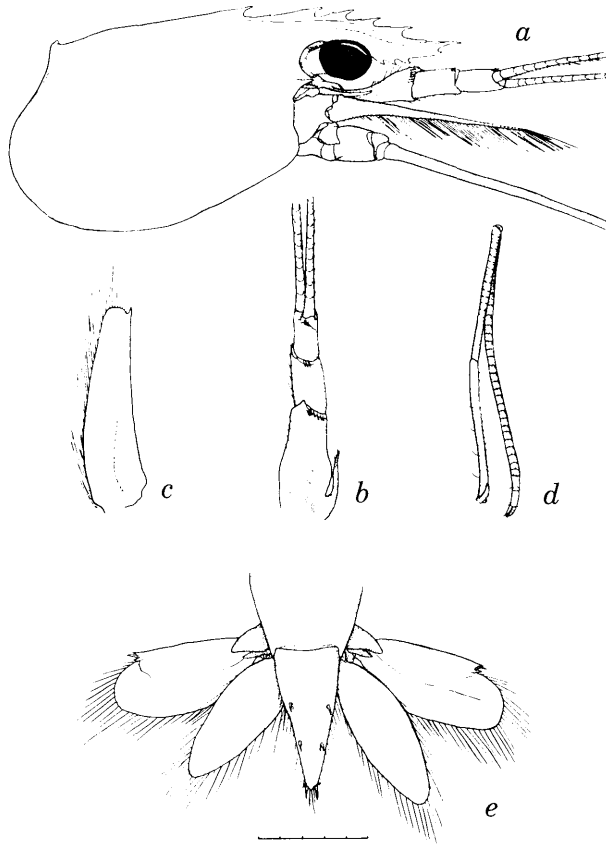


Fig. 90. *Lysmata wurdemanni* (Gibbes). a, Anterior portion of body in lateral view; b, antennule; c, antennal scale; d, second leg; e, uropods and telson in dorsal view; 5 mm indicated (from Williams 1965).

Recognition characters.—Rostrum reaching distal end of second article of antennular peduncle, slightly decurved, armed dorsally with 4 or 5 teeth and ventrally with 3 to 5 teeth. Carapace smooth; carinate dorsally on anterior half with spine near base of rostrum about midway between rostral tip and posterior border; anterior margin with strong antennal spine somewhat concealing triangular ventral angle of orbit; anterolateral corner rounded. Eyes well developed. Basal article of antennular peduncle large, small ventral tooth near midlength of mesial margin; stylocerite slender, flattened, pointed, reaching a little beyond middle of article; second and third articles progressively shorter; each article with 2–5 dorsolateral spinules near distal margin; inner flagellum slender; outer flagellum with about 20 to 30 thickened basal joints. Antennal scale less than 4 times as long as wide; outer margin slightly concave, terminating in strong spine; lamella of scale subtruncate distally, about equal to spine.

Epipods on first 4 pairs of legs. First legs moderately stout, about equal, reaching to end of antennal scale; fingers about $\frac{1}{3}$ length of palm, spines

at tips of fingers darkened; carpus and hand of nearly equal length. Second legs subequal in length but much longer and more slender than first legs; chela small; carpus small; carpus divided into about 30 joints, last joint longest; merus divided into about 20 joints, and ischium into about 5 in distal half. Third to fifth legs not so slender as second; dactyls with few coarse spines on flexor surface.

Abdomen smooth; posterolateral angle of fifth and sixth segments acute. Telson tapering to tip with minute median projection flanked by 2 long, slender spines, short spine outside these on each side; armed dorsally with 2 pairs of prominent spines at $\frac{1}{3}$ and $\frac{2}{3}$ length. Uropodal exopods with outer margin ending in 2 distinct teeth, slender movable spine between these.

Measurements in mm.—Length of body: males 28 to 54; ovigerous females 38 to 55 (Wass 1955 in part).

Variation.—Individuals from the northern extreme of the range differ in some respects from those in South America (Holthuis 1959). The rostrum in South American specimens has four to seven dorsal teeth, and in specimens from the United States, four or five. Some southern specimens have stylocerites nearly as long as the basal antennular articles. In southern specimens, the tip of the lamella on the antennal scale is more truncate than in northern specimens. The second leg in Guiana material is more slender than in northern material, and the number of articulations in the carpus is higher, 33–37 as opposed to 27–31. Chace (1972) gave further details and remarked on scarcity of the species in the West Indies.

Color.—Translucent white with beautiful longitudinal and transverse markings of red.

Habitat.—Commonly found on stone jetties or among hydroids growing on piles or buoys, or in sponges (Tabb and Manning 1961); surface to 37 m (USNM).

Type-locality.—Key West, Fla.

Known range.—Great Egg Harbor, N. J., to Port Aransas, Tex.; Surinam; French Guiana; Mamanaguape, São Paulo, Brazil.

Remarks.—Ovigerous females are known in January, February, May and June from Florida (Tabb and Manning 1961; Wass 1955; Rouse 1970; USNM), January from South Carolina (USNM), April from Quintana Roo, Mexico (Chace 1972), April and August from North Carolina, May from the Guianas (Holthuis 1959), and August from Louisiana (USNM). Protandry has been observed in two European and Mediterranean species of *Lysmata* (Yaldwyn 1966a). When approached by a spiny boxfish or filefish, this shrimp begins rhythmically rocking to and fro; ascending vertically in

a peculiar walking motion, it mounts its "host" and begins picking off parasites. The shrimp will swarm over the fingers of a person, picking at cuts and dead skin (Anonymous 1975).

Genus *Spirontocaris* Bate 1888

Holthuis 1947:7.—Hayashi 1977:155.

Rostrum well developed, upper margin dentate, lower margin usually so. Carapace with armed dorsal carina and 2–4 supraorbital spines. Eyes well developed, inner basal part of stalk umbonate. Third maxillipeds with exopods. Second leg with carpus subdivided into 7 joints. Epipods on legs 1, 1–2, or 1–3.

Key to Species

(from Williams 1974c; Couture and Trudel 1968)

1. Middorsal teeth extending to or beyond posterior $\frac{1}{3}$ of carapace; spines on rostrum of nearly uniform size *S. phippsii*
Middorsal teeth falling short of posterior $\frac{1}{3}$ of carapace; spines on rostrum definitely unequal in size 2
2. Ventral margin of rostrum with 4–6 teeth; tip ascending to well-defined single point extending beyond antennal scale *S. liljeborgii*
Ventral margin of rostrum with about 2 (occasionally 3) large teeth and variable number of smaller ones (0–many); tip single or often almost equaled or surpassed by prominent ventral tooth; not extending beyond antennal scale *S. spinus*

Spirontocaris liljeborgii (Danielssen)

Fig. 91

Hippolyte Liljeborgii Danielssen 1859:5.

Spirontocaris liljeborgii.—Holthuis 1947:8 (synonymy).—1950:43, fig. 14.—Greve 1963:32, figs. 1B, D.

Spirontocaris liljeborgii.—Couture and Trudel 1968:866, fig. 7.

Spirontocaris liljeborgii.—Smaldon 1979:64, fig. 24A–D.

Recognition characters.—Rostrum deep, convex upper margin ending in acute, horizontal to slightly upturned tip reaching nearly to end of antennal scale; row of many dorsal teeth variable in size and number, smallest anteriorly and extending posteriorly along middorsal carina approximately $\frac{2}{3}$ length of carapace; ventral margin of rostrum convex, bearing 1–5 teeth variable in size, shape, and arrangement. Carapace bearing 2 supraorbital spines on each side, upper one slightly larger; suborbital lobe distinctly flanked by antennal spine; anteroventral margin almost straight; pterygostomian spine small and acute. Antennular peduncle with basal article bearing rather broad distolateral spine and ventromesial spine; stylocerite strong, acute, mesial margin tapered somewhat obliquely to tip reaching about to midlength of second article; latter bearing slender lateral spine; third article about half length of second, with slender distolateral

spine; thick ramus with short distal flagellum, slender mesial ramus longer. Antennal peduncle reaching about as far forward as stylocerite; basal article with ventrolateral spine and dorsolateral lobe; scale with lateral margin straight, lamella with rounded tip extending to about level of distolateral spine. Third maxilliped reaching beyond antennal scale, exopod and epipod present.

First 3 legs with epipods. First leg moderately stout, reaching about length of fingers beyond antennal peduncle; fingers darkened at tips, that of dactyl cleft to accommodate tip of fixed finger; palm about length of carpus; merus with small proximolateral spine. Second leg much longer and more

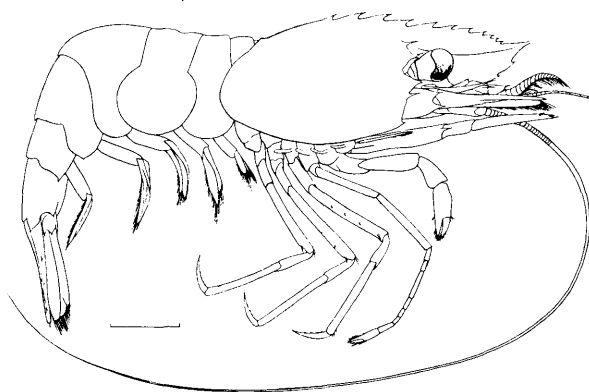


Fig. 91. *Spirontocaris liljeborgii* (Danielssen). Animal in lateral view, 5 mm indicated (from Holthuis 1950).

slender, third joint from proximal end of 7-segmented carpus longest. Third to fifth legs bearing curved spines on flexor margin of dactyls, penultimate spine strong, shorter than terminal spine but making tip biunguiculate; meri bearing small lateral spines, third with about 5–6, fourth with about 3–5, fifth with about 1–2, distalmost on each leg longest.

Abdomen with pleura of first 3 segments rounded; third with posterodorsal margin produced slightly posteriorly; fourth segment with small posteroventral spine; fifth similar though with spine directed more posteriorly; sixth with even less prominent posteroventral spine and above it an acute lateral spine with ventral shoulder overhanging base of telson. Telson with 3 pairs of terminal spines, outermost shortest, and 3–5 pairs of dorsolateral spines.

Measurements in mm.—Length of body: male 47; female 74; smallest ovigerous female (Norway) 39 (Greve 1963).

Variation.—Females are stouter than males; for a given carapace length, females have greater carapace height than males, a linear relationship probably reflecting differences in room needed for gonads (Allen 1962). The ventral part of the female rostrum is definitely convex, that of the male slightly so, but intermediates exist, and the dimorphism becomes more pronounced with age (Greve 1963). Dons (1915) showed variant rostral shapes of *S. securifrons* (= *liljeborgii*).

Color.—"Body bright red. Extremities with ribbons of red. Ends of claws and eyes brownish black" (Greve 1963). "Bright red with yellow and white spots" (Squires 1965a).

Habitat.—Mainly hard bottom, but sometimes on mud (Greve 1963; Allen 1966); 20 to 1200 m, mostly 35 to 90 m (Holthuis 1950).

Type-locality.—Lofoten, [Norway] on sandy bottom, 40 fm.

Known range.—Greenland; Nova Scotia to off Delaware Bay; arctic Alaska; Iceland; Spitzbergen and Murman coast to south coast of England and west and southwestern Ireland (Holthuis 1947, 1950; Smaldon 1979).

Remarks.—Ovigerous females in the USNM collection are from Hudson Canyon off New York in November and February, and the Gulf of Maine in September. Breeding indications in these spotty records are in agreement with times in published reports. From Foxe Basin, Frobisher and Ungava bays, Squires (1965a) found one ovigerous female in July, but 75% were ovigerous in December. They are known from November to May in southern and western Norway (Holthuis 1950; Greve 1963).

Pike (1954) showed from study of gonads and

other structures that *S. liljeborgii* is a dioecious species; no protandrous hermaphrodites have been seen. He found that most males in the Firth of Clyde, Scotland, become sexually mature by age 7–9 months; some of these may die after fertilizing females and the majority die after fertilizing females during a second year (age 18 months). His study suggested that only a small proportion of females breed in their first year, all breed during the second year, and a few appear to live for a third year. His count on egg production was 130–160 in the first year and 450–650 in the second year. Egg laying begins at the end of November and hatching is complete by the end of March. Off north-eastern England, females are ovigerous from December to April, bear 350 to 850 eggs once during the season for a period of 12–13 weeks, and a few spawn during a second year. Some individuals are thought to live up to 2½ years (Allen 1962, 1966).

The larval stages of *S. liljeborgii*, reviewed by Pike and Williamson (1961), are very similar to those of *S. spinus*, there being minor differences in spination.

Spirontocaris liljeborgii has a large mandible with flat crushing molar surface (Allen 1962, 1966). The species feeds primarily on foraminiferans and to some extent on gastropods, but also on crustaceans, hydroids, pelecypods, annelids, etc.

A bopyrid, *Hemiarthrus abdominalis*, is parasitic on this as well as other species of *Spirontocaris* (Allen 1962). No parasitized females bear eggs, and their size is generally smaller than that of unparasitized individuals.

Spirontocaris phippsii (Krøyer)

Fig. 92

Hippolyte Phippsii Krøyer 1841:575.

Spirontocaris phippsii.—Holthuis 1947:8 (synonymy).

Spirontocaris phippsi.—Leim 1921:142, pl. 6, fig. 13.—

Greve 1963:33, fig. 2C, D.—Couture and Trudel 1968:867, fig. 8.

Recognition characters.—Rostrum deep, dorsal margin about horizontal, tip reaching to or beyond antennular peduncle in males and females respectively; upper margin with rather closely spaced large teeth becoming smaller near tip and continuous with more widely spaced teeth on middorsal carina not extending beyond posterior ⅓ of carapace; some sexual dimorphism in shape and tooth number, that of females deeper with 9–13 teeth in dorsal series and 3–6 ventrally, that of males less deep with 7–12 in dorsal series and 1–4 ventrally; lateral carina slanting obliquely upward to near tip. Carapace

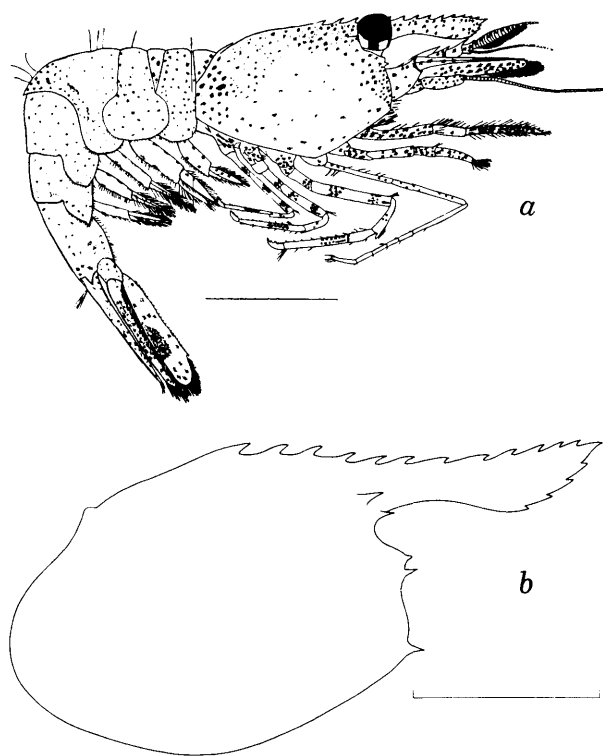


Fig. 92. *Spiontocris phippisii* (Krøyer. a, Female in lateral view, approx. 3 mm indicated (from Leim 1921); b, carapace in lateral view, 5 mm indicated (from Williams 1974c).

bearing 2 supraorbital spines on each side, upper one definitely larger; suborbital lobe distantly flanked by antennal spine; anteroventral margin almost straight; pterygostomial spine small and acute. Antennular peduncle with basal article bearing rather broad distolateral spine and ventromesial spine; stylocerite strong, acute, mesial margin tapered somewhat obliquely to tip, reaching about to dorsal margin of second article bearing strong, slender distolateral spine; thick lateral ramus with short distal flagellum, slender mesial ramus longer. Antennal peduncle reaching about as far forward as stylocerite; basal article with ventrolateral spine and dorsolateral lobe; scale with lateral margin straight, lamella with rounded tip exceeding distolateral spine. Third maxillipeds reaching beyond antennal scale, exopod and epipod present.

First 3 legs with epipods. First leg moderately stout, reaching about half length of palm beyond antennal peduncle; fingers darkened at tips, that of dactyl cleft to accommodate tip of fixed finger; palm about length of merus; merus with small proximolateral spine. Second leg much longer and more slender, third joint from proximal end of 7-segmented carpus longest. Third to fifth legs bearing curved spines on flexor margin of dactyls, penultimate spine strong, shorter than terminal spine

but making tip biunguiculate; meri bearing small lateral spines, third with about 2–7, fourth with about 2–6, fifth with 1–3, distalmost on each leg longest.

Abdomen with pleura of first 3 segments rounded; third with posterodorsal margin produced slightly posteriorly; fourth segment with small posteroventral spine; fifth similar though with spine directed more posteriorly; sixth with even less prominent posteroventral spine and above it an acute lateral spine with ventral shoulder overhanging base of telson. Telson with 3 pairs of terminal spines, outermost shortest, and 2–5 pairs of dorsolateral spines.

Measurements in mm.—Length of body: male 28; female 45.

Variation.—Variation in number of rostral spines trends toward a smaller number in males (Greve 1963). Dons (1915) showed variations in tooth pattern on the rostrum as well as the sexual dimorphism in depth for *S. turgida* (= *phippisii*). The supraorbital spine closest to the orbital margin is variably smaller than the spine posterodorsal to it, and rarely is absent (Leim 1921).

Color.—Rather large brownish red spots over body and appendages; more closely spaced on upper half, anterior and posterior end of carapace than on its remainder; also grouped on posterodorsal margin of third abdominal segment and on uropods (Leim 1921). Reddish brown with small light spots (Squires 1965a).

Habitat.—Chiefly firm bottom among algae in usually low positive temperature (Heegaard 1941); 10 to 270 m (Holthuis 1947; Squires 1965a).

Type-locality.—Spitsbergen, Norway's west coast (and Greenland?).

Known range.—Circumarctic southward to near Martha's Vineyard; northern Norway; Shumagin Islands, Alaska; Plover Bay, Siberia (Holthuis 1947; Squires 1965a).

Remarks.—In the USNM collection, ovigerous females are present from Franz Joseph Land in June, northern and northeastern Greenland from June to August, Labrador in August and Nova Scotia in September, arctic Alaska in August and September, and Foxe Basin, Canada, and Plover Bay, Siberia, in September. Breeding indications in these spotty records are elaborated by accounts of several authors. Heegaard (1941) found ovigerous females in east Greenland during July and August (as *S. turgida* = *phippisii*); MacGinitie (1955) found them at Point Barrow, Alaska, in mid-October. Squires (1965a) indicated an annual autumn spawning period for the species in Foxe Basin and found ovigerous females from June to early August around the Queen Elizabeth Islands (1968).

Summarizing Norwegian breeding records, Greve (1963) reported ovigerous females in autumn and winter from the north, but none during May to September.

Larvae of this species have not been reared in the laboratory, but Pike and Williamson (1961) reviewed published records of identifications from plankton as stage II from off Portland, Maine, and stage III from Greenland, as well as assessing status of similar larvae belonging to *Spirontocaris* and closely related genera.

Stomach contents in Foxe Basin consisted largely of foraminiferans and phytobenthos, ostracods and crustacean fragments including mysids and copepods, hydroids, small pelecypods, and rhodophytes in descending order of abundance (Squires 1965a). He (1967) thought that the species might feed selectively on ostracods in addition to detritus. He also listed cod as a predator on the Grand Banks and St. Pierre Bank.

MacGinitie (1955) reported a male parasitized by the isopod *Phryxus abdominalis*.

***Spirontocaris spinus* (Sowerby)**

Fig. 93

Cancer Spinus Sowerby 1805:47, pl. 23.

Spirontocaris spinus.—Holthuis 1947:8 (synonymy).—Greve 1963:30, fig. 1A, C.—Couture and Trudel 1968:868, fig. 9.—Hayashi 1977:177, figs. 8–9.—Smaldon 1979:66, fig. 25A-C.

Recognition characters.—Body robust. Rostrum deep, upper margin with many small irregular teeth continuous with middorsal carina running nearly full length of carapace and armed with 4 or 5 large teeth, anterior 1 or 2 often bearing a few small secondary teeth; tip not extending beyond end of antennal scale, single but often almost equaled or surpassed by prominent ventral tooth, secondary teeth may lie in distal notch thus formed as well as behind prominent ventral tooth; lateral carina turned slightly upward near tip. Carapace bearing 2 supraorbital spines on each side; suborbital lobe distantly flanked by rather strong antennal spine; anteroventral margin almost straight; pterygostomian spine small and acute. Antennular peduncle with basal article bearing distolateral spine, acute in dorsal view but rather broad in lateral view, and slender ventromesial spine; stylocerite strong, acute, mesial margin tapered somewhat obliquely to tip, reaching distal margin of second article bearing slender distolateral spine; third article about half

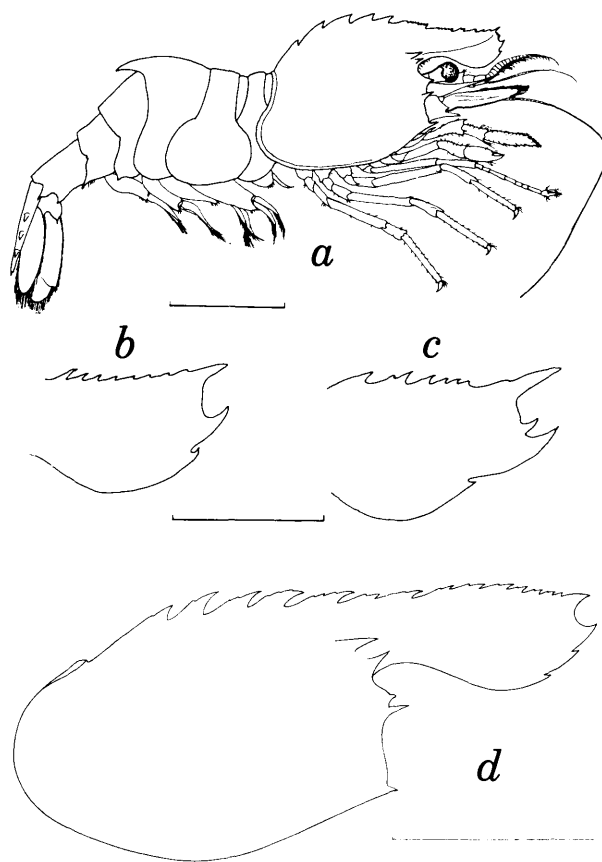


Fig. 93. *Spirontocaris spinus* (Sowerby). a, Female in lateral view; b-c, rostral variants; a, 10 mm, b-c, 5 mm indicated (from Smaldon 1979); d, carapace in lateral view, 5 mm indicated (from Williams 1974c).

length of second, with slender distodorsal spine; thick lateral ramus with short distal flagellum, slender mesial ramus longer. Antennal peduncle reaching about as far forward as basal antennular article; basal article with strong ventrolateral spine and dorsolateral lobe; scale with lateral margin about straight, lamella with somewhat rounded to subtruncate tip exceeded by distolateral spine. Third maxillipeds reaching to tip of antennal scale, exopod and epipod present.

First 3 legs with epipods. First leg moderately stout, reaching about to distal end of antennal peduncle; fingers darkened at tips, dactyl cleft at tip to accommodate tip of fixed finger; palm about length of carpus; merus with small proximolateral spine. Second leg much longer and more slender, third joint from proximal end of 7-segmented carpus longest. Third to fifth legs with dactyls bearing curved spines on flexor margin, penultimate spine strong, shorter than terminal spine but making tip biunguiculate; meri bearing lateral spines, third with

about 5–8, fourth with about 4–5, fifth with 1–3, distalmost on each leg longest.

Abdomen with pleura of first 3 segments rounded; third with posterodorsal margin produced posteriorly; fourth segment with small posteroventral spine; fifth similar though with spine directed more posteriorly; sixth with even less prominent posteroventral spine and above it an acute lateral spine with ventral shoulder overhanging base of telson. Telson with 3 pairs of terminal spines, outermost shortest, and 4–5 pairs of dorsolateral spines.

Measurements in mm.—Length of body: male 40; female 59.

Variation.—Leim (1921) found much variation in form and total number of teeth on the rostrum which may be pointed or concave anteriorly, depending on length of the ventral spine; 9–33 (\bar{x} = 18–20) dorsal spines and 2–5 ventral spines were observed. Moreover, the dorsal teeth of the carapace may number 5 or 6. Leim also noticed diversity in form of the dactyls on the third to fifth legs which may be longer and more slender than in other members of the genus. Dons (1915) illustrated several variant forms of the rostrum, and Hayashi (1977) commented on these and other variations, some of which have been the basis for nominal species or subspecies which he synonymized.

Color.—“Dull red with brown, bright red and green mottling and sometimes white marking on the legs” (Squires 1965a). Red and white with few olive-tan spots and a few chalky-white streaks (MacGinitie 1955). “Normally mottled dark red, brownish or light green. Sometimes bright red” (Smaldon 1979).

Habitat.—Hard bottom, stones, gravel, sand and algae, sometimes mud or clay (Christiansen and Christiansen 1962; Allen 1966); often associated with *Balanus* (Heegaard 1941; MacGinitie 1955); 5 to 465 m (Heegaard 1941; Holthuis 1947; Squires 1965a; Hayashi 1977).

Type-locality.—“Among oysters on the Scottish coast.”

Known range.—Circumarctic southward to near Martha's Vineyard, Mass.; northern Norway to northeastern England and Irish Sea; Shumagin Islands, Alaska; Puget Sound, Wash.; Plover Bay, Siberia; Bering Sea; Sea of Okhotsk; and Sea of Japan off Nigata Pref., Japan (Holthuis 1947; Squires 1965a; Hayashi 1977). Heegaard (1941) mapped the distribution in part.

Remarks.—Several authors have remarked that *S. spinus* is never found in large numbers (Allen

1962), although Greve (1963) considered it common off northern Norway.

Ovigerous females in the USNM collection are present from Hudson Canyon, USA, in February, Newfoundland in June and August, Gulf of Maine, northern and eastern Greenland in August, and Nova Scotia and Point Barrow, Alaska, in September. These spotty records are in conformity with more ordered findings of several authors. MacGinitie (1955) found new laid eggs at Point Barrow in early August. Greve (1963) reported ovigerous females in western Norway from February to April, northern Norway in March, and Ellesmere Land in July. Christiansen and Christiansen (1962) found them during July–August at Spitsbergen. Squires (1965a; 1967) found them off Newfoundland in June and October–November, and judged that 15% of females in Foxe Basin bore eggs that would probably hatch in autumn, thinking that if these individuals spawned twice in a lifetime, they would spawn annually. Off northeastern England, Allen (1962; 1966) found ovigerous females during December to April; the females bore one brood of 350–850 eggs per year that would be carried 12–13 weeks. He judged that the life span was up to 2½ years.

From hatching of eggs at Port Erin, Isle of Man, in April, Pike and Williamson (1961) reared larvae through early stages and studied latter stages from plankton. They described and illustrated five zoeal stages, a megalopa, and the first juvenile stage, and reviewed the work of Frost (1936), deciding that her “*Spirontocaris* A” should be referred to *S. spinus*.

Stomach contents of *S. spinus* in Squires's study (1965a) consisted of phytobenthos, foraminiferans, ostracods and infrequent other crustacean fragments, sponge spicules, small pelecypods, and hydroids. He commented especially on the massive molar process divided into two parts, describing its structure. Allen (1966) found predominantly small gastropods and bivalves with some admixture of foraminiferans and hydroids in stomachs. Cod is a frequent predator, and beluga whales occasionally eat this shrimp (Squires 1965a; 1967).

Off Northumberland, England, a good many individuals bear the isopod parasite *Hemiarthrus abdominalis* (see Allen 1962), as do individuals in Foxe Basin, Hudson Strait and northern Labrador (Squires 1965a).

Genus *Thor* Kingsley 1878

Kingsley 1878b:94.—Hemming 1958b:161.—Chace 1972:129.

Carapace with antennal spine; rostrum short, inclined ventrad, toothed above and below. Antennules with outer flagellum very stout; third article with broad movable plate at anterodistal margin.

Mandible without palp; with incisor process. (Holthuis 1955.)

Without ovigerous females, the following species are difficult to distinguish.

Key to Species

(Adapted from Chace 1972)

1. Merus of first leg armed with 1–2 spines (tiny) on distal half of flexor margin; eggs not very large, increasing from 0.36 to 0.74 mm in major diameter during development *T. dobkini*
 Merus of first leg unarmed on distal half of flexor margin 2
2. Dactyls of fourth and fifth legs commonly armed with 4 or 5 (rarely 3 or 6) spinules on flexor margin proximal to distal pair of spines; eggs large and few, increasing from 0.66 to 1.40 mm in major diameter during development *T. floridanus*
 Dactyls of fourth and fifth legs commonly armed with 3 (sometimes 2 or 4) spinules on flexor margin proximal to distal pair of spines; eggs not very large, increasing from 0.36 to 0.73 mm in major diameter during development *T. manningi*

Thor dobkini Chace

Fig. 94

Thor floridanus.—Dobkin 1968:1–7. (Not *T. floridanus* Kingsley 1878b.)

Thor dobkini Chace 1972:133, fig. 57a-y.

Recognition characters.—Rostrum inclined ventrad; tip not reaching distal margin of basal antennular article; dorsal margin usually armed with 4, sometimes 5 (rarely 3 or 6) teeth, posterior tooth in line with or slightly posterior to rear margin of orbit; ventral margin with single distal tooth, making tip bifid. Supraorbital tooth barely discernible, obtuse. Eyes well developed, cornea broader than and as long as eyestalk. Antennule with basal article large; stylocerite reaching beyond distal margin of second article and armed with small lateral tooth at base; second and third article short, second with curved lateral spine reaching $\frac{2}{3}$ length of distal article, latter with triangular dorsal scale. Antennal scale overreaching antennular peduncle by at least $\frac{1}{3}$ length; nearly straight lateral margin terminating in stout spine, lamella greatly exceeding spine; a ventrolateral spine on basal article of peduncle. Third maxilliped reaching a little beyond tip of antennal scale; last article bearing slender spine.

First legs reaching about as far as distolateral tooth of antennal scale; fingers slightly more than $\frac{1}{2}$ length of palm, carpus about as long as palm; merus nearly $\frac{1}{4}$ longer than carpus, armed with 1 or 2 movable spines distal to midlength of flexor

margin; ischium little more than $\frac{1}{3}$ length of merus. Second leg slightly overreaching antennal scale; fingers shorter than palm; carpus subdivided, joints decreasing from proximal end in order of 3, 6, 4, 1, 2, 5. Third leg of male prehensile, subchelate, overreaching antennal scale by length of dactyl and $\frac{3}{4}$ of propodus; dactyl with about 16 closely appressed spinules on flexor margin, propodus more than twice length of dactyl, distal $\frac{1}{3}$ of flexor margin oblique and densely spinose. Third leg of female not prehensile, similar to fourth but without microscopic comblike spines at distal end of propodus. Fourth leg not prehensile; dactyl usually bearing 5 (less commonly 3, 4, or 6) spines on flexor margin of propodus.

Abdomen smooth; pleura of segments 1–3 broadly rounded, those of 4–6 with posteroventral angles acute; sixth segment nearly twice as long as fifth but shorter than telson not including terminal spines. Telson elongate, triangular, with 3 or 4 pairs of prominent dorsal spines a little remote from edges and spaced equidistantly in posterior $\frac{3}{4}$ of length; tip with median point and usually 3 pairs of subequal spines, outer pair shortest. Uropodal exopods with outer edge ending in small spine flanked mesially by strong movable spine.

Measurements in mm.—Length of carapace: males 2.0; females 3.4.

Color.—Red eyestalks, red marks (USNM).

Habitat.—Grass flats and offshore reefs; to depth of 19 m (USNM).

Type-locality.—Punta Rassa (near mouth of Caloosahatchee River), Lee County, Fla.

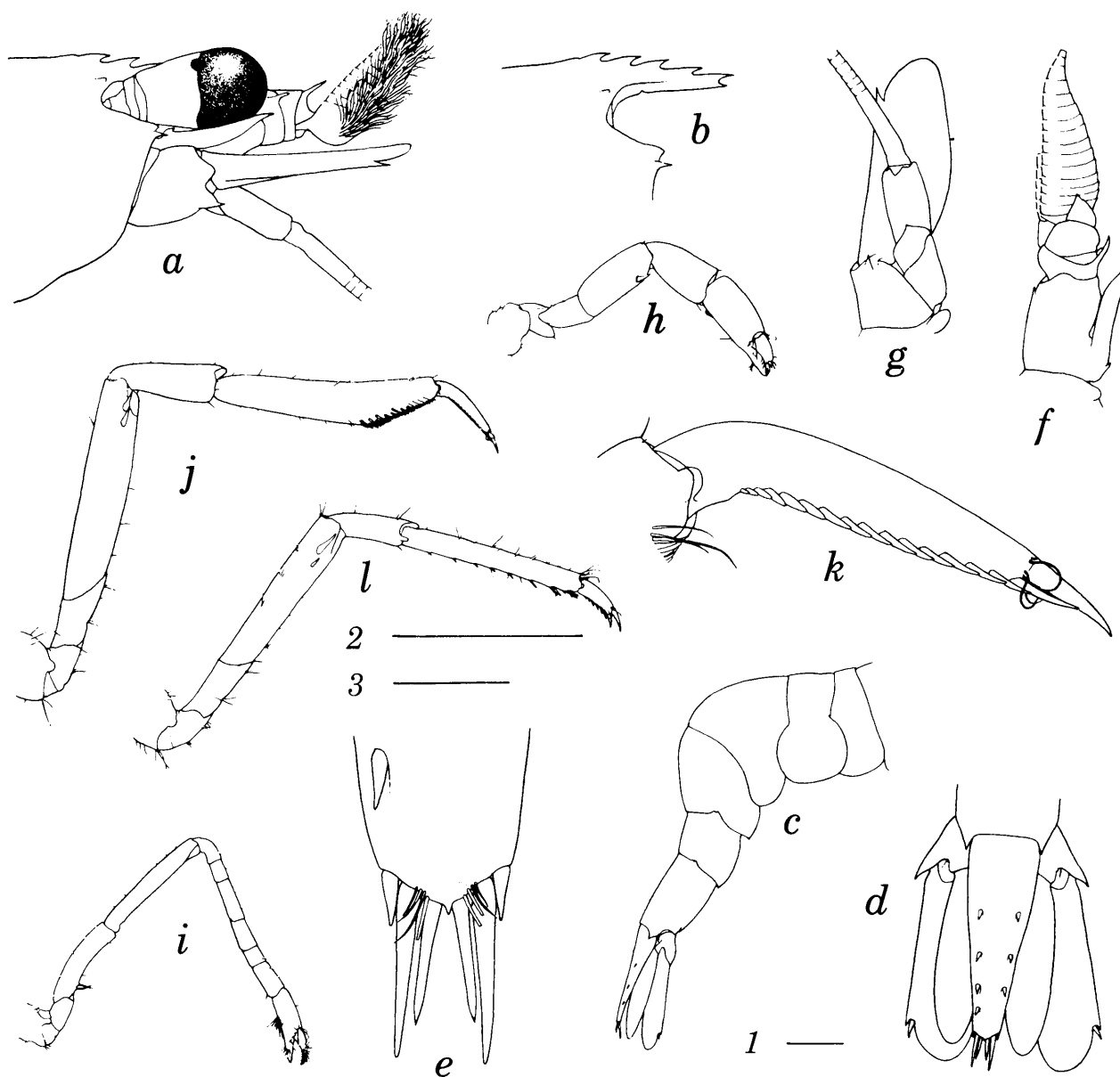


Fig. 94. *Thor dobkini* Chace. Male: a, anterior region; b, rostrum; c, abdomen; d, telson and uropods; e, end of telson; f, right antennule; g, right antenna; h, right first leg; i, right second leg; j, right third leg; k, same, dactyl; l, right fourth leg. Scales: 1(c)=1 mm; 2(e, k)=0.3 mm; 3(all others)=1 mm (from Chace 1972).

Known range.—Off Shackleford Bank, N. C., to Yucatan; Louisiana; north coast of Cuba.

Remarks.—Chace (1972) determined that *T. dobkini* is a protandrous hermaphrodite. Males are smaller than females.

***Thor floridanus* Kingsley**

Fig. 95

Thor floridanus Kingsley 1878b:95.—Chace 1972: 136, fig. 58.

Thor species Dobkin 1968:1–18, figs. 1–9.

Recognition characters.—Rostrum inclined ventrad, tip not reaching distal margin of basal antennular article; dorsal margin usually armed with 4 or 5 teeth, posterior tooth in line with or slightly posterior to rear margin of orbit; ventral margin with single distal tooth, making tip bifid (sometimes unarmed). Supraorbital tooth barely discernible, obtuse. Eyes well developed, cornea broader than and about as long as eyestalk. Antennule with basal article large; stylocerite sharp, reaching slightly beyond distal margin of basal article and armed with small lateral tooth at base; second and third articles short, second with curved

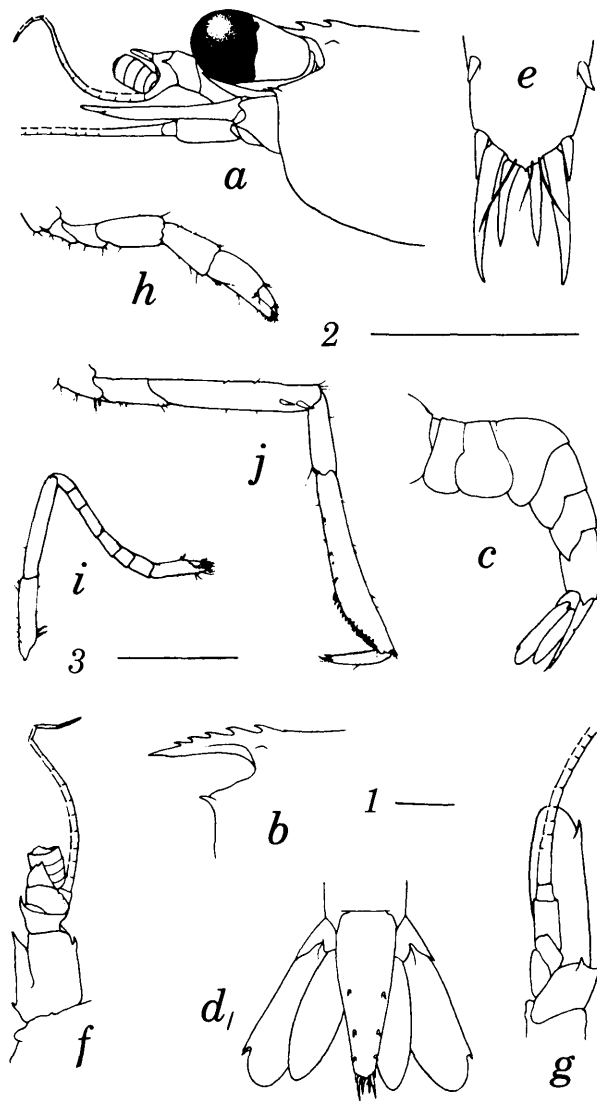


Fig. 95. *Thor floridanus* Kingsley. Male: a, anterior region; b, rostrum; c, abdomen; d, telson and uropods; e, end of telson; f, right antennule; g, right antenna; h, right first leg; i, right second leg; j, right third leg. Scales: 1(c) = 1 mm; 2(e) = 0.3 mm; 3(all others) = 1 mm (from Chace 1972).

lateral spine reaching beyond midlength of distal article, latter with triangular dorsal scale. Antennal scale overreaching antennular peduncle by nearly $\frac{1}{2}$ length; nearly straight lateral margin terminating in stout spine, lamella greatly exceeding spine; a ventrolateral spine on basal article of peduncle. Third maxilliped reaching slightly beyond tip of antennal scale, last article bearing slender spines.

First legs reaching about to end of antennal peduncle, fingers slightly more than $\frac{1}{2}$ length of palm, carpus about as long as palm; merus somewhat longer than carpus, unarmed in distal half of flexor margin; ischium at least $\frac{1}{2}$ length of merus. Second leg overreaching antennal scale by about length of chela; fingers shorter than palm; carpus subdivided, joints decreasing from proximal end in order of 3, 6, 4, 1, 2, 5 (but at least one variant 4, 6,

3, 1, 5, 2). Third leg of male prehensile, subchelate, dactyl bearing about 13 closely appressed spines on flexor margin; propodus more than twice length of dactyl, distal $\frac{1}{3}$ of flexor margin oblique and densely spinose. Third leg of female not prehensile, similar to fourth but without microscopic comblike spines at distal end of propodus. Fourth leg not prehensile, dactyl usually with 4 or 5 (rarely 3 or 6) spines on flexor margin in addition to distal pair. Fifth leg similar but fringe of stout setae distally on flexor margin of propodus.

Abdomen smooth; pleura of segments 1–3 broadly rounded, those of 4–6 with posteroventral angles acute; sixth segment nearly twice as long as fifth but shorter than telson not including terminal spines. Telson elongate, triangular, with 3 pairs of prominent dorsal spines a little remote from edges and distributed in posterior $\frac{3}{4}$ of length; tip with median point and usually 3 pairs of subequal spines, outer pair shortest. Uropodal exopods with outer edge ending in small spine flanked mesially by strong movable spine.

Measurements in mm.—Length of carapace: males 1.3–1.6, females 1.5–2.3 (Chace 1972).

Habitat.—Grass flats; on *Halimeda*; to depth of 59 m.

Type-locality.—Key West, Fla.

Known range.—Black Rocks off New River, N. C.(?); to Yucatan.

Remarks.—Chace (1972) determined that this is the species of *Thor* whose larval development was discussed by Dobkin (1962; 1968). Ovigerous females are known in Florida throughout the year, although most abundantly so from May through July, and from Quintana Roo, Mexico, in April, North Carolina from June to September, South Carolina and Louisiana in August, and northern Gulf of Mexico in October. In southern Florida, Dobkin hatched eggs and reared larvae in temperatures of 11°–31°C. Larvae fed *Artemia* developed through two stages (described and figured) in 2–4 days, metamorphosing to postlarva after 48 h in temperatures of 25°C or higher. Dobkin attempted to cross mate this species with another having many small eggs. Although females of such matings produced eggs, none were viable. At the same time, within-species matings resulted in production of viable eggs. Three generations of *T. floridanus* were reared from the captive populations.

Imperfect protandry may be developed in this species (Chace 1972).

Both Broad (1957b) and Sandifer (1972) reared a species of *Thor* attributed to *T. floridanus* from ovigerous females collected at Beaufort, N. C., in August. In each case the larvae usually passed through 8 zoeal stages before metamorphosing to postlarvae (Sandifer's varied from 6 to 10 stages). On a diet of *Nitzschia closterium* or *Nannochloris* sp.,

larvae studied by Broad metamorphosed in 16 days. Sandifer's specimens, with experimental diets of starvation, algae, live *Artemia* nauplii, and mixed algae and *Artemia*, completed larval development in 14 to 29 days. Of non-starved groups, best survival to metamorphosis was among those fed the combination diet.

The true identity of these many-staged larvae is open to question since Dobkin reared few-staged larvae of true *T. floridanus*. Broad stated that his larvae differed from those reared at Bermuda by Lebour (1940a). Markham and McDermott (1981) recorded *T. amboinensis*, *T. floridanus*, and *T. man-*

ningi from Bermuda, thus it is not possible to single out which species from Beaufort was reared unless parent material from Broad and Sandifer's rearings is still available for study.

Thor manningi Chace

Fig. 96

Thor manningi Chace 1972:137, figs. 59–60.—Carrvacho 1979:464.

Recognition characters.—Rostrum inclined ventrad, variable in length, tip reaching from short of

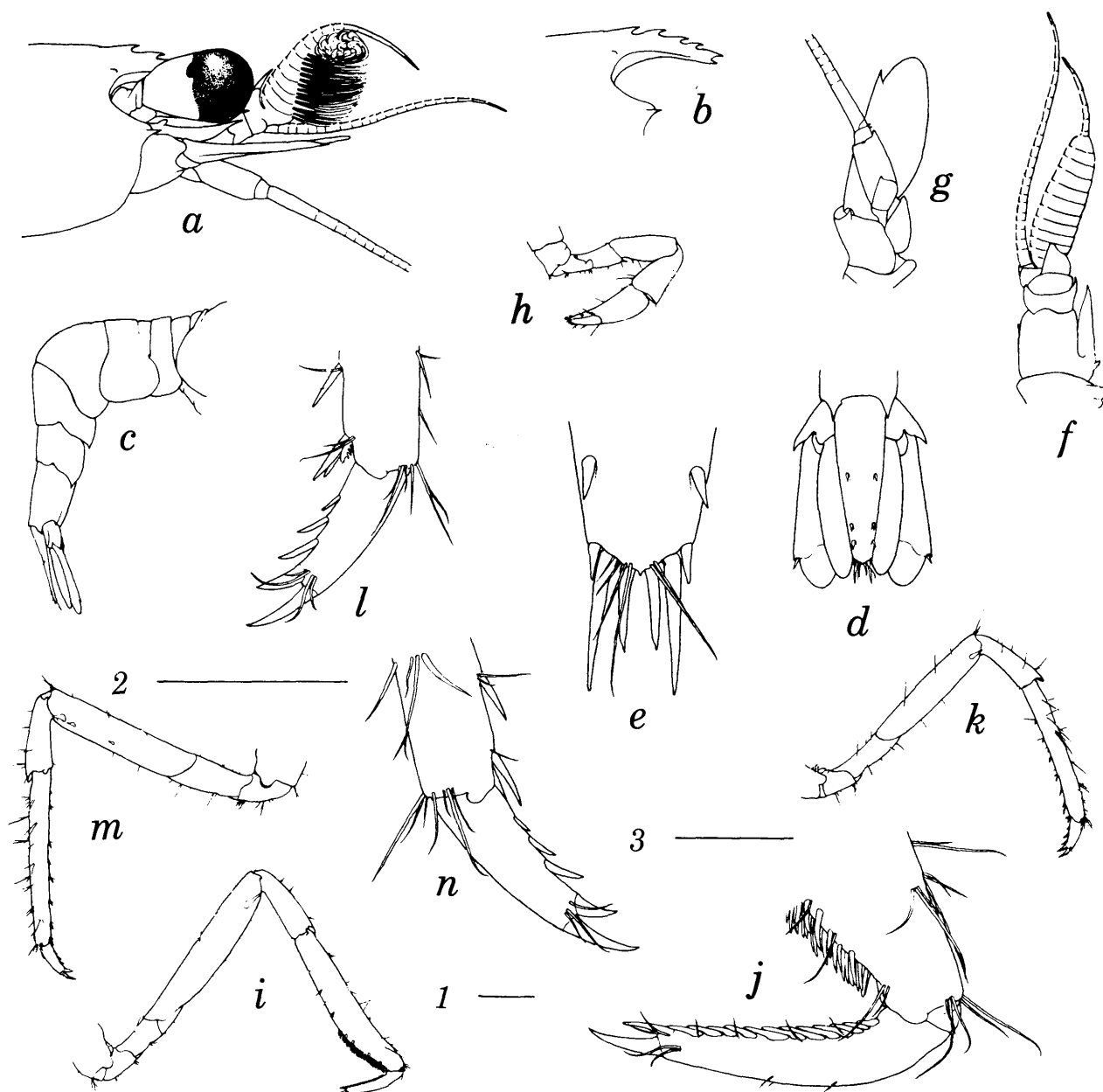


Fig. 96. *Thor manningi* Chace. Male: a, anterior region; b, rostrum; c, abdomen; d, telson and uropods; e, end of telson; f, right antennule; g, right antenna; h, right first leg; i, right third leg (prehensile); j, same, dactyl; k, right fourth leg; l, same, dactyl; m, right third leg (nonprehensile); n, same, dactyl. Scales: 1(c) = 1 mm; 2(e, j, l, n) = 0.3 mm; 3(all others) = 1 mm (from Chace 1972).

distal margin of basal antennular article to overreaching second article; dorsal margin usually armed with 4, sometimes 3 (rarely 5 or 2) teeth, posterior tooth usually in line with or slightly posterior to rear margin or orbit; ventral margin with single distal tooth, making tip bifid (rarely unarmed). Supraorbital tooth barely discernible, usually obtuse, rarely acute. Eyes well developed, cornea broader than and subequal in length to eyestalk. Antennule with basal article large; stylocerite sharp, usually reaching slightly beyond distal margin of second article and armed with small lateral tooth at base; second and third articles short, second with curved lateral spine reaching beyond midlength of distal article, latter with triangular dorsal scale. Antennal scale overreaching antennular peduncle by at least $\frac{1}{3}$ length, nearly straight lateral margin terminating in stout spine, lamella greatly exceeding spine; strong ventrolateral spine on basal article of peduncle. Third maxilliped reaching about as far as tip of antennal scale, last article bearing slender spines.

First legs reaching about midlength of antennal scale; fingers about $\frac{3}{4}$ length of palm, carpus about as long as palm; merus longer than carpus, unarmed on distal half of flexor (ventral) margin; ischium at least half length of merus. Second leg overreaching antennal scale by at least length of fingers; fingers shorter than palm; carpus subdivided, joints decreasing from proximal end in order of 3, 6, 4, 1, 2, 5. Third leg of functional males prehensile, subchelate, dactyl bearing 9–13 closely appressed spines on flexor margin; propodus more than twice length of dactyl, distal $\frac{1}{3}$ of flexor margin oblique and densely spinose. Third leg of fe-

males and nonfunctional males not prehensile, similar to fourth but without microscopic comblike distal spines on propodus. Fourth leg not prehensile; dactyl usually with 3 spines on flexor margin (rarely 2, 4 or 5) in addition to distal pair.

Abdomen smooth; pleura of segments 1–3 broadly rounded, those of 4–6 with posteroventral angles acute; sixth segment nearly twice as long as fifth but shorter than telson not including terminal spines. Telson elongate, triangular, with 3 or 4 pairs of prominent dorsal spines (occasionally 2 pairs, especially in juveniles, rarely 5 pairs) a little remote from edges and spaced equidistantly in posterior $\frac{3}{4}$ of length; tip with median point and usually 3 pairs of subequal spines, outer pair shortest. Uropodal exopods with outer edge ending in small spine flanked mesially by strong movable spine.

Measurements in mm.—Length of carapace: functional males 0.8–1.6; males with non-prehensile third leg 0.7–0.9; ovigerous females 1.4–2.5 (Chace 1972).

Habitat.—Common on grass flats from tide line to 11 m, living and dead coral, submerged timbers, among algae and hydroids; sometimes associated with sea anemones, *Bartholomea*; to depth of 44 m (Chace 1972).

Type-locality.—English Harbour, Antigua Island.

Known range.—Beaufort, N. C., to Yucatan and through West Indies to Curaçao; Islas Tres Marias, off west coast of Mexico (Chace 1972).

Genus *Tozeuma* Stimpson

Stimpson 1860:26.—Holthuis 1955:112.

Key to Species

(Adapted from Chace 1972)

1. Rostrum unarmed dorsally; third maxillipeds with rounded tip on terminal article *T. carolinense*
 Rostrum armed with series of teeth both dorsally and ventrally; third maxillipeds with pointed tip on terminal article *T. serratum*

Tozeuma carolinense Kingsley

(Arrow shrimp)

Fig. 97

Tozeuma carolinensis Kingsley 1878b:90.—1880:413.—Schmitt 1935a:155.

Tozeuma carolinense.—Rathbun 1901:114.—Hay and Shore 1918:391, pl. 27, fig. 2.—Williams 1965:83, fig. 67.—Ewald 1969:510–514, figs. 1–20.—

Coelho and Ramos 1972:153.—Chace 1972:141.
Angasia carolinensis.—Holthuis 1947:17, 61.

Recognition characters.—Body elongate, compressed. Rostrum slender, almost twice as long as remainder of carapace, inclined slightly upward distally, its dorsally thickened, smooth and rounded part tapered gradually from broadened base to attenuated tip, abruptly narrowing throughout length to ventral lamellate part deepest anterior to orbit

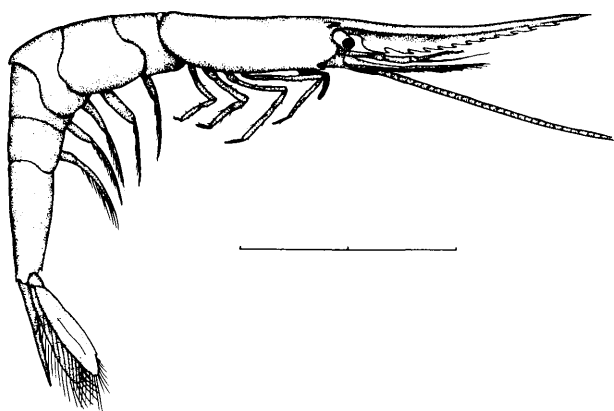


Fig. 97. *Tozeuma carolinense* Kingsley. Female in lateral view, 10 mm indicated (from Williams 1965).

and drawn to slender tip, ventral border with many (up to 19 or more) appressed teeth. Carapace smooth, polished; strong spine at either side of base of rostrum; anterior margin produced into triangular tooth below eye; anterolateral angle with spine. Eyes well developed. Antennular peduncle rather slender; first article longest, slender stylocerite reaching beyond distal margin of article up to $\frac{1}{2}$ length of second article; second and third articles progressively shorter; outer flagellum thick and much shorter than inner, outer ramus reaching tip of antennal scale. Antennae longer than rostrum; antennal scale lanceolate, less than half length of rostrum; basal antennal article with strong ventrolateral spine on anterior border. Third maxillipeds short, extending about to tip of pterygostomian spine; terminal article with tip rounded, about 2.5 times longer than broad and about 1.5 times length of penultimate article; both articles slightly spooned laterally, beset with stiff marginal setae and with smaller setae over mesial surface.

Legs relatively short; first pair very short, stout, hand inflated, fingers curved, closing completely, spines on fingers sometimes dark colored; second pair slender, longer, reaching about to base of spine on first antennal article; carpus with 3 joints, proximal joint nearly as long as merus; legs 3 to 5 with comblike spines on curved dactyls.

Abdomen smooth; strongly bent between third and fourth segments; third segment of male bearing low dorsal hump; fifth segment with spine at each side of posterior border; sixth with spine at posterolateral angle and broad spine at base of telson. Elements of tailfan long and narrow. Telson with 1 pair of dorsal spines at midlength, another at $\frac{3}{4}$ length; tip with strong pair of mesial spines flanked by weak lateral pair. Uropodal exopods with outer border terminating in small spine flanked mesially by movable spine.

Measurements in mm.—Length of body: male 40; ovigerous females 28 to 54 (Ewald 1969).

Variation.—The humped third abdominal segment is pronounced in young individuals of both sexes.

Color.—Apparently varying to some degree depending on background and feeding habits (Ewald 1969); shades of green from light yellowish green to rich deep green, or occasionally brownish or red in beds of *Diplanthera wrightii* and *Zostera marina* (see Bryce 1961); purple on alcyonarian corals *Antillogorgia* and *Pterogorgia* (see Voss 1956); nearly colorless (Verrill 1922; Ewald 1969, for juveniles).

Habitat.—Common in beds of vegetation or similar habitats in shallow water; this species often swims in a vertical position and rests in a clinging position on blades of grass. It blends well with the background because of shape and color and is aptly named "arrow shrimp." Larvae are common in plankton of shallow coastal water around south Florida. Surface and intertidal to 75 m (Holthuis 1947; Ewald 1969; Rouse 1970).

Type-locality.—Fort Macon, N. C.

Known range.—Vineyard Sound, Mass., through Gulf of Mexico to Yucatan and southward to Colon, Panama; through West Indies to Curaçao; Pernambuco to Bahia, Brazil (Coelho and Ramos 1972).

Remarks.—Ewald (1969) gave a history of the specific name. Bryce (1961) gave general ecological observations on *T. carolinense* along with a detailed study of larval development. The adults apparently feed by grazing on faunal and floral growths on marine grasses and alcyonarians.

In North Carolina, ovigerous females are present from May to October, with one doubtful record in February. Elsewhere they have been taken year-round in Florida (Ewald 1969; Rouse 1970), their proportion to non-ovigerous but mature females always very high, and in a recorded period of December to August (USNM) in the West Indies and Gulf of Mexico.

Ewald collected ovigerous females from grass flats near Bear Cut and alcyonarians near Soldier Key off Miami, Fla., held them in the laboratory until eggs hatched, and reared the larvae through to metamorphosis on a diet of *Artemia* nauplii. Developing animals were held in water of 32–36‰ salinity at 15°, 20°, and 25°C in chambers alternating 12 h periods of light and dark. The developing larvae exhibited no distinct stages but passed through 5 to 13 intermolts ending in the postlarval stage, those from adults on alcyonarians passing through more stages than those from marine grasses. Provenzano and Dobkin (1962) found the same variability.

Bryce (1961) found that larvae hatched from

ovigerous females reared in culture dishes at fluctuating temperatures in an air conditioned room (during summer) usually passed through eight or nine larval stages before metamorphosing into postlarvae. However, the larvae did not always transform at these stages, and one group reared in early fall continued molting for an indefinite number of stages. One individual passed through 25 larval molts before the experiment was terminated. Variations in larval stages and examples of asymmetry were discussed, as were the effects of diet and temperature.

Ewald noted longer intermolt periods and a greater number of intermolts in lower temperatures, but mortalities were similar in the three levels tested.

***Tozeuma serratum* A. Milne Edwards**

Fig. 98

Tozeuma serratum A. Milne Edwards 1881:16.—1883, pl. 32.—Chace 1972:141.

Recognition characters.—More robust than *T. car-*

olinense. Body elongate, compressed. Rostrum slender, from about 1.4 to 2 times as long as remainder of carapace, inclined slightly upward distally, its dorsal part thickened and stiffened by dorsolateral carina, tapering from broadened base to attenuated tip and bearing 5 teeth on proximal $\frac{2}{3}$ of upper margin; abruptly narrowing throughout length to ventrally lamellate part deepest anterior to orbit and drawn to slender tip, ventral border with 10–14 teeth. Carapace smooth, polished; strong spine at either side of base of rostrum; anterior margin produced into triangular tooth below eye; anterolateral angle with spine. Eyes well developed. Antennular peduncle rather slender; first article longest, slender stylocerite reaching beyond distal margin of article and up to $\frac{1}{2}$ length of second article; second and third articles progressively shorter; outer flagellum thick and much shorter than inner, latter not reaching tip of antennal scale. Antennae longer than rostrum; antennal scale lanceolate, slightly over $\frac{1}{2}$ length of rostrum; basal article with strong ventrolateral spine on anterior border. Third maxillipeds long, extending to base of terminal article of antennal peduncle;

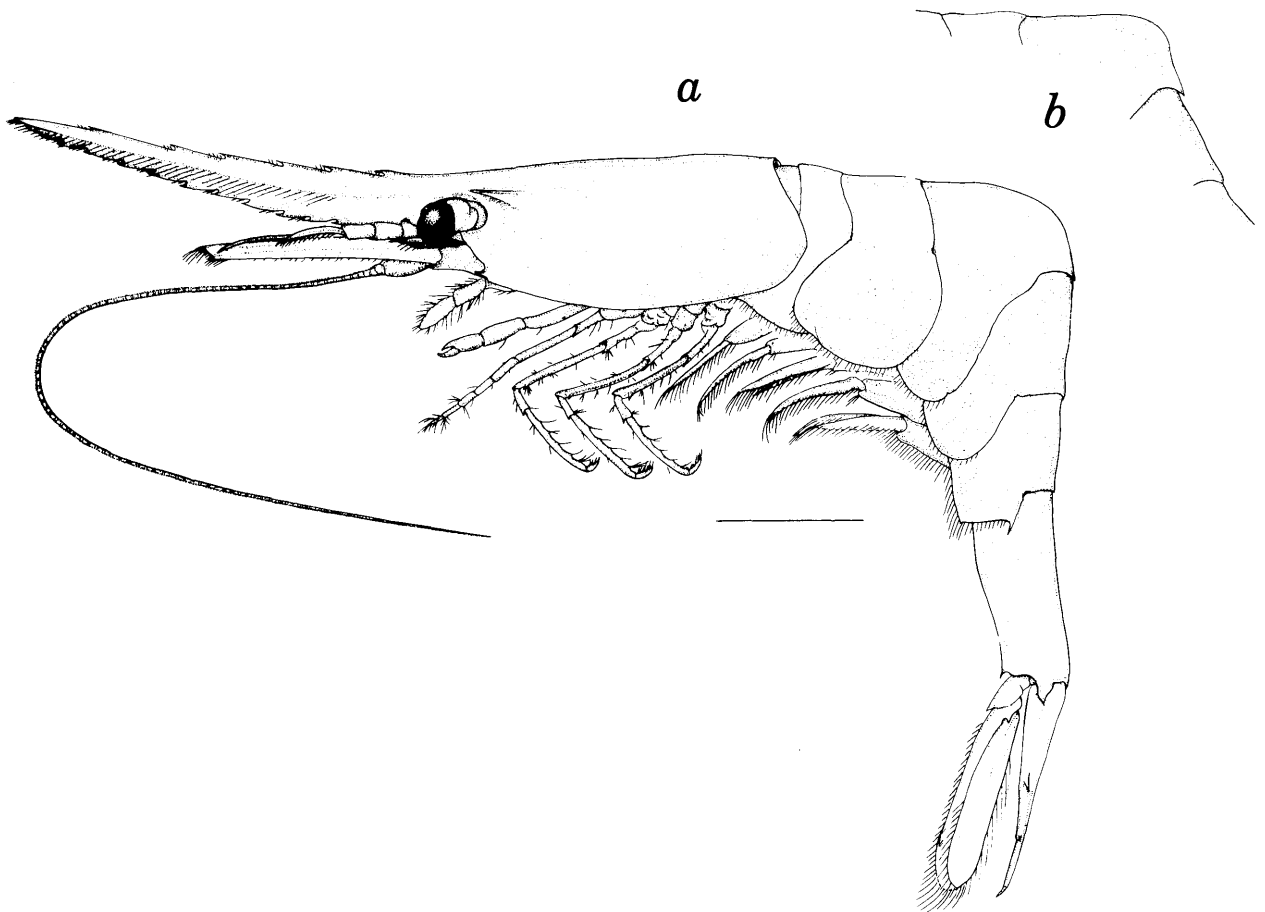


Fig. 98. *Tozeuma serratum* A. Milne Edwards. *a*, Female in lateral view; *b*, male abdomen, dorsal aspect of segments 2–5 in lateral view, 3 mm indicated (USNM 120102).

terminal article with pointed tip, about 2.9 times longer than broad and about 1.3 times length of penultimate article; both articles slightly spooned laterally, beset with stiff marginal setae and with smaller setae over mesial surface.

Legs relatively short; first pair very short and not much stouter than succeeding legs, palm and carpus of nearly equal length, fingers straight, tips corneous and crossed; second pair slender, longer, exceeding spine on first antennal article by length of chela, carpus with 3 joints, decreasing in length from proximal end in order 1, 3, 2; legs 3 to 5 with comblike spines on curved dactyls.

Abdomen smooth; strongly bent between third and fourth segments; third segment of male bearing low dorsal hump; fifth segment with spine at each side of posterior border; sixth with spine at posterolateral angle and broad spine at base of telson. Elements of tail fan long and narrow. Telson with 1 pair of dorsal spines at midlength, another at $\frac{3}{4}$ length; tip with strong pair of mesial spines flanked by weak lateral pair. Uropodal exopods with outer border terminating in small spine flanked by movable spine.

Measurements in mm.—Length of body: holotype 55; ovigerous females 40–50 (USNM).

Habitat.—4.6 to 102 m.

Type-locality.—Off Barbados.

Known range.—Nonamesset Island, Mass.; off Capes Hatteras and Lookout, N. C. (Herbst, et al. 1978; USNM), Cape Canaveral, extreme southern

and northwestern Florida, Colombia and Barbados (Chace 1972; USNM).

Remarks.—Ovigerous females are known in June from Massachusetts and eastern Florida, and at an unrecorded date from Colombia where they were associated with a hydroid.

Family Processidae

Body smooth; rostrum short, slender, apex bifid or simple, ventral border never armed. Carapace armed at most with antennal spines. Eyes relatively large, cornea well developed. Antennule with well developed stylocerite on peduncle, flagella simple, shorter ventromesial ramus thickened proximally. Antennal scale well developed. First leg with right side (usually) chelate, left with unopposed simple dactyl (except in symmetrically chelate *Ambidexter*). Second legs slender, carpus always, merus usually, and ischium occasionally subdivided; ischium with inner basal enlargement; right leg often longest. Third to fifth legs slender. (Abridged from Manning and Chace 1971.)

Manning and Chace's recent exhaustive account of processids from the northwestern Atlantic, followed by Hayashi's (1975) monograph, are so thorough that further elaboration is hardly necessary except for addition of geographic and depth records. For convenience, a key, short descriptions, and selected figures are given for species known to occur in the area covered here.

Key to Genera

- | | |
|-------------------------------------|-----------------|
| 1. First legs with exopod | <i>Nikoides</i> |
| First legs without exopod | <i>Processa</i> |

Genus *Nikoides* Paulson 1875

Manning and Chace 1971:7.

Nikoides schmitti Manning and Chace

Fig. 99

Nikoides schmitti Manning and Chace 1971:8, figs. 3–5.—Chace 1972:142.—Carvacho 1979:466.

Processa aff. *P. guyanae*.—Herbst, Williams and Boothe 1979:990, table 1.

Recognition characters.—Rostrum slightly deflexed, extending to cornea or slightly beyond anterior margin of eye; apex bifid, obscured by numerous long setae, lower tooth longer; lower margin sinuous, convex proximally, slightly concave distally. Antennal spine well developed. Eyes moderately large, corneal width twice or more greatest

width of antennal scale. Antennular peduncle with stylocerite broadly rounded, bearing small lateral tooth in largest specimens. Antennular peduncle extending to end of or beyond antennal peduncle by less than length of distal article; length of antennal scale about 4–6 times greatest width, distal spine overreaching blade in male, falling short of anterior margin in female.

First legs with exopods not extending beyond midlength of merus; right leg of pair chelate. Second legs decidedly unequal; right larger, overreaching antennal scale by chela, carpus, and half of merus, ischium with 3, merus with 23–24, and carpus with 43–49 joints, carpus about 13 times as long as chela in males, about 10 times in females; left overreaching antennal scale by chela and about $\frac{1}{3}$ of carpus; ischium not noticeably jointed, merus with 5, carpus with 17–18 joints, carpus more than 8 times length of chela, merus about 5 times. Third

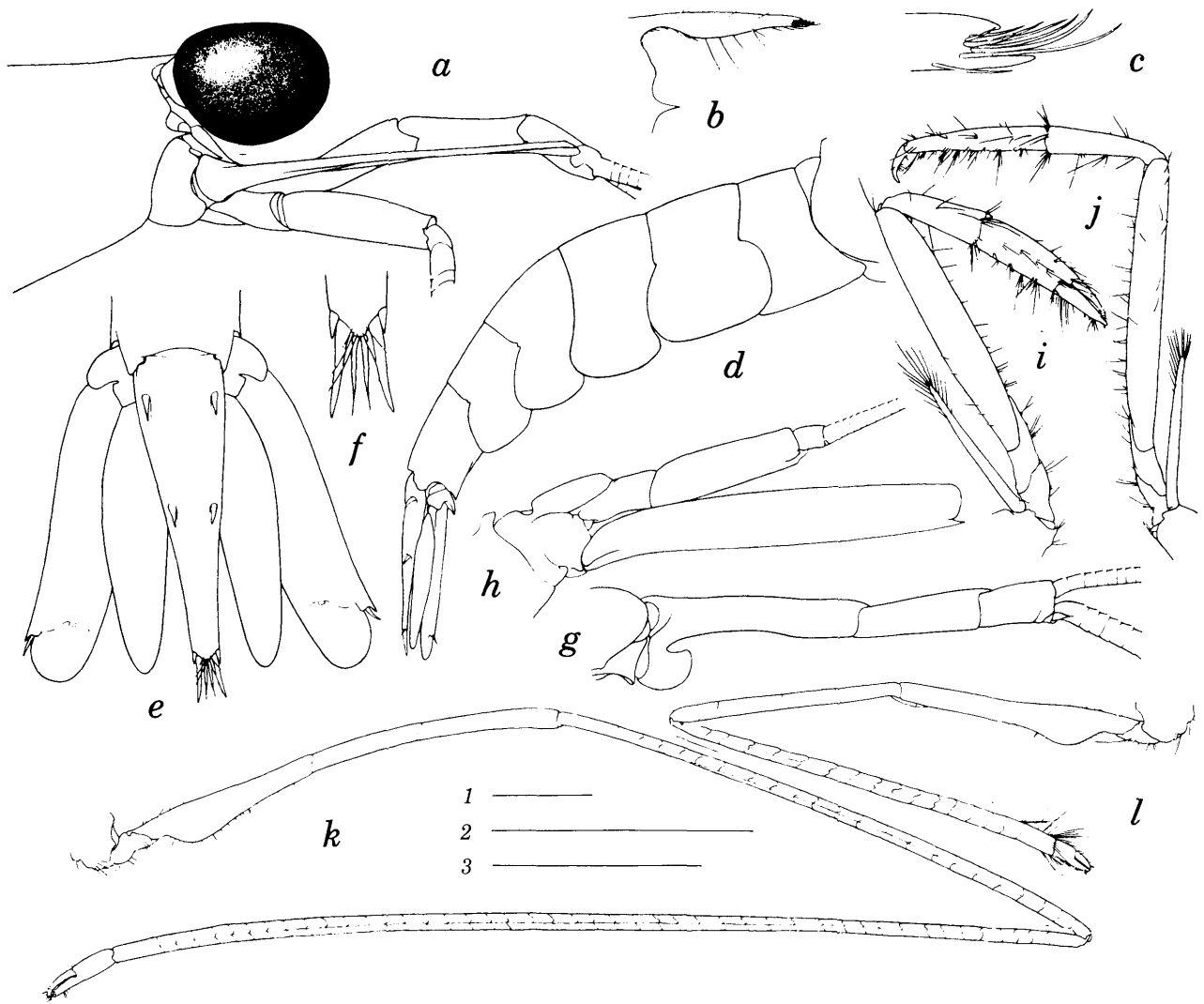


Fig. 99. *Nikoides schmitti* Manning and Chace. Male: *a*, anterior region, lateral view; *b*, rostrum; *c*, same, distal end; *d*, abdomen, lateral view; *e*, telson and uropods, dorsal view; *f*, tip of telson; *g*, right antennular peduncle, dorsal view; *h*, right antenna, dorsal; *i-j*, right and left first legs; *k-l*, first and left second legs. Scales: 1(*d*)=2 mm; 2(*c*)=0.5 mm; 3(all others)=2 mm (from Manning and Chace 1971).

to fifth legs slender; propodus-dactyl comparative lengths: third 3 times, fourth and fifth less than 3 times.

Fifth abdominal segment rounded posterolaterally; sixth abdominal segment less than twice as long as fifth, angled or bluntly spined posterolaterally; lobe above articulation of uropod usually unarmed. Telson about or slightly more than 1.5 times as long as sixth abdominal segment, length more than 3 times greatest width; 2 pairs of dorsal and 2 pairs of distal spines; anterior dorsal pair set in proximal $\frac{1}{4}$, posterior pair at midlength, distance between anterior margin and anterior pair less than half distance between pairs of dorsal spines; apex rounded.

Measurements in mm.—Carapace length: male 5.3; female 8.6; ovigerous females 7.0–8.8.

Habitat.—High salinity estuaries and shallow marine waters to 35 m.

Type-locality.—1.25 km south of Garden Key, Tortugas, Monroe County, Fla.

Known range.—E of Cape Lookout, N. C. (Herbst, et al. 1979; USNM), Biscayne Bay and Dry Tortugas; Guadeloupe and the Guianas.

Remarks.—Herbst, et al. (1979) mistakenly placed representatives of this species in *Processa*. Additional material from east of Cape Lookout, N. C., is now in the USNM collection. Ovigerous females are known from Florida in April and July, the Guianas in July, and North Carolina in August.

Genus *Processa* Leach 1815

Manning and Chace 1971:12.

Key to Species

(Adapted from Manning and Chace 1971)

1. Pleura of fifth abdominal segment with posterolateral spine; corneal width twice greatest width of antennal scale *P. fimbriata*
 Pleura of fifth abdominal segment rounded or angled posterolaterally, lacking distinct posterolateral spine 2
2. Antennal spine absent 3
 Antennal spine present 4
3. Second legs asymmetrical, right leg with 10–15 meral and 19–29 carpal joints, left leg with 3–4 meral and 13–15 carpal joints; rostrum not markedly deflexed anteriorly *P. bermudensis*
 Second legs symmetrical, with 5 meral and 10–14 carpal joints; rostrum deflexed anteriorly *P. vicina*
4. Second legs symmetrical, with 4–6 (usually 6) meral and 10–15 (usually 11) carpal joints; rostrum anteriorly deflexed *P. hemphilli*
 Second legs asymmetrical, more meral and carpal joints than above; rostrum not deflexed 5
5. Lobe on sixth abdominal segment above articulation of uropod produced into posterior spine; stylocerite with strong lateral spine, anterior margin evenly concave from inner angle to lateral spine *P. profunda*
 Lobe on sixth abdominal segment above articulation of uropod unarmed; stylocerite with lateral tubercle *P. guyanae*

Processa bermudensis (Rankin)

Fig. 100

Nika bermudensis Rankin 1900:536, pl. 17, figs. 2, 2a, 2b.

Processa bermudensis.—Manning and Chace 1971:15, figs. 6a–o, 7a–o.—Hayashi 1975:78 (key).

Recognition characters.—Rostrum almost straight, not extending beyond eye; apex slightly deflexed, bifid tip obscured by long setae, lower tooth longer; lower margin convex proximally, concave distally. Antennal spine absent. Eyes moderately large, corneal width more than twice width of antennal scale. Antennular peduncle with stylocerite obtusely rounded laterally, inner margin projecting farther than outer, unarmed. Antennal peduncle extending about to midlength of second article of antennular peduncle, basal article lacking ventrolateral spine; length of antennal scale 5.6 times its greatest width, distal spine overreaching blade.

Second legs unequal; right longer, overreaching antennal scale by chela and nearly all of carpus, merocarpal articulation extending beyond eye, ischium with 5 indistinct, merus with 10–15, and carpus with 19–29 joints; left overreaching antennal scale by chela and slightly less than $\frac{1}{2}$ of carpus, ischium undivided, merus with 3–4, and carpus with 13–15 joints. Third to fifth legs slender; propodus-dactyl comparative lengths: third about 3.6, fourth more than 4, fifth more than 3.5.

Fifth abdominal segment rounded posterolaterally; sixth abdominal segment less than twice as long as fifth, lobe above articulation of uropod rounded, unarmed. Telson about 1.5 times as long as sixth abdominal segment; 2 pairs of dorsal and 2 pairs of distal spines; anterior dorsal pair set in proximal $\frac{1}{4}$, posterior pair set at midlength, distance between anterior margin and anterior pair less than half distance between pairs of dorsal spines; apex produced into sharp median point. Abdominal sternites unarmed.

Measurements in mm.—Carapace length: male 3.4; female 5.8; ovigerous females 3.3–6.

Color.—“Background light with many small, red chromatophores and fewer, larger white ones scattered over body; eyes light green; distal segment of third maxilliped and bases of third, fourth and fifth pereopods and pleopods red; abdomen with transverse red bar across third somite; eggs yellowish” (Manning and Chace 1971).

Habitat.—Shallow marine waters including high salinity estuaries; grass flats, sand and shells; 1.8 to 45 m (Christoffersen 1979).

Type-locality.—Harrington Sound, Bermuda.

Known range.—Bermuda; North Carolina near Cape Hatteras to northwestern Florida; Veracruz, Mexico (Ray 1974); Cuba; Puerto Rico; Guadeloupe; Peninsula de Arago, Estado Sucre, Venezuela, in *Sargassum* (UNC-IMS 1854); Bahia and Rio de Janeiro, Brazil (Christoffersen 1979).

Remarks.—Manning and Chace (1971) discussed

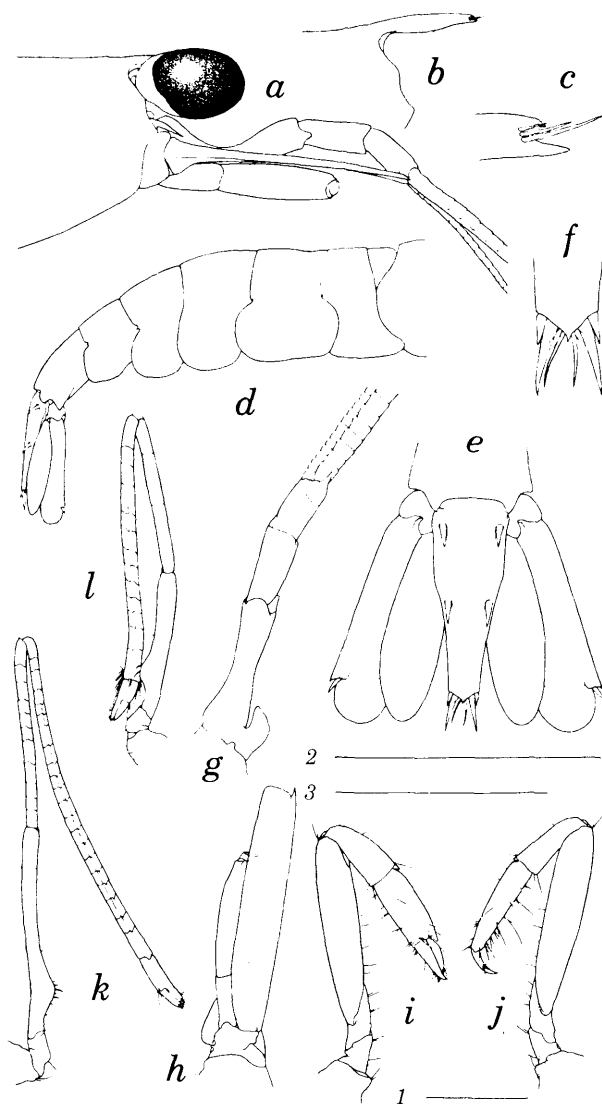


Fig. 100. *Processa bermudensis* (Rankin). Male: *a*, anterior region, lateral view; *b*, rostrum; *c*, same, distal end; *d*, abdomen, lateral view; *e*, telson and uropods, dorsal view; *f*, tip of telson; *g*, right antennular peduncle, dorsal view; *h*, right antenna, dorsal view; *i-j*, right and left first legs; *k-l*, right and left second legs. Scales: 1(*d*) = 2 mm; 2(*c*) = 0.5 mm; 3(*f*) = 1 mm, all others = 2 mm (from Manning and Chace 1971).

other processids occurring with this species in Puerto Rico. It also occurs with *P. hemphilli* in nocturnal surface plankton in Bogue Sound, Morehead City, N. C.

Ovigerous females are known virtually the year round in various parts of the range: March, July, August, December in Florida; April to October in Bermuda; June in Cuba and Puerto Rico; November in Bahia, and December in Rio de Janeiro, Brazil.

Lebour (1941) showed that *P. bermudensis* larvae are common in the plankton almost throughout the year in Bermuda, and adults were commonly found

in the dredge at night. Gurney (1936c) described eight larval stages.

Processa fimbriata Manning and Chace

Fig. 101

Processa fimbriata Manning and Chace 1971:19, figs. 8a-p, 9a-o, 10a-c.—Chace 1972:143.—Pequegnat and Ray 1974:254, fig. 67.—Hayashi 1975:76 (key).—Christoffersen 1979:367.

Recognition characters.—Rostrum straight, not extending to anterior margin of eye, lower margin evenly convex; apex bifid, obscured by few short setae, lower tooth longer. Antennal spine present. Eyes moderately large; corneal width about 1.6 times greatest width of antennal scale. Antennular peduncle with all of terminal article extending beyond antennal peduncle; stylocerite truncate anteriorly, with tiny outer spine. Length of antennal scale about 4 times greatest width, distal spine not overreaching blade; basal antennal article with outer spine.

Second legs asymmetrical; right stronger, overreaching antennal scale by chela and all but 1 or 2 proximal joints of carpus, merocarpal articulation extending to end of scale; ischium undivided, merus with 13–16, carpus with 31–40 joints, ischium longer than merus; left overreaching antennal scale by chela and less than $\frac{2}{3}$ of carpus, ischium undivided, merus with 4–6, and carpus with 15 joints, ischium slightly longer than merus. Third to fifth legs slender; propodus-dactyl comparative lengths: third 3.6, fourth more than 4, fifth more than 3; latter slightly less in males than in females, 4 or 5 spines on flexor margin, outer surface of propodus with scattered tufts of setae in females, completely obscured by short setae in males.

Fifth abdominal segment with small posterolateral spine; sixth abdominal segment with blunt posterolateral spine; lobe above articulation of uropod produced into blunt, triangular projection. Telson almost twice as long as fifth abdominal segment, length 3 times greatest width; with 2 pairs of dorsal and 2 pairs of distal spines, anterior dorsal pair set at end of proximal $\frac{1}{3}$, posterior pair beyond midlength; distal spines as in *P. bermudensis*; apex produced into sharp point. Abdominal sternites 1–5 with median ventral spine.

Measurements in mm.—Carapace length: male 4; ovigerous and non-ovigerous females 6.3.

Color.—Transparent, eyes black (Manning and Chace 1971).

Habitat.—Associated with sponges and on broken shell and coral bottom; intertidal to 50 m.

Processa guyanae Holthuis (1959)

Fig. 102

Processa guyanae Holthuis 1959:115, figs. 18, 19.—Manning and Chace 1971:22.—Christoffersen 1979:368.

Processa tenuipes Manning and Chace 1971:31, figs. 17a-v, 18a-c.—Hayashi 1975:80 (key).

Recognition characters.—Rostrum slender, convex dorsally, not exceeding eye; apex deflexed, bifid, obscured by long setae, lower tooth longer. Antennal spine small but distinct. Eyes of moderate size, corneal width more than twice greatest width of antennal scale. Antennular peduncle with stylocerite subtruncate anteriorly, anterior margin sinuous with blunt lateral angle or tubercle. Length antennal scale about 6.5 times greatest width, small distal spine not overreaching blade. Antennal peduncle reaching about to midlength of second article of antennular peduncle, basal antennal article with small but distinct outer spine.

Second legs strongly asymmetrical; right longer, overreaching antennal scale by chela, carpus, and slightly less than half of merus, merocarpal articulation extending well beyond eye, ischium divided into 4 (sometimes indistinct), merus into 18–28, and carpus into 48–69 joints; left overreaching antennal scale by chela and 4 distalmost joints of carpus, ischium not noticeably jointed, merus with 5–9, and carpus with 17–26 joints. Third to fifth legs slender; propodus-dactyl comparative lengths: third 4, fourth 4, fifth 6–7; latter with carpus longer than propodus, merus shorter than carpus.

Fifth abdominal segment bluntly angled posterolaterally; sixth abdominal segment less than twice as long as fifth, angled posterolaterally; lobe above articulation of telson unarmed. Telson slightly more than 1.5 times as long as sixth abdominal segment, length slightly more than 3 times greatest width, 2 pairs of dorsal and 3 pairs of distal spines; anterior pair of dorsal spines set near end of proximal ¼, posterior pair beyond midlength; distance between anterior margin and anterior spines more than distance between pairs of spines; apex produced into slender spine.

Measurements in mm.—Carapace length: male 10; ovigerous females 5.9–12.

Habitat.—Fine sediments through grades of sand, gravel and shells to coral and rocks; 31 to 331 m.

Type-locality.—NW of the Coppename River [Surinam] 6°54'N, 56°14'W, 49 m.

Known range.—Off Cape Hatteras, N. C., to eastern Gulf of Mexico, including northern coast of Cuba; Surinam, Ceará, Brazil, to Uruguay.

Remarks.—Christoffersen (1979) synonymized the southern *P. guyanae* and northern *P. tenuipes*.

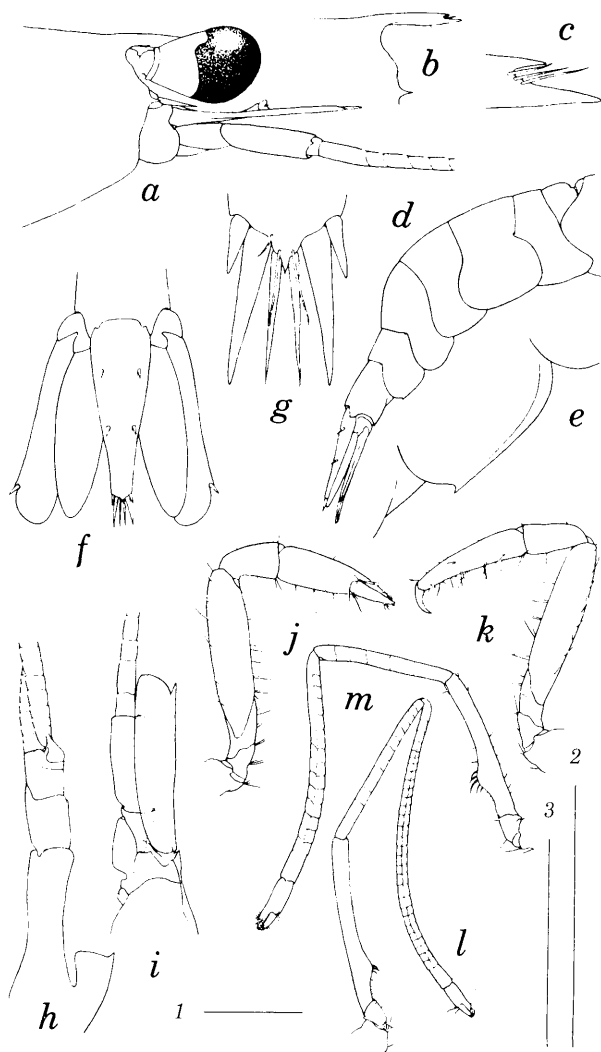


Fig. 101. *Processa fimbriata* Manning and Chace. Male: a, anterior region, lateral view; b, rostrum; c, same, distal end; d, abdomen, lateral view; e, margin of fifth abdominal pleuron; f, telson and uropods, dorsal view; g, tip of telson; h, right antennular peduncle, dorsal view (of female); i, right antenna, dorsal view; j-k, right and left first legs; l-m, right and left second legs. Scales: 1(d) = 2 mm; 2(c, g) = 0.5 mm; 3(e) = 1 mm, all others = 2 mm (from Manning and Chace 1971).

Type-locality.—Off East Key, Tortugas, Monroe County, Fla.

Known range.—Off New River, N. C., to Rio de Janeiro, Brazil (Christoffersen 1979).

Remarks.—A similar species, *P. riveroi*, is known from Puerto Rico. Manning and Chace (1971) suggested that there is a habitat difference, specimens of *P. fimbriata* being found in sponges, as noted also by Pearse (1932b, 1950) from *Spheciospongia vespara*, *Hircinia strobilina*, and *Aulospongos schoemus*.

Ovigerous females are known from Florida in July–August, and the Bahamas in November–December (Manning and Chace 1971). Christoffersen (1979) reported them from Bahia, Brazil, in November, and Espírito Santo and Rio de Janeiro in January.

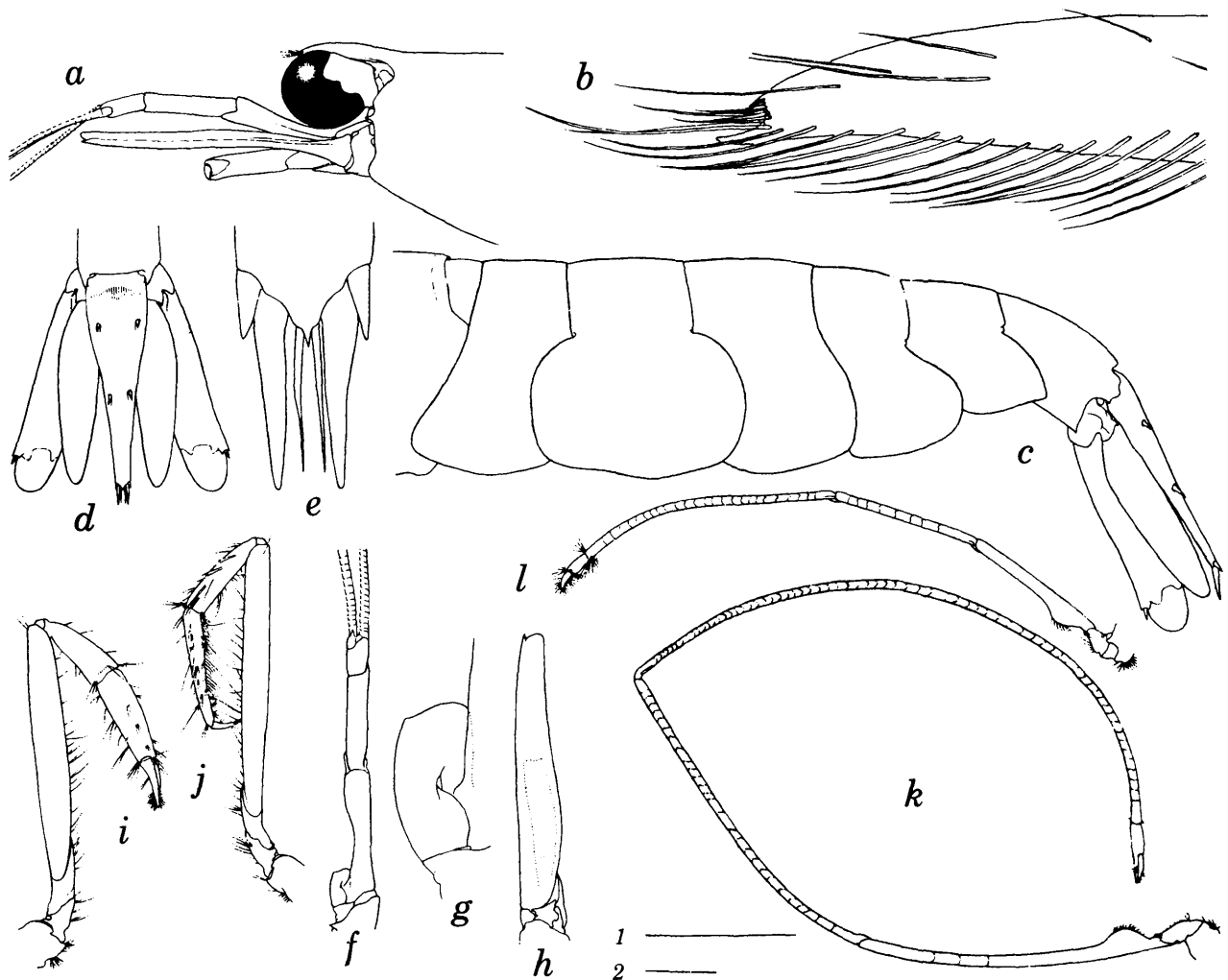


Fig. 102. *Processa guyanae* Holthuis. Ovigerous female: a, anterior region, lateral view; b, rostrum, distal portion; c, abdomen, lateral view; d, telson and uropods, dorsal view; e, tip of telson; f, right antennular peduncle, dorsal view; g, same, stylocerite; h, right antenna, dorsal view; i-j, right and left first legs; k-l, right and left second legs. Scales: 1(b, e)=0.5 mm, (g)=1 mm; 2(i-j)=1 mm, all others=2 mm (from Manning and Chace 1971).

Ovigerous females are known from Cuba in January, Florida in April, and North Carolina in April, May, and October. From south of the equator they are known from Uruguay in January and April, and from the Brazilian states of Rio Grande do Sul in January and May, São Paulo in May, August and December, and Rio de Janeiro in May and November (Christoffersen 1979).

Processa hemphilli Manning and Chace

Fig. 103

Processa hemphilli Manning and Chace 1971:23, figs. 11a-o, 12a-i.—Hayashi 1975:78 (key).—Carvalho 1979:466.—Christoffersen 1979:370.

Recognition characters.—Rostrum slightly deflexed, tapering distally, not exceeding eye; apex bifid, obscured by numerous setae, lower tooth longer. Antennal spine well developed. Eyes large, corneal width 1.6 times greatest width of antennal scale. Antennular peduncle with stylocerite subtruncate anteriorly, margin sinuous with small outer spine. Length antennal scale almost 6 times greatest width, distal spine exceeded by rounded terminal margin. Antennal peduncle slightly exceeding proximal article of antennular peduncle, basal antennal article unarmed.

Second legs symmetrical, overreaching antennal scale by slightly more than length of chela, ischium unsegmented, merus with 4, carpus with 10 joints. Third to fifth legs slender; propodus-dactyl comparative lengths: third 3, fourth 2.5, fifth less than 3.

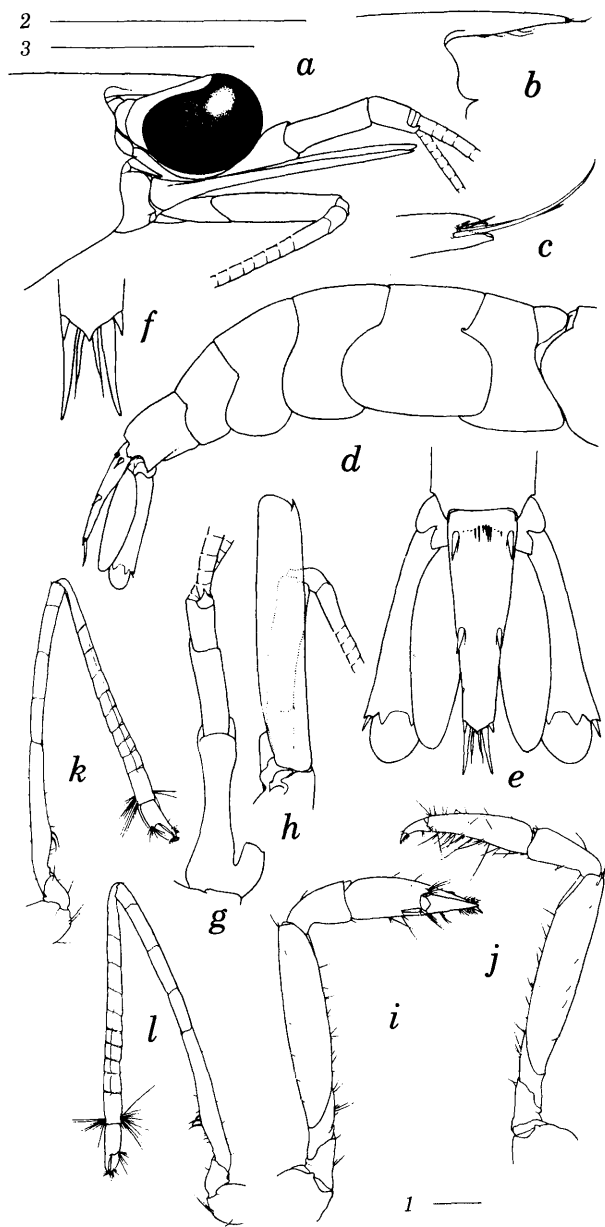


Fig. 103. *Processa hemphilli* Manning and Chace. Female: a, anterior region, lateral view; b, rostrum; c, same, distal end; d, abdomen, lateral view; e, telson and uropods, dorsal view; f, tip of telson; g, right antennular peduncle, dorsal view; h, right antenna, dorsal view; i-j, right and left first legs; k-l, right and left second legs. Scales: 1(d)=2 mm; 2(c)=0.5 mm; 3(f)=1 mm, all others=2 mm (from Manning and Chace 1971).

Fifth abdominal segment obtusely angled posterolaterally, unarmed; sixth abdominal segment subequal in length to fifth, with acute posterolateral angle, lobe above articulation of uropod angled but unarmed. Telson slightly more than 1.5 times as long as fifth abdominal segment, length slightly more than 3 times width; 2 pairs of dorsal and 2 pairs of distal spines, anterior dorsal pair set in proximal $\frac{1}{4}$, posterior pair set beyond midlength,

distance between anterior margin and anterior pair of spines about $\frac{1}{4}$ distance between pairs of dorsal spines; distal spines and apex as in *P. bermudensis*.

Measurements in mm.—Carapace length: female 3.9; ovigerous females 3.75.

Habitat.—Over mud, sand, shells, and algae; 1.8 to 154 m.

Type-locality.—Marco, Collier County, Fla.

Known range.—E Cape Lookout, and Bogue Sound, N. C.; E coast of Florida; NW Florida (Saloman 1979); Guadeloupe; Rio de Janeiro, Brazil, to Province of Buenos Aires, Argentina (Christoffersen 1979).

Remarks.—This is the species referred to by Williams (1965) as close to *P. wheeleri*. It occurs nocturnally with *P. bermudensis* in surface plankton in Bogue Sound, N. C., off the Institute of Marine Sciences, Morehead City. Specimens are in the UNC-IMS collection. Manning and Chace (1971) pointed out that similar species occur in the eastern Atlantic and Red Sea, and Carvacho thought his material from Guadeloupe might be intermediate.

Camp, et al. (1977) reported ovigerous females off central eastern Florida in May; Christoffersen (1979) reported them in December, April and August from São Paulo, January, April and August in Rio Grande do Sul, and December and August from Panama, Brazil.

Processa profunda Manning and Chace

Fig. 104

Processa profunda Manning and Chace 1971:25, figs. 13a-g, 14a-g, 15a-e.—Chace 1972:211.—Hayashi 1975:79 (key).

Recognition characters.—Rostrum almost straight, apex slightly deflexed, bifid, obscured by numerous long setae, lower tooth longer. Antennal spine present. Eyes moderately large; corneal width about twice greatest width of antennal scale. Antennular peduncle with terminal article and about half of second article extending beyond antennal peduncle; stylocerite with strong, acute lateral projection, anterior margin concave, sloping proximomesially. Length of antennal scale about 6.5 times greatest width, distal spine slightly overreaching rounded anterior edge of blade; basal antennal article with slender outer spine.

Second legs asymmetrical; right longer, overreaching antennal scale by chela, carpus and distal articles of merus; merocarpal articulation extending beyond eye; ischium with 3, merus with 21–22,

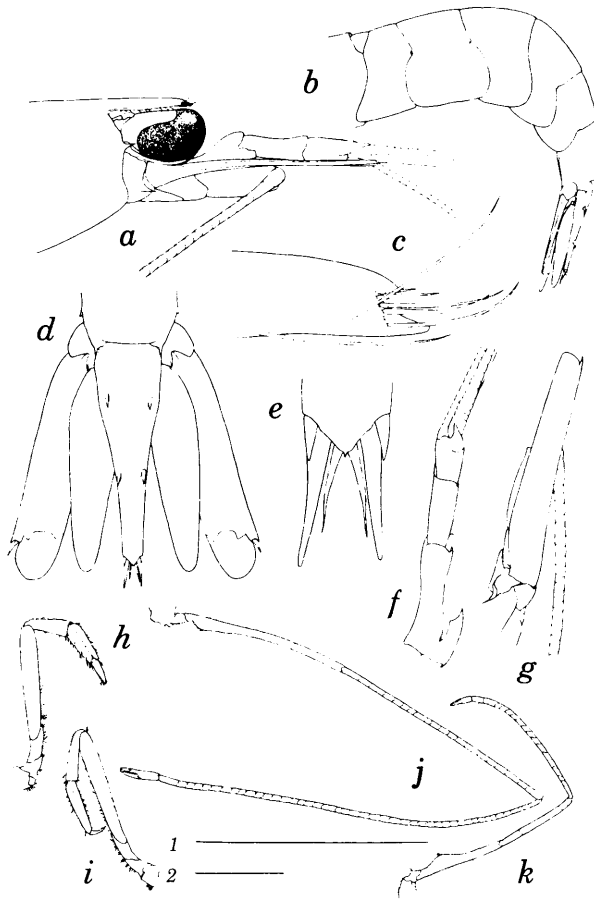


Fig. 104. *Processa profunda* Manning and Chace. Male: a, anterior region; b, abdomen; c, distal end of rostrum; d, telson and uropods, dorsal view; e, tip of telson; f, right antennule; g, right antenna; h, right first leg; i, left first leg; j, right second leg; k, left second leg. Scales: 1 (b)=0.5 mm; 2 (e)=approx. 0.5 mm, (a, d, f, g)=2 mm, (c, h-k)=4 mm (from Manning and Chace 1971).

carpus with 45–56 joints, ischium shorter than merus; left overreaching antennal scale by chela and about $\frac{1}{3}$ of carpus, ischium undivided, merus with 5, and carpus with 18–21 joints, ischium slightly longer than merus. Third to fifth legs slender; propodus-dactyl comparative lengths: third 4, fourth slightly more than 3; fifth leg extending beyond antennal scale by $\frac{1}{2}$ of carpus and distal articles.

Fifth abdominal segment rounded posterolaterally; sixth abdominal segment with posterolateral spine; lobe above articulation of uropod produced into small, sharp spine. Telson slightly more than 1.5 times as long as sixth abdominal segment, length about 3.5 times greatest width; with 2 pairs of dorsal and 2 pairs of distal spines, anterior dorsal pair set at end of proximal $\frac{1}{4}$, distal pair beyond midlength; distal spines as in *P. bermudensis*; apex produced into sharp point.

Measurements in mm.—Carapace length: male 7.2; female 10.0; ovigerous females 9.3–10.8.

Habitat.—28 (USNM) to 346 m.

Type-locality.—Gulf of Mexico off the west coast of Florida, 202 m.

Known range.—Southeast of Cape Hatteras; off South Carolina; Gulf of Mexico off southern and western Florida; Surinam (USNM).

Remarks.—The shallowest record is that off Cape Hatteras.

Ovigerous females are known from the Gulf of Mexico in March and April, and from Surinam in July.

Processa vicina Manning and Chace

Fig. 105

Processa vicina Manning and Chace 1971:34, figs. 19a-x, 20a-m.—Hayashi 1975:78 (key).

Recognition characters.—Rostrum sinuous or convex dorsally, not exceeding eye; apex deflexed, bifid, obscured by long setae, lower tooth longer. Antennal spine absent, lower orbital angle an inconspicuous lobe. Eyes moderately large, corneal width 2.5 times greatest width of antennal scale. Antennular peduncle with stylocerite obtusely rounded laterally, mesiodistal apex armed with minute tubercle in some specimens. Length antennal scale about 6.5 times greatest width, distal spine overreaching blade. Antennal peduncle extending to about midlength of second article of antennular peduncle, basal antennal article unarmed.

Second legs symmetrical, overreaching antennal scale by chela and distal 3 articles of carpus, merocarpal articulation of second legs not extending beyond eye; ischium undivided, merus with 5, carpus with 10–14 joints. Third to fifth legs slender; propodus-dactyl comparative lengths: third 4, fourth 5, fifth almost 4.

Fifth abdominal segment rectangular posterolaterally; apex of pleuron rounded; sixth abdominal segment less than 1.5 times as long as fifth, bluntly angled posterolaterally, lobe above articulation of uropod irregular in outline, unarmed. Telson about 1.5 times as long as sixth abdominal segment, length slightly more than 3 times greatest width, 2 pairs of dorsal and 2 pairs of distal spines, anterior pair of dorsal spines set in proximal $\frac{1}{4}$, posterior spines beyond midlength, distance between anterior margin and anterior pair of dorsal spines less than $\frac{1}{3}$ distance between pairs of spines; distal spines and apex as in *P. bermudensis*.

Measurements in mm.—Carapace length: male 4; female 5.3; ovigerous females 4.3–5.3.

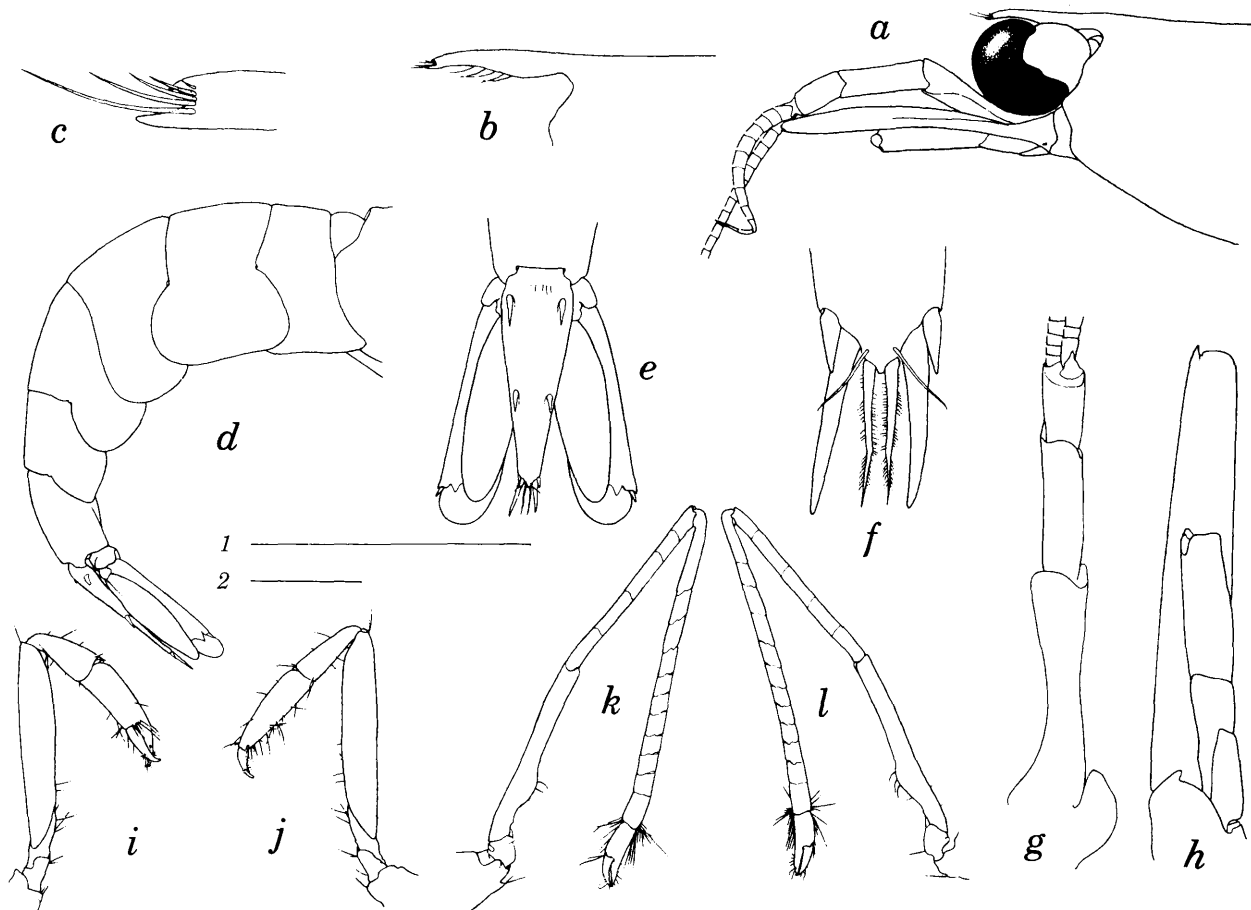


Fig. 105. *Processa vicina* Manning and Chace. Male: *a*, anterior region, lateral view; *b*, rostrum; *c*, same, distal end; *d*, abdomen, lateral view; *e*, telson and uropods, dorsal view; *f*, tip of telson; *g*, right antennular peduncle, dorsal view; *h*, right antenna, dorsal view; *i-j*, right and left first legs; *k-l*, right and left second legs. Scales: 1(*c*, *f*) = 0.5 mm; 2(*d*) = 4 mm, (*k-l*) = 0.5 mm, all others = 1 mm (from Manning and Chace 1971).

Habitat.—Over fine substrates, 2 to 223 m (Saloman 1979; Wenner and Read 1982).

Type-locality.—Off North Carolina, 34°35'30"N, 75°45'30"W, 59 m.

Known range.—SE Cape Lookout, N. C., northwest Florida, off Isla Margarita, Venezuela.

Remarks.—Ovigerous females are known from Florida in February, and North Carolina in October (Manning and Chace 1971).

Superfamily Pandalioidea

Family Pandalidae

Rostrum long and slender, laterally compressed, armed with teeth or spines. Eyes well developed. Mandibles with incisor process and a 2- or 3-jointed palp. First pair of legs simple or microscopically chelate; second pair long, slender, chelate, carpus subdivided.

Key to Genera and Species

1. Rostrum articulated with anterior margin of carapace *Pantomus parvulus*
 Rostrum fixed to carapace in normal way 2
2. Third maxillipeds with exopod. *Dichelopandalus leptocerus*
 Third maxillipeds without exopod [*Pandalus*] 3
3. Rostrum dorsally toothed throughout length; abdomen with small median spine on posterior edge of third and fourth segments, median crest on third segment *Pandalus borealis*

- Rostrum with distal portion toothless dorsally; abdomen with no median spines or crest on segments. 4
4. Rostrum upturned at about 45° angle; distolateral spine of antennal scale exceeding extremely narrow lamella. *P. propinquus*
- Rostrum upturned at considerably less than 45° angle; distolateral spine of antennal scale not exceeding somewhat narrowed lamella *P. montagui*

Genus *Dichelopandalus* Caullery 1896

Caullery 1896:379.—Rathbun 1929:9.—Holthuis 1955:122 (synonymy).

Dichelopandalus leptocerus (Smith)

Fig. 106

Pandalus leptocerus Smith 1881:437.—1884:367, pl. 5, fig. 1.

Dichelopandalus leptocerus.—Rathbun 1929:10, fig. 7.—Couture and Trudel 1968:865, fig. 6.

Recognition characters.—Rostrum curved very slightly upward in distal $\frac{2}{3}$ and tapering to slender tip, from 1.3 to 2 times as long as remainder of carapace; dorsally armed with 11–13 spines, movable except for distalmost remote from others and very near tip, usually only 2 spines (rarely 4) posterior to orbital margin; ventrally with 6–8 fixed teeth longest and most erect toward proximal end, proximal tooth curved. Surface of carapace and abdomen roughened with short, irregular, transverse, punctate ridges giving rise to bristlelike short hairs; antennal spine strong; anteroventral margin slightly convex; pterygostomial spine small. Eyes large, ocellus present dorsally. Antennular peduncle exceeding antennal peduncle by about length of distal article, basal article with conspicuous subdistal eye brush; stylocerite short, rounded distally. Basal antennal article with small ventrolateral spine; antennal scale long, narrow, subtrun-

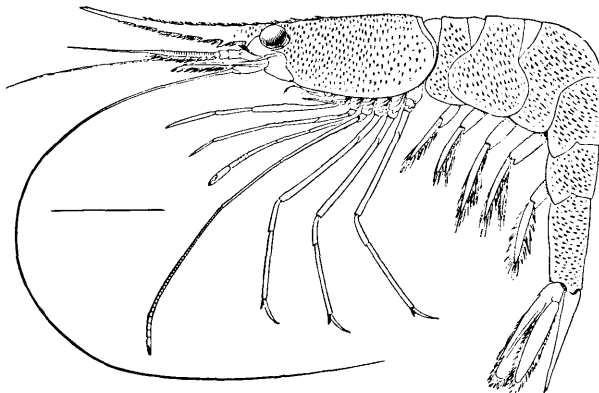


Fig. 106. *Dichelopandalus leptocerus* (Smith). Female in lateral view, 10 mm indicated (from Smith 1884).

cate blade slightly overreached by small distolateral spine. Third maxilliped with tip not reaching to end of antennal scale, slender exopod about $\frac{1}{3}$ length of ischium, epipod present.

First 4 legs with epipods. First leg slender, with microscopic chela. Second legs unequal; right leg scarcely reaching tip of first leg, carpus usually divided into 5 unequal segments, chela about $\frac{1}{2}$ length of carpus; left leg much longer with carpus divided into 52–64 segments. Third, fourth, and fifth legs slender; dactyls long, slender, curved, and armed only near base with few spinules on flexor margin.

Abdomen rounded dorsally; pleura of first segments rounded, small spine posterolaterally on fifth and sixth, and latter with broadly buttressed spine overlapping base of telson.

Measurements in mm.—Length of body (including rostrum): male 90 (USNM); female 98 (Smith 1881).

Variation.—A few specimens examined by Smith (1881) had 6 or 8 segments in the carpus of the left second leg, and one female had the right second carpus composed of about 18 segments. Smith felt that these variations might be attributable to injury and regeneration.

Habitat.—Common over sediments containing organic matter (Wigley 1960); surface to 790 m, -0.1° to 16.7°C (Williams and Wigley 1977, summary).

Type-localities.—Off Cape Cod, Mass., U. S. Fish Commission Stn. 372, $[41^{\circ}40'\text{N}, 69^{\circ}28.5'\text{W}]$, 128 m; off Block Island, R. I., Stn. 870, $[40^{\circ}02'36''\text{N}, 70^{\circ}22'58''\text{W}]$, 283.5 m; off Newport, R. I., Stn. 873, $[40^{\circ}02'\text{N}, 70^{\circ}57'\text{W}]$, 183 m; off Block Island, R. I., Stn. 878 $[39^{\circ}55'\text{N}, 70^{\circ}54'15''\text{W}]$, 260.6 m.

Known range.—Newfoundland Banks to off Oregon Inlet, N. C.; Shumagin Bank, Alaska (Rathbun 1929; Squires 1965).

Remarks.—Ovigerous females are recorded in the USNM collection from off the northeastern tip of Cape Cod to off the mouth of Chesapeake Bay during July to November, and from Hudson Canyon in February. A larva which Stephensen (1935) described as an early stage of *Pandalus propinquus* was regarded by Pike and Williamson (1964) as *D. leptocerus*. The latter authors described the larval development of *D. bonnierii* (northeastern Atlantic) from laboratory rearing through stage VI, and in-

licated that more stages were found in plankton. Haynes (1976) included comparative remarks on pandalid larvae.

Wigley (1960) stated that this species is most common in depths of 80–145 m off the northeastern United States and is the only pandalid common on Georges Bank and south of Cape Cod.

Uzmann and Haynes (1968) described a chytrid-like parasite from the gills of *D. leptocerus* and illustrated stages of its life cycle that could be deduced from available samples. In preserved trawl samples taken in June, January, and October, infection rates were 52%, 54% and 95% respectively. Diseased shrimp occurred at 79 of 126 sampling locations from southern Nova Scotia to off southeastern Long Island. Gross microscopic examination indicated that the parasite is confined to the branchial lamellae and suggested that the disease must have serious effects on respiratory efficiency of the host as it progresses. High incidence in all parts of the range suggests that the parasite may be an important cause of natural mortality in *D. leptocerus*, and undetected mature sporangia may indicate that terminal stages of parasite development are liberated from moribund shrimp not trawled from above the bottom.

Genus *Pandalus* Leach 1814

Holthuis 1950:28.—1955:123 (synonymy).—Hemming 1958:52.

Rostrum long, upper border with movable spines. Carapace smooth, without carinae, antennal and pterygostomian spines present. Eyes large, cornea broader than eyestalk. Antennule with elongate flagella, outermost with thickened basal joints; stylocerite broad and rounded.

Third maxilliped and all legs without exopods, all except first legs with epipods. First leg with microscopic chela; carpus and merus approximately equal in length, both longer than propodus; ischium about as long as propodus, thin but remarkably broad close to articulation with merus. Second legs unequal; left long and slender, right shorter and stouter; carpus of both subdivided into many segments. Last 3 legs long and approximately similar in structure, dactyl sickle-shaped with spinules on flexor margin, propodus approximately 3 times length of dactyl, carpus nearly half length of propodus, merus much longer than propodus; merus and carpus with longitudinal row of movable spines.

Pleura of first 3 abdominal segments rounded, that of fourth more narrowly so, fifth ending in posterolateral spine, sixth distinctly longer than fifth. Telson narrow, 2 longitudinal rows of movable spines, outermost very short.

Pandalus borealis Krøyer

(Northern shrimp, pink shrimp)

Fig. 107

Pandalus borealis Krøyer 1838a:254.—Rathbun 1929:8, fig. 4.—Holthuis 1950:31, fig. 9.—Coulture and Trudel 1968:863, fig. 3.—Smaldon 1979:92, figs. 35B, 38A, B.—Holthuis 1980:138.—Butler 1980:128.

Recognition characters.—Rostrum slightly up-curved, as long as or slightly longer than carapace; row of 12–16 movable dorsal spines extending into anterior $\frac{1}{3}$, normally 4 of these behind posterior orbital margin; 6–8 fixed ventral teeth, strongest proximally. Antennular peduncle exceeding antennal peduncle by length of distal article; basal article with conspicuous subdistal eye brush, distal 2 articles about equally short. Basal antennal article with small ventrolateral spine and distolateral lobe above it; antennal scale long, blade narrowed distally to rounded tip exceeding distolateral spine, slightly convex laterally. Third maxilliped with tip reaching about tip of antennal scale.

Legs as in generic diagnosis.

Abdomen with distinct, sharp dorsal crest on third segment, small median spine on posterior margin of third and fourth segments.

Measurements in mm.—Length of body including rostrum: male to 120; female to 170, but usually less. The slender rostrum is often broken. Rasmussen (1953) employed short carapace length (rear edge of orbit to rear edge of carapace) as a standard measure. He found the ratio of total length to this length to average 5.3 ($scl \times 5.3 = tl$).

Variation.—Makarov (1935) described a subspecies, *P. borealis eous*, from the northern Pacific on the basis of a longer rostrum and distally more rounded antennal scale on which the lamella exceeds the distal spine. Both Butler (1971) and Holthuis (1980) stated that while this subspecies is often recognized, its status remains doubtful; cursory examination of selected specimens indicates that these characters are variable. Butler (1980) did not mention the Pacific subspecies.

Color.—Thickly sprinkled with small red stellate spots, closer on tail; flagella of antennules banded with narrow white and broad red rings; antennae deep red (Rathbun 1929). Darker red due to concentration of red dots on dorsal surface, including other areas such as along ventral margin of carapace, distal part of rostrum, distally on abdomen and proximal part of telson, as well as fifth legs (Butler 1980).

Habitat.—Soft mud or sediment high in organic matter, but occasionally on sand and gravel to rocky

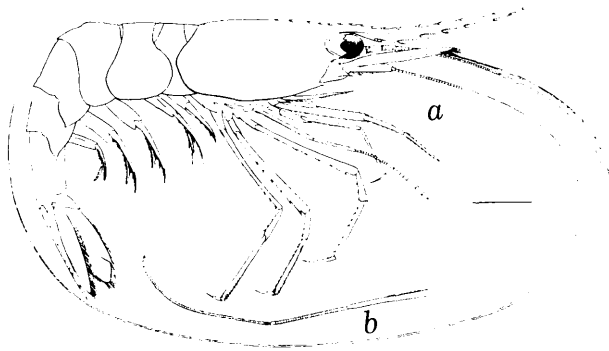


Fig. 107. *Pandalus borealis* Krøyer. a, Lateral view; b, second leg with subdivided merus, carpus, and tiny chela; 10 mm indicated (from Holthuis 1950).

substrate; -1.4° to 13.6°C , 30 to 1150 m (Makarov 1967; Williams and Wigley 1977, summary); going into deeper water with increasing age (Allen 1966; Warren and Sheldon 1966).

Type-locality.—Sydprøven, Julianehaab, and Fiskenaeset, Greenland.

Known range.—Discontinuously arctic boreal. Northern Atlantic: Greenland southward to Martha's Vineyard, Mass.; Iceland; Novaya Zemlya, Franz Josef Land and Spitsbergen, southward to northern Europe including Britain. Northern Pacific: Bering Sea (and part of Chukchi Sea) southward, stragglers to San Diego; Hokkaido and Honshu, Japan, and South Korea to about $35^{\circ}30'\text{N}$ (Ito 1976). Distribution depicted by Allen (1959).

Remarks.—Species of *Pandalus* are fished commercially and their biology has been the subject of active investigation during much of this century. The greatest concentrations of these species are centered along the southern and western coast of Scandinavia, western Greenland, the Gulf of Maine, and from the Gulf of Alaska along the northeastern Pacific coast to Washington and Oregon, with some outlying populations beyond these regions (Bae 1963; Butler 1964a, 1971, 1980; Gulland 1970; Hjort and Rudd 1938; Holthuis 1980; Horsted and Smidt 1956; Ivanov 1969; Rasmussen 1953; Ronholt 1963; Squires 1965a; Scrivener and Butler 1971). Landings of shrimp (mainly *P. borealis*) from New England, for example, were reported as over 6 million pounds per annum during the 1974–78 period (Pileggi and Thompson 1980), and this represents a great decline in recent years from landings that exceeded 10 million pounds annually in the early 1970's. Landings of shrimp from a far more extensive area in the eastern North Pacific (*Pandalus jordani*, *borealis* which dominates in Alaska, *hypsinotus*, *platyceros*, and *Pandalopsis dispar*) totaled nearly 160 million pounds per annum during the 1974–78 period (ibid 1980). Barr (1970)

stated that the domestic Alaskan catch had been as much as 40 million pounds, plus Japanese and Soviet catches of 70 million pounds per annum. Ito (1976) reported a catch of about 4,700 tons in Japan in 1972. The relative importance of pandalids in fisheries is similar in other parts of the range, and this has led to a call for thorough knowledge of the biological potential of the group. The tremendous amount of literature can be no more than briefly and selectively summarized here.

Pandalus borealis is a protandrous hermaphrodite, as are other species of the genus. During studies in British Columbia, Berkeley (1930) described six larval stages from laboratory rearing and plankton. She found that larvae of *P. borealis* hatch mainly in late March-early April, pass through early larval stages at a depth of $91 + \text{m}$, but then migrate to shallower water where they spend the summer transforming, and by winter join older shrimp in deeper water. By their second autumn (the following year) individuals of this group produce their first and only sperm, and at the end of that winter they change into females and live more than a year as females. To that basic life history outline a number of authors have added details. Larval stages reared in Alaska in flasks submerged at sea (Haynes 1979) confirmed the larval development as described by Berkeley. Kurata (1964) described seven larval stages from laboratory rearing of eggs hatched in Hokkaido, comparing these to the work of Berkeley and Lebour (1940). He felt that stage III larvae begin to move toward the coast. Makarov (1967) found five stages plus a last stage on the Kamchatkan shelf during May-July and compared this occurrence to that in the western Gulf of Alaska where larvae are released in April and May. The earliest account of larvae is that of Sars (1900) who described and illustrated eight larval stages plus the postlarva, and adult, including some data on other pandalids.

In *P. borealis* and some similar crustaceans, the factor responsible for sexual differentiation is the androgenic hormone (Berreur-Bonnenfant and Charniaux-Cotton 1966). In presence of an androgenic hormone, the germinative tissues of these animals give rise to secondary spermatogonia during development of the male phase. When level of the hormone diminishes, development of the female phase takes place with concurrent oogenesis. Histological studies confirm gonadal changes that accompany the secondary sexual changes (development of appendix masculina on second pleopods and spines on first three abdominal sternites during male phase and regression of these features at onset of female phase [see also Allen 1959; Carlisle 1959, a, b]). Parasitism by bopyrids pro-

duces effects that are distinguishable from the normal phases.

Both the life span and ages at which sexual maturity and sex reversals occur are greatly influenced by temperature (latitude) (Rasmussen 1953, 1967; Horsted and Smidt 1956). In high latitudes, the shrimp may not mature as males until their third year and change sex in the sixth year, whereas in areas such as the North Sea maturity is reached in 18 months, and more than 30% may never show male characters (Allen 1959); in deep fjords of Norway where conditions are more like the far north, the shrimp have the northern life pattern. Sex reversal in individuals showing male characters occurs before they are 27 months old in the south part of the range, and the shrimp as a whole do not live more than 38 months. In the Gulf of Maine, the average life span is 3.5 years, but may extend to 4.5 years for a few individuals (Haynes and Wigley 1969). These shrimps function first as males; most of the female phase spawn only once, 20% at 2.5 years, 70% at 3.5 years, and 10% at 4.5 years. In British Columbia the life history is similar. From a series of studies Butler (1980) amplified Berkeley's earlier work; almost as many females as males mature at 18 months, and males begin sexual change in spring when about 2 years old, passing through four or five transitional molts during summer to become functional females. By age 30 months all are females.

In summary, these populations are composed of three general sexual categories (Jagersten 1936): (1) primary females which mature early, their male characters being repressed; (2) secondary females in which male characters are repressed soon after they appear, becoming females in their second year; and (3) hermaphroditic females in which male potentialities are repressed after function as males (Allen 1959). Rasmussen (1953) was able to predict proportions of immature males and females from the size range of the age group at the beginning of the breeding season.

Haynes and Wigley (1969) and others found that clutch size increased with shrimp size. In the Gulf of Maine, females spawn 800–3,400 (\bar{x} = 2,400) eggs in August–September, and hatching occurs in March–April. The females migrate from deeper to shallow areas during the maturation period, hence it is ovigerous females in the nearshore and estuarine areas that make up the bulk of the commercial catch. Allen (1966) found that females off the Northumberland coast of England bear 300–1,500 eggs in one brood per year borne from November to May, and he judged these animals to live for 2.5 years. At the end of the first breeding period (1.5 years) approximately 35% are primary or second-

ary females, as opposed to the 5%–10% primary females predicted from Rasmussen's data. In southern Norway, the shrimp spawn during mid-October to early December (Rasmussen 1953) and eggs hatch during late February to April, the number of eggs varying from about 460 to 2,700, depending on size. In Greenland, Horsted and Smidt (1956) found a comparable range (180–3,800; \bar{x} = 1,300) depending on age and size. Ito (1976) found 579 to 4,904 (\bar{x} = 2,219) in Japan during October–December. In general, the colder the earlier the spawning, the longer the incubation period, and the later the hatch. Maximum size attained is the same regardless of latitude, but shrimp in colder waters take much longer to reach large sizes. For example, length-weight relations of shrimp from the Gulf of Maine are similar for males and non-ovigerous females (Haynes and Wigley 1969). Ovigerous females are about 1.4 g heavier for any given length than non-ovigerous ones, and the growth rate of the population is faster at ages of 2 years and older than that of any other population of *P. borealis* reported to that date.

These variations naturally influence the productivity and renewal of stocks, hence the commercial fishery. Jensen (1967) gave a short history of the *P. borealis* fishery which developed in this century in the North Sea and Skagerak. The fishing season in the Skagerak is mainly March to October by fishermen from Denmark, Norway, and Sweden, with maximum effort during summer. The Norwegian effort is to large part carried out in winter when shrimp carry roe, like that in Maine. Great diminution of relative abundance of larger shrimp was evident during the 1950's. In Greenland, Horsted and Smidt (1956) recorded generally increasing yield as the fishery developed, but concern was expressed that the stocks not be taxed too heavily. Fluctuations in that fishery are mainly due to uncontrollable natural variations in density presumably caused in most cases by water temperature (Smidt 1969). Squires (1968a) noted that some populations near Newfoundland live throughout the year in temperatures close to 5°C, apparently maturing into females in their fourth year and spawning annually in the next two or three years that they live. But some populations live in temperatures close to 0°C; the proportion of females in these is low and natural mortality may ensue before most males become females. Such cold water populations appear to be scarcely self propagating and not likely to withstand intensive fishing. Dow (1967) summarized the association of fishery yields with temperature in the Gulf of Maine in a set of tables, stating that high yields have consistently been associated with a set of temperatures that range

from 0° to 16°C in the October-July period, allowing a two-year lag for growth and development. Temperatures higher or lower than the optimum seem to result in diminished yield.

Temperatures of less than -1°C are deleterious (Horsted and Smidt 1956); indeed, Ekman (1953) questioned whether the species could reproduce in high arctic waters, but a number of authors (including Christiansen and Christiansen 1962) have shown that arctic populations such as those around Spitsbergen within the influence of the Gulf Stream do reproduce (ovigerous in July).

Stomach contents of *P. borealis* are very finely divided, but include copepods and larvae of other carideans (Allen 1966), benthic and planktonic microorganisms (Hjort and Rudd 1938; Horsted and Smidt 1953; Squires 1965a); the latter author showed that the incisor process of the mandible is sharp and the molar bears a shearing cusp at the edge of the grinding surface. The species often forms a large part of the diet of cod (Blacker 1957).

A number of parasites have been recorded from pandalids (bopyrid isopods, *Hemiarthrus* species; rhizocephalans, *Sylon hippolytes* and similar forms; and microsporidia); occurrences of these forms is summarized by Butler (1980). Margolis and Butler (1954) noted an unusual infection of *P. borealis* by a nematode, *Contaracaecum*, usually found in the digestive tract of fishes.

Pandalus montagui Leach

(Striped pink shrimp)

Fig. 108

Pandalus montagui Leach 1814:432.—Smith 1887:662[58], pl. 13, fig. 2.—1879:87.—Calman 1899:30, pls. 1–4, fig. 1.—Kemp 1910:86, pl. 10, fig. 8.—Rathbun 1929:8, fig. 5.—Holthuis 1950:28, fig. 8.—Couture and Trudel 1968:863, fig. 4.—Simpson, Howell, and Warren 1970:1230, fig. 1.—Smaldon 1979:94, fig. 39A-B.—Holthuis 1980:141.

Pandalus annulicornis Leach 1815a, pl. 40.

Pandalus levigatus Stimpson 1854:58 (sic *longivatus*, Couture and Trudel 1968).

Recognition characters.—Rostrum upcurved at considerably less than 45° angle, as long as or slightly longer than carapace; row of 10–12 movable dorsal spines extending about ½ its length and remote, tiny subdistal spine making tip bifid, normally 4 (rarely 3) of spines behind posterior orbital margin; 5–6 (rarely 7) fixed ventral teeth, strongest proximally. Antennular peduncle exceeding

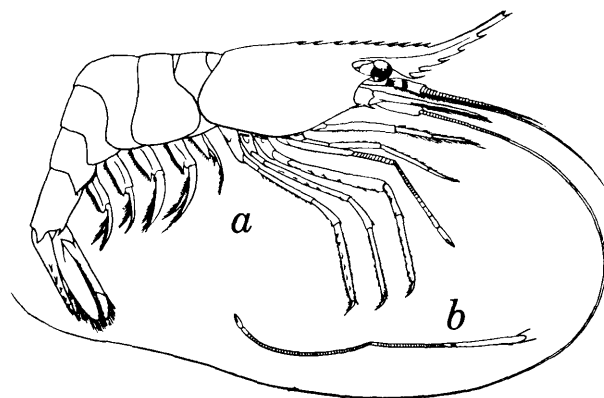


Fig. 108. *Pandalus montagui* Leach. a, Lateral view; b, second leg with subdivided merus, carpus, and tiny chela; 10 mm indicated (from Holthuis 1950).

antennal peduncle by about length of distal article; basal article with conspicuous subdistal eye brush, distal 2 articles equally short. Basal antennal article with acute ventrolateral spine and distolateral lobe above it; antennal scale long, blade narrowed distally to rounded tip not usually exceeded by distolateral spine, almost straight laterally. Third maxilliped reaching about to tip of antennal scale.

Legs as in generic diagnosis.

Abdomen with dorsal side rounded, no carina or knob present.

Measurements in mm.—Maximum length: Norwegian coast and North Sea 160, southeastern England 90, Ungava Bay 108, Labrador 130, Maine 110 (Simpson, et al. 1970, summary); total length = 4.5 × carapace length (Mistakidis 1957).

Color.—“Usually semi-translucent, with red chromatophores giving overall pink color,” often with oblique red lines on carapace, becoming more horizontal on abdomen (Smaldon 1979); “usually very pale yellow, with narrow blue lines on back” (Stimpson 1854). Kemp (1910) gave a detailed color description.

Habitat.—Prefers hard sandy bottom with variable amounts of gravel and shell where the polychaete, *Sabellaria spinulosa*, is present (southeastern England, Mistakidis 1957); gravel to mud (Allen 1966); sand and gravel, -1.0°C to 21°C, below 10°C in western Atlantic but in reduced numbers below 6°C (Couture and Trudel 1969); 5 to 790 m (Williams and Wigley 1977, summary).

Type-locality.—Zetland (= Shetland Islands).

Known range.—Boreo-arctic; Greenland to Rhode Island; Iceland; northern Europe including British Isles (Williams and Wigley 1977, summary). Heegaard (1941) mapped the distribution.

Remarks.—A northern and eastern Pacific form long known as *P. montagui tridens* Rathbun was af-

forded full species rank by Butler (1980) who compared adult morphology of rostrum, spines on dactyl of legs 3–5, relative lengths of dactyl/propodus, and morphology of larvae from the eastern Atlantic, Quebec, and the eastern Pacific. Although there is overlap in the features examined, the geographically separated Atlantic and Pacific populations seem distinct. Squires (1965a) thought that differences in color alone indicated specific separation. Butler also demonstrated minor differences in adults of the eastern and western Atlantic populations and thought that this should be studied further.

Much of the literature on *P. montagui* was cited by Scrivener and Butler (1971), and biological data were summarized by Simpson, et al. (1970). A fishery exists off southeastern England where annual yield has been estimated at about 800,000 lbs. (Mistakidis 1957).

Pandalus montagui like *P. borealis* (see above) is a protandrous hermaphrodite; transformation from male to female phases is broadly as that described for *P. borealis*, though some males may breed more than once, and proportion of primary females is higher (30%–35%) than in that species (Mistakidis 1957; Allen 1963).

Spawning at the mouth of the Thames River, England, begins in November (possibly October) approximately 10 to 12 weeks after the first sign of ovarian maturity, and continues through February, with stragglers ending in March (Mistakidis 1957). The larger females spawn first, followed by females which are spawning for the first time, some of which spawn before one year of age. It is probable that hatching there occurs in late February or early March to April (Mistakidis 1957; Allen 1966). The number of eggs is correlated with body size (136–3,796 observed), the mean for large shrimp (14–17 cl) running around 2,500. Following the hatch, females molt and lose the ovigerous setae. Older individuals tend to move offshore in winter toward higher salinities and temperatures but return in some instances to shallows in spring. Those males that do not transform in the first year move to deeper water and mature a second time (Allen 1963; 1966). Whereas the males move to deeper water in March, females do not do so until October.

Along the Gaspé, Quebec, coast spawning begins in July at the time offshore migrations are most evident, and during this time maturing males migrate more than immature males (Couture and Trudel 1969). The male phase there appears to last three years at most; after the second year most males transform to females which mostly live at least two years longer (Couture and Trudel 1969a). Eggs

hatch the following June, thus incubation lasts longer than in Europe because the temperature is lower.

From eggs hatched at Port Erin, Isle of Man, and Millport, Scotland, Pike and Williamson (1964) reared 9–11 larval stages at 10°C, with stage X and XI, when present, showing some megalopal characters. At 18°C no larvae developed beyond stage V, although this larva appeared identical to that reared at 10°C. Larvae from plankton were comparable except that those in stage VI molted directly to the megalopa. Earlier work on larvae was reviewed.

Growth is rapid during the first year but then tapers off; males attain a length of 44 mm by November of the first year in England, females approximately 50 mm, but increase stops during winter. The species lives to an age of 3–4 years in the Thames estuary, but this cannot be judged by size alone (Mistakidis 1957).

Food of *P. montagui* is mainly polychaetes (Mistakidis 1957; Allen 1963), but includes crustaceans, small lamellibranchs, hydroids and algae, depending on substrate. Squires (1965a) reported phyto-benthos, fragments of amphipods and calanoid copepods, occasionally polychaetes, pelecypod shells, ophiuroids and euphausiids. Warren and Sheldon (1967), by analysis of sand grains in stomachs and by timing rates of passage through the gut, were able to determine the main feeding ground for a population off England; sand is a natural tag.

Predators recorded are *Gadus merlangus* and *G. luscus*, *Pleuronectes* sp., *Raja* sp., and *Cottus* sp. in southeastern England (Mistakidis 1957), and cod, seals (Squires 1957) and guillemots (Tuck and Squires 1955) off eastern northern Canada.

An incidence of about 3% infestation by the bopyrid *Hemiarthrus abdominalis* is recorded (Mistakidis 1957; Allen 1963). Allen (1966a) found the parasite also on *Spirontocaris liljeborgii*, *S. spinus*, and *Eualus pusiolus*, but never on *P. borealis* even though it is abundant in samples taken off Northumberland, England, a fact noted by others off Norway. Moreover, the parasite has a clear preference for the hippolytid species. Hosts show a great difference in response to the parasite; there is no specific difference between parasites from different host species; egg size of the parasite does not vary with host nor with size of adult parasite, although size of parasite is related to size of host. No more than one *H. abdominalis* female is found on a host; only female hippolytids are parasitized, but *P. montagui* males, females and transitionals are all parasitized (in numbers 7, 93, and 14 respectively in samples examined). There, 85% of these belonged to host

year-class 1 which constitutes about 60% of the total population; 30% of this population were primary females, but there was no evidence to show that transition from male to female is accelerated by the parasite. The parasite breeds year-round. Presence on hippolytids prevents ova from becoming mature but seems only to retard growth of ova, reduce their size, and prolong incubation time during which they may regress in size on *P. montagui*.

Marr (1958) pointed out that *P. montagui* has no statocyst and does not respond to inertial stimulation, but possesses an additional sense which enables it to respond to water movement when it is rotated; this sense normally augments response to visual and tactile stimuli. Of four possible mechanisms to give information about displacement (image displacement on retina, inertial stimuli; tactile stimuli or passage of water over surface) no crustacean is known to use more than three to control direction of movement.

Pandalus propinquus G. O. Sars

Fig. 109

Pandalus propinquus G. O. Sars 1869:148.—Smith 1887, pl. 13, fig. 1.—Calman 1899:32, pls. 1–4, fig. 2.—Kemp 1910:89, pl. 11, figs. 1–4.—Couture and Trudel 1968:864, fig. 5.—Williams 1974c:13, fig. 33 (key).—Smaldon 1979:96, fig. 40.

Recognition characters.—Rostrum upcurved at about 45° angle, longer than carapace; row of 8–10 movable dorsal spines extending about to base of upturned part, and remote, tiny subdistal spine making tip bifid, normally 3 of spines behind posterior orbital margin; 5–7 fixed ventral teeth, strongest proximally. Antennular peduncle exceeding antennal peduncle by about length of distal article; basal article with conspicuous subdistal eye brush, distal 2 articles equally short. Basal an-

tennal article with acute ventrolateral spine and distolateral lobe above it; antennal scale long, blade exceedingly narrowed distally to truncate or slightly angled tip exceeded by distolateral spine, slightly concave laterally. Third maxilliped reaching about to tip of antennal scale.

Legs as in generic diagnosis.

Abdomen with dorsal side rounded, no carina or knob present.

Measurements in mm.—Length of body: 150 off Norway but usually 70–90 (Wollebaek 1908); 110 (Smith 1881).

Variation.—Right and left chelipeds may be reversed (Calman 1899).

Color.—Carapace often uniform red; transverse bands of red on first to fourth abdominal segments; fifth segment pale red with darker dots, sixth segment and tail fan darker red; shrimp from deep water with pale red legs except for colorless second pair, those from shallow water with carpus and propodus of last three pairs milk white (Kemp 1910). Rostrum yellowish toward tip (Rathbun 1929).

Habitat.—Over sediment of medium to high organic content (Wigley 1960); 2.6°–9.9°C; 20 to 2,000 m, mainly 165 to 350+ m (Williams and Wigley 1977, summary).

Type-localities.—Lofoten near Skråva, Guldbrandsøy, and Brettesnes, rare in depths of 200–300 fm.

Known range.—North Atlantic deep-sea species (Stephensen 1935); Davis Strait; Newfoundland Banks to Delaware; Iceland; NW Europe (distribution illustrated, Heegaard 1941).

Remarks.—Ovigerous females are known from the Hudson Canyon off New York in November and February (USNM). Squires (1965a) stated that *P. propinquus* is not hermaphroditic. Ovary development indicated that almost 80% of the females off eastern Canada would be ovigerous in autumn, and one female with eggs in an advanced state of development was taken in April. Indications were that the majority of the population spawns annually.

Pike and Williamson (1964) reared larvae of *P. propinquus* from eggs taken at Millport, Scotland, in April to stage VII. None were found in plankton. Parents of this group were of the type known from shallow water (see Kemp 1910). The authors pointed out that the first larvae ascribed to *P. propinquus* by Stephensen (1916) were later shown to be *P. borealis*, but his stages I and II that were subsequently described from Greenland appear to be correctly identified. Comments were given on other of Stephensen's larvae. Haynes (1976, 1978a) reviewed the literature on pandalid larvae, described his method for rearing larvae in flasks suspended



Fig. 109. *Pandalus propinquus* G. O. Sars. Carapace and antennal scale (arrow) in lateral view, 10 mm indicated (from Williams 1974c).

in the sea, reiterated the comment of Pike and Williamson (1964) that *P. montagui* and *propinquus* may develop through more larval stages when reared in the laboratory than in nature, and noted that *P. borealis* under laboratory conditions prolongs molt periods from 10–15 days to as much as 5 weeks and may have as many 11 zoeal stages before reaching postlarva.

Stomach contents consist of phyto-benthos, crustacean fragments (copepods, euphausiids, amphipods and isopods), and lesser amounts of polychaetes and small gastropod shells (Squires 1965a). Mandibles of the species resemble those of *P. borealis* and *montagui*.

Genus *Pantomus* A. Milne Edwards 1883

Rathbun 1901:117.—Hemming 1958b:159.

Pantomus parvulus A. Milne Edwards

Fig. 110

Pantomus parvulus A. Milne Edwards 1883, pl. 26, fig. 1, la.—Rathbun 1901:118.—Schmitt 1935a:138.—Williams 1965:88, fig. 71.

Recognition characters.—Rostrum longer than carapace, articulated with anterior margin of carapace; basal portion with 3 dorsal spines; lower margin with numerous slender overlapping spines; terminal half directed upward; tip bifid, lower prong longest. Carapace carinated on anterior half and armed with 3 spines, posterior 2 near together and movable, anterior spine adjoining articulation of rostrum; antennal and pterygostomial spines present. Eyes large. Antennular peduncle with basal article excavate above and longer than nearly equal second and third articles combined; stylocerite wide, broadly pointed, inner margin sinuous, tip reaching to midlength of cornea; upper flagellum about twice diameter of lower flagellum at base. Antennal scale, slender, reaching $\frac{2}{3}$ length of rostrum, broadest near base; distolateral spine exceeded by lamella.

Third maxilliped and first pair of legs reaching to tip of antennal scale. Second pair of legs longer than first; carpus subdivided; one leg with 15 to 17 carpal joints, other leg shorter, with 10 to 12 carpal joints. Third to fifth legs progressively longer than second pair.

Abdomen with third segment broadly carinate on posterior half; sixth segment elongate, 2.5 times length of fifth. Telson nearly as long as sixth segment, slender; sides concave, tapering to tip ending in small, median, bulblike enlargement; 2 pairs of spines at tip, outer pair longest and sinuous at

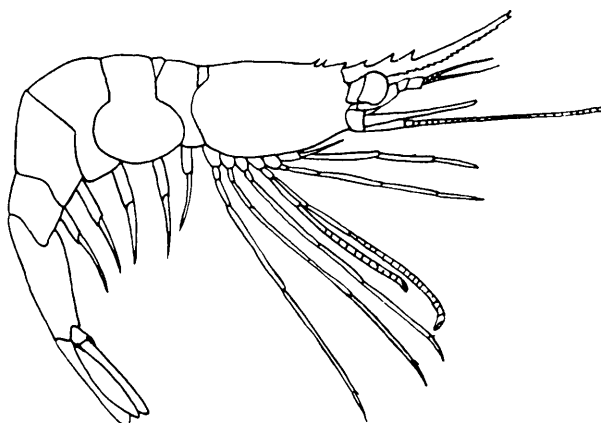


Fig. 110. *Pantomus parvulus* A. Milne Edwards. Animal in lateral view (from A. Milne Edwards 1883).

base, inner spines shorter, arising on terminal bulb; a row of 7 or 8 small dorsolateral spines on each side in distal $\frac{2}{3}$ of length. Uropods long, narrow; exopod with lateral border ending in slender movable spine.

Measurements in mm.—Length of body: ovigerous female, approximately 30.

Variation.—Among four of the syntypes, the rostrum varies somewhat in length and the number of carpal segments in the second legs is subject to variation.

Habitat.—137 to 454 m.

Type-locality.—Northern part of Yucatan Bank, 23°13'N, 89°16'W, 153.6 m.

Known range.—Cape Lookout, N. C., to Yucatan, Mexico; Puerto Rico; St. Croix, V. I.; Surinam (USNM).

Remarks.—The Catalogue of the Books, Manuscripts, Maps and Drawings in the British Museum (Natural History), vol. VI, Supplement, 1922, lists Milne Edwards' 1883 paper as follows: "The title-page (wanting to this copy), the 'Liste des Planches,' and many of the plates themselves are lithographed. Only fifty copies were issued and sent mostly to fellow workers, but few were sold, (See letter by the Author in 'Ann. and Mag. Nat. Hist.' Vol. vi, 1890:471)."

Ovigerous females in the USNM collection are from Mayaguez Harbor, P. R., in January, off west Florida in March, Surinam in July, and North Carolina in October.

Superfamily Crangonoidea

Family Crangonidae

First pair of legs subchelate, stouter than second. Second pair of legs slender, equal; carpus not subdivided; chelate (minutely) or simple. Rostrum small, usually dorsally flattened, not toothed.

Key to Genera and Some Species

(Modified from Couture and Trudel 1968)

1. Dactyls of fourth and fifth legs broadened, modified for swimming, unlike third *Argis dentata*
 Dactyls of fourth and fifth legs not broadened, digitiform, like third. 2
2. Second legs chelate 3
 Second legs reduced and simple, not chelate *Sabinea*
3. Second legs short, not extending beyond merus of third leg . . . *Pontophilus*
 Second legs long and slender, extending far beyond merus of third leg. . . 4
4. Integument smooth; antennal scale with blade narrowed distally
 *Crangon septemspinosus*
 Integument sculptured, rugose and hairy; antennal scale with blade rounded
 and broad distally *Sclerocrangon boreas*

Genus *Argis* Krøyer 1842

Holthuis 1955:134.—Hemming 1958b:153.—
 Squires 1964a:461–462.

Argis dentata (Rathbun)

Fig. 111

Nectocrangon dentata Rathbun 1902:892.—1904:138,
 figs. 76–77.

Argis dentata.—Rathbun 1929:21, fig. 27a-d.—
 Squires 1964a:461–466 fig. 1B.—Couture and
 Trudel 1968:880, fig. 20.

Recognition characters.—Integument smooth and
 shining. Carapace somewhat sculptured, low me-

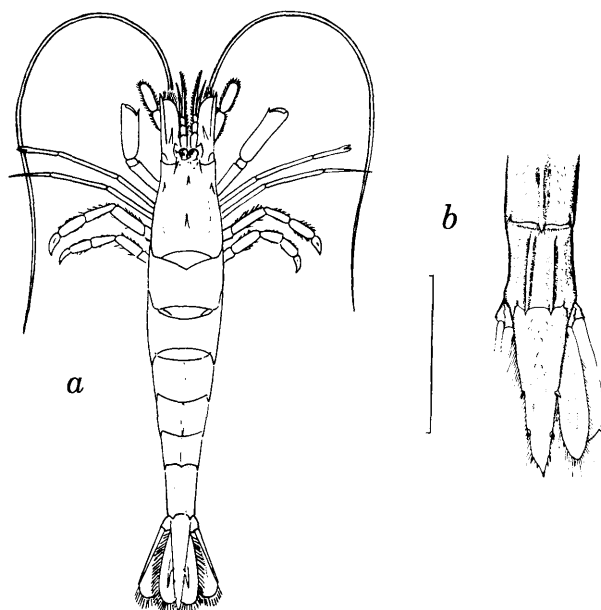


Fig. 111. *Argis dentata* (Rathbun). a, Animal in dorsal view (from Couture and Trudel 1968); b, posterior abdominal region in dorsal view, 10 mm indicated (from Squires 1964a).

dian dorsal carina running from rostrum nearly to posterior margin bearing 2 acute spines, distance between them greater than from anterior spine to anterior margin and about equal to or less than distance from posterior spine to posterior margin of carapace; hepatic and antennal spines present, hepatic spine on variably developed lateral carina. Orbits coalesced, raised and projecting anterodorsally; rostrum reduced to short, elevated spine. Eyes immediately below rostrum, very close together, their peduncles parallel in line with body, relatively larger in males than in females and bearing blunt distal tubercle. Antennule with first article of peduncle long; stylocerite broad, exceeding distal edge of cornea, sinuously truncate distally and bearing rather blunt anterolateral spine; second and third articles progressively shorter, flagella about as long as peduncle. Antennal scale extending to tip of antennal peduncle, broad, somewhat convex laterally, its broadly rounded to slightly truncate tip equaled or slightly exceeded by distolateral spine.

Subchela of first legs about 5 or more times as long as width across palm. Dactyls of fourth and fifth legs subspatulate.

Abdomen with median dorsal carina extending from first to fifth segment; sixth segment (42%–58% length of carapace) bearing 2 high carinae, each ending in small sharp tooth or spine on either side of posterior margin above base of telson; transverse proximal ridge not joining proximal ends of carinae but often bearing fringe of short setae. Telson with 2 blunt carinae armed with 3 pairs of spines on terminal half, middle pair of spines nearer to distal than proximal pair. Outer ramus of uropod distinctly shorter than inner.

Measurements in mm.—Length of carapace: males to 31 (Squires 1965a); females to 30 (USNM).

Color.—Brown (Squires 1965a).

Habitat.—Rock and sand, sand, mud with scat-

tered smaller stones (Frechette, et al. 1970); 0 to 320 m, -1.6° to 6.9°C (Williams and Wigley 1977, summary).

Type-locality.—Off Sitkalidak Island, Alaska, $57^{\circ}00'\text{N}$, $153^{\circ}18'\text{W}$, 126.6 m, *Albatross* Stn. 2855.

Known range.—Smith Sound, NW Greenland through arctic Canadian islands to Dease Strait and southward to SSW of Nova Scotia; Bering Sea to Sitka and SE coast of Kamchatka. Nesis (1963) summarized this range as arctic-boreal or lower arctic boreal.

Remarks.—There has been some confusion in generic placement of this species, but Squires (1964a) in establishing a neotype for *Argis lar* not only distinguished that species from *A. dentata* but reemphasized precedence of *Argis* over *Nectocrangon*.

From studies off Grand Rivière in the Gulf of St. Lawrence, Couture in a series of publications (especially 1968) showed that migrations of *A. dentata*, like those of *Pandalus montagui*, appear to be related to temperature. From samples taken in 18 to 110 m water, *A. dentata* was absent at 18 m where temperatures may reach 10°C . In spring at 55 m, the population is composed equally of juveniles and adults, but at the end of summer when temperatures at that depth reach 4.5°C only some young females remain. Frechette, et al. (1970) and Couture and Filteau (1971) showed that *A. dentata* is a protandrous hermaphrodite. Duration of the male phase is two years and span of the female phase is three years. Primary females may live five years or more. In young populations, males are more numerous than females, but older populations are composed of females only. Their samples showed that females had an average carapace length of 6.8 mm at six months, 11.1 at 1.5 yr, 14.3 at 2.5 yr, and 18.1 at 4.5 yr; males reached 6.4 at six months, and 9.1 at 1.5 yr. The length-frequency curves are typical of protandric species.

These results were confirmed by morphological and histological observations. Some females retain a remnant of the vas deferens. The androgenic gland degenerates in old males. In some transitory forms, the genital system is intermediate between male and female, i.e., the vas deferens and androgenic gland are atrophied and the gonad is full of young oocytes.

Ovigerous females from the southeast Canadian study area were first seen in mid-September with recently spawned eggs. Eggs in that locality mostly hatch in late spring, but a few females carry eggs in an advanced state of development as late as June (Squires 1965a). Ovigerous females from the Bering Sea are recorded in the USNM from June to early September. Squires (1965b) described two

zoal stages and the megalopa from plankton. Stage I was taken during the first plankton hauls of the season in Ungava Bay on June 24. Stage II appeared on July 3. Stage III and IV were never taken, although hauls continued until August 29. Megalopae were taken from August 11 to 20. Since considerable change occurs between stage II and stages III, IV or V, Squires considered that these were also present though never taken in plankton nets. Couture (1968) reported the first young females on the bottom in mid-August in the southeast Canadian area.

Makarov (1967) found larvae of *A.* (= *Nectocrangon*) *lar* to be very similar to those of *A. dentata*. He judged larval life to be less than one month and all larvae hatched from a local population to occur over a two-month period, May 1–July 1.

Squires (1965a) reported *A. dentata* from cod stomachs in the northwestern Atlantic. Its own stomachs contained phyto-benthos, occasionally a predominance of crustacean fragments, foraminiferans and small bivalves, and, infrequently, gastropods, ostracods and polychaetes.

Two ovigerous female shrimp from the Chukchi Sea identified as *Argis lar* bore egg capsules of a gastropod (*Buccinum* sp.?) attached among the eggs attached to their pleopods (McCauley 1964). Since attachment was by what appeared to be an expansion of the egg capsule and there was more than a single age group present, it was assumed that such attachment by the snail is not accidental and may even be a normal pattern.

Genus *Crangon* Fabricius 1798

Holthuis 1955:134.—Hemming 1958b:108.—Williams 1965:88.

Crangon septemspinosus Say

Fig. 112

Crangon septemspinosus Say 1818:246.—Williams 1965:89, fig. 72.—Squires 1965a:78.—Couture and Trudel 1968:879, fig. 18.—Haefner 1979:2. *Crango septemspinosus*.—Hay and Shore 1918:396, pl. 27, fig. 9.—Rathbun 1929:20.

Recognition characters.—Rostrum shorter than eyestalks, unarmed, tip obtuse. Carapace somewhat depressed, subcylindrical; dorsal surface with small appressed spine back of rostrum; anterior margin with suborbital spine obtuse; antennal spine strongly produced, equaling or slightly exceeding eyes and with minute spine below; hepatic spine well developed; anterior portion of carapace with

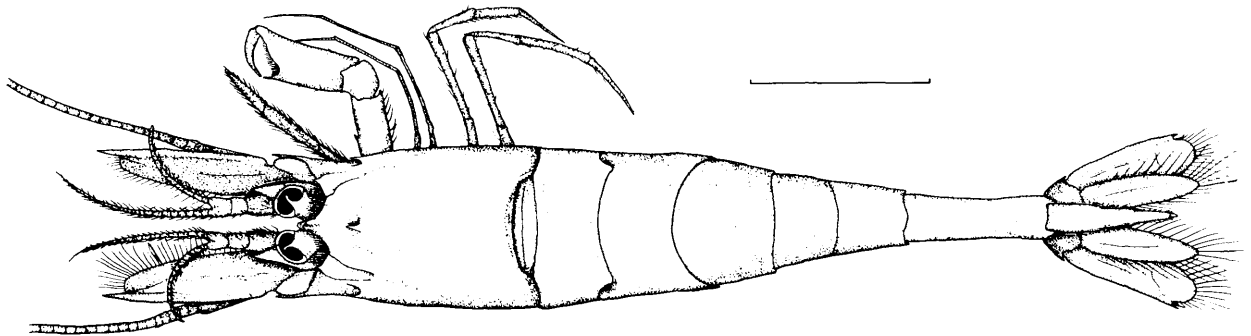


Fig. 112. *Crangon septemspinosa* Say. Ovigerous female in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

2 impressed lines, 1 originating in fissure in superior margin of orbit, another originating lateral to suborbital spine, both uniting above hepatic spine and disappearing posteriorly; broad groove below and anterior to hepatic spine. Eyes moderately developed. Antennular peduncle with basal article hollowed out above, stylocerite broad, cupped longitudinally forming portion of socket for reception of eye, tip reaching nearly to end of article; second article of peduncle slightly shorter than third; inner flagellum hairy below, a little longer than antennal scale, broadest in posterior half, lamella tapering to narrow rounded tip; lateral border slightly convex; well-developed lateral spine exceeding lamella and as long as distal width of blade. Third maxilliped reaching nearly to tip of antennule, hairy.

First legs strong, subchelate; hand less than 3.5 times as long as wide, palm with strong spine at distal end of finger; merus with small spine on lower margin. Second legs almost filiform; chela minute, hairy. Third legs stronger; fourth and fifth normal.

Abdomen, viewed dorsally, tapering from broad first and second segments to narrow sixth segment. Telson slender, tapering; with 4 small spines above on lateral border, first pair at $\frac{2}{3}$ length, second midway between these and acute tip; tip flanked by 3 pairs of movable spines, median pair longest and stoutest. Uropodal exopods with lateral border ending in spine flanked mesially by longer movable spine.

Measurements in mm.—Length of body: ovigerous females from North Carolina, 25 to 60; from Delaware: males 47; females 70 (Price 1962).

Color.—Ash-gray with numerous irregular, stel-

late, blackish-brown spots or speckled with gray, imitating the color of sand; color subject to considerable variation in shade, tail often darker (various authors).

Habitat.—Usually near bottom over sand: low-water mark to 90 m, rarely to 450 m.

Type-locality.—"Bay shores and inlets of the sea" [east coast of United States].

Known range.—Primarily subarctic-boreal (Haefner 1979) although extending beyond these limits; northern part of Gulf of St. Lawrence, doubtfully Baffin Bay (Squires 1965a) to east Florida; Arctic Alaska southward to Shumagin Islands, Alaska; Sea of Okhotsk; and Ranshima, Hokkaido, Japan.

Remarks.—A recent publication (Haefner 1979) so completely summarizes the extensive literature dealing with distribution, environmental tolerance, osmoregulation, pigmentation, reproduction, larval development, age and growth, habitat, distribution, parasites and disease, and commercial fishery for this species that an abridged review here is superfluous.

Genus *Pontophilus* Leach 1817

Kemp 1910:159.—Rathbun 1929:21.—Holthuis 1955:136.—China 1966:204.—L. H. Pequegnat 1970:112.—Couture and Trudel 1968:881.

Carapace usually with longitudinal dentate carinae; rostrum depressed. Second pair of legs chelate and very short, rarely reaching distal extremity of merus of first pair; dactyls of last 2 pairs flattened but not spatulate.

Key to Species

1. Carapace with dorsolateral suture extending from notched orbital margin to dorsal branchial region 2
Carapace lacking dorsolateral suture *P. gorei*
2. Tip of rostrum falling far short of distal edge of eyes *P. brevirostris*
Tip of rostrum reaching about to distal edge of eyes *P. norvegicus*

***Pontophilus brevirostris* Smith**

Fig. 113

Pontophilus brevirostris Smith 1881:435.—1882:35, pl. 7, figs. 1, 1b.—L. H. Pequegnat 1970:113.—Williams 1974c:14, fig. 37 (key).

Recognition characters.—A rather small species. Carapace with 3 spines on middorsal carina and frequently a smaller fourth one in front of anteriormost spine just behind base of rostrum; first lateral carina bearing 2 spines and often a rudimentary spine behind these; second lateral carina armed with single spine and not extending beyond midlength of carapace. Suborbital spine short and acute, antennal spine stronger and acute. Rostrum short, tridentate, median tooth slightly longer than laterals, falling far short of distal edge of cornea and not extending beyond suborbital spine. Antennular peduncle with basal article longer than second and third combined, second longer than broad; stylocerite acute, tip reaching nearly to distal margin of basal article. Antennal peduncle extending nearly to tip of antennal scale; latter concave laterally, distolateral spine equal to or slightly overreaching broad lamella.

First legs lacking spine on flexor margin of merus.

Abdomen with first 4 segments rounded dorsally; fifth somewhat flattened, with subdorsal carinae diverging slightly and below on each side another nearly parallel carina; sixth segment also flattened, subdorsally carinate. Telson usually sulcate, shorter than inner ramus of uropods.

Measurements in mm.—Length of body: male 37 (USNM), female 36 (Smith 1881).

Variation.—Occasionally there are only two spines on the middorsal carina.

Habitat.—13 to 426 m (L. H. Pequegnat 1970).

Type-localities.—Material described from a series of U. S. Fish Commission Stations (*Fish Hawk*) 865–867, 870–874, 877 and 878, 119 to 283 m, off Martha's Vineyard, Mass., constitutes the type-series (Smith 1881). In 1882, Smith essentially repeated the original description, gave locality data for specimens studied from Stations 314–315, 321, 327, 333, 344–345, and illustrated a mature female from Station 873, one of the stations listed in the original description. Two females from this lot, 40°02'N, 70°57'W, 183 m, are in the type collection of the USNM as are many syntypes from Stations 865–67, 871, and 872.

Known range.—Gulf of Maine to Gulf of Mexico off Dry Tortugas and Cuba (Williams and Wigley 1977; L. H. Pequegnat 1970).

Remarks.—There are ovigerous females in the USNM collection from off Chesapeake Bay in March, North Carolina and Florida in April and

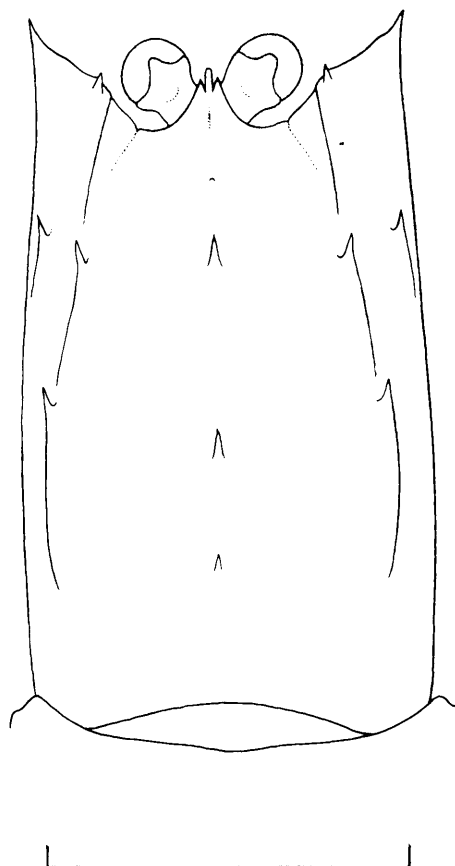


Fig. 113. *Pontophilus brevirostris* Smith. Carapace and eyes in dorsal view, 5 mm indicated (from Williams 1974c).

June, and off Martha's Vineyard and Long Island from June to September.

***Pontophilus gorei* Dardeau**

Fig. 114

Pontophilus gorei Dardeau 1980:563, figs. 1–4.

Recognition characters.—A tiny species. Carapace broad and slightly depressed, smooth; single strong, dorsomedial spine behind rostrum; suborbital spine dorsal and posterior to antennal spine from which faint longitudinal lateral carina extends posteriorly; pterygostomian spine strong and equal to or slightly exceeding distal edge of eye, minute spine posteroventral to it directed somewhat mesad. Rostrum extending slightly beyond distal edge of cornea, depressed, tip spatulate and laterally expanded, 2 blunt lateral spines. Eyes well developed, minute notch present on posterior orbital margin. Antennular peduncle shorter than flagella; stylocerite broad at base, anterior margin concave, distolateral acute tip reaching nearly to end of basal article; second article with minute distolateral spine, third article shorter than second.

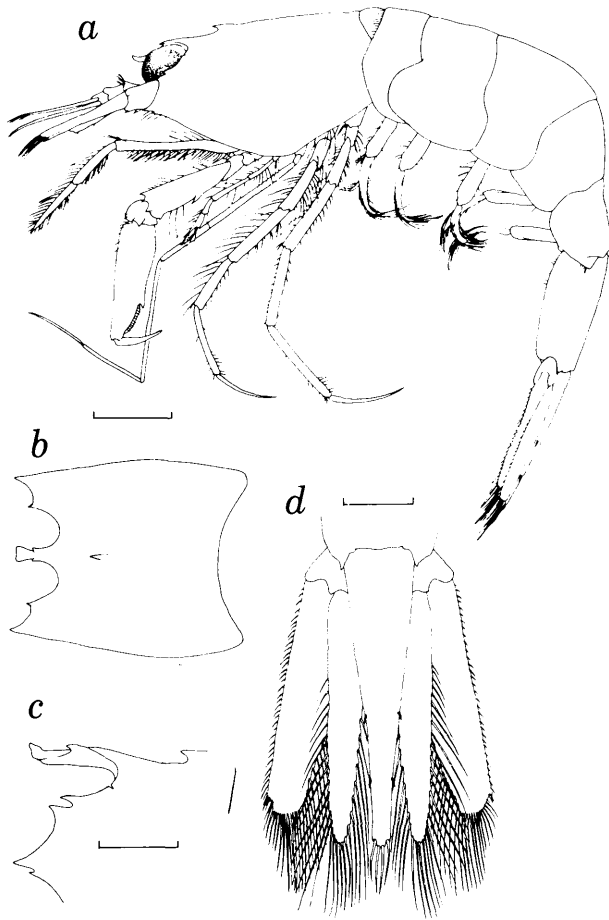


Fig. 114. *Pontophilus gorei* Dardeau. *a*, Female in lateral view; *b*, carapace in dorsal view; *c*, same, anterior in lateral view; *d*, telson and uropods; *a-b*, 1 mm, *c-d*, 0.5 mm indicated (from Dardeau 1980).

Antennal scale exceeding antennal peduncle, rather broad proximally, slightly concave laterally, lamella with somewhat rounded to slightly angled tip, reaching about same level as distolateral spine.

First leg with subchela $\frac{1}{3}$ as wide as long; strong spine on flexor margin of merus.

Abdomen smooth, tapered to narrow, elongate sixth segment; fifth segment with blunt posterolateral tooth. Telson narrow, longer than sixth segment; truncate tip bearing 3 pairs of spines, lateral pair minute; 2 pairs of lateral spines on distal half. Uropods long and narrow, inner slightly exceeding telson, outer shorter.

Measurements in mm.—Length of carapace: male 1.9, female 2.5 (Dardeau 1980).

Habitat.—Rarely 9, 37 to 182 m (Dardeau 1980).

Type-locality.—135 km due W Sanibel Island Light, [Fla.], 26°24'N, 83°22'W, 55 m.

Known range.—Off Georgia; off SW Florida, Cape San Blas and Padre Island, Tex.

Remarks.—Dardeau (1980) summarized all known

information on this species and compared it with other members of the genus.

Ovigerous females were reported from southwestern Florida in April, June, August, and October.

One specimen from off Padre Island, Tex., was taken from the stomach of a sea robin, *Prionotus rubio*.

Pontophilus norvegicus (M. Sars)

Fig. 115

Crangon norvegicus M. Sars 1861:248.

Pontophilus norvegicus.—M. Sars 1862:183.—1868: 242, pl. 1, figs. 1–25, pl. 2, figs. 17–37.—Kemp 1910:162, pl. 21, fig. 9*a-b*.—Rathbun 1929:21, fig. 26.—Squires 1965a:86.—Couture and Trudel 1968:881, fig. 21.—Williams 1974c, fig. 36 (key).—Smaldon 1979:109, figs. 41A, 48.

Recognition characters.—Carapace somewhat depressed, with 3 anteriorly directed spines on median dorsal carina, occasionally a small tubercle in front of first; 2 spines on anterior part of first lateral carina and 1 spine on second lateral carina in front of median anterior tooth; suborbital spine acute, antennal spine acute and strong. Rostrum extending to anterior margin of eyes, narrow and triangular with small anteriorly directed basal tooth at each side, slightly hollowed dorsally. Antennular peduncle with basal article longer than second and third combined, second longer than broad; stylocerite acute, tip reaching nearly to distal margin of basal article. Antennal peduncle extending beyond that of antennule but exceeded by antennal scale; latter concave laterally, distolateral spine not exceeding broad lamella.

First legs lacking spine on flexor margin of merus.

Abdomen with first 4 segments smooth, fifth with faint traces of posteriorly divergent carinae, sixth with 2 submedian carinae. Telson usually sulcate, shorter than inner ramus of uropods.

Measurements in mm.—Length of body: 80 (Rathbun 1929); male 55, female 76 (Wollebaek 1908). Squires (1965a) gave carapace length as: male 12, female 19.

Variation.—Small individuals have a relatively longer rostrum than adults and in some juveniles the posterior spine of the median and first lateral carina may be absent (Kemp 1910).

Color.—Carapace and abdomen pale dull reddish brown dorsally, often mottled and darkened on last three abdominal segments; carapace with two conspicuous oblique bands of white, traces of white on first two abdominal segments (Kemp 1910). Brown (Squires 1965a).

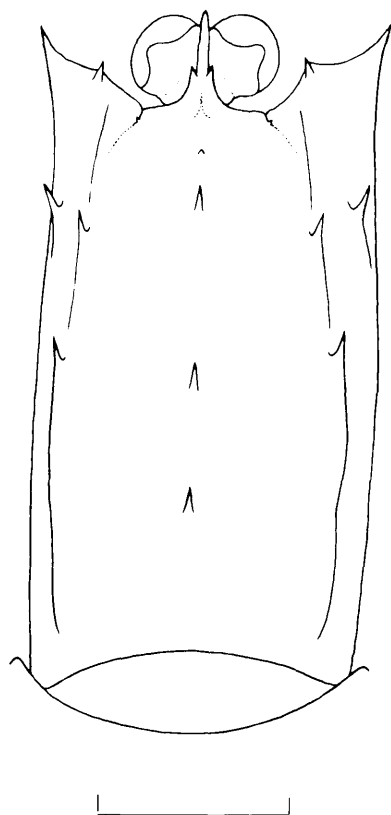


Fig. 115. *Pontophilus norvegicus* (M. Sars). Carapace and eyes in dorsal view, 5 mm indicated (from Williams 1974c).

Habitat.—Mud, sand, gravel and stones (Smith 1879), 50 to 1450 m (Sivertsen and Holthuis 1956) but usually 200 to 500 m (Smaldon 1979); never temperatures below 0°C (Heegaard 1941).

Type-locality.—Florøen (= Flora), Manger, and in Bundefjorden at Christiania [Oslo, Norway], 55 to 91 m.

Known range.—Greenland to Maryland and points southeast (38°41'N, 73°06'W) (Williams and Wigley

1977); Iceland; Spitsbergen; Murman coast and northwestern Europe including British Isles to Bay of Biscay; Balearic Islands (Forest 1965). The distribution was partly mapped by Heegaard (1941).

Remarks.—Wollebaek (1908) recorded ovigerous females off Norway from October to April, all females in spring having well-developed eggs. Larvae were found in surface layers from April on into summer. Sars (1890) described and illustrated the second larval stage, and Stephenson (1916, 1935) reported larvae from Greenland.

In the USNM crustacean collection, ovigerous females are known from southeast of Nantucket in July and off Martha's Vineyard and New York from August to November, and New York in February. Squires (1965a) remarked that about 90% of the females taken off Newfoundland and Labrador are ovigerous in autumn, first reaching maturity at about 10 mm carapace length, but that no ovigerous females were seen by him in June and July. Frost (1936) recorded larvae there in spring and fall.

Squires (1965a) found stomach contents to include phytobenthos, crustaceans, polychaetes and foraminiferans. The mandible was described.

Dahl (1944) reported an unusual occurrence of the rhizocephalan parasite *Sylon hippolytides* on *P. norvegicus* where it was attached to the mouth opening rather than as usual on the under surface of the abdomen.

Genus *Sabinea* Ross 1835

Rathbun 1929:22.—Holthuis 1955:133.—Hemming 1958b:160.—Couture and Trudel 1968:882.

Second legs short, simple, not chelate.

Key to Species

1. Rostrum with acute tip reaching beyond eyes; telson ending in acute tip flanked by 1 or 2 spines *S. sarsii*
- Rostrum with rounded tip scarcely exceeding eyes; telson with narrow but truncate tip bearing 8 or more spines or stout setae *S. septemcarinata*

Sabinea sarsii Smith

Fig. 116

Sabinea Sarsii Smith 1879:59, pl. 11, figs. 6–8.—1886:655 [51], pl. 10, figs. 3, 3a, 4.

Sabinea sarsii.—Rathbun 1929:22, fig. 29.—Couture and Trudel 1968:883, fig. 22b-c.—Williams 1974c:13, figs. 5A-B (key).

Recognition characters.—This species is generally similar to *S. septemcarinata* except in a few characters as follows: Carapace with dorsal carina sharper and its teeth somewhat more prominent and usually more numerous; lateral carinae distinct and rather regularly dentate. Rostrum with acute tip reaching beyond distal edge of eyes, its middorsal carina sharper and higher. Abdomen with pattern

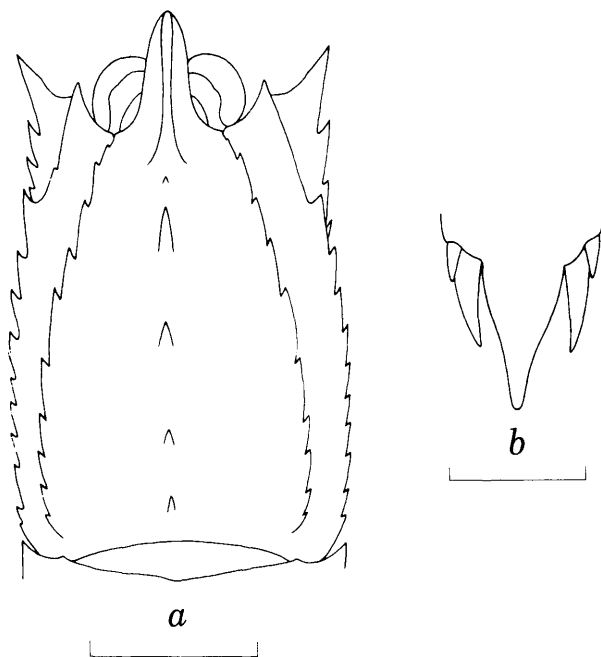


Fig. 116. *Sabinea sarsii* Smith. *a*, Carapace and eyes in dorsal view; *b*, tip of telson; *a*, 5 mm; *b*, 0.5 mm indicated (from Williams 1974c).

of sculpture more distinct. Telson ending in strong, acute tip flanked by 1 or 2 smaller spines; tip reaching to or slightly beyond inner ramus of uropods.

Measurements in mm.—Length of body: male 62 (Smith 1879), female 72 (Wollebaek 1908).

Variation.—In adults the telson terminates in an acute tip longer than its breadth at the base (separated from body of telson by an emargination at each side and from which an inner larger and outer smaller spine arise); in juveniles the tip may be triangular and flanked by three spines of nearly equal length on each side (Smith 1879).

Color.—Grayish brown (Squires 1965a).

Habitat.—Shells and sand, gravel, coarse gravel, stones and sponge (Smith 1879); -0.6° to 4.1°C (Squires 1965a), usually above 1.75°C (Blackler 1957); 48 to 710 m (Williams and Wigley 1977).

Type-localities.—Smith described a syntypic series from: Georges Bank, 110 m; Gulf of Maine, about ESE from Cape Sable, Nova Scotia, $42^{\circ}40'\text{N}$, $66^{\circ}58'\text{W}$, 205 m; Le Have Bank, $42^{\circ}44'\text{N}$, $64^{\circ}36'\text{W}$, 110 m (female USNM 39950); and Lofoten Islands, coast of Norway.

Known range.—Davis Strait to ESE Nantucket ($40^{\circ}01'\text{N}$, $65^{\circ}53'\text{W}$); Iceland; N Europe. The distribution was mapped by Stephensen (1935).

Remarks.—Squires (1965a) observed egg laying in late summer and fall in the western North Atlantic, with hatching in spring. Ovigerous females in the USNM collection are from Georges Bank in

autumn. Wollebaek (1908) reported females from the Barents Sea with partly filled ovaries in July and ovigerous females in the first half of September; Dons (1915) reported the latter from Norway in April, July and August. G. O. Sars (1890) described a very young stage in development.

Stephensen (1935) found *S. sarsii* north to about 60° latitude in Greenland but stated that it is a boreal species and is rare under arctic conditions. Christiansen and Christiansen (1962) found it rare in Isfjorden, Spitsbergen, but Blackler (1957) stated that it was numerous.

Stomach contents have included amphipod and copepod fragments, polychaetes and phytobenthos (Squires 1965a).

Fontaine (1977a) described a relationship in the northwestern Atlantic between the prosobranch gastropod, *Lora cancellata cancellata*, and female *Sabinea sarsii* (27.3% of those ovigerous examined) and *S. septemcarinata* (4.8%, same) which bear ootheca of the snail on the second sternite of the abdomen under the egg mass. Eggs of the shrimp and mollusc have synchronous growth; at hatching time young molluscs are fully developed in the ootheca. This relationship is judged to be a non-parasitic association for transportation, but presence of the egg capsules reduces egg number in the shrimp. The association was not observed on *Pontophilus norvegicus*, *Sclerocrangon boreas* or *ferox*, *Sabinea hystrix*, or *Argis dentata*, although an analogous association involving *Argis lar* was reported from the Chukchi Sea (McCauley 1964).

Sabinea septemcarinata (Sabine)

Fig. 117

Crangon Septemcarinatus Sabine 1824:ccxxxvi, pl. 2, figs. 11–13.—Hemming 1958c:141.

Sabinea septemcarinata.—Ross 1835:1xxxii.—Smith 1879:57, pl. 11, figs. 5, 9–13.—Rathbun 1929:22, fig. 28a-c.—Couture and Trudel 1968:882, fig. 22a.—Williams 1974c:13, figs. 34A-B (key).

Recognition characters.—Carapace with median carina and 3 lateral carinae on each side, all variously toothed; median carina with up to 5 moderate teeth, anteriormost minute, second to fourth about equal, fifth smaller and near posterior margin, sometimes missing in smaller individuals; first lateral carina distinct and irregularly dentate posteriorly, but obscurely toothed on anterior $\frac{1}{3}$; second laterals terminating in short tooth at outer angle of orbit, but not distinctly dentate near anterior margin of carapace; third laterals strongly dentate anteriorly but armature becoming small or obso-

lete posteriorly. Rostrum tongue shaped, nearly horizontal, and bearing median dorsal carina most prominent near rounded tip; scarcely exceeding distal edge of eyes. Antennules and antennae with flagella relatively longer in males than in females; stylocerite broad and ending in strong, acute tip.

Abdomen with middorsal carina doubled on first segment and with 2 laterals on each side, second lateral ending in small, acute tooth on anterior margin; fifth segment similarly ridged but with second lateral carina obsolescent. Telson subtruncate, tip narrower in male than in female, armed with even number of spines or stout setae, 8 to about 14 (subject to wear); tip usually falling short of inner ramus of uropods.

Measurements in mm.—Length of body: male 45 (Smith 1879), ovigerous female 37–90 (Wollebaek 1908). “Length four inches” (Sabine 1824).

Color.—Varied red and white above, white beneath (Sabine 1824). Light brown, slightly darker or more reddish brown than *S. sarsii* (Squires 1965a). Dorsally with fuzzy edged brown spots resembling tufts of moss and a few yellowish green spots; under surface light with few red and reddish-orange spots, especially on legs; eyes green (MacGinitie 1955).

Habitat.—An arctic species (Stephensen 1935), usually in water below 1.5°C (Blacker 1957); occurs on a variety of substrates but most common on mud or mud mixed with small stones, shells, gravel and sand; 0–10 to 406 m, but most frequent from 80 to 200 m (Heegaard 1941; Christiansen and Christiansen 1962).

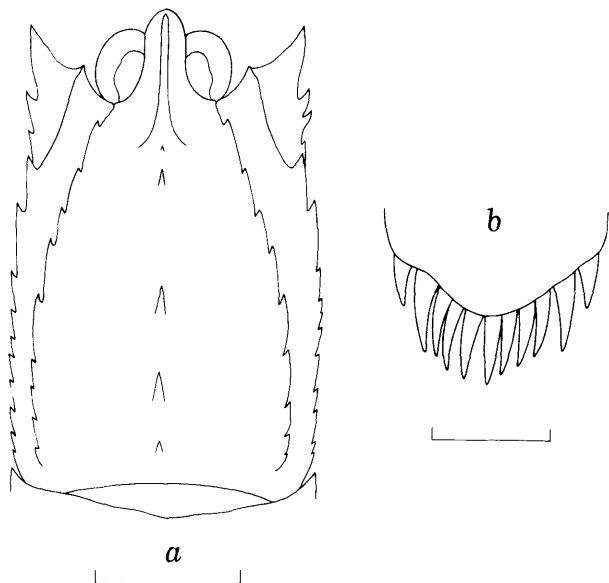


Fig. 117. *Sabinea septemcarinata* Sabine. a, Carapace and eyes in dorsal view; b, tip of telson; a, 5 mm; b, 0.5 mm indicated (from Williams 1974c).

Type-locality.—West coast of Davis Strait.

Known range.—Arctic Canada and Alaska to Point Barrow and Chukchi Sea (Makarov 1941); Greenland southward along eastern Canada to Massachusetts Bay; Iceland (except south coast); north of Faroes; Norway from 67°N through Barents Sea, White Sea, Kara Sea, and eastward to Wrangel Island (summary in Christiansen and Christiansen 1962, and mapped by Heegaard 1941).

Remarks.—Christiansen and Christiansen (1962) remarked that *S. septemcarinata* and *Sclerocrangon boreas* are the only decapods able to live on the soft mud near glaciers in the Arctic. They found ovigerous females at Isfjorden, Spitsbergen, from early July to early August. Heegaard (1941) stated that the females are ovigerous throughout the year, although he discussed differences of opinion regarding the spawning season. In the USNM collection they are present from Franz Joseph Land in June, and off Massachusetts and Nova Scotia from July to September. MacGinitie (1955) reported them from Point Barrow in September. Squires (1965a) found the breeding cycle to vary among populations, some larvae hatching in May–June, others in October, but he regarded egg laying as annual. In Hudson Bay (1967) he thought only 46% of females were potentially ovigerous each year, although numbers in the samples were small. Around the Queen Elizabeth Islands he (1968) found ovigerous females in July and August where 72% were thought to be potentially ovigerous annually. Maturity of gonads was considered to be an indication of cold adaptation. In his view, percent of females potentially ovigerous annually will indicate whether or not individuals of a population are under stress because of prevailing low temperatures. Of shrimp species taken in arctic waters, only five (*Eualus gaimardii*, *Spirontocaris phippisii*, *Lebbeus groenlandicus*, *Sabinea septemcarinata*, and *Sclerocrangon boreas*) provided numbers sufficient (but low) for assessment. These appeared to have good adaptation to low temperature and long arctic winters since most mature individuals appeared to spawn annually for the two or three times they probably spawn in a lifetime.

Sars (1890) described and illustrated the first and last larval stages of *S. septemcarinata*, and Stephenson (1916) described and illustrated an early juvenile stage which may be ascribed to this species (Stephenson 1935). Frost (1936) reported larvae in spring around Newfoundland and off Labrador.

Stomach contents consist of phytobenthos and detritus, polychaetes, crustaceans including euphausiids and amphipods, foraminiferans and hydroids, with some change in proportion in different areas. The shrimp was taken from stomachs of

beluga whales in southeastern Hudson Bay (Squires 1967).

Genus *Sclerocrangon* Sars 1883

Sars 1885:14.—Kemp 1910:139.—Rathbun 1929:20.—Holthuis 1955:136.—Hemming 1958b:161.

Zarenkov (1965), in restricting *Sclerocrangon*, erected three new genera to receive certain species of the genus that were included up to that time, the new treatment reflecting adaptations to burrowing, increase in body size, change in fecundity, egg size, and mode of larval development. Makarov (1968) amplified some of these conclusions with special reference to larval development, and Butler (1980) discussed other characters of the new genera.

Sclerocrangon boreas (Phipps)

Fig. 118

Cancer boreas Phipps 1774:190, pl. 12, fig. 1.

Crangon Boreas.—Sabine 1824:ccxxxv.

Sclerocrangon boreas Sars 1885:15.—Rathbun 1904:133.—1939:20.—Squires 1957:477, figs. 1A, B.—Couture and Trudel 1968:880, fig. 19.

Recognition characters.—Occurring in 2 forms in western Atlantic, a shallow water and a deep water-arctic form differing somewhat in sculpture and armature, see "Variation." Integument sculptured, rugose and hairy. Rostrum rather broad, exceed-

ing eyes; tip acute to acuminate and with subterminal, median ventral projection; low median dorsal carina nearly continuous with middorsal carina of carapace bearing usually 3 teeth, middle one sometimes doubled, higher and thinner in juveniles; thickened edges of rostrum continuous with orbital margin and raised posterior margin of cephalic groove, and in turn with prominent lateral carina on each side; obsolescent longitudinal ridges above and below lateral carina. Hepatic spine present. Anterior margin with small, acute suborbital spine; prominent antennal spine long, wide-spread, bent somewhat mesially and barely exceeding rostrum; small pterygostomian spine hidden beneath. Stylocerite broad, truncate anteriorly but with distolateral spine. Antennal scale about twice as long as wide, convex laterally, rounded lamella exceeding distolateral spine.

Subchela more than twice as long as wide, distal margin obliquely transverse, spine obliquely longitudinal; merus with upper distal spine, carpus with lower distal spine.

Abdomen with median carina on first 5 segments, that on sixth doubled; dorsal tubercle on first segment variably produced forward; pleura each with 1 or more spines. Telson sulcate; 2 pairs of lateral spinules on terminal half, acuminate tip exceeding movable spine at each distolateral corner.

Measurements in mm.—Length of body: male 78; female 114 (USNM); that given by Rathbun (1929) as 120 is probably a female.

Variation.—Squires (1957) remarked that specimens from Ungava Bay differed considerably from the description given by Rathbun (1929) and from specimens found by him in shallow waters around Newfoundland, although those from deeper water there correspond with the Ungava material. In the form with a double middle dorsal tooth, the posterior member of the pair is reduced. The two forms were considered to be variants of the same species and were compared in illustrations and a table. His specimens (1965a) from deep water were larger than those from shallower depths.

Color.—Bright red marked with spots of reddish brown (Rathbun 1929). Brown (Squires 1965a). Brown and tan with few flecks of chalky white, green and yellow; eggs orange (MacGinitie 1955).

Habitat.—Arctic-boreal (various authors) on a variety of bottoms from fine mud to rock (Heegaard 1941; Blacker 1957; Christiansen and Christiansen 1962), often among *Balanus*; shore to 280 m (Wollebaek 1908).

Type-locality.—Near coast of Spitsbergen (in stomach of seal).

Known range.—East and west Greenland south to Cape Cod and SE of Nantucket (40°16'N,

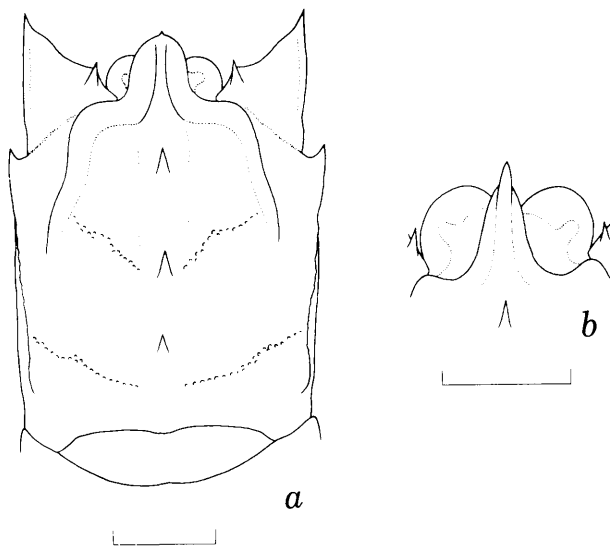


Fig. 118. *Sclerocrangon boreas* (Phipps). a, Carapace and eyes of adult in dorsal view; b, rostrum and eyes of juvenile; a, 5 mm; b, 2.5 mm indicated (from Williams 1974c).

67°26'W, Williams and Wigley 1977); arctic Canada and N coast of Alaska, Chukchi Sea (Makarov 1941) south to British Columbia (Butler 1956); Iceland excluding south coast; Faroes; Norway N of approximately 67°N and northward and eastward to Spitsbergen, Franz Joseph Land, Novaya Zemlya, White and Kara seas. The distribution is well mapped by Heegaard (1941).

Remarks.—MacGinitie (1955) regarded *S. boreas* as the most abundant large shrimp at Point Barrow, Alaska. He found ovigerous females there in September, sometimes washed ashore, bearing eyed embryos. Christiansen and Christiansen (1962) found ovigerous females in July at Isfjorden, Spitsbergen, among fairly abundant catches of the species and Blacker (1957) reported them in that area from May to October. Ovigerous females in the USNM collection are from from the Bering Sea in June, northwestern Greenland (see also Stephensen 1935), Alaskan panhandle and, Prince Edward Island, Canada, in August, and off Cape Cod in September. Squires (1965a) found about 65% of females from Foxe Basin and Labrador to be potentially ovigerous in late autumn, and they appeared to mature late at a carapace length of about 23 mm (~75 mm tl). In the Queen Elizabeth Islands (1968) 85% were potentially ovigerous in July and August. He considered that females spawn annually in these areas during their reproductive period, evidence that they are well adapted to reproduce in cold water.

The eggs are large (2.6–2.85 mm dia.), rather few in number, having been counted as up to 488 per female, and from all published accounts undergo an almost direct development (Heegaard 1941; Makarov 1967, 1968). In the latter paper, Makarov reviewed older work on the larval development obtained from embryos and added new data on development from work carried out in the Sea of Okhotsk. He described and illustrated two larval stages, both advanced, concluding that the younger is brief, representing the first stage after hatching, and that the second is a longer-lived postlarval stage. Neither stage is pelagic or free living, being passed under the abdomen of the female. The larvae are tightly covered by the pleopods of the female and cling with hooked dactyls on their fourth and fifth legs to one another, the egg shells and strings during the first stage, and with their chelae during the second stage. Seldom are they found dislodged in plankton.

Squires (1957, 1965a, 1967) reported *S. boreas* to be preyed upon by cod (*Gadus morhua*), the longhorn sculpin (*Myoxocephalus octodecimspinosus*), ringed, bearded and harbor seals, and the beluga whale. Food in stomachs of the shrimps was phy-

tobenthos, polychaetes, crustacean fragments (gammarid amphipods, ostracods, isopods and copepods), small pelecypod shells, ophiuroids, sponge spicules and foraminiferans. The mandibles were described.

The species at Point Barrow occasionally harbors a small clam, *Hiatella arctica*, under spines of the carapace, and bears egg capsules of the leech, *Crangonobdella murmanica*, on the pleopods (MacGinitie 1955).

Infraorder Astacidea

Superfamily Nephropoidea

Family Nephropidae

Eyes well developed or reduced, always present as movable appendages. Telson with lateral and/or posterolateral spines. Chelipeds equal or unequal, but fingers always considerably less than twice as long as palm; teeth on cutting edges placed in one plane. Fifth leg without true chela. Abdominal pleura large, triangular or ovate, usually ending in a point. Antennal scale, if present, with inner margin evenly curved, unarmed.

Holthuis (1974) amplified this general definition, that essentially covers the key characters, with great detail concerning the pattern of grooves, ridges, spines and teeth on the carapace, structure of the eyes, mouthparts, sternal armature, abdomen, pleopods, uropods, telson, and branchial formula.

Subfamily Nephropinae

Rostrum dorsoventrally depressed, with lateral and sometimes ventral (but no dorsal) teeth. Carapace without branchiostegal spine, but distinct postorbital spine, other spinules may be present. Body may be granulate. Lateral margin of telson with at most 3 small spines. Antennal scale present. Sternites of second to fifth abdominal segments each with sharp median spine in male. (From Holthuis 1974.)

Genus *Homarus* Weber 1795

Holthuis 1974:815.

Paraphrasing Holthuis (1974:815, including fig. 24): Essentially smooth, chelate lobster. Rostrum bearing lateral and sometimes ventral teeth. Carapace with postorbital and antennal spines present; distinct median dorsal groove extending from rostrum to posterior margin, subdorsal carinae low. A

set of other connecting grooves as follows: post-cervical distinct in upper part, lower part faint and almost entirely replaced there by intercervical connecting with cervical; urogastric, cervical and antennal distinct; gastroorbital and hepatic obscure. Thoracic sternum narrow; sternites between first to third legs with narrow single or double median or submedian ridges; that between fourth legs with 2 posteriorly divergent ridges in male, bearing sperm receptacle in female.

Chelipeds prominent, rather smooth and asymmetrical; major crusher with gaping fingers and molariform teeth in addition to smaller teeth; minor cutter without gape, cutting edges straight and armed with numerous nearly uniform small denticles, larger teeth if present neither molariform nor on cutting edge.

Abdomen smooth, no carina separating tergites from pleura. Telson narrowing posteriorly to convex terminal margin, short transverse proximal ridge and pair of posterolateral spines present. Exopods of uropods with transverse suture. Sternites of second to fifth segments with median spine in male, spines usually absent or greatly reduced in female. Male with first pleopods modified into rigid copulatory stylets.

The fossil record for the Nephropidae ranges back to the mid-Jurassic, and that of *Homarus* to the Cretaceous of North America and Europe (Glaessner 1969).

***Homarus americanus* H. Milne Edwards**

(American lobster)

Fig. 119

Homarus americanus H. Milne Edwards 1837:334.—
Holthuis 1974:818.

Recognition characters.—This species is distinguished by generic characters.

Measurements in cm.—Total length, rostrum to end of telson: large male 64.3, female 61, but both usually much smaller (Wolff 1978).

Habitat.—Cool to cold temperate waters, shore to 480 m, usually found between 4 and 50 m (Holthuis 1974).

Type-locality.—Long Branch, New Jersey.

Known range.—Strait of Belle Isle, Newfoundland, to Cape Hatteras, N. C., and occasionally southward as far as off Rich Inlet, ENE Wilmington, N. C. (Holthuis 1974; Williams and Williams, 1981).

Remarks.—The American lobster has been the subject of such extensive study and reportage in the literature that attempt to summarize this information here seems an inadequate endeavor. The classic monographs of Herrick (1896, 1911) gave an exhaustive treatment of reproduction, embryology, larval and postlarval development, molting and growth, autotomy and regeneration, size, integumental glands and sense organs, variation in color and structure, structure of reproductive organs, predators, parasites and disease, ecology, and an extensive list of references.

Other bibliographies have been prepared by Everett (1972) who summarized fishing methods along with cited references, Lewis (1970) who compiled references on the genus *Homarus*, and Logan (1975) who reviewed literature concerning energy and physiology.

Holthuis (1974) provided a compendium of taxonomic and descriptive information on members of the superfamily Nephropoidea in the Atlantic Ocean. Phillips and Cobb (1977), and Cobb and Phillips (1980) edited a set of papers on lobsters, including *H. americanus*, that are not singled out here but which summarize much that is known of the group on molting and growth, sensory physiology, habitat and behavior, comparative studies on larvae, and comparative ecology among genera of nephropids.

Excellent general accounts of life history, ecology, fisheries and culture were provided by Cobb (1976), Dexter (1952), Scott (1973), Taylor (1975, general reading), Templeman (1966), and Wilder (1954); most of these papers provide further references.

Selected recent papers have treated: economic analysis of the lobster fishery and its response to environmental and other pressures (Bell and Fullenbaum 1975; Dow 1977); movements, migration and growth (Cooper and Uzmann 1971; Hughes and Mathiessen 1962; Uzmann, et al. 1977); mating (Templeman 1934; Bliss 1968); fecundity (Saila, et al. 1969); incubation (Branford 1978); larval and juvenile survival in culture (Sastry and Zeitlin-Hale 1977); comparative studies on growth and temperature tolerance (Gruffydd, et al. 1975); morphogenesis of larval mouthparts (Factor 1978); control of crusher-cutter development in juveniles (Lang, et al. 1978); genetic similarity of eastern and western Atlantic species of *Homarus*, with evidence for geologic age of divergence (Hedgecock, et al. 1977); and trophic relationships of *H. americanus* (Evans and Mann 1976; Breen and Mann 1976; Mann 1973).

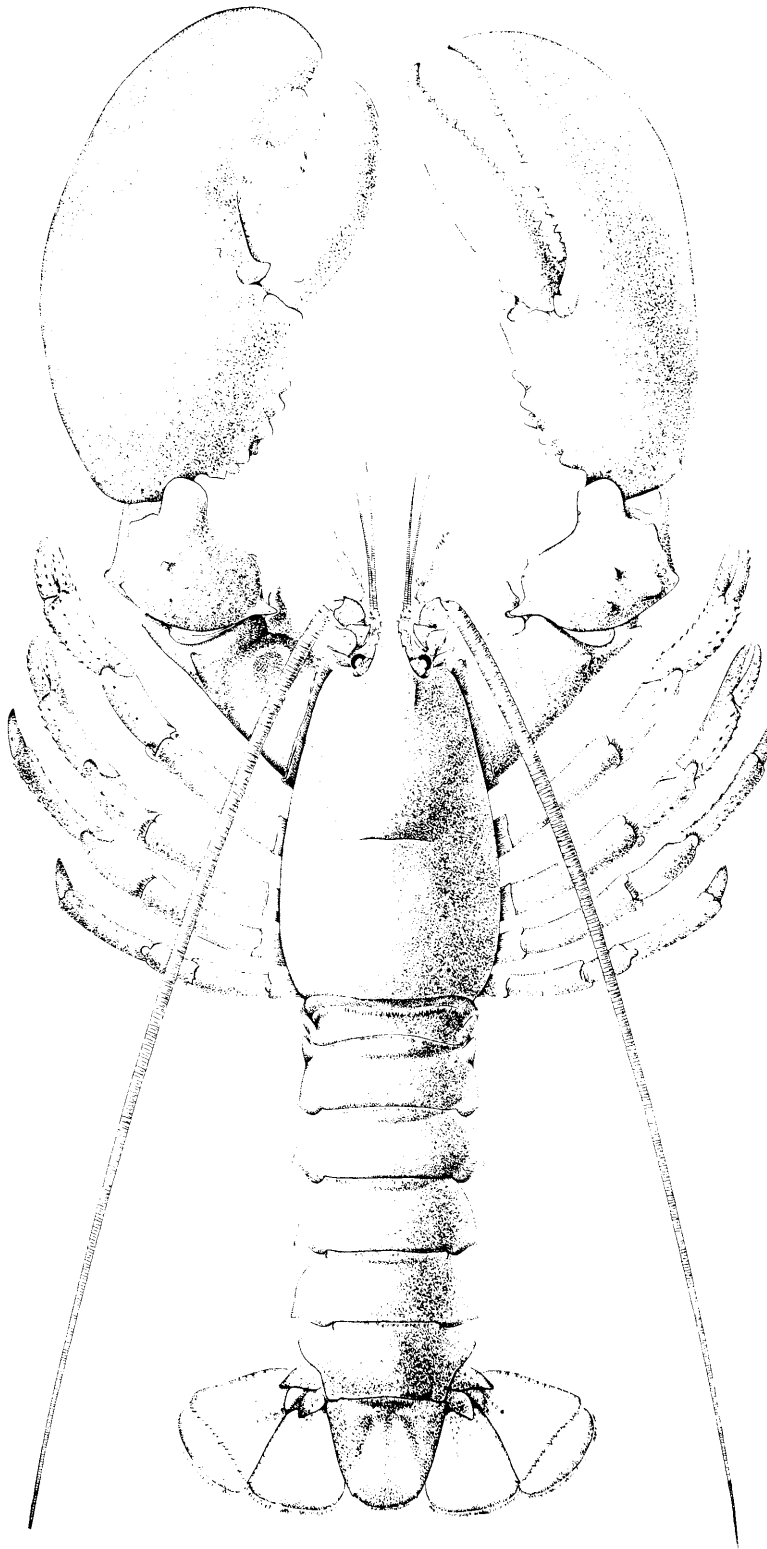


Fig. 119. *Homarus americanus* H. Milne Edwards. Male in dorsal view, much below natural size (from original by J. H. Emerton, specimen from Eastport, Maine, R. Rathbun 1884).

Infraorder Palinura

Carapace cylindrical or dorsoventrally depressed, without prominent rostrum but commonly spinose, fused laterally with epistome; antennal peduncle with 5 articles; third maxilliped pediform; abdomen well developed. (Adapted from Glaessner 1969.)

Superfamily Palinuroidea

First article of antennule fused with epistome. Antennal scale absent. All legs nearly equal in length and none chelate except subchelate last pair in females. First abdominal segment without pleopods; tail fan divided into soft membranous and striated posterior and harder anterior parts.

Family Palinuridae

Carapace subcylindrical. Eyes not enclosed in separate orbits formed by edge of carapace. Antennae not flattened but furnished with large, long, rather rigid, multiarticulate, usually spinose flagellum.

The fossil record for the family Palinuridae extends back to the Cretaceous in North America (Rathbun 1926, 1935).

Genus *Panulirus* White 1847

White 1847b:69.—Hemming 1958b:174.

Panulirus argus (Latreille)

(Spiny lobster, crawfish)

Fig. 120

Palinurus argus Latreille 1804:393.

Panulirus argus.—White 1847b:69.—Hay and Shore 1918:398, pl. 28, fig. 3.—Crawford and deSmidt 1922:291, figs. 265–271.—Schmitt 1935a:172, fig. 36.—Williams 1965:91, fig. 73.

Recognition characters.—Carapace covered with strong spines arranged more or less in regular longitudinal rows; spines above orbits very large, compressed, and curved upward and forward. Eyes large and prominent. Antennules nearly $\frac{2}{3}$ length of body; peduncles slightly exceeding antennal peduncle; outer flagellum shorter and thicker than inner, and strongly ciliated distally. Antennal segment with pair of spines in front, weaker pair about halfway to eye, strong median spine and weaker spines below insertion of antennules. Antennae very

large, heavy, exceeding body by more than length of carapace; peduncle with numerous strong spines; flagellum stout, stiff, line of cilia along inner margin and ringed with spines at intervals.

Legs rather weak, tips acute and bristly; female possessing small subchela on fifth legs with concave opposed surface formed between distal portion of propodus and proximal portion of dactyl.

Abdomen smooth, each segment crossed by furrow more or less distinctly interrupted at middle; pleural angles each produced into strong, sharp, backwardly directed tooth deeply notched and serrated on posterior margin. Pleopods absent from first segment of abdomen; exopod of pleopods broad, laminate; endopods missing in males, females with endopods of second pleopods laminate, last 3 endopods bifurcated. Proximal division of telson with rather strong spines; distal division with weak spines and setae in longitudinal lines. Uropods hard proximally, membranous distally; basal article bispinose, row of denticles along margin of hard part, and lines of minute spines and setae on upper surface of membranous part.

Measurements in cm.—Length of body from orbit to tip of telson: to approximately 45 (18 inches), occasionally larger.

Variation.—Aside from individual variations which will not be discussed here, the species exhibits marked allometric change with age as well as sexual dimorphism. These features, discussed in detail by Crawford and deSmidt (1922), are summarized here. Antennae of the young are longer in proportion to the body than in adults. Setae present on the young disappear in the adult and the sharpness of spines on the body tends to diminish with age, except for those on anterior portions of the carapace.

As pointed out in the description, only the females have chelate fifth legs. In adult males, the second pair of legs is extraordinarily developed. They are long, rarely used in walking, and the dactyl is long, curved, and provided with a brush of setae. The length of the dactyl, its curvature and setation increase with age. Sexual differences in the pleopods are given in the description.

Males have a relatively more inflated and longer carapace than females. Conversely, in females the abdomen represents a greater proportion of total length of the body than in males. Maximum lengths of the two sexes, however, are about the same (Creaser 1952). The posterior margin of the sternum in males is narrower than the comparable structure in females and the sternum is longer.

Color.—Coloration largely separable into two groups, (1) lightly colored individuals ranging from light gray and tan to shades of green and light

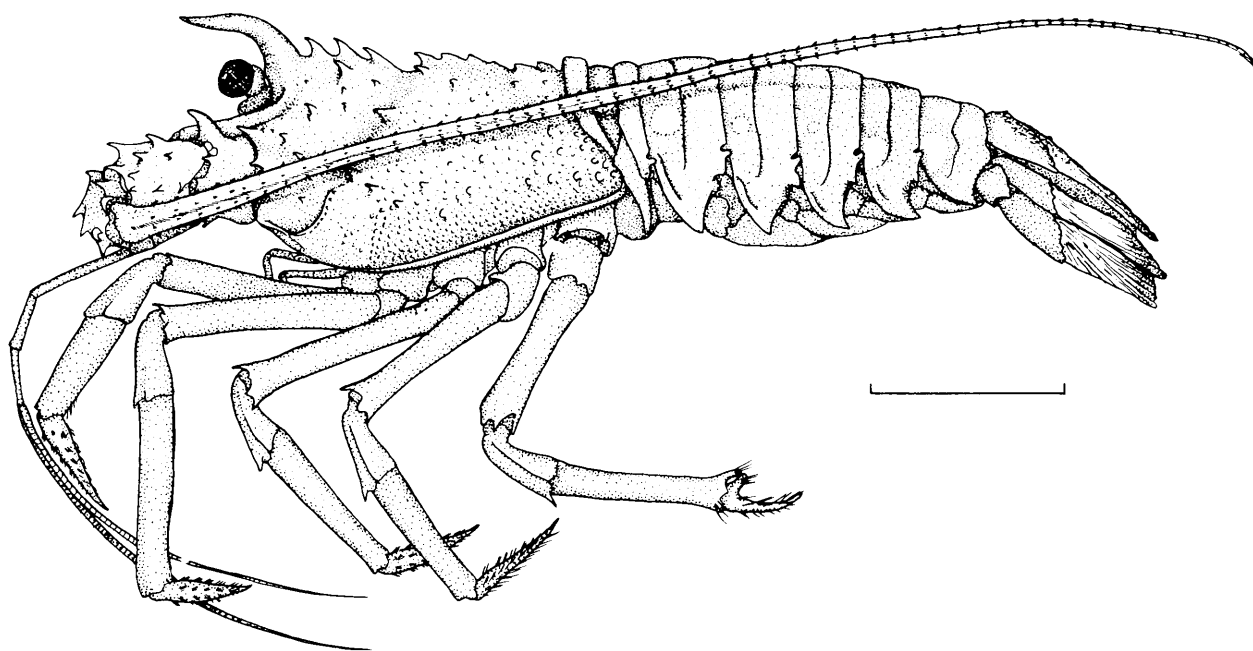


Fig. 120. *Panulirus argus* (Latreille). Female in lateral view, approx. 5 cm indicated (from Williams 1965).

brown, and (2) darkly colored individuals varying from shades of red to deep brown and blue. Abdomen spotted with yellowish ocelli; posterior margin of each segment edged with yellow or orange, lower angles of segments marked with bluish or greenish tints and sometimes additional colors. Tail fan crossed by bands of orange, yellow, and black, fringed with white. Pleopods usually orange, about half of surface covered by a black blotch. Legs striped longitudinally with blue. Ventral surfaces of body light yellow; thoracic sternum marked with irregular radiating stripes.

Young with coloration of carapace arranged in transverse bands, usually three, middle one dark; antennae frequently ringed with alternate light and dark bands; legs ringed with blue (Crawford and deSmidt 1922).

Habitat.—On reefs or among rocks, among growths of sponges or other objects which afford protection or places of concealment; low-tide mark to depths of about 91 m. Experimentally, lobsters at Bermuda have withstood depths of 457 m (Creaser and Travis 1950). Lobsters tend to aggregate in dens.

Type-locality.—Erroneously given as East Indies ("des Grandes-Indies").

Known range.—North Carolina through Gulf of Mexico and West Indies to Rio de Janeiro, Brazil; Bermuda.

Remarks.—A number of papers have been published concerning the general ecology of *Panulirus argus*. Only a selective summary of this work can be given here. The most comprehensive single

general treatment is that of Crawford and deSmidt (1922) for the species in Florida, but substantial additions to this work have been given by Berrill (1975), Clifton, et al. (1970), Dawson (1949, 1954), Dawson and Idyll (1951), Herrnkind (1969, 1970, 1975), Herrnkind and McLean (1971), Joyce (1974), Lewis (1951), Lewis, et al. (1952), Marshall (1948), and Smith (1951). Biological notes on the species in Cuba were given by Buesa Mas (1961) and in Puerto Rico by Mattox (1952). Creaser (1950, 1952), Creaser and Travis (1950), and Sutcliffe (1952, 1953, 1957) discussed the species in Bermuda. Alves and Paiva (1976), Paiva (1971, 1973, 1976), Paiva and Pitombeira (1962), Paiva and Saraiva da Costa (1971), and Santos and Correa Ivo (1973) discussed biology and fisheries in northeastern Brazil, and Squires and Riveros (1978) discussed fishery biology of the species off Colombia. Finally, in a series of review articles, Labisky, et al., Lyons, Menzies and Kerrigan, and Simmons (1980) gave a history of the Florida spiny lobster fishery and the lobster resource, and a general summary of larval development and recruitment.

North Carolina must be regarded as the extreme northern edge of the range of this species. Concentrations of the species large enough to be exploited commercially occur in southern Florida, the Caribbean and West Indies southeast to northeastern Brazil, and at Bermuda. A population may exist in deep water in the northern Gulf of Mexico (Moore 1962). Differences in growth rate and breeding habits may exist among these areas.

Panulirus argus grows to a large size. In its first

year of life it reaches a length of about 5 cm (measurements of this species often given in inches in U.S.A.) and, though growth in the young individuals is more rapid than in older animals, increments in length after that time are about 2.5 cm a year. Adults of 41 cm length are approximately 16 years of age, the males attaining somewhat greater length than females.

After juvenile stages are past, molts average about 2 ½ times per year, occurring most frequently from March to July and from December to February, at least in the Florida area. Among captive animals, molts without growth can occur. About 12 days elapse from the first sign of molting until the new exoskeleton is hard enough to resist denting, though hardening of the new shell is not complete until the 28th day. Travis (1954, 1955a, 1955b, 1957) gave an exhaustive study of the molting process among spiny lobsters near the age of sexual maturity. This work is beyond the scope of the present summary, but her findings show that molting among captive adolescent animals is largely confined to the warmer months at Bermuda and is more frequent than among Florida specimens. Other evidence shows that growth of the young is more rapid in Bermuda than in Florida, and that sexual maturity is reached sooner.

The mating season in Florida was formerly judged to extend from March through July but evidence now indicates that it is more extended. Buesa Mas (1961) reported mating in June and November in Cuba. Sexual maturity is reached in females as small as 15 cm long, but ovigerous females under 20 cm in length are rare. Mating pairs are judged to be about the same age, and mating usually occurs in the hardshell state. At the time of mating the male places a waxy spermatophore on the thoracic sternum of the female. Prior to spawning, the female scratches the surface of this packet with the chelate fifth legs. The actual egg laying is accomplished in about one-half hour, during which the female lies partially on her back forming a trough of the underside of her abdomen with the aid of the exopods of the pleopods. Eggs extruded from the oviducts pass backward from the bases of the third legs over the spermatophore and become attached to the endopods of the last three pairs of pleopods. After spawning, the spermatophore appears eroded as if enzymatic action had partially destroyed it. The eggs hatch in about one month. A second mating and egg laying may occur about a week after the hatch of the first batch and at this time the ovary is spent and the spermatophore almost completely eroded away. Molting of females during this season occurs only after spawning.

Direct evidence from the studies in Bermuda

shows that females may lay eggs twice in a season. The number of eggs laid depends on the size of the individual, and the second brood is smaller than the first. Estimates show that a 23-cm female can lay 500,000 eggs, a 30-cm female 1,118,656, a 38-cm female 2,566,916. A second laying by a 33-cm female consisted of 1,008,788 eggs. Thus, it is estimated that a 38-cm female might lay 4 million eggs a season. Buesa Mas (1961) found that 93% of ovigerous females in Cuba exceed 18 cm total length. At Dry Tortugas, Davis (1975) found the smallest ovigerous females (cl 78 mm) to be larger than the 45 mm reported by Smith (1951) but comparable to minima given by other workers for Bahama Bank (74 mm) Bermuda (85–90 mm), Panama (69 mm) and Antigua (80–90 mm). He also found, contrary to Creaser's figures for Bermuda (1950), that reproductive activity tends to decline in females larger than 125 mm cl, and other workers have agreed.

Kanciruk and Herrnkind (1976) found that reproductive activity is greater in deeper water than in shallows. At Bimini in autumn males exceed females in size for a given depth, but females outnumber the males in the deeper range: 16–19 m, 54.8% female; 20–25 m, 65.2% female; 60% of the latter showed recent reproductive activity. The authors estimated 3.7 molt cycles per year for females of 87.4 mm cl (\bar{x}), and on this basis the animals spent 6–9 days with whole spermatophores before oviposition, 20–30 days with eggs, 38–56 days without eggs but with eroded spermatophores, for a total of 84–125 days exclusive of the days following molt before mating. In Puerto Rico, the spawning season may be similar to that in Florida, for 22% of females in the commercial catch are ovigerous in September and 18% in October.

In Bermuda and elsewhere, there is apparently a movement of females from shallow to intermediate depths and from deeper water to these depths for spawning. Aside from these movements, there is evidence in Bermuda that the lobsters exhibit considerable homing tendencies, often moving as much as 5 miles against strong tides to return to the place of original capture. Adults tagged in Florida, on the other hand, have moved as much as 100 miles in 100 days (Smith 1954). Early studies of movement in these lobsters have been augmented by observations, especially off southern Florida, of a remarkable queuing behavior (Herrnkind 1969, 1970, 1975; Herrnkind and Cummings 1964; Herrnkind and McLean 1974). Autumnal mass migrations involve diurnal movements of thousands of lobsters in single-file queues of up to 50 individuals maintained by tactile cues received through the inner antennular rami, legs and antennae. The movements are directional, but

no special animals are singled out as leaders. Individuals captured in migration maintain queues indoors for up to several weeks whereas at other times the queues last only for hours. The overlapping bodies are thought to help in protecting each other, and movements in formation reduce drag during locomotion, thus the queuing behavior may conserve energy and be a consequence of the evolutionary role of migration in the species (Bill and Herrnkind 1976).

The adaptive significance is unknown. Waning daylight in autumn seems to be a triggering mechanism. One result is redistribution to new feeding grounds. In some years the migration has been so great that lobsters spilled out of the water onto rocks. The mass marches often mean windfall profit to fishermen when hundreds are sometimes clustered in small places. *Panulirus argus* is considered to be more vagile than the relatively sedentary *P. guttatus* (see Gregory 1979).

The larva of the spiny lobster is a flattened, leaf-shaped, planktonic organism which, before its identity was known, was given the name phyllosoma. Development of the phyllosoma larvae of *P. argus* has been studied off Florida and at other points in the Atlantic Ocean from the West Indies to the southeastern coast of the United States and north of Bermuda. Bigelow and Sears (1939) found phyllosoma larvae (*P. argus*?) off Chincoteague Bay in July, 1929. Eleven stages have been described from plankton. In Florida, the bulk of freshly hatched larvae appear between June and August, the last stages being taken in December and January. The first postlarval, or puerulus, stages appear in inshore waters from January to March. Thus, larval development is judged to require six months, and during that time the larvae may be swept hundreds of miles from the spawning place. (Feliciano [1956] described a prenaupliosoma stage which may at times be freed in the water but this has yet to be confirmed.) The puerulus is shaped like a miniature adult, but is about 17 mm long, colorless, and has a soft exoskeleton. It is non-planktonic and settles in shallow water. Ten postlarval stages have been distinguished. Stages I through III avoid light, but later stages show no such reactions. At the end of the first year, at the eleventh postlarval stage, the young are approximately 5 cm long.

Aside from reactions of the very young postlarvae to light, Hess (1940) showed that freshly molted adults are sensitive to light in many regions of their bodies, but as soon as the body is again sclerotized no such reactions are apparent. Sutcliffe (1956) demonstrated that in clear, shallow water lobsters sought cover in bright moonlight. He concluded that movements attributed to tidal responses were actually responses to light.

Stridulation by spiny lobsters (Palinuridae) has been described by a number of workers (Moulton 1957) and in *P. argus* it is produced primarily by a toothed ridge mesial to the bases of the antennae and extending anteriorly from beneath each eye. A corrugated membrane at the base of each antenna is played against this ridge, producing sound when the membrane is moved proximally. Two types of sound are produced, a slow rattle normally produced by animals in small groups, and a rasp which accompanies defensive behavior. A squeaking sound is also produced in an unknown manner, by vibration of the body, when a specimen is held in the hand of an observer. The effect of these sounds on other lobsters or marine life is unknown.

Pearse (1932a) determined the freezing point of *P. argus* blood at Tortugas (range -1.86° to -2.39°C).

Panulirus argus is preyed upon by the jewfish, *Epinephelus itajara*, the Nassau grouper, *E. striatus*, and mutton snapper, *Lutjanus analis* (see Randall 1967), and other large predators (Clifton, et al. 1970). It in turn preys on a variety of invertebrates including molluscs and sea cucumbers.

Family Scyllaridae

(Spanish lobsters)

Carapace depressed; exoskeleton thick, hard, sculptured or tuberculate; orbits excavated in margins of dorsal surface. Antennae short and broad with flat scalelike, stiff articles. Mandibles with 1-jointed palp. Legs simple except minutely chelate fifth pair in female.

The fossil record for the family Scyllaridae extends from the lower Cretaceous (Glaessner 1969), and from the lower Eocene of the Gulf Coast in North America (Rathbun 1935).

Key to Genera and Species

(Adapted from Lyons 1970)

1. Exognath of outer maxillipeds without flagellum; terminal article of antennae with edge cut into deep lobes distally [*Scyllarus*] 2
- Exognath of outer maxillipeds with flagellum; terminal article of antennae with edge nearly smooth or crenulate distally *Scyllarides nodifer*

2. Gastric and all lateral prominences on carapace sharp; second article of antennular peduncles cylindrical; pleura of fourth abdominal segment sharply rectangular or acute laterally *S. depressus*
Prominences on carapace blunt; second article of antennular peduncles flattened dorsally; pleura of fourth abdominal segment rounded laterally. 3
3. Pregastric tooth on carapace nearly always bilobed, incised; first to fourth abdominal segments with deep, narrow median notch in posterior margin *S. americanus*
Pregastric tooth on carapace rounded, entire; first to fourth abdominal segments with very shallow, broad median notch in posterior margin *S. chacei*

Genus *Scyllarides* Gill 1898

Gill 1898:99.—Verrill 1922:18.—Hemming 1958b:94.

Scyllarides nodifer (Stimpson)

Fig. 121

Scyllarus nodifer Stimpson 1866:48.—Stimpson 1871b:123.

Scyllarides americanus Verrill 1922:24, pls. 5–6.

Scyllarides nodifer.—Holthuis 1960b:153.—Williams 1965:98, fig. 77.—Lyons 1970:7, figs. 3–5, 19, pl. 1, pl. 2c.

Recognition characters.—Adult carapace longer than wide, subtruncate in front, coarsely and unevenly granulate, granules elevated, not crowded, each surrounded by more or less complete circle of stiff hairs; anterolateral corners forming nearly right angle terminating in an obtuse tooth; cervical notch and groove well marked with numerous denticles on margin in front of and behind notch; posterior transverse groove deep and conspicuous; gastric area with large, broad-based, promi-

nent median ridge divided into smaller anterior and larger posterior part, each part ending in an anterior, large, conical, obtuse or bilobed tubercle with other similar but smaller tubercles and coarse granules around and behind apex; cardiac region with prominent but less elevated area with larger tubercles than on adjacent surface; similar ridge on each branchial area. Orbits large, with prominent, thick borders, anterior notch wide and deep.

Antennae with distal article broader than long, edges broadly and evenly rounded, minutely lobulate and crenulate, fringed with short, closely placed hairs; exposed portion forming a half oval, upper side covered with small, rough granules and small pits bearing tufts of short hairs in large adults, smoother in small individuals. Penultimate movable article distinctly wider than long; broader than distal article; distal lobe terminating in nearly right-angled point in large adults, armed with spine in smaller specimens; edges dentate with many small teeth and some larger ones, a larger stout tooth near inner curve of both antennae separated by space about equal to orbit of eye. First movable article irregularly 4-lobed above; small outer lateral lobe with about 3 denticles; median or distal lobe



Fig. 121. *Scyllarides nodifer* (Stimpson). Female in dorsal view, approx. $\times 0.5$. Bob Simpson photo (from Williams 1965).

swollen and coarsely granular; inner lobe swollen and coarsely granular; inner lobe obliquely oblong with inner edge truncate and denticulate; prefrontal or rostral lobe a little broader than long, widest distally, swollen laterally, with concave sides and median groove.

Outer maxillipeds large, basal articles stout. Legs projecting beyond carapace; first pair stouter than others, propodus considerably swollen, dactyl stout; fifth pair with propodus most slender; merus and carpus of all pairs, except carpus of first, with finely serrulate carina ending in sharp distal tooth; carpi, except first, with lateral carina ending in distal tooth; meri of last 4 legs with ventrolateral carina ending in sharp spine distally (carina sharpest on legs 3 and 4) and each with blunter mesial spine distally.

Underside of bases of legs and sternum roughly sculptured, 1 larger acute or pyramidal elevation on sternum opposite base of each leg.

Abdomen strongly sculptured, elevated areas coarsely granulated and hairy, much like carapace. Second to fourth segments with median, elevated, obtuse ridge, covered with large granules; fifth segment with slight ridge. Pleura large, angular; that of second segment largest, subacute, both edges with dentations about as large as adjacent granules, those of third to sixth segments more minutely dentate on posterior border, nearly smooth or minutely crenulate on anterior border. Telson broader than long, subtruncate distally; posterolateral angles broadly rounded; granulated and hairy proximally, covered with numerous forked ridges and grooves distally becoming fine near edge. Uropods broad, sculptured as telson. Sternum of second segment in males bearing sharply raised, serrate, heavily sclerotized ridge.

Measurements in mm.—Length of carapace: male, 93.8, female 103.1 (Lyons 1970); female, 127. Larger specimens have been observed.

Variation.—Smaller specimens have a smoother integument than adults, but prominences on the carapace and fourth abdominal segment are more pronounced than on adults. The carapace and fourth abdominal segment are wider than long until a length of about 30–40 mm is reached (Lyons 1970).

Color.—Body covered with irregular small brown spots on grayish brown to yellowish background; many orange-red tubercles on edges, across ridge near rear edge of carapace, base and edges of antennal lobes; darker red spots at sides of gastric region, on anterior lobes of carapace and at middle of first abdominal segment; underparts yellow with darker yellow and brown spots; legs banded with red and purple; flagella of antennules purple.

Habitat.—Mud, shell, coral, and sandy bottoms; 2 to 91 m (Lyons 1970).

Type-locality.—Florida Keys.

Known range.—Bermuda; Cape Lookout, N. C., to Florida and throughout Gulf of Mexico to Yucatan (Lyons 1970); a postlarva from S of Long Island (29°11'N, 71°56'W) was taken in the stomach of a lancetfish (*Alepisaurus*). Sims (1968) described larvae of *Scyllarides* sp. from 400 mi. E Cape Cod and 300 mi. E of Cape May, N. J., light, indicating long distance dispersal via the Gulf Stream.

Remarks.—Abstracting notes on individual scyllarid species from the comprehensive account of Lyons (1970) would be needless duplication of effort, but a few general conclusions from his work follow. There was no evidence of external fertilization from his own observations or in published accounts on *Scyllarides* or *Scyllarus*. Ovigerous females of *Scyllarides nodifer* are known from late May to early August off west Florida, with some evidence for two spawnings in a single season.

In a comprehensive treatment, Lyons reviewed the confusing larval and postlarval stages of scyllarids that have been given a variety of names, including generic designations by early workers before the affinities were understood, although the life histories of these lobsters are still incompletely known. According to Lyons, development passes through larval or phyllosome stages into a transparent postlarva, and from this into pigmented juvenile stages. Juvenile *S. nodifer* was distinguished from similar *S. aequinoctialis* both by description and illustration. In *Scyllarides nodifer*, as in *Scyllarus americanus*, *chacei*, and *depressus*, there is a dramatic decrease in relative size of the pleopods at the molt from postlarva into first juvenile, and the pleopods then remain reduced in size until the genital pores appear, after which there is successive increase as the animals approach maturity. Apparently there is little need for these appendages between the early natant stage and the reproductively active stages.

Commensals of *S. nodifer* are barnacles, ectoprocts, hydroids, sponges, annelids, and bivalve molluscs, they being noted on all but very young individuals or recently molted adults (Lyons 1970). One stalked barnacle, *Octolasmis hoeki*, was found on oral appendages, gills, and inner lining of the carapace near the gills in 50% of the specimens examined.

Predators on *S. nodifer* noted by Lyons were grouper, red grouper, *Epinephelus morio*, gag grouper, *Mycteroperca microlepis*, and tiger shark, *Galeocerdo cuvieri*. Lyons reviewed Randall (1967) who found that scyllarid lobsters made up 1% to over 45% of food by volume in a series of West Indian fishes.

Catch of *Scyllarides* in the lobster trap fishery (Lyons 1970) and in trawl samples off Mississippi (Franks, et al. 1972) is insignificant. Lyons plotted

carapace length-weight relationships for samples of males and females.

Genus *Scyllarus* Fabricius 1775

Fabricius 1775:413.—China 1966:203.—Glaesner 1969:R475.

Carapace flattened, width at anterolateral corners equal to or slightly greater than length in midline; middorsal ridge and oblique ridge on each side prominent. Antennules with first articles broad, flattened, and immovable, second article much narrower and elongate; third and fourth articles slender; flagella short; abdomen, including telson, much longer (nearly twice) than carapace; pleura of first segment incised in center of lower edge, second broad and pointed distally. Anterior pleopods of male with both rami slender, flattened, hairy on outer border; remainder with exopods small and lamellate, endopods rudimentary. Anterior pleopods of female with both rami broad and flattened; exopods of remainder lamellate, endopods slender and with long silky hairs. Legs stout, extending beyond carapace; first legs stoutest, remainder progressively more slender; second pair longest; dactyls of first pair somewhat serrate on lower border, remainder simple; fifth legs of females subchelate. Third maxillipeds stout, basal articles prismatic.

Scyllarus americanus (Smith)

Fig. 122

Arctus americanus Smith 1869b:119.

Scyllarus americanus.—Bouvier 1925:448–450 (part).—Holthuis 1960b:152.—Williams 1965:96, fig. 75.—Lyons 1970:25, fig. 9.

Recognition characters.—Carapace with surface squamose in part dorsally, a little squamose below lateral borders posteriorly, lightly tuberculate toward epistome, with feathered setae (some darkened) between squames; middorsal ridge with anterior (pregastric) eminence large, bilobed anteriorly, gastric eminence sharper and more elevated, cardiac eminence not so sharp, bilobed; 2 coalesced blunt spines over each orbit large and somewhat separated from ridges over branchial areas. Rostrum short, rounded at tip, blunt keel-like middorsal tubercle above. Anterior border of carapace emarginate. Orbits deeply excavated, margins broad, with broad anterior notch; blunt tooth on proximal (fixed) antennal article in center of notch. Anterolateral corners of carapace spini-



Fig. 122. *Scyllarus americanus* (Smith). Ovigerous female in dorsal view, approx. $\times 1.5$. Bob Simpson photo (from Williams 1965).

form, lateral borders roughened with squames; rather deep notch behind orbit and another one farther back. Area between posterior marginal groove and posterior margin of carapace faintly squamose and traversed almost always by single distinct groove.

Second antennular article elongate, flattened above, anterior margin obliquely truncate. Antennae spatulate, somewhat punctate, surface variably covered with feathered setae; distal article with irregularly rounded anterior border cut into 6 somewhat separated lobes, edges ciliated, mesial lobe short, spiniform, next much larger and less pointed, following 3 about equal in length, tips rounded, lateral lobe about twice width of intermediate lobes; penultimate article short, bilobed in dorsal view; proximal movable article triangular in outline, edges spinose, 2 lateral spines larger than 4 variably sized mesial spines, prominent ridge running to apical spine nearly dividing article in half.

Second, third, and fourth tergites of abdomen (and to some extent first) with arborescent furrows running inward and forward toward midline. First to fourth segments with median notch in posterior margin fairly deep and narrow; fourth segment

elevated, more or less ridgelike in midline. Third to fifth pleura rounded distally, sixth with narrowly rounded anterolateral lobe. Sternum triangular, broad at base; smooth with furrows ciliated; male with low tubercle in center of fifth sternite, female similar.

Measurements in mm.—Ovigerous female: length of carapace 25, width 29; length of abdomen 45. Females larger than males (Lyons 1970).

Habitat.—Low-tide mark to 46 m (Lyons 1970); many taken in 2–6 m by bait shrimpers in Biscayne Bay and off central west Florida.

Type-locality.—Egmont Key, Fla.

Known range.—Off Bogue Inlet, N. C., to Campeche Banks off Mexico, and Venezuela.

Remarks.—Ovigerous females have been reported from southern Florida in January, March and April (Robertson 1968b), and in September (Williams 1965). Sims (1966) found them off west Florida from February to May, and Lyons (1970) reported them from Cuba in May and September. From numerous records, Robertson thought that spawning may occur throughout the year, at least in southern parts of the range, with a peak in spring and summer.

Robertson (1968b) gave a detailed, illustrated descriptive account of larval development in the laboratory, finding that it passed through six or seven stages to reach postlarva in 32 to 40 days at 25°C, and maybe less than 30 days at 30°C, on a diet of brine shrimp nauplii. Final stage phyllosomas were obtained in various salinities ranging from 23.2 to 38.6‰. Larval life is lengthened at lower temperatures (20°C), but such larvae did not metamorphose to postlarvae. Larval life of *S. americanus* is probably shorter than that of other genera in the family, including *Scyllarides*, its success in culture owing to an ability of all stages to feed well on *Artemia* nauplii. Feeding is a problem in the culture of phyllosomas, for the latter stages seem to have more difficulty than earlier ones in catching brine shrimp nauplii, and it seems that changing morphology of the larvae indicates a change in food with increasing age. Mouthparts of larger phyllosomas are relatively small in relation to overall size. Some authors have indicated that food of these later stages is scyphozoan medusae.

Robertson, agreeing with some previous authors, thought that distribution of both larvae and adults indicates a relatively inshore habitat where in some areas salinity may fluctuate. Evidence for this distribution is further offered by presence of *S. americanus* in the stomach of a snakefish and *Scorpaena brasiliensis* at an 18 m station (Lyons 1970).

Scyllarus americanus has been found fouled with serpulid worms, balanoid barnacles, and once with

the holdfast of an alcyonarian coral on the carapace, but is much less frequently burdened with such animals than *Scyllarides nodifer* (see Lyons 1970).

Scyllarus chacei Holthuis

Fig. 123

Scyllarus americanus.—Hay and Shore 1918:399, pl. 28, fig. 2.—Bouvier 1925:448–450 (part), pl. 7, fig. 3.—Boone 1930:84, pl. 23, fig. A.—Schmitt 1935a:174 (part), fig. 39.—Holthuis 1959:126.

Scyllarus chacei Holthuis 1960b:152.—Williams 1965:95, fig. 74.—Lyons 1970:27, fig. 10.

Recognition characters.—Carapace with surface squamose in part dorsally, lightly squamose below lateral borders, with feathered setae (some darkened) between squames; middorsal ridge with anterior (pregastric) eminence large, rounded, gastric eminence higher, upturned, cardiac eminence somewhat smaller than pregastric; 2 coalesced



Fig. 123. *Scyllarus chacei* Holthuis. Male in dorsal view, approx. $\times 2$. Bob Simpson photo (from Williams 1965).

spines over each orbit large and somewhat separated from ridges over branchial areas. Rostrum short, rounded, sides nearly parallel. Anterior border of carapace emarginate. Orbits deeply excavate, with broad anterior notch, blunt tooth on proximal (fixed) antennal article in center of notch. Anterolateral corners of carapace spiniform, lateral borders roughened and another spine farther back; area between posterior marginal groove and posterior margin of carapace nearly smooth but traversed by 2, seldom 3, distinct parallel grooves.

Second antennular article elongate, flattened above, anterior margin obliquely truncate. Antennae spatulate, somewhat punctate; distal article with irregularly rounded anterior border cut into 7 elongate, somewhat separated, lobes with rounded ends, edges ciliated; mesial 2 lobes shortest and sharpest, lateral lobe obliquely truncate and broadest; penultimate article short, bilobed in dorsal view; proximal movable article cordate, a prominent ridge throughout length to spiniform tip, a less conspicuous and irregularly shaped mesial ridge, edges spinose.

Second, third, and fourth abdominal tergites (and to some extent first) with arborescent furrows running inward and forward toward midline; first to fourth segments with median notch in posterior margin very shallow, fourth segment not elevated in midline. Third to fifth pleura rounded distally, sixth with rounded anterolateral lobe. Sternum triangular, broad at base, smooth with furrows ciliated; male with slight midventral elevation on fifth plate, elevation less evident in female.

Measurements in mm.—Length of carapace: male 21.6, female 24.2 (Lyons 1970); 19, length of abdomen 35 (Williams 1965).

Habitat.—"On bottoms composed primarily of sponge, dead and living coralline algae, and dead shell, with little sand but much silt" (Lyons 1970); 11 to 329 m.

Type-locality.—North-northwest mouth of Marowijne River, about 20 miles off coast of Surinam.

Known range.—Off Cape Hatteras, N. C., through Gulf of Mexico, West Indies, and Caribbean Sea to off Cape São Roque, Brazil.

Remarks.—Ovigerous females have been reported from Florida in late January (Lyons 1970) and March, South Carolina in July, Surinam in August and September, and northeast Brazil in November (USNM).

Robertson (1968a) hatched and reared phyllosomas of *S. chacei* in the laboratory until transformation of postlarvae; both phases were identical to analogues from plankton and indistinguishable from developmental stages of *S. americanus*. Lyons (1970) agreed with this judgment. Lyons noted

considerable variation in exopod development on postlarvae of *S. chacei*, finding development more prominent in planktonic than in benthic animals, but seemed to suggest that this may result from staging variations in metamorphosing from larva to postlarva.

Lyons further characterized *S. chacei* as one of the most common and widely ranging western Atlantic scyllarids, occurring mainly beyond depths frequented by *S. americanus*; samples throughout the range indicate general abundance. He plotted carapace length-weight relationships for samples of males and females.

Scyllarus depressus (Smith)

Fig. 124

Arctus depressus Smith 1881:429.

Scyllarus arctus paradoxus Rathbun 1900:309 (part).

Scyllarus depressus.—Bouvier 1915:291.—Lyons 1970:30, figs. 11–13.—Robertson 1971:841 ff., figs. 2–33.

Scyllarus americanus.—Bouvier 1925:447, pl. 8, fig. 2.

Scyllarus nearctus Holthuis 1960b:151.—Williams 1965:97, fig. 76.

Recognition characters.—Carapace with surface squamose in part dorsally, but only on or near ridges and sides, smooth below except sinuous submarginal row of tubercles and lightly granulate area posteriorly, densely ciliate above between squames and on smooth areas. Rostrum short and acute; pregastric tooth above it about same size, gastric tooth larger, acute, all 3 of these directed forward. Cardiac eminence blunt, bilobed at apex. Gastric tooth and cardiac eminence with squames at base, rostrum and pregastric tooth in smooth area. Lateral ridges ending anteriorly in forwardly directed spine. Front emarginate with small projection about halfway between rostrum and orbit. Orbits deeply excavated, upper border composed of 2 spines coalesced at base, lower border an inflated ridge more or less interrupted by 2 subequal spines at anterolateral corner; anterior notch partially occupied in middle by large serrulate tooth on first (fused) antennular article and another eminence forming articulation of second antennal article. Anterolateral corners of carapace drawn out to strong spine, lateral border with notch behind eye and another less definite notch behind anterior end of branchial ridge. Posterior margin of carapace with sharp but broadly opened notch in midline; area between posterior marginal groove and posterior margin of carapace traversed by 2 rows of squames.

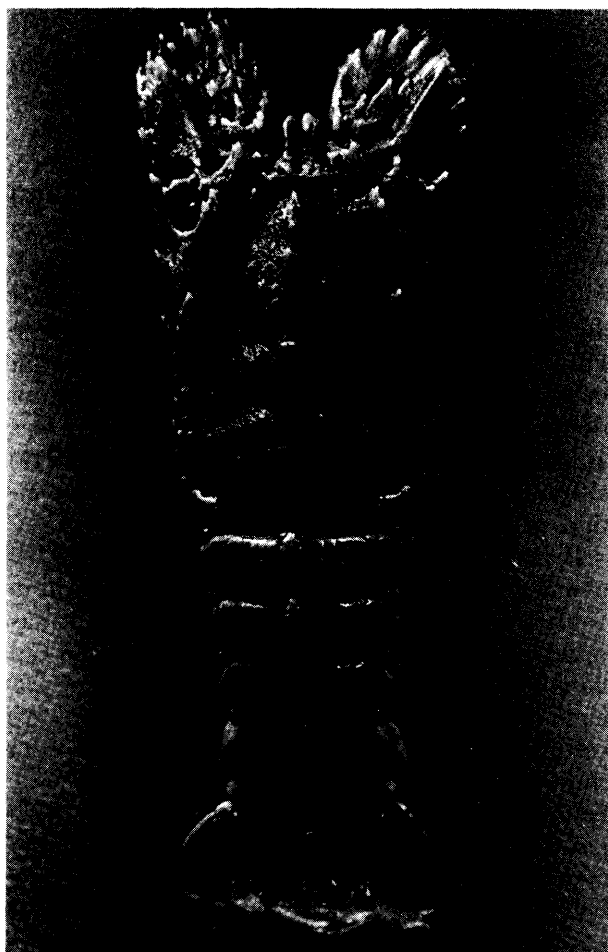


Fig. 124. *Scyllarus depressus* (Smith). Male in dorsal view, approx. $\times 1.5$. Bob Simpson photo (from Williams 1965).

Anterior border of first antennular article with low teeth or irregularities; second article cylindrical with flattened, rounded distal projection; succeeding articles slender, flagella short. Antennae fairly smooth, ciliated, edges densely covered with longer feathered setae; distal article semi-elliptical in outline, edge broken into 6 well-separated lobes with narrowly rounded tips, inner lobe smallest, outer broadest and subtruncate, suggestion of seventh lobe mesially; penultimate article short, irregularly spined and lobed; first movable article roughly triangular with apex formed by strong spine, 2 spines on outer border and 3 spines on inner border, apical spine and first 2 inner spines with small spurs on mesial borders, third spine at posteromesial border smaller, definite ridge running across article from articulation to apex.

Second to fifth abdominal segments (and to some extent first) with arborescent furrows running inward and forward toward midline. First to fourth segments with median notch in posterior margin deep and narrow. Third and fourth with distal edge

of pleura rounded anteroventrally, angled at posteroventral corner; fifth broadly rounded distally; sixth with anteroventral lobe broad and rounded. Telson with 4 flattened spines at distal edge of hard portion. Each ramus of uropods with spine at same level on outer margin.

Sternum triangular, narrower in males than in females, smooth, a little pubescent in grooves. Males with strong, shelflike protuberance on sternite between last pair of legs, and with strong sharply ridged shoulder extending over genital pore. Female with low eminence on sternite between last pair of legs.

Measurements in mm.—Ovigerous female: carapace length 24, width 26; abdomen, length approximately 50. Male carapace length 23.8 (Lyons 1970, in part).

Habitat.—Bottom associations similar to those of *S. chacei*; 29 to 263 m (Lyons 1970).

Type-locality.—South of Martha's Vineyard, $40^{\circ}05'39''N$, $70^{\circ}23'52''W$, 157.3 m, *Fish Hawk* Stn. 872.

Known range.—Off Martha's Vineyard, Mass.; off Cape Hatteras, N. C., through Gulf of Mexico and West Indies to State of São Paulo, Brazil.

Remarks.—Both Lyons (1970) and Robertson (1971) reviewed the history of this species, agreeing that Smith's specimen of *Arctus depressus*, originally acknowledged as a probable immature stage, is the holotype of *Scyllarus depressus*. The larval description of Bouvier (1925) agrees both with Smith's specimen and with the results of modern work.

Ovigerous females are known from southern Florida in January and October (Lyons 1970), and off North Carolina in June (Williams 1965) and November (Sandifer 1971). Lyons (1970) entertained the possibility that spawning occurs throughout the year. Planktonic phyllosomas were taken in Florida Straits from January through May, the final stages in April and May (Robertson 1971); from this the spawning season was judged to be fall-winter-spring. Seven larval stages were reared from eggs that hatched and developed in the laboratory. Later phyllosomas were obtained from plankton and some of these metamorphosed into postlarvae. The complete series of nine or ten phyllosoma stages plus postlarvae, described and illustrated, were estimated to have a minimal life span of about 2.5 months in water temperature of $25^{\circ}C$, and longer in lower temperatures. Sandifer (1971) also reared the first two phyllosomas of *S. depressus* in the laboratory from eggs of a female taken off Cape Lookout, N. C.

Lyons (1970) noted that postlarvae have been taken mostly in depths inhabited by adults, but one studied by him occurred at a station where bottom

depth was 2400 m, and another was from off Cape Charles, Va. Sims (1968) gave records of *Scyllarus* sp. larvae from 600 mi. east of Cape Cod, showing that phyllosomas can be transported great distances in oceanic currents.

Infraorder Anomura

Section Thalassinidea

Superfamily Thalassinioidea

Family Callianassidae

Carapace elongate, slender, separated by cervical groove into long anterior (gastric) and short posterior (cardiac) region. Rostrum little developed, nearly always unspined. Linea thalassinica present (Callianassinae) or absent (Callianideinae). Without pleurobranchs. Ocular peduncles more or less dorsoventrally depressed, contiguous, cornea usually subdistal. Antennal scales reduced. First maxilliped with large foliaceous exopodite, non-flagellated, reduced endopodite and well-developed epipodite generally composed of anterior and posterior lobe; second with often foliaceous exopodite and epipodite reduced or absent; third frequently without exopodite, endopodite pediform, subpediform or operculiform and epipodite reduced or absent. First legs chelate, usually unequal; second legs chelate; third simple; fourth simple or subcheliform; fifth subchelate or chelate. Pleopods 1 and 2 present in both sexes (except some

males), 3–5 foliaceous, provided with appendix interna. (After de Saint Laurent 1973.)

Genus *Callianassa* Leach [1814]

Leach [1814]:400.—Hemming 1958b:142.—Biffar 1971a:648.—de Saint Laurent 1973:514.

The genus *Callianassa* has a fossil record extending back to the Upper Cretaceous (Glaessner 1969). Fossil chelae of *Callianassa* are occasionally found in fossil burrows called *Ophiomorpha* by paleontologists, and *Ophiomorpha* is known to range at least as far back as the Permian (Frey and Mayou 1971), although there is no suggestion that these two entities are always associated with each other.

Biffar (1971a) regarded Stimpson's (1866, 1871b) genus *Callichirus* "to be subgeneric at best," but de Saint Laurent (1973) divided the family Callianassidae into two subfamilies (Callianassinae and Callianideinae) and subdivided the Callianassinae into eight genera including *Callichirus* Stimpson. According to de Saint Laurent, the known species from the western Atlantic formerly placed in *Callianassa* belong in *Callichirus*. The differences between *Callianassa* and *Callichirus* depend upon mouthparts and seem somewhat overlapping. For the time being, therefore, I am retaining the well-known name *Callianassa* for these species, awaiting further research which may place de Saint Laurent's system on a firmer basis.

Key to Species of *Callianassa*

1. Uropods narrow, about 4 times longer than broad *C. major*
 Uropodal endopods not much longer than broad 2
2. Eyestalks with pointed tips slender, curved outward and upward; uropodal
 exopods composed of 2 fused parts, shorter, narrower anterior and
 underlying broader posterodistal parts both terminating in dense fringe
 of marginal setae *C. atlantica*
 Eyestalks with obliquely rounded tips lacking projection; uropodal exopods
 bilobed, underlying posterodistal parts having posterior lobe fringed with
 single row of plumose setae and larger anterior lobe with compound fringe
 of plumose setae *C. biformis*

Callianassa atlantica Rathbun

Fig. 125

Callianassa stimpsoni Smith 1873c:549, pl 2, fig. 8.—
 Hay and Shore 1918, pl. 29, fig. 5.

Callianassa atlantica Rathbun 1926:107.—de Man
 1928a:37.—Rathbun 1935:104.—Schmitt 1935b:
 4.—Williams 1965:102, fig. 79.—1974c:16, figs.
 43A-B (key).

Recognition characters.—Integument smooth, shining, thin, almost membranous. Carapace about 1/3 length of abdomen, thin but with oval thickened plate on gastric region. Rostrum small, acute, flanked by small triangular prominence at each side on frontal margin. Eyestalks small, flat, contiguous mesially; pointed tips slender, curved outward and upward; cornea small, situated on outer border. Antennular peduncles about 1/2 length of cara-

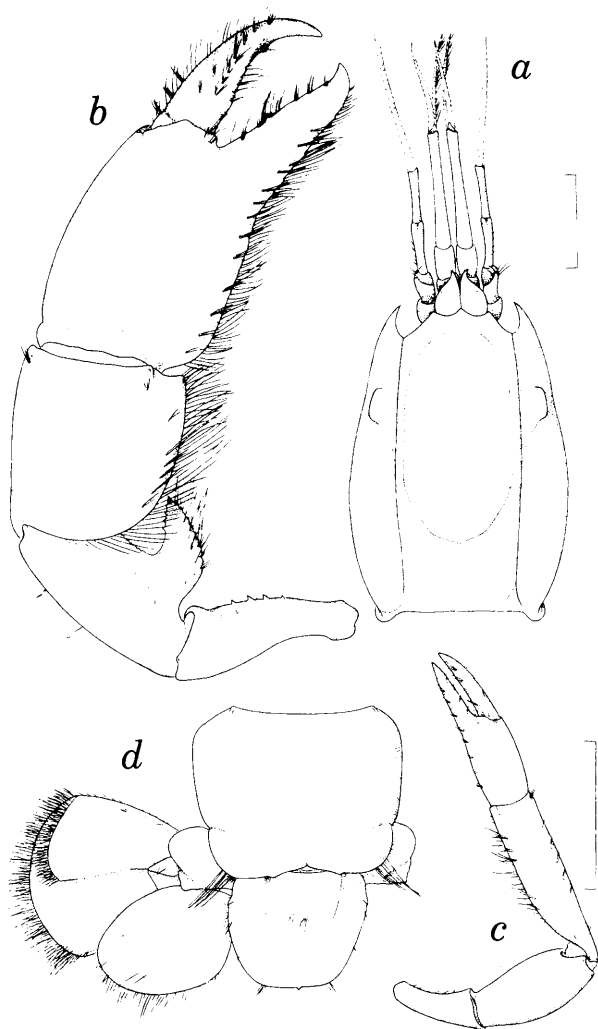


Fig. 125. *Callianassa atlantica* (Rathbun). Male: a, carapace, eyes, antennules, antennae in dorsal view; b, major (right) cheliped, c, minor (left) cheliped, external view; d, sixth abdominal segment with telson and left uropods; a, d, 5 mm; b-c, 1 cm indicated (USNM 14096).

pace; flagella about as long as distal article of peduncle, densely hairy below. Antenna slender, longer than carapace; peduncle much shorter than that of antennules, bent between second and third articles. Third maxilliped operculiform; dactyl slender.

Chelipeds unequal, showing sexual dimorphism. Larger cheliped of male with fingers about equal in length, hairy, tips incurved; cutting edge of dactyl with long, low, truncate tooth at base, smaller teeth distally; fixed finger with small teeth; palm hairy below, upper border ridged along proximal $\frac{2}{3}$; carpus as wide as but shorter than palm, upper and lower border ridged; merus articulating with carpus by extreme upper angle, prominent denticulate tooth on lower border

proximally; ischium with 6 or 7 subacute teeth on lower border. Smaller cheliped of male slender with fingers little longer than palm; carpus 4 times as long as broad distally, little longer than palm, half again as long as merus; merus twice as broad as long. Larger cheliped of female less toothed than in male; smaller cheliped as in male.

Abdomen with third to fifth segments about equally wide, each with small patch of fine hairs on posterolateral angle; sixth segments broader than long. Male with no pleopods on first and second segments. Female with uniramous pleopods on first segment; remainder well developed in both sexes. Telson nearly as long as broad; subtruncate distally, corners rounded. Exopods of uropods broader than endopods; exopod composed of 2 fused parts, anterior lobe shorter and narrower than its much larger underlying posterodistal lobe, both lobes fringed with dense marginal setae.

Measurements in mm.—Length of body: male 59; female 68.

Habitat.—Muddy shores and bottoms (Sumner, et al. 1913a, b); shoreline to approximately 38 m.

Type-locality.—“Our species ranges from the coast of the Southern [United] States north to Long Island Sound” (Smith 1873c).

Known range.—Bass River, Nova Scotia, to Georgia; Franklin County, Fla.

Remarks.—Both de Man (1928) and Schmitt (1935b) pointed out that Rathbun renamed this species because the name *stimpsoni* was preoccupied by a fossil species of *Callianassa*. To *Callianassa atlantica* itself is attributed a fossil record extending from first appearance in the Upper Miocene of North Carolina and Virginia, and a later occurrence in the Pleistocene of Maryland to the Recent (Rathbun 1935).

The species has been collected in areas ranging from salty estuaries to offshore fishing banks. Frankenberg and Leiper (1977) reported it as dominant from June through November in grab samples from fine sand off Georgia, apparently in association with *Pinnixa chaetoptera*.

Ovigerous females have been taken in Massachusetts and South Carolina in July. Sandifer (1973c) described two zoeal stages from plankton near the mouth of Chesapeake Bay that he attributed to this species. Sandifer (1973d) found these larvae in samples from July to September, and most abundantly near the bottom. Fish (1925) reported larvae (as *C. stimpsoni*) at Woods Hole from July to October, and Deevey (1960) found a *Callianassa* larva (considered *C. atlantica*) in Delaware Bay during January, March, and July to October. Sandifer considered all identical larvae from New England to be this species.

Callianassa biformis Biffar

Fig. 126

Callianassa biformis Biffar 1971b:225, fig 1.

Recognition characters.—Integument smooth, shining, thin, almost membranous. Carapace about $\frac{1}{4}$ length of abdomen, thin but with oval thickened plate covering anterior $\frac{3}{4}$. Rostrum small, acute; front broadly rounded at base of antennae. Eye-stalks flattened, shorter than first antennular article, irregularly rounded at tips; cornea small, central and subterminal. Antennular peduncle shorter than antennal peduncle, fringed with long, sparse setae laterally.

Chelipeds unequal, showing sexual dimorphism. Males with major cheliped showing 2 forms. Stronger form having palm smooth and round externally, little longer than carpus, margins entire. Opposed margin of propodal finger with broad, rounded tooth centrally, inconspicuously serrate distally, tip upturned and subacute; rounded notch at base of finger near articulation of dactyl. Dactyl hooked distally, cutting edge finely serrate and with broad, rounded proximal tooth. Carpus little longer than merus, similar to palm, margins entire except for few tubercles proximoventrally. Merus with strong proximoventral hook, margin of hook serrate and setose, acute distally, remainder of ventral

margin with irregular denticles, dorsal margin with rounded denticles on proximal half separated by tufts of fine elongate setae. Ischium with distinct, distally directed spur or hook on proximodorsal margin; distodorsal margin with tufts of fine, long setae separated by rounded denticles; ventral margin with 5 to 7 subacute spines along proximal half.

Weaker form with propodus proportionally narrower; fixed finger deeper proximally, cutting edge with series of rounded denticles and lacking median tooth; notch between fingers shallower; dactyl narrow, hooked distally, cutting edge with series of small rounded teeth but lacking large proximal tooth.

Small cheliped of male identical to both chelipeds of female. Palm subquadrate, width increasing distally, propodal finger deep proximally, acute at tip, series of acute denticles on cutting edge; dactyl curved, slightly longer than palm and equal to fixed finger, cutting edge entire or with few serrations. Carpus narrow, elongate, a bit longer than merus. Merus with midventral spine; ischium without spur, spines or dorsal elongate hairs. First walking legs chelate.

Abdomen long, gradually widening from anterior end to almost equally broad third to fifth segments, sixth narrower. Uropods broad; exopod composed of 2 fused parts, narrow anterior lobe nearly as long as its much larger underlying posterodistal lobe, latter lobe composed of 2 parts separated by marginal indentation, anterior part and fused anterior lobe both densely fringed with plumose setae, but posterior part fringed with single row of plumose setae. Telson slightly wider than long, truncate posteriorly, lateral margins convex, 2 small spinules at each posterolateral corner.

Measurements in mm.—Length of body: males 32; ovigerous females 27.

Habitat.—Primarily intertidal, occasionally subtidal, in fine mud or sand and in salinities ranging from 10 to 30 but usually around 25‰ (Biffar 1971b). Dörge (1977) found it both on protected mud flats in high salinity estuaries and from 10-m depths seaward on nearshore bottoms in Georgia.

Type-locality.—South end of Sapelo Island, mouth of Doboy Sound, McIntosh County, Ga.

Known range.—Bass River, Yarmouth and Nantucket Sound, Mass. (Williams and Wigley 1977); Chesapeake Bay (?); North Inlet, S. C. (Holland and Polgar 1976), to McIntosh County, Ga.; Franklin County, NW Fla. (USNM).

Remarks.—Biffar (1971b) pointed out that this species has been confused with juveniles of *C. atlantica*. He named the species for the two forms of large chelae found in the males. The cause for this condition is not known; "the full range of variation

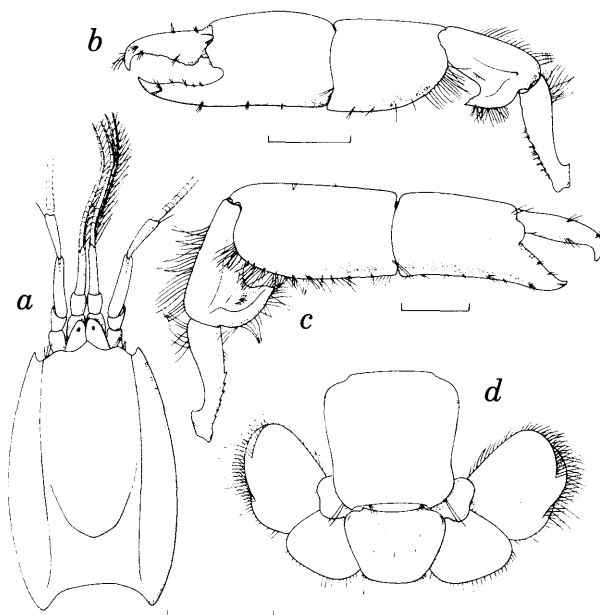


Fig. 126. *Callianassa biformis* Biffar. Male: a, carapace, eyes, antennules, antennae in dorsal view; b, major (strong form) cheliped, c, major (weak form) cheliped, external view; d, sixth abdominal segment with telson and uropods. a-b, d, USNM 135053 (paratype); c, USNM 135052 (holotype); a, c, d, 3 mm; b, 2 mm indicated.

in sizes of the chelipeds of both forms clearly shows that differences between juvenile and adult morphology are not sufficient to explain the situation." These and other polymorphic conditions are known in other species of *Callianassa* (Poore 1975).

Ovigerous females are known in June and July. Sandifer (1973c) described four zoeal stages of a *Callianassa* (species A) that he referred questionably to *C. biformis*. These zoeae were identical to stages Kurata (unpubl.) reared from *C. biformis* in Georgia. Sandifer (1973d) found the larvae in low concentrations in bottom samples from lower Chesapeake Bay over a temperature range of 18.8° to 27.6°C and salinities of 25.7 to 32‰ during July to September.

Callianassa major Say

Fig. 127

Callianassa major Say 1818:238.—Schmitt 1935b.—Williams 1965:100, fig. 78.—Rodrigues 1971:192, figs. 1–20.—Coelho and Ramos 1972:161.
Callichirus major.—Hay and Shore 1918:407, pl. 29, fig. 10.—de Man 1928a:30.

Recognition characters.—Integument more or less thin and membranous, chelipeds and oval plate covering anterior $\frac{3}{4}$ of carapace being most hardened parts. Rostrum minute, somewhat obtuse; similar projecting lobe at each side on margin of front. Cornea minute, situated at about middle of outer margin of flattened and pointed ocular peduncles. Antennular peduncles about $\frac{2}{3}$ as long as carapace, stout, densely hairy below; each with 2 flagella about as long as distal article of peduncle. Antenna slender, longer than carapace, peduncle bent between second and third article.

Chelipeds unequal, showing sexual dimorphism. Males with major cheliped rather large; granular along proximal lower edge of carpus, lower surface of merus and over most of ischium; propodus and carpus about equal in length, twice as broad as merus and more than 3 times as broad as ischium; merus with strong tooth on lower proximal border; fingers strong, dactyl hooking over outside fixed finger, strong tooth near base. Major cheliped of female weaker, not granular; propodus and carpus proportionately shorter than in male; merus without tooth on lower proximal border; dactyl hooking over inside fixed finger. Minor cheliped of male and female similar, small; fingers weak, meeting only at tips; carpus as long as hand and somewhat wider. Chelipeds and first 3 pairs of walking legs much compressed; margins of distal articles on first 2 pairs especially sharp; first walk-

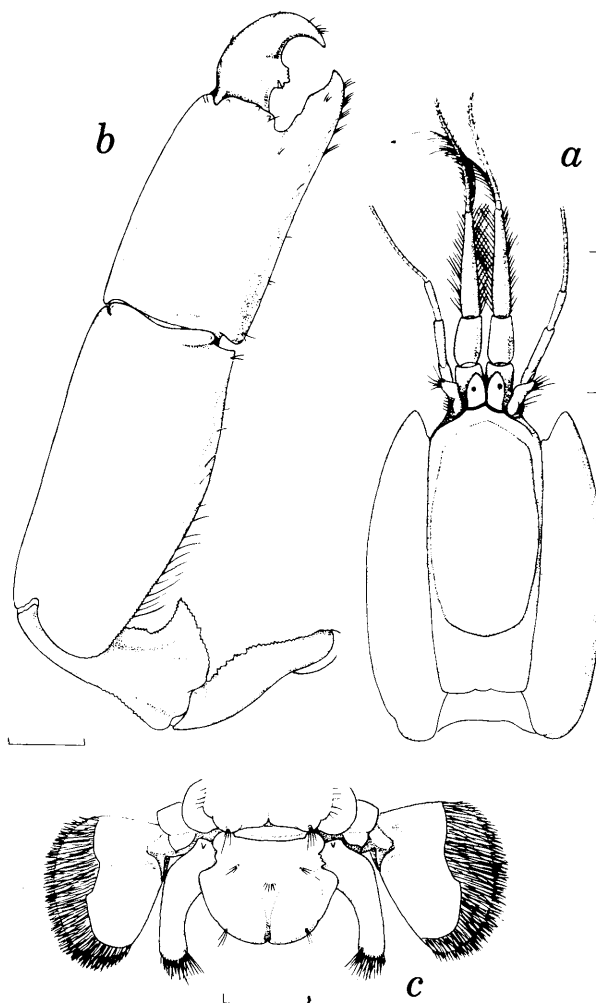


Fig. 127. *Callianassa major* (Say). Female: a, carapace, eyes, antennules, antennae in dorsal view; b, major (right) cheliped, external view; c, sixth abdominal segment with telson and uropods; a, 1 cm; b-c, 3 mm indicated (USNM 122451).

ing legs chelate, long hairs on lower margin; second legs with propodus transverse, it and small triangular dactyl densely hairy along margins; third and fourth walking legs with last 2 articles hairy, last legs subcylindrical.

Abdomen long, gradually widening from anterior end to third segment, then narrowing slightly to sixth; sixth segment deeply grooved above. First 2 pleopods small and slender in male, larger and definitely biramous in female; remaining pleopods broad and overlapping. Uropods with exopod broad, rounded distally; distal half covered with mat of dense short hair becoming longer on border; endopod narrow, obliquely truncate, hairy at tip only. Telson with inflated area on each side giving notched or fissured appearance.

Measurements in mm.—Length of body: males 95; females 92; ovigerous females 80 (Lunz 1937b).

Color.—Transparent gray except for porcelain

white chelipeds and hardened portion of carapace (Lunz 1937b). Yellowish digestive glands and red female or orange male gonads show through integument (Rodrigues 1971).

Habitat.—Burrows in sandy shores on or near open ocean; intertidal zone to 2 m.

Type-locality.—Bay shore of St. Johns River in east Florida, near low-water mark.

Known range.—Beaufort Inlet, N. C., to Cape Canaveral, Fla.; Grand Terre Island to Timbalier Island, La.; Espírito Santo and São Paulo, Brazil (Rodrigues 1965, 1971).

Remarks.—Biffar (1971a) gave a key to the western Atlantic species of *Callianassa* along with a summary of biological literature. Ovigerous females are known from Georgia in June, North Carolina in June and July, and Louisiana in June.

For many years *C. major* was known only from a single specimen from Beaufort, N. C., and early descriptions of specimens from South Carolina and Florida, but new investigations have supplied much detail. Burrowing habits of the form prevent easy detection by the casual observer using conventional methods of collection. Such habits no doubt also enhance chances for fossilization, for the genus is abundant in Cretaceous through Cenozoic deposits of the Gulf coastal plain, and somewhat less abundant in later deposits down to the Recent (Rathbun 1935; Weimer and Hoyt 1964).

Lunz (1937b) determined the habitat and abundance of the species in South Carolina and his studies were closely followed by those of Willis (1942) in Louisiana, Pearse, et al. (1942) and Pohl (1946) in North Carolina, and recently Rodrigues (1971) in Brazil. Weimer and Hoyt (1963, 1964) and Hoyt and Weimer (1964), from studies in Georgia, linked modern environments of the animal to Pleistocene and older deposits containing fossil tubes like those of *Callianassa*.

The animals live in deep burrows on sandy beaches that either face the open ocean or are close to it. In Louisiana, the burrows occupy a band from the intertidal zone to a distance of over 30 m from shore in 5 to 6 feet (2 m) of water, and in Georgia in similar parts of the foreshore to perhaps greater depths. Estuaries are tolerated to some degree in Brazil. Felder (1978) showed that the lower lethal limits of salinity are 7–8‰ and that blood osmotic regulation fails below 20‰. Blood magnesium is slightly hyperregulated at acclimation salinities less than 30‰. The tubular burrows, usually vertical to the surface, are divided into three parts. The mouth, about 5 mm in diameter, opens into the upper part, 5 to 20 cm long and 5 to 8 mm in diameter. From this the middle part, 10 to 15 cm long and often angled, widens gradually to approximately 20 mm.

The third part, 20 mm wide, is the longest. An approximate average depth of the whole burrow is 146 cm with variations usually from 60 to over 210 cm. Frey and Mayou (1971) reported living shrimp from burrows as deep as 4 m in Georgia. Branches are common and arise most often from the middle part. Characteristically, the burrows are lined with a brown material secreted by the animal (Weimer and Hoyt 1964), apparently collophanite (amorphous calcium phosphate) which is thinnest in the upper and thickest (3 to 7 mm) in the lower part. The burrows often end in an enlarged pocket lined with crushed shell, and in some the lined tube extends below the pocket. Say's (1818) general account agrees well with this description. (Some collections have been made by removing the mouth of the burrow, dropping pebbles or debris down the hole, waiting for the animal to appear at the exposed surface, then jabbing a shovel into the sand below the animal thus cutting off escape into the burrow.)

In captivity, the animals burrow in sand head-first with the anterior appendages until a shallow pit is constructed, then they reverse themselves and continue to burrow tailfirst. Though the shrimp emerge voluntarily from their burrows at times, such behavior is probably infrequent and may be confined to the breeding season (Lunz 1937b). The species is well fitted for a fossorial life by virtue of the slender, elongate body, thin exoskeleton, and flattened hairy appendages adapted for burrowing, carrying sand, sifting food, and pumping water for feeding and respiratory currents. Examination of gut contents has shown an amorphous mass containing sand grains, diatoms and other algae, and many bacteria.

Burrow mouths are often surrounded by fecal pellets which resist rapid disintegration in water. On some South Carolina beaches, such pellets were washed together in patches measuring up to 3×15 m and piled to a depth of about 0.5 mm; wave action sometimes concentrates the pellets along the beach to form thin layers of clay (Weimer and Hoyt 1964). Mouths of burrows are not uniformly scattered but tend to be clumped in patches or tracts, often as dense as three or four openings per square foot ($.09\text{m}^2$). Chimneylike structures at the mouths of burrows noted by Say (1818) apparently are formed when shifting sand exposes the main portion of the burrow. A small, raised ridge of sand often surrounds burrow mouths, but many are not marked or may be located in a depression.

Frankenberg, et al. (1967) investigated the trophic significance of fecal pellets by measuring rates at which the material was produced, its content of organic carbon and nitrogen, and its ingestion by other

animals. Results indicated deposition of 456 ± 46 to $2,600 \pm 670$ pellets/m²/day, depending on population density, and that a *C. major* population occupying an area of about 200,000 m² produces about 280×10^6 pellets/day. Carbon and nitrogen contents of the pellets were 3% and 0.3% of dry wt. Aging the pellets had no effect on carbon content but halved the nitrogen in 48 hrs. Ingestion experiments indicated that pellets were eaten by hermit crabs, probably by blue crabs, and possibly by several other beach inhabitants. This fecal material may concentrate carbon in a readily exportable state.

Thompson and Pritchard (1969) considered species of *Callianassa* to have limited euryhalinity.

In Brazil, one or two specimens of *Pinnixa angeloi* are frequently found in the upper narrow part of

the burrows of *C. major*, and a bivalve (*Ceratobornia cema*) and reddish copepod (*Hemicyclops* sp.) inhabit deeper parts of the gallery (Rodrigues 1971). The same author reported ovigerous females nearly year round in São Paulo, Brazil, and also worked out the larval development of the species (1966), describing and figuring three zoeal stages.

Family Axiidae

Carapace with rostrum and cervical groove, lacking linea thalassinica. Antennular flagella well developed, both movable and fixed antennal thorns present though sometimes minute. First legs with large chelae, second legs with small chelae. (After Borradaile 1903; Glaessner 1969.)

Key to Genera and Species

1. Uropodal exopod lacking transverse suture *Axius serratus*
 Uropodal exopod with transverse suture distally 2
2. Eyes normal with pigmented, rounded cornea; antennal thorn long
 *Axiopsis jenneri*
- Eyes lacking pigment, stalks short and flattened obliquely on distal surface;
 antennal thorn very short. *Calocaris templemani*

Genus *Axiopsis* Borradaile 1903

de Saint Laurent 1972:347, 354.

Both Borradaile (1903) and de Man (1925) separated *Axiopsis* from *Calocaris* on the basis of degree of arch in the dorsal surface of the carapace. That unsatisfactory distinction has been followed by most workers, but de Saint Laurent (1972) separated these taxa on a firmer basis in discussing the characters differentiating subgenera of *Calocaris*, which she raised to generic rank (*Calocaris* and *Calastacus*). Both of the latter lack pigmented eyes whereas *Axiopsis* (*Axiopsis*) has mobile, pigmented eyes.

Axiopsis jenneri (Williams), new combination

Figs. 128–129

Calocaris (*Calastacus*) *jenneri* Williams 1974d:451, figs. 1–10.

Recognition characters.—Carapace compressed, nearly smooth, almost straight along middorsal line in lateral view but gradually deflexed from gastric region to tip of rostrum; midline sharply rounded and elevated posteriorly but not keel-like; scattered setae in densest tufts on gastric region. Gas-

tric region with 4 interrupted and spiny dorsal carinae parallel to middorsal keel. Rostrum slightly exceeding eyes, tip upturned, 1–3 marginal spines on each side, low median dorsal keel extending to cephalic groove, notched at base (orbit) for reception of eyes in erect position. Eyestalks cylindrical, cornea well developed. Antennular peduncle with second article equaling rostrum. Antennal peduncle with terminal article exceeding antennular peduncle, strong dorsolateral spine of second article reaching proximal border of cornea; antennal thorn (scale) slender, curved, exceeding cornea.

Chelipeds strong, asymmetrical and clothed with numerous tufts of conspicuous, silky, plumose setae obscuring fingers and portion of hands. Major chela stout; fixed finger nearly straight, crushing edge with strong tooth proximally or at midlength, and some smaller teeth; dactyl curved, with strong tooth more or less opposing teeth of fixed finger; crest of propodus with few spines and tubercles, inner face with patch of tubercles near base of fixed finger; merus with row of spines on proximoven-tral margin. Minor chela more slender, fingers agape proximally but distal half of opposed edges straight and finely serrate, prominent triangular tooth at middle of fixed finger diverging outward from cutting edge and opposite it an internal

shoulder on dactyl; external row of coalesced tubercles and/or spines parallel to proximal margin of fixed finger near articulation of dactyl.

Abdomen and telson nearly twice length of carapace; segments smooth and almost uniformly arched; pleura of short first drawn to acute posteroventral point, anteroventral margins of 2–5 broadly rounded, their posterior corners nearly rectangular, of sixth broadly rounded. Tail fan with thick, long, plumose setae on caudal margin. Telson longer than broad, evenly rounded caudally, lateral margin with proximal lobate process and marginal spines distal to it as well as submarginal spines, unequal pair near distolateral corners movable. Uropodal endopods with 2–4 lateral marginal spines; exopods with transverse distal suture bordered by row of strong, fixed spines and movable one at distolateral corner, lateral margin with 2–4 spines.

Measurements in mm.—Length of carapace including rostrum: male 12.4; female 10.5.

Variation.—Ornamentation (setae, tubercles,

spines) increases in size with increasing size of the animal. The rostrum is often asymmetrically toothed. Fingers of the chelipeds gape less in smaller specimens. The major chela may be on either right or left sides with no indication of regeneration when it is on the left.

Color in life.—"Ground color 'flesh' to off-white (pinkish white) with longitudinal trending, cross-banded maculations of orange red. Most dense orange-red color on posterior part of carapace where red is also deepest in intensity. Abdomen with first segment quite light, others progressively darker caudad; lightest areas at articulations dorsally, deepest colors at pleural junctures. Basal articles of antennules and antennae with bands of color equal in intensity to darker parts of abdomen. Color on legs more washed out. Pubescence light greenish tan." (From Williams 1974d.)

Habitat.—Near edge of continental shelf; 85–232 m (Wenner and Read 1982).

Type-locality.—E Cape Lookout, N. C., 34°18'N, 76°01.2'W–34°17.1'N, 76°01.3'W.

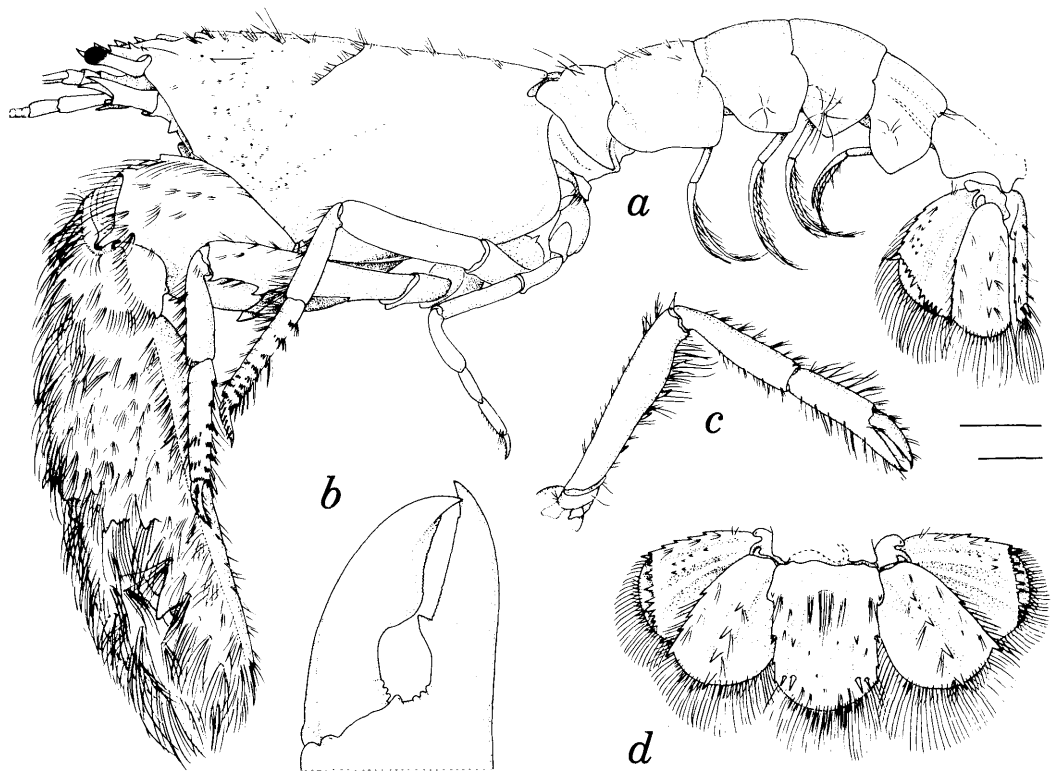


Fig. 128. *Axiopsis jenneri* (Williams). Male: a, lateral view; b, fingers of chela with setae removed, inner view; c, second leg; d, telson and uropods; 2 mm indicated, upper a, c, d; lower b (from Williams 1974d).

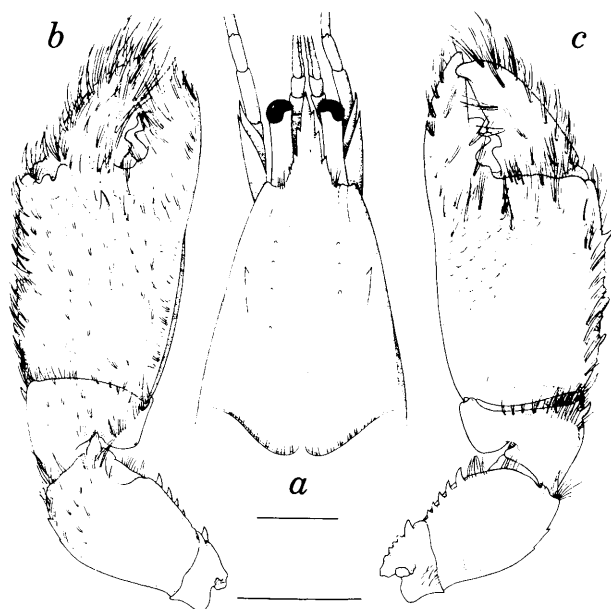


Fig. 129. *Axiopsis jenneri* (Williams). Male: *a*, anterior carapace, eyes, antennules, antennae in dorsal view; major (right) chela, *b*, external, *c*, internal view; *a*, 2 mm, *b*, *c*, 5 mm indicated (from Williams 1974d).

Known range.—Off Cape Lookout, N. C.

Remarks.—The species closely resembles *Axiopsis* (= *Calocaris* [*Calastacus*]) *hirsutimana* and *oxypleura* from the Gulf of Mexico and northern South America (Boesch and Smalley 1972; Williams 1974d).

Genus *Axius* Leach 1815

de Man 1925:8.

Fossil members of the genus range back to the Oligocene (Glaessner 1969).

Axius serratus Stimpson

Fig. 130

Axius serratus Stimpson 1852:222.—Smith 1879:55, pl. 10, figs. 4, 4a.—1881:435.—Rathbun 1929:25, fig. 32.—Williams 1974c:17, figs. 46A-B (key).

Recognition characters.—Carapace smooth, few scattered setae; compressed and drawn to rounded ridge posteriorly; cervical groove deep; lateral carinae on gastric region continuous with rostral margin and mesial to them a pair of shorter carinae. Rostrum elongate triangular, about 5–8 forward trending spines on each side and upturned spine at tip, prominent median carina. Eyestalks

with pigmented cornea nearly hidden beneath rostrum. Antennal peduncle with terminal article partly exceeding rostrum and reaching about to middle of penultimate article of antennal peduncle; antennal thorn (acicle) long, extending about to end of penultimate article.

Chelipeds asymmetrical, sparsely setose, dactyls hooking over ends of fixed fingers; upper and lower margins of palms crested, lower crest flattened ventrally and ornamented under both inner and outer crenate edges with row of long setae; lower crest continued and becoming obsolescent on carpus; upper edge of merus smooth, lower margin with 3 or 4 spines; tips of fingers calcareous on major, corneous on minor chela. Second legs flat-

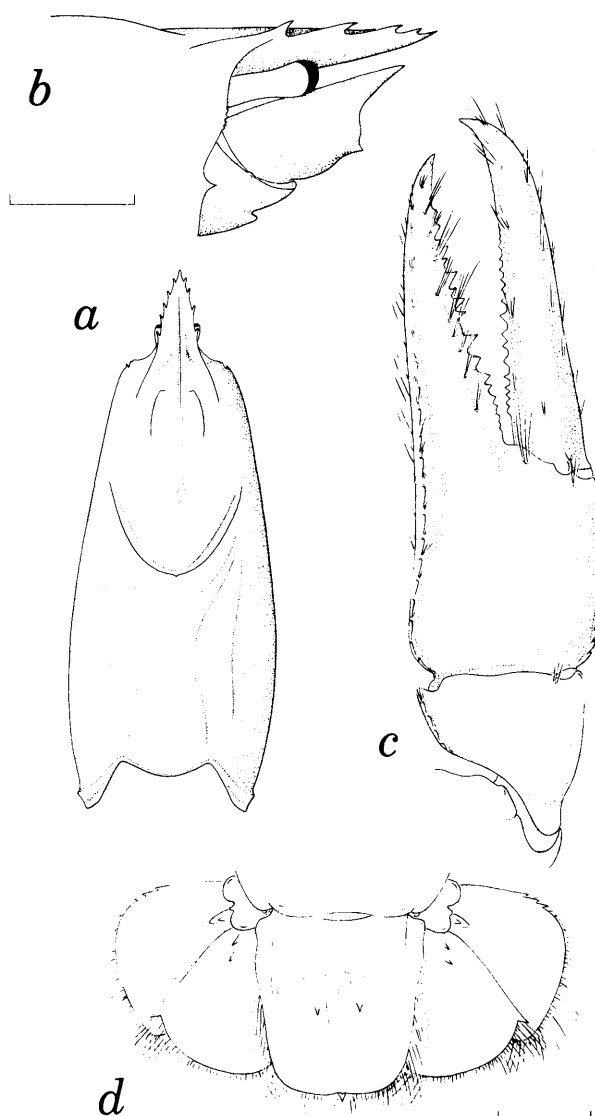


Fig. 130. *Axius serratus* Stimpson. Male: *a*, carapace, dorsal view; *b*, rostrum, eye, base of antenna, lateral view; *c*, chela and carpus, left, external view; *d*, telson and uropods; *a*, *c*, *d*, 5 mm; *b*, 3 mm indicated (USNM 20864).

tened, chelate, especially long silky setae on lower margin and moderately long ones on upper margin; last 3 legs with distal articles densely setose.

Abdomen broad, depressed and smooth; pleura of first segment drawn to fairly acute point, of segments 2–5 more or less rounded, sixth rounded but with 1 or 2 small marginal spines. Telson somewhat truncate, distal margin with median spine. Uropods with stiffening ribs; endopod with prominent proximal spine, smaller ones at distolateral corner and submarginally on central rib; exopod with about 3 small marginal spines distally.

Measurements in mm.—Carapace length including rostrum: male 30; ovigerous female 33. Total length: male 82; ovigerous female 83.

Variation.—The major chela may be on the right or left side; spines on pleura of the sixth abdominal segment may be absent.

Habitat.—Mud or sand (a burrower); 20–100 m.

Type-locality.—Off Scituate, Mass., 37 m.

Known range.—Strait of Canso, Nova Scotia, to Long Island Sound.

Remarks.—Almost nothing has been known of the biology of this species until recently. In 1954, a causeway constructed across the Strait of Canso between Nova Scotia and Cape Breton Island led to alteration of the environment in a harbor associated with industrialization and development (Pemberton, et al. 1976). Study of the area showed that *Axius serratus* constructed burrows more than 2.5 m deep with openings up to 3 cm in diameter in water depths of 7.5 to 11.5 m, most abundantly in polluted sediments barren of living Foraminifera, molluscs, and ostracods. Average density of the burrows, often interconnected, was 9/m². Shrimp retreated more than 2.5 m deep to avoid suction dredges, then reestablished burrows overnight in overburden freshly filling the excavated area.

An ovigerous female is known from the Sheepscot River, Me., in October (USNM 80514). Juveniles and larvae are known from Long Island Sound in August and September in depths of 23–30 m (R. N. Reid, personal communication). Smith (1879) gave the location of the dry type-specimen at the time he wrote, made from it the illustrations reproduced in part by Rathbun (1929), and reported the species from the stomach of a flounder (*Glyptocephalus cynoglossus*) taken 5 mi. SE Cape Ann, Mass.

Genus *Calocaris* Bell 1853

de Saint Laurent 1972b:354.

Calocaris templemani Squires

Fig. 131

Calocaris macandreae.—Rathbun 1929:25, fig. 33.

Calocaris templemani Squires 1965:2, figs. 1; 2A-B, CtC, CtD; 3Ct; 4; 5Ct; 6.—Williams 1974c:17, figs. 47A-B (key).

Recognition characters.—Carapace with middorsal carina extending full length and continuing well out on rostrum; cervical groove distinct; gastric region with carina on each side converging to merge with rostral margin and bearing 3–4 spines. Rostrum angled downward, 4–5 spines on each side pointing upward and forward. Eyestalks rudimentary, lacking pigment, with flat oblique surface facing anterolaterally but anterior edge almost rectilinear. Antennular peduncle with terminal article exceeding antennular peduncle; second article with very short lateral spine and antennal thorn (acicle) equally small.

Chelipeds essentially similar, sometimes slightly unequal in size; fringed with many long setae; dactyl with ridge on each side fringed with setae for its whole length, cutting edge with 2 large teeth separated by gap; propodus with 6 or 7 smaller

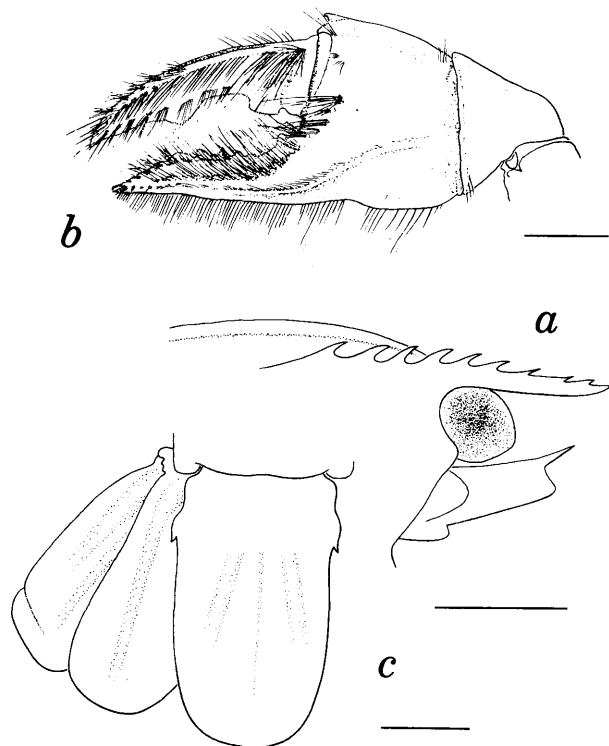


Fig. 131. *Calocaris templemani* Squires. a, Ocular region, lateral view; b, left first chela and carpus, external view; c, telson and left uropod. a, c (from Williams 1974c), 2 mm; b (from Squires 1965), 1 mm indicated.

teeth increasing in size proximally, prominent ridge on inner and outer surface of lower margin forming somewhat flattened edge, upper margin with prominent ridge ending in distal spine.

Abdomen with rounded pleura fringed with long simple setae and few setae near edge especially on segment 5, dorsal tuft of long simple setae at each side of midline on segments 2–5. Telson and uropods rounded terminally, few small carinal and lateral spines.

Measurements in mm.—Holotype: total length 44; carapace 14.

Color.—Pale pink.

Habitat.—Soft mud; 200–600 m [?], 650–700 m.

Type-locality.—Hermitage Bay, Newfoundland, 260 m.

Known range.—(Greenland?); the type-locality; Gulf of Maine; SE Cape Lookout, N. C., 34°14.8'N, 75°46.7'W–34°16.2'N, 75°44.9'W, 650–700 m.

Remarks.—This rare species was confused for years in published reports with *C. macandreae* Bell of the eastern Atlantic until Squires (1965) described it as new and clearly distinguished the two. Because few specimens have been taken, the depth range is largely unknown. The type is a mature hermaphrodite from 4.9°C water. Both sexual condition and habitat suggest a biology similar to that of *C. macandreae* in which eggs are carried 8–9 months, larvae have no significant pelagic phase, 1- to 3-year-olds have both testis and ovary, testes peak in the third year and degenerate in the fourth leaving the vas deferens filled with sperm, ovaries continue to develop and first eggs are laid at age 5 years, next eggs are laid at age 7 and possibly another clutch at age 9, animals molt annually after the fifth year and may attain an age of 10 (Buchanan 1963).

The species may occur in deeper water in the southern part of its range.

Family Laomediidae

Carapace longer than broad; rostrum well developed; linea thalassinica present. Fixed antennal thorn absent, scale reduced to flattened vestige or absent. First legs large, equal, chelate or subchelate. Abdominal pleura well developed, sutures usually present on rami of uropods. (After Borradaile 1903; de Man 1928b; Goy and Provenzano 1979.)

Genus *Naushonia* Kingsley 1897

Chace 1939b:524–530.

Naushonia crangonoides Kingsley

Fig. 132

Naushonia crangonoides Kingsley 1897:96, pl. 3, figs. 8–10.—Thompson 1903a:2, pls. 1–3.—Chace 1939b:529, figs. 1–14.—Williams 1974c:16, figs. 42A–B (key).—Goy and Provenzano 1979:352–357, figs. 1–5; 6A, E; 7A; 8A, G, H.

Recognition characters.—Carapace somewhat cylindrical, arched downward and depressed anteriorly, slightly granulate; cervical groove well marked in middle but not reaching well-impressed line (linea thalassinica) extending from anterolateral angle to posterior margin; pair of low anterolateral crests on each side of gastric region, lateral one more anterior than mesial and almost merging with rostral margin. Rostrum flattened, extending slightly beyond eyes, broadly rounded, margin tipped with small corneous spine and minutely spi-

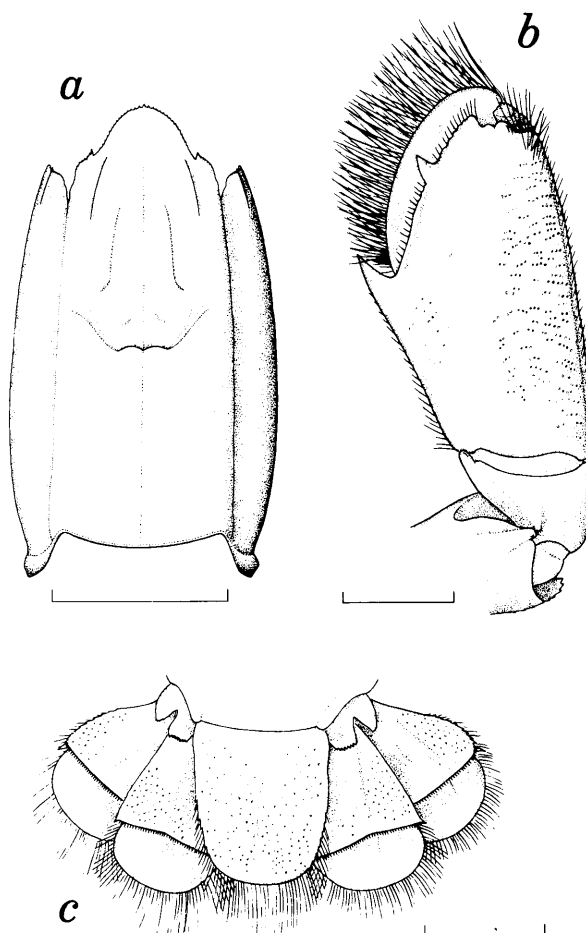


Fig. 132. *Naushonia crangonoides* (Kingsley). Female: a, carapace in dorsal view; b, chela, carpus and distal merus, inner surface; c, telson and uropods; a, 5 mm; b, 2 mm; c, 3 mm indicated (USNM 102278).

nulose elsewhere; anterior margin of carapace similarly spinulose. Eyes not visible from above, pigmented part of cornea tiny. Antennules with short flagella, inner ramus shorter than outer. Antennae with broad scale spinulous on outer margin, tip reaching to or beyond base of terminal antennular article.

Chelipeds flattened, subchelate, raised crest along external margin from propodus to ischium; dactyl regularly curved, tapered to sharp point and toothless, folding to reflexed position when closed, outer margin with fringe of dense, long setae; propodus covered with many low, transverse rugae, twice as long as broad, prehensile margin with large, acute terminal tooth, prominent central tooth and variable smaller ones largest distally; carpus triangular; merus about twice length of ischium, spinulose on distal margins. Second legs shortest, somewhat flattened, dactyls setose. Remaining legs slender, dactyls slightly curved, almost hairless, lacking spines on outer surface but comb of spinules on ventral surface.

Abdomen about $\frac{1}{3}$ longer than carapace, smooth; telson $\frac{1}{3}$ longer than broad, tip regularly and broadly rounded, posterolateral margins variably spinulose; uropods broadly rounded, transverse suture on both rami, proximal part of exopod with slightly spinulose lateral margin ending in strong movable spine.

Measurements in mm.—Length of body: male 26; female 36.

Variation.—The rostrum is variably spinulose, the tip not always spined, and the anterior part of the carapace is usually more granulate than other parts. Rugation of the chelipeds is variable.

Habitat.—Sand and mud near shore to 14 m.

Type-locality.—Naushon Island, Mass.

Known range.—Bass River, Vineyard Sound and Elizabeth Islands, Mass., to Bogue Sound, N. C.

Remarks.—Thompson's (1903a) complete account of this species at Woods Hole includes a well-illustrated, detailed description of adult and larval stages as well as biological notes and comparisons with other thalassinideans. She studied the type male and an ovigerous female dug from "a burrow with a peculiar funnel-shaped mouth" in sand at a depth of about 10 inches at Ram Island, Woods Hole Harbor, in July, 1899. From plankton she reconstructed a larval development consisting of five stages, the first appearing in mid-July but the last not until near the end of August. Fish (1925) found larvae at Woods Hole in July-September. Sandifer (1973d) reported larvae in plankton from Virginia coastal waters and lower Chesapeake Bay at least in July and August, and summarized the above published accounts of larvae as well as others in Narragansett Bay in August (Hillman 1964) and

Delaware Bay in August-October (Deevey 1960). Goy and Provenzano (1978) reared first stage zoeae taken in the mouth of Chesapeake Bay off Cape Henry, Va., in June and July to early juvenile stages in the laboratory in salinity of 25‰ at 25°C in a darkened incubator. Six or seven zoeal stages and a postlarva (described and illustrated) developed on a diet of *Artemia salina* nauplii, but early juveniles fed only on detritus and did not burrow. Thompson (1903a) also recorded notes on the first two postlarval stages (6 and 10 mm long). These colorless stages crawled on the bottom, hid but did not burrow in sand supplied them, and ate considerable diatomaceous matter but did not take animal matter during the period of observation. In all movements, the abdomen was extended and the chelipeds held stiffly in front, "thumbs" pointed inward and "elbows" not flexed. She pointed out that these stages closely resemble the adult.

The record from North Carolina is based on a postlarval specimen 10 mm long, lacking all legs except one of the fifth pair, that was taken in nocturnal surface plankton on flood tide at the UNC-IMS pier, 22 May 1966.

From larval stages reared in the laboratory, Goy and Provenzano (1979) followed subsequent development to the fifth juvenile stage, describing and illustrating their material as well as comparing it with existing museum collections in a general review of the genus, and revising Chace's key.

Langton and Brodeur (1978) reported and illustrated remains of three specimens of *N. crangonoides* taken along with *Callinassa atlantica* Rathbun and other organisms from the stomach of a rougetail stingray, *Dasyatis centroura* (Mitchell), caught in October off the mouth of Chesapeake Bay at a depth of 16 m. They felt that this confirmed Sandifer's (1973d) suggestion that a breeding population of *N. crangonoides* must exist near the mouth of Chesapeake Bay.

Specimens of *N. crangonoides* are by far the largest recorded for this rare genus. Adults of only four species are known, the one listed here, one from Puerto Rico and Yucatan (USNM), one from southern California, and one from French Somaliland, that were discussed and keyed out by both Chace (1939) and Goy and Provenzano (1979). Goy and Provenzano (1978) compared larvae of *N. crangonoides* to those of other Laomedidae that are recorded.

Family Upogebiidae

Carapace with rostrum well developed, spinous, cervical groove delimiting anterior and posterior region of about equal size; linea thalassinica present. Ocular peduncles cylindrical, cornea terminal.

Antennal scale reduced. First maxilliped with slender exopod provided with terminal flagellum, endopod short and epipod rudimentary or absent; second with slender exopod and very short epipod turned internally; third with exopod, endopod pediform, without dentate crest, epipod vestigial or absent. Neither pleurobranchs nor epipods on legs; first legs equal, chelate, subchelate or simple; second to fourth legs simple; fifth subchelate or chelate. First pleopod present in female only, second to fifth similar, foliaceous, without appendix interna. Exopod of uropods not lobed. (After de Saint Laurent 1973.)

Genus *Upogebia* Leach [1814]

Leach [1814]:400.—Hemming 1958b:143.

The genus *Upogebia* has a fossil record extending back to the Upper Jurassic (Glaessner 1969).

Upogebia affinis (Say)

Fig. 133

Gebia affinis Say 1818:241.

Upogebia affinis.—Hay and Shore 1918:408, pl. 29, fig. 9.—Schmitt 1935b:196.—Williams 1965:103, fig. 60.—1974c:16, figs. 44A-B (key).—Thistle 1973:23 (key).

Recognition characters.—Integument, except dorsal part of carapace and of legs, more or less membranous. Carapace about half as long as above, anteriorly rugose and covered with short, rigid hairs. Rostrum large, flanked on each side at base by large spine, spiny beneath in midline. Small upcurved spine behind eye on anterior margin, and minute lateral spine behind cervical groove. Eyestalks concealed, pubescent above; corneal surface small. Antenna little less than twice as long as carapace.

Chelipeds stout, fringe of long hairs below; hands with external, dentate ridge above, median row of acute spines and internal line of stiff hairs; fixed finger curved, dactyl longer, denticulate above at base, cutting edges of both fingers toothed near base; carpus grooved on outer face with row of small teeth on inner margin, and 6 acute spines along distal margin above; merus with small spine above and row of spines beneath. First pair of walking legs hairy at tips and along lower margin; merus with strong spine at base. Remaining legs hairy at tips.

Abdomen gradually increasing in width from first to fourth segment, fifth narrower posteriorly, sixth subquadrate; lateral portions of third and fourth segments densely pubescent and all with pleura

marked off by an impressed line. Tail-fan densely hairy distally. Uropodal endopods truncate, with median rib and costate outer border; exopods rounded distally and with 2 ridges. Telson broad, subquadrate, with impressed median line.

Measurements in mm.—In an analysis of sexual dimorphism, Thistle (1973) found no difference in overall length of mature males and females; mature shrimp ranged from 27 to 60. Slightly larger specimens are known.

Variation.—Schmitt (1935b) mentioned variability in spination of the lower border of the rostrum and multiple spination or lack of spines behind the cervical groove. Juveniles often lack these spines.

Color.—Gray, blue or yellowish gray dorsally, tinged with light blue medially on tail-fan and on fifth abdominal segment, interlaced with uniform light lines; and oblique blue spot on side of carapace at base of antenna extending posterodorsally; underparts light (various authors).

Habitat.—Burrows on estuarine mud flats and in shallow estuaries; intertidal to 29 m.

Type-locality.—Georgia.

Known range.—Wellfleet, Mass., to Rockport, Tex. (Hedgpeth 1950); through West Indies to Estado de São Paulo, Brazil (Coelho 1966b, 1970; Gomes Corrêa 1968).

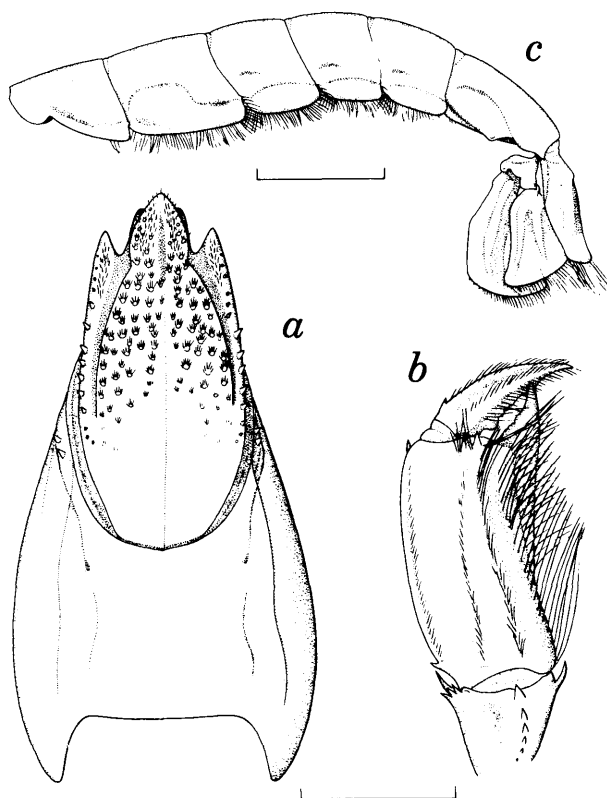


Fig. 133. *Upogebia affinis* (Say). Female: a, carapace in dorsal view; b, chela and carpus, right external view; c, abdomen, lateral view. a-b, USNM 66612; c, USNM 41747; 5 mm indicated.

Ecological observations on *U. affinis* in North Carolina were reported by Pearse (1945). The species inhabits muddy situations in estuaries where salinities are fairly high; experiments show that it is an osmo-conformer above 75‰ seawater, and a strong hyperosmotic regulator in lower salinities down to a lethal limit of 10‰ seawater (Thompson and Pritchard 1969). Its burrowing habits are similar to those of *Callianassa*. Wass (1955) found burrows prevalent in Florida where the marine grass *Halodule wrightii* stabilizes muddy substrates. Dörge (1977) found it associated with marsh creek banks and the marsh side of point bars close to the ocean in Georgia. Burrows examined by Pearse were 30 to 50 cm deep with openings about 30 cm above low-tide mark (McCloskey and Caldwell [1965] reported 60 cm depths). Burrows were often branched, containing several individuals, each in its own branch, and showed one to eight small openings at the surface. In communal burrows Pearse often found two or three ovigerous females and one or two juveniles. Like the burrows of *Callianassa*, those of *U. affinis* are narrowest in the upper part, and Pearse concluded that the animals seldom leave their confines.

In captivity, *U. affinis* made only feeble attempts to burrow. In nature, however, the animals are active and pump water vigorously from the anterior to posterior end of the body by flapping movements of the pleopods. Food is apparently strained from the water by the hairy mouthparts and walking legs, and probably consists largely of organic materials swept in the water current.

Rouse (1970) found ovigerous females nearly year round in southwestern Florida. Hay and Shore (1918) reported them throughout the summer in Bogue Sound, N. C., and they are known from Georgia in March. Sandifer (1973b) described four zoeal stages from plankton in lower Chesapeake Bay and York River, Va., in a salinity range of 13.02 to 32.34‰, and reviewed work of other students of the larvae, mentioning occasional occurrence of a fifth zoeal stage in culture. He found planktonic larvae to be common to fairly abundant from June to October, with peak numbers in July when temperatures ranged between 25° and 27°C. Hay and Shore (1918) found juveniles in plankton tows from early April to late October in North Carolina; and Fish (1925) reported larvae at Woods Hole from

mid-July to the latter part of October, but most abundant in early August. A single female may produce about 10,000 eggs at a time. They are borne on the first four pairs of pleopods. In captivity, more zoeae were hatched at night than in daytime. Pearse cited MacGinitie (1934) for evidence that *U. affinis*, like members of the genus *Callianassa*, may live several years, though there is no evidence supporting this idea for the former.

The commensal alpheid, *Leptalphoeus forceps*, occurs in burrows of *U. affinis* (see Williams 1965). *Upogebia affinis* is one item in the diet of two species of hake in Georgia estuaries (Sikora, et al. 1972).

Upogebia affinis is commonly parasitized in North Carolina by the bopyrid, *Pseudione upogebiae*. Pearse (1952a) described a parasitic isopod, *Phyllodurus robustus*, from a Florida specimen. McCloskey and Caldwell (1965) reported a parasitic fungus, *Entomomyces callianassae*, from the gut of *U. affinis* near Beaufort, N. C., suggesting a link between presence of the fungus and muddy environment, whereas *Callianassa major* in clean sandy habitats nearby contained none.

Section Paguridea

(Hermit crabs)

The hermit crabs have a nomenclatural history as contorted and diverse as their body forms. Modern workers such as Provenzano (1959), Forest and de Saint Laurent (1967), Mayo (1973), and McLaughlin (1974), on the basis of both adult and larval morphology, have followed MacDonald, et al. (1957) in organizing the family categories. This system is followed here, although it raises the categories one grade above that used by Glaessner (1969) and leaves the term Paguridea between infraorder and superfamily.

A bibliography of this group was published by Gordan (1956), compiling most references since Alcock (1905). The pagurids have a long fossil record in North America, species of *Paguristes*, *Petrochirus*, and *Pagurus* being known from the Cretaceous, and *Dardanus* from the Eocene (Rathbun 1935; Glaessner 1969), as well as these and other horizons in other parts of the world; *Clibanarius* may occur in the Eocene of Egypt (Glaessner 1969).

Superfamily Coenobitoidea

Family Diogenidae

Key to Genera and Some Species

1. Abdomen coiled for housing in gastropod shells; chelae and distal articles of walking legs not forming opercular face 2

- Abdomen secondarily straightened for housing in rock cavities or sponges;
 chelae and distal articles of walking legs forming opercular face *Cancellus ornatus*
2. Paired appendages present on first 2 abdominal segments of male and first
 abdominal segment of female; fingers opening and closing horizontally
 *Paguristes*
- No paired appendage on anterior abdominal segments in either sex. . . 3
3. Fingers of chelipeds opening and closing horizontally *Clibanarius vittatus*
- Fingers of chelipeds opening and closing obliquely or almost vertically . . 4
4. Chelipeds markedly unequal, left much larger than right. *Dardanus*
- Chelipeds not markedly unequal, right usually slightly larger than left
 *Petrochirus diogenes*

Genus *Cancellus* H. Milne Edwards 1836

Mayo 1973:6.

Cancellus ornatus Benedict

Fig. 134

Cancellus ornatus Benedict 1901b:772, figs. 1–2.—
 Mayo 1973:18, figs. 5–8.

Recognition characters.—Anterior shield of carapace shorter than maximum width. Inflated anterior margin with rounded postorbital indentations between lateral projections and rostrum, occasionally 1 or more tiny spinules at lateral terminations; a crescentic depression behind this, its anterior border running parallel to rim, but becoming wider behind ocular peduncles and diamond shaped behind rostrum. Rostrum broadly triangular with slightly concave sides, barely exceeding blunt lateral projections. Central gastric region relatively smooth, but with light transverse sculpturing anterolaterally and behind frontal depression. Round to oval gastric pits near posterolateral margin of shield. Calcified portion of cardiac region broader than long, posterior margin straight but corners rounded. Eyestalks $\frac{2}{3}$ to $\frac{3}{4}$ length of shield, nearly parallel sided in dorsal view but broadening proximally, narrowest at point even with antennal acicle; triangular part of eyescales armed with distal spinule. Antennular peduncle reaching cornea when extended. Antennal flagellum longer than eyestalk; acicle reaching about $\frac{1}{3}$ length of eyestalk and armed with usually 3 anterior or anterolateral teeth and 1 on inner margin behind these.

Chelipeds and first pair of walking legs with carpi, propodi and dactyls forming irregularly tuberculate opercular face; propodi of each with longitudinal concavity, that of second legs bound on each side, and that of chelae mesially, by series of compound tuberculate lobes separated by narrow transverse fissures, and of chelae laterally by rounded reticulate face bearing transverse ridges

or irregularly spaced tubercles; carpi rimmed by raised margins of more or less coalesced tubercles; corneous tips on fingers broad and on dactyls of walking legs spinelike.

Abdomen ellipsoidal, covered with many short setae. Female with 4 biramous pleopods on either right or left side, large females with hardened strips at base of and mesial to pleopods. Sixth abdominal tergite broadly hexagonal, $\frac{1}{3}$ broader than long, anterior part larger than posterior, rounded transverse carina extended to blunt triangular lateral projection. Ridge on each side of anterior margin armed with 8–11 strong uneven spines, single spine (sometimes bifid) anterior to each lateral projection, and more or less toothed ridges on posterior and posterolateral borders.

Measurement in mm.—Anterior shield: males and females, length to 9.4.

Variation.—Spinination and tuberculation become less accentuated with increasing age (Mayo 1973).

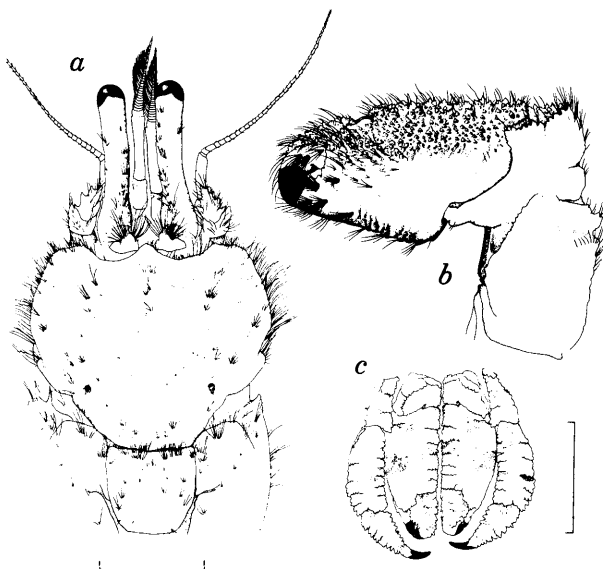


Fig. 134. *Cancellus ornatus* Benedict. Male: a, anterior part of body in dorsal view. Female: b, right cheliped; c, chelipeds and second legs in frontal view; 5 mm indicated (from Mayo 1973).

There are minor sexual differences in ornamentation of the opercular face, the longitudinal groove of the palm being more distinct in females and the tubercles more irregular. These and other minor differences have suggested the existence of a similar second species to some authors, but Mayo took a conservative view. Pleopods of females may be on either side of the abdomen.

Color.—In recently preserved specimens, dark violet on a cream-colored background with scattered red and orange markings, mainly in depressions. Large dark violet patches on carapace, particularly on anterior sculptured areas; a distinct red spot on each side of shield just anterior to gastric pit, and a broad pigmented spot on side of thorax below lateral margin of carapace; anterolateral corners of cardiac region also with a concentration of color.

Opercular surface with somewhat rectangular areas of pigmentation creating checkerboard effect with legs drawn together; undersurface of legs and coxal segments cream with scattered red markings, ambulatories generally cream with violet spots and banding, and some red spots.

Dorsal surface of ocular peduncles violet with small diffuse patches of red and white or cream-colored tubercles; undersurface white with orange patches and an indistinct longitudinal line along lateral surface. Maxillipeds with pigmented band around most segments. Antennules pale orange or cream with yellow flagella. Eye scales with patches of color on cream background; antennal acicles with red markings and a pigmented band around middle of fifth peduncular article.

Symmetrical red patches on sixth abdominal tergite and telson; uropods cream and slightly nacreous with light red patches.

One striking female had brownish violet on brownish red instead of violet. In preservation the violet seems to fade quickly, but other colors persist longer (paraphrased from Mayo 1973).

Habitat.—Members of this secondarily almost symmetrical hermit crab species are not associated with mollusk shells. Of the 10 specimens reported here or elsewhere, 8 are females, 2 are males. Each was a solitary specimen. Both males were associated with siliceous sponges at depths of 55–366 m; females associated with housing were in calcareous rock at 73–110 m.

Type-locality.—Northeast Gulf of Mexico between Mississippi Delta and Cedar Keys, Fla., 28°45'N, 85°02'W, 55 m.

Known range.—Off Cape Fear, N. C., 33°43'N, 76°40'W to 33°42.7'N, 76°40.2'W, 90–110 m (*Eastward* Stn. 1087, UNC-IMS 2397) (Herbst, et al. 1978) through eastern Gulf of Mexico, Greater and Lesser

Antilles, to near Los Abrolhos off central Brazil in a depth range of 37–366 m.

Remarks.—Mayo (1973) gave a full review of the genus *Cancellus*, pointing out probable close relationships among *C. ornatus* and *C. viridis* of the western Atlantic and *C. tanneri* of the eastern Pacific Ocean. The ovigerous female from North Carolina was collected in April in porous calcareous rock.

Genus *Clibanarius* Dana 1852

Dana 1852:122.—China 1966:254.

Clibanarius vittatus (Bosc)

(Striped hermit crab)

Fig. 135

Pagurus vittatus Bosc [1802]:78, pl. 12, fig. 1.

Clibanarius vittatus.—Hay and Shore 1918:410, pl. 30, fig. 9.—Provenzano 1959:371, fig. 5D.—Holthuis 1959:141, figs. 26, 27.—Williams 1965:120, fig. 97.—Forest and de Saint Laurent 1967:104.—Coelho and Ramos 1972:170.—Felder 1973:32, pl. 3, fig. 20.

Recognition characters.—Anterior shield of carapace subquadrate, distinct groove behind anterior margin, few tufts of hairs along lateral margin. Front with rostrum acute, triangular, slightly more prominent than lateral projections. Eyestalks almost as long as width of shield, nearly cylindrical, cornea not dilated, right eyestalk occasionally slightly shorter than left; eye scales narrow, approximate at tips but well separated at bases, margin with 1 to 4 spines, terminal largest. Antennal peduncles reaching to at least $\frac{3}{4}$ length of eyestalks; acicles acute, with 3 to 5 spines on inner margin, flagella reaching tips of walking legs.

Chelipeds equal, sparsely hairy; hands thick, inflated, twice as long as broad, covered thickly above, sparingly below, with variable, somewhat blunt spines, few darker than color of hands and with tufts of setae springing from bases; fingers opening horizontally, heavy, toothed and somewhat gaping at base, distal cutting edges corneous, extending along upper side; carpus as long as palm. Walking legs (legs 2 and 3) exceeding chelipeds by over half length of dactyls, tips corneous; 2 distal articles with numerous bundles of hairs.

Measurements in mm.—Anterior shield: male, length 17.4, width 14.4; female, length 14.9, width 12.5.

Color.—Greenish to dark brown with longi-
tudi-

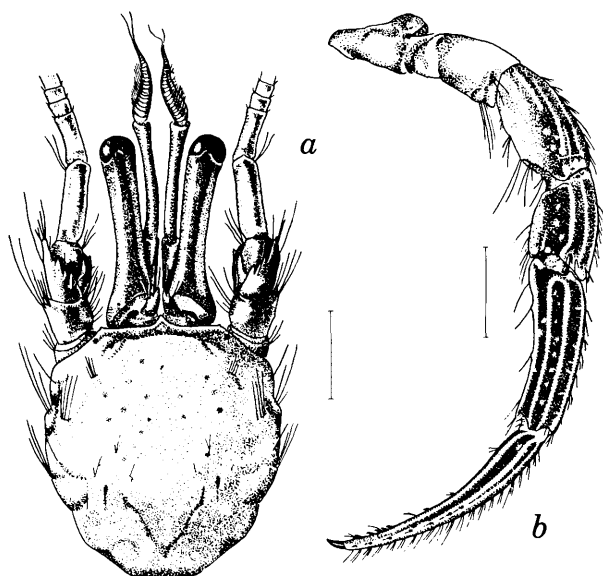


Fig. 135. *Clibanarius vittatus* (Bosc). a, Anterior part of body in dorsal view; b, third leg; a, 1 cm; b, 5 mm indicated (from Holthuis 1959).

nal stripes of gray to white; antennular peduncles light above, dark laterally, with orange flagella; tubercles on outer surface of chelae bluish white; propodus of walking legs with 4 pairs of light, longitudinal stripes continuous with similar stripes on dactyl and carpus, 1 of ventral stripes usually somewhat diffuse (Provenzano 1959; Holthuis 1959).

Habitat.—Common on harbor beaches, especially on borders of mud flats (Pearse, et al. 1942) in a variety of gastropod shells (Holthuis 1959); often on rock jetties or high on bay shores (Whitten, et al. 1950); near water line to 22 m.

Type-locality.—"Les côtes de la Caroline."

Known range.—Potomac River, Gunston, Va., to Florianopolis, Santa Catarina, Brazil (Forest and de Saint Laurent 1967).

Remarks.—This large species is one of the commonest conspicuous hermit crabs of the shore region of the Carolinian Province. Holthuis (1959) gave a history of its early recognition by explorers and naturalists, and Forest and de Saint Laurent (1967) discussed variation.

Ovigerous females have been reported from Surinam in July and August, North Carolina in June (Kircher 1967), South Carolina in July and August (Lang and Young 1977), Florida in October (Provenzano 1959), and spring in Texas (Fotheringham 1975). In one experiment at 25°C in salinities ranging from 15 to 40‰ (Kircher 1967) there were usually 5 zoeal stages (occasionally 4) and a glaucothoe. Survival to first crab stage occurred at salinities of 25, 35 and 40‰, was highest at 20‰,

but low in all cases. Total development time to first crab stage ranged from 57 days at 35‰ to 91 days at 25‰. Lang and Young (1977) studied larval development in South Carolina in filtered 25‰ sea water at 25°C under light conditions of 15 L/9 D hours, describing and illustrating larval stages as found by Kircher and passed through in about 76 days. Young and Hazlett (1978) showed by experiment in an array of salinities (15–30‰) and temperatures (15°–35°C) that no development occurred in any salinity at 15°C, but that partial development occurred in all other test conditions. Metamorphosis to juvenile crab was noted only at salinities of 25 to 30‰ in combination with temperatures of 25° to 30°C. Development time was decreased at higher temperatures, and it was suggested that the geographic distributional limits in the north are governed not by adult tolerances (survival at 5°C) but by inability of the species to establish a breeding population where time for larval development and metamorphosis is not sufficient. Larvae require two months to reach metamorphosis at 25°C, a condition not met north of Virginia.

In Texas populations the largest crabs, almost all of which are males, begin to leave the shore in early summer, but the smaller females remain until autumn (Fotheringham 1975). In spring, smaller crabs return to the shore area one month in advance of large crabs. The species aggregates in the shallow sublittoral zone in winter; individuals have been found buried in the substrate at 4°C when air temperature was subfreezing. Also in this zone a large hermit is more likely to find a large shell than in the littoral. Fotheringham (1976; 1976a) showed that *C. vittatus* maintained in shells smaller than preferred grow more slowly than those in shells of preferred size and that clutch size is highly correlated with crab size. Shell shortages may limit population size by denying room for growing young, stunting growth, or forcing females into shells that restrict brood size. *Clibanarius vittatus* females bore 1,481–30,520 eggs. Commensals, including polychaetes, gastropods, a hydroid, and xanthid crabs, consumed eggs or zoeae in the laboratory. Such egg predators were encountered in large shells occupied by males more frequently than in shells of the size range occupied by females, however. Fotheringham found a 1:1 overall sex ratio and implied, along with other evidence (1976b), that males monopolize large shells, thereby stunting females and holding down their egg production, thus influencing population structure. The species may migrate to the littoral in spring to breed.

Wright (1973) showed that *C. vittatus* is stung by the hydroids *Podocoryne carnea* and *Hydractinia*

echinata, and almost always avoids shells harboring them.

Behavior studies (Hazlett 1968a) show that aggressiveness in *C. vittatus* increases with size and that interacting crabs probably react to absolute size rather than relative size differences. If two animals are very different in size and their paths cross, they probably will not alter their behavior. If they do react, the larger will not execute a display (Hazlett 1972) nor will it react to execution of display by the smaller. If either retreats, it will almost certainly be the smaller. If the two are similar in size, they will probably interact and probability of the larger winning will not be much above chance. From experiments, it is clear that feeding behavior can be initially elicited by chemical stimuli which affect receptors in the antennules (Hazlett 1968b). Sight of a piece of fish does not act as a stimulus, though it can act as a stimulus for orientation once the response has been elicited chemically. Grasping ac-

tion is oriented primarily by visual stimulus; dark objects seem more effective than light colored. Hazlett (1966b) also briefly described courtship and mating.

Caine (1975), analyzing the relationship between feeding and masticatory structures, found stomach contents of *C. vittatus* to be composed of 40% scavenged material, 40% detritus, and the remainder presumably of muddy substratum.

Clibanarius vittatus is far more capable of resisting desiccation than are *Pagurus longicarpus* and *P. pollicaris*, an adaptation that enables it to survive intertidal exposure, especially during high daytime temperatures in summer (Young 1978a).

Genus *Dardanus* Paulson 1875

Paulson 1875:96 (translation).—Hemming 1958:163.—Provenzano 1959:372.

Key to Species

1. Propodus of second left walking leg conspicuously hairy, with lateral longitudinal ridge paralleled by groove; ridge crossed by rugae . . . *D. fucosus*
Propodus of second left walking leg not hairy, without lateral longitudinal ridge or groove; rugae arranged in herringbone pattern . . . *D. insignis*

Dardanus fucosus Biffar and Provenzano

Fig. 136

- Pagurias insignis*.—Benedict 1901b:141(part).
Dardanus venosus.—Verrill 1908a:441, text-figs. 58, 59; pl. 26, figs. 4a, 5a.—Schmitt 1935a:201, fig. 62 (part).—Provenzano 1959:374, fig. 6 (part).—Holthuis 1959:153.—Cerame-Vivas, Williams, and Gray 1963:157.—Williams 1965:123, fig. 99.
Petrochirus diogenes.—Provenzano 1963c:242, figs. 1–8.
Dardanus fucosus Biffar and Provenzano 1972:782, figs. 1A–4A, 5B, 6B.

Recognition characters.—Anterior shield of carapace slightly longer than width of front, nearly smooth but shallow cordate depression behind front, few tufts of hairs near sides and scattered elsewhere; anterior margin lacking rostrum, lateral projections between bases of eyestalks and antennae prominent, roughly triangular, blunt, surmounted by blunt spinule, and hairy on frontal edge. Eyestalks stout, slightly constricted in middle, extending to tips of antennal peduncles or slightly beyond, tuft of setae just behind dilated cornea; eye scales widely separated, inner margins straight, tips bearing several spines. Antennular peduncles

exceeding cornea by $\frac{1}{3}$ length of terminal peduncular article. Acicles short, reaching midlength of eyestalks, armed with small sharp spines.

Chelipeds unequal, left much larger than right; opposed edges of fingers with low white teeth, tips dark, corneous, spooned. Major chela with outer surface covered by scalelike tubercles separated by fan-shaped fringes of appressed hairs, inner surface smooth, mesial margin bearing row of about 7 sharp at least partially horny-tipped spines continued as row of decreasing appressed spines on dactyl and as well-developed spines on carpus; carpus with smaller sharp spines and few setae scattered over surface. Minor chela narrower, lacking scalelike tubercles on outer surface and with long setae rather than appressed bristles. Walking legs (legs 2 and 3) with dactyls longer than propodi, longest in first pair; second left walking leg markedly different from others, with dactyl and propodus broadened, fringed with hairs and with lateral longitudinal ridge paralleled by groove, ridge crossed by numerous rugae; dactyl with shallow groove on ventral margin bounded at each side by row of setae in tufts.

Measurements in mm.—Anterior shield: male, length 18.8, width 17.8; ovigerous female, length 11.7, width 11.

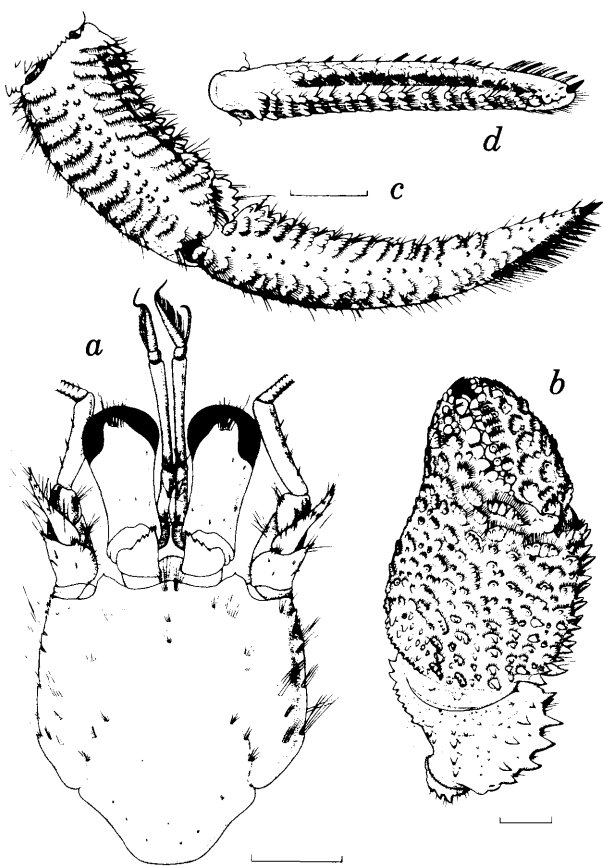


Fig. 136. *Dardanus fucosus* Biffar and Provenzano. Male: a, anterior part of body in dorsal view; b, left chela and carpus, external view; c, second left walking leg, propodus and dactyl, lateral view; d, same, dactyl, ventral view; a-d, 5 mm indicated (USNM 103342).

Variation.—Prominence of surface ornamentation varies individually and increases somewhat with age. Variations include tuberculation of the major palm, and density of the fringe of setae and tuberculation of the external surface of the second walking leg (Biffar and Provenzano 1972).

Color.—Palm of large cheliped basically purple or reddish purple, tubercles dark purple or blue. First and second walking legs with narrow bands of brown-orange on merus, carpus, and propodus, width of band on carpus or propodus about 0.2–0.3 length of segment. Cornea, in life, bluish or greenish with broad black bar running horizontally when viewed from front (paraphrased from Biffar and Provenzano 1972).

Habitat.—The species occurs on a variety of mud, shell, and coral bottoms at depths ranging from that of an eel grass bed in the moat at Ft. Jefferson, Loggerhead Key, Tortugas, to 134 m off Tobago (Young 1978 reported it to 365 m). Specimens from the Carolinas are often in the bryozoan, *Hippoporida*, “Texas longhorn shells” (Deichmann 1954).

Type-locality.—Off French Guiana-Brazil border, 5°29'N, 51°37'W, 64 m, Oregon Stn. 4202.

Known range.—Near Cape Hatteras, N. C., 35°02'N, 75°26'W, to off Amapá, extreme northern Brazil, 4°2'N, 50°33'W.

Remarks.—*Dardanus* contains species of such remarkable similarity that identification is a problem. The newly described *D. fucosus* was formerly called *D. venosus*, which is a strictly tropical western Atlantic species (Biffar and Provenzano 1972). These authors pointed out morphological differences in both adults and larvae. The best character for separating adults is presence of a shallow ventral groove on the dactyl of the second left walking leg in *D. fucosus*, and lack of this in *D. venosus*. Nowhere in the Carolinian Province should the two species normally occur together.

Ovigerous females are known more or less year round: in February from the Guianas and extreme northern Brazil, May from Guyana, June from Florida, July from Panama to French Guiana, September from North Carolina and the Guianas, October from Venezuela, and in November from extreme northern Brazil (Biffar and Provenzano 1972), also July to September in Georgia.

The glaucothoe described by Provenzano (1963b) as that of *Petrochirus diogenes* was later found to be *D. fucosus* (Provenzano 1968; Biffar and Provenzano 1972).

Dardanus insignis (Saussure)

Fig. 137

Pagurus insignis Saussure 1858:453, pl. 3, figs. 20, 20a.

Dardanus insignis.—Verrill 1908a:446, text-fig. 60; pl. 26, figs. 4b, c, 5b.—Williams 1965:124, fig. 100.

Recognition characters.—Anterior shield of carapace longer than width of front, with scattered clumps of setae, roughened slightly near anterior and anterolateral margins. Anterior margin lacking rostrum; lateral projections on front triangular, thickened, prominent, surmounted by blunt spinule, and hairy on frontal edge. Eyestalks stout, slightly constricted in middle, exceeding tips of antennal peduncles, tuft of hairs at base of dilated cornea; eye scales prominent, well separated, serrated distally with strong mesial pair of spines separated somewhat from smaller more lateral series of 4 spines by notch often obscured by tuft of setae. Antennal peduncles somewhat exceeding eyestalks. Acicles long, reaching to base of cornea, with few spines and hairs arranged in spiral line

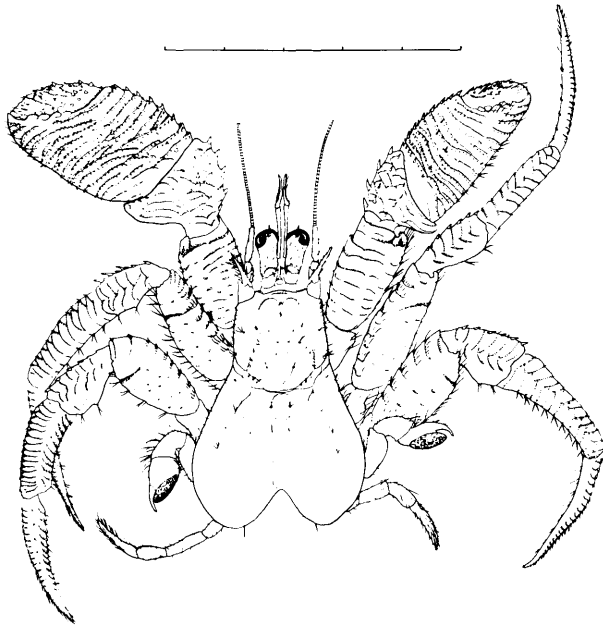


Fig. 137. *Dardanus insignis* (Saussure). Anterior part of male in dorsal view, 5 mm indicated (from Williams 1965).

originating on inner surface at base and curving across dorsal surface to termination on lateral surface near tip.

Chelipeds heavy, left larger than right, covered with ciliated, tuberculate rugosities becoming bolder and more diagonal distally on hands and fixed fingers; dactyl of major chela with ciliated rugosities somewhat diagonal, those on minor dactyl irregularly arranged; opposed edges of fingers with heavy white teeth, tips dark; spine on crest of meri, outer surface of carpi, and hands, largest spines on upper mesial border; row of spines on lower mesial border of merus and ischium. Walking legs (legs 2 and 3) strong, with rugose pattern similar to chelipeds and forming herringbone pattern on outer surface of propodus of large second left walking leg; dactyls of walking legs with crest of spines dorsally, that of left second with crest of spines also ventrally and continued on propodus.

Measurements in mm.—Anterior shield: male, length 17.5, width 15.5; ovigerous female, length 10.6, width 10.6.

Color.—Ground color yellowish; rugosities tan near body becoming maroon on chelipeds and first two pairs of walking legs distally, proximal rugae on hands with reticulate maroon pattern on yellowish background; anterior shield mottled tan; eyestalks banded alternately with maroon, yellow, and tan.

Habitat.—In both shells and calcareous worm tubes (Hazlett 1966); some specimens have been found in the bryozoan "Texas longhorn shells"

(Deichmann 1954); 22 to 260 m (Wenner and Boesch 1979; Wenner and Read 1982).

Type-locality.—Guadeloupe.

Known range.—Off Oregon Inlet, N. C., 31 m (Cerame-Vivas, et al. 1963), to Port Aransas, Tex.; through West Indies to Guadeloupe.

Remarks.—Until the above northern record, another NE of Cape Hatteras, 35°21'N, 74°53'W, 101 m (Musick and McEachren 1972) and a third on the reef SE of Cape Lookout, 70–90 m (Cain 1972) were established, this species was known only from beyond the 183-m curve in the Carolinas. Ovigerous females are known from Georgia in June, and Florida in March, April, June–August.

Provenzano (1963b) described the glaucothoe stage of *D. insignis* in plankton from south Florida, comparing it to glaucothoes of similar species. Hazlett (1966a) described aspects of the behavior of *D. insignis*, an active species, comparing cheliped and leg displays, body posture and shell fighting to those of *Petrochirus diogenes*. Kellogg (1971) observed *D. insignis* kill and remove a *Fasciolaria hunteri* from its shell prior to using the shell for new housing.

Genus *Petrochirus* Stimpson 1858

Stimpson 1858:233 (71).

Petrochirus diogenes (Linnaeus)

Fig. 138

Cancer Diogenes Linnaeus 1758:631.

Petrochirus bahamensis.—Hay and Shore 1918:410, pl. 30, fig. 6.—Schmitt 1935a:206, fig. 66.—Provenzano 1959:378, fig. 8.—1961:153.

Petrochirus diogenes Holthuis 1959:151.—Williams 1965:122, fig. 98.—Provenzano 1968:147, figs. 1–12.

Recognition characters.—Anterior shield of carapace flattened, about as broad as long, rough, uneven, and with scattered tufts of hairs; front trilobate, rostrum about as long as lateral projections. Eyestalks straight, moderately dilated distally, with tuft of setae above corneal surface and scanty tufts along length; eye scales broad basally, acute anteriorly with indistinct serrations. Antennular peduncles equaling or exceeding eyestalks. Antennal peduncles shorter than eyestalks; acicle slender, hairy, and minutely spined.

Chelipeds massive, subequal, right slightly larger; hands and carpi coarsely roughened with grouped tubercles separated by appressed setae on upper and, to some extent, lower surfaces, becoming spi-

nose along inner margin; fingers opening obliquely, major chela with fingers tuberculate on crushing edges, minor chela with fingers somewhat spooned, cutting edges sharp, tips corneous. Walking legs (legs 2 and 3) with carpus ornamented above as chelae; propodi similar with clusters of hairs beneath; dactyls with slightly twisted rows of spines and dense setae; propodi and carpi, especially of first walking legs, with dorsal row of dark-tipped spines.

Measurements in mm.—Anterior shield: male, length 36, width 34; female, length 20, width 20.

Color.—Generally reddish; chelipeds reddish except between fingers, and white spots on carpal articles; antennal and antennular peduncles longitudinally striped with red and white, antennal flagella transversely banded with red and white (Provenzano 1959).

Habitat.—Mud, mud and shell, and sand bottoms. Common on shrimping grounds near Tortugas, Fla. (Provenzano 1959), off Mississippi between 18 and 92 m (Franks, et al. 1972), in the western Gulf of Mexico (Hildebrand 1954, 1955), and southeast of Cape Lookout, N. C., in about 33 m, but young are found also in Beaufort, N. C., harbor (Kellogg 1971); in *Thalassia* beds in Belize (B. Kensley, personal communication); to 128 m off South Carolina (Wenner and Read 1982).

Type-locality.—Near shores of Bahama Islands (Catesby 1743 [1754 ed. in Holthuis 1959]).

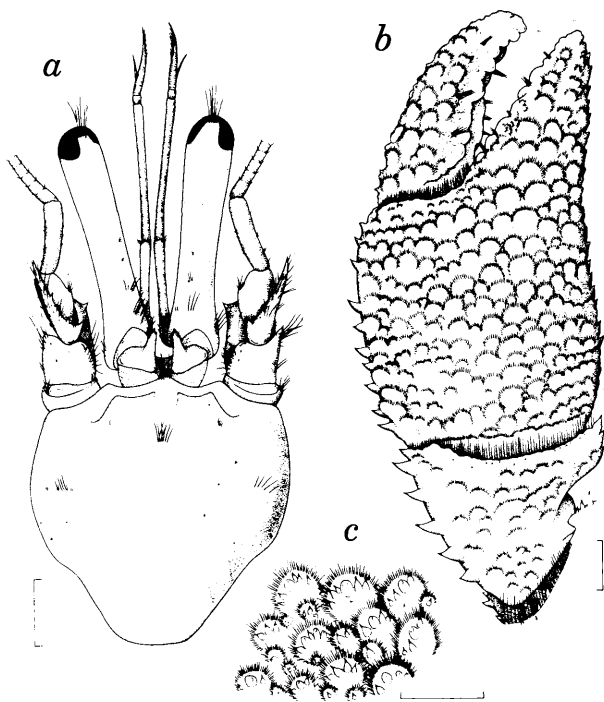


Fig. 138. *Petrochirus diogenes* (Linnaeus). Female: a, anterior part of body in dorsal view; b, right chela and carpus, external view, and c, grouped tubercles enlarged; a-c, 5 mm indicated (USNM 136870).

Known range.—Off Cape Lookout, N. C., through Gulf of Mexico and West Indies to off Ilha de São Sebastião, Brazil, 23°42.5'S, 45°14.5'W (Forest and de Saint Laurent 1967).

Remarks.—The genus *Petrochirus* has a reported fossil record extending from the Cretaceous to the present in North America (Rathbun 1935). Toulou (1911) considered the Miocene form from Panama to be conspecific with the living species in the West Indies region, but Rathbun (1918a) considered it as distinct (*P. bouvieri*) and possibly ancestral to the modern species.

Petrochirus diogenes is the largest hermit crab in the Carolinian fauna and this feature, plus its coarsely tuberculate, ruddy appendages, makes it conspicuous. The species inhabits tun and murex shells on the North Carolina scallop ground off-shore, but the young in harbor channels are usually in *Polynices* or *Terebra dislocata* shells in poor condition (Kellogg (1971). Kellogg observed a *P. diogenes* inhabiting a tun shell tear off the operculum of a *Busycon carica*, kill the mollusk and remove it from its shell in 24 hours and then adopt the shell as new housing. Caine (1975) found that scavenged material constituted 45%, prey 40% of diet, plus algae which may or may not be incidentally ingested. Kensley (personal communication) observed *P. diogenes* sifting through coarse sediments in Belize, and feeding on the exposed polychaetes. A common commensal is the porcellanid crab, *Porcellana sayana*, and other commensals on the shells carried by the crab, such as *Crepidula plana* (Say), bryozoans (*Scrupocellaria* sp.), tubicolous worms (*Hydroides* sp. and *Spirorbis* sp.) as well as other species, are mentioned by Pearse (1932b). An association between the sea anemone *Calliactis tricolor* in this and other crabs was discussed by Cutress and Ross (1969), and Cutress, et al. (1970) from studies in Puerto Rico. Randall (1967) reported *P. diogenes* from stomach contents of the Nassau grouper, *Epinephelus striatus*.

Ovigerous females are known in March from the Virgin Islands (Provenzano 1961), June from Texas, and in August from west Florida (Provenzano 1968). The complete larval development, showing some adaptability to environmental conditions, has been studied in the laboratory (Provenzano 1968). Five or six zoeal stages and a glaucothoe were described. Starved stage I larvae were not able to survive to molt to the next stage, but they survived longer at 20°C than at higher or lower temperatures. At 10° and 15°C larvae fed *Artemia* were also unable to molt and died in about the same time as starved siblings; but at 20°, 25°, and 30°C, fed larvae molted and grew. Viable glaucothoes were not obtained at 20°C; at 25°C they were obtained after

five and six zoeal stages, and at 30°C nearly all glaucothoes developed after five zoeal stages. At all temperatures the first zoeae had a longer mean duration than immediately following stages, but duration increased again in last stages, reaching a maximum in the glaucothoe. Duration of zoeal stages was 50 days at 20°C, and 25 days at the higher temperatures used. Potential planktonic life is estimated to vary from 31 to 43 days at 30°C, 37 to 50 days at 25°C, and 72 to 84 days at 20°C.

Pearse (1932a) determined the freezing point of *P. diogenes* blood (range -1.90° to -2.32°C).

Holthuis (1959) reviewed the complex nomenclatural history of the species, designated the type, restricted the type-locality, and outlined the geographic range.

Genus *Paguristes* Dana 1852

Provenzano 1959:381.—China 1966:256.—Forest and de Saint Laurent 1967:67.

Diagnosis.—Rostrum usually well developed. Eyestalks long and usually slender; eye scales usually spiniform. Chelipeds equal or subequal, left may be somewhat larger; fingers in horizontal plane, tips usually corneous, occasionally calcareous. Fourth legs with dactyl terminal, fifth pair chelate. Male with pair of modified uniramous pleopods on first 2 abdominal segments; female with pair of uniramous pleopods on first abdominal segment only.

Key to Species

(After Provenzano 1959)

1. Rostrum broadly rounded or pointed, but not advanced beyond level of lateral projections on front of anterior shield of carapace 2
Rostrum slender and definitely advanced beyond level of lateral projections on front of anterior shield of carapace 4
2. Eye scales separated, ending in an acuminate tip 3
Eye scales adjacent, ending in more than 1 terminal spine *P. hummi*
3. Anterolateral sides of anterior shield of carapace not spiny *P. lymani*
Anterolateral sides of anterior shield of carapace definitely spiny *P. moorei*
4. Anterior shield of carapace not noticeably longer than broad 5
Anterior shield of carapace noticeably longer than broad 6
5. Anterior and lateral margins of shield meeting at almost right angle
Anterior and lateral margins of shield meeting at broadly obtuse or rounded angle *P. sericeus*
Anterior and lateral margins of shield meeting at broadly obtuse or rounded angle *P. triangulatus*
6. Eye scales ending in acuminate tip *P. spinipes*
Eye scales ending in more than 1 terminal spine. *P. tortugae*

Paguristes hummi Wass

Fig. 139

Paguristes hummi Wass 1955:148, figs. 1–4.

Recognition characters.—Anterior shield of carapace longer than wide, surface with few setose tubercles. Rostrum obtuse and shorter than lateral projections, each projection often surmounted by minute spinule. Eyestalks slender, slightly constricted in midlength; eye scales mesially adjacent except for shallow indentations near bases and variably divergent tips armed with 4–7 spines anterolaterally, largest spine at tip. Antennular peduncles reaching almost to tip of eyestalks; acicles with 5 spines on inner margin, smooth laterally.

Chelipeds equal, similar, moderately spined, and

ornamented with plumose hairs longest and most dense at margins of hands; hands twice as long as wide, armed with longitudinal rows of spines on upper surface, outer marginal row with many more spines than intermediate and mesial ones; fingers agape slightly, opposed edges with few small teeth and calcareous denticles, tips corneous; carpus with spine on margins longest and densest distally; merus crested dorsally with spinules and plumose hairs. Walking legs (legs 2 and 3) with propodi $\frac{3}{4}$ length of dactyls, propodus and merus of first pair crested with spinules, second pair with tubercles only; both pairs hairy except for lateral surfaces of meri and inner surfaces of propodi.

Measurements in mm.—Anterior shield: male, length 3.8, width 3.4; ovigerous female, length 2.2, width 2.0.

Variation.—The largest specimen in the USNM collection (paratype 95594, Alligator Harbor, Fla.) is much less ornamented with spines and hairs on the chelae than is normal for other specimens in the series.

Color.—Most distinguishing mark, merus of cheliped with blue patch on inner surface bordered anteriorly by a narrow black line, followed by a similar yellow line (Wass 1955).

Habitat.—Usually found in small sponges, occasionally in *Murex*, and also in the bryozoan "Texas longhorn shell," *Hippoporidea edax*. At the mouth of Tampa Bay, Wass (1955) found it in intertidal pools in mid-October only on the south side of Mullet Key, housed in a variety of small gastropod shells, mostly *Terebra*, but some in *Olivella*, and one in a scaphopod shell.

Type-locality.—Alligator Harbor, Franklin County, Fla.

Known range.—Newport River, N. C., to off Sapelo Island, Ga.; Marco Beach, southwestern Fla., to off Isles Dernieres, La. (28°38'N, 90°55'W); intertidal to 22 m.

Remarks.—Two males, paratypes of nearly identical size (USNM 95595), occur side by side in the same opening of a sponge from Alligator Harbor, Fla. The species is found occasionally in Beaufort, N. C., harbor in shells of *Terebra dislocata* with a

good deal of fouling attached, primarily in shelly areas. It is much more abundant offshore there on rocky outcrops where a variety of sponges and algae thrive, and may feed primarily on algae (Kellogg 1971).

Ovigerous females are known from southwest Florida in February (Provenzano 1959) and northwest Florida in October (Wass 1955).

***Paguristes lymani* A. Milne Edwards and Bouvier**

Fig. 140

Paguristes lymani A. Milne Edwards and Bouvier 1893:49, pl. 4, figs. 13–22.—Williams 1965:116, fig. 92.

Recognition characters.—Anterior shield of carapace slightly broader than long, sides a little hairy and roughened by spiny granules. Rostrum often a rounded lobe falling far short of pointed lateral projections; anterior margin thickened and rounding gradually to lateral margins from lateral projections, posterolateral corners apparently notched in adults. Eyestalks somewhat dilated at base and longer than distance between apices of lateral projections of front; eye scales singly acuminate or with up to 3 unequal spines on anterior border, long hairs somewhat obscuring tip. Antennular peduncles highly variable, exceeding eyestalks by less than half to entire length of terminal article. Tips of antennal peduncles extending $\frac{2}{3}$ – $\frac{3}{4}$ length of eyestalks, slightly exceeding acicles; acicles terminated by spiny fork and often with 3 to 5 spinules on internal or external borders, external spine at base of acicle also spinulose on outer margin.

Chelipeds subequal and similar; hands about twice as long as broad, upper surface covered with rather large, well separated, tubercular granules, many with corneous tips, 4 spines on internal margin of palm; lower margin of palm concave at base of fixed finger; fingers slightly agape, terminated by corneous tips preceded by finely denticulate cutting edges, dactyl with 4 or 5 small teeth behind corneous portion; carpus with 3 rows of spines on upper surface, 4 or 5 larger ones on inner margin, about 6 on outer margin (distalmost largest), and about 6 more on upper surface near inner margin; superior border of merus armed with more or less pointed projections, feebly rugose externally; spines on palm, carpus and merus obscured by long hairs. Walking legs (legs 2 and 3) with long hairs, particularly on upper and lower borders of dactyls; spines on crest of carpus, propodus and base of dactyl, and somewhat reduced ones on inner and outer

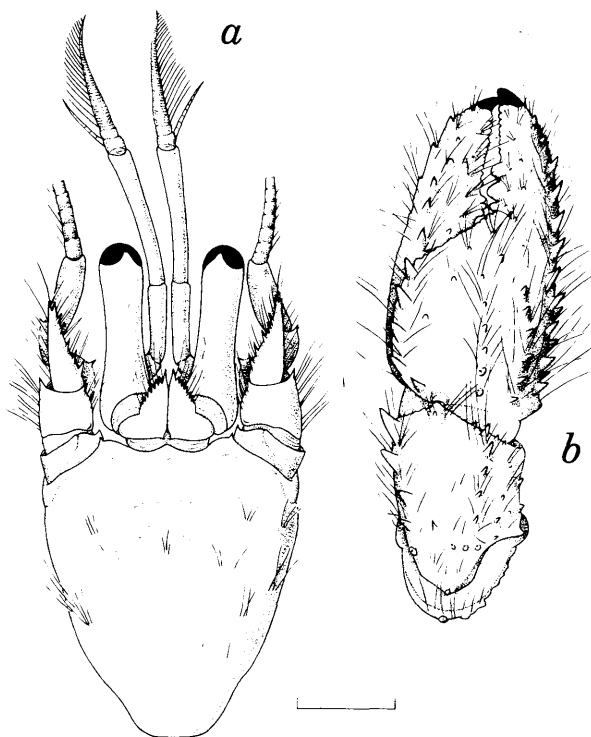


Fig. 139. *Paguristes hummi* Wass. Male: a, anterior part of body in dorsal view; b, right chela and carpus, external view; paratype, 1 mm indicated (USNM 98954).

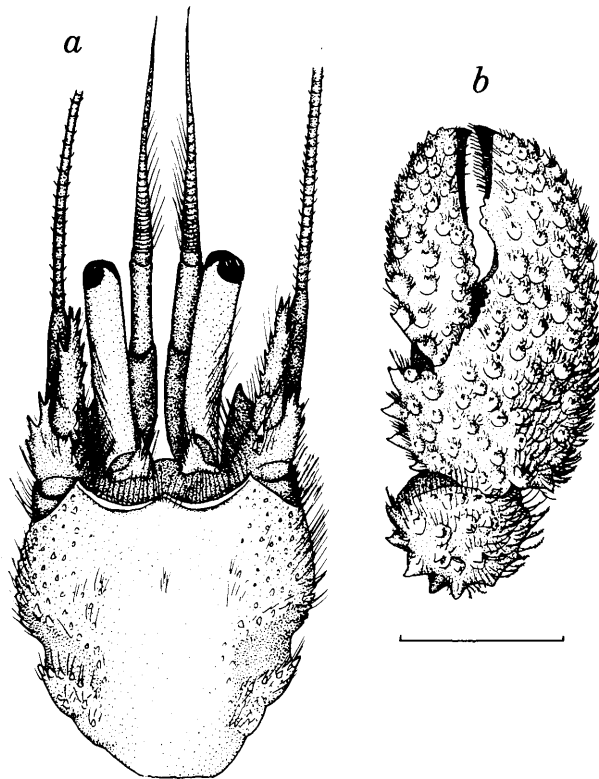


Fig. 140. *Paguristes lymani* A. Milne Edwards and Bouvier. *a*, Anterior part of body in dorsal view; *b*, right chela and carpus, external view; 5 mm indicated (from Williams 1965).

sides of propodus and carpus where rows appear mixed with hairs; dactyls arched, somewhat shorter than combined length of 2 preceding articles, and each terminated by conical claw.

Measurements in mm.—Anterior shield: male, length 7.5, width 7.9; ovigerous female, length 6.4, width 7.0.

Variation.—The spination of the chelipeds may vary in strength and density. Length of the antennular peduncles, in relation to the eyestalks, is highly variable. The eye scales become more dentate with age. The rostrum and lateral projections of the front may reach a common level, and small individuals tend to be hairier than large ones (Milne Edwards and Bouvier 1893). Proportion of the anterior shield changes with age; in young individuals it may be longer than wide.

Habitat.—Museum and published records show that this species has been found housed in small to medium-sized shells belonging to the families Cassididae, Dentaliidae, Nassariidae, Ovulidae, Muricidae, Trochidae, Turridae, and Volutidae; 27 to 1600 m.

Type-locality.—Sand-Key [Fla.], 27 m.

Known range.—Southeast of Cape Lookout, N. C. (150–180 m); Florida Keys to Swan Island off Honduras; through West Indies to Guyana.

Remarks.—Ovigerous females have been taken in February from North Carolina and Florida, May and June from Florida, and November from Guyana.

Paguristes moorei Benedict

Fig. 141

Paguristes moorei Benedict 1901c:144, pl. 4, fig. 3.—Williams 1965:115, fig. 91.

Recognition characters.—(Taken from female holotype.) Anterior shield of carapace slightly longer than broad; upper surface of carapace with few scattered hairs and irregular punctations, more or less iridescent. Rostrum short, obtusely pointed, slightly less advanced than more acute lateral projections. Eyestalks slender, slightly dilated distally, slightly longer than width of anterior shield (8.6 mm); eye scales not adjacent, anterior process acute. Antennular peduncle slightly exceeding eyestalk when extended. Antennal peduncle extending slightly beyond middle of eyestalk; flagellum not exceeding tips of legs, with scattered setae; acicles bispinose at tip (right spine on right acicle broken), row of 4 strong spines on proximal $\frac{2}{3}$ of inner side (right acicle with single external spine).

Chelipeds subequal but of similar form, mesial margins nearly straight; hands short and thick,

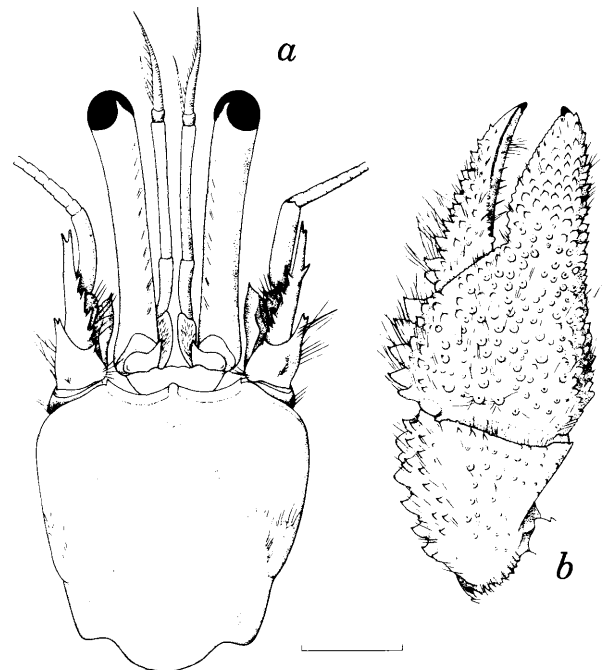


Fig. 141. *Paguristes moorei* Benedict. Female: *a*, anterior part of body in dorsal view; *b*, right chela and carpus, external view; 3 mm indicated (USNM 29207, holotype).

covered dorsally with many tubercles and hairs, but nearly smooth ventrally, row of strong spines on upper mesial border of palm, edges of fingers fitting closely; carpus similar to hands but with fewer tubercles in 2 rows, largest tubercles on mesial upper border; merus prismatic with tubercles on angles. First walking legs (leg 2) with row of spines along upper margin of carpus and propodus.

Measurements in mm.—Anterior shield: holotypic female, length 8.5, width 8.3.

Color.—Yellowish, eyestalks deep orange or crimson below and white above (Hay and Shore 1918).

Habitat.—From near edge of continental shelf.

Type-locality.—Puerto Rico.

Known range.—Edge of continental shelf off Cape Lookout, N. C.; Florida Straits (Hazlett 1966a); Puerto Rico.

Remarks.—*Paguristes moorei* was recorded by Cerrame-Vivas and Gray (1966) as a tropical form occurring off North Carolina. Hazlett (1966a) noted aspects of behavior, comparing the species' displays with those of *P. spinipes* as most active at 15°C, and shell fighting as similar to that of *Clibanarius anomalus*.

Paguristes sericeus A. Milne Edwards

Fig. 142

Paguristes sericeus A. Milne Edwards 1880:44.—Milne Edwards and Bouvier 1893:46, pl. 3, figs. 14–22.—Provenzano 1961:155.—Williams 1965:117, fig. 93.—Provenzano and Rice 1966:54, figs. 1–10.—Pequegnat and Ray 1974:242, fig. 44.

Paguristes tenuirostris Benedict 1901b:143, pl. 4, fig. 1.

Paguristes rectifrons Benedict 1901b:145, pl. 4, fig. 7.

Recognition characters.—Anterior shield of carapace nearly as broad as long, flattened, with several spines on each side; anterior margin as long as ocular peduncles, making nearly right angle with lateral margins; lateral projections low but each terminating in small spine. Rostrum with acute tip often reaching along approximately $\frac{1}{2}$ length of eye scales. Eyestalks slightly narrowed in middle; eye scales small, acuminate at tip. Antennular peduncles extending almost to tips of eyestalks. Antennal peduncles slightly exceeding acicles, terminal article armed with 2 spines; acicles straight, terminated by spiny fork and with 2 or 3 spines on internal and external borders.

Chelipeds subequal, rather short and broad; upper surface of hands and carpi with soft, silky, yellow hairs nearly obscuring surface, many strong granulations becoming corneous at tips scattered

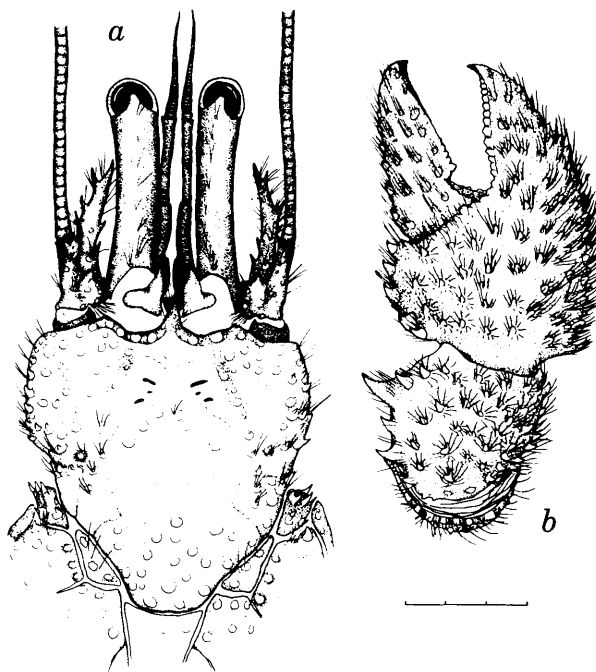


Fig. 142. *Paguristes sericeus* A. Milne Edwards. a, Anterior part of body in dorsal view; b, right chela and carpus, external view; 3 mm indicated (from Williams 1965).

over upper surface; cutting edges of fingers finely and evenly toothed, terminal parts corneous. Walking legs (legs 2 and 3) reaching beyond extended chelipeds; dactyls regularly curved, dactyl of first walking leg 1.5 times length of propodus, of second as long as propodus and carpus combined.

Measurements in mm.—Anterior shield: male, length 11.7, width 9.7; ovigerous female, length 5.9, width 5.8.

Variation.—Provenzano and Rice (1966) pointed out that shape of both the anterior carapace and eyestalks change through development, being quite different even in adults of different sizes. In these, the anterior margin becomes straighter and the eyestalks longer and more slender with increasing age. These differences led Benedict (1901b) to describe *P. tenuirostris* and *rectifrons* as distinct. Spines on sides of the cephalic shield may be worn off occasionally.

Color.—Body orange-red with numerous irregular white spots having darker border of red than general body color; eyestalks usually solid red, occasionally with white spots distally, cornea azure, almost green (from live specimens, and Provenzano 1959, 1961; Provenzano and Rice 1966).

Habitat.—Coral rubble and sand, found in *Strombus*, *Murex*, and *Oliva* (Provenzano 1961, and various authors); 9 to 145 m.

Type-locality.—23°34'N, 83°16'W [near Dry Tortugas, Fla.], 66 m.

Known range.—Off Cape Lookout, N. C.; West Flower Garden Bank, NW Gulf of Mexico to Virgin Islands.

Remarks.—Ovigerous females are known from the Virgin Islands in April (Provenzano 1961) and Florida in May and July (Rice and Provenzano 1965). Illustrations in Milne Edwards and Bouvier (1893) are inaccurate in a number of features; details of the telson and anterior carapace are not shown clearly (Provenzano and Rice 1966).

In addition to their work on allometric changes in body form, Rice and Provenzano (1965) reared and described two zoeal stages and the glaucothoe. In 36–38‰ water at 15°–25°C, half of the larvae were starved, half fed. At 15°C none survived first zoea; at 20° and 25°C both fed and starved larvae survived second zoea. The fed larvae proceeded through glaucothoe and three crab stages at 25°C, and to second crab in 20°C. Starved larvae survived to the glaucothoe stage at 25°C. Total mean time for development to first crab was about 50% greater at 20°C (16.1 days) than at 25°C (10.9 days).

***Paguristes spinipes* A. Milne Edwards**

Fig. 143

Paguristes spinipes A. Milne Edwards 1880:44.—Williams 1965:118, fig. 95.—Forest and de Saint Laurent 1967:68.

Paguristes visor Henderson 1888:78, pl. 8, fig. 3.

Paguristes armatus Hay 1917:73.

Recognition characters.—Anterior shield of carapace convex, considerably longer than broad; frontal margin thickened and drawn out into almost straight-sided, acute rostrum, with tip considerably exceeding rather obtuse lateral projections. Eyestalks considerably longer than greatest width of front but not quite so long as length of anterior shield, somewhat contracted in middle and slightly bent laterally, not much dilated distally; eye scales acuminate. Antennular peduncles extending nearly to tips of, or a little beyond, eyestalks. Antennal peduncles extending about $\frac{1}{2}$ – $\frac{1}{3}$ length of eyestalks; acicles straight, terminated by spiny fork, and with 2 or 3 spines on internal and external borders.

Chelipeds subequal and similar in form, narrow but massive; hands less than half as broad as long; upper surface of hands and carpi covered with conical spines, many with corneous tips, strongest on superointernal border, fingers more than half as long as whole of propodus and terminating in corneous tips, opposed edges with numerous small

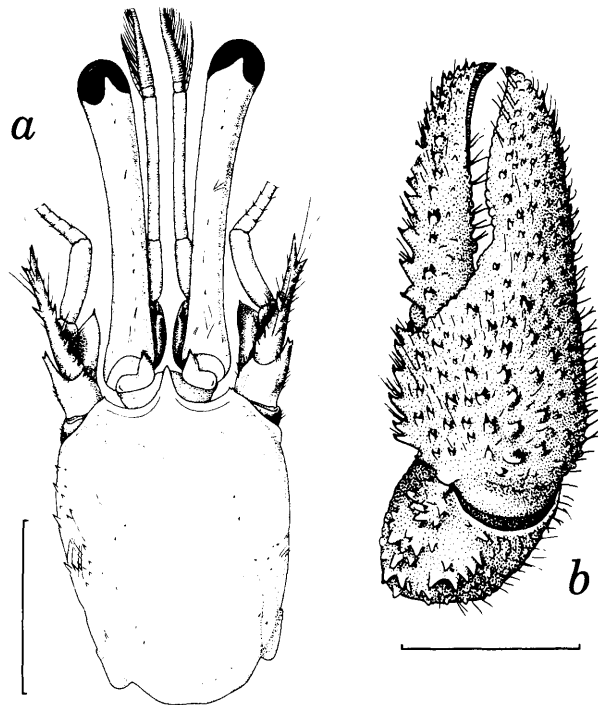


Fig. 143. *Paguristes spinipes* A. Milne Edwards. *a*, Anterior part of body in dorsal view; *b*, right chela and carpus, external view; *a*, 5 mm; *b*, 3 mm indicated (from Williams 1965).

teeth. Walking legs (legs 2 and 3) extending a little beyond chelipeds, ornamented with tufts of setae most numerous and rigid on dactyls; dactyls regularly curved and half again as long as propodi; crest of spines on carpus and propodus extending along part of dactyl of first walking legs, but reduced, and present on carpus only of second walking legs.

Measurements in mm.—Anterior shield: males, length 11.9, width 7.8; female, length 9.5, width 6.6.

Variation.—The eyestalks are somewhat shorter than the front in young individuals but much longer in adults; they are frequently unequal in length. The cardiac region is calcified but the areas lateral to it are variably calcified (Milne Edwards and Bouvier 1893). The antennular peduncles may be shorter than the eyestalks, and the antennal peduncle only half as long as the eyestalks.

Color.—A spot of orange-red on external and internal faces of first walking legs, less definite on 2 following pairs; occasionally, traces of red coloration on anterior part of cephalothorax (Milne Edwards and Bouvier 1893). In alcohol, nearly white, each cheliped with conspicuous orange-yellow band across merus and faint trace of similar band on each walking leg (Hay and Shore 1918).

Habitat.—This deep-water hermit has been taken from shells of *Cassis* and *Xenophora*; 72 to 640 m (Wenner and Read 1982).

Type-locality.—Grenada, 168 m.

Known range.—Gulf Stream south of Cape Lookout, N. C.; off Cape Canaveral to Florida Straits, Sarasota, Fla.; Barbados to Pernambuco, Brazil.

Remarks.—Hazlett (1966a), listing *P. spinipes* as one of the more common deep-water hermits in the Straits of Florida, noted that it was not active at any time in temperatures of 15° or 25°C.

From ovigerous females captured in September off Yucatan in 240–320 m depths, Provenzano (1978) reared larvae and described development of three, rarely four, zoeal stages and a glaucothoe at 20°C. Duration of larval life at this temperature was at least six weeks, far in excess of the planktonic duration known for other members of the genus. He noted that there is evidence of widespread abbreviated development in the genus.

Paguristes tortugae Schmitt

Fig. 144

Paguristes tortugae Schmitt 1933:7, fig. 4.—Provenzano 1959:388, fig. 11A-B, 12D.—Williams 1965:119, fig. 96.—McLaughlin and Provenzano 1974:171, figs. 3; 4a; 5a-c; 6a,b,e,f; 7a-c; 8a-c; 11a; 12a-c; 13a,b,e,f; 14a-d,i.

Recognition characters.—Anterior shield of carapace noticeably longer than broad, dorsolateral surface and margins with numerous small spines or spiniform tubercles; rostrum triangular, in advance of lateral projections, each surmounted by spinule. Eyestalks slender, straight, as long as greatest width of anterior shield, with distinct, often irregular, dark bands distally; eye scales separated by rostrum, anterior process armed with 3 or 4 spines (occasionally 2) decreasing in size from median spine outward. Antennular peduncles reaching to base of cornea or slightly beyond. Antennal peduncles reaching to $\frac{3}{4}$ length of eyestalks; flagella not reaching to tips of chelipeds, setae sparse and moderately short; acicles obscured by hairs, armed with 1 spine on inner edge and at least 3 on outer edge.

Chelipeds equal, thickly covered with hairs, mesial margins of chelae and carpi straight, fitting closely together when retracted; hands with forwardly directed, hooked spines on mesial upper surface (4 or 5); inner margin, outer half, and outer margin of fixed finger; hairs arising along anterior part of base of tubercles giving squamose appearance; palms with dorsal surface flat or slightly convex, margins not appreciably elevated; dactyl with 7 more or less distinct, transverse rows of small,

horny-tipped tubercles, largest on upper margin; fingers with tips corneous, more or less spooned; lower surface of chela smooth except for some tufts of hairs. Walking legs (legs 2 and 3) with heavy fringes of hairs along upper and lower margins and some tufts on lateral surfaces, outer surface smooth; dactyls somewhat longer than propodi, tips dark, corneous, row of similar colored spinules on ventral border; inner surface of dactyls and propodi with squamiform tubercles near upper and lower margins, more pronounced where bases of hairs coincide with squamous tubercles. First walking legs with upper surface of propodus serrate, and few denticles at base of dactyl; 2 rows of spines on carpus, 1 on upper margin and 1 on upper part of inner surface, shallow groove on upper part of inner surface extending distad from carpus. Second walking legs with single row of spines on carpus; merus with 1 or 2 rows of small spines or spinulose protuberances and an anteroventral spine.

Measurements in mm.—Anterior shield: male,

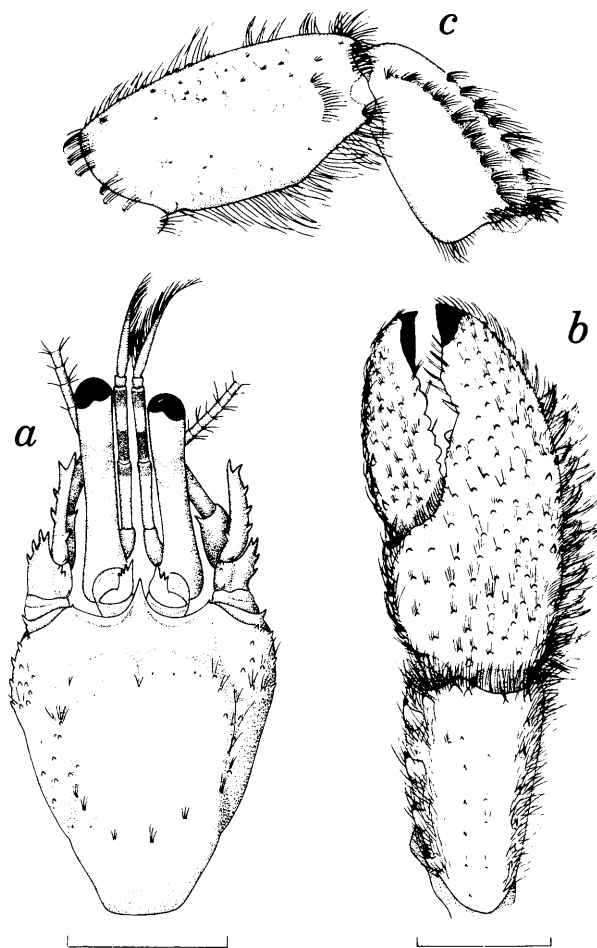


Fig. 144. *Paguristes tortugae* Schmitt. Male: a, anterior part of body in dorsal view; b, chela and carpus, external view; c, right second walking leg, merus and carpus, lateral view; a, 3 mm; b-c, 1 mm indicated (USNM 151492).

length 7.0, width 5.3; ovigerous female, length 5.0, width 3.7.

Color.—"In life: General body color varying from white to red or reddish-orange; ocular peduncles white, circumscribed with 1 or 2, often irregular or interrupted, bands of black near base of cornea; segments of antennular and antennal peduncles each circumscribed with band of black distally. Chelipeds white, pink or reddish, spines usually dark red or reddish-orange. In preservative: Color fading to uniform straw color; ocular peduncles often retaining traces of banding at bases of corneae" (McLaughlin and Provenzano 1974).

Habitat.—The holotype was taken among *Porites*, and part of the type-series in shells of *Astraea* and *Calliostoma*. Usually found on hard or shelly bottom (Tabb and Manning 1961) or in vicinity of corals; intertidal to 91 m (McLaughlin and Provenzano 1974).

Type-locality.—Off Fort Jefferson Dock, Garden Key, Dry Tortugas, Fla.

Known range.—Reefs off Beaufort, N. C., to southern and southeastern Florida; through West Indies to northern Brazil; (?) northern Gulf of Mexico.

Remarks.—McLaughlin and Provenzano (1974) revised the *P. tortugae* complex, treating seven very similar species. Identification of *P. tortugae* in the Atlantic part of the Carolinian Province is simplified because it is the only species of the group known to occur north of southern Florida.

Ovigerous females have been reported from February to October in Florida (Provenzano 1959), in June in North Carolina and August in South Carolina (Holthuis 1959). Behavior of glaucothoes is erratic when first entering shells, few animals being successful on first trial. Even early crab stages are subject to considerable error, suggesting that functional behavior patterns are a result of experience as well as inherited factors (Hazlett and Provenzano 1965).

***Paguristes triangulatus* A. Milne Edwards and Bouvier**

Fig. 145

Paguristes triangulatus A. Milne Edwards and Bouvier 1893:40, figs. 6–12.—Williams 1965:118, fig. 94.

Recognition characters.—Carapace somewhat hairy toward sides, and with scattered hairs on anterior shield; shield little longer than broad; front with thickened margin and pointed rostrum reaching

well beyond broadly angular, sometimes slightly spined, lateral projections. Eyestalks long, slightly dilated but obliquely compressed at tips, line of hairs along dorsal side; eye scales acuminate, somewhat rugose on internal border. Antennular peduncles with about $\frac{1}{4}$ – $\frac{1}{2}$ of terminal article extending beyond eyestalks. Antennal peduncles extending to base of cornea or as little as $\frac{3}{4}$ length of eyestalks; acicles reaching about to middle of eyestalks, spinose on internal and external borders, tip often bifurcate.

Chelipeds subequal, similar, upper surfaces tuberculate and hairy; inner margin of hands, carpi, and bases of dactyls with strong spines corneous at tips; upper surfaces of carpi and meri with few spines and spiniform tubercles corneous at tips. First walking legs (leg 2) with spiny crest on carpi, propodi, and base of dactyls; crest obsolescent on second pair; both pairs setose dorsally, dactyls curved, about as long as 2 preceding articles together. Dactyls of right side a little weaker than left and laterally compressed; proximal end of first left dactyl with cross section in form of curvilinear triangle, broadly rounded internal face forming base and obtusely pointed external face serving as apex; second left dactyl somewhat strong.

Measurements in mm.—Anterior shield: male, length 10, width 9.4; ovigerous female, length 7.5, width 7.0.

Color.—Legs and anterior part of cephalothorax tinted pink (Milne Edwards and Bouvier 1893); eyestalks pink (Benedict 1901b); eyestalks white or

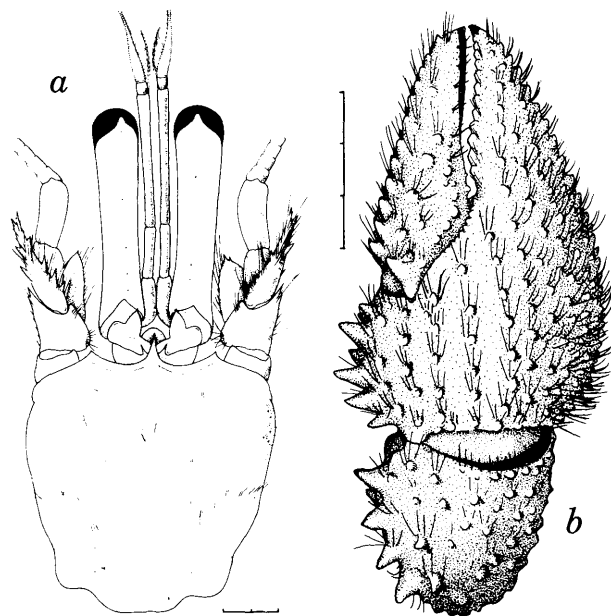


Fig. 145. *Paguristes triangulatus* A. Milne Edwards. *a*, Anterior part of body in dorsal view; *b*, right chela and carpus, external view; *a*, 2 mm; *b*, 3 mm indicated (from Williams 1965).

scarlet, antennal peduncle white, body and legs mottled white (specimens from Georgia).

Habitat.—The species has been observed in *Murex* (see Milne Edwards and Bouvier 1893), *Distorsio*, and *Phalium* shells; 12 to 150 m.

Type-locality.—Barbados, 136 m.

Known range.—Off Oregon Inlet, N. C. (12 m), to Tortugas, Fla.; Barbados; Trinidad.

Remarks.—Cerame-Vivas and Gray (1966) listed *P. triangulatus* as a tropical species in the Carolinian Province. Ovigerous females are known from Florida in August and October.

Superfamily Paguroidea

Family Paguridae

Key to Genera and Some Species

(In part from McLaughlin 1981)

1. Ischium of third maxilliped with mesioventral accessory spine near anterior end of mesial dentate crest; vas deferens of male not protruding . . . 2
 Ischium of third maxilliped without mesioventral accessory spine near anterior end of mesial dentate crest; left vas deferens of male protruding and spirally coiled *Iridopagurus caribbensis*
2. Hands more or less extended, not operculiform; fingers opening and closing horizontally; females without paired pleopods on first abdominal segment 3
 Hands operculiform, often flexed at nearly right angle to carpus, fingers opening and closing obliquely or at right angle to long axis of limb; females with paired pleopods on first abdominal segment, "Pylopagurid-like" genera 4
3. No paired appendages on first abdominal segment of either sex *Pagurus*
 Paired, short, slender pleopods on first abdominal segment of male (next 4 segments have unequally biramous appendage on left side) *Tomopaguroopsis problematica*
4. Propodus of fourth legs with 1 row of scales 5
 Propodus of fourth legs with 2 or more rows of scales 7
5. Uropods symmetrical or nearly so *Pylopagurus discoidalis*
 Uropods markedly asymmetrical 6
6. Spines of chelae with basal rosettes *Rhodochirus rosaceus*
 Spines of chelae without basal rosettes *Phimochirus holthuisi*
7. Left chela triangular in cross section, dactyl and fixed finger not dorsoventrally flattened *Anisopagurus pygmaeus*
 Left chela not triangular in cross section, dactyl and fixed finger dorsoventrally flattened *Manucomplanus corallinus*

Genus *Iridopagurus* de Saint Laurent-Dechancé 1966

de Saint Laurent-Dechancé 1966:152.

Iridopagurus caribbensis (A. Milne Edwards and Bouvier)

Fig. 146

Spiropagurus caribbensis A. Milne Edwards and Bouvier 1893: 116, pl. 8, figs. 26–30.

Spiropagurus dispar.—Williams 1965:133, fig. 108.
Iridopagurus caribbensis.—de Saint Laurent-Dechancé 1966:167, figs. 14, 27, 32, 37.

Recognition characters.—Carapace smooth but with hairy tracts on anterior shield and especially on anterior portion of membranous branchial areas; anterior margin with broadly rounded rostrum and equally advanced acute lateral projections. Eye-stalks with cornea dilated, width slightly more than half length of stalk; stalk slightly exceeding proxi-

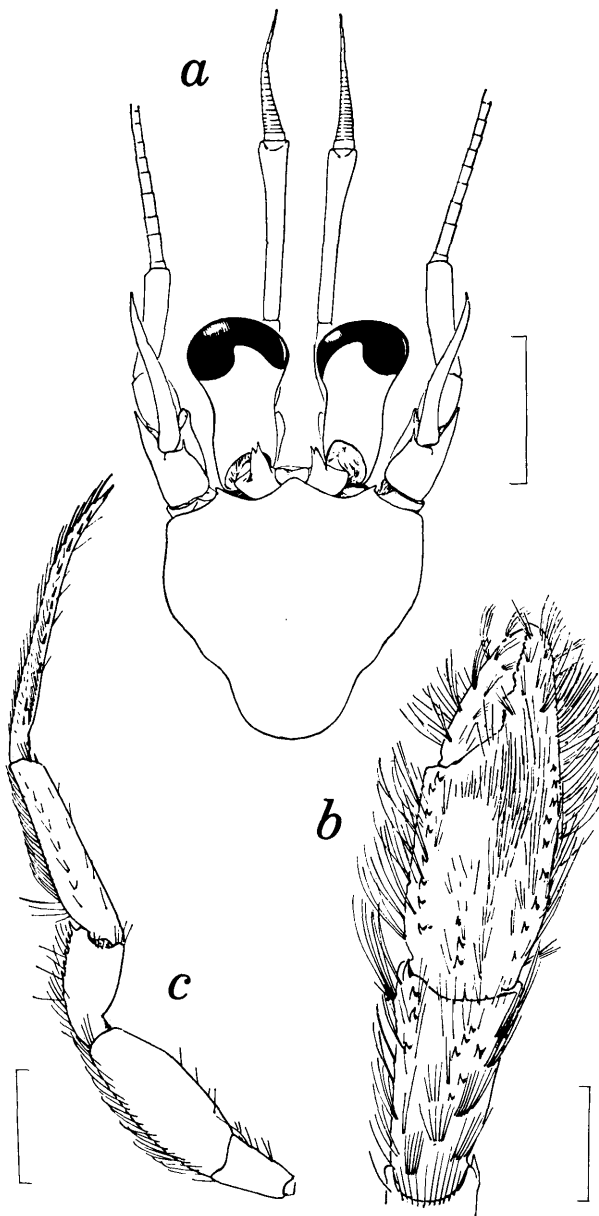


Fig. 146. *Iridopagurus caribbensis* (A. Milne Edwards and Bouvier). *a*, Anterior part of body in dorsal view; *b*, right chela and carpus, external view; *c*, left first walking leg, internal view; *a*, 5 mm; *b*, 2 mm; *c*, 10 mm indicated (from de Saint Laurent-Dechancé 1966).

mal end of terminal article of antennular peduncle and reaching about midlength of terminal article of antennal peduncle; eye scales somewhat triangular, with abruptly narrowed acute tip directed slightly laterad, and slightly exceeded by strong subterminal spine. Acicles slender, longer than eyestalks, reaching end of terminal article of antennal peduncle. Third maxillipeds lacking accessory spine near anterior end of mesial dentate crest.

Chelipeds elongate, setiferous, right chela larger than left. Major cheliped with fingers $\frac{1}{3}$ – $\frac{1}{2}$ length

of palm, cutting edges of fingers toothed; palm ornamented with dorsal submarginal row of distinct spines on each side and short central row proximally; carpus shorter than palm, with scattered spines dorsally. Minor cheliped similar but narrower; palm less spiny, and fingers with row of fine denticles on opposed edges. Two pairs of walking legs (legs 2 and 3) elongate, slender distally, somewhat less pubescent than chelipeds, propodi lacking ventral row of setae distally, carpi with low crest of spines.

Left vas deferens of male extended and prominent.

Measurements in mm.—Anterior shield: male, length 3.18, width 3.31.

Habitat.—This rare species has been found in depths of 15 to 50 m (de Saint Laurent-Dechancé 1966), 10 to 180 m (Young 1978).

Known range.—ESE of Charleston, S. C. (32°34'N, 79°05'W); WSW of Panama City, Fla. (30°19'N, 86°15.5'W); southern Florida, Virgin Islands, and Guadeloupe.

Remarks.—De Saint Laurent-Dechancé (1966) erected the genus *Iridopagurus* for reception of western Atlantic and eastern Pacific pagurids having an external, extended left vas deferens, triangular eye scales, and third maxillipeds lacking an accessory spine next to the mesial dentate crest on the ischium. She restricted *Spiropagurus* to the Indopacific and eastern Atlantic. She also pointed out distinctions between *I. dispar* and *I. caribbensis* which were synonymized by Williams (1965) following Provenzano (1961). The color notes given by Williams (1965) apply to *I. dispar*.

Small ovigerous females are known from Georgia in June. These specimens and others even smaller (shield length 1.3 mm) show the broad cornea described by de Saint Laurent-Dechancé (1966) but have acicles not reaching the distal edge of the eye. Relative length of the acicle may lengthen with increasing age.

Genus *Pagurus* Fabricius 1775

McLaughlin 1974:37.

Diagnosis.—Anterior shield well calcified. Eye scales usually triangular. Chelipeds unequal, right considerably larger than left, both oriented in horizontal plane; fourth legs subchelate, propodal rasp usually well developed. Third maxillipeds widely separated at base by sternum. Males with coxae of fifth legs equal, gonopores paired, no protruding vas deferens; females with gonopores paired. No paired pleopods in either sex, abdomen well developed, uropods asymmetrical. (After McLaughlin 1974.)

Key to Species

1. Eye scales unarmed or with single (rarely 2) subterminal spine 2
 Eye scales armed with 2 or more spines (small species). *P. carolinensis*
2. Width of major chela less than $\frac{1}{2}$ length. 3
 Width of major chela at least $\frac{1}{2}$ length. 10
3. Palm of small (left) chela triangular in cross section, upper surface divided
 by longitudinal ridge into 2 obliquely sloping facets 7
 Palm of small (left) chela not triangular in cross section, either oval or flat-
 tened and spiny dorsally 4
4. Length of eyestalks not more than 3.5 times greatest width. 5
 Length of eyestalks more than 3.5 times greatest width *P. annulipes*
5. Eye scales triangular; rostrum obtuse but definitely exceeding obsolescent
 lateral projections; major chela 3 or more times longer than wide
 *P. piercei*
 Eye scales rounded distally; rostrum obtuse but about equaling lateral pro-
 jections; major chela 2.5 (or less) times longer than wide 6
6. Chelipeds subcylindrical, relatively smooth on outer surface; eye scales
 somewhat rounded distally, dorsal surface shallowly excavated
 *P. longicarpus*
 Chelipeds not subcylindrical, relatively spiny on outer surface and setose;
 eye scales rounded distally but not excavated on dorsal surface.
 *P. defensus*
7. Palm of small (left) chela with conspicuous longitudinal ridge crested bear-
 ing single row of elevated sharp principal spines slanted inward; anterior
 part of sternite between third legs somewhat rectangular (almost twice as
 wide as long), its setae usually few and short. *P. pubescens*
 Palm of small (left) chela with broad longitudinal ridge crested bearing sharp
 or blunt spines (tending to form double row) not slanted inward 8
8. Eyestalks moderately to noticeably stout with definitely dilated cornea;
 moderate to large species in cold temperate or deeper offshore water. .9
 Eyestalks slender, curved slightly outward, cornea only very slightly dilated;
 tiny Carolinian species. *P. hendersoni*
9. Chelipeds both sharply spined and setose on upper surfaces; anterior part
 of sternite between third legs almost semicircular, its setae usually many
 and long *P. arcuatus*
 Chelipeds bluntly spined (occasionally sharply) but not setose on upper sur-
 faces *P. politus*
10. Dactyl of major chela with sharply produced angle on mesial margin
 *P. pollicaris*
 Dactyl of major chela without sharply produced angle on mesial margin. .11
11. Impressed spot (or spots) dorsally on chelae at base of fixed fingers
 *P. impressus*
 No impressed spots dorsally on chelae, hands normally inflated and often
 with broad longitudinal red-orange stripe persistent in alcohol
 *P. acadianus*

Pagurus acadianus Benedict

Fig. 147

Pagurus acadianus Benedict 1901a:454, unnum-
 bered fig.—Rathbun 1929:26, fig. 34.—Wil-
 liams 1974c:19, fig. 53.

Recognition characters.—Anterior shield of cara-
 pace usually as wide as long, truncate posteriorly.

Rostrum pointed but broader than long, well ad-
 vanced beyond lateral projections each sur-
 mounted by small spine. Eyestalks constricted at
 midlength, dilated distally and obliquely deeper
 than broad, only half as long as width of shield;
 eye scales broadly concave on upper surface, each
 armed with subterminal spine. Antennular pe-
 duncles exceeding eyestalks by about length of ter-
 minal article. Antennal peduncles exceeding eye-

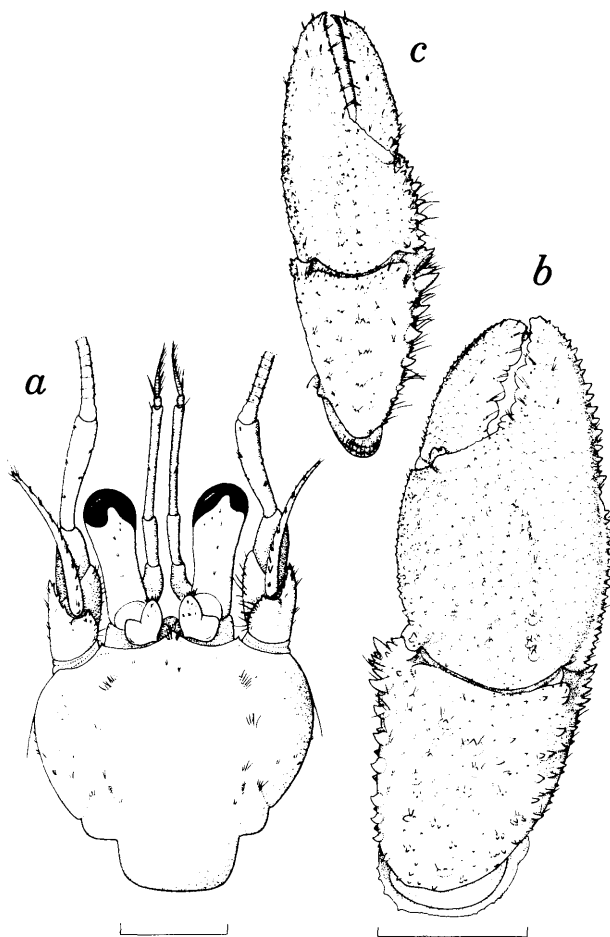


Fig. 147. *Pagurus acadianus* Benedict. Male: *a*, anterior part of body in dorsal view; *b-c*, right and left chelae and carpi in external view; *a*, 5 mm; *b-c*, 10 mm indicated (USNM 171680).

stalks by $\frac{2}{3}$ length of terminal article; acicles slender, curved outward and unarmed, nearly reaching terminus of peduncle.

Right cheliped much larger than left; hand sharply granulate above, granules a bit appressed below, row of short strong spines on lateral border and mesial border of dactyl, fingers with heavy calcareous teeth on opposed edges; carpus less granulate but more sharply spined. Minor cheliped much smaller, somewhat similarly ornamented, but compound row of prominent spines on mesial border of palm, tips of fingers corneous, and fewer spines on carpus. First and second walking legs (legs 2 and 3) with dactyls longer than propodi; dactyls smooth and convex laterally, concave mesially and with row of small corneous spines on upper and lower mesial borders and tufts of sparse setae in rows on upper border.

Measurements in mm.—Anterior shield: male, length 16.9, width 16.9; male, length 17.9, width 17.4; female, length 10.0, width 10.0; female, length 13.6, width 13.1.

Variation.—The anterior shield is slightly longer than wide in some individuals.

Color.—Upper surface of both chelae with broad longitudinal red-orange stripe often persistent in alcohol.

Habitat.—Low-water mark to 485 m (Williams 1974c).

Known range.—Grand Banks of Newfoundland and Gulf of St. Lawrence to mouth of Chesapeake Bay.

Remarks.—Details on distribution of this prominent member of the shelf fauna have been outlined by Bousfield (1958), Brunel (1970), and Squires (1966). Grant (1963), in a survey of a population in Salisbury Cove, Me., during two summer months, found about 20 individuals inhabiting a 147 m² area of rocky bottom. Low recapture after marking and release indicated transiency. Order of shell preference in laboratory tests, confirmed by field observation, descended from *Buccinum* through *Thais* to *Littorina*. It was suggested that shells such as *Buccinum* which have a higher internal volume/weight index are definitely preferred. Behavioral studies in the laboratory indicated that although the crabs had no visual orientation to shells they had been occupying, they were able to recognize these upon contact.

From eggs hatched and reared in the laboratory, Roberts (1973) described and figured four zoeal stages and a glaucothoe. Specific differences between *P. acadianus* and *P. bernhardus* based on adult morphology are borne out by differences in eggs and larval stages, though the species are closely related. Eggs of *P. acadianus* are slightly smaller than those of *P. bernhardus*, dark green rather than very dark purple, and larvae of the latter (from plankton) are markedly larger. There is similarity also to the larvae of *P. pubescens*, and probably as well to those of *P. arcuatus* which remain to be described. Ovigerous females have been collected from Cape Cod Bay in January and March.

Pagurus annulipes (Stimpson)

Fig. 148

Eupagurus annulipes Stimpson 1860a:243.

Pagurus annulipes.—Provenzano 1959:407 (part, not fig. 18).—Williams 1965:130 (part, not fig. 105).

Recognition characters.—Anterior shield of carapace as wide as or wider than long, truncate posteriorly. Rostrum rounded, about as long as rounded lateral projections of front. Eystalks nearly straight, shorter than front, slightly constricted in middle, cornea not dilated; eye scales flat, broad and

rounded, but with 1 or 2 spines on anterior border. Antennular peduncles exceeding eyestalks by about $\frac{1}{3}$ of distal article. Antennal peduncles nearly reaching or exceeding tip of eyestalks; acicles slender, curving outward, reaching about middle of last article of antennal peduncle; flagella exceeding major cheliped, adorned with long setae.

Chelipeds unequal, right much larger than left. Major cheliped long, subcylindrical, moderately and evenly granulate, except subspinose in some individuals, and variably hairy above, granules tending to be arranged in rows on palm; dactyl less than $\frac{1}{2}$ length of hand; carpus nearly twice as long as broad, spinulose along inner margin. Minor cheliped much shorter, compressed, thickly ciliate and somewhat spinulose in rows above; hand slightly shorter than carpus; fingers gaping and shorter than palm, cutting edges very finely and evenly spined distally, comblike spines of dactyl and hooked tips of both fingers corneous. First and second walking legs (legs 2 and 3) slender, compressed, with dactyls longer than propodi; carpus of left leg with distal spine on dorsal margin with or without spines on dorsal margin; carpus of right leg with several spines on dorsal margin.

Measurements in mm.—Anterior shield: male, length 2.25, width 2.56.

Variation.—Males have a tendency to attain larger sizes than females, and proportionately larger che-

lipeds (Provenzano 1959). There is considerable variation in sharpness of granules on the chelipeds as well as in length and density of hairs.

Habitat.—Fairly common on a variety of bottom types in Massachusetts, and on shelly bottom in the Beaufort Harbor, N. C., area. Offshore in North Carolina the species is found in dredge and grab samples on sand and broken shell bottom. Kellogg (1971) found it abundant in the Newport River, N. C., where tidal currents sweep the bottom, usually in *Anachis avara* shells, but mature males also in *Nassarius vibex* shells which are larger. It occurs from near low tide mark to 26 m (Musick and McEachren, 1972) and has been taken along with numerous juvenile *Cancer irroratus* from stomachs of flounders (*Paralichthyes dentatus*) caught 15 mi. ESE of Oregon Inlet, N. C., in 37-m water.

Type-locality.—Beaufort Harbor, N. C.

Known range.—Vineyard Sound, Mass., to at least northern Florida (McLaughlin 1975).

Remarks.—Three similar species have been confused under the name *P. annulipes* (McLaughlin 1975). The southern limits for distribution of *P. annulipes* now seem established; Rouse (1970) reported it absent from the warm waters of southern Florida. *Pagurus bonairensis* Schmitt, having short setae on the antennal flagella rather than long ones as does *P. annulipes*, ranges from the northern Gulf of Mexico southward along the Florida coast and through the Caribbean (Rouse 1970; McLaughlin 1975). *Pagurus stimpsoni* (A. Milne Edwards and Bouvier, 1893) apparently is the Gulf of Mexico counterpart of *P. annulipes*, ranging from west Florida to Texas, but its exact status remains to be worked out (McLaughlin 1975).

Ovigerous females of true *P. annulipes* are known from about May to September in Massachusetts (Nyblade 1970) and almost year round in the Newport River, N. C. (Kellogg 1971). Nyblade (1970) described four zoeal stages and a glaucothoe for *P. annulipes* larval development and showed that Thompson's (1903b) early work erroneously attributed *P. longicarpus* larvae to *P. annulipes* and vice versa. At room temperature ($24^{\circ} \pm 2^{\circ}\text{C}$) in undiluted sea water at Woods Hole, four zoeal stages were passed in 14.8 days. Duration of the glaucothoe stage was not determined.

W. B. and F. J. Vernberg (1970) found that individuals of this species from the Cape Hatteras region exhibit some ability to adjust metabolic rate seasonally. In February, 30°C was an upper lethal limit, but not in June.

A bopyrid isopod, *Pseudasymmetrione markhami*, has been reported from the gill chambers of *P. annulipes* taken near Beaufort, N. C. (Adkison and Heard 1978).

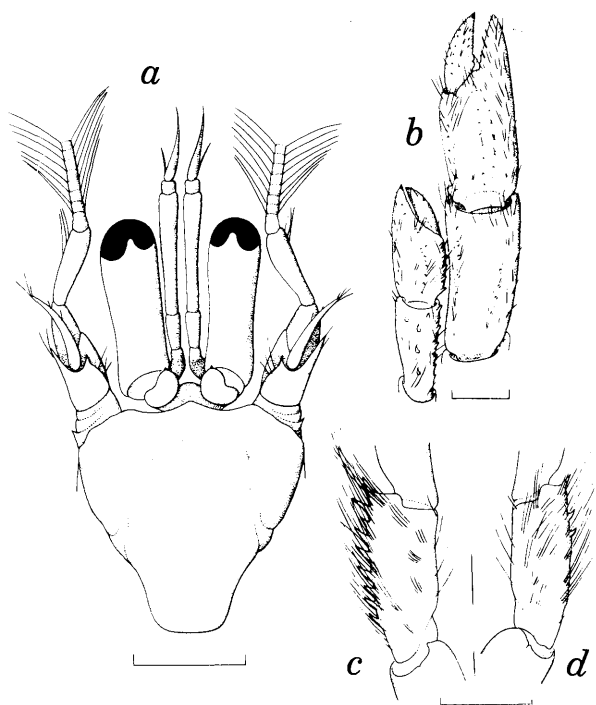


Fig. 148. *Pagurus annulipes* (Stimpson). Male: a, anterior part of body in dorsal view; b, chelae and carpi in external view; c, carpus of right first walking leg; d, same, left; a-d, 1 mm indicated (USNM 34076).

***Pagurus arcuatus* Squires**

Fig. 149

Eupagurus pubescens.—Stimpson 1859:89 (not *kroyeri*).—Smith 1879:47.—Benedict 1896:99, fig. A.—Rathbun 1929:28, fig. 37.

Pagurus arcuatus Squires 1964: 361, figs. 1C, 2C, 5.
Pagurus banksensis Nesis 1964:667, fig. 4 part 2.

Recognition characters.—Anterior shield of carapace about as broad as long, lightly sculptured, few scattered setae, frontal margin inflated. Rostrum rounded, broader than long but tipped with small spine, well advanced beyond reduced lateral projections, each surmounted by small submarginal spine. Eystalks slightly constricted at middle, obliquely deeper than broad, length a bit more than half width of shield; eye scales narrow, concave, each tapering to strong subterminal spine. Antennular peduncles exceeding eystalks by about $\frac{1}{4}$ length of terminal article; acicles moderately stout, curved outward and reaching to near tip of eystalks.

Right cheliped much larger than left but upper surface of both moderately to sharply spinose and hairy; longitudinal, erect spiny ridge running full

length of minor hand, becoming double row of spines on palm, giving it curvilinear triangular shape in cross section. Major carpus with scattered spines or tubercles tending to form rows, row of spines on mesial margin becoming clustered near articulation with hand; minor carpus smoother. Walking legs (legs 2 and 3) with dactyls longer than propodi, nearly smooth, few scattered setae.

Sternite between third legs with anterior portion almost semicircular (nearly as long as broad), setae many and long.

Measurements in mm.—Anterior shield: male, length 14.9, width 13.9; ovigerous female, length 8.0, width 8.3.

Variation.—The semicircular sternal plate may be asymmetrical, but it always bears numerous long setae.

Habitat.—Often abundant on a variety of bottoms such as mud, sand, gravel, sandy-shell, sponges, rocks (Smith 1879), sometimes in association with *Epizoanthus*; low water mark to 270 m (Williams 1974c).

Type-locality.—Grand bank (Southeast Shoal) 43°30'15"N, 49°55'30"W, 55 m.

Known range.—Greenland to off Virginia Capes.

Remarks.—Squires (1964) untangled the misidentifications applied to this species and its close relative, *P. pubescens*, and McLaughlin (1973) elaborated on separation of the two. Both species are boreal or cold temperate forms whose latitudinal ranges overlap in the western Atlantic (Van Engel and Sandifer 1972, as *P. bernhardus*).

Ovigerous females are known from the Cape Cod–Grand Bank region in summer, and off Virginia in May.

***Pagurus carolinensis* McLaughlin**

Fig. 150

Pagurus near *bonairensis*.—Pearse and Williams 1951:143.

Pagurus brevidactylus.—Provenzano 1959:413, fig. 20.—Williams 1965:132, fig. 107.—Forest and de Saint Laurent 1967:116, 120.—McLaughlin 1974:41.

Pagurus carolinensis McLaughlin 1975:365, figs. 4–6.

Recognition characters.—Anterior shield of carapace slightly longer than broad. Rostrum short, usually broadly rounded and about on line with triangular lateral projections. Eystalks swollen at base, tapering toward cornea; eye scales armed along anterior border with 3 to 6 spines. Antennular peduncles reaching at least to tips of eye-

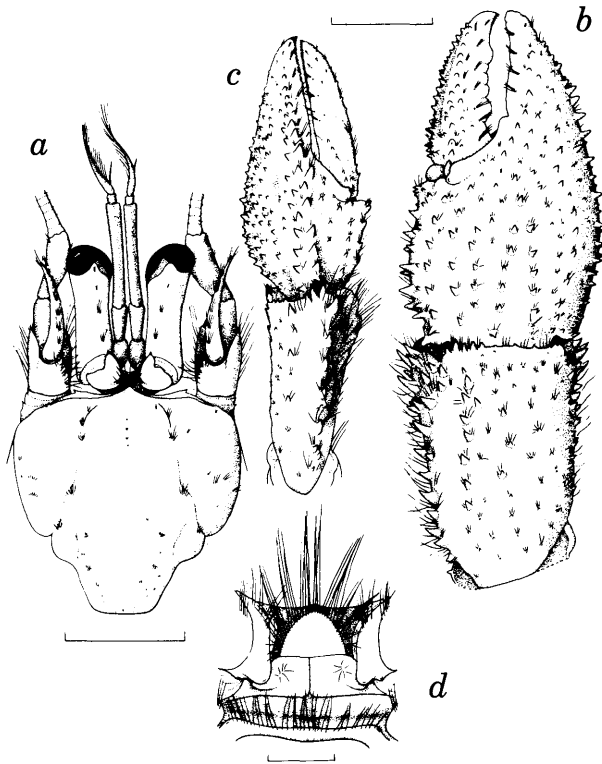


Fig. 149. *Pagurus arcuatus* Squires. Male: a, anterior part of body in dorsal view; b-c, right and left chelae and carpi, external view; d, sternite between third legs; a-c, 5 mm; d, 2 mm indicated (USNM 77444).

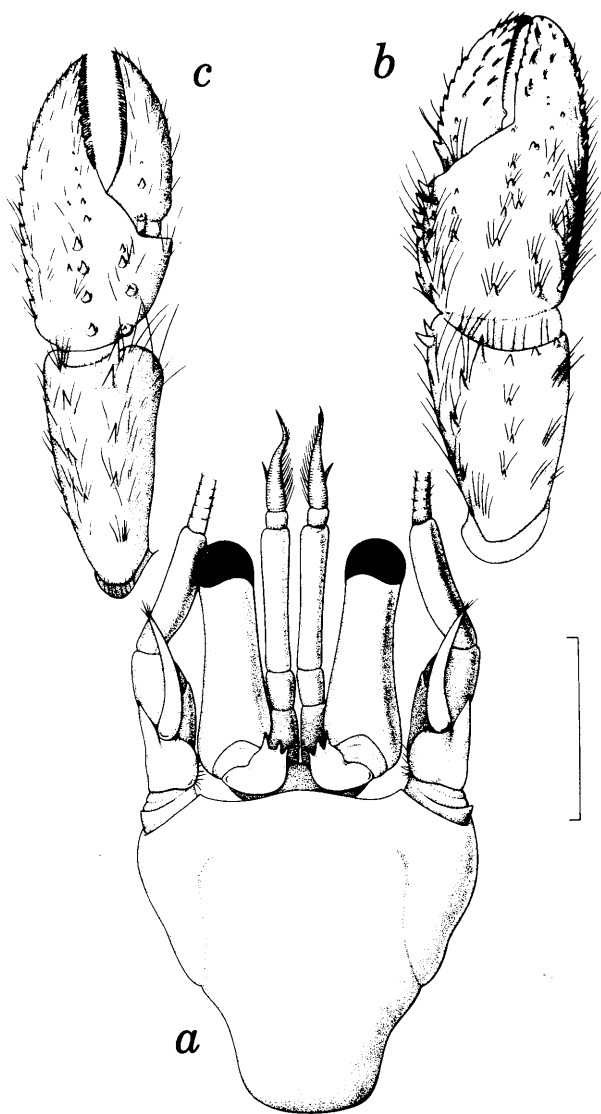


Fig. 150. *Pagurus carolinensis* McLaughlin. Male: *a*, anterior part of body in dorsal view; *b-c*, right and left chelae and carpi, external view; 1 mm indicated (USNM 90074).

stalks. Antennal peduncles slightly exceeding eyestalks; acicles reaching to base of cornea or slightly beyond.

Chelipeds unequal in males, right larger than left, equal or subequal in females; finger tips corneous, spooned. Hands covered with fine hairs, outer margin edged with very short spines, upper surface with small spines or tubercles; carpi with strong spines above. Walking legs (legs 2 and 3) with long, fine, inconspicuous hairs; dactyls shorter than propodi and with 5 to 8 conspicuous spines along inferior margin; propodi with only 1 or 2 inconspicuous spinules along inner margin.

Measurements in mm.—Anterior shield: ovigerous females, length 2.0, width 1.81; length 1.66, width 1.66.

Color.—Walking legs each characteristically colored with 6 rust-red, or maroon stripes on propodus, carpus, and merus, fewer on dactyl; stripes longitudinal and interrupted at ends of each article; ground color of walking legs yellow; hands brown with almost white fingers, not striped; carapace with scattering of red and white pigment in fresh specimens (Provenzano 1959).

Habitat.—The species seems to prefer hard bottoms in areas where water circulation is fairly good (Provenzano 1959); 2 to 53 m.

Type-locality.—Black Rocks, off New River, North Carolina.

Known range.—Newport River (Kellogg 1971) and Cape Lookout, N. C., to southern Florida.

Remarks.—This species for many years was confused with *P. brevidactylus* (Stimpson) sensu stricto which is distributed in Bermuda and from northeastern Florida to northern South America. *Pagurus brevidactylus* has spinier hands than *P. carolinensis*. Provenzano (1959) called attention to sexual dimorphism in *P. carolinensis*. In females the hands are nearly the same size and the right hand is spooned and serrate along the inside margin of the fingers, whereas in males the right hand is not only the larger but the finger tips appear more acuminate and the opposing margins of the fingers each bear a tooth. Many small specimens from Georgia have rather stout eyestalks, and lengths of dactyls and propodi of the walking legs are equal.

Ovigerous females have been collected from June to August and November in North Carolina, March to August in Florida, and July to October in Georgia.

Pagurus defensus (Benedict)

Fig. 151

Eupagurus defensus Benedict 1892:7.

Pagurus defensus.—Williams 1965:127, fig. 102.

Recognition characters.—Anterior shield of carapace broader than long, subcordate. Rostral projection broadly rounded, lateral processes triangular, armed at apex with short spine. Eyestalks stout, much dilated and flattened distally; eye scales broad, rounded, anterior margin forming semicircle, armed with subterminal spine. Antennular peduncles extending beyond eyestalks by $\frac{2}{3}$ or more length of terminal article. Antennal peduncle extending beyond eyestalks by about $\frac{1}{2}$ length of terminal article; acicle curving outward and extending somewhat beyond eyestalk.

Chelipeds unequal, right larger than left. Major chela little wider than carpus, fingers slightly agape,

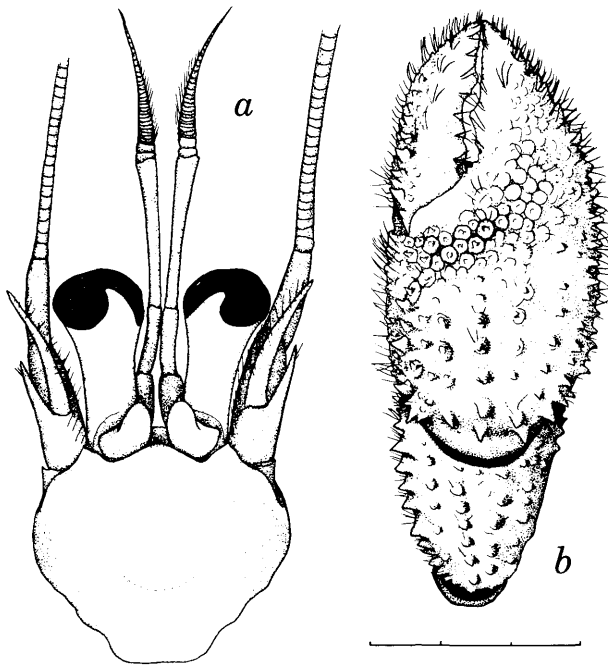


Fig. 151. *Pagurus defensus* (Benedict). Female: *a*, anterior part of body in dorsal view; *b*, right chela and carpus, external view; 3 mm indicated (from Williams 1965).

margins set with comb of long slender spines; upper surface with more or less diagonal rows of spines on palm; irregularly but closely set plates near base of fixed finger and occasionally on dactyl, spine or tubercle usually arising from center of each plate; carpus with 3 rows of sharp spines, 1 on outer margin, 1 on upper surface and 1 on inner surface. Minor chela extending to base of major dactyl; hand armed with spines as in opposite member but hairier and no spine-bearing plates present; fingers agape; carpus with double crest of spines, outer margin convex, inner margin straight and flat; merus compressed. Walking legs (legs 2 and 3) long and slender, dactyls lightly setose, longer than preceding 2 articles together; propodus and carpus with crest of spines.

Measurements in mm.—Anterior shield: male, length 5.9, width 6.5; female, length 3.1, width 3.7.

Variation.—There is considerable variation in length of spines on the chela and amount of hair on the major chela; fingers of the chelae do not gape in small individuals.

Habitat.—Twenty-five to 90 m.

Type-locality.—Gulf of Mexico between Delta of Mississippi River and Cedar Keys, Fla., 55 m.

Known range.—Cape Hatteras, N. C., to Georgia; Tortugas, Fla., to Alabama.

Remarks.—Cerame-Vivas and Gray (1966) listed this species from tropical Caribbean waters along the North Carolina shelf.

Ovigerous females have been taken south of Ocracoke Inlet, N. C., in July, and a mature female from 25 m about 25 mi. SE of New River Inlet, N. C.

Pagurus hendersoni Wass

Fig. 152

Pagurus hendersoni Wass 1963:144, figs. 5a-f.

Recognition characters.—Anterior shield of carapace a little longer than wide, smooth, rounded laterally, few scattered setae. Rostrum broadly rounded, slightly exceeding more sharply tipped broad lateral projections. Eyestalks shorter than shield but slender, slightly curved outward, and with slightly dilated cornea; eye scales oval, slightly concave, with prominent subterminal spine. Antennular peduncles equaling eyestalks when extended, those of antennae nearly as long. Acicle unarmed, reaching about $\frac{2}{3}$ length of eye.

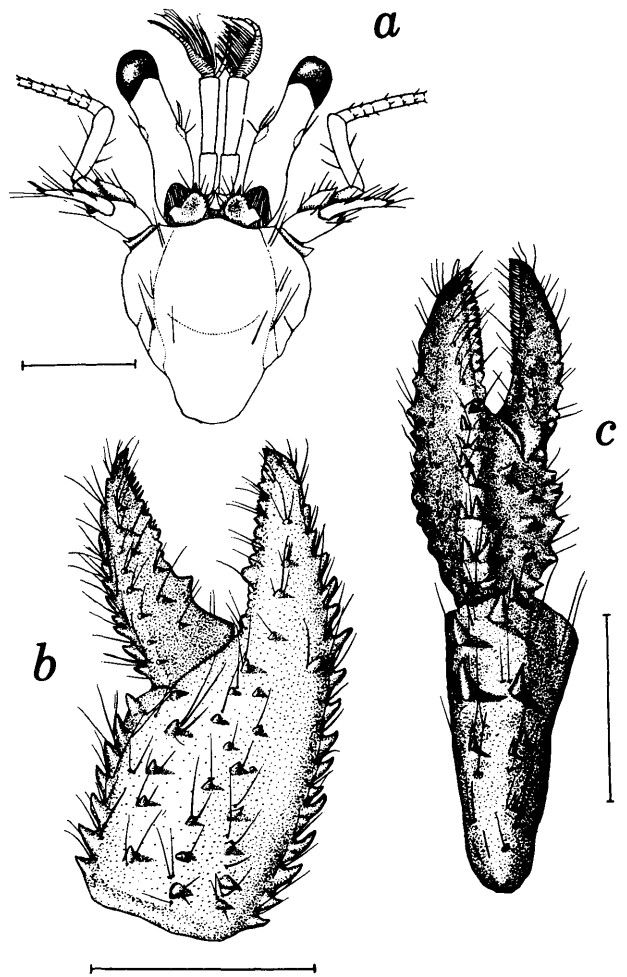


Fig. 152. *Pagurus hendersoni* Wass. Female: *a*, anterior part of body in dorsal view; *b*, right chela; *c*, left chela and carpus, external views; 1 mm indicated (from Wass 1963).

Right cheliped larger than left, strong, short and stout; chela rounded above and armed with obtuse spines in irregular rows except for 2 rows on dactyl, outer margin with strong teeth; carpus with strong mesiodorsal spines forming 2 rows distally; usually a row of slender spines laterally flanked by denticles on margin; merus with stout spine on inner ventral angle, few low denticles on opposite angle and distodorsal spine directed forward from margin. Minor chela with prominent dorsal ridge on palm bearing generally double row of spines extending on propodal finger where it bears a few denticles, row of widely spaced denticles between ridge and bluntly serrate outer margin, blunt spines along mesial margin and others parallel on upper surface; finger spooned, cutting edge of dactyl corneous, fixed finger with calcareous teeth; carpus with spinules proximally and strong spines distally on upper surface; merus with 1 or 2 spines ventrally on inner margin and irregular row of spinules on outer margin. Walking legs (legs 2 and 3) with dactyls longer than propodi.

Measurements in mm.—Anterior shield: female, length 1.8, width 1.7.

Variation.—Spination of the chelae varies; one mature female has a nearly smooth major chela.

Type-locality.—Pourtales Plateau, 10 mi. S Key West, Fla., 229 m “rocky (coral).”

Known range.—Off Georgia, 31°26'30"N, 79°42'15"W, 89–77 m; Florida Straits and Dry Tortugas.

Remarks.—Only the type-series and four specimens from Georgia are known; all are ovigerous females (in August) except one juvenile. This is a tiny species notable for the longitudinal ridge on the minor chela, slender eyes, and usually well-armed chelipeds.

Pagurus impressus (Benedict)

Fig. 153

Eupagurus impressus Benedict 1892:5.

Pagurus impressus.—Provenzano 1959:399, fig. 15.—Williams 1965:129, fig. 104.

Recognition characters.—Anterior shield of carapace about as broad as long, flattened; narrow longitudinal notch at anterolateral corners. Rostrum much rounded, in line with somewhat more angular lateral projections of front. Eyestalks shorter than width of shield, cornea dilated and flattened; eye scales with moderately slender, acuminate, slightly excavated anterior lobe, subterminal spine large. Antennular peduncles exceeding eyestalks by about $\frac{3}{4}$ length of terminal article. Antennal pe-

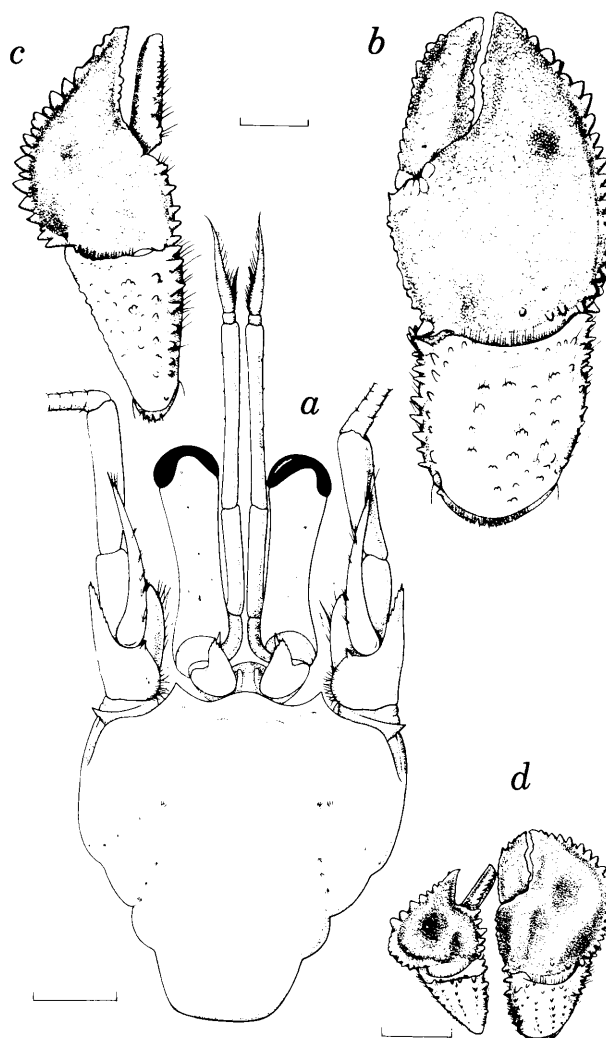


Fig. 153. *Pagurus impressus* (Benedict). Ovigerous female: a, anterior part of body in dorsal view; b-c, right and left chelae and carpi, external view; d, same, smaller female. USNM 102669, a, 3 mm, b-c, 5 mm indicated; USNM 122725, d, 5mm indicated.

duncles slightly exceeding cornea; acicles curving outward, reaching to base of cornea, hairy on mesial edge.

Chelipeds unequal, right much larger than left, upper surfaces of palms dented; both covered with small, closely crowded granules, outer margins bearing enlarged granules or small spines. Dactyl of major cheliped with rounded angle on mesial border near tip followed by marginal spines or granules, tips of fingers calcareous and hooked; carpus with longitudinal rows of small spines often obscured by irregularly arranged additional spines, row of well-developed spines along inner edge. Minor cheliped reaching to angle of major dactyl; row of spines along inner margin of hand and carpus; fingers somewhat spooned behind hooked, corneous tips, cutting edges well defined, dactyls with mesial border tuberculate; carpus with sev-

eral rows of small spines. First and second walking legs (legs 2 and 3) with dactyls much longer than propodi; first pair with row of small, well-defined spines along upper margin of propodus and carpus; second pair with spines reduced.

Measurements in mm.—Anterior shield: male, length 12.9, width 13.0; ovigerous females, length 10.8, width 10.9; length 3.9, width 3.9.

Variation.—There is considerable variation in the depth of dents on upper surfaces of the palms. Older individuals tend to have uniformly shallower dents than juveniles or small adults in which palms vary from nearly smooth to deeply pitted. Specimens from the Gulf of Mexico population seem to have somewhat smoother hands than many from the Atlantic shelf.

Color.—Hands solid rust to chocolate brown, other appendages brownish with alternating thin bands of light color; antennae, antennules, and peduncles yellow; eyestalks brown above, bright blue below with bright scarlet at base of eyestalks (Provenzano 1959).

Habitat.—On sandy bottom, grassy flats or pilings; occasionally found in sponges (Wass 1955), often in a species of *Ficulina* in North Carolina; 1 to 33 m. Kellogg (pers. comm.) found young *P. impressus* in the Newport River, N. C., estuary.

Type-locality.—Boca Ciega Bay, inner shore of Pine Key [mouth of Tampa Bay], Florida (from holotype jar label).

Known range.—Off Diamond Shoals, N. C., to near Cape Canaveral, Fla.; Florida Bay, near Flamingo, north to vicinity of Pensacola, Fla. (Cooley 1978); Port Aransas, Tex.

Remarks.—Ovigerous females have been taken in January and February in Georgia and the Carolinas, and February and April in Florida. The species is rare in southern Florida (Rouse 1970; Tabb and Manning 1961).

Türkay (1968) recognized a subspecies, *P. i. zilchi*, from Isla de Margarita, Venezuela, that is very close to typical *P. impressus*.

Pagurus longicarpus Say

Fig. 154

Pagurus longicarpus Say 1817:163.—Provenzano 1959:394, fig. 13.—Williams 1965:125, fig. 101.

Recognition characters.—Anterior shield of carapace subcordate, truncate posteriorly, about as long as broad. Rostrum obsolete, hardly as advanced as lateral projections of front. Eyestalks stout, 2 to 3 times longer than broad, much shorter than width of anterior shield, cornea dilated; eye scales with

concave, oval anterior lobe armed with subterminal spine. Antennular peduncles exceeding eyes by $\frac{1}{2}$ – $\frac{3}{4}$ length of terminal article. Antennal peduncles exceeding eyes by about $\frac{1}{3}$ length of terminal article; acicles slender, curved sinuously outward, reaching to tip of cornea; flagella exceeding tip of major cheliped.

Right cheliped much larger and longer than left, subcylindrical, devoid of hairs except for few short setae along inner edges of fingers; width of hand less than $\frac{1}{2}$ total length, palm lightly crested and minutely dentate along outer margin, upper surface minutely granulate and with 2 incomplete rows of subspinous tubercles and scattered smaller ones. Left cheliped smaller, hairier, similarly formed but relatively broader; fingers with cutting edges distally, gaping at base. First and second walking legs (legs 2 and 3) with dactyls longer than propodi, extending about as far as chelipeds.

Measurements in mm.—Anterior shield: male, length 7.25, width 7.5; ovigerous female, length 4.5, width 5.0.

Color.—Color varies with locality; specimens from west Florida lighter than those of east coast; upper surface of chelipeds and all walking legs iridescent; posterior carapace light green; hand white with median diffused pigment stripe, carpus with dorsal stripe and on each side; walking legs with dactyl unstriped, propodus with lateral stripe, merus with single lateral muddy brown stripe and transverse stripe from lower margin to broad pigmented area on upper surface; antennae with dark

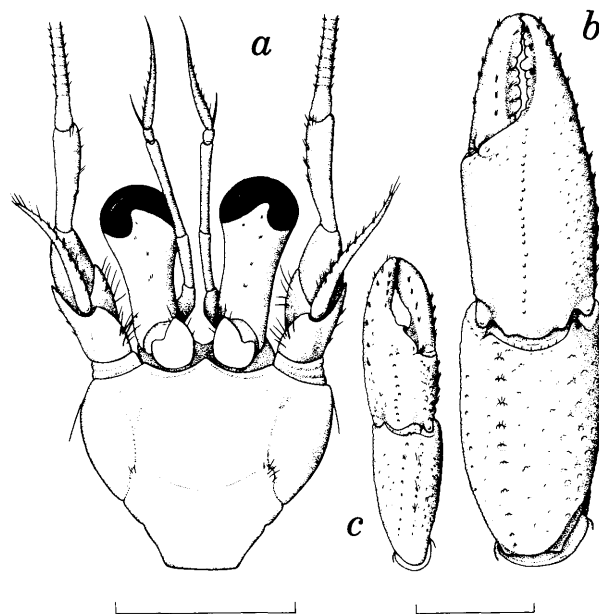


Fig. 154. *Pagurus longicarpus* Say. Male: a, anterior part of body in dorsal view; b-c, right and left chelae and carpi, external view; 5 mm indicated.

bands alternating with shorter white bands. Young may have transverse band on each article of walking legs rather than stripe; lateral stripes of major cheliped with V-shaped appearance in dorsal view (Provenzano 1959, from west Florida specimens).

Habitat.—Common on harbor beaches, in harbor channels and along shallow littoral on a variety of bottoms, but usually soft substrate (Kellogg 1971); to 200 m (Wenner and Boesch 1979).

Type-locality.—"Inhabits bay shore" [east coast of United States].

Known range.—Minas Basin and Chignecto Bay (Bousfield and Leim 1960; E. L. Bousfield, personal communication) to Hutchinson Island, Fla. (Camp, et al. 1977); southwestern Florida to coast of Texas (Provenzano 1959; Rouse 1970; Whitten, et al. 1950).

Remarks.—*Pagurus longicarpus* is one of the commonest decapod crustaceans in shallow water along the coast of the eastern United States. Like other easily collected crustaceans, it has been the subject of a number of ecological, physiological, and behavioral studies. Provenzano (1959) suggested that the Atlantic coast and Gulf of Mexico forms, with a hiatus between their ranges, may be subspecifically distinct.

The general habitat of *P. longicarpus*, summarized above, has been commented upon by other authors (Pearse, et al. 1942; Allee 1923). Allee concluded that the ubiquity of this hermit crab prevents it from being of aid in distinguishing shallow-water communities. Functional morphology of the mouthparts (Roberts 1968a) is related to a diet of diatoms, detritus and algae (Sanders, et al. 1962) as well as occasional infaunal invertebrates. Caine (1975) found that the diet is 45% scavenged material, 10% algae, and 40% detritus and sand. Scully (1978) described utilization of surface foam as food in very shallow water and reviewed food studies on hermits.

In Narragansett Bay, Rebach (1974) showed by experiment and field observation that the species has seasonal migratory and burrowing responses, burrowing preferably in sand as temperatures lower in fall to around 10°C and at the same time moving to deeper water, finally coming to occupy grounds greater than 5 m deep at 1.3°–1.7°C in winter where no hermits at all occur in summer. During spring, the hermits return to water along the strand. Kinne, et al. (1963) found that *P. longicarpus* has no osmoregulatory capacity.

The breeding season varies with latitude. In Massachusetts it extends mainly from early May to mid-September (Bumpus in Sumner, et al. 1913b), but an ovigerous female has been collected on April 23 from Cape Cod Bay. Farther south breeding ex-

tends into winter: February in North Carolina; March through July in Georgia; September to April in Florida (Dragovich and Kelly 1964; Wass 1955, in part); winter in Texas (Fotheringham 1975).

Roberts (1970; 1971a, b, c) reared four zoal stages and a glaucothoe from females taken at Gloucester Point, Va. In finger bowls of unfiltered sea water (19–22‰) no prezoal stages were observed except when culture conditions were sub-optimal. In conjunction with Nyblade (1970) he showed that Thompson's (1901, 1903b) *P. longicarpus* larvae were really *P. annulipes*. In an array of salinities (18–30.5‰), development through the glaucothoe extended 21.6–24.4 days and in lower salinities a few days longer, indicating broad adaptation to estuarine salinities. Larvae can detect a salinity reduction of 2.5‰ and probably less. Mortality of isolated glaucothoes is unaffected by shell presence or absence, but in mass culture unprotected animals are cannibalized. Among available shells, 50% of the glaucothoes entered a shell after 24 hr, up to 93% after 48 hr, and a few which failed to enter a shell did so immediately after molt to the first juvenile instar. Intermolt duration was not significantly affected by shell presence or absence.

Shell selection in hermit crabs has been studied by a host of workers. Reese (1962), basing experiments largely on *P. longicarpus*, showed that natural occurrence of hermit crabs in certain species of shells is explicable by at least two factors: an actual preference for certain species of shells, and relative abundance of shells of different species in different habitats. The two factors may operate singly or together. Hermits tested were able to discriminate among at least three species of shells, regardless of whether or not they had previous experience with the shells. The crabs were also able to discriminate among conspecific shells of different weights, and they selected shells of a specific weight relative to their own. Inception of shell-entering behavior occurs in the glaucothoe stage, appears to be composed of innate components, and is fully expressed when the glaucothoe enters its first shell except that the glaucothoe shows little visual orientation to shells.

Fotheringham (1976; 1976a) observed that *Clibanarius vittatus*, *Pagurus pollicaris* and *P. longicarpus* have broadly overlapping shell utilization patterns along the Texas coast. Wright (1973) showed that species of *Pagurus* (*longicarpus* and *pollicaris*) offered clean shells or shells bearing colonial hydroids, *Podocoryne carnea* or *Hydractinia echinata*, chose the hydroid-covered shells, whereas *Clibanarius vittatus* avoided the latter. *Pagurus* species were not stung by the hydroid zooids, and indeed were occasionally seen eating hydroids from a neigh-

bor's shell. Wright thought that they may thus gradually gain immunity to stings.

Pagurus longicarpus may mature four months after settling from the plankton and reach its asymptotic size within the next eight months. This rapid growth may enable it to preempt shells which are required for the successful brooding of a large clutch of eggs. Growth rates of crabs in preferred shells are greater than those of crabs in small shells (Fotheringham 1976, 1976a), but observed molting rate was the same in either case. Ovigerous females bore 260–4,054 eggs.

In another vein, conditioned and natural behavior of *P. longicarpus* have been studied. Spaulding (1904) found the crab able to profit by experience in vision and taste experiments, and able to learn faster than *P. pollicaris*. Fink (1941) claimed deconditioning of fear-reflex activity over a period of 18 days; older crabs responded more slowly than young ones. Hazlett (1966b) showed the results of work with shell-less crabs, as that of Allee and Douglas (1945), to be atypical because shell-less crabs do not occur in nature. Evacuation of the shell is not a matter of force. Actions of an attacking crab which result in eviction of the loser are at a signal level. Rapping and shaking are negative situations which the defender would avoid if possible; an evacuation is one means of avoiding them. The loser of a shell fight is not physically damaged in any way. First reactions of an attacker are to attain an opposed position directly or to turn the other crab over and over with its ambulatories. Weight of shell is an important factor in selection. The attacker is visually and, in a recently molted defender's case, chemically oriented to shells of approximately the right size. "Rolling" allows more judgment of size. "Signals" reduce physical damage. Hazlett (1972) also showed that in *P. longicarpus* intensity of display is inversely proportional to distance from an intruder (another crab or a mirror).

Autotomy and regeneration in this species received attention from Morgan (1900, 1901) and Haseman (1907), though investigations on this subject with other species now supersede the early studies. The first three pairs of legs have a fracture joint near their bases, hence can be autotomized, but the last two pairs lack these and cannot be autotomized. Injuries distal to the fracture plane result in autotomy and regeneration; those proximal to the plane do not result in autotomy. Injured abdominal appendages are readily regenerated. Hazeman carried this work farther showing that when the chelipeds were removed at their breaking joint they differentiated from the tip proximally, but the first two pairs of clawed (walking?) legs differentiated from the base toward the tip.

Direction of differentiation in the cheliped can be reversed by injuring the developing bud.

Kropp and Perkins (1933) showed that in *P. longicarpus*, and other remotely related decapods, the chromatophore activity substance in the eyestalk will induce contraction of chromatophores in other species, and postulated that the substance is genetically similar throughout the group.

Fraenkel (1960) emphasized the importance of exposure duration in determining an upper temperature tolerance limit of 36°C for *P. longicarpus*.

Finally, Reinhard (1944, 1945) and Reinhard and Buckeridge (1950) discussed parasitism in *P. longicarpus*. An examination of 8,000 crabs showed a 1% infestation with a larval acanthocephalid belonging to the genus *Polymorphus*. The worm was found in the abdominal cavity (?) usually attached to the hind gut or sometimes among tubules of the hepatopancreas. The usual number of cysts per host was one, though as many as three occurred. Reinhard also described an entoniscid isopod, *Paguritherium alatum*, from this species. Entering the crab's body through the dorsal side of the eyestalk, and remaining in contact with this point of entry, the parasite elongates with but little damage to thoracic organs, but becomes greatly distended in the abdominal region. There it restricts the hepatopancreas and nearly obliterates the gonads as it grows. Infestation does not externally modify the male host. In females, the parasite reduces size of the first three pleopods, especially length of the endopod, and causes partial or complete loss of ovigerous hairs on the external surface of the endopod and protopod. Thus, secondary sexual characters of the female crab are altered. One percent of the crabs investigated were infested with this parasite.

Pagurus piercei Wass

Fig. 155

Pagurus piercei Wass 1963:147, figs. 7a-g.

Recognition characters.—Anterior shield of carapace as broad as long, combs of stiff setae arranged serially to either side of gastric region. Frontal margin with broadly obtuse rostrum advanced beyond obsolescent lateral projections. Eyestalks shorter than width of shield, equally swollen at base and cornea, with combs of setae dorsally and laterally; eye scales triangular, each terminating in spinule. Antennular peduncles when extended exceeding eyestalks by nearly full length of terminal segment, those of antennae by 1/3 of terminal segment. Acicles unarmed, exceeding eyestalks.

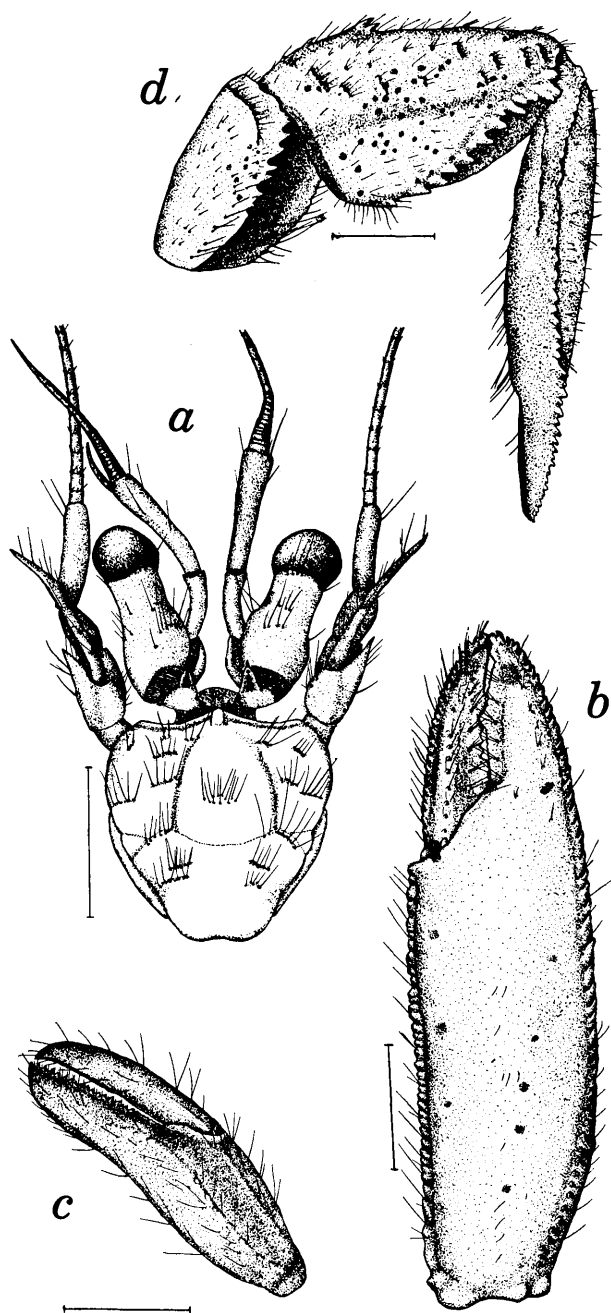


Fig. 155. *Pagurus piercei* Wass. Male: *a*, anterior part of body in dorsal view; *b-c*, right and left chelae, external view; *d*, right cheliped, lateral view. USNM 106599, holotype, 1 mm indicated (from Wass 1963).

Right cheliped much larger than left, elongate; chela over 3.5 times as long as wide, margins finely serrate, upper surface smooth and with fine setae; carpus and merus excessively swollen; carpus twice as broad as propodus, armed with row of strong teeth on mesial margin, series of smaller teeth on ventromesial and ventrolateral margins, and a few dorsal spines; merus with row of teeth on ventrolateral margin. Minor chela over 3 times as long as

wide, fingers elongate and spooned, fine setae most noticeable ventrally; merus and carpus each with 3 short spines on lateral anteroventral margin; carpus with few denticles and numerous setae dorsally. Walking legs (legs 2 and 3) slender, minute distodorsal tooth on carpus and row of ventral spinules on dactyls; rasp of fourth leg with single row of scales.

Measurements in mm.—Anterior shield: holotype male, length and width 1.6.

Color.—"Specimen in alcohol two months. A faint red persists in narrow longitudinal stripes on walking legs and in a few spots on major chela" (Wass 1963).

Habitat.—The holotype was taken from a piece of coral hooked from the bottom by a fisherman (Wass 1963); 73–260 m (Wenner and Boesch 1979).

Type-locality.—39 mi. SE Port Aransas, Tex., 73 m.

Known range.—Type-locality and 30°51'30"N, 79°58'W off Georgia.

Remarks.—Wass (1963) noted that this species is probably associated mainly with reefs and not taken by usual methods of collecting. The specimen from Georgia is a juvenile male in which the carpus and merus of the large cheliped are not relatively so swollen as in the holotype.

Pagurus politus (Smith)

Fig. 156

Eupagurus sp. Smith 1881:428.

Eupagurus politus Smith 1882:12, pl. 2, fig. 5.—

1883:27, pl. 4, fig. 4.—Fowler 1912:579.

Pagurus politus.—Rathbun 1905:16.

Recognition characters.—Anterior shield of carapace broader than long, smooth. Rostrum broadly rounded and not reaching level of acute lateral projections, each armed with short spine. Eyestalks about 1.25 times longer than distance between lateral projections of front, cornea distinctly dilated, stalk depressed; eye scales small, concave dorsally, narrow, each armed with small submarginal spine at tip. Antennular peduncles exceeding eyestalks by about $\frac{2}{3}$ length of terminal article. Antennal peduncles reaching slightly beyond eyestalks; acicles slender, sinuously curved, reaching tip of terminal article.

Right cheliped larger than left; both chelae similarly ornamented dorsally with numerous rounded, slightly appressed to spiniform tubercles; minor chela with low, central longitudinal ridge dorsally giving hand curvilinearly triangular shape in cross section, dactyl smooth dorsally; tubercles somewhat more widely spaced on carpi, minor carpus

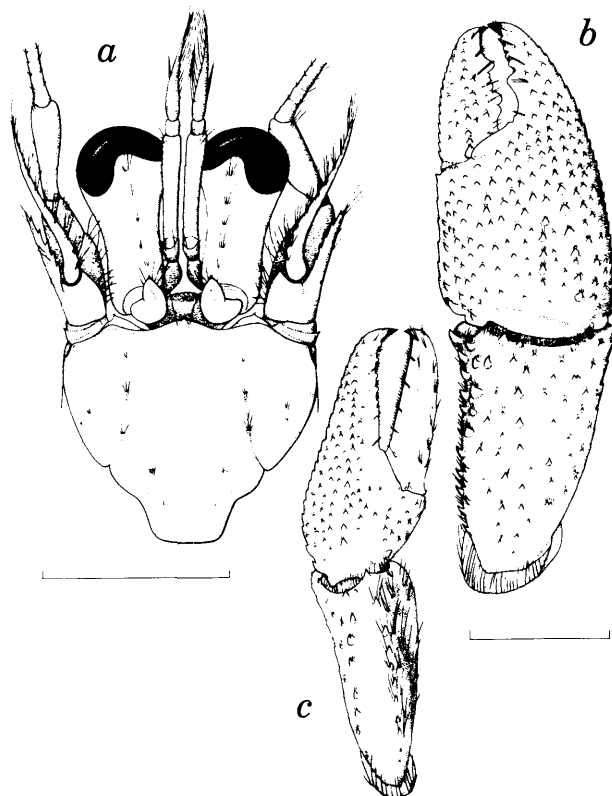


Fig. 156. *Pagurus politus* Smith. Male: *a*, anterior part of body in dorsal view; *b-c*, right and left chelae and carpi, external view; 5 mm indicated (USNM 5899).

with smooth longitudinal tract between mesial marginal row of sharp tubercles and median dorsal row; both chelae nearly devoid of hairs, those of females slightly more hirsute. Walking legs (legs 2 and 3) with curved dactyls much longer and more slender than propodi, each dactyl with ventral row of fine corneous spines distally.

Measurements in mm.—Anterior shield: male, length 12.9, width 14.1; ovigerous female, length 6.4, width 7.1.

Color.—Generally pale orange, tips of chelae and walking legs white, eyes black (Smith 1882).

Habitat.—Essentially an offshore form recorded mostly near edge of continental shelf and on continental slope; (20?) 30 to 1170 m.

Type-localities.—Not designated in original description, but syntypes from four localities off New Jersey to Massachusetts were indicated by Smith (1882). The male he illustrated, is in the type collection of USNM (21452), from off Martha's Vineyard, Mass., 40°03'48"N, 70°45'54"W, 130 m, *Fish Hawk* Stn. 922; others in the collection of MCZ, Harvard University, are from U. S. Fish Commission Stn. 309, 40°11'40"N, 68°22'10"W, 556 m, and Stn. 310, 39°59'16"N, 70°18'30"W, 475.5 m.

Known range.—Georges Bank to off Dry Tortugas, Fla. (Williams 1974c).

Remarks.—Though *P. politus* is a species abundantly represented in the USNM collection, there are few references to it in the literature. Pilsbry (1907) referred to occurrence of the barnacle *Poecilasma kaempferi novaengliae* on the carapace of a specimen taken off Martha's Vineyard. The species is occasionally associated with carcinoecia of *Epi-zoanthus*.

Many records of ovigerous females indicate a long, if not year round, breeding season throughout the length of the range.

Hazlett (1966a) listed *P. politus* as strongest in a ranking of *Pagurus* species on the basis of pagurid behavior expression. He characterized it as a large crab, very active at 15°C, which holds the shell off the substrate, avoids conspecifics in the light, less in red light, and has three kinds of cheliped display.

Pagurus pollicaris Say

Fig. 157

Pagurus pollicaris Say 1817:162.—Provenzano 1959:401, fig. 16.—Williams 1965:128, fig. 103.

Recognition characters.—Anterior shield of carapace subcordate, slightly longer than broad, truncate posteriorly. Rostrum slightly less advanced than lateral projections of front, lateral projections rounded but with inferior anterolateral spinule. Eyestalks moderately stout, not so long as width of anterior carapace, nearly straight, cornea dilated; eye scales with round tipped, slightly concave anterior lobe armed with inferior subterminal spine. Antennular peduncles exceeding eyestalks; acicles slender, curved outward, reaching to or beyond base of cornea, hairy mesially.

Chelipeds unequal, right much larger than left, both covered with small, closely spaced, often elevated and sharpened granules, outer margins with enlarged granules or small spines. Major chela stout, hand flattened; dactyl with prominent, projecting angle on mesial border; carpus with tubercles tending to be larger and more widely spaced than on hand, subspinose and ciliated on upper surface; merus with few squamiform tubercles. Minor chela with inner border dentate, dactyl without projecting angle, dentation of inner border continued on inner dorsal border of carpus. First and second walking legs (legs 2 and 3) with dactyls much longer than propodi; first pair with small, well-defined spines along upper margin of propodus and carpus; second pair with spines reduced.

Measurements in mm.—Anterior shield: males, length 21.3, width 19.2; length 20.7, width 19.9; ovigerous females, length 17.8, width 18.7; length 14.7, width 13.9.

Color.—Color varies with locality, individuals from west Florida being lighter than those of northeastern states. Chelipeds basically white with gray margins mesially, tips of dactyls, and with dark area in center of upper surface; remainder of body light gray-tan; eyestalks brown below cornea; hairs on antennules rusty brown (Provenzano 1959, for west Florida form). Massachusetts form reddish brown.

Habitat.—Deep channels of harbors and littoral waters; also found in shallow estuaries near ocean; near low-tide mark to 112 m (Wenner and Boesch 1979).

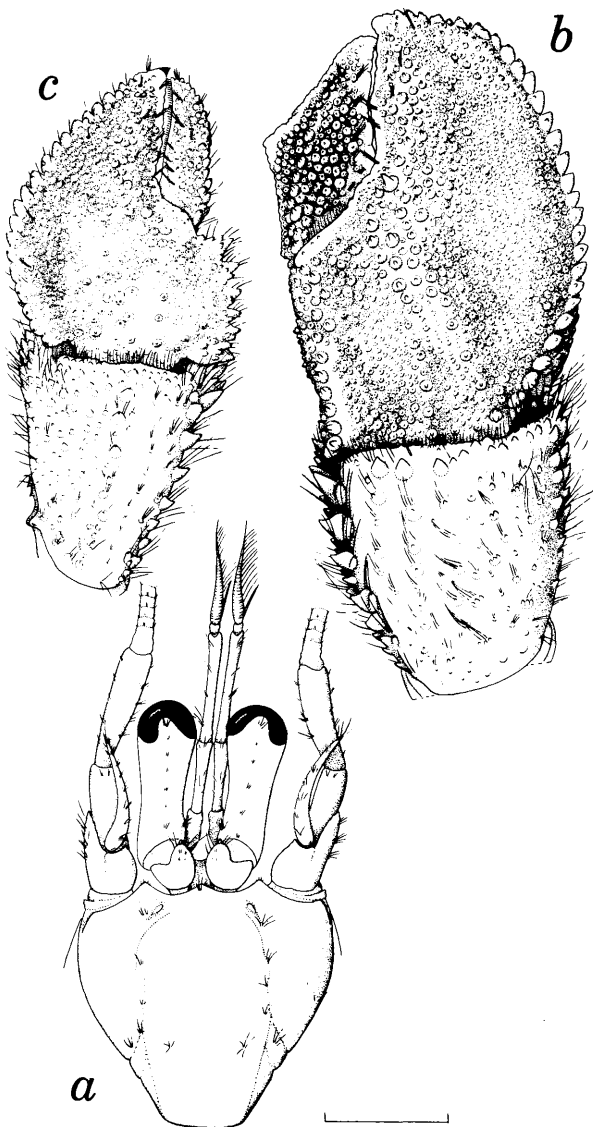


Fig. 157. *Pagurus pollicaris* Say. Female: a, anterior part of body in dorsal view; b-c, right and left chelae and carpi, external view; 5 mm indicated (USNM 173576).

Type-locality.—[East] "coast of the United States."

Known range.—Grand Manan, New Brunswick, to northeastern Florida; Key West, Fla., to Texas (Provenzano 1959, in part).

Remarks.—Differences in color between Atlantic and Gulf populations as well as the disjunct distribution suggest existence of two subspecies (Provenzano 1959).

Blake (1953) reported *P. pollicaris* from the Pleistocene of Maryland.

Ovigerous females have been reported in March, November, and December in Florida (Provenzano 1959; Dragovich and Kelly 1964), January and February in North Carolina, winter in Texas (Fotheringham 1975), April in Chesapeake Bay, and from early spring to the end of June in Massachusetts by Nyblade (1970) who also described four larval stages and a glaucothoe from laboratory rearings. In these experiments the larvae were maintained at $24^{\circ} \pm 2^{\circ}\text{C}$ and $16^{\circ} \pm 0.5^{\circ}\text{C}$ in constant light. In the first regime the four zoeal stages were passed in 15.2 days, 56.7 days in the second. Duration of the post-larval stage was not determined. Johnson (1964) gave details on the male reproductive system.

Chapple (1969a, b, c), by dissection, sectioning of tissues, experiments and substitution of a transparent plastic facsimile of a *Polynices* shell, demonstrated that *P. pollicaris* carries the shell by the columella in the crook of the abdomen, and also described components in the abdomen (including musculature and its innervation) responding to calculated forces bearing on it. Fotheringham (1976; 1976a) observed that *Clibanarius vittatus*, *Pagurus longicarpus*, and *P. pollicaris* have broadly overlapping shell utilization patterns along the Texas coast. The latter may mature four months after leaving the plankton but does not reach its asymptotic size for approximately three years. *Pagurus pollicaris* grew significantly faster in shells of preferred size than in small shells, but molted at the same rate in each. Shell weight and internal volume affect egg clutch size in this species. Females were observed with 514–10,961 eggs. Meiss and Norman (1977a, b) compared the stomatogastric ossicles and musculature to that in penaeideans, astacideans and brachyurans, finding the structure to reflect generally accepted concepts of the phylogenetic position of the anomurans. Caine (1976) found spacing of the longitudinal bars in the gland filter of the gastric mill to be directly related to particle size in diet among six species of hermit carbs. Among these, *P. pollicaris* had a finer filter than progressively coarser *P. longicarpus*, *Clibanarius vittatus*, and *Petrochirus diogenes*. Stomach contents of *P. pollicaris* were 50% flocculent detritus, 35% scavenged material

and 15% sand grains (Caine 1975).

Kellogg (1971) found small individuals in *Nassarius obsoletus* and *Terebra dislocata* shells, but larger individuals in *Polynices* and *Busycon*. The species is prone to cloaking the shells with anemones, *Calliactis tricolor*, whenever possible, and individuals can be seen stealing the anemones from each other in aquaria (Anonymous 1975). The polyclad turbellarian *Stylochus zebra* is a commensal with *P. pollicaris* from Massachusetts to North Carolina, but there and south of this region the turbellarian lives in association with other hermits, feeding mainly on the shell encrusting *Crepidula plana* (see Lytwyn and McDermott 1976).

Sikora, et al. (1972) found *P. pollicaris* in stomachs of two species of hake, *Urophycis regius* and *U. floridanus*, in Georgia estuaries. In aquaria, *P. pollicaris* will eat the jellyfishes *Cyanea capillata* or *Stomolophus meleagris* in absence of other food (Phillips, et al. 1969).

***Pagurus pubescens* Krøyer**

Fig. 158

Pagurus pubescens Krøyer 1838:314 [86].—Squires 1964:359, figs. 1A, 2A, 6.—McLaughlin 1973:564, figs. 1B, 2B, 3B.

Eupagurus kroyeri Stimpson 1859:89 [43].—Smith 1879:48.—Benedict 1896:99, fig. B.

Pagurus kroyeri.—Rathbun 1929:27, fig. 36.

Recognition characters.—Anterior shield of carapace a little longer than broad, lightly sculptured, few scattered setae, frontal margin inflated. Rostrum with rectangular to obtuse tip slightly dilated distally, length about half width of shield; eye scales ovate, each tipped by strong submarginal spine. Antennular peduncles exceeding eyestalks by nearly full length of terminal article. Antennal peduncles exceeding eyestalks by about half length of terminal article; acicles unarmed, slender and curved sinuously outward, exceeding eyestalks.

Right cheliped much larger than left; hand and carpus armed with small to medium-sized spines most prominent on margins of hand and mesial margin of carpus where they become clustered near articulation with hand; few strong single and smaller compound spines on anterior margin of carpus. Minor chela with distinctive, central, longitudinal ridge of single-file spines on palm tending somewhat mesad along its crest to form abrupt slight overhang, but gradually sloping laterally and anteriorly to margin of hand and propodal finger; dactyl and part of palm mesial to ridge rather

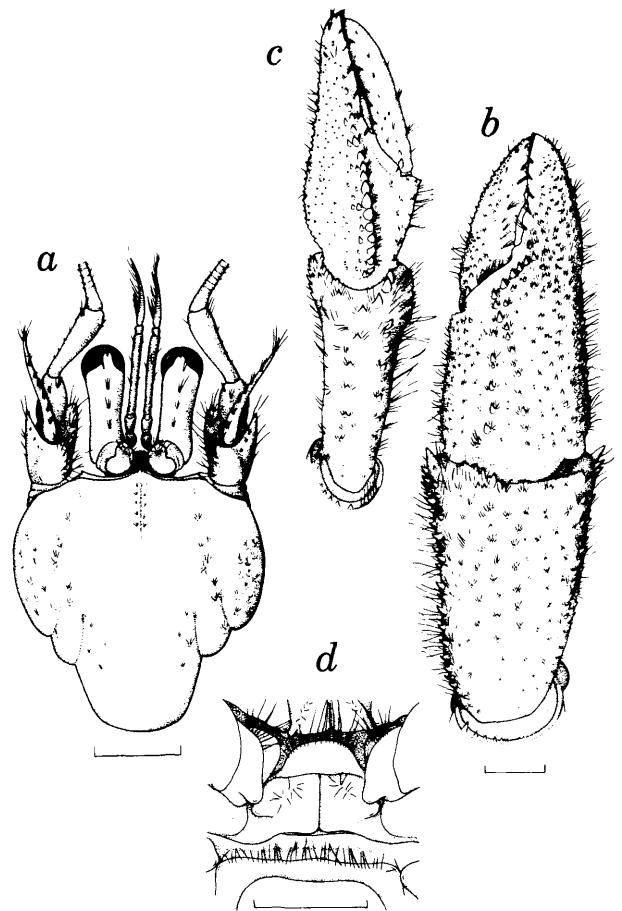


Fig. 158. *Pagurus pubescens* Krøyer. Male: a, anterior part of body in dorsal view; b-c, right and left chelae and carpi, external view; d, sternite between third legs; 5 mm indicated (USNM 98058).

smooth; lateral margin of hand with row of moderate spines, carpus laterally expanded anteriorly and armed with clustered spines; scattered hairs on both chelipeds, longest on carpi and ventral surface of hands. Walking legs (legs 2 and 3) with dactyls longer than propodi, smooth laterally but spined mesially, both articles with scattered tufts of setae.

Anterior part of sternite between third legs somewhat rectangular (almost twice as wide as long), its distal edge bearing short, sparse setae.

Measurements in mm.—Anterior shield: male, length 17.6, width 16.6; ovigerous females, length 11.6, width 11.0; length 8.3, width 7.8.

Variation.—The anterior portion of the sternite between the third legs is basically rectangular but varies somewhat in shape, and the setae on its distal edge are usually sparse but may be either short or long. The eye scales vary in width and some have supernumerary spines on tubercles on the mesial margin. The rostrum varies in acuteness at the tip.

Habitat.—This species has been reported from a wide variety of bottoms in arctic, subarctic, and boreal waters (Smith 1879; Squires 1957), tending to occur in deeper water in the southern parts of its range. Squires (1966) reported it occurring from 4 to 550 m, but mostly from 10 to 110 m, and in temperatures of -1.6° to 4.6°C in the northerly parts of its range.

Type-locality.—W. Greenland (Squires 1964).

Known range.—West Greenland, Foxe Basin, and Hudson Bay to off Cape Hatteras; Spitzbergen, Novaya Zemlya, and Barents Sea to Faeroes, Hebrides, England (except south coast), and southwestern Ireland (partly summarized in Williams 1974c).

Remarks.—Bousfield and Laubitz (1972), and Brunel (1970), gave further details on distribution in southeastern Canada. McLaughlin (1973) elaborated further distinctions between *P. pubescens* and the seemingly related *P. bernhardus* of Europe, showing morphological differences in both larvae and adults and at the same time questioning the possibility of hybridization between the two as was proposed by Jennings (1972).

Breeding season has not been reported in detail from the broad area of distribution. Squires (1962) recorded spawning in Frobisher Bay, Baffin Island, in autumn, and there are ovigerous females in the USNM collection from the northeastern Grand Banks in June, upper St. Lawrence estuary in July, and off Virginia in March.

Genera of the *Pylopagurus* Group

The genus *Pylopagurus* sensu lato has been split into a number of new genera (McLaughlin 1981). This somewhat heterogeneous assemblage has the following main characters, but the reader should see McLaughlin's revision for ample diagnoses of the new taxa: Right chela enlarged in form of operculum more or less exactly closing orifice of crab's protective housing, flexing at right angle on limb and prevented from complete extension by anterior edge of carpus, lower surface regularly convex; left chela more or less reduced; fingers of both flexed chelae moving in plane perpendicular to axis of body, those of minor chela ending in corneous tips. Frontal margin with 3 acuminate to obtuse projections. Fourth legs subchelate to nearly chelate; fifth chelate with well-developed rasp on fingers. Female with pair of pleopods behind last thoracic sternum followed by 4 unpaired pleopods along left side; male lacking first pair and with only 3 along left side. (Modified after A. Milne Edwards and Bouvier 1893.)

Genus *Anisopagurus* McLaughlin 1981

McLaughlin 1981:6.

Anisopagurus pygmaeus (Bouvier)

Fig. 159

Eupagurus pygmaeus Bouvier 1918:11, fig. 4.

Pagurus pygmaeus.—Provenzano 1959:410, fig. 19.

Anisopagurus pygmaeus.—McLaughlin 1981:6.

Recognition characters.—Anterior shield of carapace longer than wide and relatively smooth. Rostrum obtuse and slightly in advance of each lateral projection surmounted by slightly subterminal spine. Eyestalks shorter than width of anterior shield, wide at base, constricted in middle; eye scales with elongate anterior lobe armed along anteromesial margin with 3 to 5 spines. Antennular peduncles extending beyond eyestalks by about half length of terminal article. Antennal peduncle also

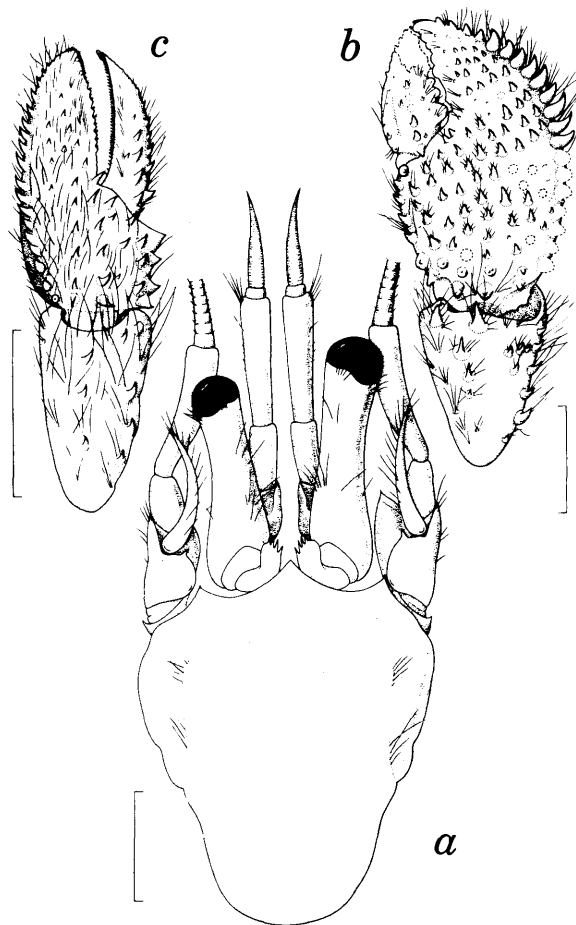


Fig. 159. *Anisopagurus pygmaeus* (Bouvier). a, Anterior part of body in dorsal view; b-c, right and left chelae and carpi. USNM 122457, a-b, male; USNM 48763, c, female; 1 mm indicated.

exceeding eyestalks; unarmed acicle curving outward, with tip reaching to or beyond base of cornea.

Chelipeds unequal, right much larger than left, both with some long, fine setae. Major chela sub-oval, more or less rimmed with row of strong, forward projecting spines; upper surface covered with smaller, nearly blunt, forward trending spines; carpus with 3 or more strong spines on upper anteromesial surface and 2 or more located laterally near short row of spines along lateral margin. Minor chela twice as long as broad; fingers spooned, with comb of fine corneous teeth on opposed edge distally; upper surface with many blunt spines (occasionally sharp), some formed into 2 central longitudinal rows; carpus with double row of strong forward-projecting spines on upper surface. First and second walking legs (legs 2 and 3) with dactyls shorter than propodi, variable number of spines on both articles.

Measurements in mm.—Anterior shield: male, length 2.5, width 2.9; ovigerous females, length 1.76, width 1.76; length 1.88, width 1.63.

Variation.—The lateral projections are obsolescent in some mature females and juveniles, their position being indicated only by the submarginal spine.

Color.—" . . . antennules are light, transparent blue; the antennae faintly purple with white bands; eyestalks clear; cephalothorax creamish with a green tinge; chelipeds and the first two proximal segments of each walking leg a brilliant vivid scarlet (no. 4-D6 in Maerz and Paul, *A Dictionary of Color*); and the distal segments of the ambulatories are colored by sequential bands of light blue-orange-dark blue-light blue-orange-yellow-dark blue-light blue-yellow. The bands of color go completely around the legs. The tips of the cheliped dactyls are light scarlet to white. The eggs are yellow-orange." (Hazlett 1966b.)

Habitat.—Hazlett (1966b) working in Curaçao found this small species limited to waters with open circulation and on a substrate of medium to large rocks with space between them and covered with a heavy, encrusting, red-scarlet algal growth (instead of the usual brown or green algae or detritus). Crabs were found in a meter or less of water, and during day always hidden beneath rocks and stones. *Pagurus brevidactylus* sensu stricto and *Phymochirus* (= *Pylopagurus*) *operculatus* were present in the same microenvironment; mostly this was in rock piles constructed by fishermen for breakwaters. To 82 m.

Type-locality.—Bahia de Socapa (= Zocappa) near Santiago de Cuba.

Known range.—Off Little River Inlet, S. C.;

southern Florida, including Tortugas, to Puerto Rico; Curaçao; to 82 m.

Remarks.—Ovigerous females are recorded in May from Cuba, July from Tortugas, August from South Carolina, and Hazlett (1966b) observed them in Curaçao.

Glaucothoes of *A. pygmaeus* oriented poorly in their first contact with shells (Hazlett and Provenzano 1965), some individuals making several attempts over periods of days before entering shells. Young crabs interact little with each other, but the older crabs do. In other studies, Hazlett (1966a, b) placed *A. pygmaeus* low in a ranking of *Pagurus* species expressing pagurid behavior. Shell fighting involves rapping and shell shaking; raps may be as many as 113/min, most of the motions being equal to the length of the eyestalks but some are half the length of the cephalothorax. Activity is mainly nocturnal. Mating behavior was observed in some detail.

Genus *Manucomplanus* McLaughlin 1981

McLaughlin 1981:6.

Manucomplanus corallinus (Benedict)

Fig. 160

Eupagurus corallinus Benedict 1892:23.

Pagurus corallinus.—Hay and Shore 1918:412, pl. 30, fig. 4.

Pylopagurus corallinus.—Williams 1965:134, fig. 110.

Manucomplanus corallinus.—McLaughlin 1981:6.

Recognition characters.—Anterior shield of carapace subcordate, smooth, truncate posteriorly. Rostrum obtuse, produced beyond rounded, unarmed lateral projection of front. Eyestalks stout, falling far short of tip of antennular peduncle, largest distally, cornea dilated; eye scales sharply pointed and with prominent subterminal spine. Antennal peduncle nearly as long as that of antennule; acicle reaching nearly to tip of cornea.

Chelipeds unequal, right larger than left and operculiform. Upper surface of major chela flattened or slightly excavated, covered with small, slender spines becoming flattened and mushroom-shaped on fixed finger as well as a few on dactyl; hand fringed with spines, often alternately large and small, becoming longer near tips of fingers, inner surface with spinose tubercles between base of dactyl and recess receiving carpus, recess bounded by crest; carpus approximately as long as palm, upper surface thickly set with sharp, spiny

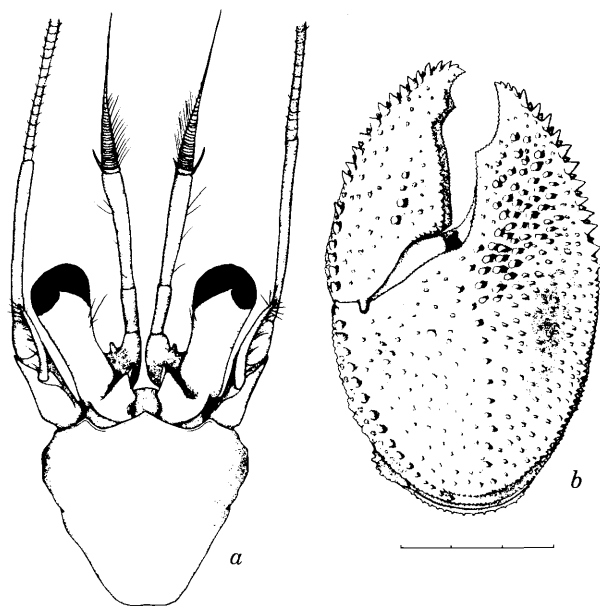


Fig. 160. *Manucomplanus corallinus* (Benedict). a, Anterior part of body in dorsal view; b, right chela, external view; (from two specimens) 3 mm indicated (from Williams 1965).

granules, margin with rows of small spines; merus compressed, quadrilateral when viewed laterally. Minor chela with hand broad, flattened; fingers broad, gaping at base; carpus compressed, surmounted by inner row of small and outer row of larger spines; merus compressed. Carpus and propodus of first walking leg and carpus of second crested with acute spines; dactyls setose, row of movable, distally pointing spines on ventral margin.

Measurements in mm.—Anterior shield: male, length 3.5, width 4.1; ovigerous female, length 2.4, width 2.6.

Color.—Large cheliped with merus and carpus blotched red and white; small cheliped and walking legs banded with same color (Benedict 1892).

Habitat.—In tunicates, sponges, stony corals, and bryozoans; 38 to 91 m (Wenner and Read 1982).

Type-locality.—Off Key West, Florida.

Known range.—Off Cape Lookout, N. C., to Gulf of Mexico between Cedar Keys, Fla., and Mississippi Delta; off Cape Catoche, Yucatan; a mutilated ovigerous female, probably of this species, off French Guiana (USNM 119889).

Remarks.—Ovigerous females have been taken off South Carolina in March, southern and western Florida in March and June, Georgia in June, and French Guiana (?) in September.

A specimen from Georgia was housed in a bryozoan "Texas longhorn shell."

Metabolically as well as geographically, this spe-

cies is tropical in affinities (W. B. and F. J. Vernberg 1970).

Genus *Phimochirus* McLaughlin 1981

McLaughlin 1981:4.

Phimochirus holthuisi (Provenzano)

Fig. 161

Pylopagurus operculatus.—Holthuis 1959:157, fig. 31.

Pylopagurus holthuisi Provenzano 1961:162, fig. 3.

Phimochirus holthuisi.—McLaughlin 1981:4.

Recognition characters.—Anterior shield of carapace about as long as wide, subcordate. Rostrum obsolete, hardly in advance of semi-acute lateral projections; anterolateral angles sloping posterolaterally without shoulders. Eyestalks about 3 times longer than wide, cornea dilated; eye scales slender, grooved dorsally, each ending in acute tooth or spine. Antennular peduncles extending slightly beyond cornea. Antennal peduncles not exceeding cornea; acicles simple, unarmed, reaching past posterior margin of cornea.

Chelipeds unequal, right larger than left and operculiform. Major chela slightly longer than greatest width, upper surface inflated, margins thin, slightly upturned and serrated; mesial margin of palm ending in prominent acute projection at base of dactyl, low rounded granules distributed over distal surface of palm and on fixed finger; dactyl with shallow groove on dorsal surface between 2 rows of round granules; carpus with 4 low appressed teeth on mesiodorsal margin, prominent mesiodistal tooth, and low ridge on distolateral margin; merus rounded dorsally in lateral view, ventral spine at anterolateral corner, anteromesial margin irregularly serrated and pair of small spines on dorsal anterior margin. Minor chela narrow, fingers spooned, tufts of heavy setae between fingers and on ventral surface; carpus with spine on anterodorsal-lateral-mesial margins and row of spines behind latter. Dactyls of walking legs longer than propodi, strong row of spines ventrally and weaker mesiodorsally; propodus with 1 or more weak ventral spines; merus with anterior dorsal tooth.

Measurements in mm.—Anterior shield: male, length 4.4, width 4.4; ovigerous (?) female, length 3.9, width 3.6.

Color.—"Anterior carapace with symmetrically placed pairs of short, longitudinal dark stripes. Posterior carapace markings blue. Blue spots on

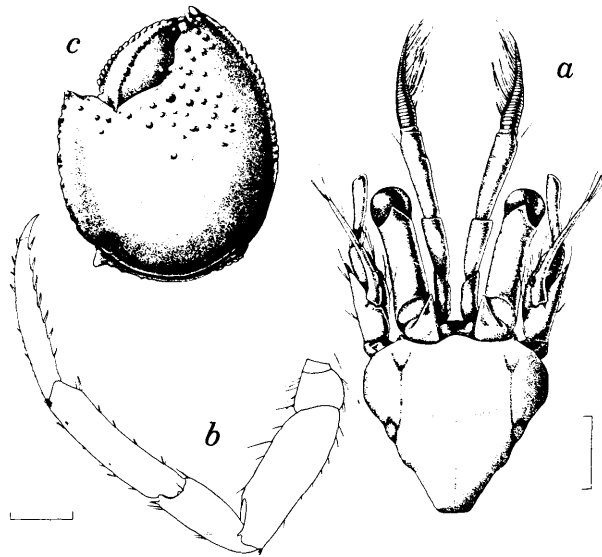


Fig. 161. *Phimochirus holthuisi* (Provenzano). a, Anterior part of body in dorsal view; b, first walking leg; c, right chela, external view; a, 5 mm; b-c, 2 mm indicated (from Holthuis 1959).

dorsal surface of abdominal somites. Eyestalks with thin ring of brownish pigment on proximal third. Antennules with brownish-yellow pigment band around ultimate and penultimate segments. Antennal scale and peduncle with spots of similar color. Major manus white distally, on dorsal surface very diffusely colored proximally with faint reddish-purple. (Paratype, with a few small scattered orange spots on dorsal face of merus.) Major carpus irregularly but diffusely colored with purple, anterodorsal margin with alternating white and dark spots. Merus blotched with purple. Minor manus colored similarly to walking legs which have on the dactyl a brownish longitudinal stripe on each side, another on the dorsal margin and one ventrally. Propodus with two stripes on each side, a fifth on dorsal margin, ventral stripe very diffuse. Stripes otherwise imposed on a diffuse yellow background which forms a band around each segment" (Provenzano 1961, from holotype).

Habitat.—Shell, sand, mud and coral bottoms; 15 to 104 m.

Type-locality.—Sand patch on coral rock bottom, 4½ mi. SE Ram's Head, St. John, Virgin Islands, 15–18 m.

Known range.—Off Oregon Inlet, N. C. (Herbst, et al. 1978), to Alabama (?); through West Indies to Surinam.

Remarks.—The species is closely related to *Phimochirus* (= *Pylopagurus*) *operculatus*. An ovigerous female taken off Alabama in March (USNM 102504) is questionably referred to this species; it has relatively longer eyestalks and eye scales than the holotype male and an acute rostrum exceeding each

lateral projection surmounted by an outwardly directed spinule. The major chela is missing from this specimen.

The deepest recorded occurrence is off Georgia, 30°51'30"N, 79°58'W. Specimens are recorded from stomachs of large adult hogfish, *Lachnolaimus maximus*, at St. John (Provenzano 1961).

Genus *Pylopagurus* A. Milne Edwards and Bouvier 1893

McLaughlin 1981:2.

Pylopagurus discoidalis (A. Milne Edwards)

Fig. 162

Eupagurus discoidalis A. Milne Edwards 1880:41.

Pylopagurus discoidalis.—A. Milne Edwards and Bouvier 1893:76, pl. 6, figs. 7–14.—Williams 1965:134, fig. 109.—McLaughlin 1981:2.

Recognition characters.—Anterior shield of carapace strongly calcified, subcordate, smooth, truncate posteriorly; anterior margin with large, sharp-pointed rostrum extending beyond middle of eye scales; lateral projections rudimentary, low and rounded, borders lateral to them very oblique. Eyestalks short, thick, widest distally, shorter than length of frontal border, not reaching middle of terminal article of antennular and antennal peduncles, cornea large; eye scales narrow, lanceolate. Acicles without spine and deflected a little outward, varying from shorter than to slightly exceeding eyestalks.

Chelipeds unequal, right larger than left. Major chela in form of operculum adapted to close openings in *Dentalium* shells or similar tubes; chela flexing at right angle on carpus and incapable of complete extension, upper surface smooth, flattened or slightly excavated, nearly discoidal in outline, surrounded by raised border with finely crenulate edge, lower surface slightly wrinkled with lines; fingers compressed, internal border of dactyl with rounded tubercles; carpus short, dilated in front, external surface ornamented with granulations following feebly squamose irregular lines (occurring also on hand back of edge forming operculiform portion), and with few denticles on anterior border. Minor cheliped shorter, chela oval, very fine denticles on lateral border; fingers agape at base and terminating in corneous tips; carpus with some spines on crest. Walking legs reaching tip of major chela, dactyls setose and with lanceolate, corneous terminal claw well developed.

Measurements in mm.—Anterior shield: male,

length 5.5, width 4.4; ovigerous female, length 3.9, width 3.5.

Variation.—The large chela may be elongate, but becomes more discoidal with advancing age (Milne Edwards and Bouvier 1893).

Color.—Whitish but with large areas of reddish on hands, on each article of legs, and ring of same color near base of eyes; reddish color may extend over anterior part of cephalothorax (Milne Edwards and Bouvier 1893).

Habitat.—The species has been taken from *Dentalium* shells and from annelid tubes of similar shape; 55 to 930 m.

Type-locality.—Montserrat, 220 m.

Known range.—ENE Oregon Inlet, N. C. (Provenzano 1963a), through eastern Gulf of Mexico and West Indies to mouth of Amazon River, Brazil.

Remarks.—Ovigerous females are known from the northern Gulf of Mexico in March, and are recorded in November from southern Florida and Brazil.

Hazlett (1966a) stated that living only in scaphopod shells [?] seems to have affected behavior patterns in this species; the crab can move quickly but not backward because the housing digs into sand, therefore the crabs tend to withdraw into their shells during aggressive interactions. As they walk, feed, etc., the major hand is at an oblique angle to the carpus, thus always in a "presentation" position; cheliped extension is from this position when two

come together. Other movements of the small chelae were also discussed.

Genus *Rhodochirus* McLaughlin 1981

McLaughlin 1981:3.

Rhodochirus rosaceus (A. Milne Edwards and Bouvier)

Fig. 163

Pylopagurus rosaceus A. Milne Edwards and Bouvier 1893:97, pl. 7, figs. 10–17.—Hay and Shore 1918:413, pl. 30, fig. 5.—Williams 1965:135, fig. 111.

Pylopagurus acutus Forest and de Saint Laurent 1967:148, figs. 114, 120–123.

Rhodochirus rosaceus.—McLaughlin 1981:3.

Recognition characters.—Anterior shield of carapace subcordate, truncate posteriorly; anterior margin with 3 projections, rostrum obtuse and falling short of strong lateral projections, each terminating in minute spine; sides of dorsal surface and anterior surface with few tufts of setae. Eye stalks stout, shorter than anterior shield, distinctly dilated distally and with 3 or 4 tufts of setae in line along upper surface; eye scales subacute anteriorly, each ending in slender subterminal spine. Antennal peduncle extending beyond eye, flagellum slender and longer than body; acicle strongly curved, reaching almost to distal edge of cornea.

Chelipeds unequal, right much larger than left. Both chelae capable of being bent down at right angle to carpus to form, either singly or together, an operculum closing orifice of cavity inhabited by crab. Both margins of major chela, and outer margin of minor chela, armed with row of close-set, conical teeth; upper surface of both hairy and covered with closely crowded, rosettelike tubercles each consisting of central larger tubercle surrounded by smaller ones; major chela with longitudinal ridge on each finger, ridge on minor propodus much weaker, concavity on propodi of each between central ridge and lateral margin; inner surface of major hand slightly rugose between base of dactyl and recess receiving carpus. Carpus of major cheliped with scattered sharp spines and hairs dorsally, strongest along mesial margin; merus with cross striae on upper surfaces, its anterior edges serrated with teeth in single row. Minor cheliped similar but hairier and with crest of spines on carpus. Walking legs of medium length, first and second of left side, and second of right side exceeding large

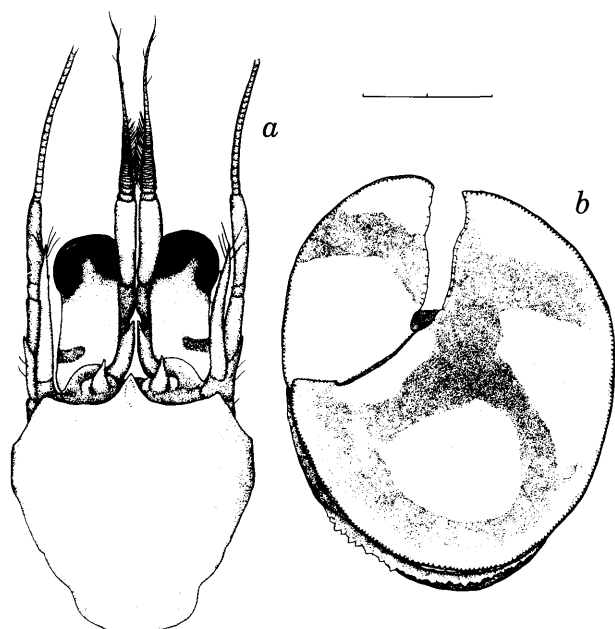


Fig. 162. *Pylopagurus discoidalis* (A. Milne Edwards). Ovigerous female: a, anterior part of body in dorsal view, eyestalks showing color pattern; b, right chela, external surface showing color pattern; 2 mm indicated (from Williams 1965).

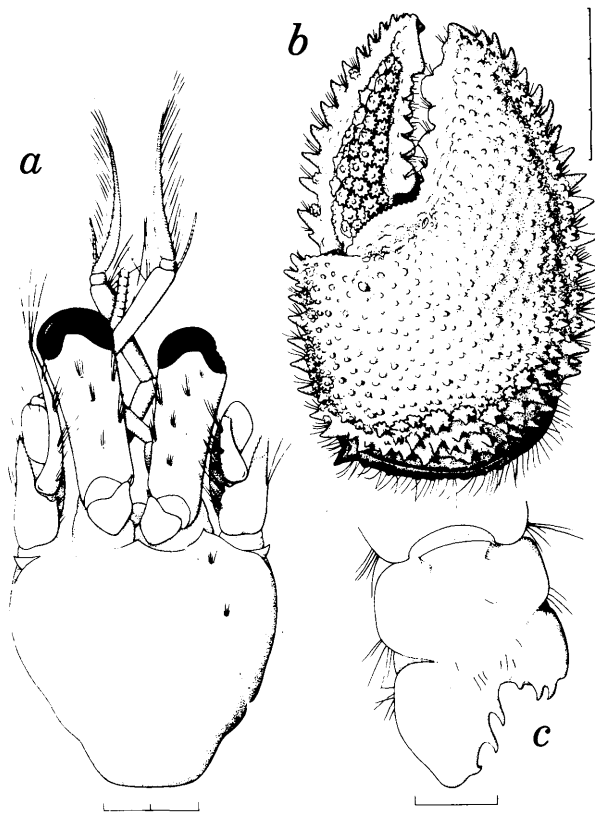


Fig. 163. *Rhodochirus rosaceus* (A. Milne Edwards and Bouvier). a, Anterior part of body in dorsal view; b, right chela, external view (from Williams 1965); c, telson. a, MCZ, holotype female, 2 mm; b, 3 mm; c, holotype female, 1 mm indicated.

chela, articles setose on dorsal margin, dactyls with row of ventral spines.

Measurements in mm.—Anterior shield: male, length 5.3, width 5.6; ovigerous female, length 3.7, width 3.9; holotype female, length 5.5, width 5.6.

Color.—Some specimens faded in alcohol retain alternate, longitudinal, light and orange to reddish stripes on dorsal and lateral surfaces of the walking legs, and tints of reddish on the chelipeds and eyestalks.

Habitat.—The holotype was taken from an unknown species of the molluscan genus *Antillophos* (= *Phos*); 119 to 168 m; (70–90 m, Cain 1972).

Type-locality.—Grenada, 168 m.

Known range.—South of Cape Lookout, N. C.; Grenada, and Surinam.

Remarks.—An ovigerous female is known from Surinam in September. The record listed from off Western Dry Rocks, Key West, Fla. (Williams 1965), is an incorrect identification.

Forest and de Saint Laurent (1967) compared their new species, *Rhodochirus* (= *Pylopagurus*) *acutus*, to *P. rosaceus* saying that it seemed closer to the form described by Hay and Shore (1918) and Williams (1965) from North Carolina than to *Rhodo-*

chirus (= *Pylopagurus*) *rosaceus* but that comparison of the type of *P. rosaceus* with specimens of Williams and the type of *P. acutus* would be necessary to verify this hypothesis. I have not seen the type of *P. acutus*, but reliance on good illustrations (Forest and de Saint Laurent 1967), the holotype of *P. rosaceus*, and specimens from the Western Atlantic yields the following information.

The type of *P. rosaceus* is a damaged, partly decalcified female specimen which was imperfectly illustrated by Milne Edwards and Bouvier (1893). Their illustration shows the eyestalks and eye scales too close together and lateral projections of the shield devoid of spines. The left side of the shield is now fractured and the right side broken and folded over, but, when laid in position, the right lateral projection exceeds the level of the obtuse rostrum and is tipped by a tiny spine directed laterad. From the type and comparative material, it seems evident that there is considerable variation in the rostrum. In material from North Carolina (USNM 51046, 102719) the rostrum is obtuse, but in a lot of 12 specimens from French Guiana (USNM 103481) the rostrum is obtuse in 6, intermediate in 2, and acute in 4. None of the above are exactly like the holotype; all except 102719 have tiny spines on the lateral projections, but though rostrums vary in length, none are as advanced as shown by *P. acutus* (Forest and de Saint Laurent 1967). Telson spines are bluntest in the type of *P. rosaceus*, but acute in most of the other material except a male from 51406. On balance it seems that all of these are probably one species, more acutely spinose in southern parts of their range, becoming less so with age.

Genus *Tomopaguropsis* Alcock 1905

Alcock 1905:136.

Tomopaguropsis problematica (A. Milne Edwards and Bouvier)

Figs. 164–165

Eupagurus? *problematicus* A. Milne Edwards and Bouvier 1893:151, pl. 11, figs. 1–10.

Tomopaguropsis problematica.—Alcock 1905:137.

Recognition characters.—Anterior shield of carapace fairly smooth but grooved at sides, slightly wider than long, truncate posteriorly. Rostrum acute, extending between eye scales and well advanced beyond acute, divergent, spiniform tips of lateral projections. Eyestalks somewhat dilated at cornea, a bit longer than distance between lateral

projection of front; anterior projection of eye scales formed as a bent triangle directed outward distally and tipped by tiny spine, dorsal surface convex. Antennular peduncles exceeding eyestalks by about $\frac{3}{4}$ length of terminal article. Antennal peduncle about length of eyestalk; acicles rather stout, curved outward and extending to tip of peduncle.

Chelipeds superficially similar in shape but right larger than left. Major chela with irregular short setae dorsally, surface a bit uneven but essentially smooth except for few tubercles or low spines along mesial margin; dactyl of female less than half length of hand, with 2 or more sometimes conspicuous teeth proximal to conspicuous tooth at midlength of propodal finger; carpus rather smooth dorsally but row of low, well-separated spines on mesial margin and 1 or 2 near anterior border. Minor hand shorter, narrower, more uneven, and with finger proportionately thicker in lateral view; carpus a bit

spinier and hairier than opposite member. Walking legs (legs 2 and 3) little longer than chelipeds, rather stout, conspicuously setose dorsally, dactyls longer than propodi.

Measurements in mm.—Anterior shield: male, length 3.5, width 3.88; female, length 5.0, width 5.25.

Habitat.—13.7 to 528 m.

Type-locality.—Near Sand Key [SSW Key West, Fla.], 228.6 m.

Known range.— $1\frac{3}{4}$ mi. NE Cape Lookout, N. C.; southern Florida and Bahamas; Barbados; off Honduras ($16^{\circ}39'N$, $82^{\circ}29'W$).

Remarks.—I left this species out of the Carolinian fauna in 1965 because the single specimen known from near Cape Lookout, N. C., had a question mark on the jar label after the vessel name

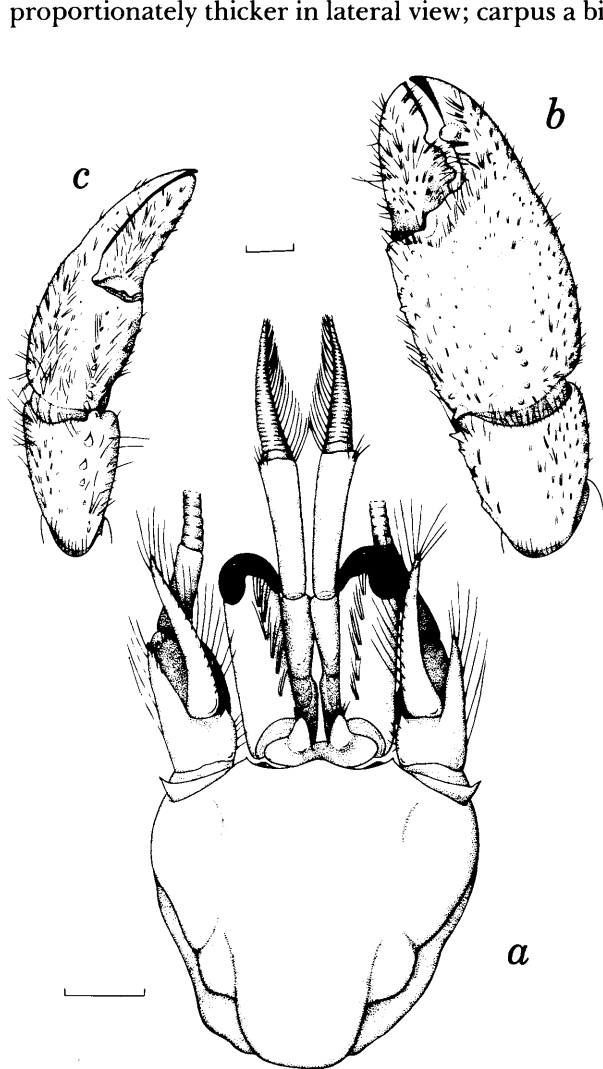


Fig. 164. *Tomopaguroopsis problematica* (A. Milne Edwards and Bouvier). Male: *a*, anterior part of body in dorsal view; *b-c*, right and left chelae and carpi, external view; 1 mm indicated (MCZ, holotype).

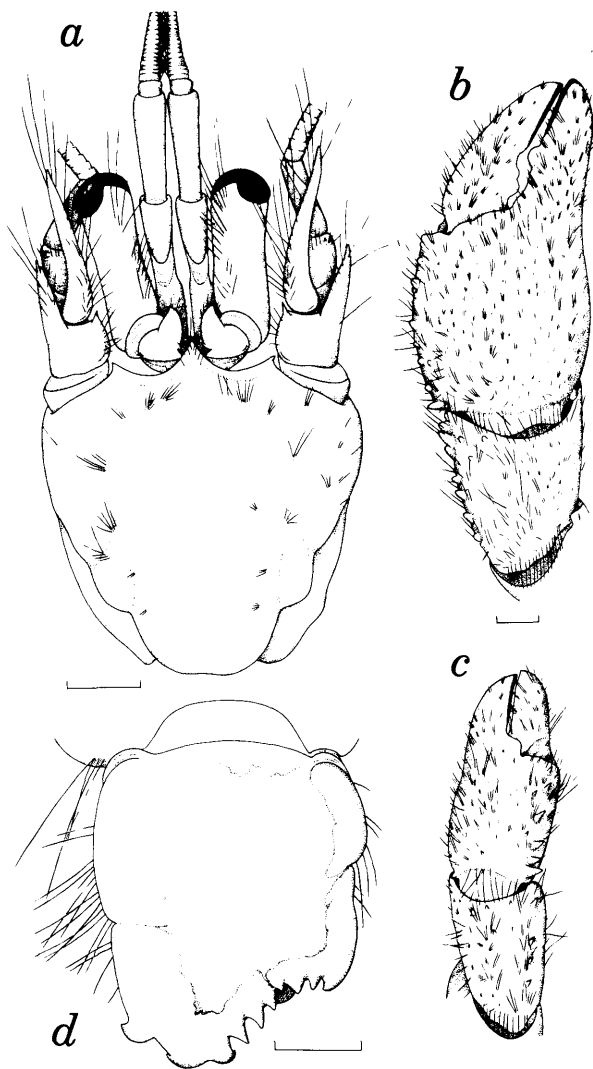


Fig. 165. *Tomopaguroopsis problematica* (A. Milne Edwards and Bouvier). Female: *a*, anterior part of body in dorsal view; *b-c*, right and left chela and carpi, external view; *d*, telson; 1 mm indicated (USNM 102720).

(made out in 1958). I now consider this record valid. The specimen was collected by the *Fish Hawk* in 1902 in sample 7302, the first sample taken in that cruise off North Carolina. There is no question concerning the locality marked in either the *Fish Hawk* records or the USNM (102720) catalog entry.

Family Lithodidae

Crablike; abdomen more or less firm, often segmented, bent under thorax. Tail fan not developed, uropods absent. First pair of legs chelate; fourth pair like third; fifth pair very small, folded under carapace to give superficial appearance of only 4 pairs of legs (Rathbun 1929).

Genus *Lithodes* Latreille 1806

Latreille 1806:39.—Rathbun 1929:29.—Balss 1957:1592.—Hemming 1958b:175.

Lithodes maja (Linnaeus)

Fig. 166

Cancer maja Linnaeus 1758:629.

Lithodes Maia.—Bell 1853:165, fig.

Lithodes maia.—Bouvier 1896:10, 24.—Selbie 1921:56, pl. 9, figs. 1–4.—Rathbun 1929:29, fig. 39.

Lithodes maja.—Stephensen 1935:8.—Holthuis 1950:141, figs. 51, 52, 53.—Balss 1957:1592, fig. 1170.—Squires 1965a:110.

Recognition characters.—Carapace pyriform in outline, about as long as broad, exclusive of rostrum and marginal spines; margin somewhat reflexed and armed with numerous long, strong spines, anterolateral ones strongest; dorsal surface ornamented with numerous spines and tubercles, regions distinct and elevated except sunken hepatic area. Rostrum prominent, elongate, bifurcated at tip, armed on basal $\frac{1}{3}$ with 2 divergent spines and near base with 2 or more divergent dorsal-dorsolateral spines; prominent, forwardly curved, median ventral spine between divergent eyestalks.

Chelipeds unequal, shorter than adjacent walking legs; merus and carpus armed with strong, sharp spines on mesial and dorsal surfaces; hands with scattered moderate spines on mesial margin and sharp tubercles dorsally; fingers spooned at tips, about as long as palm and finely serrate on opposed cutting edges of smaller chela, shorter than palm and with broad calcareous teeth on opposed cutting edges of larger chela, tufts of stiff setae on

fingers of both hands. Second to fourth legs similar, elongate, cylindrical proximally to compressed distally and strongly spined on merus, carpus and propodus; each dactyl somewhat compressed, curved, terminating in slender corneous tip, and armed proximally with prominent lateral and mesial spine, usually smaller pair of dorsal spines, and 2 or more still smaller appressed spines on external (dorsal) surface, sparse row of very slender spines ventrally. Fifth legs reduced and folded beneath carapace in gill chamber, each ending in tiny, spatulate, hairy chela.

Abdomen greatly modified, permanently folded beneath cephalothorax; first and second segment fused in broad, calcified, tuberculate and spiny, nearly vertical curved plate; remaining segments more or less molded into flattened, tuberculate, plastronlike structure composed of tuberculate leathery central portion bounded by radiating, calcified, paired plates of third, fourth and fifth segments and unpaired sixth, in turn bounded by narrow calcified marginal plates (in males) and telson; third to fifth segments symmetrical in males, but strongly asymmetrical in females with plates of third, fourth and fifth segments much enlarged on left side and narrow marginal plates lacking on left.

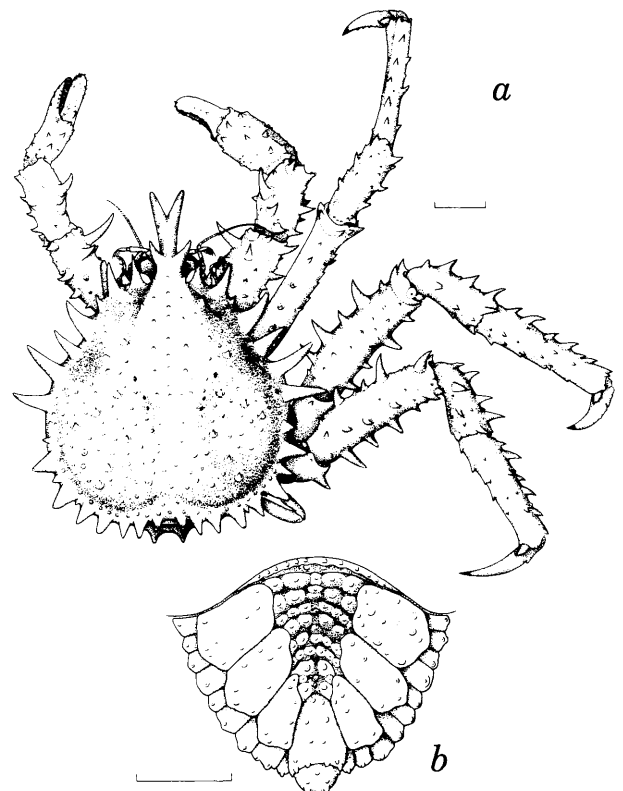


Fig. 166. *Lithodes maja* Linnaeus. Male: a, dorsal view, walking legs of left side not shown; b, abdomen; 10 mm indicated (USNM 2015).

Measurements in mm.—Extreme length of carapace including spines at least 145 in large specimens, sex unknown (Selbie 1921), but usually smaller. Kampf and Kittel (1952/53) pictured specimen with leg span of about 40 cm.

Variation.—Spinination varies individually and the rostrum is not always provided with dorsal spines on the basal third.

Color.—"Madder brown, tubercles and spines tipped with vinaceous cinnamon; legs obscurely banded with two shades of the brown" (Rathbun 1929); yellowish red, spines darker, under surface paler (Bell 1853); bright red with dull spines (Holtuis 1950).

Habitat.—Essentially a boreal species from moderate depths but not found in waters below 0°C and rare below 2.5°C (Blacker 1957); 65–790 m (Rathbun 1929; Selbie 1921; Squires 1965a, 1966; Stephensen 1935).

Type-locality.—*Habitat in Oceano Europaeo.*

Known range.—East and west Greenland to Sandy Hook, N. J.; Iceland; Spitsbergen; Barents Sea and North Sea to Netherlands and Belgium, Western Scotland to Isle of Man, and western Ireland to County Cork (Christiansen and Christiansen 1962; Hillis 1966; O'Riordan 1968; Rae and Lamont 1963; Selbie 1921; Squires 1966).

Remarks.—In European waters, ovigerous females are known from December to March (Holtuis 1950) and in December and April from Bear

Island south of Spitsbergen (Blacker 1957); in the northwestern Atlantic, about 60% of females are ovigerous in autumn (Squires 1970). MacDonald, et al. (1957) summarized knowledge of larval development and described the eggs; two zoeal stages and a glaucothoe are known from laboratory hatchings and plankton.

Old individuals may be greatly overgrown with fouling organisms such as calcareous worm tubes (Sivertsen 1953).

Section Galatheidea

Superfamily Galatheoidea

Family Galatheidae

Carapace longer than wide, often ornamented with transverse, ciliated lines. Rostrum distinct and strongly pointed, projecting beyond eyes. Antennular peduncle elongate. Antennae with 4-jointed peduncle. Chelipeds greatly elongated, slender. First, second, and third walking legs well developed; last leg feeble, reduced in size. Abdomen bent upon itself but not folded under thorax; males with pair of sexually modified pleopods on segments 3, 4 and 5; females with rudimentary pleopods on second segment, fully developed pleopods on 3, 4 and 5.

Key to Genera and Species

(Adapted from Chace 1942)

1. Rostrum rather broad, concave or flattened above, margins toothed *Galathea rostrata*
Rostrum slender, occasionally very finely serrate but toothless; supraocular teeth at base [*Munida*] 2
2. Posterior margin of carapace unarmed, no median spines on cardiac region 3
Ridge along posterior margin of carapace armed with spines, 1 or more spines on cardiac region, rostral spine slightly shorter than supraocular spines *M. longipes*
3. Basal segment of antennular peduncle with distolateral spine longer than distomesial spine; a large species *M. valida*
Basal segment of antennular peduncle with distomesial spine longer than distolateral spine 4
4. Merus of third maxillipeds with single spine on lower margin 5
Merus of third maxillipeds with 3 or 4 spines on lower margin. *M. irrasa*
5. Supraocular spines reaching to distal edge of or beyond cornea; a medium-sized to large species *M. iris iris*
Supraocular spine not reaching to distal edge of cornea; a small species. *M. pusilla*

Genus *Galathea* Fabricius 1793

Fabricius 1793:471.—Hemming 1958b:143.—Baba 1969:9.

***Galathea rostrata* A. Milne Edwards**

Fig. 167

Galathea rostrata A. Milne Edwards 1880:47.—Hay and Shore 1918:402, pl. 29, fig. 4.—Chace 1942:30.—Haig 1956:2.—Williams 1965:105, fig. 81.

Recognition characters.—Carapace somewhat flattened; transverse ciliated ridges prominent, at least 4 continuous for entire width; lateral margins with number of acute spines, each spine at end of ridge.

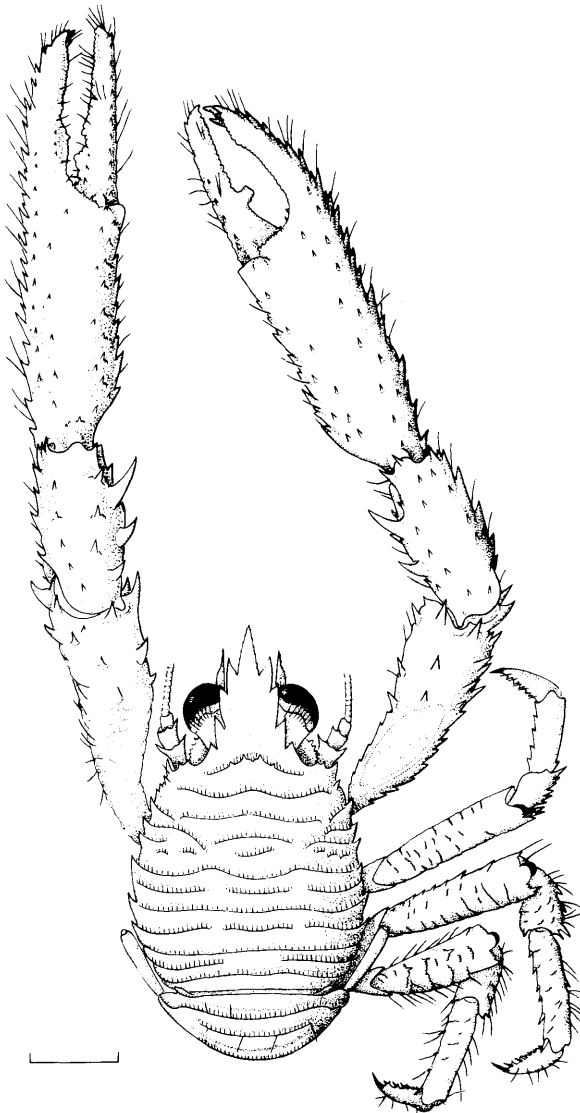


Fig. 167. *Galathea rostrata* A. Milne Edwards. Male in dorsal view, walking legs of left side not shown; 2 mm indicated (USNM 9604).

Front prolonged into broad, shallowly excavated rostrum armed with usually 4 strong, anteriorly pointing spines on each side, and prominent, narrowly triangular tip. Merus of third maxillipeds with 3 or 4 spines on lower margin.

Chelipeds nearly twice as long as body, comparatively heavy; with rows of spines or spiniform granules along margins and appressed, squamiform, ciliated granules on surfaces; a few larger spines on carpus and distal end of merus. Hand little shorter than body; opposed edges of fingers finely serrate, nearly straight in juveniles but increasingly uneven in adults; chelipeds often asymmetrical in males with fingers of larger hand gaping.

Abdomen with transverse striae similar to those on carapace but lacking lateral spines.

Measurements in mm.—Length of carapace including rostrum: male 10.6, ovigerous female 9.6.

Color.—Ground color off-white, cream, and light yellow; mottled with orange and reddish orange especially on legs, less evident on body; spines red or tipped with red; a single small circular reddish spot in center of each branchial region; a white band on propodi of walking legs; distal half of fingers white (from specimen recently preserved in formalin).

Habitat.—Has been taken from the coral, *Oculina diffusa*, in the northeastern Gulf of Mexico (S. Alexander, personal communication), and ivory tree coral (see below); 18 to 92 m.

Type-locality.—16 miles north of Jolbos Islands [Yucatan Peninsula] at 26 m.

Known range.—Off Cape Hatteras, N. C., to southern Florida, northwestern Florida to Mississippi Delta, and off Cape Catoche, Yucatan, Mexico (Gore 1979). A Block Island, Rhode Is., record (2155 m) is either an error or an accidental occurrence.

Remarks.—Ovigerous females are known from Yucatan in January and February, off western Florida from January to April, off northeastern Florida in March and April, and North Carolina in March (Milne Edwards and Bouvier 1897; Gore 1979; USNM, and UNC-IMS records).

Gore (1979) described larvae of *G. rostrata* reared under laboratory conditions. Ovigerous females taken with a clump of ivory tree coral in a cloth bag by a lock-out diver on 15 April 1977 in 80 m, 12°C water off eastern Florida were returned to the laboratory and maintained until eggs hatched. Variation in duration and number of zoeal stages appeared to be temperature-dependent; larvae reared at 15°C developed through five zoeal stages and attained megalopa stage in 52 days, whereas larvae cultured at 20°C passed through four of five zoeal stages, reaching megalopa in 18 or 23 days.

respectively. Some variation in morphology of stages was noted and compared to that in other larval galatheids.

Genus *Munida* Leach 1820

Leach 1820:52.—Milne Edwards and Bouvier 1897:20.—China 1966:256.—Zariquiey Alvarez 1968:281.

Munida iris iris A. Milne Edwards

Fig. 168

Munida iris A. Milne Edwards 1880:49.—Milne Edwards and Bouvier 1894:256.—1897:21, pl. 2, figs. 2–7.—Benedict 1902:310.—Pequegnat and Pequegnat 1970:131.

Munida caribaea.—Smith 1881:428.—1883:40, pl. 3, fig. 11.—1884:355.—1886:643 (not *Munida caribaea* Stimpson 1860a:246 or *Munida caribaea*.—Milne Edwards 1880:49).

Munida sp. indet.—Smith 1882:22.

Recognition characters.—Carapace narrowed both anteriorly and posteriorly, sides arcuate, adorned with transverse lines of iridescent pubescence, spiny. Rostral spine much longer than supraocular spines; latter not extending to distal edge of cornea. Gastric area with pair of spines behind supraocular spines and 2 or (usually) more spinules more or less transversely in line with these on each side, spine close to each hepatic region; 1 or more spines on each triangular area near cephalic groove; 1 to 4 spines (plus occasional tubercles) on each branchial region behind cervical groove; long antero-lateral spine followed by 6 (occasionally 5) lateral spines. Basal article of antennular peduncle with mesial spine longer than distal lateral spine, slender spine dorsal to latter somewhat variable in length. Merus of third maxillipeds with single strong spine on lower margin, distal spinule may be absent or present.

Chelipeds very long and slender, usually subcylindrical; covered with ciliated, squamose rugosities becoming progressively finer and more widely spaced distally; merus with longitudinal rows of spines. Fingers straight except occasionally gaping near base in one or both hands of large individuals, varying from as long as to $\frac{3}{4}$ length of palm, prehensile edges with single row of closely spaced, fine serrations interrupted by few larger teeth; tips hooked and crossing. Walking legs with mesiodorsal distal spine on carpus, merus with prominent distal spines and mesiodorsal row of spines.

Second segment of abdomen (apparent first)

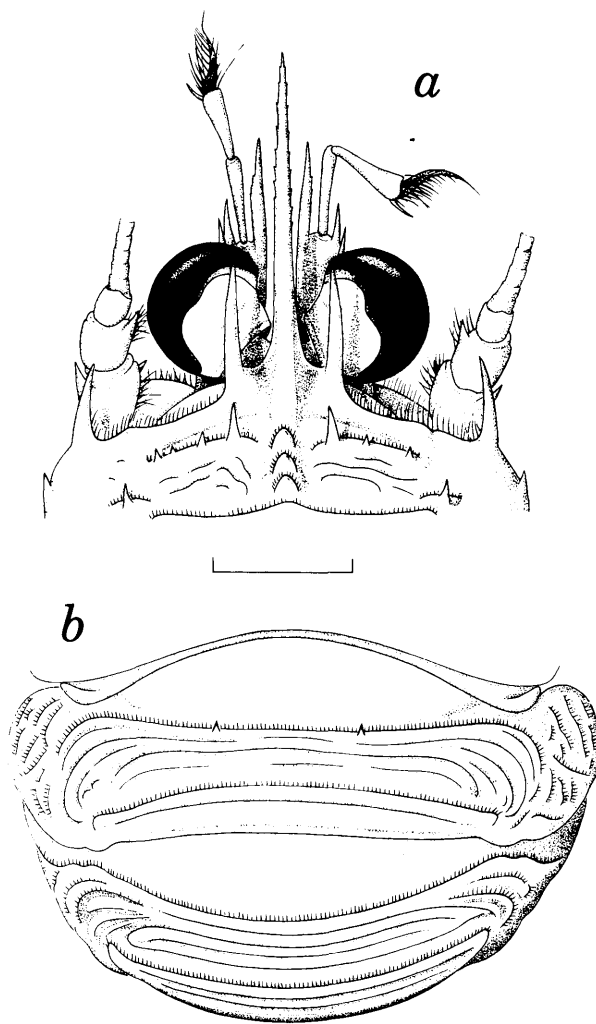


Fig. 168. *Munida iris iris* A. Milne Edwards. Female: a, frontal region and appendages in dorsal view; b, second, third, and part of fourth abdominal segments, dorsal view; 5 mm indicated (USNM 48811).

armed with pair of spinules on anterior margin, occasionally a second or third small pair.

Measurements in mm.—Length of carapace including rostrum: male 47, female 45, ovigerous females 12.6 to 44. Length of unusually large disarticulated left chela with gaping fingers 228.

Habitat.—43 to 613 m (Wenner and Boesch 1979; Wenner and Read 1982).

Type-locality.—Off Barbados, 382 m, Blake Stn. 274.

Known range.—SSE of Martha's Vineyard, Mass., through southeastern Gulf of Mexico to near Cozumel Island, Yucatan, and through Caribbean islands to off mouth of Amazon River.

Remarks.—This species is the most abundantly represented *Munida* from the western Atlantic in the USNM collection, some lots containing hundreds of specimens. The eastern Atlantic form, recognized as *M. iris* by Milne Edwards and Bou-

vier (1897), was regarded as a subspecies (*M. iris rutlanti*) by Zariquey (1952a, 1952b).

Musick and McEachran (1972) found *M. i.* associated mainly with *Homarus americanus* and *Cancer borealis* which together probably form a stable "nucleus of a shelf-edge upper slope decapod fauna which also includes *Nephropsis aculeata*, *Bathynectes superba* [= *longispina*], and *Rochinia crassa*," along the Chesapeake Bight.

The breeding season as shown by ovigerous females is long, perhaps year round in parts of the range. Present records are as follows: southern Florida, February to August; Georgia, May; North Carolina, June and October; southern New England, August and September; Delaware capes to off Chesapeake Bay, October; off Amazon River, November.

Williams and Brown (1972) analyzed age and reproductive condition of a sample of 251 *M. iris* taken at a depth of 275 m off North Carolina in June (Eastward Stn. 9888). The sample contained 63.7% females, representing a statistically significant departure from a 1:1 male-female ratio, including both parasitized and non-parasitized individuals. Of 160 females, 135 were ovigerous, bearing an estimated average of 7,900 eggs each. There was a highly significant statistical difference between the mean size of large males and females in this sample, but both comparisons with other species and measurements given above indicate that the two sexes reach comparable carapace lengths. Sizes of males in the sample apparently fitted into 3 groups: (1) small, 19 mm or less in length of carapace; (2) intermediate, 20-22 mm (including the mean size, 21.3 mm); and (3) large, 23-26 mm. All males in the latter group had markedly enlarged chelipeds, much larger than females of comparable size, and a few males in the intermediate group showed this development. Such allometry in this and other species of *Munida* is correlated with attainment of sexual maturity.

Two males in the sample harbored attached barnacles, *Trilasmis* (*Poecilasma*) *inaequilaterale* (Pilsbry) on the chelipeds. Two ovigerous females possessed long, thin, white colored unidentified worms coiled within the egg masses on the underside of the abdomen. Twenty-five specimens were parasitized by bopyrid isopods later identified as *Anuropodione carolinensis* (see Markham 1973). Of non-ovigerous females, 56% were infested with the bopyrid, but overall incidence of parasites in the sample was 10%.

Munida irrasa A. Milne Edwards

Fig. 169

Munida irrasa A. Milne Edwards 1880:49.—Hay and Shore 1918:402, pl. 28, fig. 8.—Chace 1942:46.—

Haig 1956:3.—Williams 1965:105, fig. 82.—Pequegnat and Pequegnat 1970:132.—Scelzo 1973:163.

Munida caribea.—Young 1900:403.—Türkay 1968:249.

Recognition characters.—Carapace narrowed anteriorly, adorned with transverse lines of iridescent pubescence, spiny. Rostral spine much longer than supraocular spine, latter not extending to distal edge of cornea. Row of 6–10 spines across gastric region (pair behind supraocular spines largest) in addition to 1 or 2 on each hepatic region, 2 to 5 on each triangular area and 1 to 4 on either side behind cervical groove on mesial portion of each branchial region; anterolateral spine long, followed by 6 distinct lateral spines. Basal article of antennular peduncle with distomesial spine longer than distal lateral spine, slender spine dorsal to latter somewhat variable in length, occasionally diverging anterolaterad. Merus of third maxillipeds with 3 or 4 spines on lower margin.

Chelipeds 3 or 4 times as long as carapace, subcylindrical except for somewhat flattened and broadened hand of large, mature males; covered with ciliated, squamose to tuberculiform rugosities becoming progressively finer distally; merus with rows of spines continued but reduced on carpus and hands. Fingers usually straight; prehensile

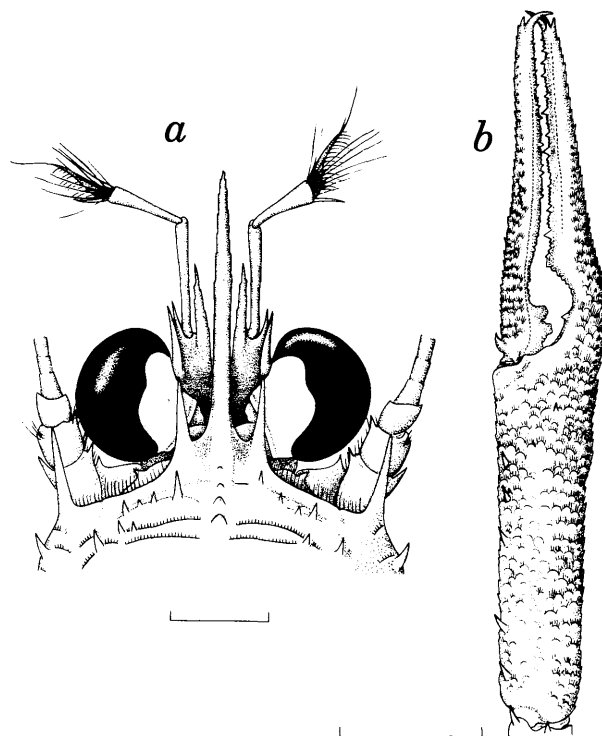


Fig. 169. *Munida irrasa* A. Milne Edwards. Male: a, frontal region and appendages in dorsal view; b, right chela, external view; a, 2 mm; b, 5 mm indicated (USNM 136629).

edges with single row of fine serrations interrupted by few larger teeth, meeting throughout except gaping at base in large, mature males; tips hooked and crossing. Most prominent spines on walking legs at distal end of merus and carpus.

Abdomen without spines.

Measurements in mm.—Length of carapace including rostrum: male 18.8; ovigerous females 4 (Chace 1942) to 15.4.

Habitat.—14 to 475 m.

Type-locality.—Not designated with certainty; syntypes from 10 localities in the Gulf of Mexico and Caribbean (MCZ).

Known range.—Off Cape Lookout, N. C., through eastern Gulf of Mexico and Caribbean Sea to 34°14'S, 51°40'W off Uruguay; "600 mi. off St. Davids, Bermuda" (USNM).

Remarks.—The Uruguay record from R/V *Walter Herwig* was reported as 41°40'W longitude by Scelzo (1973) but is recorded as above in USNM.

The name *Munida caribaea* in its various spellings has caused confusion, but as Faxon (1895) pointed out, Stimpson's (1860a) *M. caribaea* "is absolutely indeterminable from his brief notice of it, and the types were burned in the great Chicago fire." Faxon recommended that the name be dropped, a practice followed by most authors thereafter, although Young (1900) and Türkay (1968) recognized forms under this name whose descriptions most closely fit that of *M. irrasa*.

***Munida longipes* A. Milne Edwards**

Fig. 170

Munida longipes A. Milne Edwards 1880:50.—Hay and Shore 1918:402, pl. 28, fig. 9.—Schmitt 1935a:178.—Chace 1942:47.—Pequegnat and Pequegnat 1970:132, fig. 5–3.

Recognition characters.—Carapace narrowed both anteriorly and posteriorly, sides arcuate; depressed and somewhat unevenly arched dorsally; adorned with strong transverse lines of raised, lightly ciliated, close-set, fine tubercles; cervical groove fairly deep. Supraocular spine reaching about to distal edge of cornea, rostrum shorter except in some juveniles. Gastric area with pair of strong spines behind cervical groove on each branchial region and often behind each a smaller spine, sometimes even a third still smaller; median spine usually on raised cardiac region (rarely additional clustered spinules); pair of strong spines on posterior margin; strong anterolateral spine followed by irregular row of marginal spines, third and fourth superior in size and position to remainder. Basal article of antennular peduncle with distolat-

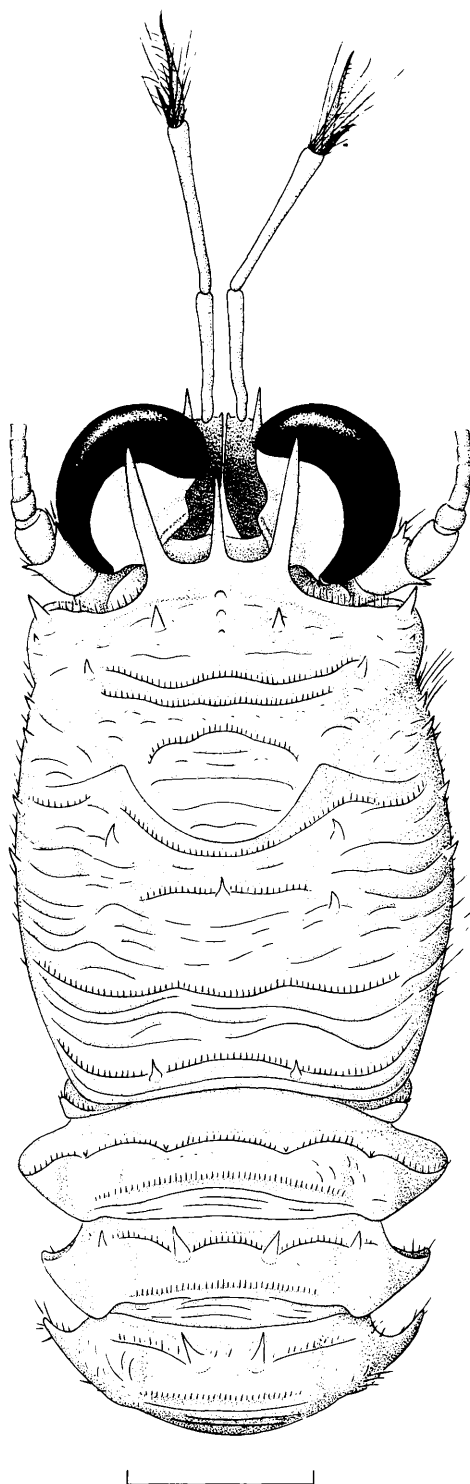


Fig. 170. *Munida longipes* A. Milne Edwards. Body of male in dorsal view; 5 mm indicated (USNM 92857).

eral spine much longer than distomesial spine. Merus of third maxillipeds with single spine on lower margin.

Chelipeds long and slender, usually subcylindrical but palms slightly expanded, covered with many ciliated rather sharply tuberculiform rugosities tending to form rows except on fingers. Fingers straight, smooth, about $\frac{1}{3}$ or less length of palm,

prismatic in cross section; prehensile edges meeting throughout length, each with single irregular row of small teeth; tips hooked and crossing, fixed finger with strong subterminal spine externally at base of hooked tip. Walking legs as long as chelipeds; rows of well-developed spines on meri and few similar spines on carpi.

Abdomen unevenly arched dorsally, 4 spines on anterior margin of second (apparent first) and third segments, and 2 spines on fourth.

Measurements in mm.—Length of carapace including rostrum: male 18, female 18, ovigerous female 22.

Habitat.—40 to 618 m (Wenner and Read 1982).

Type-locality.—Not designated with certainty; syntypes from 7 localities off Cuba and the Lesser Antilles (MCZ).

Known range.—SE Cape Lookout, N. C., through Gulf of Mexico to British Honduras, and through West Indies to Curaçao.

Remarks.—There is considerable variation in number of the smaller spines and spinules on the carapace. Not all setae are iridescent, but some are so along sides of the body and in tufts on the legs. This species tends to be very brittle in preservation.

Ovigerous females are known from: South Carolina and Mayaguez, P. R., harbor in January; east of Mississippi River Delta in February; northwest of St. Thomas, V. I., in March; off Tortugas, Cape Canaveral, and Alabama in April; Bahama Bank in May; off Mississippi River Delta to SE Florida in July; SE of Cape Lookout, N. C., and in western Gulf of Mexico in November.

***Munida pusilla* Benedict**

Fig. 171

Munida pusilla Benedict 1902:268, fig. 16.—Haig 1956:2.

Recognition characters.—Carapace narrowed both anteriorly and posteriorly, sides arcuate, adorned with transverse lines of iridescent pubescence. Rostral spine much longer than supraocular spines; latter short, not half length of eyes. Gastric area with pair of spines behind supraocular spine and 2 or more spinules transversely in line with these, spine close to each hepatic region; 2 or 3 spinules on each triangular area near cervical groove, 1 on each branchial region behind cervical groove; long anterolateral spine followed by 5 or 6 lateral spines. Basal article of antennular peduncle with mesial spine longer than distal lateral spine, slender spine dorsal to latter somewhat variable in length. Merus

of third maxillipeds with single spine on lower margin.

Chelipeds of male long and slender, usually subcylindrical; covered with ciliated, squamose to tuberculiform rugosities becoming progressively finer distally; merus with rows of spines continued but reduced on carpus and hands. Fingers usually straight, prehensile edges with single row of closely spaced, fine serrations interrupted by few larger teeth, meeting throughout length except occasionally gaping near base in one or both hands; tips hooked and crossing. Cheliped of female shorter and spinier. Most prominent spines on walking legs at distal end of merus and carpus.

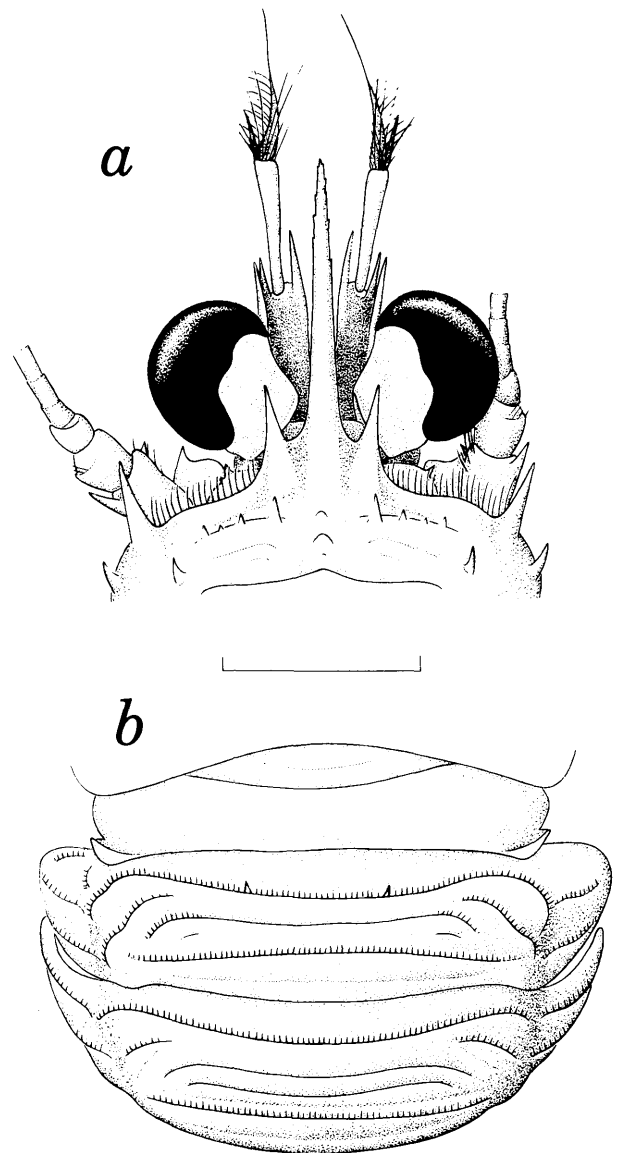


Fig. 171. *Munida pusilla* Benedict. Ovigerous female: a, frontal region and appendages in dorsal view; b, first, second and third abdominal segments, dorsal view; 2 mm indicated (UNC-IMS 2608).

Second segment of abdomen (apparent first) sometimes armed with pair of tiny spinules on anterior margin.

Measurements in mm.—Length of carapace including rostrum: male 12.6; ovigerous female 4.8 to 10.3.

Habitat.—33 to 133 m.

Type-locality.—Albatross Stn. 2405, Gulf of Mexico [south of Cape San Blas, Fla., 28°45'N, 85°02'W, 55 m].

Known range.—Off Cape Lookout, N. C., to Straits of Florida and through eastern Gulf of Mexico to Yucatan; Colombia and Trinidad.

Remarks.—*Munida pusilla* is a small species similar to *M. iris* and *M. irrasa*. There is variation in spination on the carapace and abdomen; spinules may or may not be present on the anterior margin of the second abdominal segment and, if present, seem more pronounced in larger individuals.

Ovigerous females are known from Yucatan in January, Florida from February to April and in September, and North Carolina in June.

Munida valida Smith

Figs. 172–173

Munida valida Smith 1883:42, pl. 1.—Milne Edwards and Bouvier 1894:256.—Pequegnat and Pequegnat 1970:137.

Recognition characters.—Carapace with sides almost parallel, curved mesad posteriorly, narrowed slightly anterior to cervical groove; rather evenly arched dorsally; adorned with transverse line of raised, ciliated, close-set, fine tubercles. Rostrum and supraocular spine stout; rostrum usually more than twice mesial length of supraocular spines which in turn extend to or beyond distal edge of cornea (somewhat shorter in juveniles); supraocular spines divergent and directed somewhat dorsally, rostrum broadly upturned distally. Gastric area with pair of strong spines behind supraocular spines; much smaller spine of spinule usually behind each of these; spine behind cervical groove on each branchial region; strong spine on rounded (more oblique in young) anterolateral margin and 5 or 6 marginal spines behind it. Basal article of antennule with distolateral spine longer than distomesial spine, prominent, ascending, slender spine dorsal to former sometimes obscuring it. Merus of third maxillipeds with prominent central spine and blunter distal one on lower margin.

Chelipeds elongate, subcylindrical (flattened in adults) and spiny; most of surface, sometimes including fingers, covered with short, dense pilosity. Fingers about as long as palm (variable); prehen-

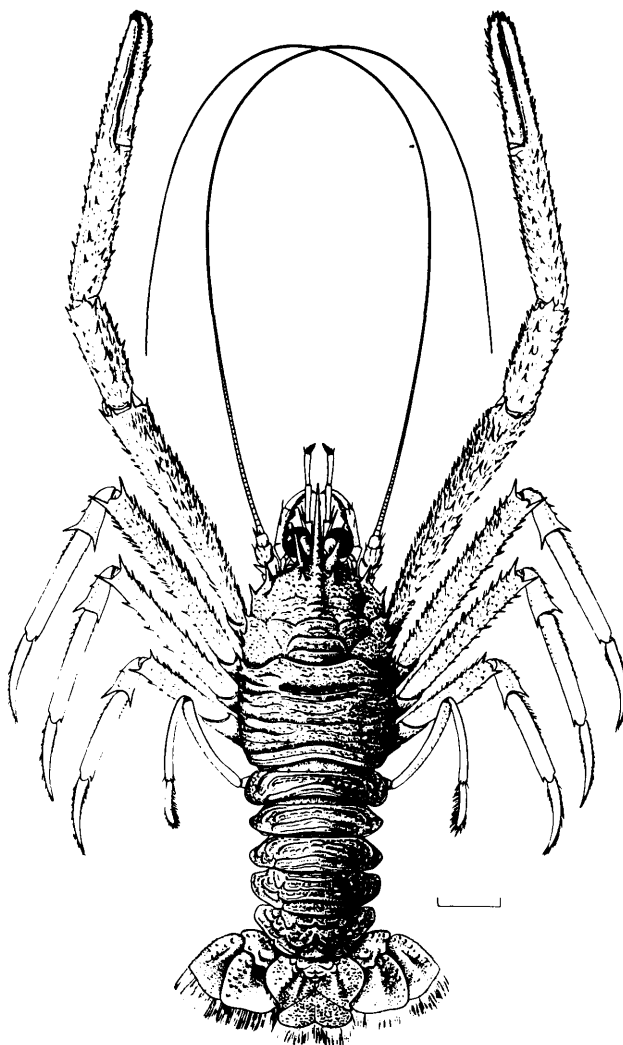


Fig. 172. *Munida valida* Smith. Male in dorsal view, 20 mm indicated (from Smith 1883).

sile edges straight, each with single row of fine teeth and hooked, crossing tips; chelae in few males noticeably broadened with fingers gaping proximally, dactyl with raised proximal tooth row or enlarged single tooth, tips occasionally spooned and finely toothed. Walking legs shorter than chelipeds, prominent acute spine on meri and carpi, propodi much smoother but with ventral row of fine acute spines.

Abdomen evenly arched dorsally, second (apparent first) and third segments with spinules on anterior margin.

Measurements in mm.—Length of carapace including rostrum: male 54, female 48, ovigerous female 49.

Habitat.—90 to 1823 m (Wenner and Boesch 1979), but shallower occurrences are known. A sample from Gerda Stn. 490, Straits of Florida, 26°37'N, 78°57'W, taken in 1- and 2-m 00-mesh plankton nets at a depth of 0–9 m between 0505

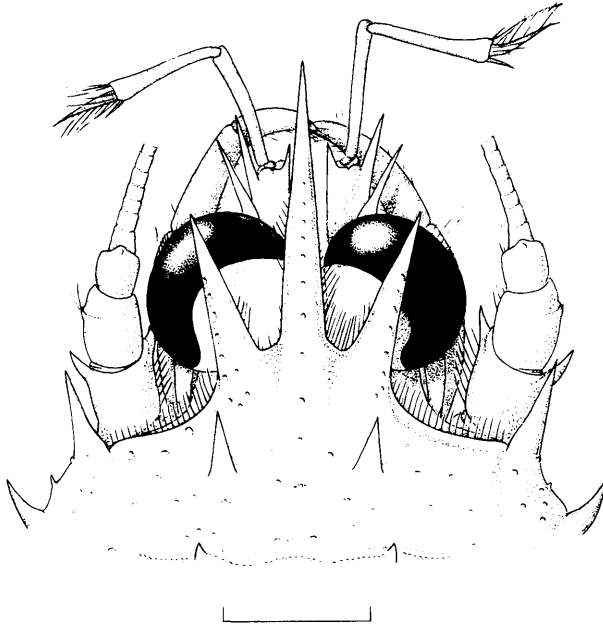


Fig. 173. *Munida valida* Smith. Male frontal region and appendages in dorsal view; 5 mm indicated (USNM 136673).

and 0605 hr over a bottom depth of 384–402 m on 3 February 1965 (USNM 136673) contains many large adults including ovigerous females.

Type-locality.—Off southern New England, *Fish Hawk* Stn. 1112, 39°56'N, 70°35'W, 448 m; Stn. 1124, 40°01'N, 68°54'W, 1171 m.

Known range.—Off southern New England through Gulf of Mexico to Golfo de Morrosquillo, Colombia, and Curaçao.

Remarks.—The original drawing by J. H. Emerton of the male specimen Smith (1883) described from *Fish Hawk* Stn. 1112 (USNM 7313) is reproduced here. Whereabouts of the female from Stn. 1124 is unknown.

Milne Edwards and Bouvier (1894) and Benedict (1902) cleared up possible confusion of this species with *M. miles*. The two species are distinct, *M. miles* having much shorter supraocular spines than *M. valida*.

Menzies, et al. (1973) listed *M. valida* as a dweller in the archibenthic zone (450–950 m) that occasionally rises to the continental shelf. They, and Rowe and Menzies (1968), showed photographs of *M. valida* oriented to bottom currents on the continental slope off North Carolina (302–800 m). These photographs suggested that some of the individuals faced north away from the Gulf Stream current (in June when the photos were taken), and still others seemed to face south in the deep counter current. An alternate suggestion was that some water may be recirculated, carried along by the Gulf Stream at low velocity, and that the crabs face away from water of “high” velocity into “low” velocity.

Ovigerous females have been recorded nearly the year round: off North Carolina in January and November; eastern and southeastern Florida in February, April and June; southern New England in August; east of Mississippi River Delta in September; western Gulf of Mexico in November.

Some specimens from Florida in the USNM collection bear sacculinid parasites. Others, especially large males, bear the barnacle, *Trilasmis* (*Poecilasma*) *kaempferi* (Darwin).

Family Porcellanidae

General form crablike. Carapace well calcified, depressed, regions usually not well defined; front often prominent but never with rostrum greatly projecting beyond eyes. Antennae inserted external to eyes, with 3 movable articles and a flagellum. Basal articles of antennules broad. Outer maxillipeds too large to be contained in buccal cavity. Chelipeds moderately elongate, usually broad, symmetrical, composed of 7 segments, bent under and held closely against thorax; males with pair of pleopods on segment 2, sometimes rudimentary or absent; females with pair of pleopods on segments 3, 4, and 5, those on 3 sometimes reduced or absent. Telson composed of 5 or 7 well-calcified pieces (Haig 1960).

Key to Genera and Species

(Modified after Chace 1942)

1. Form elongate, “hippalike”; telson much longer than broad *Euceramus praelongus*
 Form less elongate; telson usually broader than long, never much longer than broad 2
2. Lateral wall of carapace broken up into 2 or more pieces separated by membranous interspaces; front triangular or transverse in dorsal view, never with projecting teeth; carapace subquadrate 3

- Lateral wall of carapace nearly always entire; if not, front distinctly tridentate in dorsal view; carapace not subquadrate 4
3. Carapace with numerous transverse tufts of setae; chelipeds and legs setose *Pachycheles pilosus*
Carapace relatively smooth, not setose; chelipeds deeply ridged and eroded, not setose *Pachycheles rugimanus*
4. Basal antennal article small, not joining margin of carapace, articles with free access to orbit *Petrolisthes galathinus*
Basal antennal article strongly produced forward and broadly in contact with margin of carapace, movable part far removed from orbit. 5
5. Dactyls of walking legs armed with strong, fixed spines; carapace distinctly broader than long *Polyonyx gibbesi*
Dactyls of walking legs ending in simple spine, usually with small, movable accessory spinules on lower margin 6
6. Front strongly tridentate in dorsal view; chelipeds not tuberculate 7
Front trilobate in anterior view; chelipeds tuberculate *Megalobrachium soriatum*
7. Cervical groove terminating anterolaterally in shallow indentation at edge of carapace *Porcellana sayana*
Cervical groove terminating anterolaterally in distinct, longitudinal, V-shaped cleft at edge of carapace. *Porcellana sigsbeiana*

Genus *Euceramus* Stimpson 1860

Stimpson 1860b:445.—Haig 1960:187.

Euceramus praelongus Stimpson

Fig. 174

Euceramus praelongus Stimpson 1860b:445.—Hay and Shore 1918:405, pl. 29, fig. 3.—Haig 1956:7.—Williams 1965:109, fig. 86.

Recognition characters.—Carapace subcylindrical, elongate, covered with minute, irregular, transverse rugae; sides slightly arcuate; anterolateral margins with 2 small spines (more or less obtuse) on each side behind antennae. Front tridentate, rostrum about twice length of lateral spines; broad, shallow V-shaped indentation at posterior edge of carapace. Eyes well developed. Antennules short. Antennae about $\frac{3}{4}$ length of body, flagella with sparse, fine setae; basal article short, not produced forward; movable articles not far removed from orbit. Third maxillipeds large, forming subquadrate shield extending laterally almost to edge of carapace.

Legs and underparts with ornamentation similar to carapace, ridges more pronounced and setate on distal articles. Chelipeds stout, subequal; somewhat stouter in males than in females; fingers about as long as palm, more gaping in males than in females. First pair of walking legs shorter than

second and third pairs.

Abdomen small, fringed with setae, distal segments narrow; uropods reduced. Telson longer than broad, composed of 7 elements.

Measurements in mm.—Length of carapace from tip of rostrum to center of posterior indentation: males 16; ovigerous females 15.4.

Color.—Background of carapace greenish gray to greenish tan with lighter and darker line of color delineating striae and marginal furrow; a light longitudinal stripe, broadest anteriorly, along mid-dorsal line; purplish marking along lines separating major regions of carapace; legs mottled with greenish gray or tan as on carapace; suggestion of iridescence on body and legs (from specimen collected by L. McCloskey, Morehead City Harbor, N. C., Aug. 7, 1962).

Habitat.—Sandy beaches below water line, and on both smooth and broken-shell bottoms; low-water mark to 38 m.

Type-locality.—Beaufort, N. C.

Known range.—Delaware Bay (USNM; Watling and Maurer, 1976) to Aransas area of Texas coast.

Remarks.—Haig (1960) placed *Euceramus* between the group of porcellanid "genera in which the basal antennal segment is short and not broadly in contact with the anterior margin of the carapace, and the group of genera in which the basal segment is strongly produced forward so that the movable segments are far removed from the orbit."

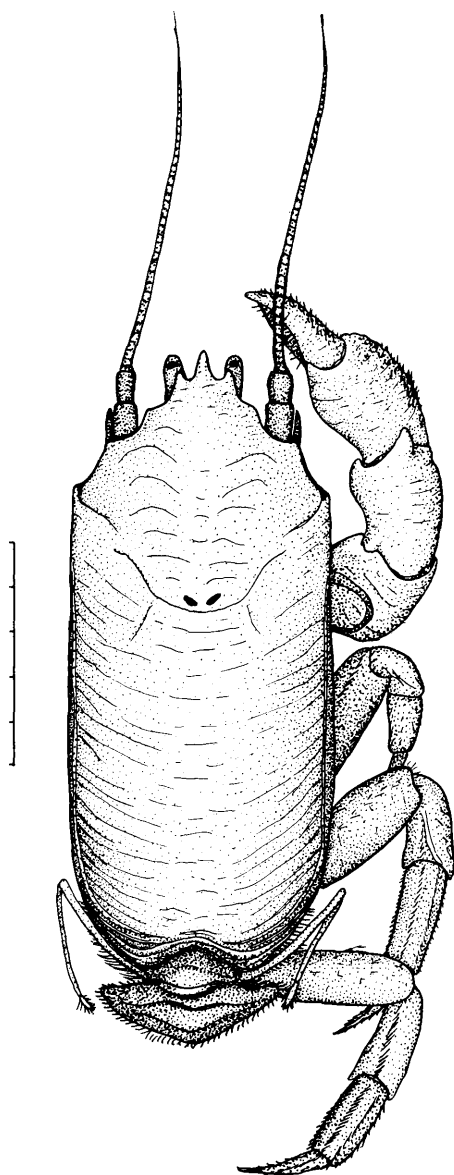


Fig. 174. *Euceramus praelongus* Stimpson. Animal in dorsal view, fifth leg only of left side shown, 5 mm indicated (from Williams 1965).

Hay and Shore (1918) and Haig (1956) remarked that *E. praelongus* is a rare species. Pearse, et al. (1942) helped to explain its apparent rarity by describing its adaptation to life in the substrate, drawing parallels to *Emerita*, *Lepidopa* and *Ogyrides*. They characterized it as a highly adapted burrower which burrows backward in subtidal sand along beaches, but it is also found on rubble-covered bottoms and the depth range indicates general adaptation to burrowing in shallow shelf waters. Rouse (1970) gave data on occurrence in southwestern Florida in temperatures of 16°–29°C over

a salinity range of 29 to 39‰. Juveniles have occasionally been taken in nocturnal surface plankton tows inside inlets in North Carolina. The animal scrapes entrapped food from the hairy antennae with setose mouthparts.

Ovigerous females are known from Florida in January (Camp, et al. 1977); Georgia in February, April and May; North Carolina in May and November; mouth of Chesapeake Bay in July; and York River, Va., in August (Roberts 1968b). Roberts (1968b) reared larvae in 21.5‰ salinity water at temperatures ranging from 25° to 28°C, finding two zoeal stages and a megalopa. He compared these to larvae of other porcellanids in a discussion and useful table. Sandifer (1973d) reported larvae in plankton from the mouth of Chesapeake Bay to some distance up York River, Va., from June to October in a temperature range of 19.3° to 37.9°C over a salinity range of 15.74 to 32.34‰, with greatest abundance in August and September. One larva in a January sample (4.9°C) may have resulted from error in sorting. Most were stage I larvae and most were in bottom samples.

Genus *Megalobrachium* Stimpson 1858

Stimpson 1858:228.—Haig 1960:212.

Megalobrachium soriatum (Say)

Fig. 175

Porcellana soriata Say 1818:456.—Hay and Shore 1918:404, pl. 29, fig. 6.

Porcellanopsis soriata.—Haig 1956:35.

Megalobrachium soriatum.—Haig 1960:229.—Williams 1965:112, fig. 89.—Felder 1973:32, pl. 4, fig. 12.—Gore and Abele 1976:17.

Recognition characters.—Carapace somewhat hexagonal, slightly wider than long; sides emarginate, unevenly and sharply tuberculate; lateral walls more or less hairy; areolations well marked, some tuberculate. Front irregularly rounded in dorsal view, median and lateral lobes produced downward in frontal view. Orbits well defined; eyes well developed. Antennae about as long as carapace; basal article strongly produced forward and broadly in contact with margin of carapace; movable article slender and removed from orbit.

Chelipeds long and heavy, roughly tuberculate; hand fringed with long hair along lower margin and with granulate tubercles in rather well-defined

rows; fingers with white, usually strongly hooked tips; carpus with 1 strong spine and some smaller spines on anterior border, dorsal aspect with tubercles irregularly arranged and appearing granulate under slight magnification; merus ornamented distally like carpus. First 3 pairs of walking legs stout, lightly setose and with sharp, curved dactyls.

Telson composed of 5 elements.

Measurements in mm.—Carapace: male, length 5, width 5.5; ovigerous female, length 4 to 5, width 4 to 5.5.

Color.—In life a dirty gray; in alcohol a rusty or grayish red.

Habitat.—Free living among corals, rocks, and sponges; in North Carolina found especially in canals of sponges taken from fishing banks offshore near Beaufort Inlet (Hay and Shore 1918; Pearse and Williams 1951). Wass (1955) found the species in sponges of the genus *Ircinia* in Florida, and Gore (USNM records) found it in *Oculina* coral off Vero Beach, Fla.; shore to 171 m.

Type-locality.—St. Catherines Island, Ga.

Known range.—Off Cape Hatteras, N. C., to Port Aransas, Tex.; West Indies to Barbados; Contoy, Mexico; Bahia Caledonia and Galeta Island, Panama.

Remarks.—This small porcellanid crab, very close to its Pacific congener, *M. tuberculipes* (Lockington), is rare in the southwestern Caribbean (Gore and Abele 1976).

Ovigerous females have been taken off the Carolinas in June, July, and August. Rouse (1970) found

them year round in southwestern Florida at temperatures of 19°–30°C in salinities of 24 to 45‰. Gore (1973) reared larval stages from an ovigerous female caught just off Vero Beach, Fla., in late June. Held in nonflowing but aerated 35‰ salinity seawater at room temperature of 25°C, the eggs hatched in nine days. A prezoal stage lasting only 10 min to 1 h molted through two subsequent zoal stages of about six days duration each before transforming to the megalopa which lived, at most, eight days but failed to transform to first crab stage. Larval stages were illustrated, described and compared to those of related species.

McCloskey (1970) discussed association of this crab with the scleractinian coral, *Oculina arbuscula*, community along the Carolinas.

Genus *Pachycheles* Stimpson

Stimpson 1858:22.—Haig 1960:131.

Pachycheles pilosus (H. Milne Edwards)

Fig. 176

Porcellana pilosa H. Milne Edwards 1837:255.

Pachycheles pilosus.—Haig 1956:11.—Williams 1965:108, fig. 84.

Recognition characters.—Carapace slightly broader than long, flattened but somewhat more convex from front to back than from side to side; lightly rugose along sides, with numerous short, transverse tufts of setae except scattered setae on frontal region. Frontal margin sinuous, slightly produced in middle, with submarginal row of setae. Anterolateral margins emarginate. Epimeral pieces of metabranchial regions separated by membranous interspaces, posterior part consisting of 1 or more pieces. Orbits deeply excavated, postorbital angle spiniform; eyes short, stout. Antenna with first movable article bearing buttressed spine on anterior margin; second article with spine near middle of anterior border; third article short, smooth.

Chelipeds unequal, stout, ornamented with numerous long, dark setae with shorter ones between; hands inflated, lateral margin of each spined and tuberculate below, obsolescent spines on inner edge of palm and dactyl; fingers short, major fixed fingers with single blunt tooth, opposed edges of minor fingers serrated; carpus with number of prominent white tubercles on proximal part, mesial border with about 3 spines; merus outlined dorsally with long setae, usually a stout spine and large white tubercle at inner distal angle. First 3 pairs of

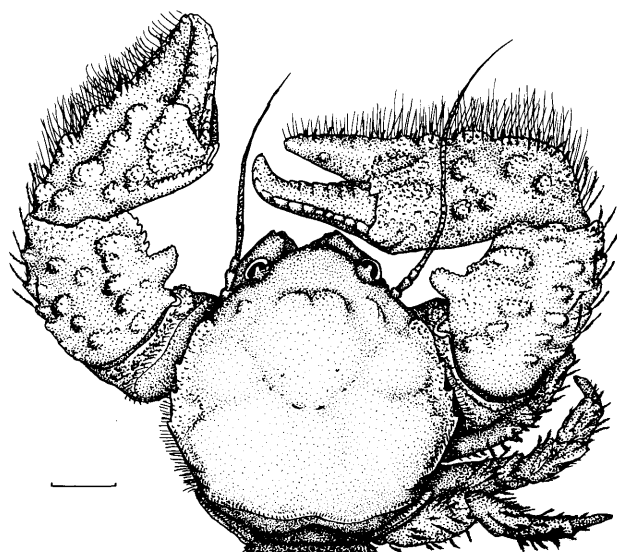


Fig. 175. *Megalobrachium soriatum* (Say). Animal in dorsal view; second, third, and fourth legs of left side not shown; 1 mm indicated (from Williams 1965).

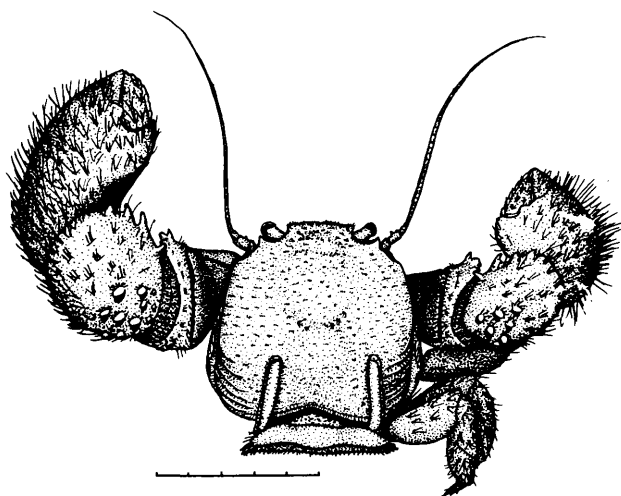


Fig. 176. *Pachycheles pilosus* (H. Milne Edwards). Animal in dorsal view; second, third, and fourth legs of left side not shown; 5 mm indicated (from Williams 1965).

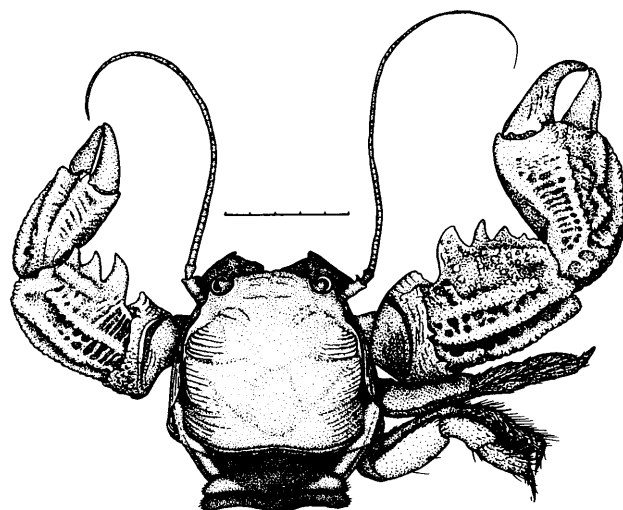


Fig. 177. *Pachycheles rugimanus* A. Milne Edwards. Animal in dorsal view; second, third, and fourth legs of left side not shown; 5 mm indicated (from Williams 1965).

walking legs with hairy covering similar to chelipeds, few spines below on dactyls and propodi.

Telson composed of 5 elements.

Measurements in mm.—Length of carapace: males 7; ovigerous females 5 to 7 (Haig 1956).

Habitat.—In corals; to 7 + m (Schmitt 1935a).

Type-locality.—Vicinity of Charleston, S. C.

Known range.—Charleston, S. C.; Key West to Sarasota Bay, Fla.; through West Indies to Tobago and Aruba.

Remarks.—Ovigerous females have been found in the West Indies from February to May (Haig 1956, in part). Rathbun (1926) reported a Pliocene species of *Pachycheles* from Central America.

***Pachycheles rugimanus* A. Milne Edwards**

Fig. 177

Pachycheles rugimanus A. Milne Edwards 1880:36.—Hay and Shore 1918:404, pl. 29, fig. 2.—Haig 1956:12.—Williams 1965:108, fig. 85.

Recognition characters.—Carapace about as long as wide, flat from side to side, convex from front to back, slightly rugose along sides; anterolateral margins emarginate; epimeral pieces of metabranchial region separated by membranous interspaces, posterior portion consisting of 1 or more pieces. Front broad, slightly produced in middle, margin projecting downward, hardly visible from above. Orbits deeply excavated, margins slightly raised, postorbital angle spiniform; eyes short, stout, retractile. Antenna with first movable article bearing slightly serrate spine on anterior margin; sec-

ond article with row of unequal spines on anterior border; third article short, smooth.

Chelipeds subequal, stout; carpus with 4 anterior spines, graded in size, proximal one largest, upper surface with 4 prominent longitudinal, tuberculate ridges, deep channels between crossed by irregular septae forming rows of oblong pits; ridges and pitted channels continued onto hand but with less regularity in arrangement, fingers tuberculate almost to tips; merus crossed by few rugae distally, rugose and serrate spine at inner distal angle. First 3 pairs of walking legs stout and with distal articles setose.

Telson composed of 5 elements.

Measurements in mm.—Carapace: male, length 8, width 7; ovigerous female, length 8, width 9.

Color.—Brownish red, fingers vermillion.

Habitat.—To depth of 145 m (Schmitt 1935a).

Known range.—Off Cape Lookout, N. C., through Florida to St. Thomas, V. I., and Contoy Island, Mexico; Pernambuco, Brazil (Coelho 1964).

Remarks.—Only a few collections of this species have been recorded from widely scattered localities. Cain (1972) gave collection data for specimens from the *Lithothamnion* reef off Cape Lookout, N. C. Ovigerous females have been taken in February and March from the Carolinas and west Florida, and in September in North Carolina, Georgia and east Florida.

Genus *Petrolisthes* Stimpson 1858

Stimpson 1858:240.—Haig 1960:21.—China 1966:250.

Petrolisthes galathinus (Bosc)

Fig. 178

Porcellana galathina Bosc [1802]:233, pl. 6, fig. 2.

Petrolisthes galathinus.—Hay and Shore 1918:404, pl. 29, fig. 1.—Haig 1956:22.—1960:36.—Williams 1965:107, fig. 83.—Coelho 1966a:56.—Gore 1970:965.—Gore and Abele 1976:21.

Recognition characters.—Carapace covered with strong, transverse, ciliated rugae, scarcely interrupted at grooves separating well-marked regions; frontal region granulate, metabranchial regions plicate. Rostrum broad, triangular, sinuous sided, with broad median depression usually covered with short pubescence. Supraorbital spine present, not distinct in large specimens; postorbital angle produced into small spine-tipped tooth; epibranchial spine strong. Eyes well developed. Antenna with first movable article bearing anteromesial, spine-tipped, lamellar lobe; second and third articles lightly rugose.

Chelipeds large, covered with strong, ciliated rugae continuing obliquely and almost unbroken across carpus and hand, broken into series of shorter rugae on fingers; hand broad, flattened,

rugae on outer margin spiniform in smaller specimens, outer margin often fringed with plumose hairs; dactyl sinuous, fingers closing closely, thick tuft of pubescence below; carpus about twice as long as wide, anterior margin with 4 to 6 strong serrate spines, row of spines on posterior margin; merus with strong rugose lobe at inner distal angle. First 3 pairs of walking legs rugose; upper margin of meri with fringe of plumose hairs, anterior margin on first and second legs with 6 to 9 spines, on third with 5 to 7, merus of first and second with postero-distal spine; all articles covered with long, non-plumose setae.

Sternum, sternal plastron, abdomen, ventral surface of outer maxillipeds, chelipeds and walking legs covered with strong striations.

Telson composed of 7 elements.

Measurements in mm.—Length of carapace: males 7 to 17; non-ovigerous females 6 to 11 (15?); ovigerous females 7 to 14 (Haig 1960; Holthuis 1959).

Color.—Grayish brown without markings in life; in alcohol, light brown with purple or dark red line and dots on rugae (Hay and Shore 1918). Spaces between rugae yellow; lower surface, including abdomen, deep red (Faxon in Haig 1960). Blue gray to white with dark reddish purple striations (R. H. Gore, personal communication).

Habitat.—Under stones and associated with sponges, corals and anemones in littoral; from sand and sand-shell bottom in somewhat deeper water (Haig 1960; Dragovich and Kelly 1964); shell hash in tide pools and intertidal regions (Gore and Abele 1976), low water mark to 54 m.

Type-locality.—Unknown.

Known range.—Cape Hatteras, N. C., through Gulf of Mexico and Caribbean Sea to Rio de Janeiro, Brazil; Ilha Trinidad off Brazil; Pacific Ocean from Isla San Lucas, Costa Rica, to off La Libertad, Ecuador.

Remarks.—Haig (1956, 1960) gave a full review of this species and Gore (1970) added notes on morphology. Ovigerous females are known from the Caribbean area from January to August, and from North Carolina and the Gulf of Mexico from June to October (Gore 1974; Gore and Abele 1976; Haig 1956, 1960; Holthuis 1959, in part; Rickner 1975; Rouse 1970). Ovigerous females from North Carolina have been found with rhizocephalans (USNM 51050).

Rathbun (1926) described a fossil species, *P. avitus*, from the Pliocene of Central America which is similar to the recent *P. galathinus*.

Randall (1967) reported *P. galathinus* from stomach contents of the dusky squirrelfish, *Holocentrus vexillarius*, rock hind, *Epinephelus adscensionis*, Nas-

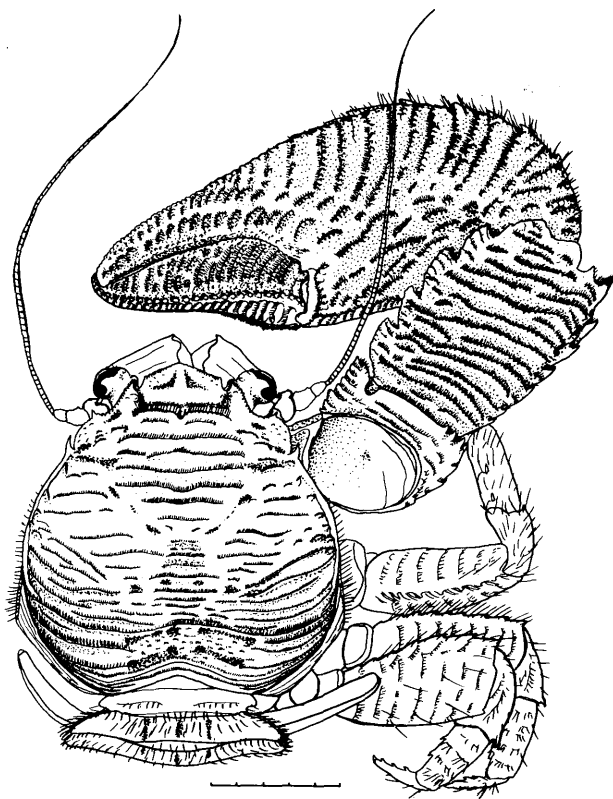


Fig. 178. *Petrolisthes galathinus* (Bosc). Animal in dorsal view, fifth leg only of left side shown, 5 mm indicated (from Williams 1965).

sau grouper, *E. striatus*, striped drum, *Equetus acuminatus*, Spanish hogfish, *Bodianus rufus*, and reef scorpionfish, *Scorpaenodes caribbaeus*.

Genus *Polyonyx* Stimpson 1858

Stimpson 1858:233.—Haig 1960:232.

Polyonyx gibbesi Haig

Fig. 179

Porcellana macrocheles Gibbes 1850:191.

Polyonyx macrocheles.—Hay and Shore 1918:405, pl. 29, fig. 8.

Polyonyx gibbesi Haig 1956:28.—Williams 1965:113, fig. 90.

Recognition characters.—Carapace smooth, finely plicate, transversely oval, about $\frac{1}{4}$ to $\frac{1}{3}$ wider than long; front hardly produced, margin slightly sinuous; posterolateral portions with scattered, feathered hairs; infolded lateral parts separated from rest of carapace by deep fissure. Orbits small; eyes small, cornea reduced. Antenna slender, about 1.5 times as long as body; basal article strongly produced forward; movable articles far removed from orbit.

Chelipeds unequal, long and distorted; inner margin of hands convex, very thinly fringed with plumose hairs, outer margin nearly straight, emarginate, densely fringed with long plumose hairs; major hand nearly twice as long as carapace; fingers short, hooked at tip, toothed on cutting edges, dactyl falciform with largest tooth in middle, fixed finger with largest tooth in proximal $\frac{1}{3}$; minor hand with straighter fingers; carpus as long as palm, thick, anterior margin produced into thin crest, subrec-

tangular proximally, fringed with fine plumose hairs, thinner fringe of shorter hairs on outer margin; merus subcubical, finely rugose above, plumose-hairy dorsolaterally, inner distal angle produced. Three pairs of walking legs sparsely hairy, dactyls with 4 corneous spines on lower margin closing against weaker spines on distal part of propodus, merus of second and third walking legs minutely spinulose below. Last legs with long tufts of hairs on chela and distal end of carpus.

Telson composed of 7 elements.

Measurements in mm.—Carapace: male, width 11; female, length 10, width 14; ovigerous females, width 8.4 to 16.

Color.—Grayish white, sometimes stained with brown. Rickner (1975a) characterized the carapace and chelipeds of males as yellowish orange to moderate brown and females as yellowish to light brownish gray with occasionally moderate yellowish brown chelipeds.

Habitat.—A common commensal of the annelid *Chaetopterus variopedatus*, seldom found outside tubes of this worm; intertidal to 47 m (Gore 1974).

Type-locality.—Coast of South Carolina.

Known range.—Woods Hole, Mass., to Uruguay (Coelho and Ramos 1972).

Remarks.—Unlike other porcellanids occurring along the east coast of the United States, *Polyonyx gibbesi* has been the subject of ecological studies. Enders (1905), at Beaufort, N. C., and Pearse (1913), at Woods Hole, Mass., studied inhabitants of the tubes of *Chaetopterus variopedatus*, finding *P. gibbesi* to be common commensals in both areas. Both authors found usually a male and a female crab in the same tube, although Enders found 6 isolated ovigerous females in the course of a summer. Pearse found the species to be strongly thigmotactic; crabs seemingly too large to enter *Chaetopterus* tubes entered and left an artificial tube at will in the laboratory.

Observed crabs usually moved backward or sideways on open sand, using the chelipeds as an aid in walking, or at times swam clumsily upside down by flapping the abdomen. They showed little ability to burrow. The respiratory mechanism seemed well adapted to life in confinement, for the respiratory currents were strong and capable of being shifted with the change in direction of water flow in the worm tubes. Crabs in an experimental tube tolerated considerable fouling of the water.

Pearse gave an excellent figure of the chelate and tufted last legs which are used extensively in the meticulous preening characteristic of this species. The plumes of hairs on the appendages, especially those on the third maxillipeds, are used as nets for capturing food from water currents. Caine (1975)

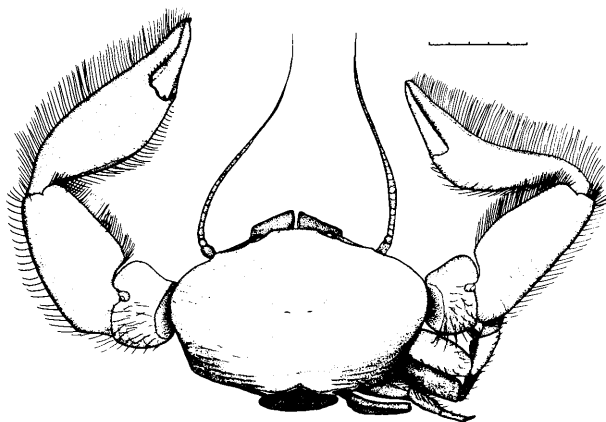


Fig. 179. *Polyonyx gibbesi* Haig. Female in dorsal view, second to fifth legs of left side not shown, 5 mm indicated (from Williams 1965).

summarized information on feeding, pointing out that the species not only "net-fishes" passively in water passing through the host worm's tube, usually near the exhalant opening, but also actively filters by alternate movements of the third maxillipeds. Stomach contents indicted a detritus-diatom mixture with some algal filaments present, and the author thought that *P. gibbesi* may gather additional food with the densely setose ventral margin of the chelipeds and probably also feeds on fecal matter of the host.

Gray (1961), reviewing the life history and ecology of the species, found the breeding season at Beaufort, N. C., to extend at least from April to December, and ovigerous females are otherwise known in January from Georgia, February and March from Florida, June to August in Texas (Rickner 1975), and July from Venezuela (Gore 1974). Usually when a pair of *P. gibbesi* was found in a tube, adult crabs of no other species were present. Gray concluded that the crabs enter worm tubes by chance, not in response to attractants.

In the years since Enders's and Pearse's studies, the proportion of *Polyonyx gibbesi* and *Pinnixa chaetoptera* at Woods Hole and Beaufort has changed. Woods Hole: 1913, 22% *Polyonyx*/78% *Pinnixa*; 1959, 66%/34%—Beaufort: 1905, 83%/17%; 1958–59, 39%/61%. Gray postulated that the more southerly species, *Polyonyx gibbesi*, has increased in the Woods Hole area because of warming climate. In the Beaufort area, decline may have resulted from hurricane damage (before the study) which destroyed many *Chaetopterus* tubes. Gray also found that *Polyonyx gibbesi* prefers less muddy bottoms than *Pinnixa chaetoptera*. He considered *Polyonyx gibbesi* an obligate commensal of *Chaetopterus*.

Craig (1974) concurred with much of Gray's analysis. He also found that the relative abundance of *Polyonyx gibbesi* in samples of intertidal *Chaetopterus* tubes steadily decreased northward, that the crabs could not withstand temperatures of 10°C for more than a few days, and that they are sensitive to dessication. However, the zoeae and adults of *Polyonyx gibbesi* were less tolerant of high temperature than comparable stages of *Pinnixa chaetoptera*, as indicated by both lethal limit and metabolic studies.

Gore (1968) described the larval development from eggs hatched in the laboratory. Among larvae held at 10°, 15°, 25° and 30°C, those held at 25°C and fed *Artemia* nauplii passed through pre-zoeal, two zoeal and megalopal stages lasting two hours, 12 and 12–14 days respectively before molting to first crab. No crab stages were obtained above or below 25°C and no megalopae below 20°C. Smith (1880b) reported swarms of zoeae of *Polyonyx gib-*

besi at the edge of tidal currents near the mouth of Narragansett Bay in summer, Hillman (1964) observed them once there in August, and Fish (1925) found them in plankton from July to October at Woods Hole. Sandifer (1973d) found the larvae to be fairly abundant in plankton from the mouth of Chesapeake Bay to lower reaches of York River, Va., over a salinity range of 15.74 to 30.37‰ with peak abundance from 20 to 25‰. The larvae were present from July to October over a temperature range of 19.4° to 28.1°C. Both zoeae and megalopae were in surface and bottom samples, with zoeal stage I making up 80% of the samples, most abundant near the bottom but stage II more abundant at the surface. Most megalopae were in bottom samples. Further south, Dudley and Judy (1971) found larvae at three stations off Beaufort Inlet, N. C.: May–November 1.6 km and 6.5 km offshore at 1–8 m, mainly 8 m; July–November 10–13 km offshore at 8 m.

Long, barbed rostral spines of the zoeae of *P. gibbesi* have been known to pierce the skin of children swimming in Quisset Harbor, Buzzards Bay, Mass., causing an itch that was alleviated soon after the youngsters dried themselves and dressed (Zinn 1954). Adults were not affected. Collections showed an unusually large swarm of zoeae in the plankton at time of the attack.

Genus *Porcellana* Lamarck 1801

Lamarck 1801:153.—Haig 1906:196.—China 1966:250.—Haig 1978:707.

Porcellana sayana (Leach)

Fig. 180

Pisidia sayana Leach 1820:54.

Porcellana sayana.—Hay and Shore 1918:403, pl. 29, fig. 7.—Haig 1956:31.—Williams 1965:110, fig. 87.—Coelho 1966a:62.—Gore 1970:963.

Recognition characters.—Carapace usually a little longer than wide, depressed; dorsal surface slightly convex, meeting lateral parts in slight shoulder a little behind base of antenna; surface minutely granulate and with fine oblique dorsal plications along sides, especially on posterolateral parts; few scattered small clumps of setae. Rostrum triangular, concave above, tip abruptly decurved, margins spinulate or tuberculate. Inner angle of orbit produced into strong tooth separated from rostrum by wide and rather deep notch; outer angle produced into broad, low tooth. Eyes well developed. Cervical groove lightly impressed, terminating an-

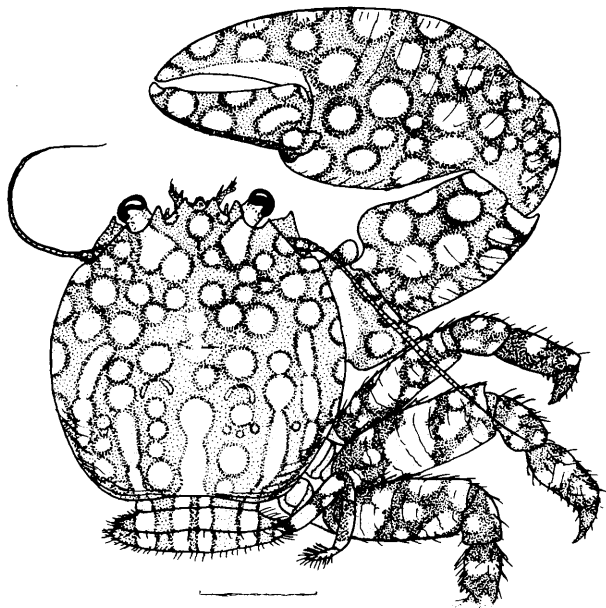


Fig. 180. *Porcellana sayana* (Leach). Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

terolaterally in shallow indentation at edge of carapace. Antennae slender, smooth, longer than carapace; basal article strongly produced forward into spinelike projection; movable articles far removed from orbit.

Chelipeds strong, heavy, finely plicate, nearly smooth in old individuals; hand as long as or longer than carapace, outer margin fringed with long setae except in old individuals; fingers short, curved and bent; proximal inner angle of carpus and distal inner angle of merus produced, forming lobes, both articles with scattered setae near dorsolateral border; anterodistal angle of carpus ending in spine. First 3 pairs of walking legs normal, with scattered setae.

Telson composed of 7 elements.

Measurements in mm.—Carapace: males, length 14 (Wass 1955), width 12; nonovigerous females, length 8, width 8; ovigerous females, length 5 (Haig 1956) to 10, width 10. Specimens with length and width equal are unusual.

Color.—Ground color reddish or rusty brown; covered on all dorsal surfaces and abdomen with complicated irregular pattern of yellowish white, yellow, and some bluish-white spots or longitudinal stripes; stripes more prominent on rear center part of carapace and on abdomen. Walking legs banded with red on proximal edge, "white stockings" on distal edge (Gore 1970). Pattern quite variable in shape and shade, some specimens being predominantly light. Andrews (1911) noted males with a "sky blue" ring between the peripheral red line and

center of some spots.

Habitat.—This species is often found in crevices in clusters of oyster shells, among rocks of jetties or as a commensal of the hermit crabs *Pagurus pollicaris* and *Petrochirus diogenes* in the shell of some gastropod. Hildebrand (1954) found specimens attached to the decorator crab *Stenocionops furcata*. Telford and Daxboeck (1978) at Barbados, West Indies, found it confined to *Strombus gigas*, the queen conch, where it clung to the inner surface of the operculum or close to that structure even when the gastropod's foot was retracted, or more abundantly in association with the hermit crabs *Petrochirus diogenes*, *Dardanus venosus* and *Paguristes grayi* when they were housed in *S. gigas* shells. The authors remarked that the porcellanid has a color pattern similar to that of the host hermits. Shallow water to 92 m (Gore 1974); (713 m?, Schmitt 1935a).

Type-locality.—Coast of Georgia and Florida.

Known range.—Cape Hatteras, N. C., around Gulf of Mexico and Caribbean Sea to Rio Grande do Sul, Brazil (Coelho and Ramos 1972).

Remarks.—This species is rather abundant off the Carolinas and in the western Gulf of Mexico (Hildebrand 1954, 1955; Rickner 1975), rare in south-western Florida (Rouse 1970), but fairly common in less than 18-m depths around barrier islands off Mississippi (Franks, et al. 1972). Ovigerous females are known to occur from January to November in various localities from the Carolinas to the Guianas. Brooks and Wilson (1883) described the first zoeal stage of *P. sayana*. A long breeding season is indicated, as is true of a close relative in the Pacific, *P. cancrisocialis*. Haig (1960) suggested that these forms may be conspecific.

Randall (1967) reported *P. sayana* from stomach contents of the Spanish hogfish, *Bodianus rufus*.

Porcellana sigsbeiana A. Milne Edwards

Fig. 181

Porcellana sigsbeiana A. Milne Edwards 1880:35.—Haig 1956:33.—Williams 1965:111, fig. 88.—Gore 1970:964.

Recognition characters.—Carapace longer than wide, evenly convex in posterior half, broadly ridged in gastric region; lateral margins thin, produced and slightly upturned; surface faintly rugose. Front strongly tridentate; rostrum exceeding narrower lateral teeth, irregularly pentagonal. Orbit with outer angle produced into broad, oblique tooth; eyes well developed. Anterolateral borders concave, ending in shoulder separated from acute

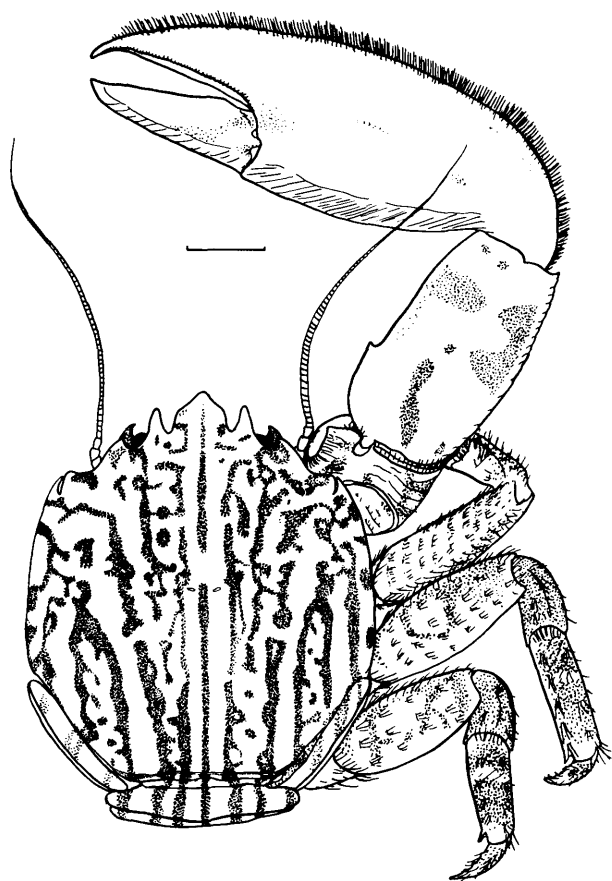


Fig. 181. *Porcellana sigsbeiana* A. Milne Edwards. Animal in dorsal view, fifth leg only of left side shown, 5 mm indicated (from Williams 1965).

marginal tooth by elongate notch at terminus of cervical groove. Antennae slender, smooth, about as long as carapace; basal article strongly produced forward in spinelike projection; movable articles far removed from orbit.

Cheliped strong, heavy, nearly smooth but slightly rugose; hand longer than carapace, outer margin fringed with setae, fingers less than half as long as palm, nearly straight, hooked at tips; length of carpus more than 1.5 times width, small spiniform tooth at outer distal angle with variable small spines mesial to it and shoulder at proximal inner angle tipped by similar spine preceded by variable smaller ones; merus with broad tooth and variably smaller ones on lobe at internal angle. First 3 pairs of walking legs with scattered tufts of setae.

Telson composed of 7 elements.

Measurements in mm.—Carapace: male, length 24, width 22; ovigerous female, length 16, width 14.5.

Color.—Irregular pattern of reddish longitudinal mottlings on white background (specimens preserved in alcohol).

Habitat.—Gore (1971) characterized *P. sigsbeiana*

as a sublittoral species; it is usually found in deeper water than the related and similar *P. sayana*; 16 to 393 m (Wenner and Read 1982).

Type-locality.—Blake Stations: 49, off delta of Mississippi River, 216 m; 36, north of Yucatan, 154 m; 142, Flannegan Passage [Virgin Islands], 49 m.

Known range.—Off Martha's Vineyard, Mass., to southwestern Caribbean Sea off Colombia (Gore 1970); West Indies to Virgin Islands.

Remarks.—This is the largest porcellanid species in the region (Benedict 1901c). Spines on the legs become worn or obliterated in old individuals.

Ovigerous females have been taken in April, May, June and November off northwest Florida, Alabama, Mississippi and Louisiana, in July off Venezuela and Colombia (Gore 1974), and in midwinter off Yucatan. Gore (1971) studied the complete larval development under laboratory conditions at temperatures of 10°, 15°, 20°, 25° and room temperature of 19°–27°C (\bar{x} = 24.4°C). Duration of stages appeared to be temperature dependent. There is a pre-zoeal stage that persists for ½ hour followed by two zoeal stages and a megalopa; the first zoeal stage lasted 8–9 days, the second 10–14 days, and the megalopa at least 15 days. Although the lowest mortality was observed at 20°C, the only crab stage reared was obtained at room temperature 33 days after hatching.

Comparing larvae of *P. sigsbeiana* with those of other porcellanids, Gore (1971) recognized two groups: a *Porcellana* group that includes *Polyonyx*, *Euceramus* and *Pisidia*; and a *Petrolisthes* group that includes *Pachycheles* and *Megalobrachium*. A third group may include aberrant *Petrolisthes* from the eastern and Indo-Pacific ocean regions. Gore included an excellent bibliography of papers on larval porcellanids.

Section Hippidea

Superfamily Hippoidea

Abdomen reduced in size, bent under thorax; appendages of sixth segment not adapted for swimming. First pair of legs simple or subchelate, second to fourth legs with last article curved and flattened. Rostrum small or absent. Third maxillipeds without epipodites.

Family Albuneidae

Carapace flattened and without wings covering legs. First pair of legs subchelate. Third maxillipeds narrow. Telson not conspicuously lengthened, almost oval.

Key to Genera

1. Eyestalks narrow, triangular. *Albunea*
 Eyestalks broad, oval *Lepidopa*

Genus *Albunea* Weber 1795

Gordon 1938:190.—China 1966:203.

Key to Species

1. Dactyl of second and third legs with blunt, rectangular lobe at base of anterior border. *A. gibbesii*
 Dactyl of second legs with asymmetrically mucronate spur, and third legs with acute, falciform spur at base of anterior border *A. paretii*

Albunea gibbesii Stimpson

Fig. 182

Albunea symnista Gibbs 1850:187.

Albunea gibbesii Stimpson 1859:78[32], pl. 1, fig. 6.—Benedict 1901c:139.—1904:625.—Hay and Shore 1918:414, pl. 30, fig. 11.—Schmitt 1935a:208.—Gordon 1938, figs. 3e, 4b.—Williams 1965:136, fig. 112 (part).

Recognition characters.—Carapace about as broad as long, convex from side to side, nearly straight from front to back; front with minute rostrum, and strong spine at either side followed by 7 to 10 slender spines; anterolateral angle with stout conical spine below *linea anomurica* projecting little if any beyond anterior border; posterior margin deeply

and broadly notched; dorsal surface with numerous irregular, more or less transverse, impressed lines, short ciliated one near front and another crossing near middle in shape of spread M being most conspicuous.

Eyestalks narrow, triangular, cornea at tip minute. Antennules about twice as long as carapace; flagella slender and densely setose above and below along inner surface, forming respiratory tube when approximated. Basal article of antenna with acute, small, lateral spine; flagellum about half as long as peduncle. First pair of legs stout, setose, all but distal articles inflated; hand subchelate; inferior distal angle of propodus produced into spine; dactyls curved and rather slender. Second, third, and fourth legs stout, hairy, and with falcate dactyls; dactyl of third leg almost rectangular at base of anterior margin and second with similar broader structure. Fifth legs weak, borne above others.

Second, third, and fourth abdominal segments with expanded pleura, fifth and sixth segments small. Female with long uniramous pleopods on second to fifth segments. Uropods consisting of rather large basal article and two small falcate blades. Telson of male ovate to ovate with bluntly mucronate tip, central shield heavily calcified, round patch of setae near basal corners and elongate V-shaped patch distally on midline, wide margins lightly calcified and thickly fringed with setae; of female ovate and well calcified overall, setae less developed.

Measurements in mm.—Length of carapace, male and female, 20.

Variation.—Spines on the anterior margin of the carapace may vary in number, spaced occasionally so close as to appear doubled. In a limited sample, males from southern Brazil appear to have a more attenuated tip on the telson than males from North America and the Greater Antilles.

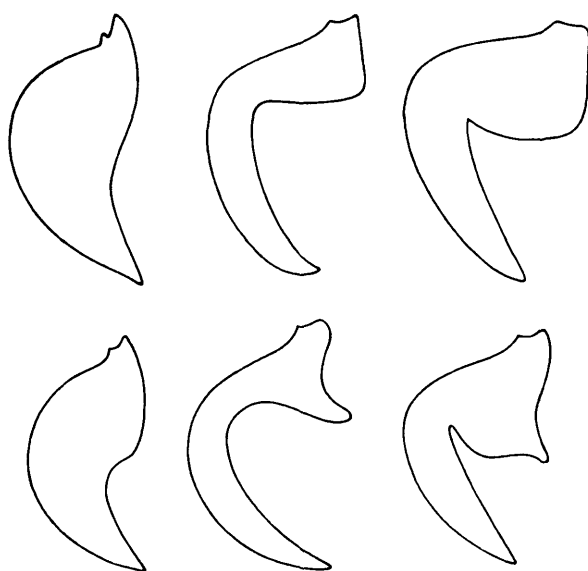


Fig. 182. *Albunea gibbesii* (upper) and *A. paretii* (lower), dactyls of second to fourth legs.

Color.—Light brown to orange-tan above, cross striae lighter, with irregularly placed iridescent areas; antennules with alternating light and dark bands; eyestalks with a white ring behind cornea; underparts light (from recently preserved specimens). Pink hand and finger (M. Gray, notes on Georgia specimen). Light purple with whitish markings, more or less iridescent (various authors).

Habitat.—Sandy bottoms; extreme low tide mark to 64 m; (70–90 m?).

Type-locality.—St. Augustine, Fla.

Known range.—East of Cape Lookout, N. C., to Texas; through West Indies to São Sebastião, São Paulo, Brazil.

Remarks.—*Albunea gibbesii* is occasionally found on exposed sandy shoals, especially at times of extremely low tides when heat from the sun warms the exposed sand and drives the animals to the surface. Occasionally specimens are found by digging, and have been taken in the Carolinas by dredging to depths of 64 m. This also may be the species reported by Cain (1972) at 70–90 m on the *Lithothamnion* reef SE of Cape Lookout, N. C.

Ovigerous females have been taken in North Carolina in June.

Pearse, et al. (1947) showed that *A. gibbesii* burrows backwards into the sand like the similar highly specialized sand dwellers, *Lepidopa websteri* and *Emerita talpoida*. These authors stated that *A. gibbesii* scrapes food from the setose antennules with the mouthparts; however, the chelate first legs and well-developed mandibles suggest feeding habits more like those of *Lepidopa* species. Function of the antennules as a possible feeding device was discussed by Benedict (1904).

Randall (1967) reported *A. gibbesii* from stomach contents of the margate, *Haemulon album*, and permit, *Trachinotus falcatus*.

Albunea paretii Guérin-Méneville

Figs. 182–183

Albunea oxyophthalmus Leach (MS) in White 1847b:57 (nomen nudum).—Snodgrass 1952, fig. 11A.

Albunea paretii Guérin-Méneville 1853:48, pl. 1, figs. 10–10a.—Rodrigues da Costa 1962:6, pl. 1, figs. 5, 7; pl. 3, figs. 1–3.—Williams 1965:137, figs. 112 (part), 113.

Albunea parettoi.—Monod 1956:37, figs. 2–9.

Albunea paretii.—Fausto-Filho 1967a:12.

Recognition characters.—Similar to *A. gibbesii*, differing chiefly in characters given in key and shape of male telson. Dactyl of second legs with asym-

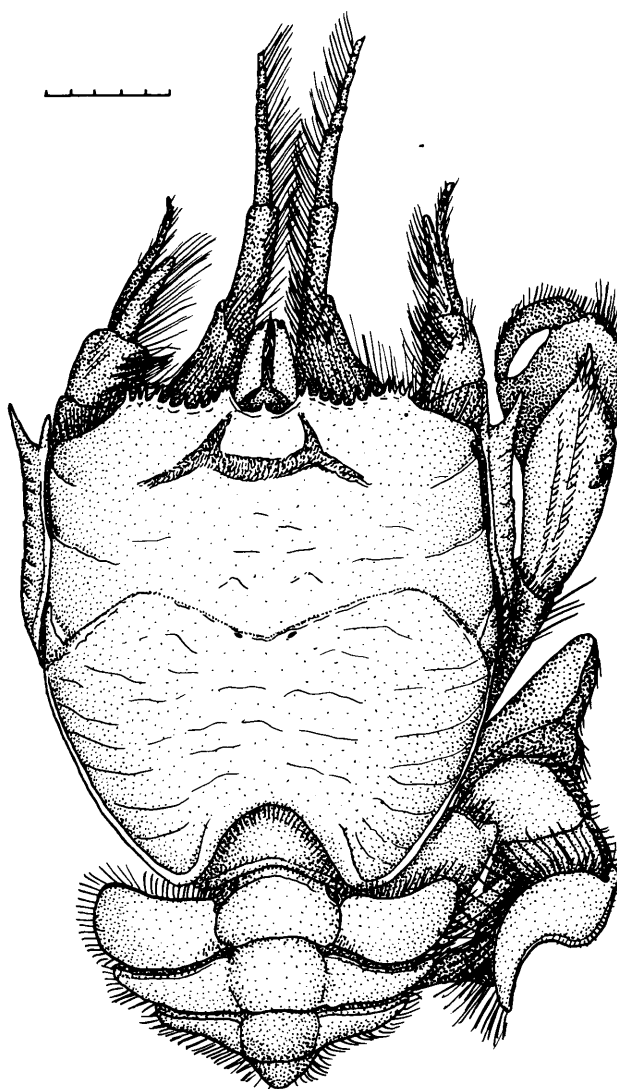


Fig. 183. *Albunea paretii* Guérin-Méneville. Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

metrically mucronate spur, of third legs with acute, falciform spur at base of anterior border. Telson of male pentagonal, central shield heavily calcified, with line of setae near each basal corner and in closed V-pattern distally along midline, wide margins lightly calcified and thickly fringed with setae; of female ovate and well calcified overall, setae much less developed.

Measurements in mm.—Length of carapace: male, 15; female, 20.

Habitat.—Sandy bottom; low tide mark to 38 m. Dörge (1977) found it associated with unprotected sand flats, shoals, and from 10 m seaward in nearshore waters of Georgia.

Type-locality.—[Uncertain], America.

Known range.—Beaufort Inlet, N. C., to Corpus Christi, Tex.; through West Indies to Santa Cata-

rina, Brazil (Coelho and Ramos 1972); West Africa from Cape Verde Islands and Senegal to Ghana.

Remarks.—Ovigerous females have been taken in June in North Carolina.

Genus *Lepidopa* Stimpson 1858

Stimpson 1858:230.—Holthuis 1960a:27.—China 1966:248.

Lepidopa websteri Benedict

Fig. 184

Albunea scutellata.—Gibbes 1850:187 (not Fabricius 1793, and H. Milne Edwards 1837).

Lepidops venusta.—Kingsley 1880:410.

Lepidopa websteri Benedict 1903:892, fig. 3.—Hay and Shore 1918:415, pl. 30, fig. 12.—Williams 1965:138, fig. 114.—Efford 1971:91, figs. 1b, k; 2j; 3r; 4h, m; 5g, i; 60.

Recognition characters.—Carapace considerably shorter than wide, slightly narrowed behind lateral spines, then widening before sides converge toward truncated posterior margin; anterior margin fringed with long setae; posterior concavity just short of being semicircular; dorsal surface traversed near front by impressed lines crossing at about middle of carapace. Rostrum narrowly acute (tip somewhat obscured by setae), its concave sides continuous with margin of ocular sinus; margin running from base of orbit almost straight out to anterolateral projection (tipped by spine) with only slight tendency to convexity; anterolateral margin extending backward and then nearly straight laterally before curving to lateral spine.

Eyestalks lamellate, irregularly oval, underside densely setose. Antennules with peduncles exceeding eyestalks; major flagella straight, slender, nearly 3 times as long as carapace, fringed mesially with setae and forming respiratory tube when approximated; second flagella exceedingly short, each extending only to end of second article of first flagella. Short antennae with broad basal article; antennal scale reduced to short point just overlapping fourth article of peduncle, fifth article only about half width of distal end of fourth; flagellum stout, curved, composed of 8 articles (first very short). Carpus of third maxilliped overlapping propodus but not reaching its distal end. First legs with broad, flat articles; dactyl turned back on propodus to form subchela. Second, third and fourth legs with terminal article bifurcate. Fifth legs much reduced, slender and folded.

Abdomen short and partly flexed beneath thorax;

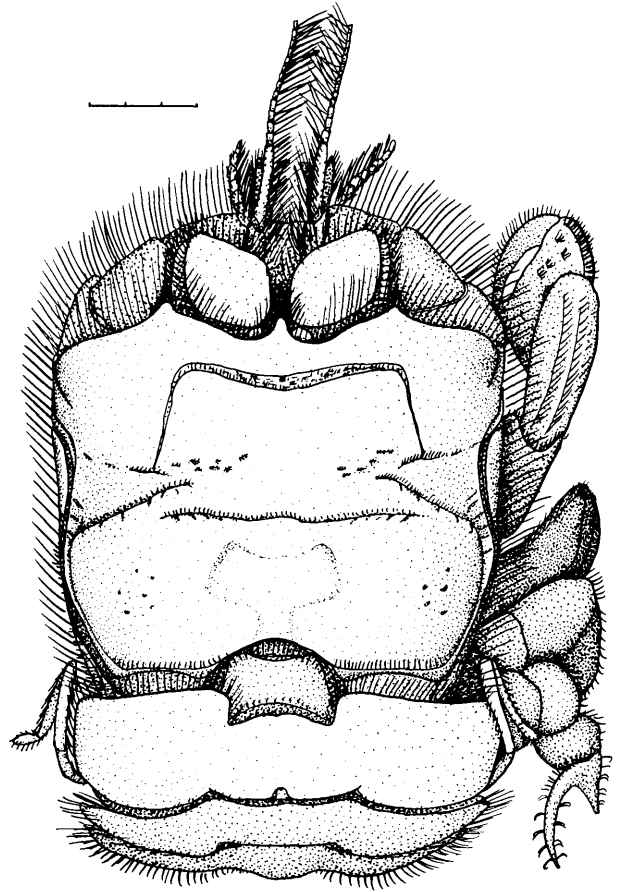


Fig. 184. *Lepidopa websteri* Benedict. Animal in dorsal view, first to fourth legs of left side not shown, 5 mm indicated (from Williams 1965).

second, third, and fourth segments with expanded pleura. Uropods small, with slender basal article and long, oval blades, their margins and those of abdominal segments fringed with long silky hairs. Telson heart shaped.

Measurements in mm.—Length of carapace, to 19 (A. M. Young, personal communication).

Color.—All parts white, iridescent, with pink being most conspicuous tint on anterior part of carapace, and blue showing along sides, in depressions of carapace, and on extremities of fifth legs; dorsal plates of abdomen faintly pink tinged, bordered by a delicate blue-green; on either side of middorsal line, pink shading into red, and blue becoming deeper in shade (from note by A. Shaftsbury, USNM).

Habitat.—Usually found on gradually sloping sand beaches of open ocean at or immediately below low tide mark (Pearse, et al. 1942); shallow water, limits unknown.

Type-locality.—Beach near Fort Macon [Carteret County], N. C.

Known range.—Around mouth of Chesapeake Bay

(larvae); Drum Inlet, N. C., to Sapelo Island, Ga.; Tampa Bay, Fla.; Ship Island and Petit Bois Island, Miss. (Efford 1971; Sandifer and Van Engle 1972a; Sandifer 1973d).

Remarks.—Efford (1969) outlined his view of evolution of the Albuneidae and (1971) revised the genus *Lepidopa*, discussed zoogeography, and reviewed all published information. The biology of *L. websteri* is best known among species in the genus but information is largely limited to the brief account given by Pearse, et al. (1942) which included detailed drawings of the specialized legs as well as a lateral view of the whole animal. The species is highly adapted for burrowing in sand, and is usually found in small numbers. It burrows backward, and at rest lies at an angle to the surface with the long antennules extended in the water above. If disturbed, the animals may descend several centimeters into the sand. Benedict (1904) commented on the possible feeding function of the antennules in the genus *Lepidopa*. In 1903, he found setae of annelids, skin of a small *Synapta* and parts of the flagella of some small crustaceans among stomach contents of *Lepidopa scutellata* (= *L. benedicti*, see Holthuis 1960a:31). Such finding would be in accord with the fact that *Lepidopa*, like *Albunea*, has well-developed mandibles (Snodgrass 1952). Under experimental conditions Howard (1969) X-rayed *L. websteri* in its U-shaped burrows. He suggested that it may be a detritus feeder.

Ovigerous females have been taken in July in North Carolina, and both larvae and juveniles have been taken in plankton tows there in July and Au-

gust. Sandifer and Van Engel (1972a) described three zoeal stages from plankton collected at six stations near the mouth of Chesapeake Bay and one location north of the Bay off the eastern shore of Virginia in July and August of 1960, 1961, and 1969. Most of these were first zoeae. Presuming an 8–10 day duration of stage I (as in *L. californica*), and taking into account the summer circulation patterns for the region, a breeding population on Virginia beaches was proposed as likely rather than transport of the larvae from North Carolina.

Family Hippidae

Carapace subcylindrical, and with wings covering legs. First legs simple. Third maxillipeds broad. Telson lengthened, lancet-shaped.

Genus *Emerita* Scopoli 1777

Heegaard and Holthuis 1960:181.—China 1966:236.

Body convex, oval. Carapace firm, crossed more or less by overlapping rugosities. Rostrum small; impressed transverse line behind rostrum and deeper more strongly curved one farther back. Anterolateral margins concave. Eyestalks long, slender, cornea small but dilated. Antennules with peduncles and flagella setose mesially, forming respiratory tube when approximated. Antennae normally held concealed beneath third maxillipeds. First legs directed forward.

Key to Species

(After Schmitt 1935a)

1. Dactyl of first leg subacute or sharply pointed distally, anteroventral extension of propodus similar; transverse rugosities more or less continuous over dorsum and continued in posterior part of carapace to inferior margin *E. benedicti*
- Dactyl of first leg rounded or obtuse distally, anteroventral extension of propodus bluntly pointed or rounded; lateral expansion of carapace smooth and punctate for greater part *E. talpoida*

Emerita benedicti Schmitt

Fig. 185

Emerita benedicti Schmitt 1935a:215, figs. 71a, b.—Lunz 1939:336.—Williams 1965:139, fig. 115A.

Recognition characters.—Carapace subcylindrical, firm; transverse rugosities more or less continuous, close set, and crossing whole of dorsum, those

on posterior part continued to inferior margin. Rostrum equilaterally triangular, separated by rounded sinus on each side from prominent and subacute tooth. Anterolateral margins concave and subserrate. Antennules about 3 times length of slender eyestalks. Antennae normally held beneath third maxillipeds, at least as long as carapace when extended; first peduncular article short, second largest with outer margin produced into strong

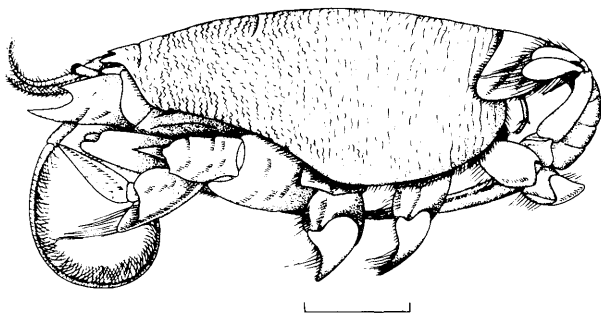


Fig. 185. *Emerita benedicti* Schmitt. Female in lateral view; 5 mm indicated (USNM 119091).

superior and much longer inferior spine; flagellum densely beset laterally with 8 rows of fringed setae, outer rows longest.

First pair of legs with articles more or less setose and with impressed, interrupted, transverse ciliated lines; dactyl subacute distally; anteroventral extension of propodus similarly pointed; carpus terminating in spine distally. Second, third, and fourth legs less strong, setose, tips curved and foliaceous. Fifth legs almost filamentous, entirely concealed beneath abdomen.

Abdomen broadest anteriorly, narrow posteriorly, flexed so that telson and sixth segment lie beneath body. Uropods turned forward, resting along sides of proximal segments. Telson elongate, lanceolate, margined with reflected setae above and inflected ones on edge; base with 2 short, impressed lines.

Measurements in mm.—Length of carapace, ovigerous female, 21.

Habitat.—Shell bottom, and probably other types (Lunz 1939) [coarse grained substrate?]; to 3.5 m.

Type-locality.—Tampa Bay, Fla.

Distribution.—Charleston County, S. C., to Veracruz, Mexico (Efford 1976).

Remarks.—Ovigerous females are known from South Carolina in June (Lunz 1939) and from South Carolina, Georgia, and Mississippi in July.

Emerita talpoida (Say)

(Mole crab; sand bug)

Fig. 186

Hippa talpoida Say 1817:160.

Hippa emerita.—Ortmann 1896 (in part):232.

Emerita talpoida.—Hay and Shore 1918:41, pl. 30, fig. 8.—Schmitt 1935a:216, figs. 74a, b.—Snodgrass 1952.—Williams 1965:140, figs. 115B, 116.

Recognition characters.—Carapace subcylindrical, with overlapping rugosities anteriorly, smoother and

polished posteriorly. Rostrum small, blunt, separated by rounded sinus on each side from more prominent and acute tooth. Anterolateral margins concave and subserrate. Antennules approximately twice length of slender eyestalks; basal article with strong external spine. Antennae nearly twice as long as carapace when extended; first peduncular article short, second largest with outer margin produced into strong, anteriorly directed spine bifid at tip with deep fissure below; flagellum densely beset laterally with 8 rows of fringed setae, outer rows longest.

First pair of legs with articles more or less setose and with impressed, interrupted, transverse ciliated lines; dactyl rounded or obtuse distally; anteroventral extension of propodus bluntly pointed or rounded; carpus terminating in spine distally. Second, third and fourth legs less strong, setose, tips curved and foliaceous. Fifth legs almost filamentous, entirely concealed beneath abdomen.

Abdomen broadest anteriorly, narrow posteriorly; flexed so that telson and sixth segment lie beneath body. Uropods turned forward, resting along sides of proximal segment. Telson elongate, lanceolate, margined with reflected setae above and inflected ones on edge; base with 2 short, impressed lines.

Measurements in mm.—Length of carapace: males 19.4; ovigerous females, 36.

Color.—Uniform pale yellowish brown (Snodgrass 1952).

Habitat.—Sandy beaches in and below surf line; to 3.5 m in winter.

Type-locality.—[East] coast of United States.

Known range.—Harwich [Barnstable County], Mass. to Horn Island, Miss.; Progreso, Yucatan, Mexico (Schmitt 1935a; Efford 1976).

Remarks.—The morphology, life history and general ecology of *Emerita talpoida*, a representative of the specialized sandy-beach fauna, have been studied by a number of workers. The spawning season lasts from winter to autumn, varying in length with latitude and season, more extended in the south than in the north. Ovigerous females have been reported in scattered records as early as February at Egmont Key, Tampa Bay, Fla. (Dragovich and Kelly 1964), are known in April from Pensacola, Fla., and as late as September at Cape Henry, Va., October in Charlotte County, Fla., and November at Flagler Beach, Fla. (USNM). Diaz (1974) found them from January to October in North Carolina, with spring and summer pulses of abundance. Hunter (1972), working in Virginia, thought the reproductive cycle to be related to temperature.

The eggs are bright orange when first laid and

gradually fade to a translucent dirty gray just before hatching. Johnson (1964) gave details on the histology of the male reproductive system and Diaz (1974) showed that large females in spring have greater numbers of and larger eggs than the smaller females of midsummer. Wharton (1924) gave a figure of the mature sperm cell. Herrick (1892:25) gave figures of developmental stages in the egg. Rees (1959) described the larval stages and a megalopa, which resembles the adult, from rearing experiments in the laboratory. He found development to last 28 days and encompass at least 6 larval stages, and Diaz (1974) added details showing some variation in development time. Shield (1973) described a constant pattern of red-colored chromatophores in each of the zoeal stages which is apparently distinctive for the species.

Sandifer (1973d) reviewed published records of larvae found in plankton. These occurrences are later than the spawning records, being as early as May off the St. Johns River in Florida, and around Beaufort Inlet, N. C., off Chesapeake Bay in June, Delaware Bay to Woods Hole in July, ranging from St. Johns River, Fla. to Woods Hole in September, and receding in autumn with records in Delaware Bay in October and at Cape Hatteras, N. C., in November. Most of these records are from along shore or in bays or lagoons near the sea. A few records show that there is some offshore movement. Dudley and Judy (1971) found larvae at 1–8 m depths at three stations off Beaufort Inlet, N. C.: 1.6 km offshore, May–September; 6.5 km offshore, May–October; 8–10 km offshore, June–October. Sandifer (1973d) reported them from a comparable station in the mouth of Chesapeake Bay. Efford (1970) pointed out that all species of *Emerita* live along continental shores, except one in Puerto Rico. All, with the possible exception of that one (da Costa 1962), have extended larval developments, and da Costa concluded that longshore countercurrent systems are essential to maintenance of the populations (also Efford 1976).

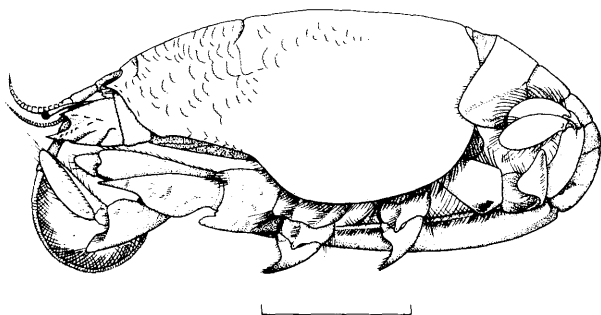


Fig. 186. *Emerita talpoida* (Say). Female in lateral view; 1 cm indicated (USNM 91082).

Wharton (1942) found megalopae and young adults distributed evenly in the wave-washed zone rather than in colonies as are adults. Megalopae swim with the abdomen extended, whereas young adults swim with the abdomen flexed. He traced development of the pleopods of females from the truly swimming appendages of the megalopae to the uniramous non-swimming pleopods of adults. Adult males lack pleopods.

Diaz (1974) was able to resolve the results of earlier observations on spawning, breeding, and growth with his own. He found that recolonization occurs in June–July and September–October, corresponding to the earlier spawning pulses if one allows time for larval development and settlement of the megalopae. With the aid of individuals tagged with corks tied to monofilament line, he observed no massive migrations, rather there is net displacement along the shore in currents moving from 10–15 m to 4–5 km/day.

Aggregations were seen clearly in fall and spring along Bogue Banks, N. C., their occurrence usually corresponding with appearance of a cusp on the beach. By midsummer, there were aggregations 5–10 m wide in bands several km long.

Females grow at rates related to time of settlement; those arriving on the beach in June might overwinter once, but those arriving in September through November could overwinter twice. Females commonly attained a carapace length of 22 mm (smallest ovigerous was 14.1 mm) and there were a few above 29 mm. Large females tend to die after spawning in spring. Males reach their maximum size in 9–10 months, commonly attaining lengths of 14 mm and occasionally as much as 19.4 mm. The sex ratio was 50% except in May, August, and September when females rise to 65% and in July when they reach a low of 43%.

Sexually mature at very small sizes, the males are neotenic, occurring in densities of up to 7/female with no correlation between size of female and number of male consorts. Multiple matings of a female with males were observed, ribbons of sperm usually being deposited between the third and fourth pairs of legs. Females had molted prior to copulation.

Efford (1967) suggested that neotenuous males in *Emerita* are probably advancing toward incipient parasitism, precocious sexual maturity insuring that many males find females and enhancing their chances of sticking on in turbulent surf. However, Wenner (1972) pointed out that deviation from 1:1 sex ratios in different size classes is apparently widespread in marine crustaceans and may have been obscured by usual methods of computation. He felt that size within class should be observed for

computing sex ratios, and that one of the types of skewed ratios could indicate sex reversal. To bolster his evidence for *Emerita*, 85 males of *E. analoga* were maintained in a cage in open water for 40 days. At the end of that time 79 survived and 16 were females. Diaz (1974) essentially repeated this experiment for *E. talpoida* but observed no sex reversal among males kept 48–85 days in aquaria and fed *Artemia* nauplii or dockside plankton in turbulent water. He analyzed groups of 100 in June–July 1972, April and October 1973, at carapace lengths of 3.5–13.9 mm. Females, some ovigerous, introduced in the same tanks with the males also had no effect. Fusaro (1978) found that differential growth rate of males and female *E. analoga* between 9 and 14 mm carapace length may account for the size frequency distribution and sex ratio pattern observed by Wenner, rather than protandry.

Wharton (1942) estimated that growth of large female *E. talpoida* may be as much as 0.08 mm per day from early June to late August. However, both Wharton and Williams (1947) noticed that there is considerable annual fluctuation in size at the same locality, and Williams further stated that there is considerable variation in size between localities in the same year.

The beautiful adaptations of this species for life in the shifting sand of the surf zone were treated by Wharton (1942) and the anatomical specializations exhaustively discussed by Snodgrass (1952). Adults can swim by means of the uropods, but they are primarily adapted for burrowing backward into wet sand. This is accomplished by rotating the uropods and fourth legs in unison (Trueman 1970, for *E. portoricensis*) and moving the first, second and third legs laterally and posteriorly in oarlike unison. Digging is initiated by tactile stimulation of the base of the telson. Like many crustaceans adapted for life in sand, the exoskeleton is ornamented with ridged burrowing sculptures (Seilacher 1973; Schmalfuss 1978). The ridges can be described as cuevas or terraces with sharp edges above steep anterior slopes. The ridge patterns are only vaguely symmetrical, and on different individuals are as different and personalized as fingerprints. Ontogenetically, ridge patterns are replicated in considerable detail except for size increase; new ridge elements are introduced as short lateral extensions of preexisting ridges, links between these, or incipient ridges in smooth areas; new incisions appear in previously simple saddles, particularly of incipient ridges, but partial disappearance of ridge elements is less common. Seilacher proposed that minute fibers pull the new cuticle off the old one in the direction of molting. At every point the pull produces V-shaped wrinkles which link with adja-

cent wrinkles to form smoothly curved pull-off saddles. Larger setae are not involved in the process because their pores are never placed in the tie-point incisions, but they influence the course of the ridges. This remains to be proved. The process does not allow formation of completely straight ridges, but for burrowing ribs the fabrication irregularity increases friction rather than reducing it, introduces chance effect in pattern, allows step by step increase of ridge length at molts, and produces frictional symmetry only in one direction (conformable with direction of molting); therefore, this type of sculpture is restricted to the carapace whereas different types of ornamentation (setate ridges) fulfill the same function in other parts of the exoskeleton.

Emerita talpoida moves up and down the beach with the tide, following shallow waves toward the water or moving up the beach with deep waves. Each time the animal is buried, the antennae are allowed to lie on the sand extended anterolaterally to strain the receding waves. Stomach contents consist of small particulate matter, the method of transferral of food from the antennae to the mouth being explained in detail by Caine (1975). Jones (1936) compared the habits of *E. emerita* to those of *E. talpoida* and devised a clever method of marking animals with string for the purpose of tracing their movements on the beach.

Edwards and Irving (1943) studied the influence of temperature and season on oxygen consumption in *E. talpoida* at Woods Hole. They found that oxygen consumption of winter animals at 12°C is about the same as that of the smallest summer animals at 17°C; consumption of winter animals at 3°C is about the same as that of summer animals at 13°C. They concluded that *E. talpoida* from the Woods Hole area become adjusted to seasonal changes in temperature in such a manner that rate of metabolism in winter is kept at a level comparable to that in summer. This explains why growth is uniform throughout the year, by their estimates, though the animals live in 2 to 4 m of water in winter rather than in the surf. The method of feeding in winter was not discussed, and Efford (1966) pointed out that *E. talpoida* cannot feed in standing water whereas *E. analoga* can do this.

Emerita talpoida tolerates sea water concentrations of 40 to 180‰ (Bursey and Bonner 1977). Crabs transferred directly from one salinity to another experience changes in hemolymph concentration toward that of the new salinity and less than two hours are required to establish a new steady state. Hyperosmotic regulation occurs over the entire range of tolerance, but may be entirely due to protein concentration of the hemolymph since its

osmotic concentration is always greater than the external medium at equilibrium (Burse 1978). Tolerance is greatly influenced by temperature, and is optimal at 20°C for test exposures of limited time.

Cronin and Johnson (1958) described a fungus from the hind gut of *E. talpoida* from the beaches of North Carolina near Beaufort.

Infraorder Brachyura

Crabs with abdomen much reduced in size, straight, symmetrical, closely bent under thorax, never used for swimming, and with uropods rarely present, never biramous. Cephalothorax depressed, fused with epistome at sides and nearly always in middle. Antennal scales immovable. Third maxillipeds broad. First pair of legs chelate and nearly always much stronger than other legs.

Borradaile's (1907) hierarchical arrangement of brachyurans, essentially adopted by Rathbun (1918b, 1925, 1930a, 1937), has been the accepted standard for American workers. However, independent lines of evidence from adult morphology of recent crabs, the fossil record, and larval studies are beginning to offer a more complex picture of evolutionary radiation in the group than the "standard" ideas based on adult morphology alone. Števcic (1971) drew the lines of evidence together, feeding a host of ideas into concise analysis which offers new views of old problems. Incorporating the more modern views, especially those derived from larval studies, the following arrangement deviates from Rathbun's standard in some respects, especially among the primitive crabs.

Key to Genera

1. Carapace firm and hard, body covered with short pubescence . . . *Dromidia*
Carapace soft and membranous, body mostly naked *Hypoconcha*

Genus *Dromidia* Stimpson 1858

Rathbun 1937:32

Carapace convex and pilose, hair often of considerable length; front narrow, hepatic region more or less concave, or excavated anteriorly. Palate strongly ridged on either side. Sternal sulci in female approximate in their extremities in either a single or more or less bifurcated tuberculiform projection between bases of chelipeds. (After Rathbun 1937.)

Section Dromiacea

Carapace subglobose or subquadrate, frontal region narrow. Last 1 or 2 pairs of legs small, subdorsal in position. Abdomen folded under thorax, penultimate segment usually without appendages; 5 pairs of appendages in female, first pair rudimentary. Lateral thoracic apodemata united in common center, forming a sternal canal. External maxillipeds with merus and ischium subquadrate (Rathbun 1937).

Superfamily Dromioidea

Family Dromiidae

Carapace subglobular, rarely flattened; no *lineae anomuricae* (a pair of longitudinal suture lines on carapace). Sternum of female traversed at least in part by 2 obliquely longitudinal grooves. External maxillipeds generally operculiform. Legs of moderate size; fourth and fifth pairs short, subdorsal in position, furnished with small hooklike nail or dactyl. Sixth segment of abdomen generally with rudimentary uropods (Schmitt 1921).

Gordon (1950; 1963) found the obliquely longitudinal sternal grooves on the females of this family to be external evidence of a pair of involuted tubes (variously developed in different species) leading from an external opening at the anterior end of the grooves posteriorly to paired spermathecae enclosed in the endophragmal system. (See also Wear and Batham 1975.)

The North American fossil record for this family dates from the Paleocene of the Gulf of Mexico coast (Glaessner 1969), though no modern species possesses a fossil record.

Dromidia antillensis Stimpson

Fig. 187

Dromidia antillensis Stimpson 1859:71.—Hay and Shore 1918:417, pl. 31, fig. 5.—Rathbun 1937:33, fig. 12, pl. 7, figs. 1–3.—Guinot-Dumortier 1959:428, fig. 4a, b.—Williams 1965:143, fig. 118.—Coelho and Ramos 1972:177.—Felder 1973:44; pl. 6, figs. 1, 3 (key).—Powers 1977:19.

Recognition characters.—Body and legs covered

with thick coat of short pubescence, leaving little but parts of fingers and tips of dactyls exposed. Carapace convex in all directions, longer than broad; frontal region longitudinally grooved along middle; front strongly deflexed, with 5 small teeth, median 3 subequal and approximately as long as distance between them at bases, teeth over eyes somewhat shorter but acute. Anterolateral margin of carapace deflected toward corner of buccal area, armed with 4 or 5 teeth.

Chelipeds rather thick and heavy; carpus dentate with small teeth at anterior angle; palm shorter than dactyl and armed with 3 blunt spines on upper margin; fingers curved, with strongly interlocking teeth. Walking legs rather slender; last pair turned forward over back and much longer than fourth pair; dactyls of fourth and fifth legs hooked, closing against unequal pair of distal spines on propodus.

Measurements in mm.—Carapace: male and female, length 32, width 31.

Color.—Quite variable. General ground color dirty yellowish green, olive buff, white, coral-mud gray, orange buff or various shades of red with lighter pubescence; fingers with bases darker than white tips, shades of orange, pink, or red; cornea of eyes gray, hazel, reddish speckled or brown; some

specimens with bluish cast on maxillipeds and antennular peduncles. Rathbun (1937) gave great detail on a number of individuals which appear to vary from light to dark in a harmonious set of colors.

Habitat.—Shore to 311 m.

Type-locality.—St. Thomas, V. I., Key Biscayne and Tortugas, Fla.

Known range.—Off Cape Hatteras, N. C., through Gulf of Mexico and Caribbean Sea to Rio de Janeiro, Brazil; Bermuda; Saint Helena (Forest 1974).

Remarks.—This species is usually found carrying a covering of compound ascidians, sponges, or zoanthoid polyps. The North Carolina records represent marginal occurrences in a favorable northern locality. Hildebrand (1955) found it common on the Campeche Banks shrimping grounds.

Rathbun (1937) reported ovigerous females from Florida and the West Indies in winter, spring and summer, and they are known from North Carolina in June. Rice and Provenzano (1966) described 6 zoeal stages and a megalopa from eggs hatched in February and reared in 100% and 75% sea water at 25°C, and in 100% sea water at 20°C. Development time in 100% sea water at 25°C averaged 40 days. At lower salinities and temperatures no developing animal passed through all stages. From eggs hatched in June and reared in 100% sea water between 25° and 28°C, development through megalopa averaged 30 days. Relationships of the species to the Dromiacea were discussed in light of larval studies.

In temperature tolerance experiments, specimens taken from an offshore reef off North Carolina in September and October died after a 7-hour exposure to 4°C (F. J. and W. B. Vernberg, 1970).

Genus *Hypoconcha* Guérin-Ménéville 1854

Rathbun 1937:44.

Front and lateral margins expanded, covering eyes and all parts of head except flagella of antennae; margin of anterior half usually hairy, also lower surface and appendages; dorsal surface very thin and membranous. Appendages capable of being folded compactly against body; fourth and fifth pairs of legs prehensile without being subchelate; dactyl lunate.

Shape adapted to fit inside valve of lamelli-branch mollusk; this protective covering held over carapace by posterior pairs of legs and insertion of angular abdomen under hinge. (After Rathbun 1937.)

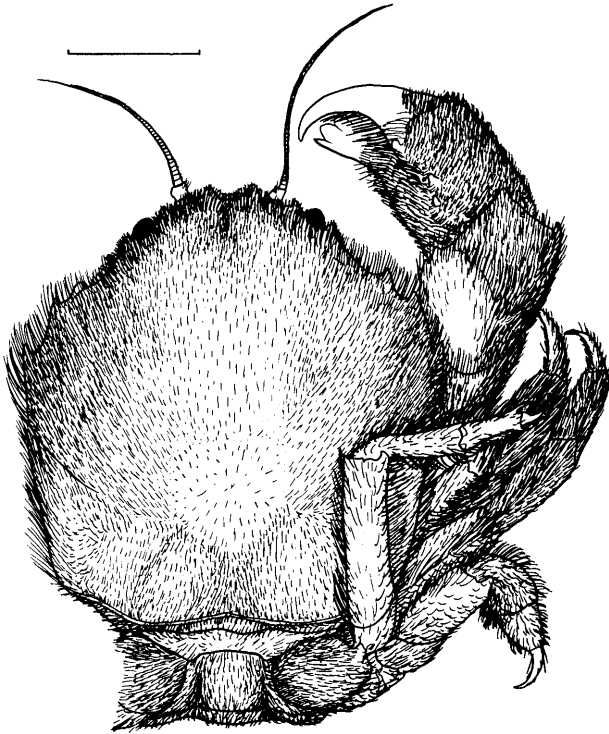


Fig. 187. *Dromidia antillensis* Stimpson. Male in dorsal view, legs of left side not shown, 1 cm indicated (from Williams 1965).

Key to Species

1. Ventral surface of carapace with 3 granulated nodules forming a triangle on either side; not hairy. *H. sabulosa*
 Ventral surface of carapace often granulate or spiny but without 3 nodules forming a triangle on either side; often hairy 2
2. Ventral surface of carapace visibly granulate; posterior side of orbit raised but never conspicuously spined *H. arcuata*
 Ventral surface of carapace with scattered, sharp granules or spines often partly or wholly concealed by thick pubescence; posterior side of orbit surmounted by a strong spine *H. spinosissima*

Hypoconcha arcuata Stimpson

Fig. 188

Hypoconcha arcuata Stimpson 1858:226.—Hay and Shore 1918:418, pl. 31, fig. 2.—Rathbun 1937:47, pl. 11, figs. 1–4.—Williams 1965:144, fig. 119.—Coelho and Ramos 1972:178.—Powers 1977:20.

Recognition characters.—Body short, broad, flattened, solid and roughly granulate ventrally. Front margin of carapace nearly semicircular in outline, margin densely ciliated, deeply fissured in middle and with shallow notch on each side near middle. Ventral surface without ridges but coarsely granulate and pubescent, sloping evenly to anterior margin, with eyes, antennules, antennae and mouthparts deeply seated in depressions; narrow fissure in front of eye for lodgment of antennal flagellum; outer posterior margin of orbit fissured. Third maxillipeds completely closing buccal cavity.

Legs all stout, hairy and coarsely granulate. First pair chelate; fingers somewhat spatulate and toothed at tip, fixed finger articulated at angle with hand. Second and third legs with sharp, corneous tips; fourth and fifth legs borne on dorsal surface, with penultimate article quite short and terminal article reduced to small contorted claw. Abdomen short and flexed so that last 2 segments lie on thoracic sternum.

Measurements in mm.—Carapace: male, length 24, width 24; female, length 24, width 25; ovigerous females, length 7.7–20, width 8.4–22.

Variation.—Most specimens are more granulated than the one figured.

Color.—Gray.

Habitat.—This curious crab is always found occupying a valve of some lamellibranch shell, preferably a clamshell (often *Trachycardium muricatum* or *egmontianum* [see Rouse 1970]) which it carries about upon its back after the manner of a hermit crab. By means of the claws on its fourth and fifth

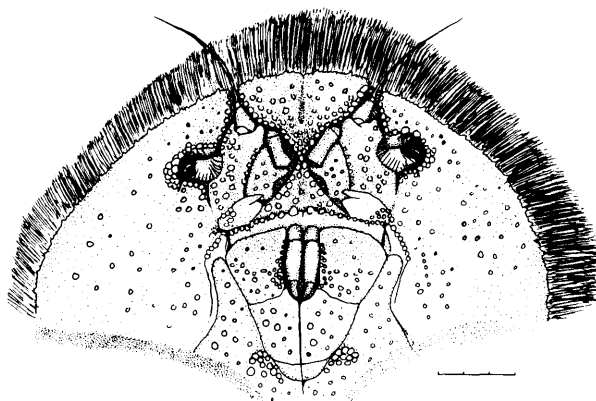


Fig. 188. *Hypoconcha arcuata* Stimpson. Anterior part of animal in ventral view, 3 mm indicated (from Williams 1965).

pairs of legs, perhaps aided by pressure of its body against the shell, it clings so tightly that removal from the shell without crushing it is almost impossible. Shallow water to 66 m (Wenner and Read 1982).

Type-locality.—South Carolina sandy shores and St. Thomas [V.I.].

Known range.—Off Cape Lookout, N. C., to west Florida; St. Thomas, V. I.; Surinam (Holthuis 1959) to Espírito Santo, Brazil.

Remarks.—Ovigerous females are known from eastern Florida in April and May. Kircher (1967, 1970) reared larvae from ovigerous females taken at an unspecified time off Cape Lookout, N. C. In controlled temperature BOD boxes at 25°C, newly hatched larvae subjected to 15, 20, 25, 30, 35 and 40‰ salinity on a photoperiod of 14 h light, 10 h dark survived to first crab stage in 25, 30, and 35‰ salinity. Three zoeal stages and a glaucothoe stage were described and figured. The early zoeae had higher survival rates in the lower salinities but the inverse was observed in later stages. There was an inverse relationship between duration and survival of each stage at a given salinity.

Kircher compared morphology of these larvae

to those of other dromiids and of the Brachyura and Anomura generally, concluding that *Hypoconcha* along with other dromiids is an anomuran, not a brachyuran, while recognizing that this placement has long been controversial.

In temperature tolerance experiments, specimens collected from an offshore reef southeast of Cape Lookout, N. C., in September and October died after 17 h of exposure to 4°C (F. J. and W. B. Vernberg 1970).

Hypoconcha sabulosa (Herbst)

Fig. 189

Cancer sabulosa Herbst 1799:57, pl.48, figs. 2–3.

Hypoconcha sabulosa.—Hay and Shore 1918:418, pl. 31, fig. 3.—Rathbun 1937:44, pl. 8, figs. 3–4, pl. 9, figs. 1–5.—Williams 1965:145, fig. 120.—Coelho and Ramos 1972:178.—Felder 1973:44; pl. 6, fig. 5 (key).—Powers 1977:20.

Recognition characters.—Body short, broad, flattened; surface nodulose, granulate, and marked by strong ridges ventrally. Carapace in old individuals pubescent above; margin densely hairy; armed anteriorly with 4 curved spines having sharp tips pointed obliquely downward followed by a few other smaller spines or raised tubercles; front between submesial pair of spines subtruncate or sloping slightly backward toward short, narrow, median fissure. Antennal fossae limited in front by pair of strong, oblique ridges arising between 2 of spines on anterior border, meeting each other in midline in front of epistome; epistome with posterior border raised into prominent ridge continuing on either side across front and some distance along

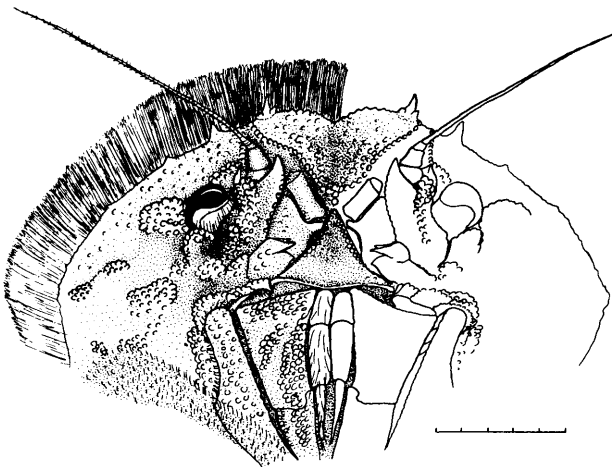


Fig. 189. *Hypoconcha sabulosa* (Herbst). Anterior part of animal in ventral view, detail of right side shown, 5 mm indicated (from Williams 1965).

sides of buccal area. Basal articles of antennae tuberculate; proximal article with strong inwardly directed tooth, distal article with tooth on each side of base of flagellum. Fissure in posterolateral margin of orbit prominent owing to development of strong ridge on either side.

Carpus of cheliped with granulate ridges, hand covered with more or less pointed tubercles. Other legs and abdomen much as in *H. arcuata*.

Measurements in mm.—Carapace: male, length 24, width 23; ovigerous female, length and width 22.

Variation.—The anterior spines may be obsolescent or in some cases doubled or tripled. The anterolateral spines vary in spacing.

Color.—Gray; or as described by Schmitt in Rathbun (1937), coral sand above with whitish-gray hairs, ground color beneath, red; rounded bosses on legs and subfrontal region reddish brown; eyes black or reddish brown; eggs orange.

Habitat.—About 3 to 82 m.

Type-locality.—Listed as "Africa" (probably an error).

Known range.—Off Cape Hatteras, N. C., through Gulf of Mexico to Bahia, Brazil.

Remarks.—Ovigerous females are known from Florida in February and June, and from North Carolina in October (Rathbun 1937, in part).

Hypoconcha spinosissima Rathbun

Fig. 190

Hypoconcha spinosissima Rathbun 1933a:185.—1937:46, fig. 14; pl. 10, figs. 1–2.—Felder 1973:44, pl. 6, fig. 4 (key).—Powers 1977:21.

Recognition characters.—Body short, broad, flattened; parchmentlike dorsum covered with short pubescence, solid ventral surface as well as legs usually densely hairy, especially in old individuals, and bearing tufts of coarse setae in hollow behind frontal notch, on eminence lateral to buccal angle, on distal edge of third maxillipeds and eminences elsewhere. Front subtruncate between antennae and divided by short, wide, median fissure followed by shallow furrow; anterolateral margin somewhat sinuous and densely hairy. Ventral surface beneath pubescence granulate and spiny, granules sparser on carapace than on appendages; spines erect and distributed as follows: 5 or 6 on anterolateral margin, longer spine at juncture of epistome with front; 1 very strong on posterior side of orbit, 1 strong curved above orbit; 1 or 2 on eminence lateral to buccal angle; row of small acute spines along anterior margin of buccal frame; 9 or 10 in irregular rows of palm of cheliped and 3 on carpus; 1 on

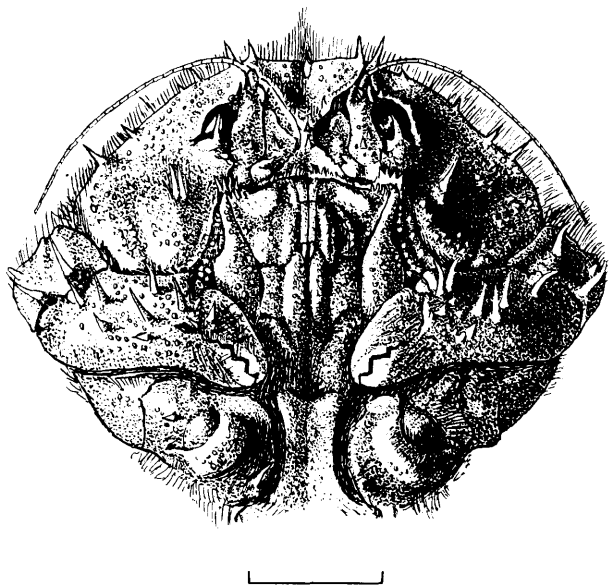


Fig. 190. *Hypoconcha spinosissima* Rathbun. Female in ventral view, USNM 55957, holotype, 5 mm indicated (from Rathbun 1937).

coxa and ischium of cheliped and first walking leg; row of short spines and tubercles on border of epistome; 6 or 7 slender spines on third maxilliped at outer angle of merus.

Legs and abdomen hairier but shaped much as in *H. arcuata*.

Measurements in mm.—Carapace: male, length 27, width 28; largest female, length 27, width 31; ovigerous female, length 25, width 26.

Variation.—Some specimens (USNM 55955 male) have a smoothly arched anterior border completely lacking marginal spines, and some nearly lack the ventral hairy covering.

Color.—Generally pinkish buff, darker parts salmon, fringing hairs primrose yellow (Rathbun 1937).

Habitat.—Sand and coarse bottom, 21 to 110 m.

Type-locality.—Off Cape Hatteras, N. C., 89.6 m.

Known range.—Off Cape Hatteras, N. C., to Gulf of Mexico off Mississippi Delta and Yucatan; Jamaica.

Remarks.—Ovigerous females are known from near Cape Hatteras, N. C., and Cape Canaveral, Fla., in October.

Family Tymolidae

Cyclodorippidae

Carapace circular or subquadrate. Third maxillipeds greatly elongated, leaving no appreciable part of buccal cavern uncovered. Legs 2–3 long, slender, subequal, articles cylindrical; legs 4–5 small, filiform, dorsal in position. Female with genital openings on coxa of third leg (second walking leg); sternal grooves well developed. Abdomen of both sexes 6- or 7-segmented. (Adapted from Gordon 1963; Sakai 1976; see also Wear and Batham 1975 for discussion of family placement.)

Genus *Clythrocerus* Milne Edwards and Bouvier 1899

Rathbun 1937:109.

Carapace rounded, sternal plastron reduced. First and second maxillipeds lacking exopods. Antennules small, completely retractile in orbito-antennal cavity. Antennae short, peduncle valviform. Walking legs short. Abdomen of female broad, cupped; that of male slender.

Key to Species

1. Front with 2 broad, platelike teeth on plane with flat, finely granulate carapace; posterolateral margin not spinulose *C. perpusillus*
- Front with 2 widely separated, fairly acute teeth depressed below level of coarsely granulate carapace; posterolateral margin spinulose *C. granulatus*

Clythrocerus granulatus (Rathbun)

Fig. 191

Cyclodorippe granulata Rathbun 1898a:293, pl. 9, fig. 1.

Clythrocerus granulatus.—Rathbun 1937:119, fig. 31; pl. 33, figs. 5–8.—Williams, McCloskey, and Gray 1968:45, fig. 3.

Recognition characters.—Surface of body and legs closely and coarsely granulate; front and posterior

orbital region depressed; remainder of carapace somewhat swollen, broader than long, lateral borders regularly rounded, narrowed in front and behind; a short, sharp spine above and near widest part; lateral margins, especially posterior half, fringed with slender spinules and some plumose hairs; branchiocardic sutures deep. Each half of bilobed front somewhat subdivided and edged with short, fine spinules; central notch partly occupied by extension of buccal cavity; cupped orbits oblique and deeply cut by a V-shaped notch above, at least

partly edged with fine spinules; eyes short.

Ischium of outer maxilliped with parallel margins, almost twice as long as merus, latter a little wider posteriorly than ischium; exognath as long as merus and widest at middle. Chelipeds rather slender, rough; both carpus and palm spinulose on inner margin in females and young males, smoother in mature males, fingers bent downward. First and second walking legs slender, cylindrical, second pair less than twice length of carapace, dactyl and propodus subequal; third and fourth walking legs shorter than carapace, propodus and dactyl of each slightly curved, dactyl flexed for grasping.

Abdomen of mature female broad, cupped; that of male slender.

Measurements in mm.—Carapace: male, length 4.4, width 4.6; ovigerous female, length 3.14, width 3.8.

Variation.—Old males in this species develop greatly elongate chelipeds which, along with the anterior parts of the carapace, are granular but less spinulose than in females or smaller males.

Habitat.—128 to 567 m.

Type-locality.—Off Trinidad, B. W. I.

Known range.—ESE Cape Lookout, and SE Cape Fear, N. C.; Honduras; southern Florida through Antilles to Venezuela and Trinidad.

Remarks.—Williams, et al. (1968) thought that variation in development of spinules in specimens from off North Carolina compared with that in specimens from tropical parts of the range might

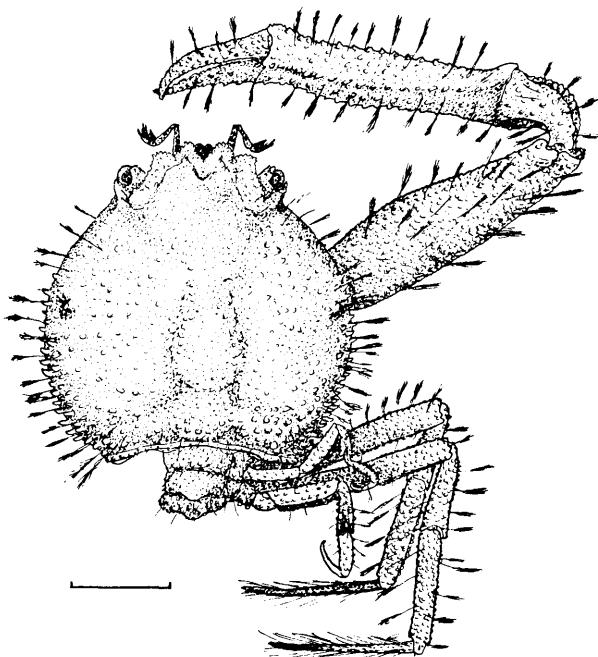


Fig. 191. *Clythrocerus granulatus* (Rathbun). Male in dorsal view, legs of left side not shown, 1 mm indicated (from Williams, et al. 1968).

be sufficient to indicate specific differences between populations. Subsequent study of more material shows that there is considerable individual variation in ornamentation, the young being relatively more spinulose than adults.

Ovigerous females are known from North Carolina in January and October.

Clythrocerus perpusillus Rathbun

Fig. 192

Clythrocerus perpusillus Rathbun 1901:90, fig. 14.—1937:111, fig. 28; pl. 33, figs. 3, 4.—Williams, McCloskey, and Gray 1968:44.

Recognition characters.—Surface of body finely granulate. Carapace flat dorsally, slightly broader than long, part behind orbits almost equally narrowed anteriorly and posteriorly, regions slightly marked, margins lightly pubescent; small, sharp spine just anterior to middle of lateral margin preceded by finely granulate, slightly indented margin. Two triangular, blunt frontal teeth in same plane as dorsal surface separated by sinus about equal to reverse of either tooth, sinus partly occupied by extension of buccal cavity slightly exceeding frontal teeth. Orbits roughly quadrilateral and oblique, preorbital angle flat, inconspicuous, postorbital angle variably dentiform, eye projecting beyond orbit.

Outer maxillipeds long and narrow. Chelipeds stout and short, about 1.5 times length of carapace, palm and dactyl with inner superior crest, fingers bent strongly inward, opposed edges meeting, propodal finger strongest; carpus with prominent anteroexternal lobe. Second walking leg exceeding first by length of dactyl; propodus and dactyl of third and fourth walking legs curved, dactyl flexed for grasping.

Measurements in mm.—Carapace: ovigerous female (Barbados), length 2.56, width 2.75; ovigerous female (North Carolina), length 2.72, width 3.04.

Variation.—Three females (2 ov) and a fragment of a fourth from North Carolina differ from Caribbean specimens in having the body slightly more rounded laterally, less granulate along margins of the carapace, the lateral spine less developed and not set off by an indented margin, and postorbital angles obsolete. These northern specimens may represent variants with spinous features less developed than in tropical members of the group, as seen in certain other brachyurans.

Habitat.—27 to 110 mm.

Type-locality.—Off Vieques [Puerto Rico], 27.4 m.

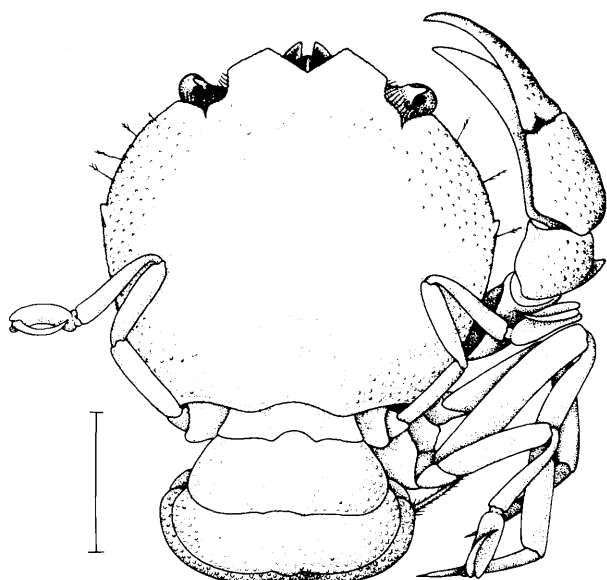


Fig. 192. *Clythrocerus perpusillus* Rathbun. Female in dorsal view, fifth leg only of left side shown, 1 mm indicated (UNC-IMS 2076).

Known range.—SE Cape Fear, N. C.; Bahama Banks; Vieques; Barbados.

Ovigerous females are known from North Carolina in January and from the Bahama Banks and Barbados in May.

Superfamily Homoloidea

Family Homolidae

Crabs with carapace rectangular, ovoid or urn-shaped, longer than broad. Eyes incompletely sheltered by orbits when retracted, terminal article of eyestalks either longer or shorter than slender basal article. External maxillipeds pediform, subpediform or suboperculiform. Sternum of female without longitudinal grooves. Gills 8, 10, 13 or 14 on each side (Rathbun 1937, modified after Gordon 1950).

Genus *Homola* Leach 1815

Rathbun 1937:62.—China 1966:204.—Zariquiey Alvarez 1968:304.—Manning and Holthuis 1981:25.

Homola barbata (Fabricius)

Fig. 193

Cancer barbatus Fabricius 1793:460.

Homola barbata.—Hay and Shore 1918:419, pl. 30, fig. 10.—Williams 1965:146, fig. 121.—Zariquiey

Alvarez 1968:304, figs. 12g, 106c.—Coelho and Ramos 1972:178.—Powers 1977:22.—Manning and Holthuis 1981:25.

Thelxiope barbata.—Rathbun 1937:63, fig. 16, pl. 15, figs. 1–2.

Recognition characters.—Carapace about $\frac{1}{4}$ longer than wide; surface granulate, spinulose, and sparsely setose; *linea anomurica* distinct and dorsal; sides nearly straight, only slightly convergent posteriorly, and extending almost vertically downward from spiny ridge running backward from behind strong spine situated at extremities of suture separating gastric and hepatic regions. Rostrum small, bifurcate at tip; 1 spine on each side at base of rostrum, 1 at outer orbital angle, transverse row of 2 behind rostrum, behind these a transverse row of 8, and farther back a small median spine. Antero-lateral parts below and behind orbits with small spines. Eyestalks long, slender at base, and abruptly enlarged below cornea.

Chelipeds of moderate size, surface granulate and hairy; merus and carpus with rows of spines. Bases of legs grouped behind midlength of carapace, placed in a dorsally curving arc on each side with fifth not only dorsal but slightly anterior to fourth. First to third walking legs with flattened articles, long, hairy and spinulose along margins. Last legs folded forward over back and subchelate.

Second segment of abdomen with large, median, conical tooth.

Measurements in mm.—Carapace including rostrum: male, length 30, width at base of lateral spines 22, posterior width 16; female, length 33, width at spines 25, posterior width 20.

Color.—"Body covered with tawny or yellowish-brown or reddish-brown hair; spines red or partly red" (Rathbun 1937).

Habitat.—55 to 682 m.

Type-locality.—Bay of Naples.

Known range.—Off southeastern Massachusetts to Rio de Janeiro, Brazil; eastern Atlantic Ocean from Portugal and Azores to Cape Verde Islands and Angola; South Africa; Mediterranean Sea.

Remarks.—Gordon (1950) discussed the anatomical structure of the spermathecae of females and copulatory apparatus of males in the genus *Thelxiope* (= *Homola*) and remarked upon the evolutionary sequence shown by these structures in the Dromiacea.

Hartnoll (1970) observed and filmed swimming individuals collected and held in the laboratory at Naples. The first, second and third walking legs beat in the frontal plane of the crab, successively stroking and feathering in planes above each other. Duration of the backward propulsive stroke is the

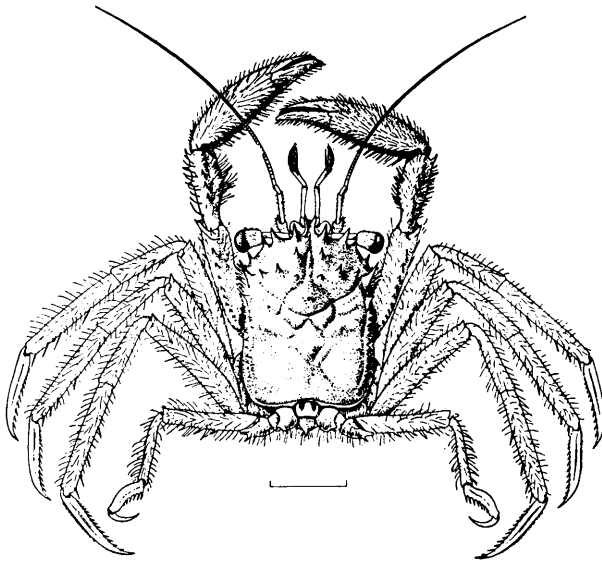


Fig. 193. *Homola barbata* (Fabricius). Animal in dorsal view, 1 cm indicated (from Smith 1887).

same as that of the forward recovery stroke. Legs of each side beat in sequence, 3–2–1, with a lag of about $\frac{1}{3}$ of a cycle between successive legs. The opposite legs of a pair beat about half a cycle out of phase. The crab swims quite rapidly and in a controlled manner, but only for short periods since it appears to fatigue rapidly. Both chelipeds and fifth legs are held in a folded position during swimming. Observation in a tank suggests that swimming is an escape reaction from benthic predators, in which case short bursts would be adequate.

In the western Atlantic Ocean ovigerous females are known nearly year round: off Nicaragua in February; Cape Canaveral, Fla., in April, and variously North Carolina to Yucatan Channel from May to September; Martha's Vineyard, Mass., in August, Delaware Bay in October, and Surinam in September.

Larvae are described from both plankton and rearing experiments. Rice and Provenzano (1970) reared seven zoeal stages in plastic trays at 20°C and 36.2‰ salinity from a female taken in Yucatan Channel. None of the larvae reached the megalopa stage, and molts were more variable than is usual in such experiments, with peaks at about 9.5, 17.5, 26.5, 37 and 48 days after hatching. The specimen that molted to 7th stage did so on the 67th day after hatching and it is estimated that it might have molted to megalopa in another two weeks, although the bizarre-shaped last stage may have been an extra stage induced by unfavorable conditions. The zoeal stages lasted about 11 weeks. Earlier, Rice (1964) described large zoeae and a

megalopa held through one molt from plankton taken in the Straits of Florida which were identified as *H. barbata*. This megalopa lived 27 days before transforming. Thus, total larval development of this species may last 15 weeks.

Differences between the western Atlantic larvae and others from the Mediterranean Sea and South Africa (Rice and Levetzow 1967) suggest that the east and west Atlantic may harbor separate species of *Homola*, differing more as larvae than as adults. Further, the views of Williamson (1965; 1967) were confirmed by the rearing experiments, indicating that the Homolidae appear to be related to the Raninidae and are close to the line of descent of the true crabs, but that the family Homolidae is well separated from the much more primitive Dromiidea and from typical Anomura.

In temperature tolerance experiments, specimens collected from a reef area SE of Cape Lookout, N. C., in September and October died after 7-h exposure to 4°C (F. J. and W. B. Vernberg 1970).

Family Latreilliidae

Carapace pyriform, extremely narrowed anteriorly and drawn into elongate gastric region, not covering bases of legs; basal article of ocular peduncle much longer than terminal article; each supraocular spine very long, divergent, with short deflexed rostrum between; *linea homolica* absent; 8 gills on either side; walking legs extremely long and slender; female abdomen with broadened segments 4–6 fused into cupped plate. (Wright and Collins 1972; Guinot 1978).

Genus *Latreillia* Roux 1830

Rathbun 1937:73.—China 1966:256.

Latreillia manningi Williams

Fig. 194

Latreillia elegans—Smith 1881:419.—1883:23.—1884:35 [7], pl. 2, figs. 2, 2a; pl. 3, fig. 1.—1886:637 [33].—Hay and Shore 1918:419 (part).—Rathbun 1937:73, fig. 18, pl. 21, figs. 1–8 (part).—Chace 1940:10.—Williams, McCloskey and Gray 1968:43, figs. 1A–D (part).—Powers 1977:23 (part).
Latreillia manningi Williams 1982:233, figs. 1b–c, 2a–e, 3a, 8.

Recognition characters.—Carapace pyriform, finely granulate; front drawn out into 2 long, divergent

horns between which a small, spinelike rostrum projects obliquely downward; each horn variably spinulose, with spine on lower side near proximal third; anterior margin of carapace with acute spine projecting downward at base of eyestalks. Eyes large, pyriform, at end of slender stalks about as long as supraorbital horns. Third maxillipeds slender and somewhat pediform.

Legs long, almost filiform, with ischial and propodal articles spinulose. Chelipeds about twice as long as body and about half as long as third walking legs, hand slightly longer than carpus, dactyl slightly less than half as long as palm. Last legs dorsal in position but not folded over back.

Abdomen in both sexes broad; female having first segment with median tubercle, second with strong median spine, third with stout spine on each lateral margin, third and remaining segments fused; abdomen of male with 6 distinct segments, spines lacking except for median spine on second segment.

Measurements in mm.—Carapace: male, length 6.5–10.9, width 3.9–6.6; female, length 8.25–12.25, width 5.6–7.25 (Williams 1982).

Habitat.—Mud, sand, shell, sponge, and fine coral bottoms, 82–474 m (Williams 1982).

Type-locality.—American Shoal Light, Florida, about 10 mi. N by $W\frac{1}{2}W$, 192–201 m.

Known range.—Nantucket Shoals off Massachusetts to off Havana, Cuba; Venezuela; Ascension I.; Frost (1936) reported a megalopa off Newfoundland.

Remarks.—Williams (1982) revised the genus *Latreillia* sensu lato, finding that *L. elegans* Roux, formerly considered to range through the Atlantic and Mediterranean, is restricted to the eastern Atlantic while the western Atlantic form was unde-

scribed. The latter, named *L. manningi*, is a less robust species, though there is some overlap in all features examined except in relative length of the legs.

Ovigerous females are known in February and May off Florida, April and August off Massachusetts, and October off Venezuela.

Cano (1893) described two larval stages of a *Latreillia* which can be attributed to *elegans*, a metazoea and a megalopa with branched horns, and he compared these to the Thalassinidea and Paguridea. Frost (1936) described a megalopa from 100-m depth off Newfoundland that was identified by R. Gurney. This was taken in a year marked by reduced Arctic current and a consequent influx of warm water.

Superfamily Raninoidea

Anterior thoracic sterna broad, posterior thoracic sterna narrow and keel-like. Posterior thoracic epimera largely exposed by reduction of branchiostegite. Female openings on coxae. Last pair of legs dorsal in position, normal or reduced in size. Posterior abdominal appendages absent in males, pleopods absent from first abdominal segment of females, uropods absent (in adults). Last thoracic segment fused with others. Sternal canal present. Thoracic nerve ganglion-chain elongate. Antennary sternum triangular, spout-shaped. Gills 8 on each side (Bourne, 1922; modified from Števíć, 1973).

Family Raninidae

Carapace remarkably elongate but not covering abdominal terga, first 4 or 5 terga lying exposed in dorsal plane of body. Last pair of legs also raised in dorsal plane of body. Antennae and antennules large, not folding into fossettes. Vasa deferentia protruding through bases of fifth pair of legs; oviducts piercing coxa of third pair of legs. Sternum broad anteriorly, narrow or linear posteriorly. A pair of respiratory orifices between tergum of first abdominal segment and coxae of last pair of legs. External maxillipeds completely covering buccal cavity, with palp concealed in repose; exopod but little longer than ischium. Gills less than 9 in number on each side. Hand flat, fixed finger extremely bent allowing dactyl to close against anterior border of hand. (Modified after Alcock 1896, and Rathbun 1937.)

Because of aberrant shape and organization, the systematic position of raninids as well as their phy-

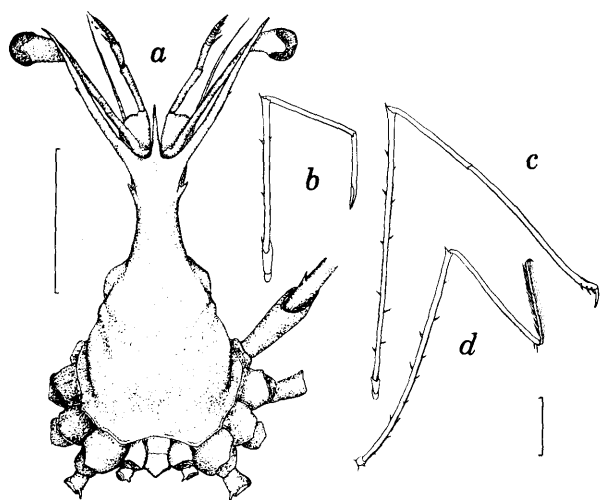


Fig. 194. *Latreillia manningi* Williams. a, Body of male in dorsal view, 5 mm indicated; b, cheliped; c, first walking leg; d, fourth walking leg; 5 mm indicated (from Williams, et al. 1968).

logeny has been interpreted in various ways (Glaessner 1969). The group has many specializations in structure and function related to burrowing in substrate, consequently it is difficult to establish which characters are primitive and which are derived. In his very readable review, Števčić (1971) regarded as secondary features the elongated body, prolonged mouthparts, narrow sternum and incompletely flexed abdomen, all related to the burrowing habit. He concluded that these are crabs which branched off the brachyuran ancestral lineage after the primary organizational level of crabs was reached. He pointed out that their larvae (citations in individual accounts below) combine brachyuran and anomuran features that tend to

link them with the homolid crabs, placing them, in his view, in an isolated position within the Brachyura near or somewhat above the Dromioidea within the Dromiacea rather than in the Oxystomata as arranged by Glaessner (1969). The first raninids occur in the Lower Cretaceous. The group as a whole rose to a peak in numbers during the Tertiary, later declining to the living forms, but the fossil forms are remarkably similar to the modern ones (Glaessner 1960, 1969). Ancestors of the raninids are not known with certainty, but according to Števčić must have been at a higher level of organization than recent forms, thus the raninids are products of regressive specialization. (See also Wear and Batham 1975.)

Key to Subfamilies, Genera, and Species

1. Frontoorbital border more than half width of carapace; carapace smooth or partly covered with transverse lines; 8 pairs of gills 2
 Frontoorbital border less than half width of carapace; carapace eroded on anterior half; 7 pairs of gills [Subfamily Symethinae] *Symethis variolosa*
2. Orbits of moderate size, slightly oblique and situated on anterior border of carapace, ocular peduncle folded almost transversely or longitudinally; last pair of legs slender [Subfamily Ranininae] *Raninoides loevis*
 Orbits large, deep cavities in lower side of carapace forming inverted V with point at rostrum, ocular peduncles folded strongly and obliquely downward and backward; last pair of legs not slender [Subfamily Notopodinae; *Ranilia*] 3
3. Hand of cheliped with spine on upper margin *R. muricata*
 Hand of cheliped without spine on upper margin *R. constricta*

Subfamily Symethinae

Genus *Symethis* Weber 1795

Rathbun 1937:24.

This genus is known as fossil from the Paleocene of Alabama (Glaessner 1969).

Symethis variolosa (Fabricius)

Fig. 195

Hippa variolosa Fabricius 1793:476.

Symethis variolosa.—Rathbun 1937:26, fig. 10; pl. 5, figs. 7–8.—Gomes Corrêa 1970:10, pl. 5, figs. 38–47; pl. 6, figs. 48–55; pl. 7, figs. 61–62.—Coelho and Ramos 1972:179.—Powers 1977:25.

Recognition characters.—Body almost entirely covered with densely packed, tiny granules. Carapace irregularly narrow-ovate, convex from side to side and anteroposteriorly, abruptly elevated transversely behind frontal region with edge of

shoulder thus formed drawn into 5 anterior processes more or less separated by eroded depressions, floor of latter and other symmetrically arranged depressions on anterior half more coarsely but sparsely granular than other surfaces; fronto-orbital border less than half width of carapace, front proper trilobate and produced anteriorly, median lobe largest, a few stiff submarginal hairs along its sides; rounded tooth at outer side of orbit separated from anterolateral tooth by concave depression. Eyes short and rudimentary but with pigmented cornea. Antennules small and concealed by massive antennal peduncles meeting along midline; latter having first article partly fused with carapace, second article with prominent, triangular prolongation longer than mesial ramus terminating in short flagellum.

Chelipeds fairly long; palm swollen, fingers longer than palm, bent mesioventrally, cutting edges sharp and armed with widely separated acuminate teeth progressively stronger distally, tips hooked. Articles of remaining legs intricately modeled and

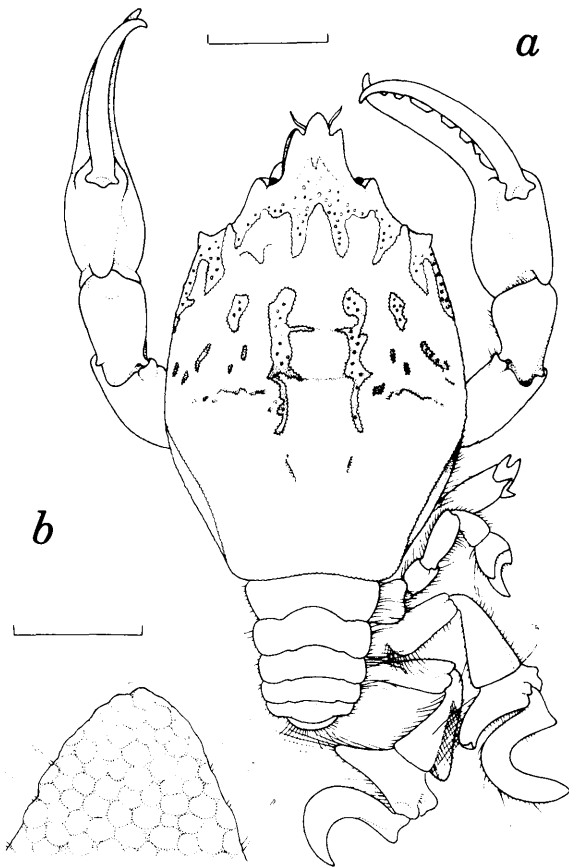


Fig. 195. *Symethis variolosa* (Weber). a, Female in dorsal view, walking legs of left side not shown; b, tip of rostrum; a, 5 mm, b, 0.5 mm indicated (USNM 155091).

densely fringed with hair except for thinner, sickle-shaped dactyls, last one least strongly curved.

Abdomen short and relatively narrow.

Measurements in mm.—Carapace: male, length 25, width 15.5; female, length 31 (est.), width 20.

Variation.—The pattern of erosion on the carapace varies and the chelipeds become somewhat more sculptured with age.

Color.—General color white; 2 pink spots in front, 2 light brown spots at middle and 2 green spots behind. Spotted with vinaceous-cinnamon. (Henderson and Schmitt in Rathbun 1937.)

Habitat.—Calcareous algae, occasionally sand (Coelho and Ramos 1972); shell hash (Goeke 1981); 18 to 137 m.

Type-locality.—"In oceano Indico."

Known range.—SE Cape Lookout, N. C., 34°10'N, 76°10'W, through western Gulf of Mexico (Goeke 1980) to Bahia, Brazil; Fernando de Noronha.

Remarks.—Both Cain (1972) and Cerame-Vivas and Gray (1966) listed this species from reef structures in tropical water off North Carolina, and F. J. and W. B. Vernberg (1970) found that animals

collected from this reef in September and October succumbed after 17-h exposure to 4°C water. Coelho (1966c) corrected the impression that the species is extremely rare in the Brazilian part of its range, finding 13 specimens at 8 stations in 27–90 m depths. Goeke (1981) further discussed the species, separating it from an east Pacific congener, described the spermathecal pits as most primitive in a series progressively coalesced in other raninids, remarked on the structure of the male pleopods and the reduced gill count, and placed the genus in a distinct subfamily.

Ovigerous females are known from southeastern Florida in July.

Subfamily Notopodinae

Serène and Umali 1972:24, 29.—Manning and Holthuis 1981:7.

Genus *Ranilia* H. Milne Edwards

Rathbun 1937:17.

Carapace broadly oval. Orbits invisible from above, together forming inverted V directed obliquely ventrad from rostrum; eyes stout. Antennae directed forward, basal article somewhat dilated mesially. Outer maxillipeds with third article longer than second. Sternal plastron linear between second legs, broadened to slightly concave, hexagonal disk between third and fourth pairs. Last (fifth) legs not remarkably reduced.

This genus has a fossil record dating from the Eocene of Hungary and the Tertiary of Europe-North America, but neither of the living species from the Western Atlantic has been reported as fossil (Glaessner 1969).

Ranilia constricta (A. Milne Edwards)

Fig. 196

Raninops constrictus A. Milne Edwards 1880:35.

Ranilia constricta.—Rathbun 1937:20, pl. 4, fig. 5; pl. 5, figs. 1–2.—W. E. Pequegnat 1970:180.—Powers 1977:24.—Manning and Holthuis 1981:7, figs. 1–2.

Ranilia atlantica.—Monod 1956:631, figs. 17–18.

Recognition characters.—Resembling *R. muricata*. Carapace oval, strongly convex from side to side, drawn to a rounded midsagittal peak anteriorly but more arched posteriorly, slightly convex from front to back; smooth posteriorly but microscopically granulate and with numerous faint, transverse,

lightly granulate wrinkles anteriorly. Rostrum slender, extending beyond innermost anterior spine; beaded anterior border of carapace with 4 spines, innermost overhanging base of orbit and fourth slightly behind external angle of front strongest, second and third reduced. Eyestalks strong, about 4 times as long as rostrum and capable of being turned back into deep, oblique orbits. Antennules small. Antennae directed forward, slightly longer than eyestalks.

Bases of legs grouped behind midlength of carapace, arranged in a dorsally curving arc on each side with fifth anterodorsal to fourth. First pair of legs subchelate, stout, flattened dorsally; merus squamous denticulate above with strong spine on superodistal margin; palm almost smooth above; distal margin of hand perpendicular, toothed; dactyl strong, smoothly curved; articles except dactyl with granulate wrinkles laterally. Dactyl of second and third pairs of legs flattened triangular, of fourth leg irregularly falciform, and of fifth narrowly and asymmetrically ovate.

Abdomen short and narrow.

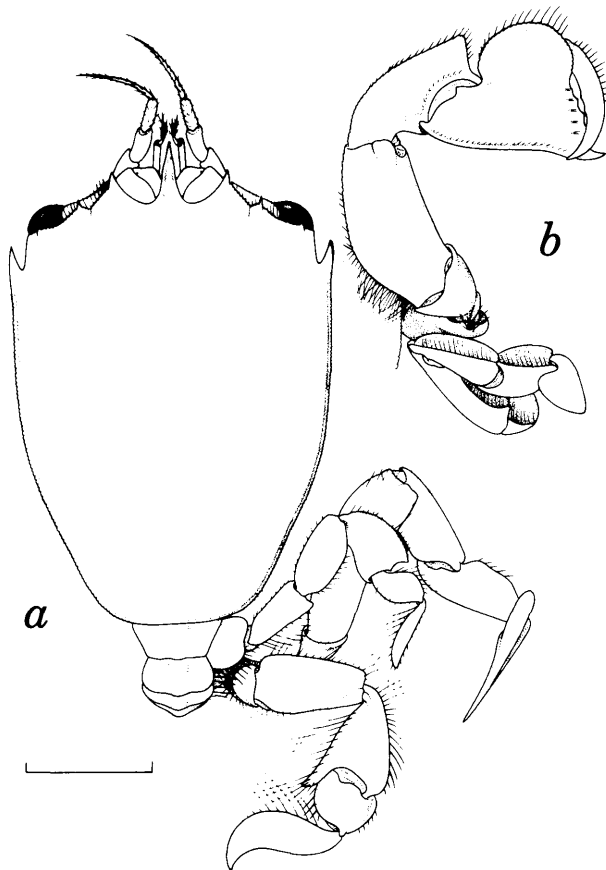


Fig. 196. *Ranilia constricta* (A. Milne Edwards). *a*, Female in dorsal view, walking legs of right side only shown; *b*, right cheliped and first walking leg, external view; 3 mm indicated (UNC-IMS 2506).

Measurements in mm.—Carapace: female, length 22.8, width 15.7 (Rathbun 1937).

Variation.—In some specimens the rostrum extends slightly beyond the innermost anterior spines of the front but in others it exceeds these spines by fully half its length. There is also variation in the eyestalks, those of some larger specimens being relatively more slender than those of smaller ones. These ill-defined differences may be attributable to growth.

Habitat.—Shallow reef water to 365 m.

Type-locality.—Near Sombrero (Florida?), 86 m (see Rathbun 1937).

Known range.—SE of Cape Fear, N. C., 33°42'N, 76°39.5'W, 140 m; Palm Beach, Fla., to Florida Straits and Yucatan Channel; Cuba; off Barbados; Ascension Island; eastern Atlantic from Sierra Leone and Annobon Island (Manning and Holthuis 1981).

Remarks.—A specimen from Cuba (USNM 48642) was caught with a handline on a reef. There appears to be great resemblance between this species and *R. fornicata* from the Pacific.

Ranilia muricata H. Milne Edwards

Fig. 197

Ranilia muricata H. Milne Edwards 1837:196.—Hay and Shore 1918:420, pl. 31, fig. 1.—Rathbun 1937:18, pl. 3, figs. 3–6, pl. 4, figs. 1–4.—Williams 1965:142, fig. 117.—Powers 1977:24.

Recognition characters.—Carapace strongly convex from side to side, slightly so from front to back, smooth posteriorly but with numerous transverse, ciliated granulate wrinkles anteriorly. Rostrum slender; anterior border of carapace with 4 strong spines on each side, innermost overhanging base of orbit, third surmounting external angle of orbit, fourth at external angle of front. Eyestalks strong, about 4 times as long as rostrum and capable of being turned back into deep, oblique orbits. Antennules small. Antennae directed forward, slightly longer than eyestalks.

Bases of legs grouped behind midlength of carapace, arranged in a dorsally curving arch on each side with fifth anterodorsal to fourth. First pair of legs subchelate, stout, flattened distally, squamous-denticulate above with strong spine on superodistal margin of merus and palm; distal margin of hand perpendicular, toothed; dactyl strong, curved; members except dactyl with granulate wrinkles laterally. Second, third and fourth pairs of legs with flattened, triangular dactyls. Fifth pair of legs with flattened, narrowly ovate, asymmetrical dactyl.

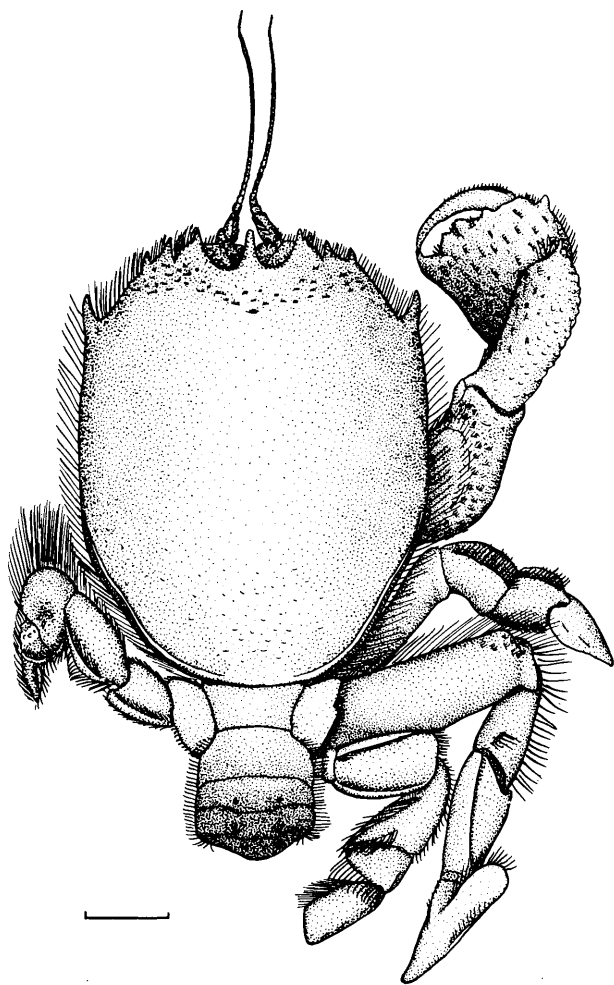


Fig. 197. *Ranilia muricata* H. Milne Edwards. Ovigerous female in dorsal view, first to fourth legs of right side shown, only fifth leg of left side shown, 5 mm indicated (from Williams 1965).

Abdomen short and narrow.

Measurements in mm.—Carapace: male, length 39, width 28; female, length 28, width 22.

Color.—Porcelain white with red, vermiculate, transverse lines on cephalothorax, and red dots and blotches on legs. Gibbes in Rathbun (1937) gave the color of dry specimens as purplish mixed with yellow and orange in places, particularly about the articulations and spines, with the latter having white tips and the chelipeds, remaining legs and abdominal segments with purplish markings.

Habitat.—This species appears to be confined to sand bottoms offshore. Specimens have been obtained in dredge hauls, and fragments of others have been taken from fish stomachs off North Carolina; 12 to 102 m.

Type-locality.—Unknown.

Known range.—Off Cape Lookout, N. C., 34°43'N, 76°40'W, to northwestern Gulf of Mexico (Goeke 1980) and Colombia; Swan Island.

Remarks.—Rathbun (1937) reported ovigerous females in April from Florida, and in September from North Carolina.

Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but died after 17-h exposure (F. J. and W. B. Vernberg, 1970).

Randall (1967) reported *R. muricata* from stomach contents of the mutton snapper, *Lutjanus analis*.

Subfamily Ranininae

Serène and Umali 1972:25, 34.

Genus *Raninoides* H. Milne Edwards 1837

Rathbun 1937:7.

Raninoides loevis (Latreille)

Fig. 198

Ranina loevis Latreille 1825:268.

Raninoides loevis.—Rathbun 1937:8, fig. 3, pl. 1, figs. 1,2.—Guinot-Dumortier 1959:426, figs. 2a-b.—Powers 1977:25.

Raninoides laevis.—Knight 1968:164–168 (passim), pl. 4, figs. a, b.—Glaessner 1969:502, fig. 313–5a, b.—Goeke 1980:147.

Recognition characters.—Carapace elongate obovate, strongly arched transversely, nearly twice as long as broad, surface mostly smooth, regions undefined; fronto-orbital border slightly less than greatest width; 4 sinuses of front continued on carapace as narrow, cilia-outlined grooves, those bordering 3-toothed rostrum slightly convergent posteriorly; tooth lateral to rostrum shorter than submedian tooth; lateralmost sinus slightly divergent; outer orbital tooth bifid, its inner branch short, dentiform, outer branch with long, slender, inward curved tip not reaching level of intermediate tooth; hepatic spine slender, slightly curved. Eyes with small, distinct stalks broadly dilated at base, orbits slightly oblique. Antennules about equal to antennae; latter with stout peduncle not concealing that of antennules, flagellum slender. External maxillipeds with merus usually shorter than ischium and edges slightly thickened and raised. Sternum broad to level of third legs, narrowed between third to fifth legs.

Chelipeds with spine near distal inner end of ischium; curved spine at inner end of ischium; curved spine at inner distal extremity of merus; carpus with



Fig. 198. *Raninoides loevis* (Latreille). *a*, Anterior part of carapace in dorsal view; *b*, distal half of right cheliped, upper surface (from Rathbun 1937).

2 unequal spines placed obliquely-transversely on distal half, outer one largest; similar spine distally on outer margin of palm and 4 irregular spines on inner margin; about 13 small spines on prehensile edge of fixed finger and a small proximal spine on outer margin of slender, slightly curved dactyl. Last (fifth) legs short, slender, arising in advance of fourth pair. Dactyls of walking legs flattened, second and third curvilinearly triangular, fourth broadly falcate, reduced fifth lobate.

Abdomen of both sexes with 7 separate segments. (Modified after Rathbun 1937.)

Known range.—S Cape Hatteras, 35°03.2'N, 75°35.1'W; around Gulf of Mexico and southern Caribbean Sea, including Leeward Islands, to Bahia, Brazil (Coelho and Ramos 1972; USNM).

Remarks.—Glaessner (1969) listed fossil *Raninoides* from the Oligocene-Miocene of northwestern North America, Chile and the East Indies. *Raninoides loevis* (the ligatured *oe* in Latreille's monograph is distinct from *ae*) resembles *R. benedicti* Rathbun, the characters upon which Rathbun separated the species being superficial ones that change with age, but male gonopods of the two are distinct, indicating a clear separation. Moreover, specimens from the Pacific formerly determined as *R. loevis* have been shown to be *R. benedicti* (see Guinot-Dumortier 1959; Knight 1968), thus the former is confined to the western Atlantic, the latter to the eastern Pacific.

Ovigerous females are known from west Florida in December and Dominica in March. Larvae of *R. benedicti* collected in September off Mexico were reared through four zoeal and a megalopa stage in about two months, each of the two major developmental steps requiring about a month for completion. From these and other plankton samples ranging from Baja California to Colombia, Knight (1968) described and illustrated larval development. Development of the Atlantic species is undoubtedly similar.

Section Oxystomata

Epistome reduced or absent. Efferent branchial channels terminating at middle of buccal area, buccal cavern produced forward and generally elongate-triangular in shape, efferent channels enclosed by elongate lamellar process of exopods of first maxillipeds. Afferent branchial openings either in front of bases of chelipeds, or at sides of endostome. Gills 6 to 9 on each side. Antennules folding either longitudinally or obliquely, rarely transversely. Male genital ducts protruding through bases of fifth legs or through fifth thoracic sternum nearby. (Modified after Alcock 1896 in Rathbun 1937.)

Superfamily Dorippoidea

Family Dorippidae

Carapace typically flat, not hiding much more than half of abdominal terga. Antennae large. First 2 pairs of walking legs remarkably long and stout; last 2 pairs of legs reduced and subdorsal in position. Genital opening of female sternal, male coxal. (Adapted from Rathbun 1937; Sakai 1976.)

Subfamily Ethusinae

Genus *Ethusa* Roux 1828

Rathbun 1937:77.—China 1966:255.

Carapace flat, truncate-oblong, broadest posteriorly, covering little more than first 2 thoracic sterna; tooth or spine at anteroexternal angle; hepatic region small; front consisting of 2 laminar teeth, each bifid. Large antennules folding obliquely and projecting beyond fossae. Antennae with basal article inserted between eyestalk and basal antennular article but at slightly lower level, flagellum long. Buccal cavern elongate-triangular, not reaching front; its basal $\frac{3}{4}$ covered by third maxillipeds having completely exposed palp, but its distal $\frac{1}{4}$ covered by stout, foliaceous processes of first maxillipeds. Efferent openings widely open in front of bases of chelipeds. Chelipeds in male often unequal. First and second walking legs long and usually rather stout; last 2 pairs short, rather slight, arising dorsal to other legs and bearing small hooklike dactyls. Abdomen of male narrow with segments 3–5 fused or partly so; that of female triangular with 7 free segments, first 3 visible in dorsal view. (After Rathbun 1937.)

Key to Species and Subspecies

1. Eyestalks long, extending beyond anterolateral spine *E. mascarone americana*
 Eyestalks short, not extending beyond anterolateral spine 2
2. Dactyls of first and second walking legs flattened *E. microphthalma*
 Dactyls of first and second walking legs not flattened. *E. tenuipes*

Ethusa mascarone americana A. Milne Edwards

Fig. 199

Ethusa americana A. Milne Edwards 1880:30.

Ethusa mascarone americana.—Rathbun 1897c:109.—

1937:78, pl. 22, fig. 2; pl. 23, fig. 2.—Williams, McCloskey, and Gray 1968:43, fig. 2.—Coelho and Ramos 1972:179.—Powers 1977:28.

Ethusa mascarone.—Bouvier 1898:65 (part).

Recognition characters.—Carapace longer than broad, regions well marked, branchial and cardiac regions equally raised; surface of body very finely granulate. Front between orbits 0.4 times as wide as distance between anterolateral angles and divided into 4 sharp, well-separated spines equally advanced, median notch deeply V-shaped; anterolateral angles broad at base but tapering to slender, acute spine; projecting obliquely forward. Eyes prominent, rather slender, directed obliquely for-

ward beyond anterolateral spine, cornea dilated; orbit broadly oblique, dorsal margin sinuous.

Chelipeds of male very unequal; major carpus and chela inflated and ovate in external view but hand compressed; fixed finger about $\frac{1}{8}$ length of palm, longer dactyl closing obliquely, opposed edges of fingers gaping and toothless; minor chela smaller and slender, hand scarcely stouter than carpus, slightly compressed fingers grooved, bent inward and downward, opposed edges toothless. Chelipeds of female equal and shaped as smaller one in male.

Measurements in mm.—Carapace: male, length 7.0, width 5.8; female, length 10.7, width 9.4 (Rathbun 1937).

Habitat.—Shallow water to 95 m.

Type-localities.—West Florida, 23.7 m, and West Florida, 26°16'N, 36.6 m.

Known range.—S of Cape Lookout, N. C. (34°06'N, 76°15'W) to Gulf of Mexico and West Indies; Maranhão to Bahia, Brazil; Golfo de California; Taboga Island, Panama.

Remarks.—Ovigerous females are known from Key West, Fla., in June.

Ethusa microphthalma Smith

Fig. 200

Ethusa microphthalma Smith 1881:418.—Rathbun

1937:82, pl. 22, fig. 3; pl. 23, fig. 3.—Chace

1940:10.—Pequegnat 1970:175.—Powers 1977:

28.

Recognition characters.—Carapace with anterior part less than half as broad as posterior swollen branchial region; dorsal surface slightly convex, pubescent, regions not deeply separated but cervical groove well marked; body microscopically granular. Front between orbits half or less than half as wide as distance between prominent anterolateral angles and divided into 4 similar and nearly equidistant, spiniform teeth, less advanced than spiniform anterolateral angles, V-shaped median sinus deeper than submedian sinus. Eyes small,

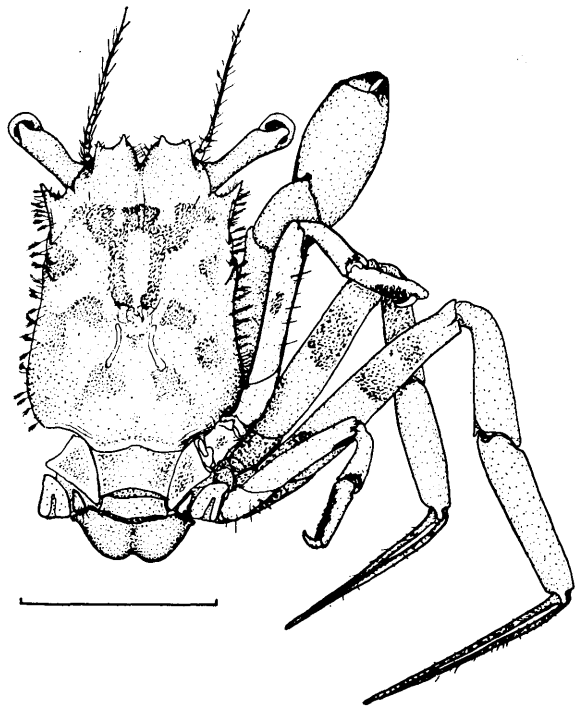


Fig. 199. *Ethusa mascarone americana* A. Milne Edwards. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams, et al. 1968).

barely visible in dorsal view, cornea terminal, not expanded, pigment black.

Chelipeds of males very unequal. Major cheliped with stout, swollen hand about 4 times higher and 2.5 times thicker than minor one; fingers much shorter than palm, tapering to tips, opposed edges oblique and unarmed. Minor cheliped and those of female small and slender, hand scarcely stouter than carpus, basal part smooth and nearly cylindrical, fingers alike, as long as palm, strongly compressed, longitudinally grooved, slightly curved mesially, opposed edges nearly straight, very finely and regularly toothed. First 2 pairs of walking legs twice as long as minor cheliped and nearly naked; dactyl longer than propodus, slightly curved, strongly ribbed, much compressed laterally, of nearly uniform breadth to short distance from acuminate tip. Third and fourth walking legs nearly alike, less than half length of first and second, slender, covered with short pubescence except on short, strongly curved dactyls.

Measurements in mm.—Carapace including spines: male, length 26, width 28; female, length 26, width 27 (Rathbun 1937). Unsexed specimen, length of carapace 65 mm [?] (Fowler 1951).

Variation.—Southern specimens are (generally) much larger than northern, have the carapace thickly covered with a short, soft pile, and the edge of the front concealed by a fringe of short hair

walking legs subequally 4-sided, ribbed, not compressed. Third and fourth walking legs shorter and (Rathbun 1937). Chace (1940) pointed out that his specimens from Cuba had anterolateral spines not reaching as far forward as the frontal spines.

Color.—Carapace salmon under dense cream-buff pubescence; cornea gray; tips of fingers white, legs light flame scarlet, darkest on dactyls to lightest on proximal half of back of merus (Schmitt in Rathbun 1937).

Habitat.—Rarely 20 m; 83 (Wenner and Boesch 1979) to 752 m (W. E. Pequegnat 1970).

Type-locality.—Off Martha's Vineyard, Mass, 260.6 m, Stn. 878, *Fish Hawk*, 39°55'N, 70°54'15"W.

Known range.—Off Martha's Vineyard, Mass., to Cuba and around Gulf of Mexico (Pequegnat, et al. 1971).

Remarks.—Chace (1940) pointed out allometric changes in proportions of the carapace. The shallowest known occurrence is that documented by Fowler (1951) off Atlantic City, N. J., along with a figure of the specimen. Ovigerous females are known in June off the Mississippi River Delta, and in July, October and November near the Florida Keys.

Ethusa tenuipes Rathbun

Fig. 201

Ethusa tenuipes Rathbun 1897c:11.—1937:87, pl. 24, fig. 3; pl. 25, fig. 3.—Williams, McCloskey, and Gray 1968:44.—Powers 1977:28.

Recognition characters.—Carapace with anterior part much narrower than posterior swollen branchial region; dorsal surface nearly smooth, slightly convex, cardiac region slightly raised, variably hairy, especially on marginal areas. Front between orbits half as wide, or less, than distance between prominent anterolateral angles and divided into 4 nearly similar and equidistant, slender teeth slightly exceeding anterolateral angles. Eyes visible from dorsal view in V-shaped orbits, cornea shorter than eyestalk but of good size.

Chelipeds of males very unequal. Hand of major cheliped with upper and lower margins convex, fingers much shorter than palm, tapering to tips, opposed edges oblique and toothless, lower margin of fixed finger straight. Minor cheliped small and slender; hand scarcely stouter than carpus, slightly compressed, a shallow groove along upper external surface; fingers compressed, grooved, with slight proximal gape and regularly dentate opposed edges. Chelipeds of female equal and shaped

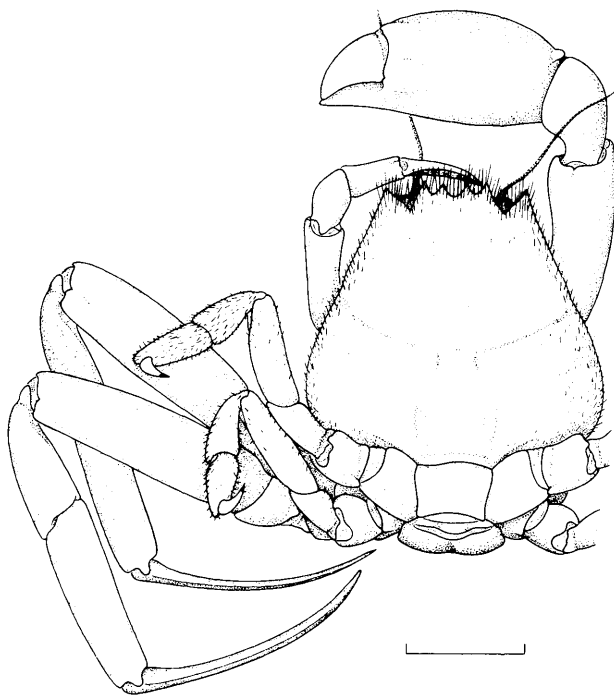


Fig. 200. *Ethusa microphthalmalma* Smith. Male in dorsal view, second to fifth legs of right side not shown completely; 1 cm indicated (USNM 66829).

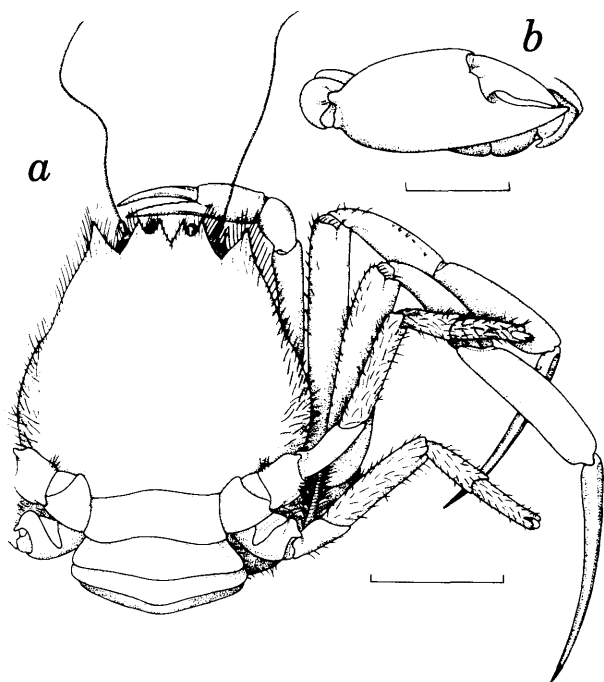


Fig. 201. *Ethusa tenuipes* Rathbun. *a*, Female in dorsal view, legs of left side not shown completely; *b*, male right chela and carpus, external view. *a*, USNM 66815, 5 mm; *b*, USNM 19855, holotype, 2 mm indicated.

as smaller one in male. Dactyls of first and second more pubescent, dactyls extremely short.

Measurements in mm.—Carapace: male, length 7.1, width 5.6; ovigerous female, length 11, width 11.1 (Rathbun 1937).

Variation.—Proportions of the carapace change noticeably with age, and relative lengths of frontal teeth and anterolateral angles vary individually.

Habitat.—25 to 216 m.

Type-locality.—Off Key West, 91.5 m.

Known range.—ESE Cape Lookout, N. C. (94–77 m); East Florida to Gulf of Mexico E of Mississippi River Delta; Cuba (Chace 1940).

Remarks.—Ovigerous females are known in April from Cuba (Chace 1940), May from Florida, and July from North Carolina and Florida.

Superfamily Calappoidea

Family Calappidae

Oxystomata of normal crablike form with abdomen hidden beneath thorax. Antennae small. Afferent openings of gill chambers in front of chelipeds. Outer maxillipeds not completely closing buccal cavity. Male openings coxal on fifth pair of legs.

Calappid species are known from the Cretaceous to the present in North America (Rathbun 1935).

Key to Genera and Some Species

1. Chelae dissimilar; large tooth on dactyl and pair of protuberances on propodus of major chela [Subfamily Calappinae] 2
 Chelipeds essentially symmetrical, no unusually enlarged teeth or protuberances. [Subfamily Matutinae] 4
2. Posterolateral region of carapace expanded into dentate, winglike projection *Calappa*
 Posterolateral region of carapace not expanded into dentate, winglike projection 3
3. Merus of cheliped bispinous on distal outer surface with lower spine strong and greatly extended laterally *Acanthocarpus alexandri*
 Merus of cheliped not bispinous on distal outer surface; carapace subcircular, small spine at lateral angle *Cycloes bairdii*
4. Carapace considerably broader than long, regularly convex above
 *Hepatus*
 Carapace nearly as long as broad, dorsal surface uneven *Osachila*

Subfamily Calappinae

Merus of external maxillipeds almost never elongate and acute, never concealing palp in repose. Legs adapted for walking (Alcock in Rathbun 1937).

Genus *Acanthocarpus* Stimpson 1871

Rathbun 1937:220.

Acanthocarpus alexandri Stimpson

Fig. 202

Acanthocarpus alexandri Stimpson 1871a:153.—

Rathbun 1937:221, pl. 69, figs. 1-2.—Chace 1940:26.—Williams 1965:156, fig. 137.—W. E. Pequegnat 1970:177, fig. 6-3.—Coelho and Ramos 1972:181.—Felder 1973:42, pl. 5, fig. 9.—Powers 1977:29.

Recognition characters.—Carapace ovate, regularly convex, widest in anterior half; surface uneven, granulate and punctate, with protuberances arranged longitudinally in roughly 5 rows centrally, and 2 shorter, intercalated rows behind orbits; all rows formed into ridges, those adjacent to midline each terminating in a spine on posterolateral margin. Posterior margin arcuate bearing low eminence at middle; inferior margin of pterygostomian region with row of 7 to 11 strong, widely spaced, oblique ridges of varying length. Orbits large, margins ciliated.

Chelipeds strong, dissimilar; merus bispinose on distal outer surface, inferior spine strong and a little longer or shorter than half width of carapace, superior spine about $\frac{1}{4}$ to $\frac{1}{3}$ length of inferior spine; hand with superior crest of 7 closely placed teeth, and oblique 6-toothed crest on outer surface extending from base of dactyl to posteroinferior angle, scattered tubercles between crests; inner surface of hand with stridulating ridge composed of about 45 oblique, closely placed striae which can be played against oblique ridges of pterygostomian region. Walking legs smooth. Sternal plastron with conical tubercle on either side of first article.

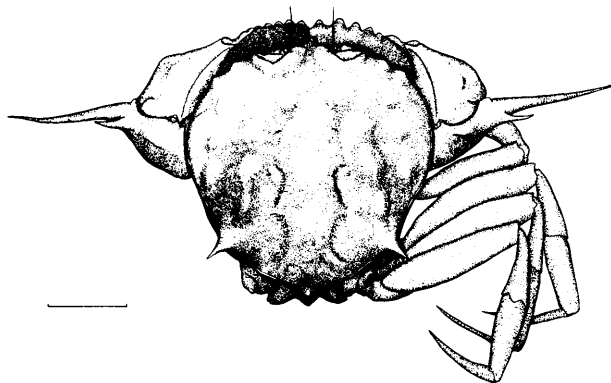


Fig. 202. *Acanthocarpus alexandri* Stimpson. Male in dorsal view, walking legs of left side not shown, 1 cm indicated (from Williams 1965).

Measurements in mm.—Carapace: male, length 41, width 42.2; female, length 39, width 41 (Chace 1940).

Color.—Dorsal surface of carapace and chelipeds pale reddish orange, deepest in hue on elevations of carapace and bases of meral spines of chelipeds; underparts white, slightly tinged with red (Rathbun 1937).

Habitat.—68 to 476 m.

Type-locality.—Off the Quicksands, Florida Keys, 135 m.

Known range.—Georges Bank off Massachusetts to west coast of Florida; Puerto Rico to Grenadines; Rio de Janeiro, Brazil (Coelho and Ramos 1972).

Remarks.—W. E. Pequegnat (1970) stated that this is by far the most abundant calappid that he collected in deeper water of the Gulf of Mexico. Oviparous females are known off Florida in June-July (Rathbun 1937), and elsewhere in the Gulf of Mexico off northwest Florida in July-August, Mississippi Delta in October, and Texas in November (W. E. Pequegnat 1970).

The stridulatory apparatus was described in detail by Hansen (1921) and reviewed along with that in other members of the genus by Guinot-Dumortier and Dumortier (1960).

Genus *Calappa* Weber 1795

Rathbun 1937:197.—China 1966:254.

Carapace strongly convex, rounded in front; posterolateral, clypeiform expansions or wings concealing flexed walking legs beneath. Front small, somewhat triangular, bilobed, projecting little if at all beyond level of small, circular orbits. Eyestalks short, thick. Antennules nearly vertical. Basal article of antennae broad, filling hiatus at inner angle of orbit. Outer maxillipeds gaping, exposing mandibles and lamellar processes of first maxillipeds. Chelipeds very large, subequal, closely fitted internally to carapace; merus with transverse winglike external expansion; compressed palms with dorsal crest, fingers of major chela with stout projecting lobule. Abdomen of adults with segments 3-5 fused. (Modified after Rathbun 1937.)

Key to Species

1. Orbits not separated from antennular sockets; surface may be moderately ridged or roughened. 2
- Orbits completely separated from antennular sockets; surface quite rough, covered with rounded protuberances and granulate. *C. angusta*
2. Carapace without flattened tooth or spine at either end of posterior margin; intermediate area on lower half of palm of cheliped concave, smooth or

- moderately granulate, not directed obliquely upward distally 3
 Carapace often with flattened tooth or spine at either end of posterior margin;
 intermediate area on lower half of palm of cheliped smooth or moderately
 granulate, somewhat narrow proximally but widening and continued
 obliquely upward distally *C. sulcata*
 3. Darker part of color pattern on carapace in interlacing bands on anterior
 half, becoming obliquely longitudinal stripes and fading somewhat on
 posterior half *C. flammea*
 Darker part of color pattern on anterior of carapace becoming reticular in pat-
 tern at midlength but fading posteriorly *C. ocellata*

***Calappa angusta* A. Milne Edwards**

Fig. 203

Calappa angusta Milne Edwards 1880:8.—Hay and Shore 1918:421, pl. 31, fig. 7.—Rathbun 1937:210, pl. 64, figs. 1–6.—Williams 1965:154, fig. 134.—Türkey 1968:251.—W. E. Pequegnat 1970:177.—Powers 1977:30.

Recognition characters.—Carapace 0.75 to 0.9 times as long as wide; anterolateral margins finely granulate with larger granules at intervals; surface covered with protuberances, granulate between. Tooth at posterolateral angle of winglike extension of carapace largest, preceded anteriorly by 4 teeth successively diminishing in size, and followed posteriorly by 2 or 3 smaller teeth successively diminishing in size, all with beaded edges. Orbit completely separated from antennular cavity.

Chelipeds with outer surface of palm not divided into 3 zones as in succeeding species, only lower and upper zones evident; upper margin with 6 to 8 teeth. Abdomen of either sex with sixth segment subquadrate; telson subtriangular, slightly longer than wide.

Measurements in mm.—Carapace: male, length 34, width 45; female, length 28, width 33.

Variation.—Posterior part narrower than middle of carapace in juveniles, wider than middle in adults.

Color.—Ground color buff to buff yellow; high spots or lumps on carapace and chelipeds red. Marginal spine of carapace, crest of chela and lumps on crest drab. Hairs of carapace, especially those of hind margin, light olive yellow; those of walking legs light citrous yellow. Merus of chelipeds practically colorless. Underparts whitish, pterygostomian region and maxillipeds suffused with pale purple (Schmitt in Rathbun 1937).

Habitat.—More abundant offshore than in inshore waters; 14 to 210 m, rarely deeper.

Type-locality.—Barbados.

Known range.—Off Cape Lookout, N. C., through eastern and southwestern Gulf of Mexico, to Venezuela (Türkey 1968) and Grenada.

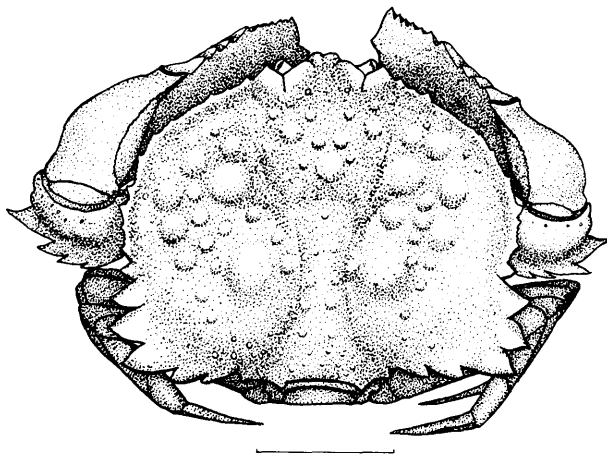


Fig. 203. *Calappa angusta* A. Milne Edwards. Animal from North Carolina in dorsal view, 1 cm indicated (from Williams 1965).

Remarks.—Ovigerous females have been taken from southern Florida in March.

Calappa angusta is the most unevenly granulate and tuberculate of the four species of *Calappa* treated here, having a central longitudinal ridged area but lacking other definite dorsal ridges. The roughness tends to be retained in adults. The teeth on the posterolateral wing of the carapace are rather blunt and there are three progressively smaller teeth behind these on the posterior margin. Flattened submesial spines or teeth on the posterior margin over the abdomen are lacking. The outer face of the chelae is rough and not zoned as in *C. flammea*.

In temperature tolerance experiments, specimens collected from an offshore reef southeast of Cape Lookout, N. C., in September and October died after 17 h of exposure to 4°C (F. J. and W. B. Vernberg 1979).

***Calappa flammea* (Herbst)**

Figs. 204–205

Cancer flammeus Herbst 1794:161, pl. 40, fig. 2.

Calappa flammea.—Hay and Shore 1918:421, pl. 31, fig. 8.—Holthuis 1958:148, figs. 28–35.—Wil-

liams 1965:152, figs. 130–131.—Felder 1973:43, pl. 5, fig. 11.—Powers 1977:30.

Recognition characters.—Carapace 1.14 to 1.42 times broader than long, varying from smaller to larger ratio with increasing size; surface granular, less conspicuously so in posterior half, tuberculate anteriorly, becoming obsolescent in adults; branchiocardiac grooves distinct. Front deeply notched anteriorly, projecting somewhat beyond orbits; anterolateral borders together forming semicircle in younger individuals, less strongly arched in adults. Posterolateral winglike expansions of carapace distinct, consisting of 5 broad teeth with beaded edges, fourth and fifth largest.

Chelipeds with outer surface of palm divided into 3 horizontal zones: lower zone with many large granules; intermediate zone, slightly sunken, with no large granules but with scattered small ones, more in some males than females; third zone occupying whole upper half of outer surface of palm, separated from intermediate zone by row of small granules, bearing many small granules and some large low granular tubercles, more densely granulated than intermediate zone in females, same in both in males. Upper margin of large hand with about 7 teeth, 6 on small hand; proximal teeth broad, low, and bifurcated. Palm with strong tooth on outer lower surface near carpus, apex of tooth approximately rectangular with sharp tip. Fingers of crushing hand somewhat stouter than on cutting hand, and with prominent projecting lobule near base of each. Merus with strong 4-toothed crest parallel with outer distal border.

Male with abdomen narrow; third to fifth segments fused, fifth segment with basal width twice median length, sixth with width greater than length, telson with length about 1.5 times width. Female with few granulations near lateral border of fourth

segment; length of telson equal to or slightly greater than width.

Measurements in mm.—Carapace: male, length 99, width 136; female, length 106, width 135.

Variation.—Juveniles may look quite unlike adults, having five low longitudinal crests on the carapace interrupted by irregularly spaced elevations; elsewhere there is uneven granulation and tuberculation. On the posterior border there are two low teeth between the submesial elevations and the posterolateral spines on each side. In juveniles, teeth with beaded edges on the winglike posterolateral expansions have acute tips; in adults, the second and third teeth may be sharp but lack pointed apices, and the fifth develops a shoulder on the inner basal part.

Color.—Ground color of carapace gray behind, shading to drab mottled with white over greater portion; reddish blue on outer surface of chelipeds becoming almost white on lower half of palm and on fingers; inner surface of chelipeds, pterygostomial regions, anterior surface of first walking legs, and small part of second walking legs reddish hued. Carapace with color pattern variable, purplish brown in interlacing bands on anterior half, obliquely longitudinal stripes on posterior half becoming lighter posteriorly. Merus, carpus, and proximal upper portion of palm striped with purplish brown, 2 distinct round spots of same color in middle of palm; upper half of palm with spots and patches of sulphur yellow on teeth and tubercles and same color mixed with ground color of merus, carpus, and part of carapace; 2 or 3 orange spots on hands near base of dactyls and spots of same near articulation of palm and carpus. Third to fifth legs, and underparts whitish. (Adapted from R. L. Barney in Rathbun 1937.)

Habitat.—This strikingly colored crab does not often occur within estuaries, but is often brought up from a few meters depth in the ocean. Those obtained in sounds or lagoons are usually small. Hildebrand (1955) listed the species as common from 10 to 30 m on the Campeche Banks. The species may spend much time buried in sand (Pearse, et al. 1942). Surface to 73 m, rarely to 262 m (Wenner and Read 1982).

Type-locality.—America.

Known range.—Woods Hole region, Mass., to Florida Keys; Gulf coast of United States and Mexico; Bahamas; Bermuda.

Remarks.—This species has a fossil record in North America dating from the Oligocene (Rathbun 1930b; Ross, et al. 1964).

The breeding range of the species extends as far northward as Cape Hatteras, but larval stages often drift beyond to southern New England. Some of

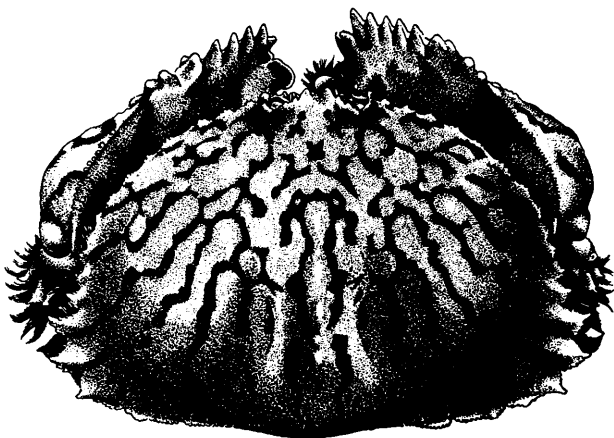


Fig. 204. *Calappa flammea* (Herbst). Female from Tortugas, Fla., in dorsal view, approx. $\times 0.66$ (from Holthuis 1958).

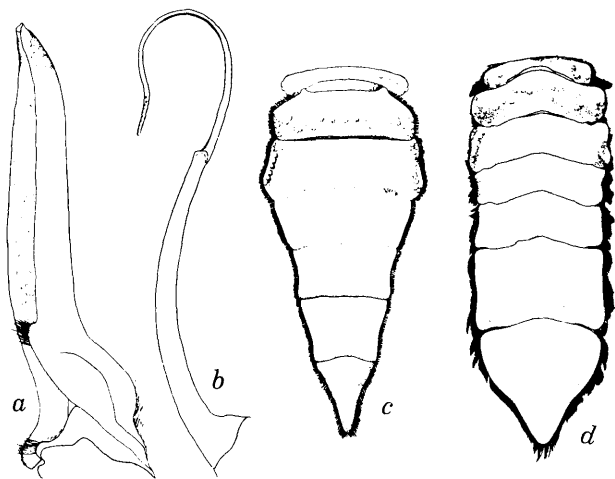


Fig. 205. *Calappa flammea* (Herbst). *a*, Male first pleopod in abdominal view, $\times 3$; *b*, male second pleopod in sternal view, $\times 3$; *c*, abdomen of male, approx. $\times 0.8$; *d*, abdomen of female, approx. $\times 0.8$; *a-c* from Tortugas, Fla., *d* from Bahama Islands (from Holthuis 1958).

these larvae are supposed now and then to survive a mild winter and develop by the next summer into the small individuals which have at intervals been taken on the coast of Massachusetts, Rhode Island, and New York. Some of the larval stages have been figured by Lebour (1944). Smith (1880b) gave a description of the megalopa of this species.

Members of the subfamily Calappinae, particularly *Calappa*, possess a large tooth on the dactyl and a pair of protuberances on the propodus of the right cheliped. With these modifications and an associated behavior pattern, these crabs can efficiently open shells of gastropods and other mollusks and feed on soft parts of enclosed hermit crabs (Shoup 1968). The crab moves over sand searching with the ambulatories, especially the first two. Intensity of search increases near food. The crab grasps the shell of a mollusk, usually trapping it between the chelipeds and the body. Using the chelae and first two pairs of legs, the crab rolls the shell over several times, frequently inserting dactyls into the aperture. The shell is normally held on the crab's right side, oriented with the aperture directed dorsally and supported by the first two pairs of walking legs. The crab grasps the edge of the aperture with the chela and positions the shell for insertion of the large tooth of the right dactyl, then inserts the tooth in the aperture, with the outside edge of the shell bridging the gap between the two heavy teeth on the propodus. The dactyl is then closed on the propodus and the bridging portion of the shell is broken. The shell is rolled and the breaking motion repeated until the contents are exposed and removed by the chela or maxillipeds.

Shoup, in his account of this process, pictured *C. flammea* but also mentioned other species of *Calappa* as well as *Cycloes*.

Complete reversal of symmetry, observed on both chelipeds of a number of specimens, has been attributed to simultaneous and approximately equal regeneration of the appendages following autotomy (Lewis 1969). Differences between these and normal chelipeds were described; the regenerated chelae are usually smaller and ornamentation is less prominent. If only one cheliped is regenerated, it becomes a minor chela no matter which side is involved.

Camp, et al. (1977) found the barnacle *Octolasmis hoeki* on the afferent branchial openings and *O. mulleri* in the gill chambers.

Randall (1967) reported *C. flammea* from stomach contents of the Nassau grouper, *Epinephelus striatus*.

Calappa ocellata Holthuis

Figs. 206–207

Calappa ocellata Holthuis 1958:158, figs. 36–40.—Williams 1965: 153, figs. 132–133.—Fausto-Filho 1967b:42, fig. 1, pl. J, figs. 1–2.—Coelho and Ramos 1972:180.—Powers 1977:31.

Recognition characters.—Carapace similar in size to *C. flammea*, having width to length ratio of 1.15 to 1.4, varying from smaller to larger ratio with increasing size; granulations much coarser than in *C. flammea*, granules larger, fewer, and more widely separated. Posterolateral winglike projections distinctly set off from anterolateral margin, teeth with slender pointed tips, more slender than in *C. flam-*

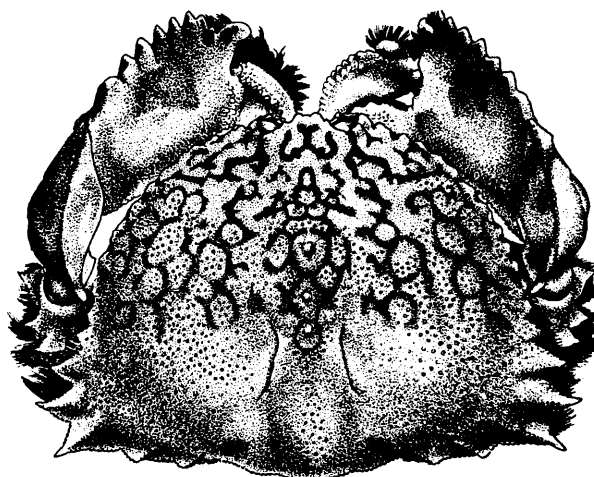


Fig. 206. *Calappa ocellata* Holthuis. Male from Curaçao in dorsal view, approximately natural size (from Holthuis 1958).

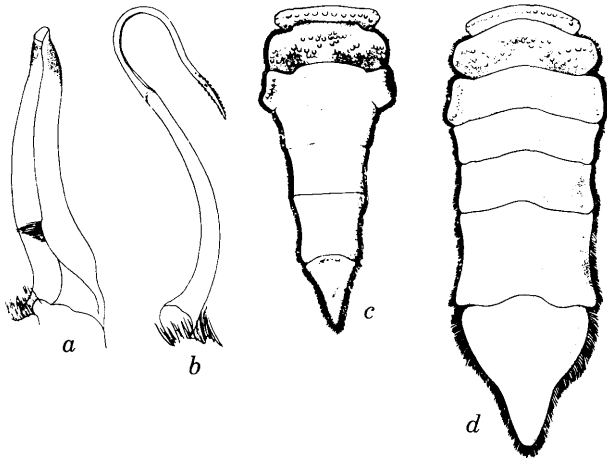


Fig. 207. *Calappa ocellata* Holthuis. a, Male first pleopod in abdominal view, $\times 3$; b, male second pleopod in sternal view, $\times 3$; c, abdomen of male, approx. $\times 0.8$; d, abdomen of female, approx. $\times 0.8$; a-d from Dutch West Indies (from Holthuis 1958).

mea, notch in basal part of fifth tooth inconspicuous.

Chelipeds similar to *C. flammea*, though second and third zones of outer palm nearly alike in both males and females. Upper margin with teeth narrower proximally than in *C. flammea*, and with bifurcation indistinct or absent. Palm with strong tooth on outer lower surface near carpus, apex sharply pointed with an acute tip. Teeth on crest of merus more sharply pointed than in *C. flammea*.

Male with abdomen narrower than in *C. flammea*; third to fifth segments fused, fifth segment with basal width less than twice median length, sixth with width equal to or less than length; seventh more slender than in *C. flammea*. Females with no granules near lateral border of fourth segment; length of seventh segment distinctly greater than width.

Measurements in mm.—Carapace: male, length 86, width 119; female, length 54, width 89.

Color.—Dark parts predominantly purple or wine red, varying from almost black to light violet or red; dark anterior portion lightening almost imperceptibly toward median transverse line in reticular pattern, but fading abruptly on posterior half, radiating lateral lines of color being continuous posteriorly but central lines interrupted on each side by superior and inferior spot of color near posterior border and base of winglike expansion, lateral lines ending in purplish spots. Areas between anterior reticulations forming ocellated light green spots which become elongate and radiate between line of color to margins, becoming nearly white posteriorly. Color varies with age and substrate (Fausto-Filho 1967b).

Habitat.—Shallow water to 80 m.

Type-locality.—Klein Bonaire, Dutch West Indies.

Known range.—Cape Hatteras, N. C., to Rio de Janeiro, Brazil; Bermuda.

Remarks.—This species is much less common than *C. flammea* from Tortugas northward and it is easily confused with that species, which it closely resembles (Holthuis 1958). The resemblance is so close that colors are useful in distinguishing the two forms. In addition to the characters given above, the terminal aperture in the male first pleopod is more widely open in *C. ocellata* than in *flammea* and the subterminal crook in the second pleopod has a narrower arc in *ocellata* than in *flammea*.

Difference in granulation of the female fourth abdominal segment in the two species is a character of limited utility.

Randall (1967) reported *O. ocellata* from stomach contents of the eyed flounder, *Bothus ocellatus*.

Calappa sulcata Rathbun

Figs. 208–209

Calappa sulcata Rathbun 1898a:289, pl. 9, figs. 3–4.—Hay and Shore 1918:422, pl. 31, fig. 6.—Holthuis 1958:179, figs. 51–54.—Williams 1965:156, figs. 135–136.—Fausto-Filho 1967b:46, fig. 3, pl. 2, figs. 5–6.—Coelho and Ramos 1972:180.—Felder 1973:42, pl. 5, fig. 10.—Powers 1977:32.

Recognition characters.—Carapace somewhat wider than long, covered with uniform granulations giving appearance of being smooth; 5 prominent longitudinal rows of tubercles on low to obsolescent ridges. Anterolateral margins crenulate and granulate, grading into inconspicuous posterolateral wings; teeth triangular, pointed. Posterior margin with tooth at each end near base of abdomen, sharper in males than in females, very low in adults, most slender and sharp in juveniles; third tooth of posterolateral wings extremely sharp and slender, pointed in juveniles.

Chelipeds with outer surface of palm divided into 3 zones as in preceding species; large tubercles of lower zone low and inconspicuous; zones 1, 2, and 3 each separated by row of sharply pointed tubercles; middle zone minutely granulate, extending horizontally but curving dorsally in distal part; upper zone smooth, except for 2 low, inconspicuous, granular tubercles near upper margin of palm; granulations on palm more distinct in females than in males; tooth on outer, lower, proximal surface of palm nearly rectangular in large individuals, slender and acute in smaller ones. Meral articles of

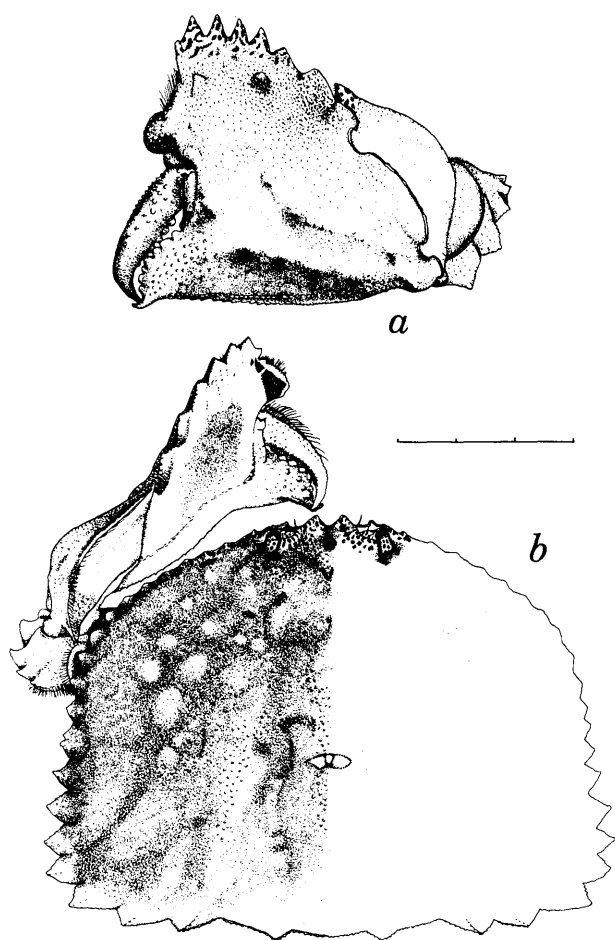


Fig. 208. *Calappa sulcata* Rathbun. *a*, Large chela in external view; *b*, female in dorsal view; 30 mm indicated (from Williams 1965).

walking legs with granules on lower surface.

Measurements in mm.—Carapace: male, length 90, width 122; female, length 92, width 119.

Color.—Varying from dark beige to light vermillion and pink. Color diminishing in intensity from front to back, becoming yellowish white or ivory at posterior margin. Three well-marked spots on carapace, one central a little behind median transverse line, and two somewhat smaller ones laterally a little anterior to it. Central spot intense ocher with an even darker ring inside it; lateral spots having lunate darker anterior and posterior lighter parts. In dark beige specimens the three spots are nearly the same color as the carapace, but somewhat wine red with lighter shades. Dorsal part of orbit with round or elongate dark vermillion punctations (Fausto-Filho 1967b).

From a large male taken at *Oregon II* Stn. 17696 off mouth of Amazon River, frozen May 12, 1975, by B. B. Collette and thawed June 24 when color notes were made: Color generally as Holthuis (1958)

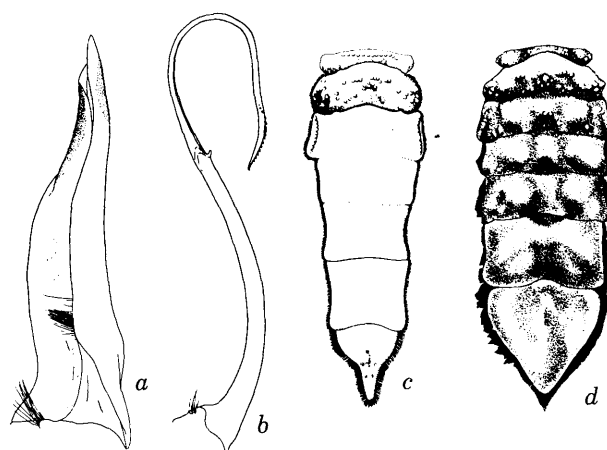


Fig. 209. *Calappa sulcata* Rathbun. *a*, Male first pleopod in abdominal view, approx. $\times 3$; *b*, male second pleopod in sternal view, approx. $\times 3$; *c*, abdomen of male, approx. $\times 0.8$; *d*, abdomen of female, approx. $\times 0.6$; *a-c* from near Margarita Island, Venezuela; *d* from Surinam (from Holthuis 1958).

and Rathbun (1937) recorded it. A 1.5-cm, round, reddish-brown spot in center of carapace and paired smaller lunate spots of similar color on each branchial region anterior to posterolateral wings in which cavity of each lunule has a yellowish hue. Many small spots on orbits, along anterior margin and crest of chelae and distalmost upper corner of cheliped carpus of granular, almost reticulated, deep reddish brown, but some tiny areas within spots showing white. Chelipeds with irregular dark area in center of each carpus and shadowy large spot with suggestion of smaller ones on upper, outer side of each palm. This surface also bears a suggestion of iridescence.

Habitat.—22 to 183 m (Cerame-Vivas, personal communication).

Type-locality.—Off Louisiana 29°24'30"N, 88°01'W, 64 m.

Known range.—Cape Hatteras, N. C., through Gulf of Mexico to Sergipe, Brazil.

Remarks.—Hildebrand (1954) reported this species (under the name *C. springeri*) as conspicuous but never abundant in the western and northwestern Gulf of Mexico at depths off 22 to 64 m. One ovigerous female was found in May off Padre Island, Tex.

Meiss and Norman (1977a, b) compared the stomatogastric ossicles and musculature to that in penaeideans, astacideans and anomurans, finding the structure to reflect generally accepted concepts of the phylogenetic position of the brachyurans.

Genus *Cycloes* De Haan 1837

Rathbun 1937:225.—Chace 1968:610.

Cycloes bairdii Stimpson

Fig. 210

Cyclois bairdii Stimpson 1860a:237.

Cycloes bairdii.—Rathbun 1937:225, pl. 69, figs. 3–4.—Fausto-Filho 1967b:54, fig. 7, pl. 4, figs. 16–17.—Williams, McCloskey, and Gray 1968:49, fig. 6.—Chace 1968:607(remarks).—Coelho and Ramos 1972:181.—Powers 1977:32.

Recognition characters.—Carapace slightly broader than long, broadest anterior to lateral spine, regularly convex, median regions well defined; surface densely and coarsely granulate, uneven or tuberculate, partly in longitudinal rows. Front with subtriangular, median notch, each submesial tooth slightly expanded on outer edge. Anterolateral margin with beaded edge, 5 or 6 denticles behind orbit; short sharp tooth or spine at lateral angle.

Chelipeds strong, dissimilar; outer surface of palm granular and divided into 3 zones, lower granular zone separated from intermediate zone by interrupted row of raised granules extending distally from single-toothed proximal crest, continuing distal crest of merus bearing 2 broad teeth and smaller granules; intermediate zone smoother, concave, extending horizontally but curving dorsally in distal part; upper zone rougher and with irregular larger granules trending in 3 obscurely oblique rows; upper margin with 9 teeth; dactyl of major chela with stridulating band of transverse ridges on inner surface. Fourth walking legs more flattened than preceding ones.

Measurements in mm.—Carapace: male, length 40,

width 43; female, length 45.8, width 49 (Rathbun 1937); fragment, width 53.5 (Chace 1968).

Variation.—Chace (1968) discussed differences in size, color pattern, granulation, extension of frontal lobes and width of abdomen, pointing out that Pacific specimens generally have more pronounced elevations than do those from the western Atlantic but that there is considerable variation even in a single locality. He also discussed possible subspecific differences between the Atlantic and Pacific populations, suggesting also that when the distributional ranges are better known, *C. deweti* from Saint Helena may prove to be a variant at the periphery.

Color.—Variable. Bright pale yellow, cream-buff or whitish with varied spots depending on color of crab—lemon yellow in irregular rows; bright red or crimson, especially laterally; white with posterior $\frac{2}{3}$ of each margined with purple; or with faint cinnamon or pale hazel markings. Eyestalks cream buff to purple. Chelipeds yellow or white outside with red to purple spots and a spot inside at articulation of dactyl; carpus with 1 or 2 dark spots at middle of outer side near upper margin. Walking legs yellow with bands of red and purple (Verrill and Schmitt in Rathbun 1937).

Habitat.—Burrows in sand or on reefs; 2.7 to 228 m.

Type-locality.—Cape St. Lucas, Mexico.

Known range.—Bermuda; ESE Cape Lookout, N. C., to Espirito Santo, Brazil, in west Atlantic; tip of Baja California to Ecuador and Galapagos Islands, including Clarion, Socorro and Cocos islands, in eastern Pacific.

Remarks.—Chace (1968) gave a key to the species and a nomenclatural history of the genus. *Cycloes bairdii* is relatively abundant off northern Brazil (Fausto-Filho and Neto 1976).

Subfamily Matutinae

Merus of external maxillipeds elongate and acute, entirely concealing palp in repose (Alcock in Rathbun 1937).

Guinot (1966, 1967), in a revolutionary approach to relationships among the genera *Aethra*, *Osachila*, *Hepatus*, *Hepatella*, and *Actaeomorpha*, only two of which occur in the western Atlantic, proposed that they be united in a subfamily, Aethrinae Dana or Hepatinae Stimpson, a taxonomic unit which would bridge the parthenopid and oxystomatid lines and give some coherence to their lineages that is not accounted for in arrangements adopted by Rathbun, and modified by Glaessner (1969). While this viewpoint has merit, in a manual

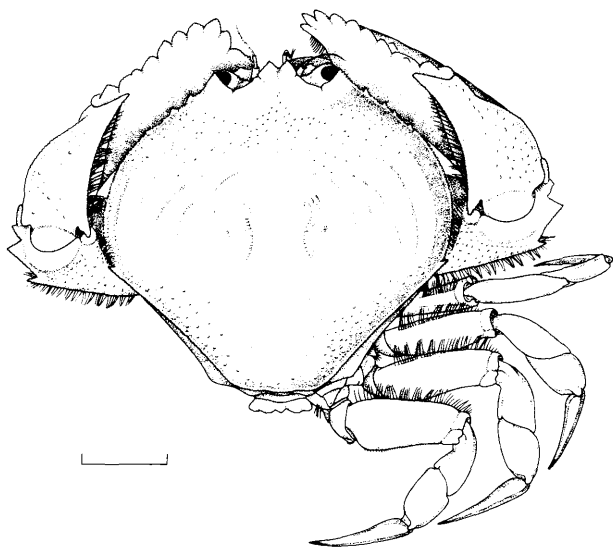


Fig. 210. *Cycloes bairdii* Stimpson. Male in dorsal view, walking legs of left side not shown; 1 cm indicated (USNM 171465).

of this kind which seeks to simplify complexities, it is best to retain the standard classification, leaving resolution of novel or classical approaches to the test of time.

Genus *Hepatus* Latreille 1802

Rathbun 1937:234.—Holthuis 1959:173.

Carapace broad, convex, regularly arcuate anteriorly, strongly narrowing posteriorly; hepatic regions large, branchial regions small. Front nar-

row, straight or nearly so, rather prominent and situated above level of lateral border continued beneath orbits to margin of buccal cavity. Orbits small, circular, level with front. Antennules oblique. Antennae at inner angle of orbit. Buccal cavity triangular, extending to level of lower border of orbits and entirely covered by external maxillipeds, with triangular merus concealing articles distal to it. Chelipeds fitting closely against lower body surface; palms with superior crest, fingers inclined downward and inward. (Modified after Rathbun 1937.)

Key to Species

1. Carapace covered with large, usually discrete spots (spots may be interconnected or form irregular, transverse stripes, proportionately small in juveniles); front noticeably tuberculate and truncate; Chesapeake Bay south
 *H. epheliticus*
 Carapace covered with small spots often aligned in transverse rows; front slightly tuberculate and obtusely bidentate; Georgia south, rare
 *H. pudibundus*

Hepatus epheliticus (Linnaeus)

(Calico crab, Dolly Varden crab)

Fig. 211

Cancer epheliticus Linnaeus 1763:414.

Hepatus epheliticus.—Hay and Shore 1918:422, pl. 37, fig. 1.—Rathbun 1937:238, pl. 70, figs. 3–4; pl. 71, figs. 1–4.—Williams 1965: 158, fig. 140.—Felder 1973:43, pl. 5, fig. 14.—Powers 1977:33.

Recognition characters.—Carapace covered with large spots, about $\frac{2}{3}$ as long as wide, convex above, regularly arcuate in front, strongly narrowed behind, almost smooth, with indistinct lines of low granules on gastric region and posterior part of branchial region. Front narrow, truncate, tuberculate, not dentate, and placed higher than continuation of anterolateral borders of carapace; anterolateral borders dentate with denticles more prominent than in *H. pudibundus*, middle denticle of each tooth projecting.

Chelipeds moderately strong; carpus and hand with lines of coarse tubercles on outer face and 3- to 4-toothed crest on superior margin of hand. Dactyls of walking legs with coating of short, dense pubescence except for tip and a narrow smooth line on each side.

Measurements in mm.—Carapace: male, length 53, width 79; female, length 60, width 88.

Variation.—In a series representing successive ages a great deal of variation is shown, the granulations

being relatively much coarser and the spots more numerous and variable in color among juveniles.

Color.—Dark gray or brownish with numerous, rather large, round or irregular spots of light red (muddy lavender to light red in young) with darker borders scattered over carapace. Spots may be coalesced in transverse rows or reticulate patterns.

Habitat.—This species is often found in depths of a few meters in channels of Beaufort, N. C., harbor, though such individuals are not so numerous or large as those taken in the ocean outside. Gunter (1950) found the species in water ranging from 28.7 to 35.2‰ salinity. Normally buried in sandy substrate (Anonymous 1975), 2–91 m (Franks, et al. 1972).

Type-locality.—Carolina.

Known range.—Chesapeake Bay to western Bay of Campeche, Mexico (Rickner 1977); Cuba; Jamaica; Dominican Republic.

Remarks.—Though this species has been recorded in depths to 91 m, Franks, et al. (1972) found it most abundant shoreward around 22 m off Mississippi, and Hildebrand (1954, 1955) found it most common shoreward of the latter depth in Texas and Mexico. Hildebrand found ovigerous females rarely in July, and Rouse (1970) found one ovigerous female in southwest Florida in January. Dudley and Judy (1971) in the vicinity of Beaufort, N. C., found females with orange eggs in August and with black eggs from May to October; larvae from June to October at 1- to 8-m depths 1.6 and 6.5 km offshore, and at 1 m in November at the latter sta-

tion; larvae present at 1- to 8-m depths from July to September 10–13 km offshore.

Earlier, Costlow and Bookhout (1962b) described five zoeal stages and a megalopa from individuals hatched and reared at 25°C in an array of salinities ranging from 20 to 40‰. Complete development took place only at 30 to 35‰, though some growth occurred in the other salinities. They pointed out that the adults are usually found in waters with salinity in the 30–35‰ range. Curiously, Kalber and Costlow (1968) and Kalber (1970) found that all the larval stages are good osmoregulators, but adults lose the ability.

Several authors noted the occurrence of the sea anemone *Calliactis tricolor* (Lesueur) on the carapace of this crab (Carlgren and Hedgpeth 1952; Hildebrand 1954, 1955), and Cuttress, et al. (1970) reviewed the association with this and other crabs. *Calliactis tricolor* lives more commonly in Puerto Rico as a commensal on *Turbo* and *Fasciolaria* shells, less commonly on *Murex* shells, inhabited by *Dardanus venosus*. Besides *D. venosus*, which is active toward the anemone, *Petrochirus diogenes* and *Stenocionops furcata* display extremely effective behavior patterns in transferring it. *Hepatus epheliticus*, on which *C. tricolor* lives in the Gulf of Mexico, occasionally showed rearing and rubbing of its carapace on the tentacles in response to *C. tricolor*. This led the anemone to transfer to the crab. *Calliactis tricolor* also transferred to *H. epheliticus* without such activity by the crab. In discussing results, the authors emphasized the variety of tactile stimuli used by different crabs. This is reflected in a flexible response pattern in the anemone.

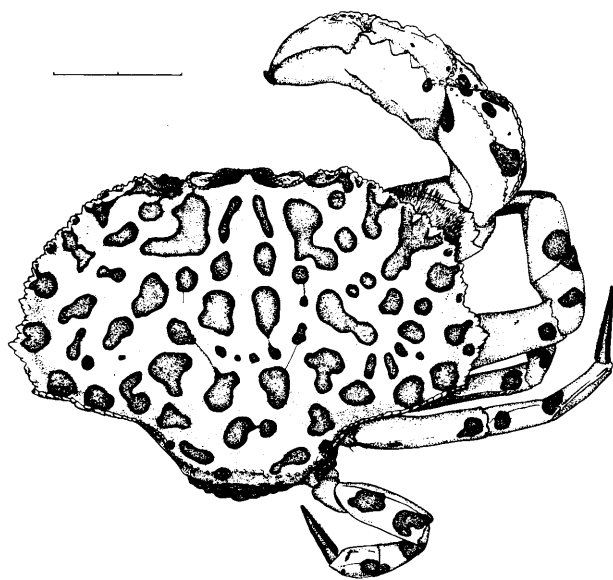


Fig. 211. *Hepatus epheliticus* (Linnaeus). Male in dorsal view, legs of left side not shown, 2 cm indicated (from Williams 1965).

Gray (1957) found that *H. epheliticus* has a large gill area in relation to its weight. He related this large respiratory area to its active nature as compared to activity of other strictly aquatic crabs with smaller gill area. In studies of metabolic tolerance, F. J. and W. B. Vernberg (1970) showed that *H. epheliticus* from the Cape Hatteras area placed in 25°C water at 10‰ salinity died within 24 h, at 20‰ were moderately active after 24 h, and in 30‰ were very active after 24 h. W. B. and F. J. Vernberg (1970) also showed that this species has metabolic adaptations to temperatures relating it to other species with southern affinities.

Johnson (1964) studied the histology of the male reproductive system.

Hepatus pudibundus (Herbst)

Figs. 212–213

Cancer pudibundus Herbst 1785:199.

Hepatus princeps.—Rathbun 1937:235, pl. 70, figs. 1–2.—Guinot-Dumortier 1960:510, fig. 10.

Hepatus pudibundus.—Holthuis 1959:167, figs. 36–38a, b.—Williams 1965:157, figs. 138–139.—Fausto-Filho 1967b:50, fig. 5, pl. 2, figs. 9–10.—Coelho and Ramos 1972:182.—Felder 1973:43, pl. 5, fig. 13.—Powers 1977:33,34.

Recognition characters.—Carapace between $\frac{2}{3}$ and $\frac{3}{4}$ as long as broad, relatively narrower in juveniles than in adults, covered with transverse lines or small spots, strongly convex. Surface smooth in adults; juveniles with 8 distinct rows of tubercles, 3 in a transverse line in broadest part of carapace, 2 others anterior and 3 posterior. Front thick, obtuse, slightly bidentate and tuberculate (and placed higher than continuation of anterolateral borders of carapace). Anterolateral margin divided into 12 or 13 more or less rectangular teeth, denticulate on margins and not projecting; anterior portion of posterolateral margin consisting of 2 rows of tubercles placed side by side with no space between, a small blunt tooth in middle of rows and another in posterior portion of this margin.

Outer face of hands with 5 rows of tubercles exclusive of marginal ones. Dactyls of walking legs with coating of short, dense pubescence, except for tip, and a narrow smooth line on each side.

Measurements in mm.—Carapace: males, length 16–60, width 21–76; females, length 14–46, width 18–62 (Holthuis 1959).

Color.—Light roseate to violet depending on quantity and size of spots, the pattern varying individually. Spots usually small, especially in center of carapace, but varying from scattered to ar-

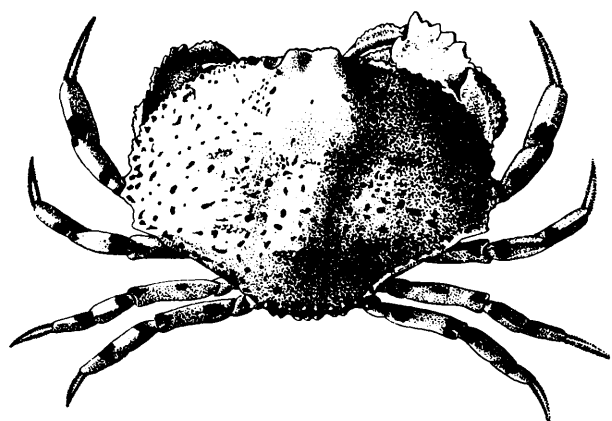


Fig. 212. *Hepatus pudibundus* (Herbst). Female in dorsal view, approximately natural size (from Holthuis 1959).

rangement in closely ranked transverse rows whose lateral ends bend posteriorly and coalesce along lateral margin of carapace. Chelipeds with upper and external parts of palm roseate, granules varying from faded to dark vermilion spots. Walking legs banded with vermilion and orange spots (Fausto-Filho 1967b).

Habitat.—Beach to 49 m.

Type-locality.—Martinique.

Known range.—Georgia to Santa Catarina, Brazil (Coelho and Ramos 1972).

Remarks.—Fausto-Filho (1967b) gave great detail on coloration as well as a figure showing the transversely banded pattern on the carapace. The figure here shows the more scattered pattern of spots. Nomura and Fausto-Filho (1966) calculated the regression coefficient of carapace width on length for males and females, pointing out no difference between the sexes although their sample of females was much smaller than that of males.

Ovigerous females are known from Guyana and

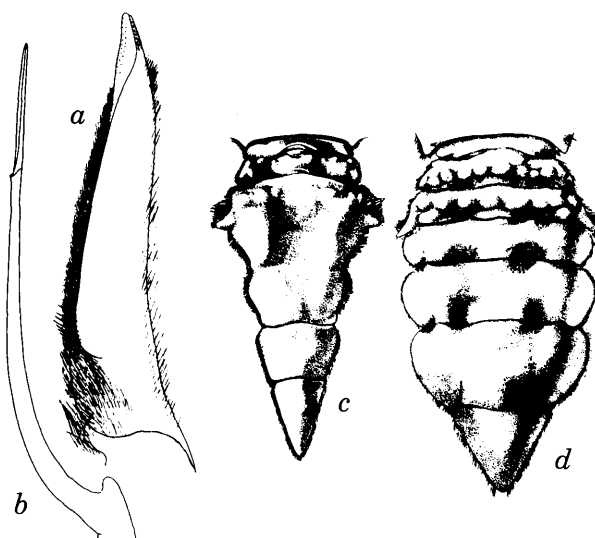


Fig. 213. *Hepatus pudibundus* (Herbst). *a*, Male first pleopod; *b*, male second pleopod; *a-b* approx. $\times 8$; *c*, abdomen of male; *d*, abdomen of female; *c-d* approx. $\times 2$ (from Holthuis 1959).

Surinam in April and September. Several of the specimens Holthuis (1959) studied carried one or more sea anemones on the carapace and one bore barnacles.

Genus *Osachila* Stimpson 1871

Rathbun 1937:248.—Hemming 1958b:17.—Guinot 1966:748.—1967:828–841 (passim).

Near *Hepatus* in all essential characters, but differing in narrower, octagonal carapace, more or less depressed and expanded at sides; very uneven surface having usually 6 chief protuberances; and much produced front forming true rostrum. (Modified after Rathbun 1937.)

Key to Species

1. Posterolateral margin of carapace shorter than anterolateral, thickened and raised, bearing 3 lobes including lateral angle, third lobe obsolescent *O. semilevis*
- Posterolateral margin of carapace about as long as anterolateral margin, not thickened and raised, bearing 4 lobes including angle, second lobe smallest *O. tuberosa*

Osachila semilevis Rathbun

Fig. 214

Osachila semilevis Rathbun 1916:652, pl. 36, fig. 1.—Hay and Shore 1918:422, pl. 31, fig. 9.—Rathbun 1937:251, pl. 77, fig. 1.—Williams 1965:159 (not fig. 142).—Powers 1977:34.

Recognition characters.—Much like *O. tuberosa*. Carapace octagonal, with 6 large protuberances, 1 mesogastric, paired metagastric, 1 cardiac, very prominent paired mesobranchial; protuberances eroded, depressions nearly smooth. Anterolateral margins continued toward buccal cavity, armed with tripartite teeth, each triad with strong central tooth

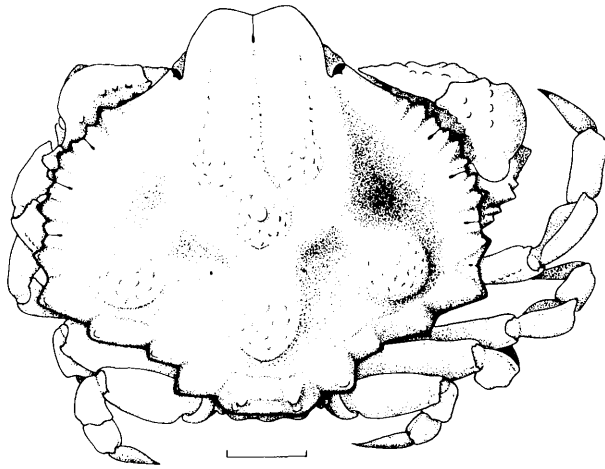


Fig. 214. *Osachila semilevis* Rathbun. Male in dorsal view, 2 mm indicated (USNM 171469).

continuing as slight ridge onto carapace and flanked on each side by minor teeth, triads separated from each other by closed or obsolescent sutures; posterolateral margin shorter than anterolateral, thickened and raised, bearing 4 lobes including lateral angle projecting laterally as far as adjacent anterolateral tooth, third lobe obsolescent, last lobe quite prominent. Front usually with narrow buttonhole-like sinus.

Chelipeds short, thick, tuberculate on outer face and with rough margins; hand stout, upper margin with 3 simple teeth; fixed finger thick, dactyl comparatively slender and straight. Walking legs of moderate size, more or less prismatic and lightly grooved. Abdomen narrow, eroded along margins and on last 2 segments.

Measurements in mm.—Carapace: male, length 10.5, width 11.6; ovigerous female, length 13, width 15.

Habitat.—23.7 to 91 m.

Type-locality.—Gulf of Mexico, 48 m.

Known range.—Off Beaufort, N. C., to northwest Florida.

Remarks.—This species has been recorded north of Florida only a few times, most recently by Cain (1972) from offshore reefs near Cape Lookout, N. C., and is much less abundant in collections than *O. tuberosa*. Ovigerous females have been taken from Florida and Georgia in August.

Osachila tuberosa Stimpson

Fig. 215

Osachila tuberosa Stimpson 1871a:154.—Hay and Shore 1918:423, pl. 31, fig. 10.—Rathbun 1937:250, pl. 77, fig. 3.—Williams 1965:159, figs.

141 and 142 (as *O. semilevis* by error).—Guinot 1966:748–755 (passim), figs. 3, 7, 15, 17.—1967:828–841 (passim), figs. 26, 31, 35.—W. E. Pequegnat 1970:178.—Powers 1977:34.

Recognition characters.—Carapace octagonal, with 6 large protuberances, 1 mesogastric, paired metagastric, 1 cardiac, paired mesobranchial; protuberances and lateral margins finely eroded. Anterolateral margins continued toward buccal cavity, armed with tripartite teeth each with strong central tooth continuing as slight ridge onto carapace and flanked on each side by minor teeth, triads separated from each other by closed or obsolescent sutures; posterolateral margins not thickened and raised, with 4 lobes, first lobe projecting laterally slightly beyond adjacent anterolateral margin, second almost obsolescent, third and fourth progressively prominent. Maxillipeds, sternum, abdomen and bases of legs eroded.

Chelipeds short, thick, tuberculate on outer face, and with rough margins; hand stout, upper margin with 3 teeth, proximal one bifid; fixed finger thick. Walking legs more or less prismatic with sharp margin and light longitudinal grooves.

Measurements in mm.—Carapace: male, length 18.0, width 18.8; female, length 18, width 20.

Color.—“Sand color with reddish cast, white below, claws and legs white.” (Henderson in Rathbun 1937.)

Habitat.—45 to 481 m.

Type-locality.—Five stations among the south Florida reefs (see Stimpson 1871a).

Known range.—Off Cape Hatteras, N. C., to

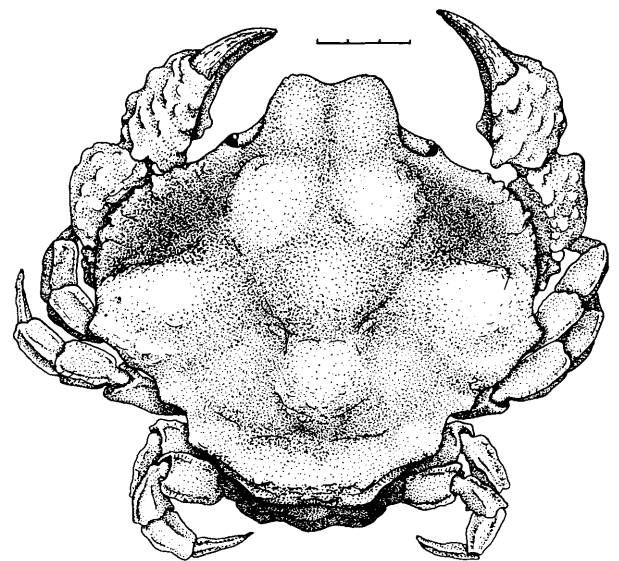


Fig. 215. *Osachila tuberosa* Stimpson. Animal in dorsal view, 3 mm indicated (from Williams 1965).

northwest Florida and Yucatan Channel (W. E. Pequegnat 1970; Springer and Bullis 1956).

Remarks.—This species is now known to occur fairly commonly on the reefs off Georgia and North Carolina. Ovigerous females are known off Georgia in June and August and at unrecorded dates off southern Florida.

Guinot (1966, 1967), in her discussion of the genus, gave a well-illustrated discussion employing this species for comparative purposes. As she suggested, the attribution of fig. 142 to *O. semilevis* in Williams (1965) is erroneous. It is in reality *O. tuberosa* and is used as the illustration for that species in this paper.

Specimens collected from reefs off Cape Lookout, N. C., in September and October died within 7 h exposure to 4°C, demonstrating the southern affinity of the species (F. J. and W. B. Vernberg 1970). In complementary salinity tolerance experiments, first zoeae maintained at 20°C expired within 16 h at 10 and 20‰ dilution, but were very active after 48 h at 30‰.

Family Leucosiidae

Crabs having carapace circular, oval, or polygonal. Eyes and orbits small, front narrow but wider than orbit. Antennules folding more or less obliquely. Antennae small. External maxillipeds completely enclosing buccal cavity, except often a small crevice in front. Afferent branchial channels occupying sides of endostome on either side of deep, median, endostomal groove serving as efferent branchial channel. Afferent channels covered by exognaths of external (third) maxillipeds, efferent channels by pair of lamellar processes of first maxillipeds. Chelipeds symmetrical. Abdomen hidden beneath thorax, commonly with third to sixth abdominal terga fused, sixth sometimes free. Vasa deferentia opening on fifth thoracic sternum near bases of last pair of legs. (Modified after Alcock 1896 in Rathbun 1937.)

Manning and Holthuis (1981) discussed the complex history of the subfamilies in the family Leucosiidae.

Key to Subfamilies, Genera, and Some Species

1. Carapace polygonal, uneven, nodular or eroded . [Subfamily Ebaliinae] 2
Carapace ovoid or hemispherical and smooth or granular 3
2. Posterior part of carapace lacking deep cavities (viewed posteriorly) *Ebalia*
Posterior part of carapace with deep, rounded cavity on each side (viewed posteriorly) *Speloeophorus*
3. Merus of external (third) maxilliped with mesial margin less than twice length of ischium [Subfamily Iliinae] 4
Merus of external (third) maxilliped with mesial margin 2 or more times length of ischium [Subfamily Leucosiinae] 5
4. Chelipeds slender; carapace not marbled, posterior half with 5 spines *Myropsis quinquespinosa*
Chelipeds robust; carapace marbled, posterior half with 3 spines *Persephona mediterranea*
5. Posterior half of carapace with 7 spines *Callidactylus asper*
Posterior half of carapace with 3 spines *Iliacantha*

Subfamily Ebaliinae

Surface of carapace uneven. Chelipeds of moderate length; fingers not very thin and elongate, dactyl moving in oblique plane. Anterior margin of buccal cavity arcuate, middle part projecting beyond pterygostomial region. Epistome and infraorbital lobe well developed. Pterygostomial margin extending either slightly or distinctly for-

ward, terminating in an indentation. Merus of external maxillipeds half or more than half length of ischium measured along inner border. First abdominal segment in female often under carapace (Rathbun 1937).

Genus *Ebalia* Leach [1817]

Rathbun 1937:123.—Hemming 1958b:15.

Key to Species

1. Carapace octagonal *E. cariosa*
Carapace hexagonal or subglobular *E. stimpsonii*

***Ebalia cariosa* (Stimpson)**

Fig. 216

Lithadia cariosa Stimpson 1860a:238.—Hay and Shore 1918:424, pl. 32, fig. 6.

Ebalia cariosa.—Rathbun 1937:125, pl. 35, figs. 6–7.—Williams 1965:147, fig. 122.—Coelho and Ramos 1972:182.—Powers 1977:35.

Recognition characters.—Carapace convex, roughly pentagonal; front truncate, lateral angles obtuse; surface uneven and covered everywhere, including other parts of body and legs, with beadlike granules, larger posteriorly and ventrally. Front narrow, upturned, and broadly notched, connected with middle protuberances by a median ridge traversing gastric region; ridge flanked on each side by sinuous, deep, broad excavation of darker color than protuberant parts. Anterolateral margin of hepatic region sinuous, hepatic region slightly prominent, delimited posteriorly by an impressed line. Pterygostomian region with large downward pointing tooth, hardly visible in dorsal view. Posterolateral margin with broad tooth, separated from bilobate intestinal region by deep sinus; cardiac and inner lobules of branchial region strongly protuberant, separated from thick intestinal lobes by deep narrow sulcus.

Chelipeds stout, a little longer than width of carapace, joints angular; merus about as broad as hand, outer margin convex and a little irregular; hands rather small, tapering to rather slender fingers. Walking legs cylindrical. Abdomen of male narrow,

triangular, with backward-projecting spine, ridge or tubercle at proximal end of penultimate segment. Abdomen of female with penultimate segment very large, nearly circular.

Measurements in mm.—Carapace: male, length 12, width 13; female, length 13, width 15.

Color.—Light gray or buff, female occasionally with two or three small red spots on abdomen; other specimens may be pale red (Rathbun 1937).

Habitat.—Below low-tide mark to 131 m (Coelho and Ramos 1972).

Type-locality.—Beaufort, N. C.

Known range.—Beaufort, N. C., to west Florida; western Gulf of Mexico (Rickner 1977); Jamaica; northeastern South America to São Paulo, Brazil.

Remarks.—This species is occasionally found in channels in the Beaufort, N. C., harbor. The species feigns death when brought on deck in a dredge haul, and thus closely resembles the pebbles and pieces of shell among which it appears to live. Ovigerous females are found at this locality throughout the summer.

***Ebalia stimpsonii* A. Milne Edwards**

Fig. 217

Ebalia stimpsonii A. Milne Edwards 1880:22.—Rathbun 1937:124, text-fig. 33; pl. 35, figs. 1–3; pl. 37, figs. 1–3.—Williams, McCloskey, and Gray 1968:46.—Powers 1977:35.

Recognition characters.—Integument everywhere covered with crowded, depressed granules. Carapace hexagonal, length and width subequal; rather

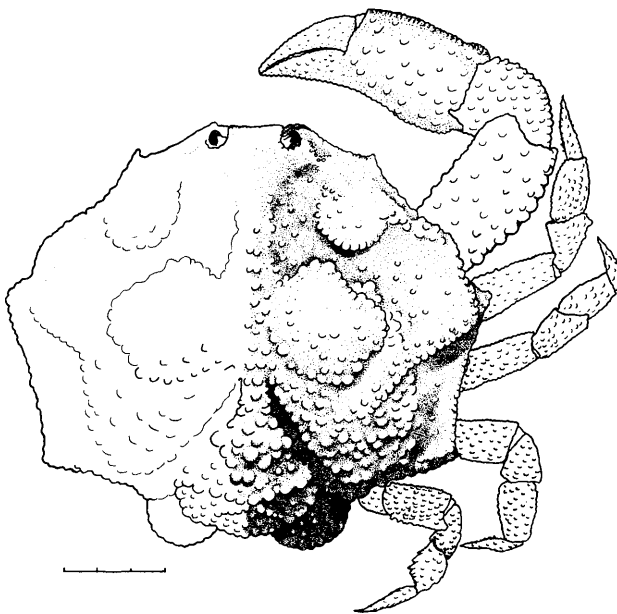


Fig. 216. *Ebalia cariosa* (Stimpson). Animal in dorsal view, legs of left side not shown, 3 mm indicated (from Williams 1965).

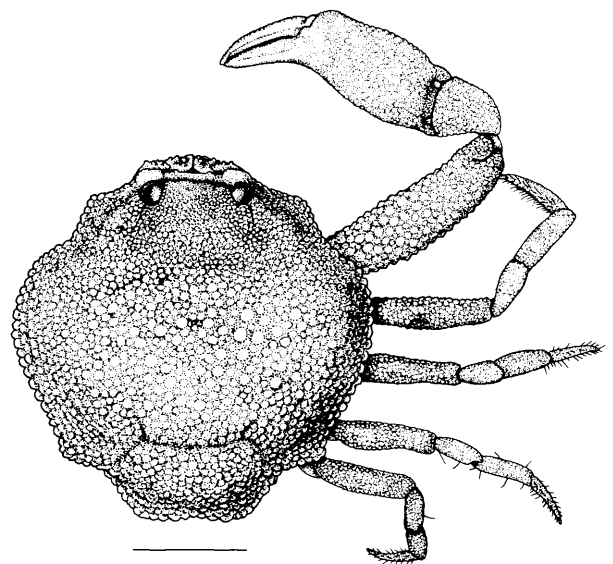


Fig. 217. *Ebalia stimpsonii* A. Milne Edwards. Female in dorsal view, legs of left side not shown, 3 mm indicated (USNM 66514).

uneven, granules smaller on anterior $\frac{1}{3}$, elsewhere a few granules prominent; front bidentate, broadly emarginate; row of outstanding granules on lateral margin; hepatic region depressed, its margin forming low, blunt prominence a little anterior to branchiohepatic suture; pterygostomian prominence farther forward, subacute; cardiac region swollen, surrounded by depression; posterolateral lobe in transverse line with middle of cardiac region; posterior margin faintly bilobed. In male, 4 posterior protuberances subrectangular, rounded at tips; in female, lobes shallower, posterior pair forming nearly horizontal line.

Chelipeds with granules coarser on merus than on hand; palm inflated proximally, fingers slender, tapering, and bent at angle to long axis of hand. Walking legs slender, covered with smaller granules.

Measurements in mm.—Carapace: male, length 5.6,

width 5.4; female, length 7.7, width 7.6.

Habitat.—Sandy mud to shelly and coral bottoms; 7.3 to 160 m (Fausto-Filho and Neto 1976).

Type-locality.—Barbados, 13.72 to 91.45 m.

Known range.—SE Cape Lookout, N. C.; west Florida to Barbados; off mouth of Amazon R., Brazil.

Remarks.—Ovigerous females are known in March from the Bahamas and May from North Carolina and the Bahamas.

Randall (1967) reported *E. stimpsonii* from stomach contents of the reef squirrelfish, *Holocentrus coryrus*.

Genus *Speloeophorus* A. Milne Edwards 1865

Rathbun 1937:141.

Key to Species

1. Lateral portions of carapace tumid, not expanded into wings; deep cavity of carapace with only 2 openings, not visible dorsally *S. nodosus*
- Lateral portions of carapace expanded into broad, flattened wings; deep cavity of carapace with 4 openings, visible dorsally *S. pontifer*

Speloeophorus nodosus (Bell)

Figs. 218–219

Oreophorus nodosus Bell 1855:307, pl. 33, fig. 8.

Speloeophorus nodosus.—Hay and Shore 1918:425, pl. 32, fig. 5.—Rathbun 1937:142, pl. 40, figs. 1–5.—Williams 1965:148, figs. 123–124.—Powers 1977:36.

Recognition characters.—Carapace convex, roughly pentagonal or hexagonal, broader than long; posterolateral angles rounded; surface nodose, evenly and thickly covered everywhere with crowded, rounded granules. Front thick, bilobed, upturned; prominent broad ridge extending backward from front to cardiac region. Hepatic region to each side with low hump, behind this, at side of gastric region, a much larger hump, and still farther back near posterior border, another of nearly equal size; posterior humps overhanging and largely containing deep cavity at either side with opening invisible in dorsal view. Subhepatic region with nodose prominence near front, and farther back 2 others of smaller size.

Chelipeds short, stout, coarsely granulate, crested along outer margin; merus with large distal and small proximal lobe; fingers thin, flat, grooved. Walking legs with dentate or narrowly lobed crests.

Measurements in mm.—Carapace: male, length

14.8, width 19.8; female, length 22, width 26.

Variation.—Carapace of males much more uneven than that of females.

Color.—Pink with a few purplish spots on carapace and rusty-brown marks on legs. Rathbun (1937) described this species as looking like a dead piece of coral overgrown with purplish and greenish algae, with patches of red ones; chelae with natural greenish cast; reticulations around whitish areas

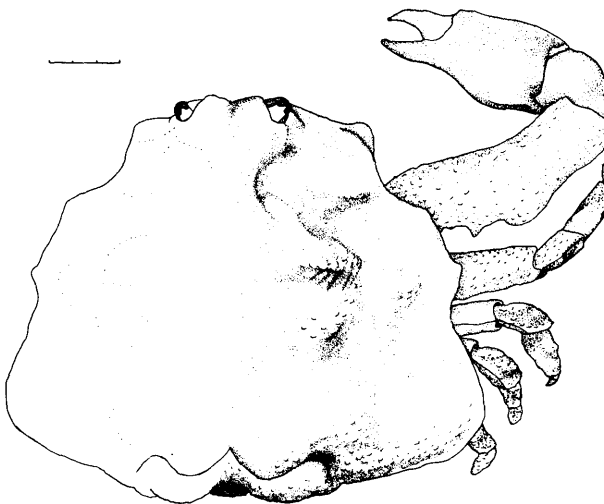


Fig. 218. *Speloeophorus nodosus* (Bell). Animal in dorsal view, legs of left side not shown, 3 mm indicated (from Williams 1965).

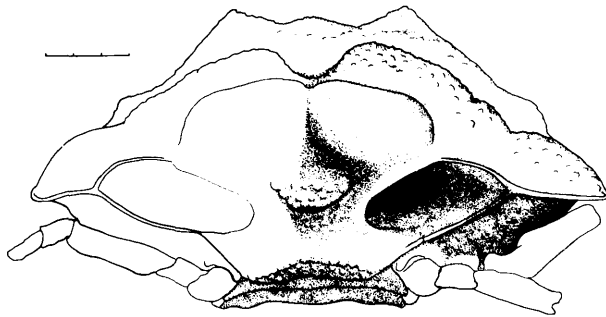


Fig. 219. *Speloeophorus nodosus* (Bell). Animal in posterior view, 3 mm indicated (from Williams 1965).

of green hue; fingers dull white with reddish and whitish spots; eyes not distinguishable from rest of body; underparts dirty white, abdomen green.

Male, bluish purple.

Habitat.—Among rocks; 2.7 to 18.3 m.

Type-locality.—Unknown.

Known range.—Florida; West Indies.

Remarks.—This species is rare in the northern part of its range and was reported by Pearse and Williams (1951) from reefs off Beaufort Inlet, N. C. The species readily plays dead when brought on deck.

Ovigerous females are known from North Carolina in April and Florida in July.

Speloeophorus pontifer (Stimpson)

Figs. 220–221

Lithadia pontifera Stimpson 1871b:115.

Speloeophorus pontifera.—Hay and Shore 1918:425, pl. 32, fig 5.

Speloeophorus pontifer.—Rathbun 1937:144, pl. 39, figs. 1–3.—Williams 1965:149, figs. 125–126.—Powers 1977:36.

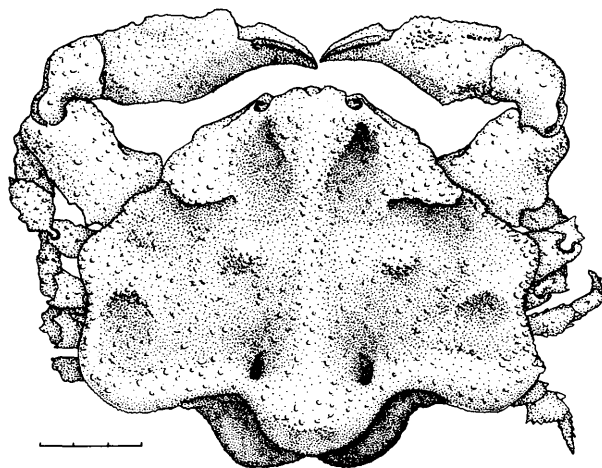


Fig. 220. *Speloeophorus pontifer* (Stimpson). Female in dorsal view, 3 mm indicated (from Williams 1965).

Recognition characters.—Carapace angular, roughly trefoil shaped, from $\frac{1}{6}$ to $\frac{1}{3}$ wider than long; surface granulate, uneven. Lateral margin of each side extended into broad wing projecting over bases of legs; anterolateral margins concave, with notch near middle; posterolateral margins broad, with deep rounded cavity to each side of intestinal region, extending toward much smaller pit on dorsal surface at side of cardiac region, narrow suture connecting cavity and pit of each side. Front narrow, produced, upturned, and with deep median sinus. Orbits small. Middorsal ridge extending from front almost to posterior margin, interrupted in middle of carapace; branchial region on each side with prominent elevation more or less divided into 2 parts, one connected by ridge to anterior angle of lateral wing, other similarly connected to posterior angle. Hepatic region small, slightly elevated; pterygostomial region prominent, with conical downward-pointing eminence visible from above.

Chelipeds of moderate size, somewhat crested; merus with 2 large triangular teeth on outer margin; fingers slender and curved. Walking legs granulate and tuberculate.

Abdomen tuberculate; segments 3 to 5 only partially fused; sixth segment with sharp backward-pointing, proximal spine.

Measurements in mm.—Carapace: male, length 6, width 8; female, length 10, width 13.

Variation.—This small species apparently attains a width of about 15 mm, and is extremely variable. The ridges and elevations of the dorsal surface may be sharp and conspicuous or low and rounded; the lateral angles of the lateral wings of the carapace may be produced or rounded off. The female is not so wide in proportion to length as the male, and is somewhat tumid on the outer posterior part of the lateral wings.

Color.—Pale red in middle, remainder white (von Martens, et al. in Rathbun 1937).

Habitat.—Low tide to 229 m.

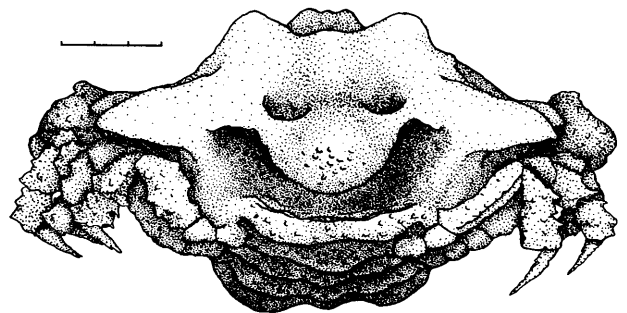


Fig. 221. *Speloeophorus pontifer* (Stimpson). Female in posterior view, 3 mm indicated (from Williams 1965).

Type-locality.—Barbados.

Known range.—Southeast of Cape Lookout and off Beaufort, N.C., to west Florida; West Indies to Barbados.

Subfamily Iliinae

Carapace almost hemispherical, surface only slightly uneven. So-called frontal teeth often being well-developed inner orbital angles. A median frontal tooth often present. Infraorbital lobe seldom well developed, roof of efferent branchial channel usually reaching same level. Epistome usually reduced. Margins of mouth and pterygostomian region in same transverse plane. First abdominal segment in female often under carapace (Rathbun 1937, for Philyrinae).

Myopsis Stimpson 1871

Rathbun 1937:164.

Myopsis quinquespinosa Stimpson

Fig. 222

Myopsis quinquespinosa Stimpson 1871:157.—Rathbun 1937:164, pl. 46, figs. 1–3.—Chace 1940:24.—Williams, McCloskey, and Gray 1968:46, fig. 4.—W. E. Pequegnat 1970:179.—Felder 1973:39, pl. 5, fig. 5.—Powers 1977:38.

Recognition characters.—Body and appendages granulate except dactyls of legs; carapace sub-spherical, a little longer than wide, narrowed anteriorly; front subacutely bidentate, elevated, anterior extremity of septa of branchial channels not extending beyond orbits; 5 posterior spines, median spine intestinal, intermediate pair marginal (equally long and more evenly conical in adult), outer smaller pair on branchial region over insertion of last legs with strongly upturned tip; tubercle at middle of lateral margin, another on hepatic region and between these a small granulated tubercle behind hepatic suture; hepatic region slightly swollen, cervical suture partly defined at hepatic region; cardiac and intestinal regions defined by faint furrows on either side.

Chelipeds very long and slender, densely granulate; merus longer than carapace exclusive of spine; palm broader than thick, upper face nearly 3 times as long as wide; fingers longer than palm, armed with minute acute teeth of variable size. Walking legs cylindrical and microscopically granulate.

Abdomen of male with segments 3–6 fused.

Measurements in mm.—Carapace: male, length exclusive of median spine 69, including median spine 73, width 68; ovigerous female, length including median spine 49, width 45.

Variation.—Granules on the body vary in size and the median posterior spine is relatively longest in immature specimens; the posterolateral spines occasionally exceed the other posterior spines in length (Rathbun 1937).

Color.—Buff to yellowish white with buff yellow to pinkish tint on legs, front between eyes darker, white beneath (Henderson and Schmitt in Rathbun 1937).

Habitat.—84 to 521 m, rarely to 1048 m (Rathbun 1937). Williams, et al. (1968) reported the species to occur mainly at depths of 120 to 160 m along the edge of the continental shelf south of Cape Hatteras and W. E. Pequegnat (1970) found it mainly between 183 and 210 m in the Gulf of Mexico, noting that it was recorded at greater depths near islands.

Type-locality.—Tennessee Reef, Florida Keys.

Known range.—South of Martha's Vineyard, through Gulf of Mexico and Caribbean Sea to Surinam.

Remarks.—Ovigerous females are known throughout the year from various parts of the range: February, Bahamas; March to May, Cuba, Florida and Panama; June, Honduras; July, North Carolina and Florida; September, Colombia and Venezuela; October, NE Gulf of Mexico; December, South Carolina and Alabama.

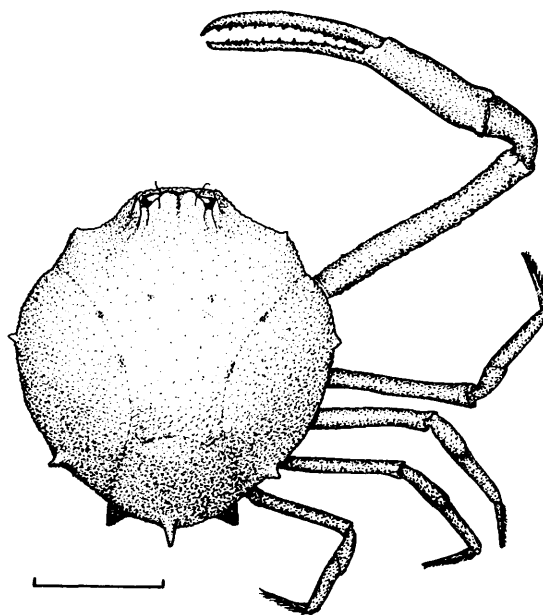


Fig. 222. *Myopsis quinquespinosa* Stimpson. Female in dorsal view, legs of left side not shown, 1 cm indicated (from Williams, et al. 1968).

Genus *Persephona* Leach 1817

Rathbun 1937:151.—Hemming 1958b:18.

Persephona mediterranea (Herbst 1794)

(Purse crab)

Fig. 223

- Cancer mediterraneus* Herbst 1794:150, pl. 37, fig. 2.
Leucosia mediterranea Lichtenstein 1815:142.
Guaia punctata.—H. Milne Edwards 1837:127.—
 Gibbes 1850:185.—Desbonne 1867:53 (in part).
Persephona punctata.—Stimpson 1859:70.—Coues
 1871:123.—Rathbun 1901:97.—Hay and Shore
 1918:423, pl. 32, fig. 9 (part of synonymy per-
 taining to northern species).—Dragovich and
 Kelly 1964:82.—Dudley and Judy 1971:9.
Persephone punctata.—Kingsley 1878c:324 [9].—
 1880:403.—Smith 1884:349.—1887:637 [33].
Persephona punctata aquilonaris Rathbun 1933a:
 184.—1937:154, pl. 42, figs. 6–7.—Behre 1950:
 23.—Hildebrand 1954:267.—Holthuis 1959:
 183 (part giving distribution of subspecies).—
 Williams 1965:150, fig. 127.
Persephona aquilonaris.—Guinot-Dumortier 1959:
 429, figs. 7, 9.—Tabb and Manning 1961:
 600.—Fausto-Filho 1968:44.—Rouse 1970:142.
 —Coelho and Ramos 1972:183.—Williams
 1974c:24, fig. 65.
Persephona mediterranea.—Guinot-Dumortier 1959:

429, 433.—Grizzle 1974:135.—Williams and
 Wigley 1977:10.—Powers 1977:39.

Recognition characters.—Carapace hemispherical, thickly strewn dorsally and laterally with granules of various sizes, and with 3 sharp, recurved spines, 1 at each end of posterior margin and 1 median just above posterior margin. Front narrow, broadly bidentate, produced and elevated, and with dentiform angles of branchial channels projecting slightly beyond it. Anterior and lateral regions bounded externally by row of beadlike granules broken anteriorly by single tubercle of larger size, and posteriorly extending to point nearly opposite termination of posterior margin.

Chelipeds subcylindrical in adult male, approximately 1.5 times as long as carapace; merus with many large tubercles; carpus and chela nearly smooth except on margins; chela somewhat flat and dilated; fingers weak.

Measurements in mm.—Carapace: male, length excluding posterior spine 60, width 58; ovigerous female, length including posterior spine 34, width 30.

Color.—Gray to grayish brown, with darker brownish irregular spots or marmorations; granules white or tinged with red.

Habitat.—This crab is sometimes taken in otter trawls but usually by dredging in shelly mud in relatively shallow water; 3.6 to 55 m.

Type-locality.—Erroneously, Mediterranean Sea.

Known range.—New Jersey through Gulf of Mexico and Caribbean Sea to Santa Catarina, Brazil.

Remarks.—Guinot-Dumortier (1959) pointed out that Rathbun's *Persephona punctata aquilonaris* is specifically distinct from her *P. p. punctata*, and that geographic ranges of the two overlap widely. According to Guinot-Dumortier, *P. punctata* has never been taken in North America, ranging from Panama (Colon, Limon Bay) through the Antilles, French Guiana to Brazil (São Paulo, see Coelho and Ramos 1972). Almost in an aside at the end of her discussion, Guinot-Dumortier pointed out that the type of the crab in the Berlin Museum represented by Herbst (1794:150, pl. 37, fig. 2) as *Cancer mediterraneus* has the characters found in *P. aquilonaris*. Both shape and spotted coloration leave no doubt of this. Although inappropriately named for a mistaken locality, the name *P. mediterranea* must stand.

The species is occasionally abundant in colonies. The purselike receptacle formed by the enormously enlarged penultimate segment of the abdomen in the female may be found filled with eggs at almost any time during spring and summer in the Carolinas. Otherwise, ovigerous females are known from Florida in February (Rouse 1970),

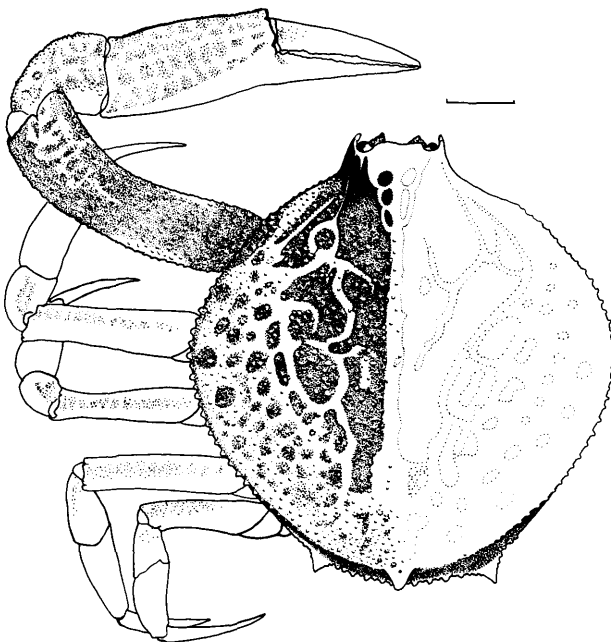


Fig. 223. *Persephona mediterranea* (Herbst). Animal in dorsal view, detail of left side shown, 5 mm indicated (from Williams 1965).

April and July, Texas in May and September, and French Guiana in September.

Subfamily Leucosiinae

Fingers slender, almost same diameter from base to near tip, either much longer than palm or, if shorter, of filiform slenderness; either opening and closing in vertical plane or, if in a nearly horizontal plane, tip of dactyl movable through an arc of about 120°; palms either short, swollen and subglobular, or tapering-cylindrical with swollen base always much broader than at origin of fingers distally (Rathbun 1937).

Genus *Callidactylus* Stimpson 1871

Rathbun 1937:192.

Callidactylus asper Stimpson

Fig. 224

Callidactylus asper Stimpson 1871:158.—Rathbun 1937:193, pl. 58, figs. 1–3.—Williams, McCloskey, and Gray 1968:48, fig. 5.—Coelho and Ramos 1972:184.—Powers 1977:37.

Recognition characters.—Carapace rounded, regularly convex except near anterior margin; upper surface ornamented with scattered, prominent granules or short capitate spinules becoming less prominent and grading into granules posteriorly; furnished with 11 or more rather blunt spines, 4 on anterior half, 7 on posterior half (3 in midline, 2 on posterior margin and 2 on posterolateral margins). Front short, orbit longitudinal with 3 distinct sutures on outer side extending to base of orbital tube; pterygostomian channel tridentate anteriorly and exceeding orbit. Hepatic region well defined, protuberant, toothed, surrounded by depressions and with strong toothlike eminence on its posterior part. External maxillipeds sharply granulated; exognath with convex lateral margin; endognath with lateral surface of merus concave, in female with row of strong setae on submesial longitudinal ridge of ischium arching over smooth channel anterior to brood chamber under abdomen lacking in male.

Chelipeds with hand longer than merus; palm short, pyriform, much swollen within proximally and somewhat twisted so that fingers move in oblique plane; fingers longer than palm, thin; delicate, laminate, curving upward and inward toward crossed tips, serrate on outer edge and armed on opposed edges with numerous needle-shaped teeth. Walking legs almost naked; propodi com-

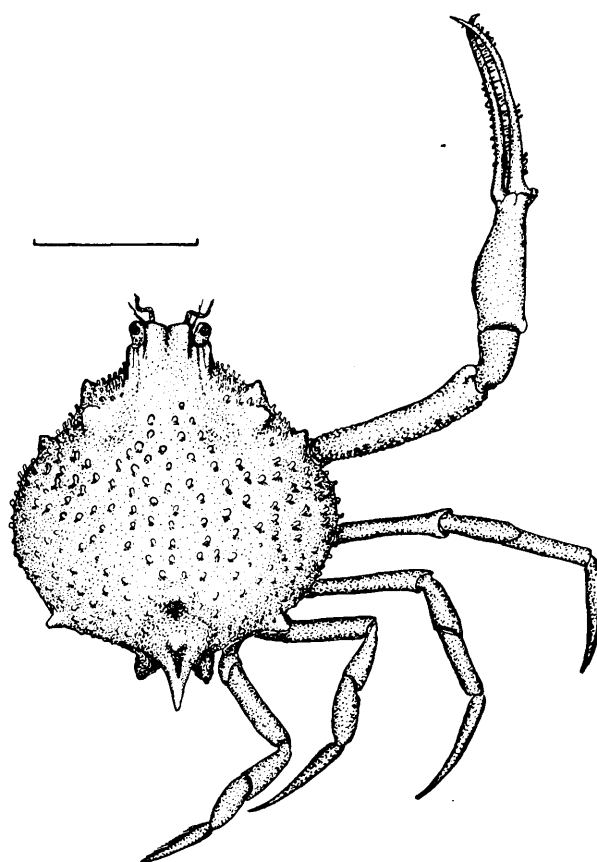


Fig. 224. *Callidactylus asper* Stimpson. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams, et al. 1968).

pressed with moderate laminate crests above and below; dactyls of first 3 pairs 3-edged, of last pair 2-edged and shorter and broader than others.

Abdomen of male with segments 3–5 fused; female with segments 4–6 fused, smooth and glossy around middle but a transverse tuberculate ridge on fourth and sparse granules on sixth segments; telson concave.

Measurements in mm.—Carapace: male, length 13.2, width 11; female, length 17.9, width 15.5 (Rathbun 1937).

Habitat.—Calcareous algae, sand and organic bottom, 27 to 393 m (Coelho and Ramos 1972).

Known range.—S of Cape Lookout, N. C. (Williams, et al. 1968), through SE Gulf of Mexico to Panama and southeastward to Alagoas, Brazil (Coelho and Ramos 1972).

Remarks.—Ovigerous females are known in February from Florida, March from Surinam, and October from Panama and Venezuela.

Genus *Iliacantha* Stimpson 1871

Rathbun 1937:183.

Key to Species in the Carolinas

1. Fingers about half as long as palm of hand *I. intermedia*
 Fingers longer than palm of hand. *I. subglobosa*

Iliacantha intermedia Miers

Fig. 225

Iliacantha intermedia Miers 1886:302, pl. 26, figs. 3, 3a.—Hay and Shore 1918:424, pl. 32, fig. 3.—Rathbun 1937:186, pl. 54, figs. 1–2.—Williams 1965:151, fig. 129.—Coelho and Ramos 1972:184.—Fausto-Filho 1975:81.—Powers 1977:37.

Recognition characters.—Similar to *I. subglobosa*, but carapace more coarsely granulate; posterior spines shorter, flattened, triangular, connectd by prominent line of granules. Front grooved above, broadly notched anteriorly, and with angles of branchial channels extending beyond it. Margin of carapace distinctly granulate; intestinal region not protuberant above median spine.

Chelipeds slender, nearly as long as carapace; merus cylindrical and granulate with coarser granulations proximally; hand smooth, somewhat inflated proximally but tapering to slender fingers; fingers about half as long as palm, incurved at tip, and denticulate on opposed margins. Male abdomen widened at convex-sided sixth segment.

Measurements in mm.—Male: carapace length 16, width 12; chela, length 13, fingers 4. Female: carapace length 27, width 21.

Color.—Gray without marking of any kind.

Habitat.—10 to 329 m.

Type-locality.—Bahia, Brazil.

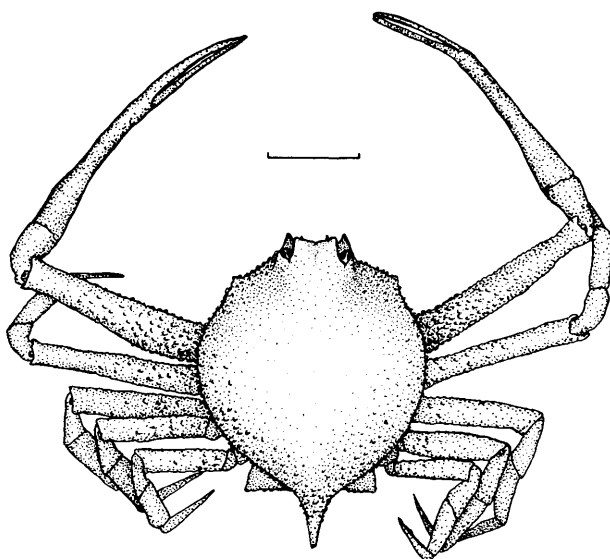


Fig. 225. *Iliacantha intermedia* Miers. Male in dorsal view, 5 mm indicated (from Williams 1965).

Known range.—Off Beaufort, N. C., to NW Florida; St. Thomas, V. I.; Venezuela; Ceará and Bahia, Brazil.

Remarks.—The young of this species and *Persephona mediterranea* have a close resemblance.

Iliacantha subglobosa Stimpson

Fig. 226

Iliacantha subglobosa Stimpson 1871a:155.—Hay and Shore 1918:424, pl. 32, fig. 2.—Rathbun 1937:185, pl. 53, figs. 1–2.—Williams 1965:150, fig. 128.—W. E. Pequegnat 1970:179.—Coelho and Ramos 1972:184.—Powers 1977:38.

Recognition characters.—Carapace orbicular, smoothly and evenly convex, finely granulate, unarmed except posterior border with 3 spines; lateral spines subtriangular, blunt; median one higher, longer, conical, and curved upward. Front grooved above, broadly notched anteriorly and with angles of branchial channels extending beyond it. Margin of carapace distinct, somewhat acute on hepatic region and anterior portion of branchial region, indistinct beyond; hepatic region swollen; intestinal region slightly protuberant above base of median spine.

Chelipeds 2.5 times as long as carapace, excluding spine, finely granulate; merus more sharply

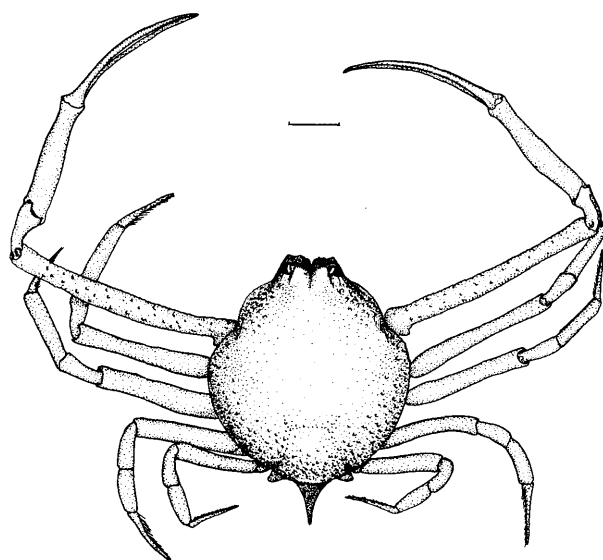


Fig. 226. *Iliacantha subglobosa* Stimpson. Female in dorsal view, 5 mm indicated (from Williams 1965).

granulate than carpus and hand; fingers slender, longer than palm, denticulate on opposed margins. Walking legs slender, smooth; merus as long as 3 terminal articles; dactyls grooved, and with 2 fringes of hair on upper and posterior surfaces. Male abdomen gradually tapering from fifth to seventh segment.

Measurements in mm.—Male: carapace length 21, width 16; chela, length 22, fingers 13.

Habitat.—16 to 915 m (Wenner and Read 1982).

Type-localities.—Three stations in Florida reefs, 73–146 m.

Known range.—Off Cape Hatteras, N. C., to northwest Florida; through eastern Gulf of Mexico and Caribbean Sea south to Alagoas, Brazil.

Remarks.—Ovigerous females have been taken in April, June and July off Florida, May off Colombia, September off Colombia and Venezuela, and in October off Venezuela.

Section Oxyrhyncha

Carapace more or less narrowed in front and usually produced to form a rostrum; branchial re-

gions considerably developed, hepatic regions small. Epistome usually large; buccal cavity quadrate, with anterior margin usually straight. Gills almost always 9 in number on each side; efferent channels opening at sides of endostome or palate. Antennules longitudinally folded (Rathbun 1925).

Superfamily Majoidea

Family Majidae

Chelipeds especially mobile, usually about same size as other legs, fingers straight. Second article of antenna well developed, generally fused with epistome and often with front. Orbits generally more or less incomplete. Hooked hairs almost always present. Male openings coxal (Borradaile 1907). Palp of external maxilliped articulated either at summit or at anterointernal angle of merus (Alcock 1895). First pleopod in male greatly exceeding second pleopod in length (Garth 1958).

Key to Subfamilies

(Modified after Garth 1958)

1. Eyes either without orbits, or with commencing orbits 2
 Eyes with complete or nearly complete orbits; basal antennal article broad, expanded to form floor to orbit **Mithracinae**
2. Male abdomen terminally broadened, terminal segment subquadrate and inserted deeply into sixth segment; male first pleopod longitudinally grooved, with rows of filamentous setae on either side of groove.
 **Oregoniinae**
 Male abdomen not terminally broadened, terminal segment subtriangular and not inserted deeply into sixth segment; male first pleopod exceedingly varied, but not as above. 3
3. Eyes without orbits; eyestalks generally long, non retractile, retractile against sides of carapace, or against acute postocular spine affording no concealment; basal (fused) antennal article extremely slender and unusually long **Inachinae**
 Eyes with commencing orbits; basal (fused) antennal article not extremely slender 4
4. Eyes with cupped postocular process into which eye retracts, and with supraocular eave or spine. **Pisinae**
 Eyes lacking postocular cup, but with tubelike housing 5
5. Eyestalks long; orbit partly protected by hornlike supraocular spine or eave, strong postocular tooth, or both; body truncate in front **Tychinae**
 Eyestalks short, relatively immobile and either concealed by supraocular spine or sunk in sides of rostrum; basal antennal article truncate-triangular; body not truncate in front **Epialtinae**

Subfamily Inachinae

Eyes without orbits; eyestalks generally long, either nonretractile, retractile against sides of carapace, or against an acute postocular spine. Basal

article of antenna extremely slender throughout its extent and unusually long. First pleopod not very stout, straight or curved, apically tapering, but apex most varying (hairy; spinose, naked, etc.; acute, blunt, bifid, etc.); second pleopod short (Garth 1958).

Key to Genera of Inachinae

(Modified after Garth 1958)

1. Seven free abdominal segments in both sexes, rostrum double. *Anomalothir*
Six free abdominal segments in male, 5 in female. 2
2. Rostrum double 3
Rostrum single 7
3. Interantennular spine present and conspicuous 4
Interantennular spine absent or inconspicuous *Collodes*
4. Eyestalks slender; carapace with 3 erect median spines *Arachnopsis*
Eyestalks not slender 5
5. Seven long, capitate dorsal spines *Aepinus*
Fewer than 7 long, capitate dorsal spines 6
6. Spine of basal antennal article equally advanced with front. . *Euprognatha*
Spine of basal antennal article not equally advanced with front *Batrachonotus*
7. Merus of outer maxilliped as broad as ischium, palp of moderate size . . 8
Merus of outer maxilliped often narrower than ischium, palp large and coarse 10
8. Postorbital tooth large, curving around side of eye *Pyromaia*
Postorbital tooth small, or if large not curving around eye 9
9. Carapace rough with spines and tubercles; legs not subprehensile *Anasimus*
Carapace smooth; legs subprehensile. *Inachoides*
10. Rostrum considerably less than postrostral length; basal antennal article often longitudinally sulcate *Podochela*
Rostrum approaching or surpassing postrostral length; basal antennal article not longitudinally sulcate 11
11. Carapace nodulose; merus of walking legs with long distal spine; rostrum sparsely spined *Metoporphaphis*
Carapace smooth; merus of walking legs with distal spine no longer than other spines; rostrum multispinose. *Stenorhynchus*

Genus *Aepinus* Rathbun

Rathbun 1925:92.

***Aepinus septemspinosus* (A. Milne Edwards)**

Figs. 227, 241c

Apocremus septemspinosus A. Milne Edwards 1879:185, pl. 35, figs. 5–5d.

Aepinus septemspinosus.—Rathbun 1925:92, text figs. 28–29, pl. 32, figs. 3, 4; pl. 219, figs. 1–3.—Coelho and Ramos 1972:207.—Powers 1977:43.

Recognition characters.—Carapace triangular in front half, broadly semicircular in posterior half; dorsal aspect bearing 7 capitate spines, 1 gastric, 1 cardiac, 2 branchial (1 on each side), 2 supraorbital (1 on each side, shorter), 1 directed obliquely backward on first abdominal segment; scattered tubercles; gastric region narrow, high, and with triangular laminate projection on each anterolateral slope with intervening tubercles; hepatic region steeply sloping to laminate marginal tooth preceded by triangular pterygostomial tooth. Rostrum short, formed of 2 shallowly rounded, nar-

rowly separated lobes, tuft of hooked hairs at base. Triangular tooth on partition between antennules. Eyes short, flat above, tubercle situated anteriorly in corneal emargination. Postocular tooth small, easily broken, close to carapace behind orbit. Basal antennal article deep, its prominent ventral crest bifurcating near anterior end with longer outer branch continuing to epistome and terminating in a lobe.

Chelipeds small, granulations trending in longitudinal lines; palm narrow, male with fingers slightly gaping proximally. Sternum of male with prominent crest between coxae of chelipeds and minor crests converging from walking legs, less-developed granulate line in juveniles. Abdomen of adult females with terminal segment coarsely pitted or tuberculate, with smooth median carina, younger females granulate.

Measurements in mm.—Carapace: male, length 6.0, width 7.1; ovigerous female, length 5.5, width 7.0.

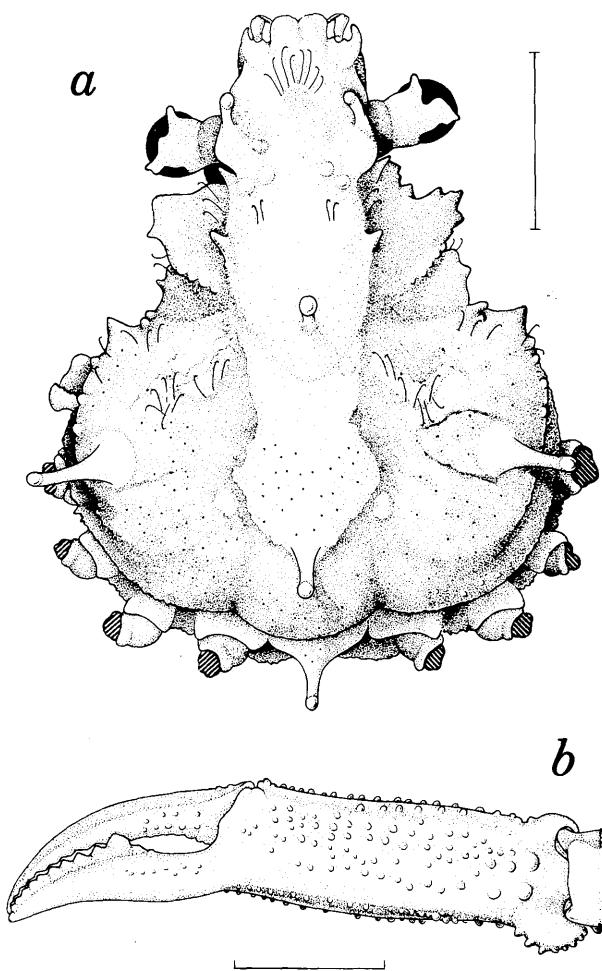


Fig. 227. *Aepinus septemspinosus* (A. Milne Edwards). a, Body of male in dorsal view; b, left chela, external view; a, 2 mm; b, 1 mm indicated (USNM 24150).

Variation.—Specimens from the Antilles are more delicate than those from the Gulf of Mexico and North Carolina, the former having more slender and divergent spines. Beside other variations given above, the supraorbital spines vary in direction.

Habitat.—Generally on calcareous algae, occasionally on detritus or mud bottom, 12.8 to 85 m (Coelho and Ramos 1972).

Type-locality.—Florida Strait, 24°55'N, 83°25'W, 67.7 m.

Known range.—S Cape Lookout, N. C., 34°10'N, 76°10'W; SW Cape San Blas, Fla., and Bahama Banks to Bahia, Brazil.

Remarks.—Only one specimen (an empty exoskeleton, UNC-IMS 2414) is known from north of the Florida Straits; it is one of the largest and most heavily spined males seen. Ovigerous females are known in February from off Cape San Blas, Fla., Vieques [P. R.], and St. Thomas.

Genus *Anasimus* Milne Edwards 1880

Rathbun 1925:64.

Anasimus latus Rathbun

Figs. 228, 241n

Anasimus latus Rathbun 1894:58.—1925:65, pl. 214.—Guinot-Dumortier 1960:177, fig. 18a, b.—Williams 1965:240, fig. 217.—Coelho and Ramos 1972:209.—Felder 1973:49, pl. 7, fig. 5.—Powers 1977:43.

Recognition characters.—Carapace broadly ovate, elevated on median line, posterior half semicircular, anterior half broadly triangular, surface covered with unequal granules. Carapace with median row of spines, 2 gastric (posterior one larger), large cardiac, 1 small backward-pointing intestinal, and long acuminate backward-projecting spine at distal end of first abdominal segment; anterior gastric spine one of transverse row of about 5; branchial region with 3 small spines or tubercles in triangular arrangement. Three anterolateral spines, 1 hepatic and 2 branchial above base of cheliped. Rostrum short, medially carinate, broadly triangular at base, ending in short, sharp, upturned spine. Eyes large; prominent supraorbital spines separated by depression, postorbital spines long, exceeding eye in large specimens. Antenna short, slightly exceeding rostrum, basal article with terminal spine and stout spine pointing downward and forward in front of eye. Pterygostomian region with row of spines and spinules continued to antennal

segment including long spine at angle of buccal cavity. Sternum of male coarsely granulate.

Chelipeds of male more than twice length of carapace, granulate; merus cylindrical; palm swollen, shorter than fingers; fingers slender, curved inward, gaping at base only, finely and evenly toothed except for larger basal tooth on dactyl. Female with chelipeds a little longer than carapace but smaller than in male, fingers not gaping. Walking legs long, slender, cylindrical, roughened except on dactyl, with numerous short, stout, appressed spinules; propodi and dactyls with double fringe of hair.

Abdomen of male with 6, female with 5 free segments; female with median tubercle on third and fourth segments.

Measurements in mm.—Male: carapace length 34, width 32; length of cheliped 83, of first walking leg 145. Ovigerous female: carapace length 25, width 25.1.

Variation.—Adults are relatively broader than the young whose rostrum and dorsal spines are relatively longer. There is some variation in count of spines but the basic pattern is recognizable. The postorbital spines are very small, pointing directly outward, being little more than tubercles in specimens 9 mm long or less.

Color.—Recently preserved specimens show dark reddish or brown rings on the legs (Holthuis 1959).

Habitat.—This species has been taken from coarse sand, coral, coral sand, and mud and shell bottom; 27 to 274 m (Wenner and Read 1982).

Type-locality.—Gulf of Mexico, east of Delta of Mississippi River, 29°14'30"N, 88°09'30"W, 124.4 m.

Known range.—Off Cape Lookout, N. C., through

Gulf of Mexico (Felder 1973) to Amapá, Brazil (Coelho and Ramos 1972).

Remarks.—Ovigerous females have been recorded from the northern Gulf of Mexico and Florida in all seasons of the year, from North Carolina in June (Williams 1965) and November (Sandifer and Van Engel 1972), the Guianas from April to August (Holthuis 1959 and USNM), and Colombia in November-December (USNM).

Sandifer and Van Engel (1972) described development of hatching eggs taken from an ovigerous female off Cape Lookout, N. C., in November. The eggs were hatched at 21°–25°C and larvae reared in 32‰ salinity sea water on a diet of *Artemia* nauplii. The larvae hatched as pre-zoeae in transit to the laboratory and most of them died during this stage. Survivors had become first zoeae by the time they were segregated into culture dishes and fed. Only a few of these molted to second stage, and two molted to megalopa after 21 days. In addition to describing development of this species, the authors reviewed literature on rearing majid crabs.

Boschma (1968) described a rhizocephalan parasite from a specimen of *A. latus* caught off Surinam.

Genus *Anomalothir* Miers 1879

Rathbun 1925:23.

Anomalothir furcillatus (Stimpson)

Figs. 229, 241a

Anomalopus furcillatus Stimpson 1871a:125.

Anomalothir furcillatus.—Rathbun 1925:24, text-fig. 6, pl. 8, fig. 2; pl. 9, fig. 2; pl. 206.—Williams 1965:236, fig. 312.—Powers 1977:43.

Recognition characters.—Carapace much elongated, almost subcylindrical, pubescent, with regularly placed tubercles. Rostrum long, from 0.66 to 1.25 times as long as remainder of carapace, bifurcated, horns contiguous for half or more of length, slightly divergent. Eyes without orbits; pre- and postorbital spines small, acute. Antenna visible in dorsal view, basal article narrow. Merus of maxilliped without notch at inner angle where palp inserts.

Chelipeds in adults longer than carapace; merus subcylindrical, with row of small spines below and less distinct row above; carpus with 3 spines on outer surface; palm unarmed, elongate; fingers short, stout, less gaping in male than in female. Walking legs pubescent; first 2 pairs long, slender; third and

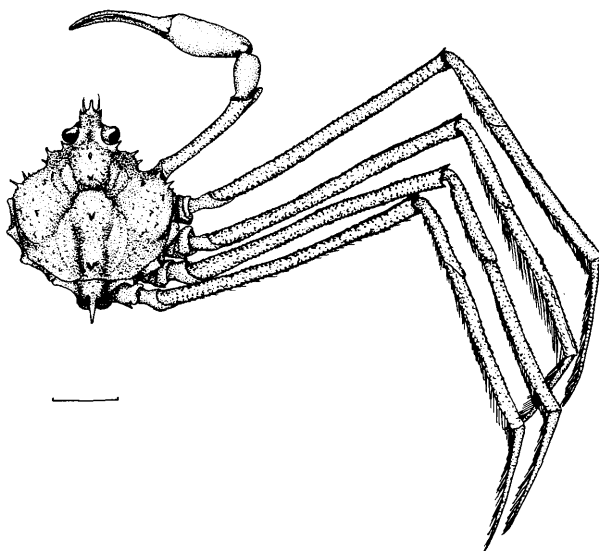


Fig. 228. *Anasimus latus* Rathbun. Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

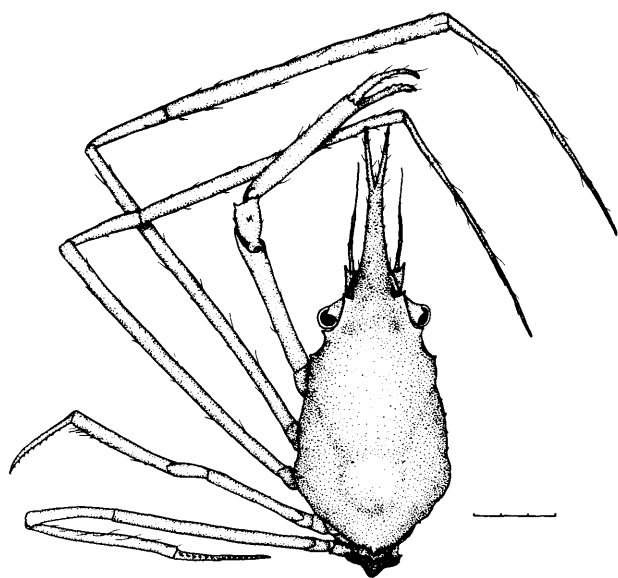


Fig. 229. *Anomalothir furcillatus* (Stimpson). Female in dorsal view, legs of right side not shown, 3 mm indicated (from Williams 1965).

fourth pairs shorter, prehensile, with dactyls spinose on inner border; third pair shortest, merus with 2 or 3 strong hooked spines beneath, propodus and curved dactyl of about equal length; fourth pair intermediate in length, nearly straight, with propodus longer than dactyl.

Abdomen of both sexes with 7 free segments.

Measurements in mm.—Carapace: male, length including rostrum 18, length rostrum to base movable antennal articles 7.5 (br.), width 5.6; female, length including rostrum 27.6, length rostrum to base movable antennal articles 15.0, width 6.6.

Color.—Light orange yellow; palms much deeper color (Henderson in Rathbun 1925).

Habitat.—Rathbun (1925) listed this form from sand, broken shell, pebbled and rocky bottom; 55 to 480 m.

Type-locality.—Off "The Samboes" [southern Florida], 225 m.

Known range.—Off Cape Lookout, N. C., through eastern Gulf of Mexico and West Indies to Grenada.

Remarks.—Though the depth range of this species is usually beyond the 200-m mark, it may occur in shallower water in the Carolinas. Ovigerous females are known from the northeastern Gulf of Mexico in March.

Genus *Arachnopsis* Stimpson 1871

Rathbun 1925:89.

Arachnopsis filipes Stimpson

Figs. 230, 241d

Arachnopsis filipes Stimpson 1871a:121.—Rathbun 1925:89, text-figs. 26, 27; pl. 32, figs. 1, 2; pl. 219, figs. 4, 5.—Williams, McCloskey, and Gray 1968:58.—Coelho and Ramos 1972:206.—Powers 1977:44.

Recognition characters.—Carapace oblong, rather narrow, somewhat truncate in front; smooth and glossy except for few hairs on anterolateral part of branchial and sides of frontal and gastric regions; dorsal aspect bearing 3 erect, slender, blunt spines, 1 gastric, 1 cardiac, and 1 on first abdominal segment; spinules and spiniform granules beneath subhepatic and pterygostomian regions; often finely denticulate along margins, lateral slopes of rostral horns, around orbits and postorbital spines. Rostrum short, formed of 2 triangular teeth widely separated at tips by shallow notch often disclosing point of interantennular spine in dorsal view. Eyes long, overreaching but capable of being drawn back beneath long postocular spine directed obliquely forward; orbital arch high, occasionally surmounted by tubercle or small spine. Basal antennal article with 2 spinulose crests on inferior surface meeting anteriorly, lateral crest continued back to angle of buccal area; small, sharp anterolateral spine directed obliquely forward with movable ar-

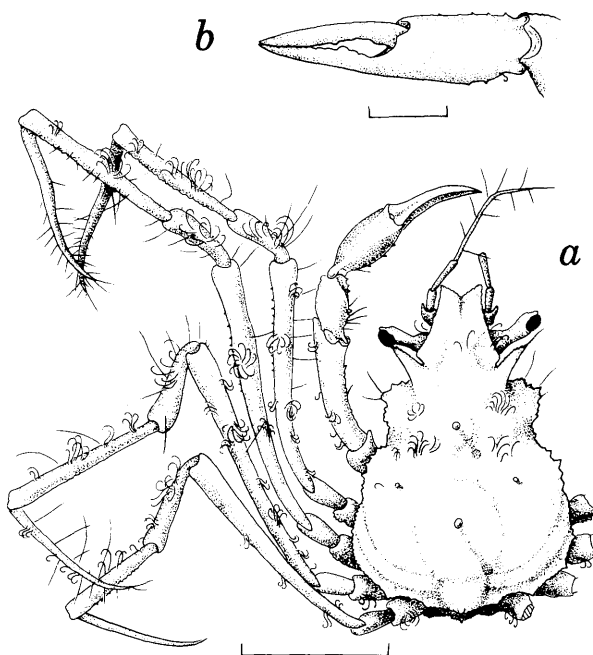


Fig. 230. *Arachnopsis filipes* Stimpson. a, Male in dorsal view, legs of right side not shown; b, left chela, external view; a, 3 mm; b, 1 mm indicated (USNM 18114).

ticle of antenna interposed between it and rostrum. Sternum, abdomen and maxillipeds granulate or spinose.

Chelipeds in male moderately enlarged, somewhat longer than carapace, curved; edges of ischium, merus and surface of carpus spinulose; propodus mainly smooth but sparse spinulation proximally, its upper and lower margins convex; fingers as long as palm, gaping except near tips; cutting edges toothed, largest tooth at middle of fixed finger, slightly smaller tooth preceding it on dactyl. Walking legs filiform, nearly equal in length.

Measurements in mm.—Carapace: male, length 7.9, width 5.1; female, length 7.5, width 5.1.

Variation.—A few specimens show a sometimes setose pair of tubercles or tiny clusters of tubercles in front of the gastric spines. Still fewer individuals have in addition a low median spine in front of the gastric spine as well as one between the cardiac spine and that on the first abdominal segment.

Habitat.—Rathbun (1925) reported the species from fine sand, shell, coral and sponge bottoms, Williams, et al. (1968) from a *Lithothamnion* reef near the edge of the continental shelf, and Coelho and Ramos (1972) from calcareous algae and sand; 27 to 238 m (rarely 366 m?).

Type-locality.—Off Conch, Carysfort and French reefs, Florida.

Known range.—SE Capes Hatteras and Lookout, N. C.; Gulf of Mexico off NW Florida; through West Indies to off Rio Grande do Norte, Brazil.

Remarks.—Mature females are common in collections studied but the only ovigerous one is a spiny variant from west of Puerto Rico in February. A number of specimens bear *Sacculina*.

In temperature tolerance experiments, specimens collected from an offshore reef southeast of Cape Lookout, N. C., in September and October died after 7 h of exposure to 4°C (F. J. and W. B. Vernberg 1970).

Genus *Batrachonotus* Stimpson 1871

Rathbun 1925:122.

Batrachonotus fragosus Stimpson

Figs. 231, 241e

Batrachonotus fragosus Stimpson 1871a:122.—Rathbun 1925:123, text-fig. 48, 1 pl. 39, figs. 1–2 (not *B. brasiliensis* Rathbun, pl. 39, figs. 3–4).—Williams 1965:238, fig. 214.—Powers 1977:44.

Recognition characters.—Male. Carapace triangular, broadly expanded behind; gastric, cardiac, and

branchial regions strongly protuberant, each surmounted by stout spine or large tubercle; intestinal region with 2 small tubercles just above posterior margin; hepatic region angular, approximating postorbital tooth. Cervical depressions deep and broad giving carapace superior outline much like frog's back. Rostrum short, formed of rounded lobes separated by shallow notch, scarcely projecting beyond antennular fossae, margin and supraorbital margin denticulate. Basal articles of antenna with dentate margins and small tooth at anterior extremity. Merus of outer maxilliped broad with prominent outer and inner anterior angles. Abdomen and sternum granulate except for smooth area between chelipeds; abdomen with 6 free segments, last 2 fused, proximal fixed segment with prominent median spine.

Chelipeds somewhat longer than carapace, spinulose; ischium with distal spine; hand slightly compressed; fingers nearly as long as palm, gaping nearly whole length, large tooth in middle of fixed finger. First pair of walking legs more than twice length of second pair, posterior pairs short.

Female. Carapace narrower behind and wider in front than male, tuberculation more uniform, spines less frequent. First walking leg little longer than second, approximately 1.5 times length of carapace. Abdomen tuberculate or granulate, with 5 free segments, last 3 fused.

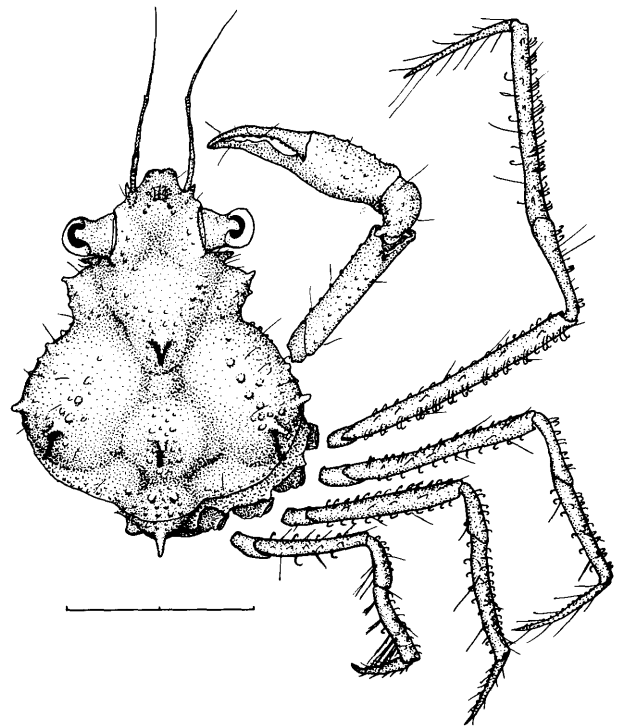


Fig. 231. *Batrachonotus fragosus* Stimpson. Animal in dorsal view, legs of right side shown in approximate position, legs of left side not shown, 2 mm indicated (from Williams 1965).

Measurements in mm.—Carapace: male and female, length 7, width 6.

Variation.—Rathbun (1925) stated that this species exhibits wide variations from the type. Some specimens have the elevated regions each surmounted by a spine, some have an abdominal spine, others, mainly females, are smoother, lacking even tubercles on the elevated regions.

Habitat.—The species has been reported from mud, sand of various grades, and broken-coral and shell bottoms; shore to 247 m (Wenner and Read 1982).

Type-locality.—South of Tortugas, [Fla.], 24°-36'40"N 80°02'20"W, 29.3 m.

Known range.—Cape Hatteras, N. C., to south-

ern and western Florida; West Indies to Barbados.

Remarks.—Coelho (1971) pointed out that *B. brasiliensis* Rathbun is a valid species which should not be synonymized with *B. fragosus*. The Brazilian species has a median tubercle (female) or spine (male) on the intestinal region but lacks a median spine on first abdominal segment.

Ovigerous *B. fragosus* are known from north-western Florida in January and Tortugas in June (USNM).

Genus *Collodes* Stimpson 1860

Rathbun 1925:105.

Key to Species

1. Carapace without median spines; basal antennal article coarsely dentate laterally *C. robustus*
- Carapace with median spines; basal antennal article spinulose laterally *C. trispinosus*

Collodes robustus Smith

Fig. 241g

Collodes depressus Smith 1881:414 (not *C. depressus* A. Milne Edwards 1878).

Collodes robustus Smith 1883:5.—Rathbun 1925:114, text-figs. 36–41, pl. 29.—Williams, McCloskey, and Gray, 1968:58.

Recognition characters.—Carapace ovate-triangular, thickly covered with granules except on gastric region. Larger than *C. trispinosus*, hepatic regions more prominent, median spines reduced to tubercles hardly larger than surrounding granules in adults. Rostrum wider than in *C. trispinosus*, its horns more widely separated at tips. Postorbital tooth broader than in *C. trispinosus*, slightly exceeding eyes in adults. Lateral margin of basal antennal article dentate; interantennular spine long and slender. Sternum of male coarsely granulate.

Chelipeds much as in *C. trispinosus*, a low tooth on dactyl opposite that on fixed finger. Remaining legs long and hairy.

Measurements in mm.—Carapace: male, length 27, width 21; ovigerous female, length 18.2, width 15.

Habitat.—Rathbun (1925) reported this species from bottoms ranging from soft sticky mud to coarse shell and sponge; 27 to 682 m.

Type-localities.—Twenty-one stations off Martha's Vineyard to off Chesapeake Bay, 1–2 to 285 m.

Known range.—North of Cape Cod, 42°12'N, 70°13'W, to southeast of Cape Lookout, N. C.

Remarks.—Williams and Wigley (1977) gave new distributional records from New England. Rathbun (1925), Williams, et al. (1968), and USNM records show ovigerous females off Virginia in March, off North Carolina in July, south of Martha's Vineyard in August–September, and off the mouth of Chesapeake Bay in October–November.

Collodes trispinosus Stimpson

Figs. 232, 241f

Collodes trispinosus Stimpson 1871a:120.—Rathbun 1925:107, text-figs. 32a, b; pl. 36, figs. 5–6.—Williams 1965:239, figs. 215, 223D.—Powers 1977:45.

Recognition characters.—Carapace ovate-triangular, covered with coarse granules except on front, anterior part of gastric region, and about bases of spines; single, slender, erect, capitate spine on gastric and cardiac regions, and first abdominal segment. Rostrum short, with 2 minute and usually well-separated horns. Eyes of moderate length, partially retractile; postorbital tooth slender, a granule on upper orbital border. Antenna with first movable article approximately as long as rostral horns; basal article of antenna twisted, with 4 or 5 spinules on outer border and with laminate crest on inner margin ending in large tooth; interantennular spine short. Merus of outer maxilliped obcordate, deeply cut on distal margin, strongly produced at inner and outer angles.

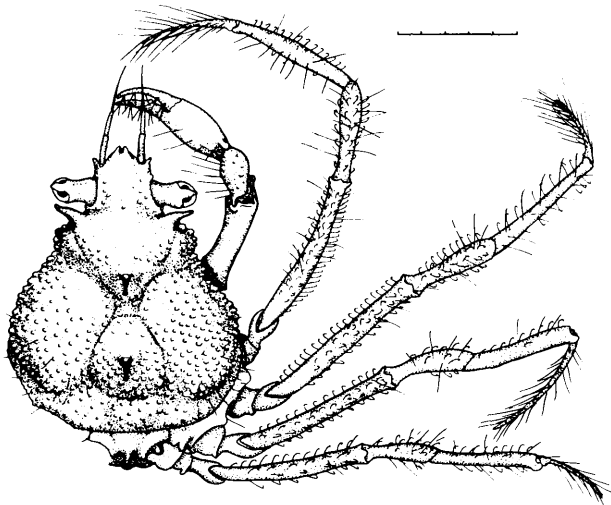


Fig. 232. *Collodes trispinosus* Stimpson. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

Chelipeds of male moderately stout, palm thick, smooth outside; surface of carpus and margins of merus and palm spinulose; fingers widely gaping, with triangular tooth near middle of fixed finger and low molariform tooth near base of dactyl. Walking legs long; first 2 pairs variably subequal; third and fourth pairs successively shorter; dactyls as long as propodi.

Measurements in mm.—Carapace: male, length 14, width 12; female, length 12, width 10.

Habitat.—Rathbun (1925) reported this species from gray sands of varying coarseness, broken shell, and gravel bottoms; 7.3 to 247 m (Wenner and Read 1982).

Type-locality.—Off the Quicksands, Carysfort Reef, and French Reef [Fla.], 62.1 to 91 m.

Known range.—Near Cape Hatteras, N. C., to south and west Florida near Apalachicola.

Remarks.—Rathbun (1925) reported ovigerous females from North Carolina in October, and they are known from Florida in March, June and July, and Georgia in June and July (USNM).

Genus *Euprognatha* Stimpson 1871

Rathbun 1925:95.

Euprognatha rastellifera Stimpson

Figs. 233, 241b

Euprognatha rastellifera Stimpson 1871a:123.—Hay and Shore 1918:454, pl. 37, fig. 7.—Coelho and Ramos 1972:207.

Euprognatha rastellifera marthae Rathbun 1925:96,

text-fig. 30, pl. 33; pl. 34, figs. 1–2; pl. 35, figs. 3–4; pl. 216.—Williams 1965:237, figs. 213, 223B.

Recognition characters.—Carapace pyriform, granulate, tubercle or short truncate spine on gastric and cardiac regions, each branchial region, and supraorbital margin. Rostrum short, with 2 small teeth or horns. Ocular peduncles short, with tubercle at emargination of cornea. Frontal teeth short, spiniform, or triangular. Postorbital projection dentiform, triangular, tapering to slender point. Obtuse antennal spines directed obliquely forward, approximately as advanced as front; interantennular spine inclined downward, equaling or surpassing front. Sides of hepatic and pterygostomian region with few small spines. Sternum granulate except for concave part between chelipeds.

Chelipeds approximately twice as long as carapace, granulate, margins spinous; hand swollen; fingers more than half length of palm, slightly gaping. Walking legs granulate, with tufts of curled setae and often small spines; first pair longest, others successively shorter.

Abdomen of males with 6, females with 5, free segments.

Measurements in mm.—Carapace: male, length 14.3, width 11.5; female, length 9.5, width 7.8.

Variation.—The spines of the carapace are often capitate. Rathbun (1925) divided the species *E. rastellifera* into a northern subspecies, *marthae* (ranging from Nantucket to southern Florida), and a southern or Caribbean subspecies, *acuta* (ranging from Cuba to Grenada and Barbados), with a region of intergradation in the Florida Keys. The southern form (*acuta*) has longer, sharper, and more slender spines than *marthae*, and a narrower, higher, and more closely and finely roughened carapace with regions more deeply separated. Likewise, the chelipeds have spines on the border of the merus well developed and legs more spinulose than in the northern form.

Rathbun pointed out that there is considerable overlap in distribution of these subspecies, listing *acuta* from as far north as Martha's Vineyard. Subspecific intergradation over such a broad range of latitude in this region of the western Atlantic seems unlikely. Rather, the variation may parallel that seen in *Callinectes sapidus* which is apparently a polymorphic species, responding perhaps to temperature by developing spines of longer mean length in tropical than in temperate waters.

Habitat.—The species has been reported from a variety of sandy and muddy bottoms; 25.6 to 708 m.

Type-locality.—Southwest of Martha's Vineyard, Mass., 40°N, 70°57'W, 155 m.

Known range.—Off Georges Bank (40°35'N,

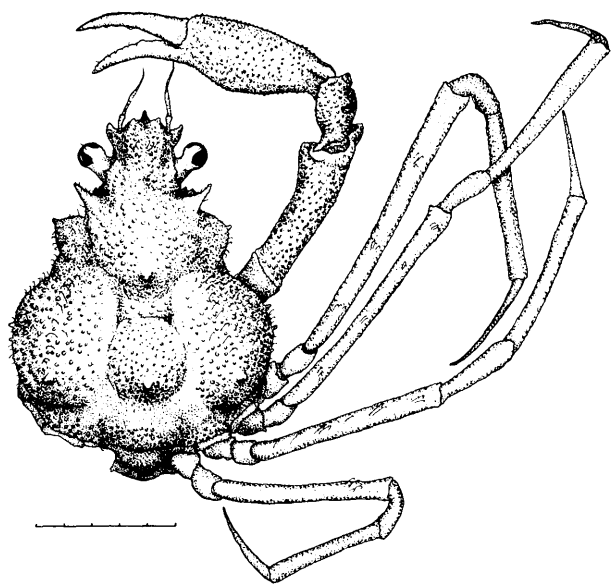


Fig. 233. *Euprognatha rastellifera* Stimpson. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

67°37'W) to São Paulo, Brazil (Coelho and Ramos 1972).

Remarks.—Ovigerous females are known virtually throughout the year: January and May off Cuba; February and June at Key West; March to June, and October off Chesapeake Bay; May off New Jersey; September off Long Island to Martha's Vineyard; and November off Georges Bank (USNM).

**Genus *Inachoides* H. Milne Edwards and Lucas
1842**

Garth 1958:95.

***Inachoides forceps* A. Milne Edwards**

Figs. 234, 240i

Inachoides forceps A. Milne Edwards 1879:199, pl. 33, figs. 4–4d.—Garth 1958:101.—Williams, McCloskey, and Gray 1968:60, 14.—Powers 1977:45.

Inachoides laevis.—Rathbun 1925:61 (part, the Atlantic specimens), text-fig. 17.

Recognition characters.—Carapace longer than broad, nearly smooth, regions protuberant and rounded; hepatic region produced to submarginal deflexed tubercle, branchial region with small tubercle on margin above base of cheliped. Rostrum tapering from triangular base to simple extremity of variable length. Supraorbital arch without sur-

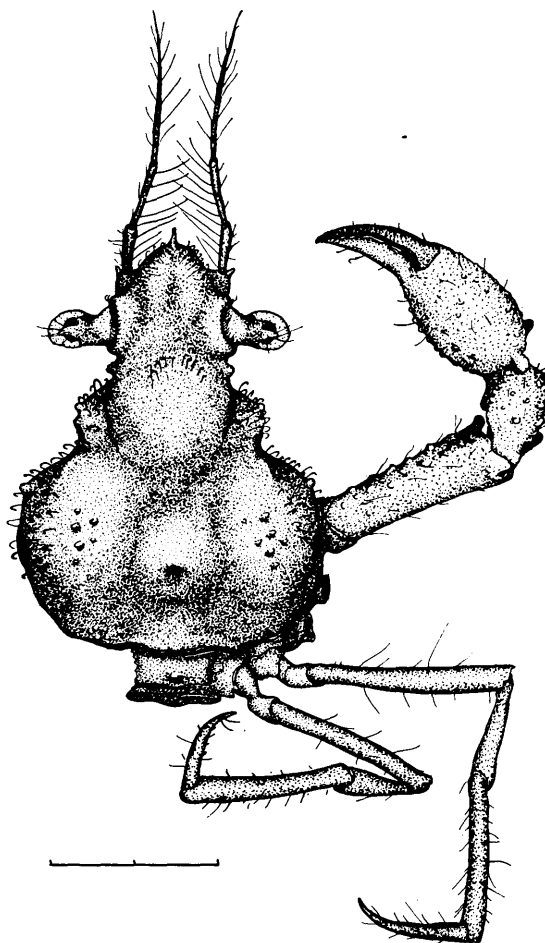


Fig. 234. *Inachoides forceps* A. Milne Edwards. Male in dorsal view, legs of left side and missing legs of right side not shown, 2 mm indicated (from Williams, et al. 1968).

mounting tubercle. Postorbital spine minute. Sparse branchial tubercles and pterygostomian tubercle on lateral region in front of base of each cheliped. Basal segment of antenna with 2 smooth or slightly spinulose ridges converging anteriorly, small spine at anterolateral angle. Outer maxillipeds with longitudinal, denticulate ridge on outer part of ischium; anterointernal corner of merus projecting sharply and obliquely forward.

Chelipeds of male long and heavy in comparison to body; merus subcylindrical; palm stout, margins convex, surface sparsely spinulose, more or less in rows; fingers curved, male with fixed finger strongly decurved leaving narrow, oval gape, large tooth at base. Walking legs similar in length, carpus and propodus subequal, dactyl falciform; first of these legs slenderest and with straightest dactyl.

Measurements in mm.—Carapace: male, length 10.7, width 8.2 (Rathbun 1925); ovigerous female, length 7.1, width 4.5.

Variation.—In restricting *I. laevis* Stimpson to the east Pacific, Garth (1958) remarked that studies in progress then on the named Atlantic varieties *I. forceps* and *I. obtusus* A. Milne Edwards, and *I. intermedius* Rathbun would show them to represent variations in *I. forceps* analogous to variants in the Pacific species which had never been named. The named varieties arose primarily from differences observed in rostral length, *I. forceps* as figured by Milne Edwards (1879) having the longest extremity. Most specimens from throughout the range have a short extremity on the rostrum corresponding to the variety Rathbun called *I. intermedius*. Only one lot of specimens from Puerto Rico (USNM 24186) seen by me approaches *I. obtusus* in lack of a rostral extremity (Rathbun 1925). Thorough study will probably bear out Garth's (1958) idea (based on gonopod morphology) that all these forms belong to a single species, and if so, Milne Edwards's *I. obtusus* (1879:199, pl. 33, figs. 3–3d) will fall into synonymy.

Habitat.—Shallow water to 20 m.

Type-locality.—Guiana and Desterro, Brazil.

Distribution.—SE Cape Lookout, N. C.; west coast of Florida to Desterro (= Florianopolis), Brazil.

Remarks.—Ovigerous females are known from Puerto Rico in January, Brazil in October, and Florida in February and November. The synonymy given by Williams, et al. (1968) errs in including references to specimens from the Pacific.

Genus *Metoporphaphis* Stimpson 1860

Rathbun 1925:19.

Metoporphaphis calcarata (Say)

Figs. 235, 240h

Leptopodia calcarata Say 1818:455.

Metoporphaphis calcaratus.—Hay and Shore 1918:454, pl. 37, fig. 5.

Metoporphaphis calcarata.—Rathbun 1925:21, text-fig. 5, pls. 6–7.—Williams 1965:243, figs. 221, 223J.—Coelho and Ramos 1972:209.—Felder 1973:48, pl. 7, fig. 2.—Powers 1977:46.

Recognition characters.—Carapace triangular, longer than broad, uneven, nodulose, each nodule sometimes surmounted by tubercle and this in turn usually with pencil of soft, hooked hairs. Rostrum as long as or longer than carapace, subcylindrical, tapering to point, often armed with 4 or 5 slender spines projecting outward alternately from opposite sides of lower surface, and with distal pair so close to tip as to give tip bi- or trispinose

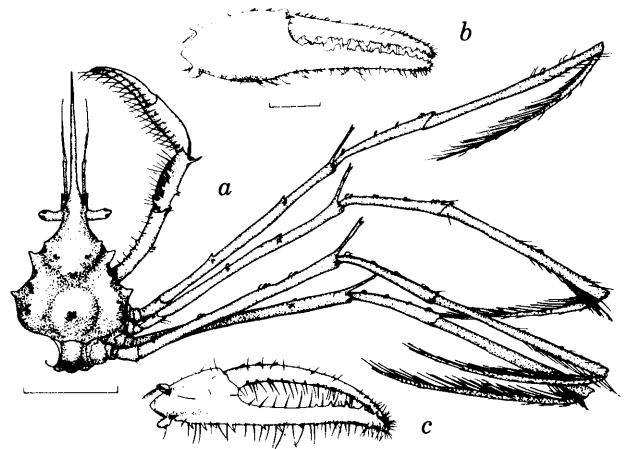


Fig. 235. *Metoporphaphis calcarata* (Say). a, Animal in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965); right chela, external view, b, male (USNM 102001), c, female (USNM 73416), 2 mm indicated.

appearance. Eyes protuberant, peduncles terminating in superior spinule projecting beyond cornea. Basal antennal article with spine below at midpoint of length, another at outer distal angle, and spinule at end of next 2 articles.

Chelipeds of moderate length, twisted, stout in male and less than half as long as first walking legs; merus with sharp terminal dorsal spine and row of smaller ventral spines; carpus with sharp dorsal spine near each extremity and row of sharp spines along mesial margin; hand broad, inflated, row of widely spaced spines along dorsomesial aspect of palm, fingers about as long as palm, bent mesially. Female with chelipeds feebler, palm shorter, fingers longer and more gaping. Walking legs slender, articles cylindrical but somewhat crooked; meri with 1 conspicuous spine and 2 smaller spines at extremity; dactyls longer than propodi, fringed with hair.

Male with 6, female with 5, free abdominal segments.

Measurements in mm.—Carapace: male, length including rostrum 21, rostrum 9.9, width 8.7; female, length including rostrum 24, rostrum 8.9, width 12.7.

Color.—Dirty gray to lemon yellow.

Habitat.—Often found among hydroids and fouling materials on hard substrates; ocean and high salinity estuaries; shallow water to 90 m.

Type-locality.—Bay of Charleston, S. C.

Known range.—Off Cape Hatteras, N. C., through Gulf of Mexico and Caribbean Sea to Rio de Janeiro, Brazil.

Remarks.—Ovigerous females have been taken nearly year round: November, March and April in

Georgia, March and August in Florida (Wass 1955), August in South Carolina, and October in North Carolina. Wass noted that this species can remain suspended in water by "rhythmic waving of its long, setae-lined legs."

Genus *Podochela* Stimpson 1860

Rathbun 1925:31.

Carapace somewhat depressed, elongate, pyriform; gastric region narrow, swollen. Body and appendages usually ornamented with curved hairs

above, straight hairs most often below legs. Rostrum arcuate or truncate, occasionally spinelike. Supraocular margin elevated or thickened. Eyes short, stout, prominent tubercle above, cornea oblique. Postorbital tooth or lobe remote from eye when present and either well developed or reduced to granule. Sutures between sternal segments of male depressed; sternum of female deeply concave, margins elevated and laminate. Abdomen with first 2 or 3 segments visible dorsally in male, 4 or 5 in female. Chelipeds of moderate length, merus curved, trigonal. Walking legs slender, subprehensile, diminishing in length from first to last pairs. (Modified after Rathbun 1925.)

Key to Species

1. Rostrum broad, rounded in front 2
Rostrum long, spiniform. *P. gracilipes*
2. Last 3 pairs of legs rather stout, dactyls less than $\frac{1}{2}$ length of propodi; cardiac region raised; pterygostomian region bearing broad, spinelike projection *P. riisei*
Last 3 pairs of legs slender, dactyls $\frac{1}{2}$ or more length of propodi; cardiac and gastric regions raised; pterygostomian region bearing long, thin lamina *P. sidneyi*

Podochela gracilipes Stimpson

Figs. 236, 241j

Podochela gracilipes Stimpson 1871a:126.—Hay and Shore 1918:454, pl. 37, fig. 6.—Rathbun 1925:47, text-fig. 13, pl. 17.—Williams 1965:243, figs. 220, 223 I.—Coelho and Ramos 1972:208.—Powers 1977:47.

Recognition characters.—Carapace with pronounced, rounded protuberance on cardiac region and 2 much smaller median protuberances on gastric region; 2 pterygostomian tubercles; small tubercle on epistome and projecting angle of buccal frame visible in dorsal view on large specimens. Rostrum long, spiniform, hairy, unarmed. Sternum of males with thick, blunt spine mesial to base of cheliped. Crests on basal article of antenna less pronounced than in *P. riisei*, article long, narrow posteriorly, with diagonal ventral ridge merging with terminal spine distally.

Chelipeds in male stout, inflated, fingers widely agape to near tip, large tooth near base of dactyl. Chelipeds slender in female. Walking legs slender, first pair 3 times length of carapace; dactyls long, nearly straight, $\frac{1}{3}$ length of propodus; propodi of last 3 pairs thickened distally; dactyls slightly scythe-shaped, $\frac{2}{5}$ length of propodus on second

pair, $\frac{1}{2}$ length on third, and $\frac{2}{3}$ length of propodus on fourth pair.

Abdomen of male with 6, female with 5, free segments.

Measurements in mm.—Carapace: male, length 14, width 9; ovigerous female, length 10.4, width 7.1.

Habitat.—Fine sand and mud to calcareous algae (Coelho and Ramos 1972); 6 to 219 m.

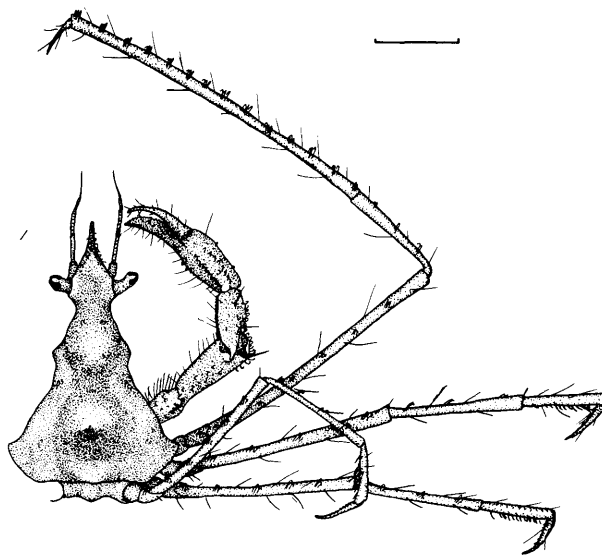


Fig. 236. *Podochela gracilipes* Stimpson. Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

Type-localities.—West of Tortugas, off Pacific and Carysfort Reefs [Fla.], 66 to 110 m.

Known range.—Off Cape Lookout, N. C., through Gulf of Mexico and Caribbean Sea to Santa Catarina, Brazil.

Remarks.—Ovigerous females are known in January from Yucatan Channel, February to July in Florida, March in Alabama and Colombia, and December in North Carolina.

Metabolic activity of first stage zoeae of this tropical species from offshore reefs near Cape Hatteras was lowest among zoeae of 6 species of *Brachyura* determined at 15°, 20° and 25°C (W. B. and F. J. Vernberg 1970).

Podochela riisei Stimpson

Figs. 237, 241k

Podochela riisei Stimpson 1860a:196, pl. 2, fig. 6.—Hay and Shore 1918:453, pl. 37, fig. 9.—Rathbun 1925:33, text-figs. 9a-b; pl. 11, figs. 1–2; pl. 208, fig. 2.—Chace 1940:56.—Williams 1965:241, figs. 218, 223G.—Powers 1977:47.

Recognition characters.—Carapace with greatest width about $\frac{2}{3}$ length, dorsal region uneven and with tufts of hairs. Rostrum broad, rounded in front, deeply excavated below for antennules, carinate above and with tuft of curled hairs. Basal article of antenna with sharp projecting ridge on each margin. Sternum of male thrown into ridge radiating to bases of legs.

Chelipeds slender in both sexes, fingers in contact throughout their length (stouter and slightly agape proximally in adult males). First pair of walking legs stouter than others, about 3 times as long as carapace; upper surface of all legs with regularly spaced tufts of stiff curled hairs.

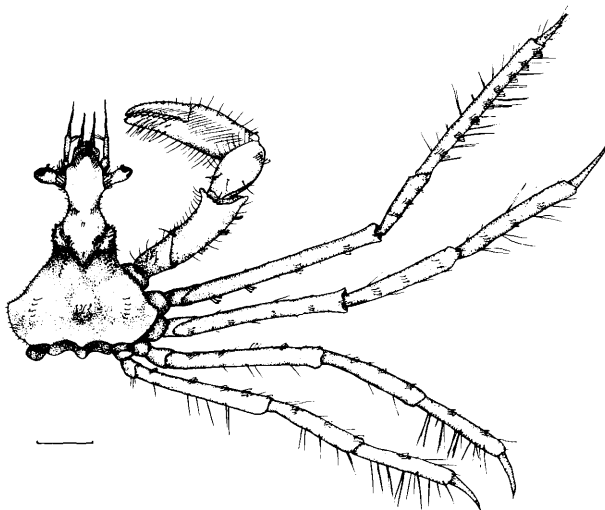


Fig. 237. *Podochela riisei* Stimpson. Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

Abdomen of male with 6, female with 5, free segments.

Measurements in mm.—Carapace: male, length 23, width 18.6; female, length 23, width 20.

Variation.—The rostrum is variable in shape and length, being nearly triangular in some specimens. Margins of the basal antennal articles are thick in old individuals but may be thin in younger ones. Sternal segments of males usually have rounded surfaces but are sometimes flattened.

Color.—Overall color light brown; legs lighter, grading to almost off-white or pale yellow; chelae and chelipeds nearly white to almost transparent; carapace darker on lateral aspects of urogastric and cardiac regions, as well as at posterolateral portions of metabranchial regions. Wass (1955) reported brick red specimens.

Habitat.—Has been taken from among hydroids on pilings, calcareous algae, on sandy bottom (Dragovich and Kelly 1974), and in rocky areas in northwestern Florida (Wass 1955); shallow water to 139 m (Wenner and Read 1982).

Type-locality.—Island of St. Thomas [West Indies].

Known range.—North Carolina to Campeche, Mexico; through West Indies to Trinidad (USNM); Rio de Janeiro, Brazil (MCZ 1832); Bermuda.

Remarks.—The largest male measured (USNM 97516) from the southeastern Gulf of Mexico bears an anemone covering all of the carapace except the "neck." The Rio de Janeiro specimen seems typical of the species, but the locality is remote from the remainder of the geographic range.

Ovigerous females are known through much of the year over the range: February in Puerto Rico, March to April in Georgia, June–July in Jamaica, September in North Carolina, June to August and November to March in Florida. Yang (1967) reared the first and second zoea, megalopa, and first crab stage in laboratory culture, and described the first zoeal stage. Hinsch (1973) found the sperm structure of *P. riisei* and *P. gracilipes* to be similar.

Rouse (1970) found the species uncommon in southwestern Florida, as did Dragovich and Kelly (1964) in salinities ranging from 20 to 45‰ over a temperature range of 15.2° to 30°C.

Podochela sidneyi Rathbun

Figs. 238, 241l

Podochela sidneyi Rathbun 1924:1.—Rathbun 1925:39, text-fig. 9c, pls. 12–13.—Williams 1965:242, figs. 219, 223H.—Felder 1973:49, pl. 7, fig. 4.—Powers 1977:48.

Recognition characters.—Closely resembling *Podochela riisei*, cardiac and posterior eminences more

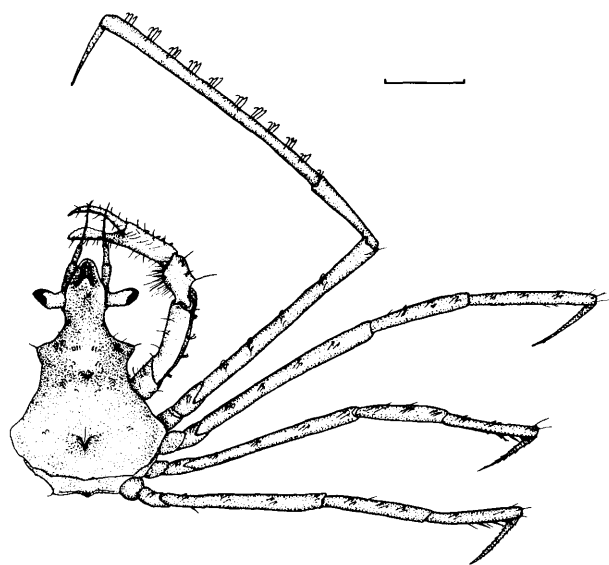


Fig. 238. *Podochela sidneyi* Rathbun. Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

produced, spiniform. Rostrum narrower at base and more triangular. Pterygostomian region bearing long thin lamina either subtriangular or produced downward in a lobe. Sternal segments flat with sharp cristate margins.

Chelipeds of adult male less inflated than in *P. riisei*; first pair of walking legs 3 or more times as long as carapace; dactyls of last 3 pairs less curved, longer and relatively more slender than *P. riisei*; dactyl of second leg up to $\frac{1}{2}$ length of propodus, of third leg to $\frac{2}{3}$, and of fourth leg to $\frac{3}{4}$ length of propodus.

Abdomen of male with 6, female with 5, free segments.

Measurements in mm.—Carapace: male, length 23, width 19.4; female, length 19.4, width 16.6.

Habitat.—A variety of bottoms including reef environment; shallow water to 187 m.

Known range.—Off Cape Hatteras, N. C., to Veracruz (Ray 1974); northwestern Cuba; Yucatan Channel.

Remarks.—Hildebrand (1954) reported the carapace of this species as decorated with hydroids and ascidians. Ovigerous females are known from October to March in Georgia, March, April, June, and September in Florida (Camp, et al. 1977; Cooley 1978), and March in Alabama.

Genus *Pyromaia* Stimpson 1871

Rathbun 1925:127.

Pyromaia cuspidata Stimpson

Figs. 239, 241m

Pyromaia cuspidata Stimpson 1871a:110.—Hay and

Shore 1918:455, pl. 38, fig. 4.—Rathbun 1925:129, text-fig. 49, pl. 41.—Boone 1927:34.—Chace 1940:57.—Williams 1965:240, figs. 216, 223E.—W. E. Pequegnat 1970:181.—Powers 1977:48.

Recognition characters.—Adult male. Carapace pyriform, approximately $\frac{2}{3}$ as wide as long; regions well marked, tumid, rough, with scattered granules, sharp tubercles and spines; often 6 large median spines (2 mesogastric, 1 urogastric, 2 cardiac, 1 intestinal), elsewhere 1 protogastric, 2 or 3 hepatic, remainder branchial. Depressions separating branchial regions from other regions somewhat pitted. Rostrum tapering to point, trigonal; upper and lateral margins spinulose. Interantennular spine acute, triangular, pointing downward and forward. Orbits large, open; supraorbital spine almost erect, directed slightly outward and forward; postorbital tooth large, curved around end of eye; anterior margin fringed with hair. Basal article of antenna long, with terminal spine, larger spine at middle of inner margin followed by row of tubercles or spinules. Tubercle at angle of buccal cavity. Outer maxilliped spinulose, longitudinal depression on ischium, merus cordate.

Legs covered with short fur, surface underneath roughened with sharp granules or spines. Merus of cheliped armed on margins, terminal spine of upper margin longest; upper margin of carpus spinulose with few spines on outer surface; hand inflated, fingers bare, grooved, uniformly toothed distally, slightly agape at base. Walking legs spinulose; meri with distal spine; first legs longest, remainder successively shorter.

First abdominal segment long, with acute backward-pointing spine; 6 free segments, last 2 fused.

Adult female. Legs almost bare; chelipeds not

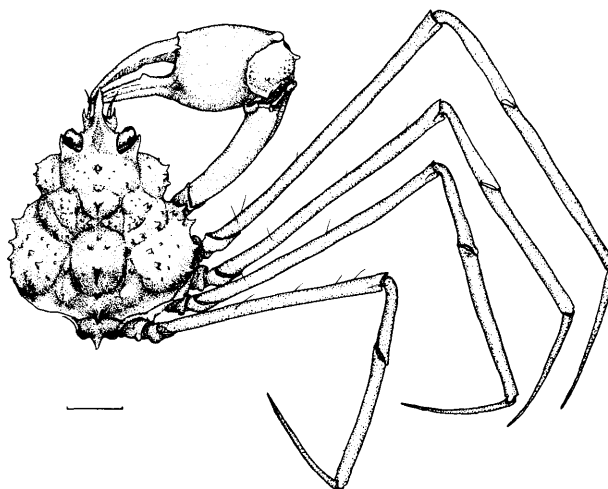


Fig. 239. *Pyromaia cuspidata* Stimpson. Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

much stronger than walking legs, dactyl longer than palm; legs shorter than in male. 5 free abdominal segments, last 3 fused.

Measurements in mm.—Carapace: male, length 41, width 32; ovigerous female, length 27, width 33.

Variation.—The young have pubescence resembling that in females, the postorbital tooth smaller than in adults, slender and directed outward in small specimens (7.5 mm long), directed outward and forward in somewhat larger forms.

Color.—Immature individuals brown, legs with lighter crossbands.

Habitat.—This species has been taken on gray mud, sand, pebble, and broken-coral bottoms; 27 to 549 m.

Type-localities.—Off Sand Key, 150 m; Alligator Reef, 170 m; the Samboes, 170 and 221 m; southwest of Sand Key, 229 m [Fla.].

Known range.—Off Cape Lookout, N.C., to west Florida; Cuba and Yucatan Channel to off Nicaragua 14°31'N, 80°41'W.

Remarks.—Ovigerous females are known off Florida in February, June and July, and off Cuba in April (USNM).

Genus *Stenorhynchus* Lamarck 1818

Rathbun 1925:13.—Garth 1958:129.—Opinion 763.

Stenorhynchus seticornis (Herbst)

(Arrow crab)

Figs. 240, 241o

Cancer seticornis Herbst 1788:229, pl. 16, fig. 91 (see Rathbun 1925).

Stenorhynchus sagittarius.—Hay and Shore 1918: 455, pl. 37, fig. 8.

Stenorhynchus seticornis.—Rathbun 1925:13, text-fig. 3, pls. 2–3.—Chace 1940:55.—Monod 1956:567, figs. 838–839.—Williams 1965:244, figs. 222, 223K.—Türkyay 1968:254.—Felder 1973:48, pl. 7, fig. 1.—Pequegnat and Ray 1974:237, figs. 11, 12.—Powers 1977:49.

Stenorhynchus seticornis.—Coelho and Ramos 1972:209.—Opinion 763.

Recognition characters.—Carapace smooth, triangular, longer than broad, diminishing in width to level of eyes and thence produced into slender, horizontal, flattened, laterally spinulose rostrum varying from slightly longer to 2.5 times as long as carapace; rostral tip acuminate. Orbits not defined; postorbital spine small, occasionally bifid. Eyes short, not retractile. Basal article of antenna slen-

der, with strong spine at middle directed downward and forward.

Legs extremely long and slender, composed of cylindrical articles, finely spinulose and bearing in addition 2 rows of spines on merus, 2 or 3 spines on carpus, and 3 terminal spines on merus. Chelipeds slender, cylindrical; hand weak; palm of male cheliped from 2.5 to 4 times as long as dactyl. First pair of walking legs from 8 to 9 times as long as postrostral part of carapace, second, third, and fourth legs successively shorter; dactyls on each pair longer than propodi.

Abdomen in male with 6, female with 5, free segments.

Measurements in mm.—Carapace: male, length including rostrum 60, width 24, rostrum to eyestalk 33.5; female, length including rostrum 59, width 21, rostrum to eyestalk 35.

Variation.—There is great variation in length of rostrum, relative length of palm and fingers, and length of legs. In old individuals the rostrum, chelipeds, and legs are pubescent.

Color.—Body ground color gray, banded dorsally with stripes of light and dark brown or black converging anteriorly as a nested series of inverted V's; one dark pair of stripes continuing united on dorsal side and another more lateral pair of like color on ventral side of rostrum. Legs reddish brown, joints darker; fingers of chelipeds bluish purple.

Rathbun (1925) summarized other color observations. The general pattern is as above, with ground color creamy white, buff, or light orange vermillion; stripes white, chestnut, brown, or black;

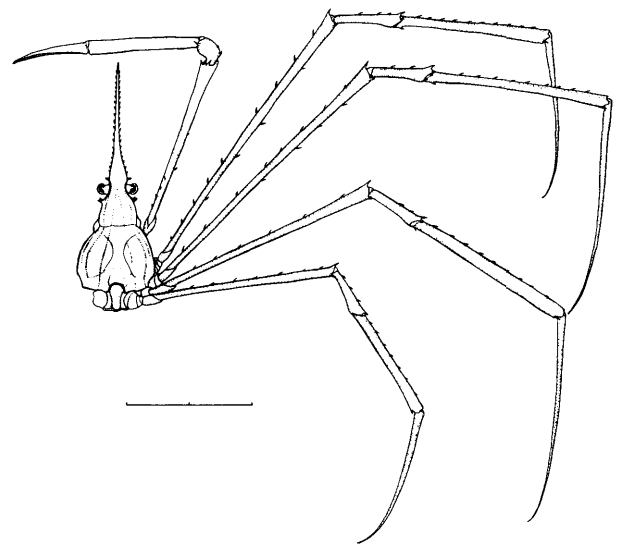


Fig. 240. *Stenorhynchus seticornis* (Herbst). Animal in dorsal view, legs of left side not shown, 30 mm indicated (from Williams 1965).

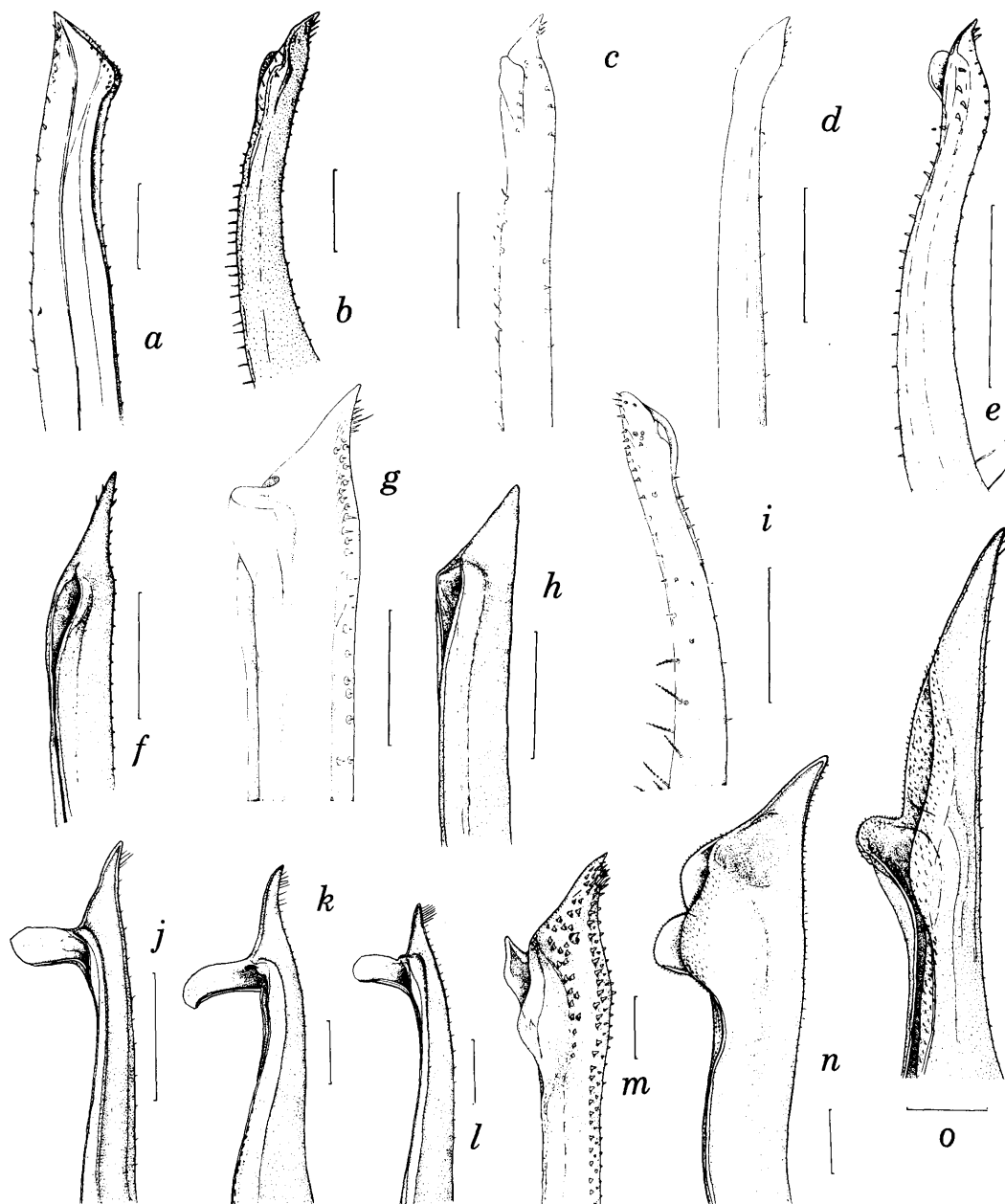


Fig. 241. Subfamily Inachinae, tips of right first pleopods of males, all sternal views except *a*, *i* abdominal: *a*, *Anomalothir furcillatus* (Stimpson); *b*, *Euprognatha rastellifera* Stimpson; *c*, *Aepinus septemspinosus* (A. Milne Edwards), USNM 24150; *d*, *Arachnopsis filipes* Stimpson, USNM 18114; *e*, *Batrachonotus fragilis* Stimpson; *f*, *Collodes trispinosus* Stimpson; *g*, *C. robustus* Smith, USNM 10085; *h*, *Metoporphaphis calcarata* (Say); *i*, *Inachoides forceps* A. Milne Edwards, UNC-IMS 2078; *j*, *Podochela gracilipes* Stimpson; *k*, *P. riisei* Stimpson; *l*, *P. sidneyi* Rathbun; *m*, *Pyromaia cuspidata* Stimpson; *n*, *Anasimus latus* Rathbun; *o*, *Stenorhynchus seticornis* (Herbst); (*a*, *b*, *e*, *f*, *h*, *j*-*o* from Williams 1965); 0.33 mm indicated.

legs reddish with bright red spots at joints; chelae purple or mauve; spine on legs and rostrum orange or red; eyes maroon.

Habitat.—This form has been dredged or trawled from a variety of bottoms—rock, coral rock, pebbles, sand, or sand mixed with broken shell; also, it has been taken from wharf piling and rock jetties. Near surface to 188 m (Wenner and Read 1982) (1465 m, Young 1978).

Type-locality.—Guadeloupe (Holthuis 1959).

Known range.—North Carolina to Santa Catarina, Brazil; Bermuda.

Remarks.—Rathbun's (1925) summary of this seemingly distinctive species, which has been followed by subsequent authors, is too inclusive. Both Yang (1967) and Barr (1975) referred the eastern Atlantic records to *S. lanceolatus* (Brulle). From studies of both larvae and adults, Yang (1967)

thought that two forms may exist in the western Atlantic, a shallow-water species to which the name *S. seticornis* can be applied correctly, and a possibly distinct deeper water form. Yang (1967) compared the adult morphology of two forms and (1976) described larval development of *S. seticornis* in laboratory culture through two zoeal stages, the megalopa and first crab stage, as well as the first zoeal stage of the deeper dwelling form.

The species as currently recognized has a tremendous recorded range in depth, but Yang thought the shallow form to occur usually from near the surface to near 90 m and the deeper form to range usually from near 40 to near 135 m. The validity of Yang's ideas remains to be determined.

Ovigerous females are known year round in the western Atlantic (see also Hartnoll 1965). Eggs hatch in 12 days at 22–25°C (Hartnoll 1965). Hinsch (1973) described sperm structure of the male. The species changes in form at the pubertal molt, relative size of male chelipeds increasing markedly. The female develops pubescence around articulation of the dactyl; there is a tooth near its base in both sexes. Moreover, the female develops a rim around the edge of the sternum which fits inside the abdomen (Hartnoll 1965).

Individuals collected from a reef southeast of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 40°C for 7 h but died after 17-h exposure (F. J. and W. B. Vernberg 1970).

Hartnoll (1966) described an entoniscid (*Acheilion occidentalis*) from specimens of *S. stenorhynchus* collected in Jamaica.

Barr (1975) studied the biology and behavior of *S. seticornis* in 22-m depths near the Tektite underwater habitat in Lameshur Bay, St. John, Virgin Islands, from July 23 to August 12, 1970, observing crabs for about 40 h in situ plus behavior of 103 crabs in the habitat entry room. The species lives there on live coral reefs, patch reefs on sand, sand, and the edge of large reefs; crabs were more abundant on coral substrate than sand but most abundant on reef edges near the coral-sand interface, usually in direct contact with stony or soft coral. Those on sand were associated with stable objects such as sponges, anemones, etc., and were smaller than the mainly larger crabs on coral.

Counts of crabs along 1 × 10 m transects in daytime, dusk, night, and dawn, showed somewhat

greater numbers at dusk and night. The crabs migrate upward at dusk, reaching heights of 1 m or more on soft coral and gorgonians by dark, and retreat at dawn, tending to hide in the same place each day. Although some small crabs may have been overlooked, proportions were 1♂:1.14♀; females measured 4.5–13 mm in carapace length (cl), males 3.5–16.5 mm. Sexes were equal in the 8-mm class, females dominated the 8.5–13 mm class, and only males exceeded this size. Both sexes are mature at 8.5–9.5 mm cl. Among 35 mature females, 28 were ovigerous.

Mating, observed in late afternoon-early evening and once at 0200 h, was described in detail. Males are the aggressors, but assume an inverted position during copulation with the upright females supporting the pair. Molting is no prerequisite, females copulate with or without eggs but in the former case old eggs soon hatched and new ones were deposited within 19 h. Hatched larvae seek the light.

Stenorhynchus seticornis tends to be an omnivorous, opportunistic scavenger, mainly on detrital particles. Self cleaning seems to be a chief activity. Barr theorized that the species is essentially a filter feeder, its body catching particles to be consumed later; the crabs crawl about exposing themselves to water currents at night but feed mostly in daylight. They prey little if at all on other living organisms and are not, themselves, important food to predators. The long, spiny appendages apparently make them difficult to eat, for fishes will take only the body of a legless or almost legless specimen and active crabs fend off approaching fishes with the walking legs and retreat to the protecting spines of a sea urchin.

Randall (1967) reported *S. seticornis* from stomach contents of the rock hind, *Epinephelus adscensionis*, red hind, *E. guttatus*, Nassau grouper, *E. striatus*, and sharp nose puffer, *Canthigaster rostrata*.

Subfamily Oregoniinae

Male abdomen terminally broadened, last segment subquadrate or transversely ovate, invaginated into sixth segment, its outer border emarginate or introverted. Male first pleopod lanceolate, longitudinally grooved, provided with numerous filamentous setae, and having bulbous base (Garth 1958).

Key to Genera and Species

(Adapted from Garth 1958; Rathbun 1925)

1. Carapace broader than long or very little longer than broad; rostrum short; adult male cheliped much shorter than walking legs. *Chionoecetes opilio*

- Carapace considerably longer than broad; rostrum elongate; adult male cheliped either longer than walking legs or very little shorter [Hyas] 2
2. Hepatic region behind postorbital spine not expanded (slightly so in large individuals); fixed basal antennal article elongate and subtriangular *H. araneus*
- Hepatic region behind postorbital spine expanded laterally; fixed basal antennal article elongate with sides nearly parallel, granulate, outer side ending in blunt tooth *H. coarctatus*

Genus *Chionoecetes* Kröyer 1838

Garth 1958:148.

Chionoecetes opilio opilio (O. Fabricius)

(Snow crab)

Figs. 242, 245a

Cancer phalangium O. Fabricius 1780:234 (not *C. phalangium* J. C. Fabricius 1775).

Cancer opilio O. Fabricius 1788:182, plate.

Chionoecetes opilio.—Kröyer 1838:249.—Rathbun 1925:233, text-figs. 88–89, pls. 84–85.—Garth 1958:150, pl. I, fig. 5; pl. 14.—Sakai 1976:185 (English text), pl. 64.

Recognition characters.—Carapace ovate in outline, length and width subequal; surface covered with very short pubescence and scattered unequal prominences, blunt, wartlike and granulate about middle but more acute anteriorly and at sides; gastric region depressed and well separated from branchial regions; paralleling channels above posterolateral margin nearly smooth but with double margins granulate; anterolateral row of marginal small teeth diminishing in size anteriorly. Rostrum short, divided into 2 flat, triangulate horns. Orbit large, shallow, open above leaving eyes visible when retracted; cornea large. Postocular tooth large, directed forward.

Chelipeds 1.5 times as long as carapace, twice as long in old individuals; fingers 1.5 times as long as palm. First 3 walking legs about twice as long as carapace, 3 times as long in old; last leg about as long as cheliped; legs slightly pubescent, meri scabrous or echinulate above; chelipeds somewhat scabrous above, muricate along angles.

Abdomen 7 segmented in both sexes, 3 proximal segments strongly granular; width in males $\frac{1}{3}$ width of sternal plastron at its penultimate segment; third and fourth segments widest. Male first pleopod with tip reflexed, almost ringed with subterminal filaments.

Measurements in mm.—Carapace: male, length

69.3, width 69.3; ovigerous female, length 53.8, width 54.5 (Garth 1958). Male, length 125.5, width 127.5 (Rathbun 1925); male, length 126, width 128 (Sakai 1976).

Color.—Light brick red above, often iridescent, yellowish white below; sides of legs shining white (Stimpson in Garth 1958). Sakai (1976) gave the color as "light brownish or copper-colored," which is faithfully shown in his plate 64.

Habitat.—Green and black mud, fine gray sand and shell (Garth 1958; Rathbun 1925); mud (Brunel 1961; Prowles 1968); 12.8 to 640 m, rarely to 2222 m (Rathbun 1925; Squires 1966). Sakai (1976) gave the bathymetric range as 20 to 1200 m; Motoh (1973) placed a lower limit for fishing at about 1500 m.

Type-locality.—Greenland.

Known range.—Western Atlantic Ocean from Greenland south to St. Lawrence estuary and Gulf of Maine; arctic Alaska (Pt. Barrow) and northeastern Siberia through Bering Strait to Alaskan Peninsula and Aleutian chain; Kamchatka; Okhotsk Sea and southward to Japan. Prowles (1968) characterized these waters as subarctic in the northeastern Atlantic and Bering Sea, and the northeast Pacific.

Remarks.—Rathbun (1925) and Garth (1958) both regarded a population from Japan as the subspecies, *C. o. elongatus* Rathbun. Sakai (1976) did not distinguish this population, but Watson (1970) in biological studies recognized its distinctness.

The species is a commercial fishery resource in the northern Pacific (Slizkin 1974). It had limited development in the northwestern Atlantic until 1966 (Brunel 1961; Wilder 1966); thereafter production increased markedly (Watson 1970). Brunel (1961) showed that catches were made off Gaspe Peninsula where the species seemed confined to water between -1° and 4°C . Males in samples attained much larger weight (mean 628 g, rarely 1268 g) than females (108 g, rarely 239 g), hence by size alone were separated in the then limited fishery. Deveau and Aucoin (1966) found greatest abundance north of Cape Breton Island in depths of 90 to 137 m, and Prowles (1968) found it most com-



Fig. 242. *Chionoecetes opilio opilio* (O. Fabricius). Male in dorsal view, third left walking leg missing, 5 cm indicated (USNM 17075).

monly in trough areas 73 to 165 m deep on mud bottom in water -1° to 2°C . Temperature tolerance experiments by McLeese (1968) and McLeese and Watson (1968) largely confirmed these early environmental observations on temperatures favored by the Canadian population.

Watson (1970) found that 50% maturity occurs in males at about 57 mm carapace width (minimum 51 mm), and at 47 mm carapace width in females (minimum 51 mm). After attainment of maturity, males show allometric growth, but females do not grow after a pubertal molt. He suggested that only hard-shelled males are capable of mating, and described the mating of a captive male and female. The female had just molted and was still in soft condition. The following day this female laid fertile eggs. Field observations indicate that new eggs are produced within a few days after a female has released a hatch of larvae, and that one mating fertilizes more than one spawning. Watson (1972) described mating behavior in which males hold females in precopulatory embrace for a period which ends when they assist females in molting, then mate. During postcopulatory embrace, both animals flex abdomens, spermatophores issue from the male's pleopods, and the female's waving pleopods draw spermatophores toward her abdomen. It is possible that emission of spermatophores by males and gathering of them by females may induce egg laying; many spermatophores were seen within egg masses soon after laying. Alternatively, the first batch of eggs may be

externally fertilized and subsequent batches may be fertilized from spermatophores stored in the spermathecae. Eggs are laid in late May to early June and hatch about 11 months later (Prowles 1968). Watson (1971) also described molting in captive crabs, showing that its duration increases with size, lasting two to nine hours. Newly molted crabs of commercial size take two to three months to harden sufficiently for commercial acceptability.

The Japanese have studied the western Pacific populations in great detail, from both purely biological and economic standpoints. Motoh (1973), from an ovigerous female taken by fishermen in the Sea of Japan in February, reared, described and illustrated the two zoeal stages and megalopa. There is a transitory pre-zoeal stage. Comparisons were made with previous studies. Haynes (1973) described the pre-zoea and first zoea of *C. opilio* from Bristol Bay, Alaska, and compared them with similar stages of *C. bairdi*. Kon (1970) estimated planktonic larval stages to last only 63–66 days in Waskawaka Bay water of 11° – 13°C , based on laboratory experiment. Ito (1968) described the first crab stage as being near the surface until June, after which they move deeper, settling to the bottom as first crab stages the following fall and winter. Sinoda (1968) thought that females reach a terminal pubertal molt but that males keep on molting annually; females at a width of 75 mm were estimated to be six or seven years old; males as broad as 165 mm were recorded.

The above account makes no pretense of review-

ing the growing body of literature on this species, but such a review was provided by Adams (1979).

Genus *Hyas* Leach 1814

Garth 1958:142.

Hyas araneus (Linnaeus)

(Toad crab)

Figs. 243, 245b

Cancer araneus Linnaeus 1758:628.

Hyas araneus.—Leach 1814:431.—Rathbun 1925: 253, text-figs. 91–92, pls. 92–93.—Christiansen 1969:116, fig. 48.

Recognition characters.—Carapace longer than broad, more or less subtriangular, broadest posteriorly, convex anteroposteriorly, but deflexed in anterior part of gastric region; hepatic region not dilated laterally, lateral margins converging throughout length, tuberculate behind postorbital tooth; surface uneven, pustulate tubercles especially on median gastric area and in oblique row on each branchial region, 2 tubercles side by side on intestinal region (may be united in young). Rostrum triangular, flat, bifid, horns contiguous. Eyes not entirely concealed when retracted; fissures above and below orbit open; postorbital tooth large, acutely triangular, cupped. Basal antennal article longer than wide, subtriangular, narrowed anteriorly; first movable article curved laterally, last article of peduncle cylindrical.

Chelipeds compressed, stout, thick in large males with fingers narrowly gaping. First walking leg longer than cheliped, following legs progressively somewhat shorter.

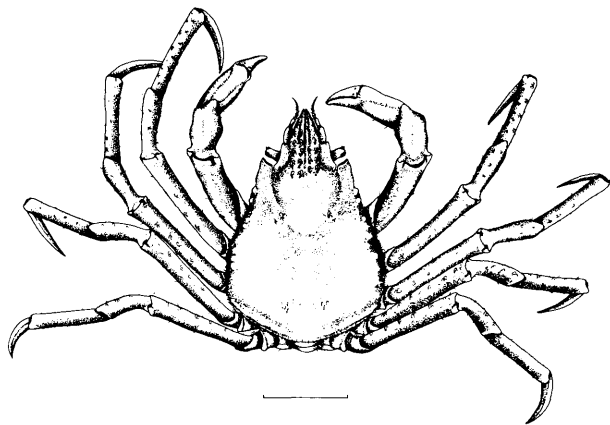


Fig. 243. *Hyas araneus* (Linnaeus). Male in dorsal view, 2 cm indicated (from Christiansen 1969).

Abdomen 7-segmented in both sexes; that of male broadest at third and fourth segments, terminal segment transversely ovate; female abdomen broadly oval.

Measurements in mm.—Carapace: male, length 95, width 75; ovigerous female, length 81, width 64.

Color.—Reddish brown dorsally and dirty white ventrally (Christiansen 1969).

Habitat.—Hard, stony, sandy and soft bottom (Christiansen 1969); commoner on soft bottom where *H. coarctatus* is rarer, the two species being complementary (Hartnoll 1963); intertidal to 350–360 m, usually less than 50 m.

Type-locality.—“Habitat in Oceano Europaeo.”

Known range.—West Greenland; Labrador to Rhode Island; between Greenland and Iceland, through British Isles and northwest France to Spitsbergen and Kara Sea; intertidal to 360 m.

Remarks.—Hartnoll (1963) studied the biology of this species along with that of *H. coarctatus* (see below) at the Isle of Man, and Christiansen (1969) gave a general summary.

Christiansen (1973) reared larvae in the laboratory and compared results with earlier work. Incubation time and larval development are nearly identical with findings for *H. coarctatus*. Small differences between the larval morphology of the species were described. Temperature influenced rate of development and survival of the larvae, the megalopa being reached in 37.8 (\bar{x}) days with 73% survival at 10°C, first crab in 57 (\bar{x}) days with 1% survival at 15°C, and no development at 20°C. Earlier (1971) she found that antibiotics aid growth and survival of this species in culture.

Hyas coarctatus coarctatus Leach

Hyas coarctatus alutaceus Brandt

(Toad crab)

Figs. 244, 245c

Hyas coarctatus Leach 1815b:329.—Rathbun 1925:258, text-fig. 93, pls. 94–97.—Christiansen 1969:118, fig. 49.

Recognition characters.—Carapace longer than broad, more or less shield shaped, broadest posteriorly; postorbital and hepatic regions dilated laterally into winglike expansion with rounded posterolateral angle, separated from branchial region by broad and deep sinus; ornamentation similar to *H. araneus* but tubercles of lateral margin extend only to posterior part of hepatic region, 1 tubercle

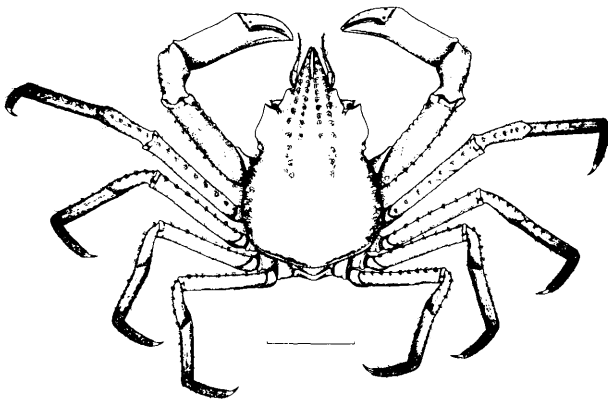


Fig. 244. *Hyas coarctatus* Leach. Male in dorsal view, 1.5 cm indicated (from Christiansen 1969).

on lateral margin just anterior to contraction, 2 large median tubercles on mesogastric region; carapace in old individuals rougher. Rostrum triangular, flat, bifid; horns contiguous, narrowly diverging or with buttonhole gape, meeting only at tips. Basal antennal article narrowing slightly forward, longitudinal margins granulated, outer side ending in blunt tooth; first movable article curved laterally, last article of peduncle cylindrical.

Chelipeds longer than in *H. araneus*, more roughly granulated in older individuals and sometimes exceeding second walking legs in length.

Abdomen as in *H. araneus*.

Measurements in mm.—Carapace: male, length 30.2, width 19.7 (off Cape Cod); male, length 51.5, width 35 (Murman Sea) (both typical form, Rathbun 1925); male, length 8–62; female, length 9–45 (Squires 1967).

Variation.—Rathbun (1925) stated that *H. coarctatus* shows great geographic and individual variation manifesting these differences in three subspecies. Other authors (Christiansen 1969; Sakai 1976) have accepted her analysis. The typical form is relatively small and has a long rostrum. The essentially Arctic and Pacific form, *H. c. alutaceus*, with shorter, broader rostrum, is also broader across the anterior carapace embracing the hepatic region. The third hairier and proportionally different form, *H. c. ursinus*, is confined to the Pacific.

Color.—Similar to *H. araneus*, perhaps more reddish dorsally (Christiansen 1969).

Habitat.—Hard, stony, sandy and occasionally soft bottom; 1 to 1650 m, usually less than 50 m (Christiansen 1969; Squires 1966).

Type-locality.—Kent near Sandgate, England.

Known range.—Two subspecies occurring in the North Atlantic merge gradually into each other. Typical *H. c. coarctatus* ranges from off North Carolina northeasterly with the trend of the Gulf Stream to northwestern Europe, thence eastward in the Arctic to the Murman Sea. This form merges

into *H. c. alutaceus* around Cape Breton Island, Newfoundland, Greenland and Iceland, continuing as that form through Davis and Hudson straits and into Hudson Bay; westerly it is found along edges of the Beaufort, Chukchi and East Siberian seas, southward through the Bering Sea, on the east to Puget Sound, and on the west to the Sea of Japan and East China Sea. The third form, *H. c. ursinus*, is known only from the Sea of Japan and Singapore (Christiansen 1969; Rathbun 1925; Sakai 1976; Squires 1966, 1967).

Remarks.—Hartnoll (1963), studying the biology of *H. coarctatus* at the Isle of Man, outlined habitat preferences and noted omnivorous feeding habits (also Squires 1965a) with a preference for crustaceans. The growing crabs enter maturity in a terminal pubertal molt which may vary greatly in size; at Isle of Man mature males varied in length from 12 to 42 mm and females from 10 to 36 mm. At this molt the female abdomen changes from narrow to broad and fringed with hairs, the shallow sternal groove with locking buttons becomes a much broadened surface without buttons and the genital openings are converted from short diagonal slits to open slits, each around the inner edge of a small dome. In males, pleopods become much enlarged and hairy. Growth is allometric; there is greater increase in size at the pubertal molt than at any other, the male chelipeds showing marked increase in size but the female chelipeds only a slight increase. Male pubertal molts occurred from January to July, usually February to June, and females from May to September, usually May to July. Both season and size determine whether there will be further molts or the molt of puberty but the two conditions overlap. Immediately after this molt, gonads enlarge in the males.

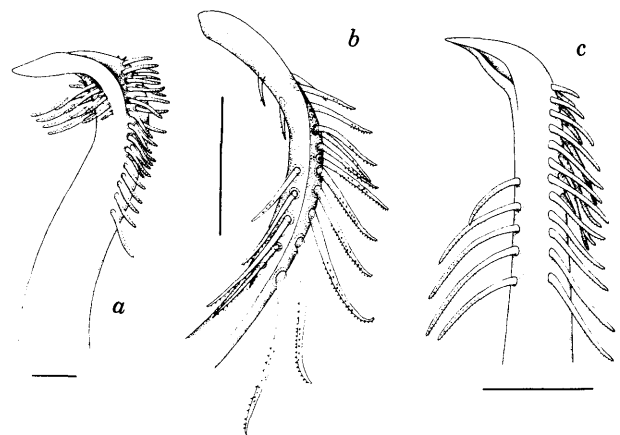


Fig. 245. Subfamily Oregoniinae, tips of male first pleopods: a, *Chionoecetes opilio* (O. Fabricius); b, *Hyas araneus* (Linnaeus) USNM 122023; c, *H. coarctatus* Leach; a, c, 1 mm (redrawn from Garth 1958); b, 0.5 mm indicated.

Hartnoll (1974) pointed out that in this species as in others (among them *Carcinus maenas*, *Ocyropsis quadrata*, *Macrocoeloma trispinosum*, *Microphrys bicornutus*, and *Stenorhynchus seticornis*) the strong positive allometry of male chelipeds, low positive allometry of female chelipeds, strong positive allometry of female abdomen until the molt of puberty, and slight positive allometry of male gonopods until puberty, followed by a negative trend, are all adaptations to mechanical considerations and utilization of available resources. The male chelae continue to be implements of aggression, defense and mating, the female abdomen is an incubatory chamber with no need to change once efficient size is reached, and male gonopods of intermediate size equip males with the capacity for mating with a range of sizes.

Post-pubertal females mate while soft and, having mature ovaries, spawn almost at once. By September females that had laid eggs in early summer again have full ovaries. Eggs laid from April to August are carried for 9–11 months until the following March or April. When larvae hatch, the females, already having full ovaries and spermathecae, lay eggs again almost immediately. Nearly 10% of mature females are in their second breeding season during April–June. Hartnoll (1963) could not determine whether any survived to lay more than two sets of eggs. A 19-mm female can carry 1500 eggs; 32-mm, 8000.

Early in his studies Hartnoll (1960) described a hermaphrodite of the species, apparently unparasitized, that had male and female systems on both sides of the body. This was the only such crab among 250 examined and at that time was the fifth such occurrence recorded for decapod crustaceans.

Larval stages in this species were studied most recently by Christiansen (1973) who reared larvae in the laboratory and compared results with earlier work. She found this species to be ovigerous the year round in Oslo Fjord, Norway. From ovigerous females collected in May and maintained in laboratory running sea water of about the same temperature-salinity as outside (6.5°C at 32.9‰ and 7°C at 34.8‰), larvae hatched the following April. One female produced new eggs a few weeks later. Larvae were reared at 10°, 15°, and 20°C, some with water temperature abruptly raised, others gradually raised to the rearing temperature, but there were no observed differences between these two sets. Hatching was observed under the binocular microscope. There is a prezoal stage which probably lasts a very short time and was never seen to swim. The two zoal stages, megalopa and first crab stage, were described.

Temperature influenced rate of development and survival of the larvae, first crab being reached in 75.7 (\bar{x}) days with 22% survival at 10°C, 57 (\bar{x}) days with 11% survival at 15°C, and attainment only of megalopa in 20.5 (\bar{x}) days with 21% survival at 20°C. None survived to first crab at this last temperature.

Subfamily Tychinae

Orbit consisting, if complete, of supraocular eave and postocular spine; intercalated spine lacking . . . [but] . . . longer spinous outgrowths on supraocular eave and on postocular spine for most part present. Shape of body elongate, somewhat truncate in front, often provided behind with median spine or outgrowth (Balss 1929; Williams, et al. 1977).

Key to Genera and Species

(Modified after Garth 1958)

1. Eyes furnished with projecting and tubular commencing orbits *Pitho lherminieri*
 Orbit completely unprotected below; eyes protected above by lamellate projection consisting of supraocular eave and outgrowth of hepatic region *Tyche emarginata*

Genus *Pitho* Bell 1835

Garth 1958:162.—Guinot 1964a:44.

Pitho lherminieri (Schramm)

Figs. 246, 259a

Othonia lherminieri Schramm, in Desbonne and Schramm 1867:20.

Pitho lherminieri.—Hay and Shore 1918:459, pl. 38, fig. 8.—Rathbun 1925:362, text-fig. 117b, pl. 128, figs. 1–2; pl. 129, figs. 1–2; pl. 252, fig. 2.—Williams 1965:246, figs. 224, 233A.—Coelho and Ramos 1972:210.—Powers 1977:61.

Recognition characters.—Carapace as broad as long in adult males, longer than broad in other individuals, narrow behind in males, broader in females, roughened with tubercles of different sizes, and

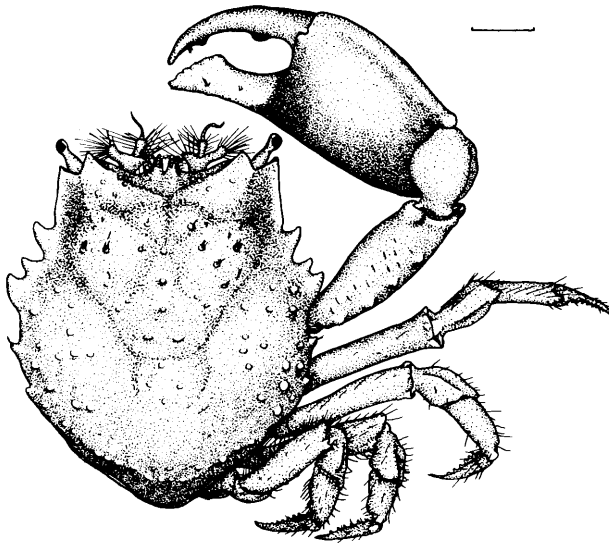


Fig. 246. *Pithecheilichium lherminieri* (Schramm). Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

adorned with scattered hooked hairs. Frontal teeth forming rostrum more advanced than orbital angles. Anterolateral margins armed with 5 strong teeth, exclusive of postorbital tooth; first tooth largest, second and third subequal, fourth and fifth much smaller, second occasionally bilobed. Orbits small, tubular, deep. Antennae short, with stiff hairs on borders; basal article lamellate, forming floor of orbit; second article flat, short, and broad; third article smaller, flattened.

Chelipeds of adult male from 1.5 times to nearly twice length of body; merus subcylindrical; carpus and hand more or less compressed and distinctly angled along margins; fingers of adult male spatulate, touching only at extremity. In female and young male, fingers short and weak, evenly dentate, with margins in contact.

Abdomen of both sexes with 7 free segments.

Measurements in mm.—Carapace: male, length 26, width 24; female, length 18, width 17.

Variation.—In females and young males the carapace is more tuberculate than in old males, the lateral teeth sharper, and the last two teeth more prominent.

Color.—Dirty brownish yellow (Schramm in Rathbun 1925).

Habitat.—This species has been found on a variety of bottoms including mud, sand, shell-sand, shell, rock and coral, and grass (Rathbun 1925); 1 to 51 m, rarely 220 m.

Type-locality.—Guadeloupe, in cavities of the keys.

Known range.—Off Beaufort Inlet, N. C., to west Florida; Veracruz, Mexico; West Indies to Islet of São Sebastião, São Paulo, Brazil.

Remarks.—Ovigerous females are known from May to November in the Bahamas and Florida, and in December from Brazil (Rathbun 1925 and USNM).

Hinsch (1973) described sperm structure of the male.

Randall (1967) reported *P. lherminieri* from stomach contents of the longspine squirrelfish, *Holocentrus rufus*.

Genus *Tyche* Bell 1835

Garth 1958:172.—Guinot 1964a:44.

Tyche emarginata White

Figs. 247–248, 259b

Tyche emarginata White 1847a:206.—Hay and Shore 1918:461, pl. 39, fig. 4.—Rathbun 1925:508, pl. 272; pl. 273, figs. 7–12.—Garth 1946:406–408, text-fig. 1.—Williams 1965:247, figs. 225, 226, 233B.—Williams, Shaw, and Hopkins 1977:890, figs. 4, 7, 10b.—Powers 1977:62.

Recognition characters.—Carapace oblong-oval, flattened, with lamellate expansions in front covering ocular peduncles, and another prolonged and bilobed behind, stout hooked hairs on rostrum and prominent elevations. Front wide, with 4 long horns, lateral horns forming anterior angles of orbit, divergent, longer and more elevated than submesial rostral horns. Ocular peduncles entirely uncovered below. Gastric region swollen, with 3 low tubercles, 2 anterior, and a third posterior and median; cardiac region depressed, with 3 small tubercles. Lateral borders straight and nearly parallel at hepatic regions, rounded at branchial regions. Dorsal surface of hepatic region concave; branchial region with large tubercle on anterior

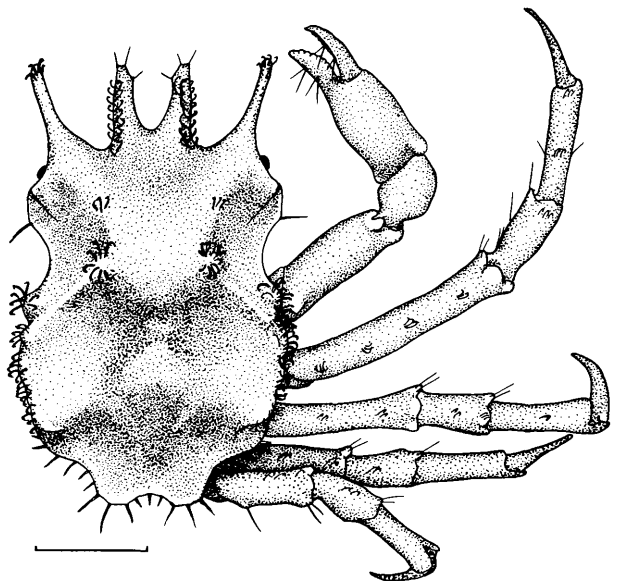


Fig. 247. *Tyche emarginata* White. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

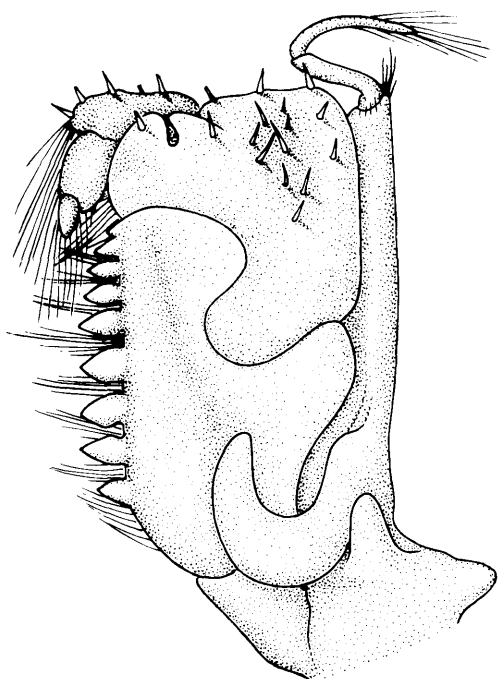


Fig. 248. *Tyche emarginata* White. Left outer maxilliped (redrawn from Garth 1946).

lobe, and prominent tuberculate crest above lateral margin. Exopod of third maxilliped with basal protuberance recurving to cover base of ischium, merus inserting deeply into outer distal portion of ischium by similar but less developed process, inner margin of ischium strongly dentate.

Chelipeds of male more than twice length of postorbital part of carapace; palms somewhat dilated and compressed; fingers gaping at base, dentate throughout length. Walking legs ornamented with stout hooked hairs; dactyls spinulose on middle third, spinules increasing in size distally.

Abdomen of both sexes with 7 free segments.

Measurements in mm.—Carapace: male, length to tip of submesial horns 19.1, width 10.8; female, length to tip of submesial horns 38, width 23.

Color.—Generally yellowish gray; carapace greenish above, with 2 triangular white spots; blackish above base of legs (various authors).

Habitat.—The species has been reported from rocky or coarse shell bottoms (Rathbun 1925); 1 or 2 to 36 m.

Type-locality.—West Indies.

Known range.—Off Beaufort Inlet, N. C.; through Bahamas to west coast of Florida.

Remarks.—Garth (1946) gave a detailed comparison of this species with its Pacific counterpart *T. lamellifrons*. He also (1952) named *T. potiguara* from northern Brazil, the type-locality of which Williams (1965) included in the distribution of *T. emarginata*. Williams, et al. (1977) gave detailed comparisons of selected mouthparts and male-female reproductive structures in the subfamily Tychninae.

Subfamily Epialtinae

Manning and Holthuis 1981:255.

Eyes without true orbits; eyestalks very short or sometimes obsolescent, either concealed beneath anteriorly produced supraocular spine, or sunk in sides of huge beaklike rostrum; postocular spine or process sometimes present, but not excavated for reception of retracted eye. Basal antennal article elongate but truncate-triangular. External maxillipeds with merus as broad as ischium. Dactyls of walking legs prehensile or subchelate; last 3 pairs of legs often disproportionately short compared with first pair (Alcock 1895 [for Acantho-nychinae]). Postocular spine not cupped (except in *Sphenocarcinus*); rostrum either simple or 2-spined; palp on third maxilliped arising from anterointernal angle of merus (Rathbun 1925). First pleopod of male medium stout, apex most varying (hammer-shaped; divided into 3 or 4 lobes; etc.); second pleopod short (Stephensen 1945).

Key to Genera and Species

1. Rostrum single or secondarily bifurcate at tip; 6 free abdominal segments in male, 5 in female *Epialtus dilatatus*
 Rostrum double, deeply forked; 7 free abdominal segments in both sexes
 *Sphenocarcinus corrosus*

Genus *Epialtus* H. Milne Edwards 1834

Garth 1958:227.

Epialtus dilatatus A. Milne Edwards

Figs. 249, 259d

Epialtus dilatatus A. Milne Edwards 1878:140, pl.

27, figs. 4–4b.—Rathbun 1925:153, text-fig. 53j, pl. 45, fig. 2.—Williams 1965:249, figs. 228, 233D.—Powers 1977:42.

Recognition characters.—Small species. Carapace broad, subpentagonal, almost smooth, with hepatic and branchial projections more or less laminate. Rostrum broad, somewhat triangular, short, bilobed at tip, slightly depressed on median line

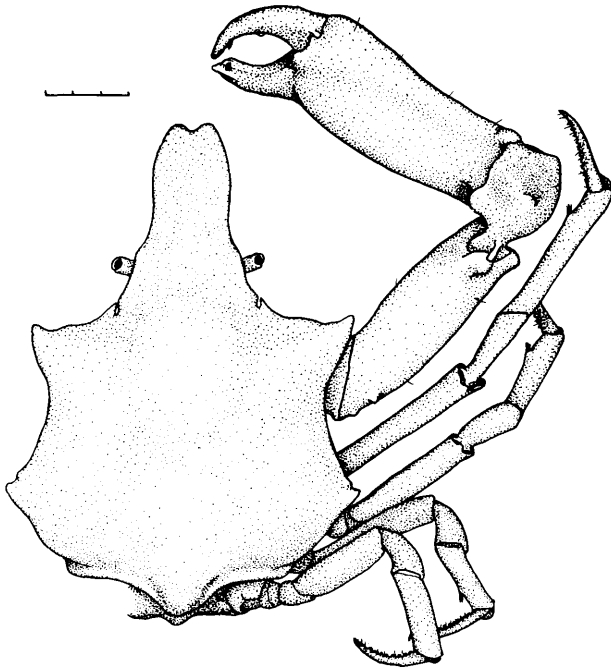


Fig. 249. *Epialtus dilatatus* A. Milne Edwards. Male in dorsal view, legs of left side not shown, 3 mm indicated (from Williams 1965).

dorsally with depression continued ventrally and limited by 2 crests uniting posteriorly in acute angle. Eyes small; preorbital angles scarcely marked; postorbital teeth minute. Basal article of antenna triangular, movable part concealed beneath rostrum.

Chelipeds moderate in size; carpus with 4 longitudinal crests; hand slightly enlarged distally, upper margin blunt, defined by depression on either side; fingers short and stout. Walking legs with slight tuft of hair on lower margin of propodi.

Abdomen of male with 6, female with 5 free segments.

Measurements in mm.—Carapace: male, length 17, width 13; female, length 10, width 8.

Variation.—Members of the genus *Epialtus* are variable in a number of respects. The hepatic expansion varies in shape and the rostrum varies from triangular to suboblong in shape. Williams and Pearse (1951) listed specimens that could not be placed with certainty in *dilatatus*.

Rathbun (1925) recognized from southwestern Florida an elongate form of *E. dilatatus* which has a longer rostrum and slightly different lateral expansions than the typical form. The complex should be reviewed as more material becomes available.

Habitat.—The species has been reported from shell reefs and coarse coral sand, and the elongate form has been found on sandy-grassy bottoms as well; 4.6 to 22 m.

Type-locality.—St. Thomas.

Known range.—Off Beaufort Inlet and New River, N. C.; southwest Florida; Yucatan; Bahamas to St. Thomas.

Remarks.—Ovigerous females are known from April through summer in Florida, June in North Carolina, September in Brazil, and November in Puerto Rico (Rathbun 1925; USNM). An ovigerous female collected in May from Biscayne Bay, Fla., produced 60 larvae whose development was followed in the laboratory (Yang 1968). Reared in bay water 33–36‰ at 25°C, larvae fed *Artemia* nauplii passed through the standard stages for spider crabs. Zoea I lasted 2.5 (\bar{x}) days; zoea II, 3 (\bar{x}) days; megalopa, 6.5 (\bar{x}) days. Only 5 individuals reached first crab and none reached the second crab stage. Yang described the stages and compared them to other known developments of Epialtinae (eight species to that date) and to representatives of other subfamilies.

Genus *Sphenocarcinus* A. Milne Edwards 1875

Garth 1958:217.

Sphenocarcinus corrosus A. Milne Edwards

Figs. 250, 259c

Sphenocarcinus corrosus A. Milne Edwards 1875, pl. 17, figs. 5–5c.—1878:136.—Hay and Shore 1918:460, pl. 39, fig. 1.—Rathbun 1925:187, text-fig. 73, pl. 62; pl. 223, figs. 3–5.—Williams 1965:248, figs. 227, 233C.

Recognition characters.—Carapace subpentagonal, broad behind, anterolateral margin concave, posterolateral margin convex. Dorsal surface deeply channeled, leaving symmetrical, coarsely punctate, or eroded elevations in regular pattern as follows: longitudinally placed, trefoil-shaped gastric, transversely placed cardiac with 2 deep posterior indentations, transversely elongate intestinal, paired laterals extending from near lateral angles to near eyes, and paired small postocular and larger supraocular elevations; margins of all elevations sharply defined with surface finely eroded. Rostrum usually longer than carapace, formed of 2 pointed horns contiguous to near tips, slightly divergent in old individuals. Eyes deeply sunk between 2 low smooth excrescences. Basal antennal article truncate, antennal flagellum hidden beneath rostrum. Epistome long, narrow.

Chelipeds weak; first pair of walking legs longer than others and exceeding length of chelipeds by more than length of dactyl.

Abdomen in both sexes with 7 distinct segments.

Measurements in mm.—Carapace: male, length 13, width 7; ovigerous female, length 23, width 11.

Variation.—Divergence of the rostral horns varies individually. In some specimens the horns are contiguous nearly to the tip, in others the horns

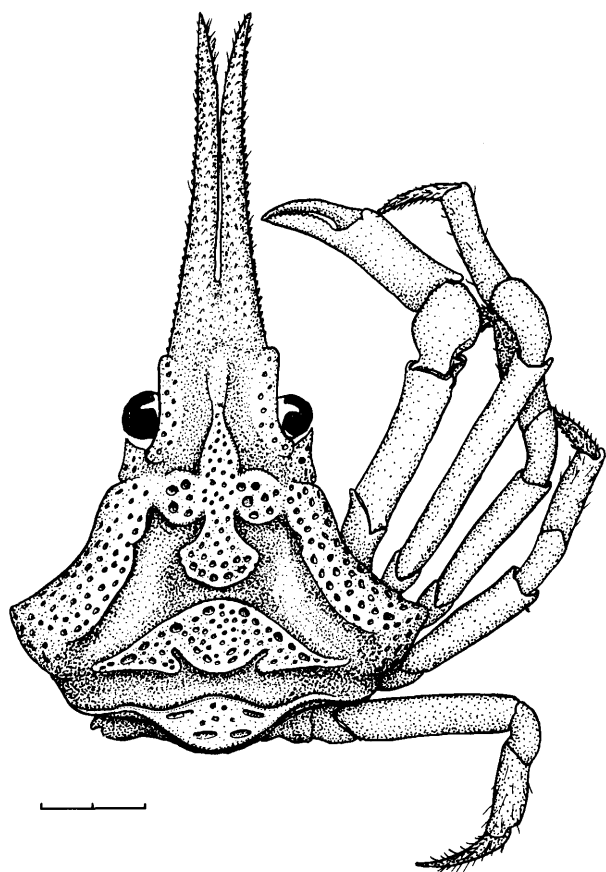


Fig. 250. *Sphenocarcinus corrosus* A. Milne Edwards. Male in dorsal view, legs of left side not shown, 2 mm indicated (from Williams 1965).

may be divergent for half their length, and in still others there is no evidence at all of bifurcation.

Color.—Orange-red.

Habitat.—165 to 271 m, rarely 365 (?) m.

Known range.—Off Cape Lookout, N. C., Gulf of Mexico (Goeke and Shaw 1980) to Barbados.

Remarks.—Ovigerous females have been reported from North Carolina in April (Rathbun 1925).

Subfamily Pisinae

Eyes with commencing orbits; each eye retractile into sometimes large, blunt, usually isolated, cupped postocular tooth or lobe, but never to such extent as completely to conceal cornea from dorsal view; usually prominent supraocular eave with anterior angle sometimes produced forward as a spine; eyestalks short. Basal antennal article broad, at least at base, anterior angle generally produced to form tooth or spine. Merus of external maxilliped broader than ischium owing to expansion of anteroexternal angle, and carrying palp at anterointernal angle. Rostrum [except in *Neodoclea* among New World forms] 2-spined; legs often very long (Alcock 1895). First pleopod medium stout to slender, usually apically somewhat tapering, but apex extremely varying (blunt, acute, filiform, straight, geniculate, etc.); second pleopod short (Stephensen 1945).

Key to Genera and Some Species

(Adapted in part from Garth 1958)

1. Intercalated orbital spine, present between supraorbital and postorbital spine 2
- Intercalated orbital spine absent 3
2. Rostrum hollowed out in form of gutter ventrally *Coelocerus spinosus*
- Rostrum not hollowed out ventrally *Nibilia antilocapra*
3. Supraocular eave and postocular process not closely approximated 4
- Supraocular eave and postocular process closely approximated (except occasionally in juveniles less than 8 mm carapace length) *Libinia*
4. Rostrum bifid for more than half its length *Rochinia*
- Rostrum bifid for not more than half its length; small species *Pelia mutica*

Genus *Coelocerus* A. Milne Edwards 1875

Rathbun 1925:446.

Coelocerus spinosus A. Milne Edwards

Figs. 251, 259i

Coelocerus spinosus A. Milne Edwards 1875:85, pl. 18, figs. 2–2b.—Rathbun 1925:446, text-fig. 130,

pl. 263; pl. 264, figs. 1, 2.—Felder 1973:49, pl. 7, fig. 6.—Powers 1977:50.

Libinia cavirostris Chace 1942a:86, pl. 27.

Recognition characters.—Covered almost everywhere except on fingers and greater part of dactyls on walking legs with short, close pile. Carapace swollen, spinose; 6 median spines (2 gastric, 1 urogastric, 2 cardiac, 1 intestinal), lateral gastric spine

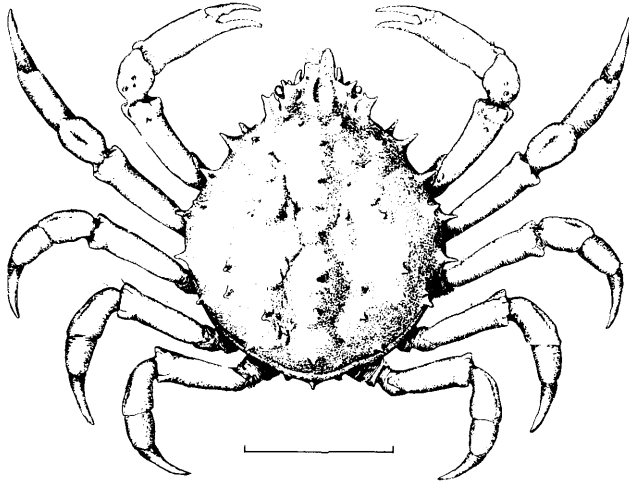


Fig. 251. *Coelocerus spinosus* A. Milne Edwards. Female in dorsal view, 5 cm indicated (from Rathbun 1893).

anterolateral to each side of anteriormost median spine; 5 spines above lateral margin, first (hepatic) strongest, small dorsal hepatic mesial to it; 6 dorsal branchial spines, 4 arranged in 2 longitudinal rows of 2 each; 1 spine above posterolateral margin in line with intestinal spine. Rostrum short, ascending extremity slightly bifid; in form of gutter open below, lateral margins folding under; longitudinal depression at base between orbits. Orbit with narrow buttonhole fissure above and below, preocular angles spiniform, postocular cup produced laterally. Basal antennal article with strong anterior tooth pointing downward, proximolateral tooth smaller; small spine immediately behind article, another at buccal angle; 2 strong pterygostomian spines.

Legs stout. Chelipeds of female no longer, but those of male longer than next leg; merus with blunt spine near each end; palms of male elongate, granulate, those of female diminishing in width dis-

tally; fingers finely toothed on cutting edges, proximal gape in male. Walking legs with short, blunt, terminal spine on merus.

Abdomen of both sexes with median spine on first 2 segments, lateral lobes on second.

Measurements in mm.—Carapace: male, length 119, width including spines 102; female, length 108, width including spines 94.

Variation.—Spines are proportionally longer and the extremity of the rostrum is more deeply bifid in the young. There is a tendency to doubling of the branchial spines.

Habitat.—17 to 71 m.

Type-locality.—Off Florida, 34.75 m.

Known range.—Off Cape Fear, N. C., to near Cape Canaveral, Fla. (B. B. Boothe, Jr., personal communication); W Florida to E of Mississippi River delta.

Remarks.—*Coelocerus spinosus* was placed in the Mithracinae by Garth (1958) but allied to *Stenocionops* in the Majidae by Rathbun (1925). The general shape of the carapace, ventral aspect of the rostrum, and conformation of the orbital region resemble those features in *Libinia* (see also Chace 1942a), and the male pleopods resemble those of both *L. dubia* and *emarginata* as well as of *Stenocionops furcata coelata* and *spinimana*. There is little doubt that the species is close to the limits of both the Pisinae and Mithracinae, but in my opinion it is most closely allied to the former.

Recent records from the southeastern United States have extended the known range of this species outside the Gulf of Mexico. An ovigerous female is known from west Florida (no date).

Genus *Libinia* Leach 1815

Garth 1958:322.

Key to Species

1. Median line of carapace with about 6 spines; spine on anterolateral angle of buccal frame *L. dubia*
 Median line of carapace with about 9 spines; anterolateral angle of buccal frame without spine *L. emarginata*

Libinia dubia H. Milne Edwards

(Spider crab)

Figs. 252, 259g

Libinia dubia H. Milne Edwards 1834:300, pl. 14bis, fig. 2.—Hay and Shore 1918:456, pl. 38, fig. 5.—Rathbun 1925:313, text-figs. 105–106; pls. 114–115; pl. 122, fig. 1.—Boone 1927:37.—Williams

1965:253, figs. 232, 233G.—Felder 1973:52, pl. 7, fig. 8.—Powers 1977:63.

Recognition characters.—Similar in general characters to *L. emarginata* but with more pyriform carapace and fewer spines; median row with but 6 spines, 2 gastric, 1 genital, 2 cardiac, and 1 intestinal; preorbital, subhepatic, and lateral spines stronger than in *L. emarginata*, but spiniform tu-

bercles few or wanting altogether. Rostrum slightly longer and more definitely bifid than in *L. emarginata*. Anterolateral angle of buccal frame armed with spine.

Measurements in mm.—Carapace: male, length 102, width including spines 82; ovigerous female, length 74, width 64; mature female, length 38, width 34.

Variation.—Dorsal spines and tubercles variable in length.

Habitat.—Found on almost all types of bottom in the shallow ocean and saltier estuaries. Occasionally, large individuals are found in pools left by falling tide. Immature individuals are often completely overgrown with sponges, hydroids, ascidians, barnacles or worm tubes, but the larger ones are usually almost clean. Near shore to 46 m.

Type-locality.—"Cotes des Etats-Unis."

Known range.—Cape Cod, Mass., to southern Texas; Bahamas and Cuba.

Remarks.—Some authors attribute a geologic record to this species extending from the Upper Miocene of Virginia (Rathbun 1935) through the Pleistocene of New Jersey (Rathbun 1935) and Maryland (Easton 1940). Glaessner (1969) more conservatively limited North American records for *Libinia* to closely related *L. emarginata*, only from the Pleistocene.

Tabb and Manning (1961) found this species common in Florida Bay, and Dragovich and Kelly (1964) reported it as the most common spider crab in Tampa Bay; Wilson (1969) found young *L. dubia* in canal-lake waters of low salinity (0–10‰) in southwestern Louisiana.

An association of this species with the jellyfish *Stomolophus meleagris* has been reported. The crabs

have been found in the subumbrellar space, and on occasion small specimens have been taken from the genital pits. Corrington (1927) found medusae with crabs between Sullivan Island and Isle of Palms, S. C., in May, and Gutsell (1928) found the association in the vicinity of Cape Lookout, N. C., in summer and fall. The crabs, found in adult jellyfishes, varied in length from 3 to 37 mm. Near the mouth of the Patuxent River, Md., in late August and early September, 1963, at depths to 3 m in water 30 m deep, Jackowski (1963) found small *L. dubia* living on and within many medusae of *Aurelia aurita*. Concurrently, numerous young harvestfish were observed feeding upon the medusae. Eleven *L. dubia* collected from 10 jellyfish had carapace lengths of 10–25 mm. Seven of these were clinging to the ventral surface of the subumbrella, two to the manubrium between oral arms, and two were in mesoglea of the umbrella. Several crabs appeared to be feeding upon a living medusa later in the laboratory. Crabs pulled fragments of tissue from the exumbrella with their chelipeds and ate them. None showed ill effect from eating or living in medusae. Incidence of crabs associated with swarms of jellyfishes (*Chrysaora quinquecirrha*, *Stomolophus meleagris*, and *Chiropsalmus quadrumanus*) in Mississippi Sound, Miss., varied from 0 to 100%, being highest in populations trawled from the bottom (Phillips, et al. 1969); moreover, any scyphomedusae introduced into aquaria containing *L. dubia* harbored some crabs within a few hours. The crabs actively fed on medusae.

Ovigerous females are recorded from January to June in Florida, May in Connecticut, August in New Jersey, and April to August in North Carolina (various authors, museum records, and H. J. Porter, personal communication).

From laboratory cultures, Sandifer and Van Engel (1971) described two zoeal stages and a megalopa, the usual developmental sequence for spider crabs. Complete larval development required about nine days in water of 22‰ salinity at 25.5°–28.5°C. Zoeal molting behavior was observed on several occasions in which zoea I molting to zoea II apparently uses its old abdominal skin as a brace against which to exert pressure while withdrawing its carapace and appendages from the old skin. This "bracing" behavior was not seen in the molt from zoea II to megalopa. Only uninjured larvae were able to "brace" and molt successfully.

Planktonic larvae of *Libinia* spp. were found in samples taken from the mouth of Chesapeake Bay to lower York River from June to October, most common in July and September, in water of 15.74 to 32.34‰ salinity and 20° to 28.1°C respectively (Sandifer, 1973d). Most of the larvae (zoea I and

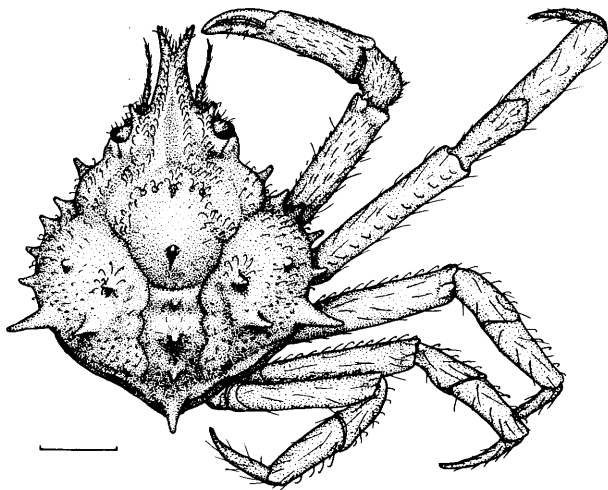


Fig. 252. *Libinia dubia* H. Milne Edwards. Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

II) occurred in bottom samples. Fish (1925) found planktonic larvae of *Libinia* spp. at Woods Hole from June to October, Hillman (1964) found them from early July to mid-September in Narragansett Bay, R. I., and Deevey (1964) found them from July to October in Delaware Bay. Larvae of *Libinia* spp. were found rarely at a station 1.6 km off Beaufort, N. C., in May, July and August at 8-m depth; at stations 6.5 km offshore they occurred rarely in July at this depth (Dudley and July 1971).

Pearse (1929), studying the survival rates of various estuarine crabs in dilutions of sea water and in air, found *L. dubia* least able to survive desiccation and dilutions of sea water. Ayers (1938), in a study of the relationship of habitat to oxygen consumption among certain estuarine crabs, found that *L. dubia* lives much of the year in relatively deep [estuarine] water where there is low oxygen content, sometimes very little. The species is correspondingly sluggish and slow. Gray (1957) showed that gill area per gram of weight in this species is small.

Pearse (1952b) reported *Octolasmis lowei* (= *mul-leri*) on the gills and mouth parts, and *Chelonibia patula* on the carapace of *L. dubia* in Texas.

Libinia emarginata Leach

(Spider crab)

Figs. 253, 259h

Libinia emarginata Leach 1815:130, pl. 108.—Hay and Shore 1918:456, pl. 38, fig. 6.—Rathbun 1925:311, text-figs. 103–104; pls. 110–113.—Williams 1965:252, figs. 231, 233H.—Felder 1973:52, pl. 1, fig. 7.—Powers 1977:64.

Recognition characters.—Carapace orbicular, about 1.16 times longer than wide, spinose and tuberculate, with dense covering of short hairs. Larger spines arranged as follows: median row of about 9 extending from near base of rostrum to posterior border consisting of 4 gastric, 1 genital, 2 cardiac, and 2 intestinal; lateral marginal spines 5 on each side; 2 subhepatic spines; 2 or 4 spines above posterior margin, aside from median spine, and about 4 dorsal branchial spines; spiniform tubercles scattered about among larger spines. Gastric region marked off by deep groove. Rostrum slightly depressed, emarginate or bifid at tip; median groove between eyes. Orbits with prominent preorbital spine, 2 spines beneath on basal article of antenna; 1 fissure above and 1 beneath. Anterolateral angle of buccal frame spineless.

Chelipeds equal, larger in male; hands granulate; fingers smooth, evenly denticulate, and about

half as long as hand. Walking legs long, hairy, unarmed, often unequal and asymmetrical (result, perhaps, of injury and subsequent regeneration).

Measurements in mm.—Carapace: male length 124, width 124; ovigerous female, length 69, width 66.

Variation.—The number of median spines in the gastric region is subject to variation in size and number.

Color.—A brownish or dirty yellow.

Habitat.—Found on almost any kind of bottom; shore to 49 m, occasionally to 124 m.

Type-locality.—Unknown.

Known range.—Windsor, Nova Scotia, to western Gulf of Mexico.

Remarks.—The young of *L. emarginata* and *L. dubia* are difficult to distinguish. Wass (1955) pointed out useful distinguishing marks. "The rostrum of *L. dubia* is much longer, forming a V; the carapace is not so wide, and there is but one spine on the intestinal region whereas *L. emarginata* has two." Andrews (1883) gave a complete anatomical study of *L. emarginata*, and Meiss and Norman (1977a, b) almost a century later compared the stomogastric ossicles and musculature to that in penaeideans, astacideans and anomurans, finding the structure to reflect generally accepted concepts of the phylogenetic position of brachyurans.

Hildebrand (1954) reported this species as the most common larger spider crab on the western Gulf of Mexico shrimp grounds. It was most common in July, at which time ovigerous females were observed. Juveniles were observed riding the bell of the scyphozoan *Stomolophus meleagris*, a habit noted by others for the young of *L. dubia*. Winget, et al. (1974) found *L. emarginata* seasonally commonest along a breakwater in Delaware Bay in

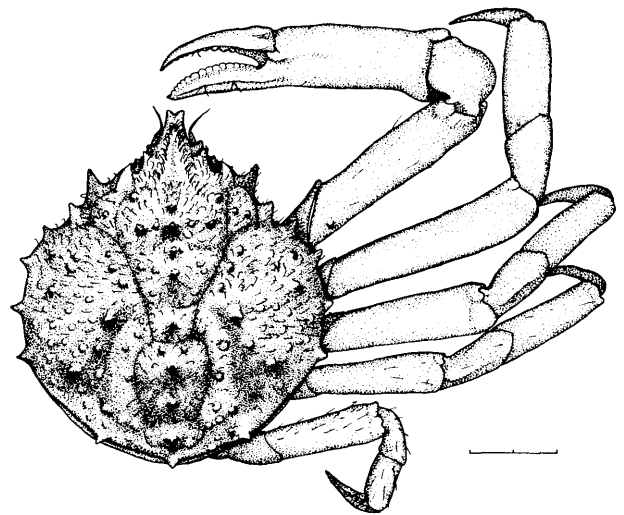


Fig. 253. *Libinia emarginata* Leach. Male in dorsal view, legs of left side not shown, 20 mm indicated (from Williams 1965).

spring and summer, and also common in mud of sloughs where no other species of crab occurred in a salinity range of 15 to 32‰. They found a male-female ratio of 3:1 in winter when the animals were less abundant.

In addition to the Texas records, ovigerous females are recorded from February to May in Connecticut, May to early September at Woods Hole, Mass. (Hinsch 1968), August in New Jersey, and March-April (H. J. Porter, personal communication) and June-August (Dudley and Judy 1971) in North Carolina. Eggs at oviposition are a bright orange-red color but change to brown as development progresses (Hinsch 1968). Ovigerous females taken in fall and spring in South Carolina and from Narragansett Bay, R. I., during summer, isolated in chambers under controlled conditions, produced broods of larvae which were reared in an array of salinities (15–45‰) and temperatures (15°–30°C) on a diet of *Artemia* nauplii, and were described and illustrated by Johns and Lang (1977). There are two zoeal stages and a megalopa. Optimal conditions for development differed for larvae from the two localities, probably showing latitudinal adaptations. At 30‰ salinity and 20°C Rhode Island larvae attained second zoea in five days, megalopa in eight and first crab in 14; South Carolina material reached the same stages in 3, 6 and 14 days at 25°C. The larvae showed no significant differences from those in plankton, but first stage larvae from South Carolina were smaller than those from Rhode Island. The zoeae cannot be differentiated from those of *L. dubia*, but megalopae of *L. dubia* have one cardiac protuberance on the carapace, *L. emarginata* two.

Bigford (1978) showed that survival is greater and development time shorter for larvae fed diets including *Artemia salina* nauplii either alone or in combination with other foods. Survival is also correlated with amount of *Artemia* nauplii fed and can probably be attributed to the high fat content in these nauplii (Sulkin 1975).

Hinsch (1969) stated that factors governing sexual maturation and onset of spermatogenesis in this species are unknown. Spermatogenesis occurs in testes of males having a carapace length as short as 19 mm; the vas deferens from these animals contained spermatophores filled with spermatozoa that appeared to be structurally identical to those of larger males at light-microscope and ultrastructural magnifications. Spermatophores are found within the vas deferens at all times of year. Hinsch (1969, 1973) described ultrastructure of sperm. More detail on structure of the vas deferens and comparison with the virtually identical structure in *L. dubia* were given by Hinsch and Walker (1974);

in fact, the same structure and function were also found for *Heterocrypta* and *Stenorhynchus*. The male reproductive tract produces sperm long before the crab has attained full size and, presumably, ability to mate. The authors observed a male *L. emarginata* mating with a female for short periods (5–7 minutes) and mating frequently with several different females over a period of several days.

In an aquarium, females produced a new brood in less than 12 hours after releasing zoeae (Hinsch 1968). When females were about to release zoeae, males in the same aquarium could be seen walking on tips of their dactyls, apparently searching, and often fighting with each other. Under these conditions, two definite behaviors were associated with release of zoeae.

First, encounters with non-gravid females or females which had either released larvae or were about to do so generally resulted in the females mating in the "hard" condition (see also Hartnoll 1969). Whether the female first mates at times of final molt to adulthood is not known. Ovigerous females with eggs in early stages of development were never observed to mate. The male first grasped legs of the female and positioned her beneath him with the sterna face to face, then with his chelae grasped the female by the hepato-ptyergostomial region. The abdomen of the female was pulled down and bent back at the same time the male's abdomen was lowered. Copulation then began and the male frequently rotated over onto his carapace holding the female above him. When copulation was completed, the male resumed a walking position, released his hold on the anterior part (head) of the female, once again grasped her by the legs and then released her.

Second, in a number of cases a female about to release zoeae would be captured by a male or fought over by two males only to be lost to a third. Eventually, a male grasped the female by the legs with his chelae, moved her behind him, their carapaces touching and the axis of their bodies at right angles to each other. The tips of his fifth legs were inserted beneath the abdominal flap to hold her in this position after which he often retreated to a protected area and stood with chelae outstretched, fending off other males. Held in this position the female released the zoeae, then cleaned remaining eggs cases from her pleopods, following which the male released her. Juvenile males or females and females with broods in early stages were never objects of this "obstetrical" behavior. Hinsch thought that predictability and specificity of these patterns suggested their possible initiation by pheromone(s).

Kalber and Costlow (1968) and Kalber (1970)

found that *L. emarginata* has larvae with osmoregulatory ability for much of the larval life before the megalopa reverts to the stenohaline pattern of adults. This could be a survival mechanism in large estuaries.

Allometric studies show that there is a 16-fold weight range for mature non-molting males, similar to that found for other male majids (Aldrich 1974). Some of the smallest of these males are capable of pursuing and mating with mature females. Mature females are ovigerous in two size categories, but the largest "old" mature females were never found with eggs. Their reproductive status is not understood. Within this great range of mature sizes, small crabs bearing many encrusting organisms appear to have lived for several years whereas larger crabs from muddy bottoms, seldom heavily encrusted, may not have lived as long. Two sets of crabs may be present, small ones that have reproduced for several years and larger ones with a shorter reproductive period. Aldrich discussed feeding strategies for these proposed groups.

Moreover, Aldrich (1976) maintained that predation of *Libinia emarginata* upon *Asterias* in absence of other food, the discovery of significant amounts of *Asterias* ossicles in newly molted crabs, and the finding together of *L. emarginata* with *Asterias* having many missing arms, suggest that under the right conditions this predation may be common. He noted that in captivity a crab eats only one arm of a starfish at a time, twisting open the dorsal side of an arm with the chelae. A starfish thus wounded autotomizes the arm and the crab eats at the open end of the detached arm. The spider crabs prefer prey of mean weight 12% of their own weight regardless of crab size; crabs fed ad libitum in 12°–13°C water ate little more than enough to sustain metabolism, but this may have been a seasonal phenomenon. In the same experiment, *Callinectes sapidus* and *Cancer irroratus* held with *L. emarginata* did not attack starfish even though starved for several weeks.

The eyes of *L. emarginata* show light-dark adaptation analogous in some respects to rods and cones of the vertebrate eye, i.e., are differentiated not for color vision but for use in dim and bright light as are the vertebrate rods and cones (Wald 1968).

Gray (1957) compared gill area in this sluggish species with that of other common littoral crabs in the Carolinas and found that it had the smallest gill area per gram body weight of any studied.

Genus *Nibilia* A. Milne Edwards 1878

Rathbun 1925:289.

Nibilia antilocapra (Stimpson)

Figs. 254, 259f

Pisa antilocapra Stimpson 1871a:110.

Nibilia antilocapra.—Rathbun 1925:290, text-fig. 97, pls. 102, 103, and 239.—Williams 1965:251, figs. 230, 233F.—Powers 1977:65.

Recognition characters.—Carapace pyriform, conspicuously spinose, much swollen, longer than wide; gastric and cardiac regions with about 18 spines of moderate size and smaller ones interspersed, largest spines surmounting summit of regions and somewhat surrounded by circle of smaller spines; other regions also well spined. Rostrum horizontal, undivided at base but moderately bifurcate for greater part of length, horns varying from $\frac{3}{5}$ to $\frac{4}{5}$ total length of rostrum. Preorbital spine ascending, slightly curved, not so advanced as base of horns; behind this a small spine on supraocular eave and a triangular (intercalated) spine or tooth on supraocular border; postocular cup terminating in a spine. Basal antennal article with strong distolateral spine, short spine just outside posterior end, and tubercle behind this in line with prominent angle of buccal cavity. Maxilliped and sternum smooth. Pterygostomian region armed with 2 rows of spines.

Chelipeds of adult male longer and stouter than walking legs; merus and carpus rough with spines above and below; chelae almost cylindrical; hand nearly as long as merus, nearly smooth, few spines near articulation with carpus; fingers agape for half of length in large males, with well-developed tooth on dactyl in gaping part. Walking legs long, slender; merus and carpus with few spines longitudinally arranged; dactyls long, stout, unarmed.

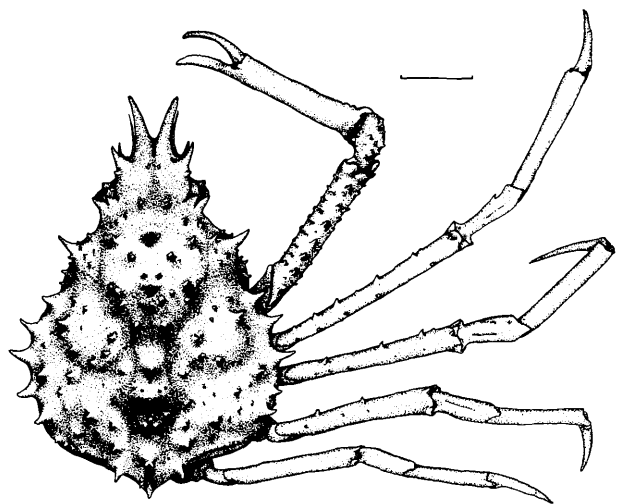


Fig. 254. *Nibilia antilocapra* (Stimpson). Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

Measurements in mm.—Carapace: large male, length 120, width 82; female, length 60, width 43.

Variation.—The young and half-grown are covered with short hair, but adults are nearly bare except for hairy dactyls on the walking legs.

Habitat.—The species has been reported from gray and coarse sand, broken-shell, and coral bottoms (Rathbun 1925); 66 to 256 m (Wenner and Read 1982).

Type-locality.—Florida, off Carysfort Reef, 95 and 109.7 m; and off Alligator Reef, 251.8 m.

Known range.—Off Cape Hatteras, N. C., to Gulf of Mexico just east of Mississippi River Delta and Gulf of Campeche; Windward Islands, West Indies, off Guyana.

Remarks.—Ovigerous females are known from St. Vincent in February, Barbados in March, and North Carolina in July and October (Rathbun 1925; USNM).

Individuals collected from a reef SE of Cape Lookout, N. C., did not survive 48-h exposure to 10°C (F. J. and W. B. Vernberg 1970).

Genus *Pelia* Bell 1835

Garth 1958:268.

Pelia mutica (Gibbes)

Figs. 255, 259a

Pisa mutica Gibbes 1850:171.

Pelia mutica.—Hay and Shore 1918:455, pl. 38, fig.

7.—Rathbun 1925:278, text-fig. 94, pl. 98, figs.

2–3.—Williams 1965:250, figs. 229, 233E.—

Felder 1973:53, pl. 7, fig. 13.—Powers 1977:65.

Recognition characters.—Small species. Carapace pyriform, greatest width approximately $\frac{2}{3}$ greatest length; swollen, devoid of tubercles, covered with sparse pubescence, gastric and cardiac regions elevated. Rostrum well developed, $\frac{2}{5}$ as long as remainder of carapace, formed of 2 more or less distally divergent horns with outer margins often parallel, furrow on basal portion. Eyes retractile. Basal antennal article long, slender, forming incomplete floor to orbit and jutting out beyond orbital margin, usually with small tooth or spine at anteroexternal angle; antennal flagellum greatly developed.

Chelipeds of mature male as long as first walking legs but stouter and almost bare, weaker in females and young males; upper and inner margin of merus dentate; carpus with longitudinal denticulate ridge; upper and lower margins of hand slightly arcuate; basal half of fingers widely agape,

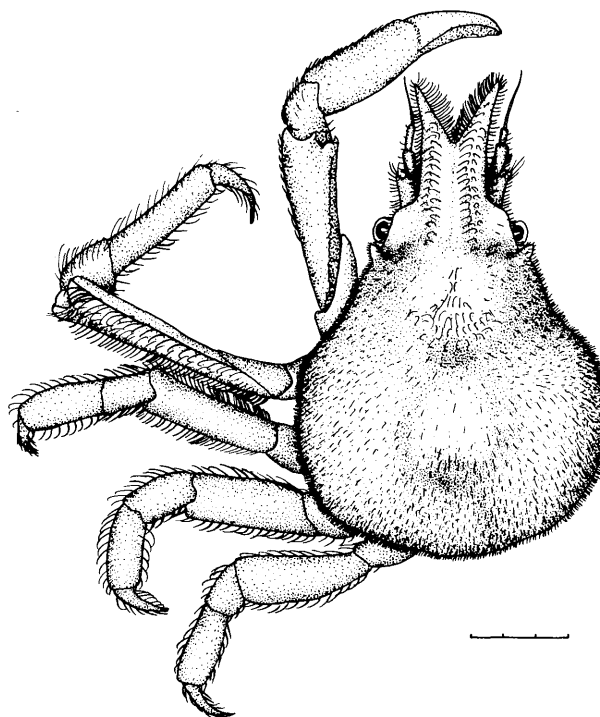


Fig. 255. *Pelia mutica* (Gibbes). Animal in dorsal view, legs of right side not shown, 3 mm indicated (from Williams 1965).

with denticulate margins on occludent parts and broad basal tooth of dactyl; fingers weaker and not agape in females and young males. Walking legs with marginal rows of stiff setae, meri much compressed, dactyls strongly curved.

Abdomen of both sexes with 7 free segments.

Measurements in mm.—Carapace: male, length 13, width 9; ovigerous females, length 5–10 (Wass 1955).

Color.—Bright red in patches on carapace and in bands on legs, spots of light red on chelipeds (Rathbun 1925).

Habitat.—This species has been found on gravelly and shelly bottoms of bays and sounds, among hydroids, ascidians, and sponges on wharf piles, and also on shelly reefs (Felder 1973; Pearse and Williams 1951). Individuals are often so covered with sponge that they are difficult to recognize. Gray (1961) reported the species from *Chaetopterus* tubes. Low-water mark to 51 m.

Type-locality.—Charleston Harbor, off White Point Battery, S. C.

Known range.—Buzzards Bay and Vineyard Sound, Mass., to off Port Mansfield, Willacy Co., Tex. (Felder 1973); Cuba, Puerto Rico, and St. Thomas, West Indies.

Remarks.—Ovigerous females are known in most months of the year in Florida (Rouse 1970), through the summer in the Carolinas, and July in Massa-

chusetts (Rathbun 1925). Hartnoll (1965) concluded that breeding was year round in Jamaica.

Genus *Rochinia* A. Milne Edwards 1875

Garth 1958:282.—China 1966:257.

Carapace pyriform or elongate-triangular; armed either with tubercles or long spines, hepatic and

branchial spines always prominent and very conspicuous. Rostrum consisting of 2 spines, usually long and slender. Eyes small, retractile against sharp postocular process commonly but little cupped; supraocular eave terminating either in forwardly directed tooth or upturned spine. Basal antennal article not very broad, sharply truncate; mobile portion of antennae freely exposed on either side of rostrum.

Key to Species

(Modified from Rathbun 1925)

1. Six spines on gastric region *R. crassa*
Less than 6 spines on gastric region 2
2. Dorsal spines or tubercles acute *R. tanneri*
Dorsal spines or tubercles mostly large and flat topped *R. umbonata*

Rochinia crassa (A. Milne Edwards)

Figs. 256, 260a

Amanthia crassa A. Milne Edwards 1879:203, pl. 28.

Rochinia crassa.—Rathbun 1925:210, text-figs. 83–84, pls. 68–69, 226.—Boone 1938:216, pls. 77–78.—Williams, McCloskey, and Gray 1968:60.—W. E. Pequegnat 1970:183.—Powers 1977:66.

Recognition characters.—Carapace convex with tendency to median carination; surface pubescent; median spines 6 (5 in juveniles), 2 anterior spines (gastric) in row, each flanked by remote spine on each side; anteriormost median spine forming first of an oblique row extending backward to spine at lateral angle of branchial region, scattered spines

mesial to row; prominent marginal hepatic spine; small spine on each side of middle above posterior margin (lacking in juveniles) and row of about 6 spines over bases of last 2 legs; from above anterior of legs (third walking leg) an irregular row of spines extending forward to anterior angle of buccal cavity. Rostrum divided into 2 stout, gradually tapering, acuminate spines, diminishing in relative length with age. Eyes small and retractile against well-developed postorbital lobe; supraocular eave bearing tubercle and ending in preocular spine. Basal antennal article with 2 spines on lateral margin pointing downward, forward and outward.

Chelipeds long, slender, tuberculate, becoming quite stout and elongate in adults; merus with distal spine and 1 or more spinules near proximal end; hand slightly compressed and distally enlarged; fingers gaping at base, tooth on dactyl in gape of males, prehensile edges with stout, close fitting teeth. Walking legs slender, diminishing noticeably in size from first to fourth, surpassing chelipeds in medium sized individuals; merus with short distal groove.

Measurements in mm.—Carapace: male, length to base of rostral horns 95, width 79.5 (Rathbun 1925); female, length to base of rostral horns 77, including horns 87, width 65.

Color.—Carapace on dorsal side diffusely mottled with light rust-orange; remainder dirty white. Merus, carpus and propodus with darker rust-orange blotches, particularly on distal parts (Williams, et al. 1968).

Habitat.—Mud and sand substrates; 66 to 860–1216 m (Wenner and Read 1982).

Type-locality.—Between Cuba and Florida, 24°15'N, 82°13'W.

Known range.—Nantucket Shoals, Mass., to Gulf

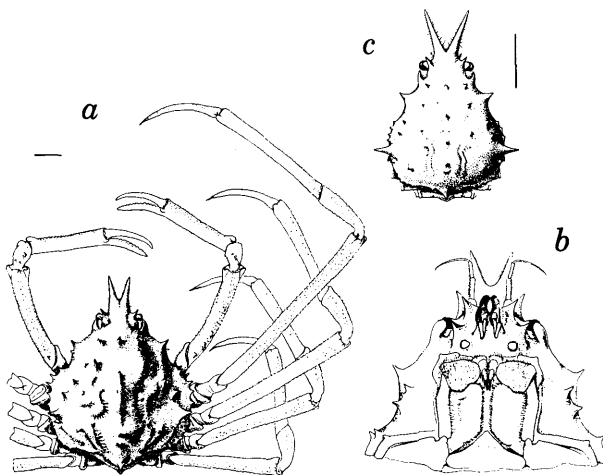


Fig. 256. *Rochinia crassa* (A. Milne Edwards). a, Female in dorsal view, walking legs of left side not shown completely; b, anterior part of same, enlarged ventral view; c, body of male in dorsal view. a, USNM 5693, c, 1 cm indicated (from Rathbun 1925 after Smith).

of Mexico off southern Texas; northern Cuba; W of Cabo de la Vela, Colombia; off French Guiana.

Remarks.—This species is the largest of the three species of *Rochinia* treated here. Ovigerous females are known from the northern Gulf of Mexico in February, August and November, and off southern Florida in June and August.

Menzies, et al. (1973) considered *R. crassa* an archibenthal species which ranges upward.

Rochinia tanneri (Smith)

Figs. 257, 260b

?*Amathia modesta* Stimpson 1871a:124.

Amathia tanneri Smith 1883:4.

Rochinia tanneri.—Rathbun 1925:216, pl. 227, fig. 1.

1.—Williams, McCloskey, and Gray 1968:60, fig. 15.—Powers 1977:66.

Recognition characters.—Small species. Carapace with fewer but relatively more prominent spines than *R. crassa*; 4 median spines of good size, 2 anterior gastrics flanked on each side by much smaller tuberculiform spine to form diamond-shaped pattern; 1 cardiac and 1 intestinal; moderate hepatic spine on each side, and branchial region with triangular arrangement of strong spine at posterolateral corner flanked mesially by 2 smaller spines. Rostral horns prominent, divergent, straight and slender. Orbit moderately open, preorbital spine

moderately developed, postorbital spine blunter. Basal antennal article with terminal anterolateral spine. Anterior angles of buccal cavity prominent, broad triangular tooth followed by 3 or 4 blunt, conical projections on pterygostomial region.

Chelipeds somewhat stouter than walking legs, similar to those of small *R. crassa*. Walking legs with short distal spine on merus of first leg, those of remaining legs reduced to tuberculiform protuberances.

Measurements in mm.—Carapace: male, length to base of rostral horns 21.6, width including spines 23.1 (Rathbun 1925); female, length to base of rostral horns 14.8, including horns 22.5, width including spines 14.8.

Habitat.—Sand, shells; 128 to 708 m.

Type-locality.—Off Delaware Bay.

Known range.—Off Martha's Vineyard, Mass., to Straits of Florida.

Remarks.—Juvenile *R. crassa* and *R. tanneri* are similar.

Rochinia umbonata (Stimpson)

Figs. 258, 260c

Scyra umbonata Stimpson 1871a:115.

Rochinia umbonata.—Rathbun 1925:222, text-fig. 85, pl. 72; pl. 73, fig. 1.—Chace 1940:63.—Williams, McCloskey, and Gray 1968:61, fig. 16.—W. E. Pequegnat 1970:183.—Powers 1977:67.

Recognition characters.—Surface covered with close tuberculiform pubescence, longer club-shaped se-

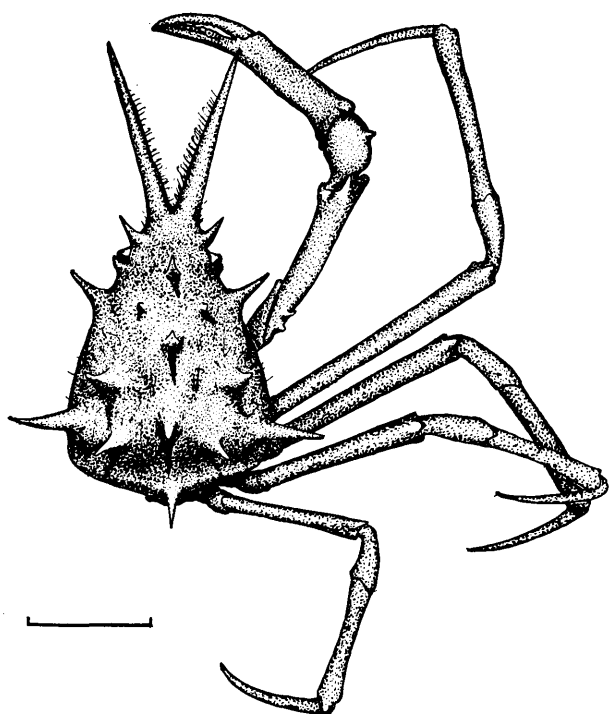


Fig. 257. *Rochinia tanneri* (Smith). Male in dorsal view, legs of left side not shown, 1 cm indicated (from Williams, et al. 1968).

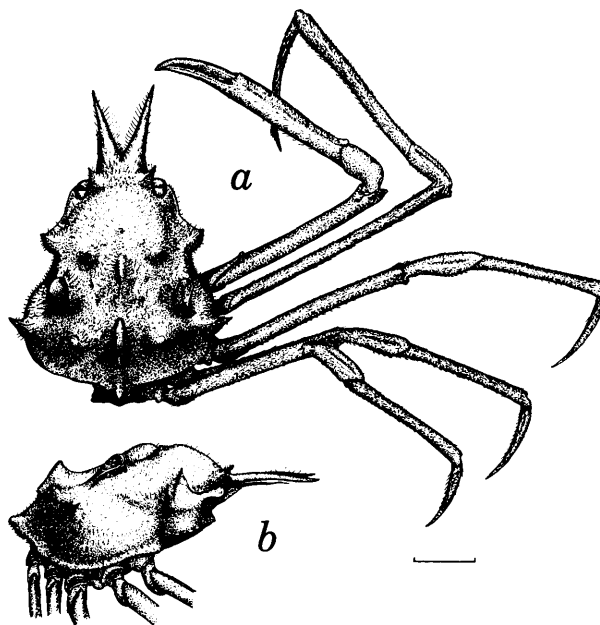


Fig. 258. *Rochinia umbonata* (Stimpson). Male: a, dorsal view, legs of left side not shown; b, lateral view of body, 1 cm indicated (from Williams, et al. 1968).



Fig. 259. Subfamilies Tychinae, Epialtinae and Pisinae, tips of right first pleopods of males: *a*, *Pitho therminieri* (Schramm), abdominal view; *b*, *Tyche emarginata* White, lateral view; *c*, *Speno-carcinus corrosus* A. Milne Edwards, sternal view; *d*, *Epialtus dilatatus* A. Milne Edwards, sternal view; *e*, *Pelia mutica* (Gibbes), sternal view; *f*, *Nibilia antilocapra* (Stimpson), abdominal view; *g*, *Libinia dubia* H. Milne Edwards, lateral view; *h*, *L. emarginata* Leach, lateral view; *i*, *Coelocerus spinosus* A. Milne Edwards, lateral view, USNM 57842; (*a-h* from Williams 1965); 0.33 mm indicated.

tae on margins of legs, and slender curved setae on rostrum, gastric region, and laterally on branchial region. Carapace with 9 tubercles on dorsal surface; 6 of these often large, flattened and irregular in shape, 1 posterior gastric, 1 cardiac, 2 on each branchial region; 3 smaller tubercles all gastric, 11 anterior, others lateral. Lateral margin with hepatic and branchial spine either triangular, flattened and somewhat appressed, or conical and projecting outward. Small tubercle on middle of posterior margin or on raised ridge parallel to posterior margin. Rostral horns divergent and varying in length. Orbits either narrow with supraocular eave somewhat convex in outline and preocular spine directed outward, or wider with eave concave and preocular spine directed outward. Basal antennal article unarmed or with inconspicuous tooth at distolateral angle. Angles of buccal cavity projecting, lobiform; subbranchial and pterygostomian regions tuberculate.

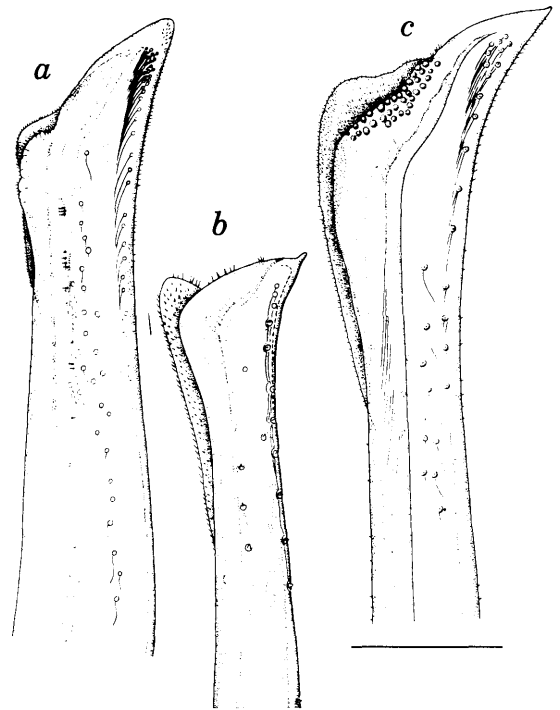


Fig. 260. Subfamily Pisinae, tips of right first pleopods of males, sternal view: *a*, *Rochinia crassa* (A. Milne Edwards), USNM 1169539; *b*, *R. tanneri* (Smith), USNM 46773; *c*, *R. umbonata* (Stimpson), USNM 11377; 0.33 mm indicated.

Chelipeds of male nearly as long as first walking legs, slightly enlarged; merus somewhat angled, upper margin tuberculate and with distal spine; carpus uneven, inner margin with thin lobe near merus; palm compressed, narrow, elongate, margins thin; fingers much shorter than palm, large tooth at base of gape in large males, prehensile edges of fingers denticulate. Walking legs slender, spine at distal extremity of merus on first pair, tubercle or spine on remaining legs.

Measurements in mm.—Carapace: male, length to base of rostral horns 54, including horns 62, width including spines 44; ovigerous female, length to base of rostral horns 57, including horns 73, width including spines 47.

Variation.—Extremely variable in ornamentation. The slender legs become extremely so in large individuals.

Habitat.—161 to 900 m.

Type-locality.—Off Sand Key, Florida.

Known range.—SE Cape Lookout, N. C., through eastern and northern Gulf of Mexico to NE of Nicaragua; through West Indies to St. Vincent.

Remarks.—Ovigerous females are known from April through June off Florida, in August off Georgia, and September off Nicaragua. Yang (1967), from an ovigerous female taken off Florida in June maintained at 10°C, hatched several prezoae and two well-developed zoeae. These were transferred

to 15°C but failed to develop further. He described the first stage, which was larger than that of other majids studied.

Subfamily Mithracinae

Carapace broadened anteriorly by outstanding, often tubular orbits; orbits formed by (1) an arched

supraocular hood, or semitubular horn, (2) hollowed postocular process, and (3) remarkable broadening or prolongation of anterior part of basal antennal article affording complete concealment to retracted eye. Rostrum often more or less deflexed (Alcock 1895). First pleopod like that in Pisinae; second pleopod short (Stephensen 1945).

Key to Genera and One Species

(Adapted from Garth 1958)

1. Intercalated orbital spine present (between supraorbital and postorbital spine); orbits not tubular 2
Intercalated orbital spine absent; orbits tubular 4
2. Legs cristate; orbits not projecting laterally beyond general outline of carapace (poor character) *Hemus cristulipes*
Legs not cristate; orbits projecting laterally somewhat beyond general outline of carapace (poor character) 3
3. Carapace ovate, usually broader than long; rostrum small (except *M. acuticornis*) *Mithrax*
Carapace broadly pyriform, longer than broad; rostrum large, usually with 2 strong divergent horns; basal antennal article armed with prominent spine at anteroexternal angle *Microphrys*
4. Lateral margin of carapace not armed with series of strong spines, but with 1 spine, usually strong, at lateral angle *Macrocoeloma*
Lateral margin of carapace armed with series of strong spines; basal antennal article very broad *Stenocionops*

Genus *Hemus* A. Milne Edwards 1895

Rathbun 1925:345.

Hemus cristulipes A. Milne Edwards

Fig. 261

Hemus cristulipes A. Milne Edwards 1875:88, pl. 16, figs. 1–1f.—Rathbun 1925:345, text-fig. 110, pl. 124, fig. 1; pl. 248, figs. 9–15.—Coelho and Ramos 1972:213.—Powers 1977:50.

Recognition characters.—Body and legs covered with depressed granules. Carapace longer than wide, thick and swollen, especially in prominent cardiac region; postorbital portion wide; gastric region high; branchial regions elliptical, each bearing 2 subacute prominences directed outward, first stronger than second. Subhepatic region deeply grooved. Rostrum small, short and wide, bicarinate dorsally, bent downward and bifurcated. Orbit with upper border unarmed but with narrow fissure; lower border incomplete; postorbital cavity receiving retracted eye; no preorbital spines. First and second movable articles of antennae wide and

flat, flagellum inserted at external angle of second. Merus of third maxillipeds long and somewhat dilated anterolaterally, exognath broad through midlength, narrowed distally.

Chelipeds small, fingers slightly gaping, strongly bent inward distally, scarcely spoon shaped. Walking legs short but strong, first longest and strongest, last pair very small; each merus wide, ornamented dorsally with thin straight crest and ventrally with lamellar prolongation bearing crenulate and arcuate border; remaining articles smaller but dactyls strong, much curved.

Abdomen of both sexes with 7 free segments.

Measurements in mm.—Carapace: female, length 7.6, width 6 (Rathbun 1925).

Habitat.—Sand, rock, and coral bottoms; in horn sponges and the coral *Porites porites*, 15 to 69 m (Powers 1977, summary).

Type-locality.—Near Contoy [Yucatan], at the entrance to the Gulf of Mexico, 21.9 to 32.9 m.

Known range.—Off Cape Lookout, N. C., and South Carolina; northwest of Gulf of Mexico and Yucatan, through West Indies to Pernambuco, Brazil (Powers 1977; Herbst, et al. 1979).

Remarks.—The dilated legs, antennal peduncle,

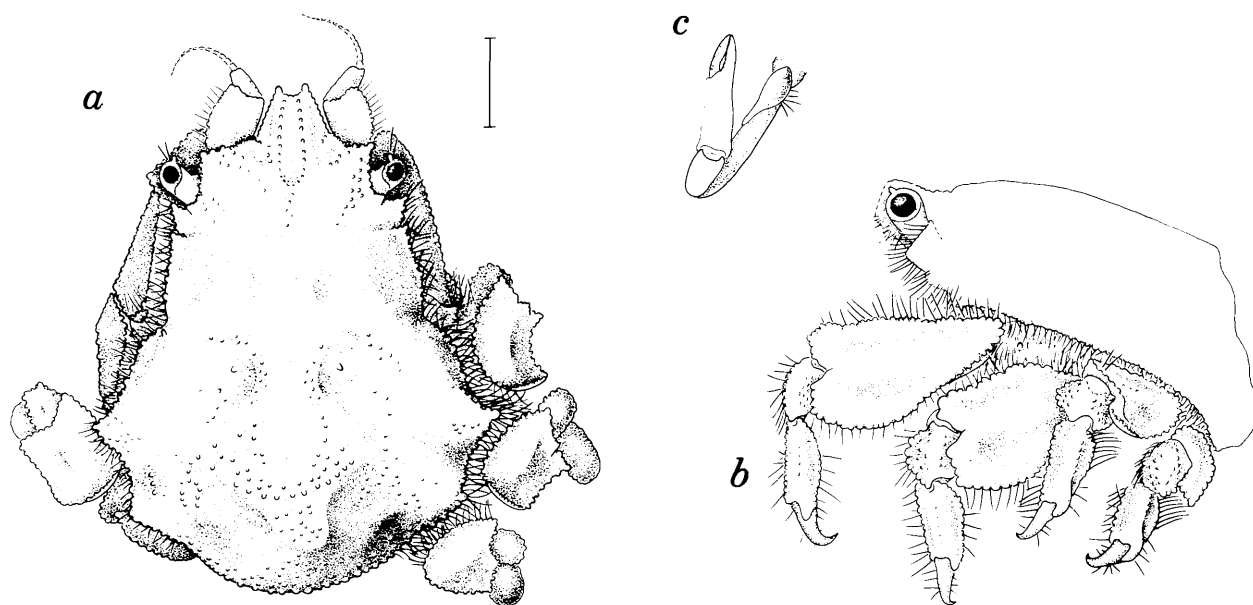


Fig. 261. *Hemus cristulipes* A. Milne Edwards. Female: *a*, dorsal view, some legs deleted; *b*, lateral view showing legs 2-5 in situ; *c*, right cheliped; 1 mm indicated (USNM 94050).

and deflexed rostrum cluster to surround a large cavity beneath the body (Rathbun 1925).

Genus *Macrocoeloma* Miers 1879

Garth 1958:412.

Carapace subpyriform or suboblong, but broadened anteriorly by projecting orbits; dorsal surface unarmed, tuberculate, or with few long spines;

margins without series of elongate lateral spines, but often with strongly developed lateral epibranchial spine preceded by smaller spines. Rostral spines well developed. Eyes retractile within roomy tubular orbits. Antennae with basal article considerably enlarged and armed distally with 1 or 2 spines; mobile part sometimes concealed by rostrum. Abdomen with 7 separate segments in both sexes. (Modified after Garth 1958.)

Key to Species

1. Carapace with fewer than 7 spines on posterior half, or if 7 some small. . 2
Carapace with 7 strong spines on posterior half *M. camptocerum*
2. Basal (fixed) antennal article armed with 2 ventral spines; rostral horns separated by U-shaped space *M. eutheca*
Basal (fixed) antennal article armed with 1 spine or sharp tubercle; rostral horns separated by space narrow or pointed at its base. *M. trispinosum*

Macrocoeloma camptocerum (Stimpson)

Figs. 262, 275m

Pericera camptocera Stimpson 1871a:112.

Macrocoeloma camptocerum.—Hay and Shore 1918:457, pl. 38, fig. 12.—Rathbun 1925:469, pl. 174, fig. 4; pl. 270, fig. 2.—Williams 1965:264, figs. 244, 245K.—Powers 1977:50.

Recognition characters.—Carapace irregularly triangular; surface covered with short, close pubescence, and, in addition, long, stiff, curled hairs on

front, gastric region, and lateral parts of branchial regions; wide at level of orbits, narrowing distinctly in hepatic portion, widening again posteriorly; 4 strong spines on dorsal region, 1 on gastric, 1 on cardiac, and 1 on each epibranchial region. Posterolateral spines subconical, regularly tapering, acute, and directed slightly backward; posterior median spine shorter, acute, obliquely erect. Rostral horns acute, rather regularly divergent from base. Distolateral spine on basal article of antenna rather slender, divergent. Orbital tubes, pre- and

postorbital spines protuberant laterally, preorbital spine curving a little forward.

Chelipeds of male strong, longer than carapace; merus with few short spinules above; carpus somewhat nodose with tubercle at inner angle; palm widest near articulation; fingers tipped with black or dark brown. Walking legs nearly smooth.

Measurements in mm.—Carapace including spines: male, length 40, width 36; ovigerous female, length 31, width 25.

Variation.—The rostral horns may be straight or slightly curved outward at tips, and range in length from $\frac{1}{6}$ to $\frac{1}{3}$ the total length of the carapace. The interspace between horns may vary from a narrow V-shape to almost a right angle. The posterolateral spine may be straight in frontal section, curved upward and nearly transverse, or directed strongly backward.

Color.—A dirty brown.

Habitat.—The species has been taken on a variety of bottoms ranging from sand with grass, or a hard smooth substrate, to rocky or coral bottoms; Rathbun (1925) reported it from predominantly coarse bottoms. About 3.7 to 24 m.

Type-locality.—Near Key West [Fla.], 3.7 to 9.2 m.

Known range.—Beaufort Harbor, N. C., around southern Florida to Alligator Harbor, Fla.

Remarks.—Encrusting organisms on the dorsal surface of the carapace are often as large a mass as the crab itself—including the sponges *Dysidea* sp.,

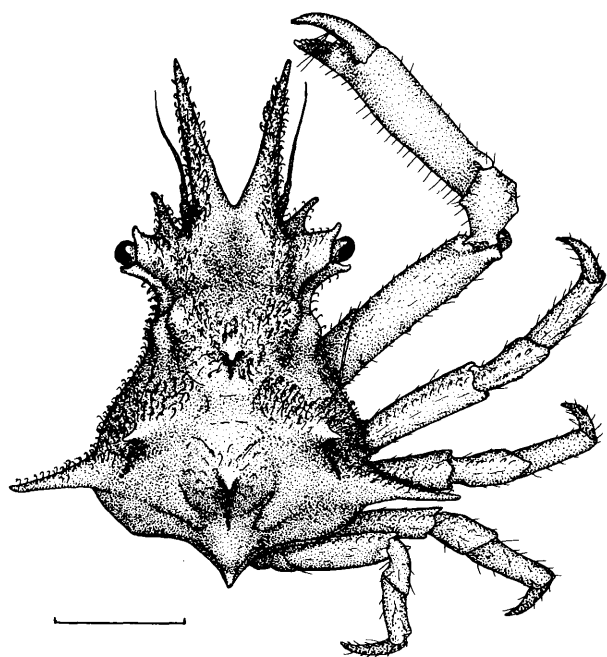


Fig. 262. *Macrocoeloma camptocercum* (Stimpson). Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

Haliclona sp., *Lissodendoryx isodictyalis*, and unidentified ascidians (Rouse 1970).

Ovigerous females are known in Florida from January to April (USNM); Hartnoll (1965) considered breeding to be continuous in Jamaica. He observed hatching of eggs in 13–14 days at 22°–25° C. From a single brood hatched in March, Yang (1967) reared the larvae singly in 50 ml plastic compartments in the laboratory. He described the stages, finding that at 25°C zoea I lived 2 days (\bar{x}) before molting, zoea II 3 days (\bar{x}), the megalopa 7–8 days, and the first and second crab stages 6 days each.

Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but died after 17-h exposure (F. J. and W. B. Vernberg (1970).

Macrocoeloma eutheca (Stimpson)

Figs. 263, 275k

Pericera eutheca Stimpson 1871a:112.

Macrocoeloma eutheca.—Rathbun 1925:485, pls. 170, fig. 1; 171, fig. 1.—Powers 1977:51.

Recognition characters.—Carapace subtrapezoidal, narrow behind orbits; median spine on gastric, cardiac and intestinal prominences, spinule on gastric region behind each orbit in line with gastric spine and at summit of each branchial region; 1 strong spine at lateral angle directed outward and backward. Rostrum small, horns slender, nearly parallel in proximal half of length with interspace U-shaped, but tips slightly divergent. Tubular orbits directed forward, upward and outward, prolonged well beyond ventral face of basal antennal article and having 4 spines, 1 pre-, 1 post-, 1 supra-ocular, and 1 ventral belonging to antennal article. Latter article in addition bearing 2 ventral spines; pterygostomian region with 4 tubercles.

Merus of rather slender cheliped with 3 marginal rows of tubercles, hand with partial row above and below as well as scattered proximally. Walking legs seem short and slight for size of body, diminishing markedly in length from first to last pair.

Measurements in mm.—Carapace: male, length without horns 32, including horns 41, width including spines 35; ovigerous female, length without horns 28, including horns 30, width including spines 26.

Habitat.—55 to 214 m.

Type-locality.—Off French Reef [Fla.], 27.4 m, and west of Tortugas, 67.7 m.

Known range.—SE of Cape Lookout, N. C.; off

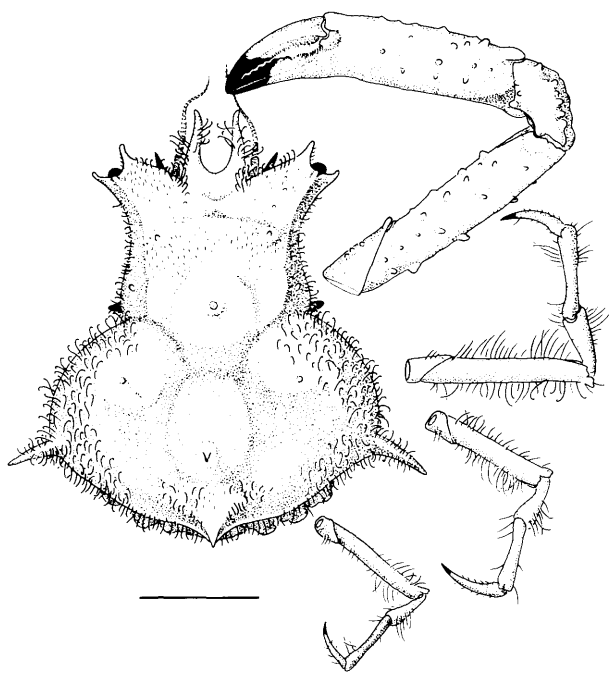


Fig. 263. *Macrocoeloma eutheca* (Stimpson). Male in dorsal view, dissociated cheliped and 3 legs of right side shown; 10 mm indicated (USNM 173637).

NW Florida through Bahama Banks and West Indies; Panama.

Remarks.—Ovigerous females are known from NW Florida in December and St. Croix in January.

Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but died after 17-h exposure (F. J. and W. B. Vernberg 1970).

***Macrocoeloma trispinosum* (Latreille)**

***Macrocoeloma trispinosum*, variety**

***Macrocoeloma trispinosum nodipes* (Desbonne)**

(Grass crab, sponge crab, decorator crab)

Figs. 264, 275l

Pisa trispinosa Latreille 1825:142.

Pericera nodipes Desbonne 1867:15, pl. 5, fig. 13.

Macrocoeloma trispinosum.—Hay and Shore 1918:457, pl. 38, fig. 11.—Rathbun 1925:466, text-fig. 132, pl. 166, fig. 1; pl. 167.—Boone 1927:40.—Williams 1965:263, figs. 243, 245J.—Coelho and Ramos 1972:217.—Felder 1973:53, pl. 7, fig. 9.—Powers 1977:52.

Macrocoeloma trispinosum, variety.—Rathbun 1925:468, pl. 168, fig. 1.

Macrocoeloma trispinosum nodipes.—Rathbun 1925:468, pl. 166, fig. 2; pl. 168, fig. 2.

Recognition characters.—Carapace irregularly tri-

angular, body and legs with velvety covering of short brown hairs, thick and swollen, wide at level of orbits, narrowing distinctly in hepatic portion, widening again posteriorly. Middorsal region much elevated and bearing 4 low, rounded tubercles or bosses, 1 on gastric, 1 on cardiac, and 1 on each epibranchial region. Posterolateral angle prolonged into long flattened spine directed obliquely outward and backward, sometimes curved upward; posterior margin with broad, median, triangular projection with tip sometimes slightly recurved. Rostrum formed of 2 somewhat flattened horns adjacent and subparallel at base, divergent distally. Upper margin of orbit deeply emarginate, pre- and postocular teeth prominent, preocular teeth curved forward. Basal article of antenna with distolateral angle produced, exceeding frontal margin, and forming broad spine directed obliquely outward at each side of rostrum.

Chelipeds of male narrow, approximately as long as carapace; merus nodose; palm with subparallel sides; dactyl approximately half as long as upper margin of palm and lightly furrowed above. Walking legs rather slender, slightly nodose.

Measurements in mm.—Carapace including spines: male, length 47, width 41; ovigerous female, length 37, width 31.

Variation.—Rathbun (1925) discussed variation in this species throughout its known range. Body shapes falling into three general series are distinguishable. In the typical form, the posterolateral prominences are narrow, with regularly tapering spines projecting beyond the general outline of the carapace, directed more or less backward, and sometimes strongly curved from base to tip with the concavity forward. The carapace is considerably constricted behind the orbits. The orbits are prominent owing to this constriction, and the pre- and postocular teeth are strong, the former directed forward and curved. The upper edge of the orbit is deeply emarginate. The four large tubercles or bosses are prominent, some or all with an acute tip, that on the gastric region sometimes nearly a spine.

In the second series, treated by Rathbun as an unnamed variety, the posterolateral prominences are wider than in the first series, less spinelike and more laminate, their posterior margins nearly transverse. The carapace is less narrowed behind the orbits, the orbital teeth less marked, though the preocular tooth is directed forward and a little curved, and the superior emargination less deep. The four large dorsal bosses are lower than in series one, but the gastric boss tends to be surmounted by a sharp tubercle or granule.

In series three, called *M. t. nodipes*, the posterolateral prominences are broader and more obtuse

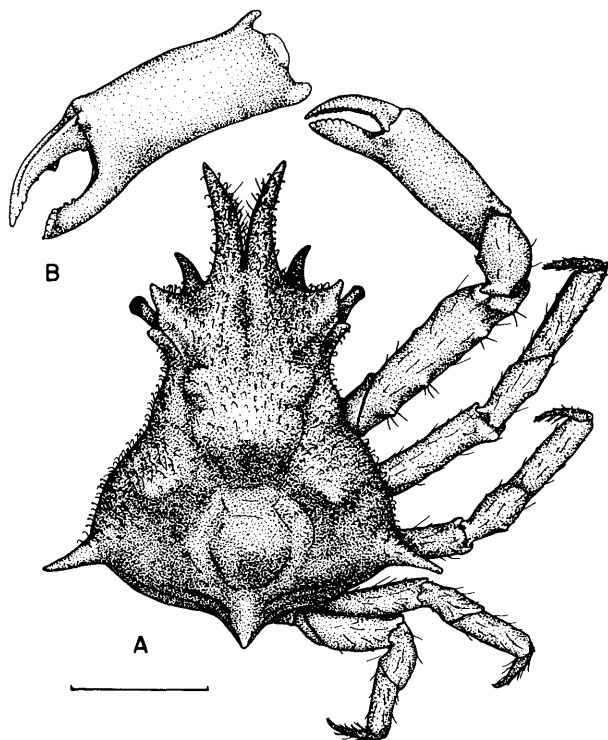


Fig. 264. *Macrocoeloma trispinosum* (Latreille). *a*, Small male in dorsal view, legs of left side not shown, 10 mm indicated; *b*, right chela of adult male in external view (from Williams 1965).

than in series two with their margins almost continuing the margin of the carapace. The carapace is constricted little or not at all behind the orbits; the preocular tooth is acute but not prominent, and the postocular tooth is blunt or subacute with both teeth somewhat more prominent in young individuals than in old ones. The orbit has a slight emargination in the upper border. The dorsal bosses are lower than in the other series, smoothly rounded and blunt.

In the three series the posterior median spine varies in a manner similar to the lateral spines, and the rostrum shows great variability in length, direction, and curvature of horns.

Color.—Hairs yellowish or reddish brown (various authors); scarlet vermilion (W. L. Schmitt, notes).

Habitat.—In North Carolina, this species has been found in seaweed in Beaufort Harbor, in the ocean on floating masses of *Sargassum*, and dredged from offshore reefs. Elsewhere it has been found in a variety of situations, from pilings, and mangrove roots to weedy rocks, coarse coral-sand, sand-shell, and broken-shell bottoms. The species is often concealed by a covering of sponge. Shallow water to 82 m.

Type-locality.—"Nouvelle Holland" (?) [error].

Known range.—Beaufort, N. C., to Alligator Harbor, Fla.; Yucatan; through West Indies to Bahia, Brazil.

Remarks.—Ovigerous females of the varieties together are known from March to December in Florida, April in Bermuda and Cuba, July in Jamaica and St. Thomas, and September east of the Mississippi River delta. Structure of the sperm was described by Hinsch (1973).

Boone (1927) reviewed an early description of decoration in the species. Randall (1967) reported *M. trispinosum* in stomach contents of the squirrel-fish, *Holocentrus ascensionis*.

Genus *Microphrys* H. Milne Edwards 1851

Garth 1958:385.

Carapace broadly pyriform, somewhat depressed, dorsally uneven and tuberculate or nodose, small marginal spine or tubercle at lateral angle of branchial region; preocular spine usually developed. Orbits small, circular, with closed fissures; eyes small. Rostral horns moderate or small, divergent. Basal article of antenna considerably dilated, armed with sizeable spine at anteroexternal angle visible in dorsal view; movable antennal parts visible dorsally. Abdomen of both sexes with 7 separate segments. (Modified after Garth 1958.)

Key to Species

1. Carapace with 2 lateral laminiform processes, 2 strong branchial spines. *M. antillensis*
- Carapace without lateral laminiform processes, 1 strong branchial spine. *M. bicornutus*

Microphrys antillensis Rathbun

Figs. 265, 275h

Microphrys platysoma.—Hay and Shore 1918:459, pl. 38, fig 9.

Microphrys antillensis Rathbun 1920:24.—1925:498, text-fig. 141, pl. 176, figs. 3–4.—Williams

1965:260, figs. 240, 245G.—Coelho and Ramos 1972:217.—Powers 1977:53.

Recognition characters.—Carapace depressed, tuberculate, and granulate, area at inner angle of branchial region finely granulate; intestinal region with 4 or more large, equal tubercles. Anterolateral wall with 2 laminiform processes, 1 on hepatic,

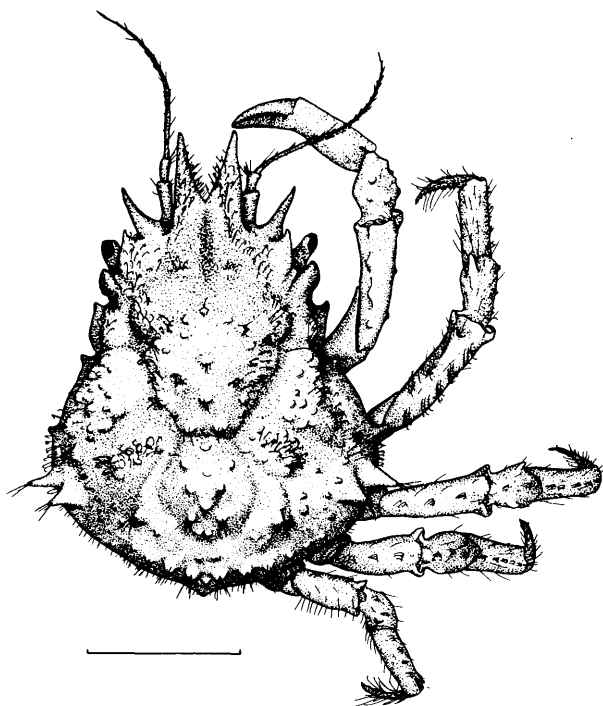


Fig. 265. *Microphrys antillensis* Rathbun. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

1 ill-defined on branchial region; hepatic process with anterior end acute, projecting outward and occasionally forward in large individuals, sometimes with outward-projecting tubercle at middle of upper edge; spine between and below level of hepatic and branchial processes. Branchial region with 3 spines, 1 forming posterolateral angle occasionally doubled. Posterior margin with row of tubercles increasing in size mesially. Rostral horns slender, rather short, directed forward. Basal article of antenna with spine at outer angle about half length of rostral spines. Preocular spines acute, about half as long as antennal spines.

Merus of chelipeds with dentate and laminate dorsal crest; carpus tuberculate; palm less than twice as long as broad; fingers widely gaping, fixed finger curved downward. Walking legs sparsely hairy and with few spines and tubercles; propodi with prominent distal laminiform process for articulation of dactyls.

Measurements in mm.—Carapace: male, length to base rostral horns 15.6, including horns 18, width 15.6; female, length to base rostral horns 14.2, including horns 16.2, width 14.6.

Habitat.—3.7 to 27 m.

Type-locality.—Off Montego Bay Point, Jamaica.

Known range.—Near capes Hatteras and Lookout, N. C., to Cape Fear, N. C.; Cuba; Jamaica; Puerto Rico; Pernambuco, Brazil.

Remarks.—Ovigerous females are known from

June to September off North Carolina, July off Florida, and November at Bimini (Rathbun 1925, and USNM).

Cain (1970) reported occurrence of the species on an offshore reef near capes Lookout and Hatteras, N. C. F. J. and W. B. Vernberg (1970) found that zoeae collected in this reef region died within three to four h at 4°C. At 10°C the zoeae were inactive but recovered if returned to room temperature after 24 h.

Microphrys bicornutus (Latreille)

Figs. 266, 275g

Pisa bicornuta Latreille 1825:141.

Microphrys bicornutus.—Hay and Shore 1918:459, pl. 38, fig. 10.—Rathbun 1925:489, text-fig. 139, pl. 175.—Williams 1965:259, figs. 239, 245F.—Coelho and Ramos 1972:216.—Powers 1977:54.

Recognition characters.—Carapace subtriangular, moderately hairy, all raised parts covered with rounded tubercles; line of 4 tubercles arching upward on intestinal region, branchial region with 2 or 3 short spines and another spine at lateral angle. Rostrum composed of 2 stout horns, divergent throughout or at base with extremities curving inward, $\frac{1}{2}$ to $\frac{1}{3}$ length of remainder of carapace. Basal article of antenna with conspicuous, flat, obtuse spine at anterior angle and marginal tubercle behind this or short, stout spine in large individuals. Preorbital angle rectangular.

Chelipeds spotted, spots persisting for many years in alcohol; merus with 3 or 4 tubercles or short, blunt spines above; carpus somewhat nodose; hand smooth; fingers gaping, hollowed out at tips. Walking legs diminishing noticeably in length from first to fourth pair, hairy, margins somewhat rough.

Measurements in mm.—Carapace: male, length 36, width 26; female, length 24, width 20.

Color.—Variable; carapace often dull yellowish brown or bright purplish rose; chelipeds grayish white, covered with small, round, purplish spots.

Habitat.—The species is common on coral reefs. It is often disguised by foreign objects such as sponges, anemones, hydroids, algae, etc., which became attached to it. Shallow water to 30 m.

Type-locality.—“Nouvelle Hollande.”

Known range.—Near Beaufort, N. C., through Gulf of Mexico (Ray 1974) to Florianopolis, Santa Catarina, Brazil; Bermuda.

Remarks.—This species is represented by a large collection in the USNM, and has been the subject of a number of studies. Hartnoll (1965) showed that the species in Jamaica has a recognizable molt of

puberty in which male chelipeds increase relatively in size, the female abdomen becomes broadened and male gonopods remain unaltered from prepubertal condition. He concluded that breeding was continuous. Other records show ovigerous females from March to August in the Caribbean area and November to January in the West Indies and northern South America (Rathbun 1925; USNM). The female mates in the hard condition. Hartnoll observed as many as four sets of fertile eggs to be laid following a single mating which probably supplies enough sperm to last through the reproductive life. A female with carapace length of 25 mm can lay 3000 eggs in a clutch. There is little delay in laying a new clutch of eggs following the hatching of a previous one. Hatching, usually nocturnal, is facilitated by the female standing on the tips of the dactyls, extending the abdomen and waving the pleopods while repeatedly thrusting the chelae into the egg mass.

From laboratory rearings, Hartnoll (1965a) described the prezoea and two zoeal stages. Yang (1967) described the first and second zoea, megalopa and first crab stage, and from several broods reared at 25°C he found the following duration of stages in days: zoea II, 3; megalopa, 5; crab 1, 4–6; crab 2, 4–8; crab 3, 9; crab 4, 5–9; crab 5, 7–11; crab 6, 11. Greatest mortality was in the first zoeal stage and the megalopa.

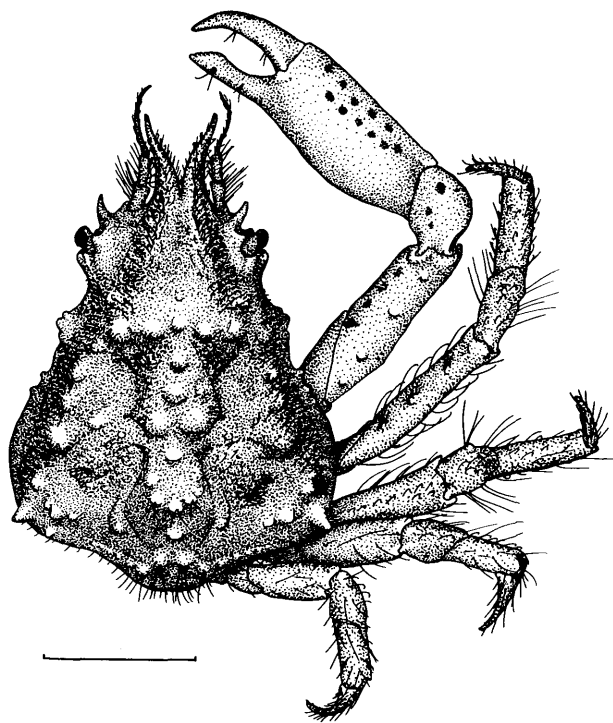


Fig. 266. *Microphrys bicornutus* (Latreille). Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

In the majids (Hartnoll 1965) there are two kinds of breeding season, continuous under essentially uniform temperature conditions (*M. bicornutus* as a model), or fixed in which one set of eggs is laid per year (*Hyas coarctatus* in cold northern water as a model). In neither of these types is the molt of puberty at a fixed point in life, i.e., at a uniform size as in some Brachyura, but this terminal feature, whether in a large or a relatively small individual, marks the group as among the most specialized of the Brachyura. There is tremendous change in this one molt.

Hartnoll (1967) also studied the effects of parasitism on this species by *Sacculina biscuspidata* in Jamaica, giving an excellent general review of sacculinid host-parasite relationships. He found 15% of the crabs infected, and multiple infections rare. Effects of parasitism on the male crabs are: relative length of the chelar propodus becomes smaller than in prepubertal males; abdomen is broadened; fringing abdominal setae are elongate, the locking mechanism is lost, but genital openings and papillae are not affected; first pleopods remain unaltered but second and succeeding pleopods may become biramous, typically with an antero-posterior gradient in masculinity; sperm ducts may remain large and filled with spermatophores containing spermatozoa, but spermatogenesis usually is stopped or reduced. Parasitized females appear as normal adults but the ovaries are small and pale; $\frac{1}{3}$ of such females observed did not copulate. As noted by others, the externa of the parasites act as substitute egg masses, effecting hormonal changes to induce this. Parasitized males can be distinguished from females by absence of female genital openings.

Pearse (1932b), working at Dry Tortugas, listed the copepod *Anthracus intermedius* from the gill lamellae (accidental guest) and a tapeworm plerocercoid, *Rhynchobothrus*, from the viscera, and (in Wilson 1935) reported a few specimens of *Cancrincola jamaicensis* Wilson from the branchial cavity of this crab. Hartnoll (1966) described a new entoniscid (*Achelion occidentalis*) from specimens of *M. bicornutus* taken in Kingston Harbor, Jamaica.

Hazlett (1972a) presented models to *M. bicornutus* to test the importance of postures of walking legs, chelae, and body during agonistic interactions. The double first ambulatory raise and spread chelipeds both elicited a significant number of responses, but multiple leg raises or lowered body posture did not. Size and sex of test animals seem to have little effect on their responses, although small crabs may retreat and slightly larger ones may respond by "freezing." Hazlett (1972b) concluded that agonistic display movements are more stereotyped than nondisplays, feeding or walking move-

ments from which they may have evolved in this species. Hazlett and Estabrook (1974) showed that a set of postures characterize the agonistic behavior patterns among individuals that meet while feeding on detritus and algae. Static factors (sex, size, color phase, hunger state) have less influence on behavior patterns shown by one animal in a fight than behavior of the other animal. The first crab to move won 70% of interactions, regardless of static factors. Camouflage of these crabs may tend to hide size.

The species lacks a tendency to match its own decorated covering with that of the background (Getty and Hazlett 1978). Lack of any tendency actively to match background may be associated with low mobility of the crabs. Animals were often found in the same habitat patch for several weeks. The authors suggest that since these crabs appear to have a moderately high rate of replacing algal decoration on their dorsal surface (every two or three

days), this tendency may be sufficient to maintain an acceptable degree of camouflage.

Randall (1967) reported *M. bicornutus* from stomach contents of the bandtail puffer, *Sphaeroides spengleri*.

Genus *Mithrax* Desmarest 1823

Carapace convex, ovate or oblong-ovate, narrowing noticeably in front. Front formed of 2 small, often pointed rostral horns, other preorbital or antennary spines or projections laterally. Orbital margins generally more or less spinous or tuberculate. Basal article of antenna wide, bearing 2 or 3 strong spines in front; second article inserted outside of orbit at base of rostrum. Merus of external maxillipeds broad, dilated on outside; exognath broad. Sternal plastron nearly circular. Abdomen of male formed of 7 free segments. (Modified after Garth 1958).

Key to Species

1. Carapace roughened to greater or lesser extent by tubercles or spinules, branchial grooves absent; spine lateral to movable articles of antenna conspicuous, pointed, or subtruncate. [Subgenus *Mithrax*] 2
Carapace smooth and bearing oblique branchial grooves, either strongly or weakly indicated; spine lateral to movable articles of antenna inconspicuous, tuberculiform [Subgenus *Mithraculus*, 1 species] *M. forceps*
2. Acute rostral horns definitely overreaching spines lateral to movable articles of antennae 3
Obtuse rostral horns only slightly overreaching spines lateral to movable articles of antennae. 4
3. In lateral view, spine at lateral angle (fourth or fifth) situated noticeably below level of preceding spines *M. acuticornis*
In lateral view, spine at lateral angle in line with preceding spines *M. spinosissimus*
4. Carapace paved with close-set, tessellate granules (concealed by short hair in young) *M. verrucosus*
Carapace not paved with such granules 5
5. Spine on or just above posterolateral margin close behind spine at lateral angle; rostral sinus U-shaped; attains large size *M. hispidus*
Tubercle on or just above posterolateral margin close behind spine at lateral angle; rostral sinus V-shaped except in old adults; never attains large size *M. pleuracanthus*

Mithrax (Mithrax) acuticornis Stimpson

Figs. 267, 275a

Mithrax acuticornis Stimpson 1870:116.—Jones 1969:381.

Mithrax (Mithrax) acuticornis.—Rathbun 1925:388, pl. 136, figs. 1–2; pl. 257, fig. 1.—Coelho and Ramos 1972:214.—Felder 1973:52, pl. 7, fig. 10.—Powers 1977:56.

Recognition characters.—Carapace distinctly longer than broad; cervical and cardiac sutures distinct; dorsal surface ornamented with spines, short and scanty on gastric region, longer and more numerous elsewhere; 5 large anterolateral spines, first or hepatic spine tending to be doubled, next 3 often with small spine in front of each, last spine in this row at lateral angle longest and below others, behind it 1 shorter posterolateral spine. Rostral horns

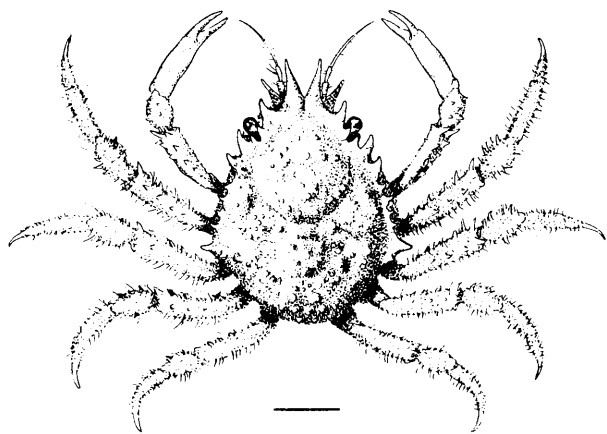


Fig. 267. *Mithrax (M.) acuticornis* Stimpson. Male in dorsal view, USNM 15817, 5 mm indicated (from Rathbun 1892).

straight with slight inward curve at tip, divergent, regularly tapering. Distolateral spine of basal (fixed) antennal article half as long as rostrum, straight or slightly curved; 2 other spines on article, 1 forming part of orbital border, other tiny spine (sometimes obsolete) at base of first movable article. Orbit armed with 1 strong ventral spine outside antennal article and 1 at outer angle, 3 above including prominent preorbital, second of these with more or less developed accessory lateral spine.

Chelipeds of male about as long and stout as first walking legs; merus with 2 rows of long spines above; carpus covered with short spines or tubercles, 3 on inner margin; palm with 1 or few dorsal spinules proximally in individuals over 18 mm long; fingers with short, narrow gape, opposed edges denticulate, larger denticle in middle of gape on dactyl. Walking legs with spines in 2 rows above on merus and carpus, especially long in first 2 pairs.

Measurements in mm.—Carapace: male, total length 24.2, without rostral horns 21.2, width including spines 22.2; ovigerous female, total length 18.5, without rostral horns 16.5, width including spines 15.0.

Variation.—Spinination is positively correlated with size.

Color.—Deep red orange, fingers somewhat purplish red with narrow white bands near bases (Henderson in Rathbun 1925).

Habitat.—Mainly calcareous bottom, occasionally sand or mud; 22 to 103 m, rarely 298 m.

Type-localities.—Off the Quicksands [Fla.], 62.6 m; west of the Tortugas, 67.7 and 76.8 m.

Known range.—Off Cape Lookout, N. C.; W Florida and Yucatan Channel through West Indies to Espírito Santo, Brazil.

Remarks.—Rathbun (1925) emphasized the ease

with which *M. acuticornis* may be confused with young *M. spinosissimus* and *M. cornutus*.

Ovigerous females are known from April to July in Florida, January in Bahia, Brazil, and May, June, and October in North Carolina.

Individuals collected from a reef southeast of Cape Lookout, N. C., did not survive 48-h exposure to 10°C (F. J. and W. B. Vernberg 1970).

Mithrax (Mithrax) hispidus (Herbst)

(Coral crab)

Figs. 268, 275d

Cancer hispidus Herbst 1790:245 (247 by error), pl. 18, fig. 100.

Mithrax (Mithrax) hispidus.—Rathbun 1925:406, text-fig. 124, pls. 145–146; pl. 147, fig. 3.—Boone 1927:38.—Williams 1965:256, figs. 236, 245C.—Coelho and Ramos 1972:215.—Powers 1977:56.

Mithrax hispidus.—Jones 1969:381.—Pequegnat and Ray 1974:236, figs. 5–10.

Recognition characters.—Carapace swollen, considerably wider than long, smooth except for some low, rounded prominences chiefly toward outer margin of branchial region, gastric tubercles faint; front wide. Rostral horns short, obtuse, separated by U-shaped notch (sometimes narrow). Preorbital angle blunt, slightly produced. Basal article of antenna with 2 teeth, inner tooth nearly as advanced as rostrum, outer smaller tooth on orbital border. Orbit with 4 tubercles on margin, 2 superior much smaller than external or inferior ones. Anterolateral margin with 4 spiniform teeth, first tooth obtuse, often bifid at tip; second longer, sharp, double, and curving forward; third and fourth slender. Posterolateral border with smaller spiniform tooth situated higher on carapace in line with 2 obliquely located tubercles, or low spine and tubercle. Subhepatic region with 2 tubercles; a few other tubercles on subbranchial and pterygostomian regions.

Chelipeds large, unequal in males, equal in females; merus with 4 or 5 spines and few tubercles on upper surface, spine on inner margin; carpus smooth; hand smooth; fingers spooned at tips, gaping, with broad low crenulated tooth near base of dactyl. Walking legs moderately stout; dactyls slender, somewhat hooked and pointed.

Measurements in mm.—Carapace: large male, length 102, width 146; ovigerous female, length 52, width 62.

Variation.—Young individuals have tubercles on the carapace more protuberant than in the old.

Color.—Nearly uniform deep brownish-red or terra cotta color above, brighter on chelipeds and

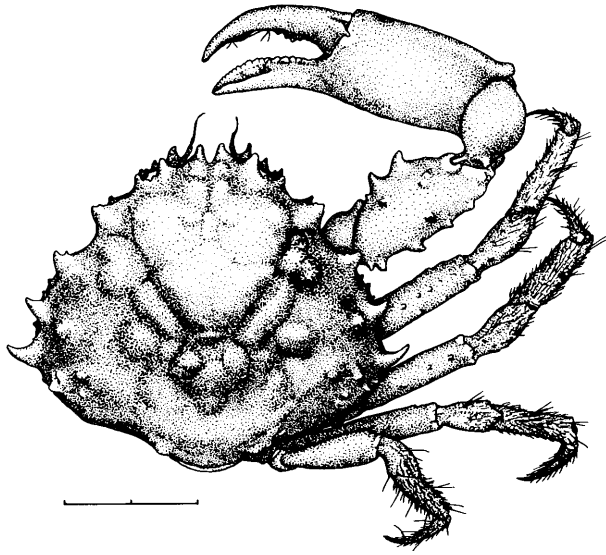


Fig. 268. *Mithrax (M.) hispidus* (Herbst). Male in dorsal view, legs of left side not shown, 20 mm indicated (from Williams 1965).

darker on legs (due to brown hairs); legs often with brighter red bands at joints; underparts of body mostly white or bluish white; legs red, speckled with pale yellow (Verrill 1908a). Body deep tan but lighter on raised areas, especially gastric and cardiac regions. Major cheliped (minor missing) with tan hand but obsolete cross rugae on inner surface lighter giving somewhat striped appearance; spines of merus lighter tan; fingers purplish near spooned tips except lighter and bluish at very edge of fine teeth along spoon. Walking legs dull reddish brown or dull maroon with cross bands of yellowish tubercles, 2 on meri (1 subproximal, 1 subdistal), indistinct band but scattered yellowish tubercles on carpi, 1 on propodi; slender dactyls with black band at base of reddish orange tips (specimen from North Carolina).

Habitat.—Commonly on rough bottom, also sand, shell, *Halodule* beds, and in sponges; shallow water to 64 m (Coelho and Ramos 1972).

Type-locality.—Unknown.

Known range.—Recorded in literature from as far north as Delaware Bay (Say 1818), off Charleston Harbor, S. C., and Georgia (Gibbes 1850). Northwestern Gulf of Mexico; Bahamas and Florida Keys through West Indies to São Paulo, Brazil; Bermuda.

Remarks.—*Mithrax hispidus* has a reported fossil record dating from Pliocene coral rock deposits in Barbados (Collins and Morris 1976).

Ovigerous females are known from off French Guiana in May, Florida in June, July and December, and St. Croix in December (USNM).

Individuals collected from a reef SE of Cape

Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but died after 17-h exposure (F. J. and W. B. Vernberg 1970).

Mithrax (Mithrax) pleuracanthus Stimpson

Figs. 269, 275e

Mithrax pleuracanthus Stimpson 1871a:116.—Hay and Shore 1918:458, pl. 38, fig. 3.—Jones 1969:382.

Mithrax depressus Milne Edwards 1875 (in part):96, pl. 20, figs. 4–4c.—Rathbun 1901:68.—Verrill 1908a:407, pl. 23, fig. 1.—Hay and Shore 1918:458, pl. 38, fig. 2.

Mithrax hispidus Rathbun 1892(in part):265.

Mithrax (Mithrax) pleuracanthus Rathbun 1925:411, pl. 150.—Boone 1927:39.—Williams 1965:257, figs. 2376, 245D.—Powers 1977:57.

Recognition characters.—Carapace not much wider than long, conspicuously tuberculate; front wide. Rostral horns shorter and wider than in *M. hispidus*, notch between horns narrower and nearly triangular, always triangular in young individuals. Preorbital angle blunt, slightly produced; orbit with 2 superior tubercles; small postorbital angle and suborbital tubercle. Basal article of antenna with 2 teeth, inner one nearly as advanced as rostrum, outer smaller one on orbital border. Spines of anterolateral border well developed, first or second inclined to be double, posterior 2 more acute and

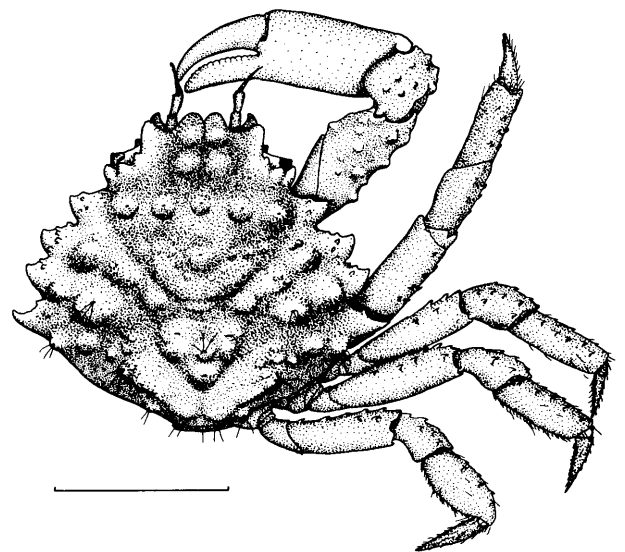


Fig. 269. *Mithrax (M.) pleuracanthus* Stimpson. Animal in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

pointed forward, small tubercles about base of spines. Gastric region with transverse row of 5 tubercles; in front of these, 2 pairs of tubercles, anterior pair at base of rostral horns. Mesogastric region with 2 tubercles on each side in transverse line. Cardiac region with 3 poorly defined tubercles. Branchial area with 4 rather strong tubercles and several smaller ones arranged more or less in 3 oblique rows radiating from cardiac region to anterolateral border.

Chelipeds large; merus with scattered low spines on upper margin, simple spine, spine and tubercle, or rounded eminence on inner margin and 5 small spines on posterior border; carpus smooth or with few low tubercles on upper surface; hands smooth; fingers slightly gaping, dentate for nearly entire length, spoon shaped at tips. Walking legs dentate and hairy.

Measurements in mm.—Carapace: large male, length 36, width 44; ovigerous female, length 16, width 19.

Variation.—In young individuals the rostral horns are wider behind and flatter than in adults; the notch between the rostral horns in extremely large individuals may be U-shaped; the large tubercle above the posterolateral margin may be spiniform but is located higher on the carapace than the similarly formed tubercle in *M. hispidus*.

Color.—Carapace yellowish white, with blotches of bright red; 2 largest red spots over branchial areas, median spot on cardiac area, pair situated farther back, small pair behind orbits, and another beneath orbits; legs yellowish white, blotched or barred with red; chelae light red with pale tips (Verrill 1908, for *M. depressus*).

Habitat.—The species, which is often encrusted with bryozoans and other organisms, is found predominantly on coarse or rocky substrates but occasionally on muddy or sandy bottom. In North Carolina it is a common species on the offshore banks and is associated with *M. forceps*. Pearse (1934) found the species in canals of the sponge *Stematumenia strobilinia* at Tortugas, Fla. Shallow water to 51 m.

Type-localities.—Key West, 3.6–9.1 m, Tortugas [Fla.] 9.1–11 m; St. Thomas.

Known range.—Beaufort, N. C., to Pensacola, Fla., western Gulf of Mexico to Yucatan Channel off Cape Catoche, Mexico; West Indies to Venezuela; Bermuda.

Remarks.—Ovigerous females are known in Florida from December to August; North Carolina in April and September; St. Thomas in July, and Venezuela in April and September (Rathbun 1925; USNM).

Yang (1967) described first stage zoeae reared

from an ovigerous female collected from Biscayne Bay, Fla.

Mithrax (Mithrax) spinosissimus (Lamarck)

Figs. 270, 275b

Maia spinosissima Lamarck 1818:241.

Mithrax (Mithrax) spinosissimus.—Rathbun 1925:383, pl. 135.—Chace 1940:67.—Williams 1965:254, figs. 234, 245A.—Collins and Morris 1976:118, pl. 17, fig. 1; pl. 18, figs. 2,3.—Powers 1977:58.

Mithrax spinosissimus.—Jones 1969:380.

Recognition characters.—Large. Carapace nearly naked, subcircular, approximately as broad as long; surface rough with short spines, those in center blunt, elsewhere sharp; cervical suture deep; hepatic and cardiac regions distinctly delimited. Rostral horns narrow, obliquely truncate and granulate at extremity, separated by U-shaped notch of equal length and breadth; 2 stout spines at base of horns and 2 more behind these but farther apart; preorbital spine stouter, truncate, and less advanced than rostrum. Orbital border with 3 small teeth exclusive of postorbital spine; suborbital margin with 1 acute spine outside antennal segment and larger truncate spine lateral to this. Antennal segment with outer small acute spine and inner spine more or less advanced than rostrum bearing small secondary lateral spine near end. Lateral margin with 6 spines, first 2 double, last and smallest one on posterolateral margin. Other spines present on suborbital, subhepatic, subbran-

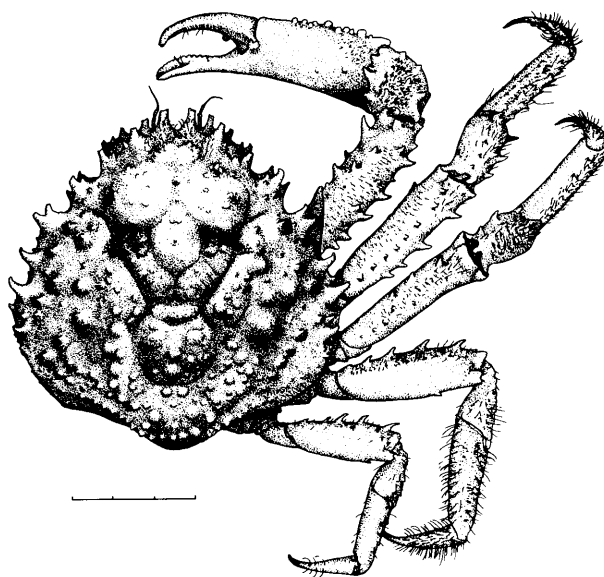


Fig. 270. *Mithrax (M.) spinosissimus* (Lamarck). Male in dorsal view, legs of left side not shown, 30 mm indicated (from Williams 1965).

chial, pterygostomian regions, and at angle of buccal cavity.

Chelipeds of adult male massive, longer than walking legs; merus armed with 8 or 9 stout spines on outer margin, others irregularly placed; carpus armed with unequal spines, about 5 on inner margin; hand deep, compressed, armed above with more or less double row of spines and on inner surface with 2 to 4 spines proximally; fingers curved leaving wide gape, strong tooth near middle of dactyl, tips spooned with edges crenate preceded by few low tubercles. Adult female with chelipeds no longer and not much stouter than first pair of walking legs; hand tapering somewhat distally; fingers narrowly gaping with numerous denticles on cutting edges. Walking legs of both sexes spinose and coarsely hairy; propodi elongate and compressed.

Measurements in mm.—The largest species of *Mithrax* in the region. Carapace: male, length 170, width 184; female, length 77, width 80.

Variation.—In large males, spines on the chelipeds tend to become blunt and tuberculiform. In medium-sized individuals, the carapace is relatively longer than in the largest, spines are sharper, rostral horns curve inward at the sharp tips, the carapace is covered with short hair, chelipeds of both sexes are small, and the gape extends only half the length of the fingers. In small individuals, the spines are even more accentuated, rostral horns are $\frac{1}{5}$ as long as the carapace, there are two spines on the suborbital margin outside the antennal segment, chelipeds are no longer or stouter than the first walking legs, and gape of the fingers is less than in large individuals.

Color.—Bright carmine; vinous red with yellowish tints; or cephalothorax dark red; walking legs brick red and chelipeds rose red with yellow fingers (various authors including Rathbun 1925).

Habitat.—The species is often covered with encrusting organisms and found among rocks; shallow water to 179 m.

Type-locality.—"Ile-de-France." Locality erroneous.

Known range.—North (?) and South Carolina to Nicaragua, and through West Indies to Barbados and Venezuela.

Remarks.—Collins and Morris (1976) reported *M. spinosissimus* from Pliocene and Pleistocene coral rock in Barbados. Ovigerous females are known possibly year-round in southern Florida (Hazlett and Rittschof 1975; Bohnsack 1976), and are reported in March, May and June from Cuba (Rathbun 1925; Chace 1940) and January in Venezuela (Provenzano and Brownell 1977).

The latter worked out larval development from

captured females under primitive laboratory conditions, finding that at 24–28°C in seawater of 34–36‰ salinity the larvae developed from hatching to first crab in about six days. Stages include a non-swimming prezoaea, two zoeae, and a megalopa.

Hazlett and Rittschoff (1975) and Bohnsack (1976) found from study of a population in a canal in the Florida Keys that the crabs are herbivorous, living primarily on algae scraped from rocks at night. Population density there was highly correlated with crevice density, clusters of 2–11 crabs often living together, but females often exclude other females from crevices and presence of many females in an area restricts their movements. The nocturnal animals usually forage within 4 to 6 m of a crevice, but if they do not return to this shelter they will move an average of 12.9 m to another crevice by dawn. The extent of daily movement is inversely correlated with spider crab density, especially for females, with no correlation between animal size and measure of movement; males relocate more than females. Presence of spiny lobsters usually excludes crabs from crevices.

Claw meat in the large crabs is a limited food resource. The crabs cannot be trapped, removal of a claw from a living crab is often fatal, and slow growth of an estimated 18 months between molts precludes quick regeneration after removal.

Mithrax (Mithrax) verrucosus H. Milne Edwards

Figs. 271, 275c

Mithrax verrucosus H. Milne Edwards 1832:cl. 7, pl. 4 (col.) [+ unpaginated description].—Jones 1969:119.

Mithrax (Mithrax) verrucosus.—Rathbun 1925:400, pl. 144.—Boone 1927:39.—Williams 1965:255, figs. 235, 245B.—Coelho and Ramos 1972:215.—Collins and Morris 1976:119, pl. 17, fig. 7, pl. 18, figs. 5–6.—Powers 1977:58.

Recognition characters.—Mature males, large to medium-sized. Carapace covered with flattened, closely crowded granules, nearly naked, granules covered with small pits, cervical suture deep; branchial region with few dorsal spines on outer part, front and orbit with truncate spines. Rostral horns short, separated by deep notch. Preorbital spine directed somewhat outward, 4 other spines on orbital margin aside from 3 on broad basal antennal article. Anterolateral margin with 8 spines, first 6 in pairs, anterior spines of each pair smaller, spines in first 2 pairs more or less united at base; single posterolateral spine, and below lateral margin a row of about 9 spines.

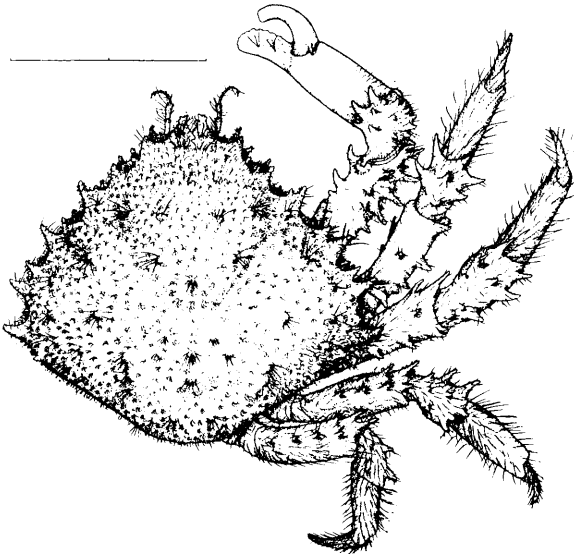


Fig. 271. *Mithrax (M.) verrucosus* H. Milne Edwards. Male in dorsal view, legs of left side not shown, 20 mm indicated (from Williams 1965).

Chelipeds stout; outer margin of merus with 6 sharp spines, approximately 6 spines on upper surface; inner margin of whole cheliped armed with blunt spines or lobes, 11 on ischium, 4 on merus, 2 or 3 on carpus; carpus with dorsal surface smooth or slightly tuberculate proximally; palm unarmed, elongate, somewhat swollen, fingers gaping with large tooth near middle of dactyl, edges of spoon-shaped tips slightly crenulate, 2 bunches of hair inside spoon. Walking legs covered with coarse hair, meri and carpi spiny.

Measurements in mm.—Carapace: male, length 51, width 65; ovigerous female, length 35, width 43.

Variation.—Females, juveniles, and most immature males differ from mature males in that the carapace is covered densely with hair; rostral horns of females and immature males are shorter and farther apart but horns of the young are sharper; spines on the inner margin of the chelipeds are sharper, the carpus is more or less spiny dorsally, and the palm is spinulose and hairy above proximally. The degree of spination on the chelipeds also varies individually.

Color.—Dark red; color largely concealed by hairiness, carapace dark dull red, pincers olive above and lighter olive below, tips claret, teeth white, underparts maroon flecked with white and yellow (various authors and Rathbun 1925).

Habitat.—This species lives near shore among rocks, where it hides in holes. It is nocturnal, and has been caught with the aid of a light while feeding.

Type-locality.—Robert Bay, Martinique.

Known range.—Charleston, S. C.; Campeche

Banks; through West Indies to Fernando Noronha Island, Brazil.

Remarks.—Collins and Morris (1976) reported *M. verrucosus* from Pliocene and Pleistocene coral rocks in Barbados.

Ovigerous females are known from Cuba in April and Florida in July and August.

Randall (1967) reported *M. verrucosus* from stomach contents of the Nassau grouper, *Epinephelus striatus*.

Mithrax (Mithraculus) forceps (Milne Edwards)

Figs. 272, 275f

Mithraculus forceps A. Milne Edwards 1875:109, pl. 23, fig. 1.

Mithrax forceps.—Hay and Shore 1918:457, pl. 38, fig. 1.—Jones 1969:382.

Mithrax (Mithraculus) forceps.—Rathbun 1925:431, pl. 156.—Chace 1940:67.—Williams 1965:258, figs. 238, 245E.—Türkay 1968:254.—Coelho and Ramos 1972:216.—Pequegnat and Ray 1974:236, fig. 1–4.—Powers 1977:55.

Recognition characters.—Carapace about $\frac{1}{5}$ wider than long, deeply sculptured in young individuals but smoother with age. Anterolateral margin with 4 tubercles or simple teeth exclusive of postorbital angle, separated by broad rounded sinuses, first tooth usually shortest, remainder usually acute and turned forward at tip. Three grooves running diagonally backward over branchial area from near first, second, and fourth sinuses of anterolateral margin, between these grooves 2 well-defined, unbroken ridges and broken ridge behind third groove. Cardiac and gastric regions crossed by less sharply defined ridges somewhat broken up into low rounded tubercles. Notch between rounded rostral horns broadly V-shaped, 2 pairs of tubercles on frontal region behind lobes of rostrum. Preorbital angle prominent, not exceeding rostrum. Orbital margin with dorsal and ventral tubercle near postorbital angle. Outer spine of fused antennal article nearly equaling rostrum.

Chelipeds strong. Merus with 2 strong spines or tubercles in front, 5 much smaller ones on posterior margin, and usually 2 on upper surface near posterior margin. Carpus smooth or with small spine or tubercle on inner margin near inner distal angle. Hand smooth, polished, somewhat tumid. Fingers widely gaping in male, with expanded hollowed-out tips; dactyl with single large tooth $\frac{1}{3}$ distance from proximal end, or with few minute teeth; fixed finger with from 1 to 3 small teeth or tubercles in

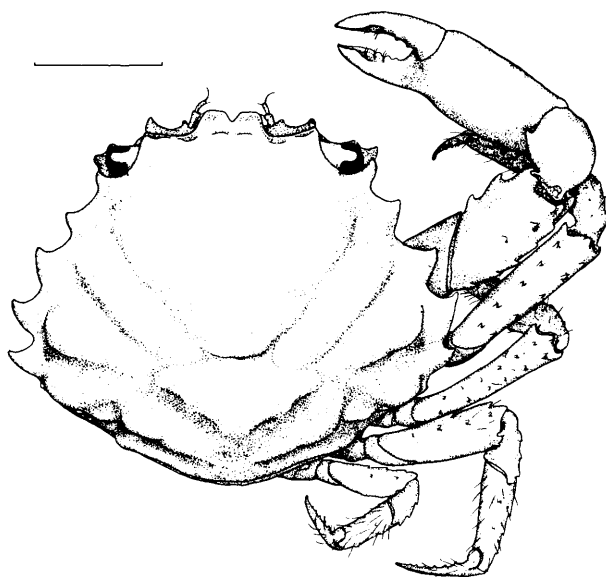


Fig. 272. *Mithrax (Mithraculus) forceps* A. Milne Edwards. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

middle. Walking legs spiny or denticulate with many fine hairs.

Measurements in mm.—Carapace: male, length 31, width 38; ovigerous female, length 20.7, width 23.3.

Color.—Red, approaching vermillion, with occasional trace of purple. Terra cotta, or uniform yellowish brown, varying to greenish brown; often with wide, pale yellow, median dorsal stripe, and legs often banded, especially in young individuals (various authors).

Habitat.—The species lives on rocky shores and reefs in crevices, under stones and dead coral; also exposed between tides and in shallow water in certain areas (Verrill 1908a; Coelho and Ramos 1972; Pequegnat and Ray 1974). In North Carolina this form is found on offshore reefs and has been found in the sponge *Stematomenia strobilinia* at Dry Tortugas, Fla. (Pearse 1934). Intertidal to 90 m.

Type-locality.—Guiana.

Known range.—From Cape Hatteras, N. C., through Gulf of Mexico to Rio de Janeiro, Brazil; Bermuda.

Remarks.—Ovigerous females have been taken virtually the year round in Florida, and from the northern Gulf of Mexico in February (Pequegnat and Ray 1974), Cuba in March (Chace 1940), Curacao in April, Barbados and Aruba in midsummer, Venezuela in September and November, North Carolina in September, and Trinidad in November (Rathbun 1925; USNM). Lebour (1944) and Yang (1967) described some of the larval stages, but Wilson, et al. (1979) reared, described and illustrated the full larval development. From ovigerous females taken in 6-m depths off St. Lucie County, Fla., in September, eggs were maintained in 36‰ salinity at 20°, 25°, and 20°–25°C on a diet of *Artemia* nauplii. They passed through a prezoal and two zoal stages plus a megalopa, developing to first crab in 14 days at 25°C and 16 days at 20°C.

Randall (1967) reported *M. forceps* in stomach contents of the squirrelfish, *Holocentrus ascensionis*, and longspined squirrelfish, *H. rufus*.

Genus *Stenocionops* Desmarest 1823

Garth 1958:401.

Carapace subpyriform, rather convex, dorsal surface uneven, tuberculated or spinous; lateral margins armed with series of long spines; preocular spine well developed. Rostrum composed of 2 strong, deflexed spines divergent from base. Orbits tubular, not strongly projecting; eyes small, retractile within orbits. Basal antennal article considerably enlarged, armed with 1 or 2 small distal spines or tubercles not visible in dorsal view. Abdomen in male distinctly 7-segmented. (Modified after Garth 1958.)

Key to Species

1. Hepatic region neither enlarged nor produced beyond general outline of carapace, armed with not more than 1 large spine 2
Hepatic region enlarged and produced separately from curve of branchial region, 3 marginal hepatic spines; carapace with 12 or 13 median spines *S. spinimana* (adult)
2. Four marginal spines behind orbit; carapace with about 4 median spines or spiniform tubercles. *S. furcata coelata*
Three marginal spines behind orbit; carapace with about 8 median spines *S. spinimana* (young)

Stenocionops furcata coelata (A. Milne Edwards)

Figs. 273, 275i

Pericera coelata A. Milne Edwards 1878:224.

Stenocionops furcata coelata.—Hay and Shore 1918:460, pl. 39, fig. 3.—Rathbun 1925:450, pl. 164.—Williams 1965:261, figs. 241, 245H.—Felder 1973:53(?).—Powers 1977:59.

Recognition characters.—Carapace oblong-ovate, approximately $\frac{3}{4}$ as wide as long, uneven, with strong spines and dense covering of short setae and many scattered, longer, hooked hairs. Rostrum consisting of 2 nearly straight diverging horns with rows of hooked setae. Orbital region broad, eyes small, retractile within tubular orbits; preorbital spine strong, suborbital and postorbital spines much smaller. Basal antennal article enlarged, armed with 1 or 2 small distal spines or tubercles not visible dorsally. Middorsal line with 4 strong spines or spiniform tubercles, 1 on gastric region, remainder on cardiac and intestinal regions, fourth spine with tip curved forward. Lateral border with 4 stout spines, 1 on hepatic, remainder on branchial region; in addition, 2 other rather stout spines on branchial region and various smaller spines toward front. Ventral surface of body, except distal articles of chelipeds, closely covered with bulbous setae hiding carapace.

Chelipeds in adult males fairly large and nodose; hand long, cylindrical, and granulate; fingers approximately half as long as palm, gaping in basal half, tooth on dactyl near base. In other individuals chelipeds weak; fingers less than half as long as palm; merus with strong spines above near distal end preceded by several smaller spines. Walking legs moderately elongate, more or less rough with clusters of hooked hairs, articles subcylindrical.

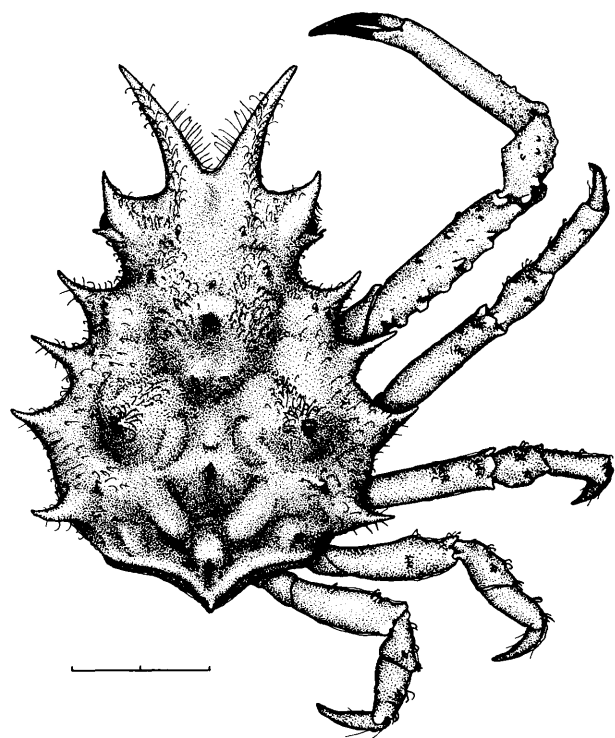


Fig. 273. *Stenocionops furcata coelata* (A. Milne Edwards). Male in dorsal view, legs of right side in part (from Rathbun 1925), legs of left side not shown, 20 mm indicated (from Williams 1965).

Abdomen in male and female with 7 distinct segments.

Measurements in mm.—Carapace: large male, length including rostrum 137, length rostral horn 26, width including spines 111; smaller male, same measurements 91, 25, 64; ovigerous female 91, 18, 68.

Variation.—Large individuals have relatively shorter rostral horns than smaller ones; juveniles are smoother than adults.

Color.—Dark red or orange red, distal half of fingers dark purplish to black.

Habitat.—Found on a variety of bottoms, including fine white sand, yellow sand, coarse gray sand, sand with algae, sandy shell, broken shell, and coral; it has been reported most often from coarse bottom (Rathbun 1925). Shallow water near shore to 110 m, rarely to 509 m.

Type-localities.—Ten miles from Jolbos Islands [Yucatan], and near Havana [Cuba], 320 m.

Known range.—Shelly reefs off Beaufort, N. C., to northwest Florida and Alabama; Yucatan Channel; West Indies to Barbados.

Remarks.—This subspecies is similar to the typical subspecies *S. f. furcata* which ranges from Georgia to Bahia, Brazil, in shallow water near shore to 64 m depth. The typical subspecies has the carapace more evenly sculptured and is less spinose than *S. f. coelata* (Rathbun 1925:449).

Stenocionops furcata may carry as many as 20–30 *Calliactis tricolor* on its carapace and legs (Cuttress, et al. 1970). When it encounters *C. tricolor* attached to another surface, the crab uses chelipeds and walking legs in stroking, scratching, and pinching movements, at first gently, then more actively, until the anemone is freed. After a period of manipulation, the crab seizes the anemone firmly in one claw and hoists it overhead to place it on the carapace. Both chelipeds usually test the carapace beforehand for free areas. The anemone relaxes completely when stimulated and manipulated in these ways, apparently in a state of general inhibition.

Ovigerous females are known in Florida from March to August (USNM).

Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but were dead after 17-h exposure (F. J. and W. B. Vernberg 1970).

Stenocionops spinimana (Rathbun)

Figs. 274, 275j

Libinia spinimana Rathbun 1892:240, pl. 30.

Stenocionops spinosissima.—Hay and Shore 1918:460, pl. 39, fig. 2.

Stenocionops spinimana.—Rathbun 1925:457, pl. 267.—Williams 1965:262, figs. 242, 245I.—W. E. Pequegnat 1970:182.—Powers 1977:59.

Recognition characters.—Carapace subpyriform, convex, covered with sparse growth of short, fine, curled hairs; 8 to 13 median dorsal spines (occasionally doubled), and numerous other spines on gastric and branchial regions; 3 anterior marginal hepatic spines, anteriormost small and occasionally absent in large individuals. Rostral horns widely divergent, straight, tapering gradually to slender tip. Orbits tubular, not strongly projecting, eyes small, retractile within orbits; preorbital spine similar in size to spine near anterolateral angle of basal article of antenna.

Merus and carpus of chelipeds with numerous spines, hand with 2 rows of spines above, 1 below, spines becoming progressively smaller distally. Walking legs with few spines; each merus with terminal spine above, and on first leg a longitudinal inner-upper row of 5 or 6 and ring of about 4 spines near distal end; on second leg a ring of 3 or 4; on third and fourth only 1 or 2 spines besides terminal spine. Carpus of first leg with 3 or 4 spines, second with 3 spinules or tubercles, third and fourth with 1.

Abdomen in male and female with 7 segments, 6 free in females.

Measurements in mm.—Carapace: large male,

length including rostral horns 130, length horns 11, width including spines 118; smaller male (holotype), same measurements 89, 10, 76; ovigerous female, length to base of broken rostrum 103, width including spines 94.

Variation.—This species exhibits great change in shape and spination with increasing size, as has been pointed out by Rathbun (1925), and Garth (1958) for related forms. Young individuals differ much in shape from adults, having a width considerably less than length (width about 70% of length including spines and rostrum), whereas the mature animals are more rounded in contour (large adult male, width about 90% of length). Adults have a thicker coating of hair than juveniles, especially on the chelipeds. Chelipeds in large adults become quite large and stout with the palm compressed (length more than twice that of carapace). The young have fewer spines than adults; the hepatic region is not expanded and bears only 1 marginal spine as opposed to 3 spines in adults.

Habitat.—Found on a variety of bottoms, from gray mud, through various grades of sand, to sand-shell, coral, and rock (Rathbun 1925); 37 to 227 m.

Type-locality.—Off Cape Lookout, N. C., 227 m.

Known range.—Off Cape Hatteras, N. C., to Florida Straits and Gulf of Mexico off Mobile Bay, Ala., and E of Chandeleur Is., off Miss. (Franks, et al. 1972).

Remarks.—Ovigerous females have been re-

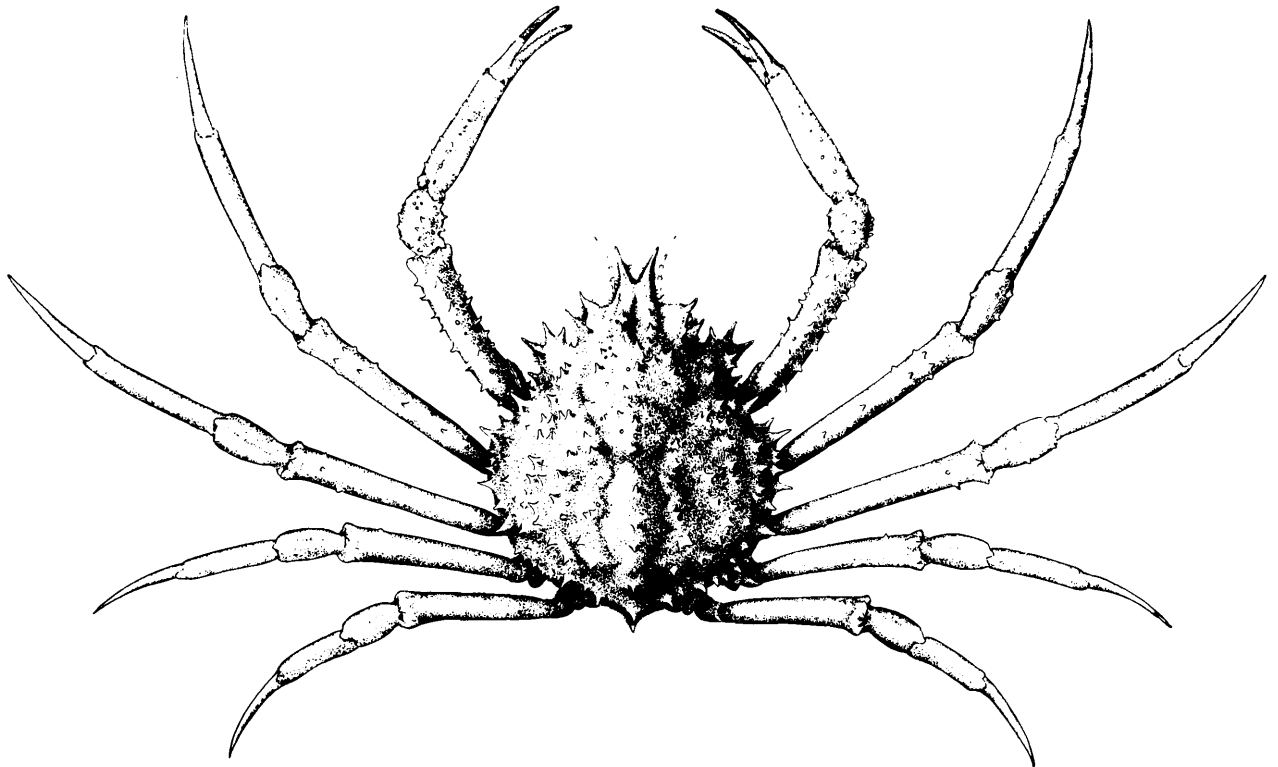


Fig. 274. *Stenocionops spinimana* (Rathbun). Holotypic male in dorsal view (from Rathbun 1892).

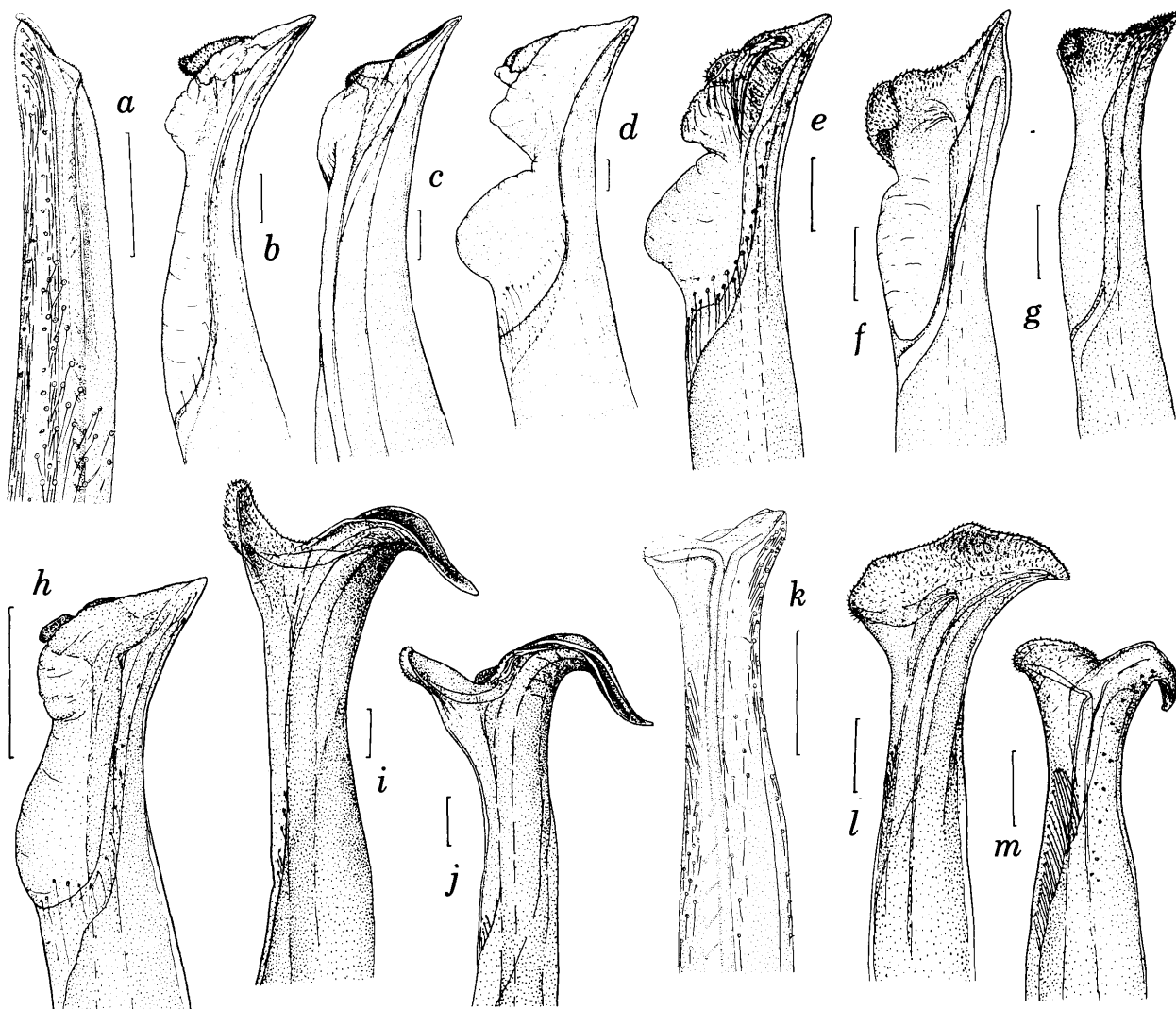


Fig. 275. Subfamily Mithracinae, tips of right first pleopods of males: a, *Mithrax (M.) acuticornis* Stimpson, UNC-IMS 2210; b, *M. (M.) spinosissimus* (Lamarck); c, *M. (M.) verrucosus* H. Milne Edwards; d, *M. (M.) hispidus* (Herbst); e, *M. (M.) pleuracanthus* Stimpson; f, *M. (Mithraculus) forceps* A. Milne Edwards; g, *Microphrys bicornutus* (Latreille); h, *Microphrys antillensis* Rathbun; i, *Stenocionops furcata coelata* (A. Milne Edwards); j, *S. spinimana* (Rathbun); k, *Macrocoeloma eutheca* (Stimpson), USNM 46932; l, *Macrocoeloma trispinosum* (Latreille); m, *Macrocoeloma camptocerum* (Stimpson); a-j, sternal view; k-m, lateral view; all except a and k from Williams 1965; 0.33 mm indicated.

ported from Florida in late summer, and from South Carolina in December (Rathbun 1925).

Superfamily Parthenopoidea

Family Parthenopidae

Eyes usually retractile within small, circular, well-defined orbits, floor of orbit nearly continued to front, leaving hiatus usually filled by second [article] of antennary peduncle. Basal antennal [article] small, deeply imbedded between inner angle of orbit and antennular fossae. Antennules folding somewhat obliquely (Alcock 1895).

Subfamily Parthenopinae

Carapace commonly equilaterally triangular, sometimes subpentagonal or ovate-pentagonal, and sometimes almost semicircular or semi-elliptical in outline. Cardiac and gastric regions usually deeply marked off from branchial regions on either side, making dorsal surface of carapace trilobed. Rostrum simple or obscurely trilobed. Chelipeds vastly longer and more massive than walking legs (Alcock 1895). First pleopod varying, more or less stout, apically tapering or not tapering; second pleopod usually short and of usual shape (Stephensen 1945).

Key to Genera

(Modified after Rathbun 1925)

1. Carapace not laterally expanded over walking legs 2
 Carapace more or less expanded to form vault concealing walking legs from dorsal view 4
2. Carapace tuberculate or eroded *Parthenope*
 Carapace smooth except for few strong spines 3
3. Efferent branchial channels opening at sides of endostome as usual in Oxyrhyncha *Solenolambrus*
 Efferent branchial channels opening at middle of projecting, triangular endostome as usual in Oxystomata *Mesorhoea*
4. Carapace greatly expanded both laterally and posteriorly; pterygostomian region smooth, not ridged *Cryptopodia*
 Carapace expanded laterally but not posteriorly; pterygostomian and subhepatic regions transversed by granulate or crenulate ridge
 *Heterocrypta*

Genus *Parthenope* Weber 1795

Garth 1958:434.—China 1966:249.

Carapace either broadly triangular or ovate-pentagonal, front pointed but short. Surface granular, tubercular or spiny. Eyes enclosed in distinct orbits, a suture above, hiatus below occupied by second article of antennal peduncle. Antennules

folding obliquely; antennae small, basal article extremely short and not reaching front, wedged between antennular fossa and large lobe constituting floor of orbit. Chelipeds usually of immense size and length, out of all proportion to short, slender walking legs; usually prismatic with borders strongly dentate; fingers shorter than palm and abruptly curved inward and a little downward. (Modified after Garth 1958.)

Key to Species

1. Carapace ovate-pentagonal, surface scarcely carinate in adult
 [Subgenus *Parthenope*] *P. agona*
 Carapace broadly triangular, carinate or tuberculate with more or less rounded sides [Subgenus *Platylambrus*] 2
2. Carapace and chelipeds very flat; spine at end of main dorsal branchial ridge small *P. granulata*
 Carapace convex, chelipeds not flat; spine at end of main dorsal branchial ridge large 3
3. Carapace much broader than long; hand with 8–12 teeth on inner, 10–12 on outer margin *P. pourtalesii*
 Carapace not much, if any, broader than long; hand with few good-sized marginal teeth, 6–8 on inner, 3–5 on outer margin *P. fraterculus*

Parthenope (Parthenope) agona (Stimpson)

Figs. 276, 280a

Lambrus agonus Stimpson 1871a:131.

Parthenope agona.—Hay and Shore 1918:462, pl. 39, fig. 5.—Gore and Scotto 1979:35, figs. 16, 17E–H, h, 18.

Parthenope (Parthenope) agonus.—Rathbun 1925:513, text-figs. 146, 178–179; pl. 275, figs. 1–3.—Türkay 1968:254.—Powers 1977:68.

Parthenope (Parthenope) agona.—Williams 1965:266, figs. 246, 252A.—W. E. Pequegnat 1970:183.

Recognition characters.—Carapace ovate pentagonal or subcircular, somewhat broader than long, sides rounded without angles. Postorbital constrictions light, not involving pterygostomian ridge continuing from lower side of orbit to point above cheliped. Depressions between regions of carapace not markedly deep; surface coarsely punctate or eroded and with numerous granules and tubercles, larger tubercles more or less spiniform and arranged as follows: 5 on gastric region, 3 on cardiac, 1 on each side of urocardiac lobe, 5 on branchial, and 1 on each hepatic region. Anterolateral

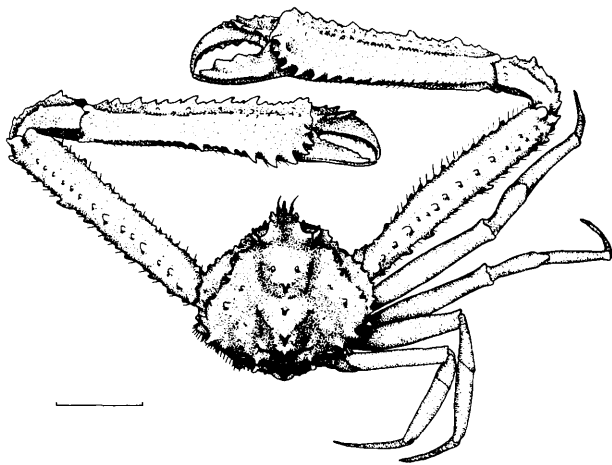


Fig. 276. *Parthenope (Parthenope) agona* (Stimpson). Male in dorsal view, position of legs reconstructed, walking legs of left side not shown, 10 mm indicated (from Williams 1965).

margin of branchial region with 6 small teeth, broad triangular tooth below and behind last tooth, and still lower on ventral surface a spine visible between ischia of cheliped and first leg. Median rostral tooth narrow, produced, denticulate at base, an acute forward-pointing tooth over each antennular cavity. Orbit with several spines on outer margin, suture above, open below; eye with small spine on upper surface. Conical spine or tubercle on each side of sternum near base of chelipeds.

Chelipeds long, slender (length of merus approximately 1.3 times width of carapace), prismatic, upper surface finely rugose. Merus and carpus with irregular row of dentiform tubercles near middle of upper surface, on inner and outer margins, and near outer margin of hand. Upper margin of hand with row of 18–20 irregular teeth, largest near base of fingers but decreasing in size both proximally and distally; outer margin with 4–6 larger teeth and many intermediate smaller ones. Walking legs long, slender, bare, and almost smooth.

Second segment of abdomen with sharp transverse crest.

Measurements in mm.—Carapace: male, length 20, width 21, length of merus 30; ovigerous female, width 16.5 (Gore and Scotto 1979).

Variation.—The rostrum may be broadly triangular or subentire instead of tridentate with denticulate margins. In young individuals it is less produced, the pterygostomian ridge is less developed anteriorly and the postorbital constriction more evident than in adults.

Color.—Light buff, somewhat marbled with purple, chelipeds and legs with broad bands of purple.

Habitat.—Reported from predominantly sandy or broken-shell bottom (Rathbun 1925); 46 to 391 m.

Type-localities.—Off the Marquesas, Carysfort Reef, and Conch Reef, 73 and 89.6 m [southern Fla.].

Known range.—Off Capes Hatteras and Lookout, N. C., and central eastern Florida; Gulf of Mexico and Pensacola, Fla., to near Ft. Myers; through Florida Straits, West Indies and Caribbean Sea to Surinam.

Remarks.—Ovigerous females have been taken from Florida in January, March, April and August–November, and off the Guianas in September (USNM).

Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but were dead after 17-h exposure (F. J. and W. B. Vernberg 1970).

Parthenope (Platylambrus) fraterculus (Stimpson)

Figs. 277, 280b

Lambrus fraterculus Stimpson 1871a:130.

Parthenope (Platylambrus) fraterculus.—Rathbun 1925:525, pls. 186–187; pl. 190, fig. 2.—Williams 1965:269, figs. 249, 252D.—Powers 1977:68.

Parthenope fraterculus.—Gore and Scotto 1979:41, figs. 19–21.

Recognition characters.—Carapace subtriangular, approximately 4-sided, posterolateral margins continuous with sides of posterior margin, and long anterolateral margins in line with rostral borders. Depressions separating branchial from cardiac and hepatic regions deep; cardiac and gastric regions connected by narrow ridge, hepatic and branchial regions by wider ridge bounded below by deep hollow visible in side view; hepatic region with large submarginal tubercle visible in dorsal view. Margin of branchial region cut into 11–13 small teeth; posterior margin with 3 equal teeth. Prominences of carapace ornamented with few large tubercles and spines as follows: 3 gastric in triangle, 1 genital, 2 cardiac, and 3 on branchial ridge. Front inclined about 45°, ending in narrow blunt tooth, blunt tooth on each side above antennules, and outside below these a small slender spine. Tubercle on preorbital lobe; orbit with small blunt tooth on inner lower angle and large tubercle between this and angle of buccal cavity. Endognath with row of 5 tubercles near outer margin.

Chelipeds of male approximately 2.5 times as long as carapace; inner, outer, and upper margins of merus with few unequal stout spines; inner and outer margin of hand armed with triangular, denticulate, unequal teeth, 6 or 7 larger ones on inner, 3 or 4 on outer margin; largest tubercle on upper

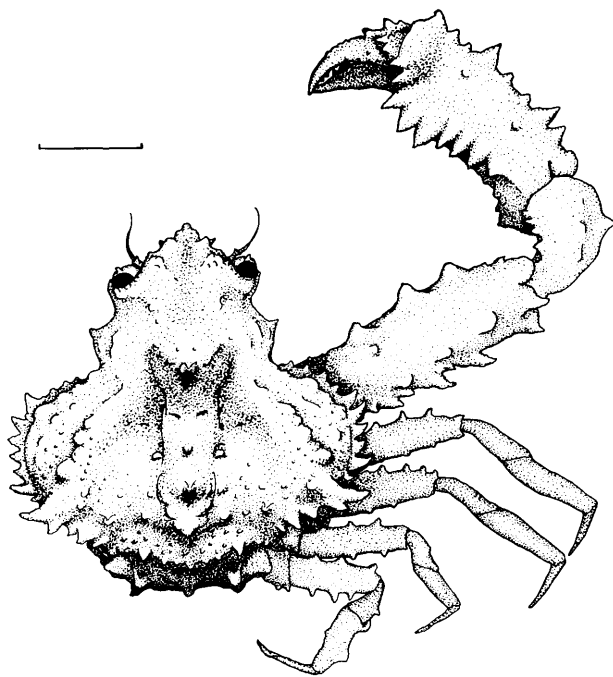


Fig. 277. *Parthenope (Platylambrus) fraterculus* (Stimpson). Male in dorsal view, position of legs reconstructed, legs of left side not shown, 5 mm indicated (from Williams 1965).

surface at proximal third conical. Walking legs with meri denticulate; dactyls furred except at tip; carpus and propodus of last pair with 2 or 3 lobes above and 5 denticles below.

Sternum and abdomen tuberculate, second to sixth abdominal segment each with large transverse tubercle.

Measurements in mm.—Carapace: male, length 16, width 17; female, length 16, width 18.

Variation.—There is great individual variation in the nature of tubercles and spines. In some individuals the prominences are low and blunt, in others high and sharp. The front varies in degree of inclination, and margins of the frontal lobes and orbits may be denticulate, entire or subentire. Gore and Scotto (1979) gave an analysis of variation.

Color.—Uniform red, eggs bright red (various authors).

Habitat.—Has been taken predominantly on rocky or shelly bottoms (Rathbun 1925; Holthuis 1959); 7.3 to 201 m.

Type-localities.—Off Sand Key, Caryfort and Conch reefs, west of Tortugas, 47.6 to 124.4 m [southern Fla.].

Known range.—Off Cape Fear, N. C.; central eastern Florida southward; Gulf of Mexico, off Cape San Blas, Fla., to Florida Straits; off Cape Catoche, Yucatan, Mexico; through West Indies to mouth of Amazon River (USNM).

Remarks.—Ovigerous females have been re-

ported in May, July, August, September, and December (Rathbun 1925; Gore and Scotto 1979; USNM).

Individuals collected from a reef southeast of Cape Lookout, N. C., did not survive 48-h exposure to 10°C (F. J. and W. B. Vernberg 1970).

***Parthenope (Platylambrus) granulata* (Kingsley)**

Figs. 278, 280c

Lambrus granulatus Kingsley 1879:150.

Parthenope serratus.—Hay and Shore 1918:463, pl. 39, fig. 7.

Parthenope (Platylambrus) serrata.—Rathbun 1925:516 (part, not pls. 180, 181, and 275, figs. 7–10 [= *P. serrata* H.M.E. restr.]).—Williams 1965:267, figs. 247, 252B.

Parthenope (Platylambrus) punctata Chace 1942a:85, pl. 26.

Parthenope (Platylambrus) granulata.—Gore 1977a: 505–523 (passim), pls. 3, fig. A; 4, figs. C, D; 5, figs. C, D; text-figs. 1A–D, 2A.

Parthenope granulata.—Gore and Scotto 1979:52, figs. 23, 24A–D, d, 25A.

Recognition characters.—Carapace depressed, convex anterolateral margin with about 11 irregularly triangular teeth in front of longer lateral spine curved obliquely backward. Posterolateral margin concave; posterior margin convex, wide, both margins together with about 7 tubercles noticeably larger than others, each terminating in indefinite longitudinal or oblique line of tubercles. Elevations of carapace ornamented with numerous unequal granulated tubercles trending in concentric rows; depression between gastric and branchial regions deep; intestinal and posterior spines protuberant, surrounded by granules. Rostrum short,

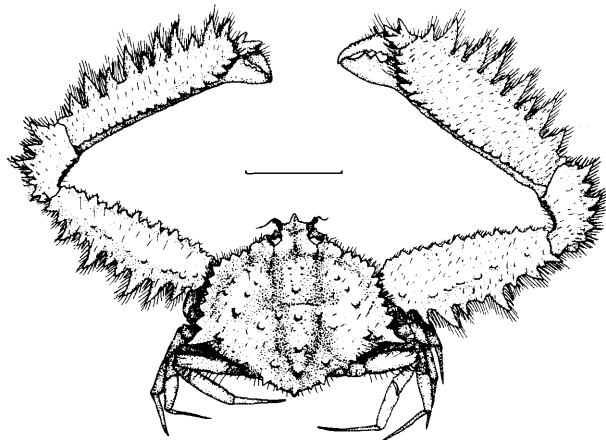


Fig. 278. *Parthenope (Platylambrus) granulata* (Kingsley). Male in dorsal view, 10 mm indicated (from Williams 1965).

tridentate, narrow at tip, and with raised margin continuous with superior wall of orbits. Pterygostomian and subhepatic regions with excavation reaching margin of orbit and, with chelipeds retracted, forming covered efferent passages.

Chelipeds, when extended, approximately 2 to 2.5 times as long as carapace, trigonal, smooth beneath, more or less tuberculate on upper surface, and with margins cut into lanceolate or acutely triangular teeth constricted at bases and fringed with fine hairs, much stronger on outer than on inner side of articles; hand with about 10 teeth alternately large and small, projecting outward or obliquely forward; fingers stout, oblique. Walking legs of moderate size, longest not exceeding merus of cheliped.

Abdomen of male with segments 3 to 5 fused, sixth segment with median spine.

Measurements in mm.—Carapace: male, length 18.2, width 25; ovigerous female, length 20, width 26.

Color.—Red somewhat mottled with gray; fingers carmine, shading to black.

Habitat.—The species has been reported from a variety of bottoms; 9.6 to 55 m, rarely 677–824 m.

Type-locality.—Tortugas, Florida.

Known range.—Off the three North Carolina capes southward around Florida to Louisiana; Bermuda; Bahia Honda, Cuba (?); St. Thomas, Virgin Is. (Gore 1977a).

Remarks.—Gore (1977a) in studying *Parthenope* species from the southeastern United States found that the species long known as *P. serrata* consisted of two forms, that listed above under its oldest name, and “true” *P. serrata* which is seemingly more tropical in distribution, ranging from the western Gulf of Mexico to Brazil.

Ovigerous females are known from North Carolina in June, from Florida in March, April, summer, and September–November, and Cuba in October (USNM; Gore and Scotto 1979).

Parthenope (Platylambrus) pourtalesii (Stimpson)

Figs. 279, 280d

Lambrus pourtalesii Stimpson 1871a:129.

Parthenope pourtalesii.—Hay and Shore 1918:462, pl. 39, fig. 6.—Gore and Scotto 1979:49, figs. 17A–D, 22.

Parthenope (Platylambrus) pourtalesii.—Rathbun 1925:521, pls. 182, 183, and 276.—Chace 1940:53.—Williams 1965:268, figs. 248, 252C.—W. E. Pequegnat 1970:183.—Powers 1977:69.

Recognition characters.—Carapace broadly ovate-

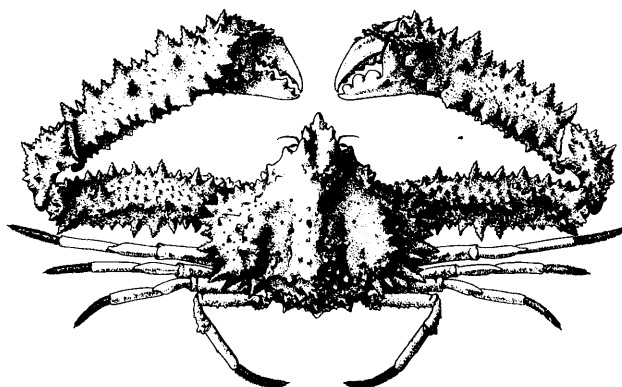


Fig. 279. *Parthenope (Platylambrus) pourtalesii* (Stimpson). Female in dorsal view, approx. $\times 0.8$ (from Smith 1887).

triangular, convex; branchial regions rather deeply separated from gastric, cardiac, and hepatic regions. Posterolateral angle marked by conspicuous lacinated spine located behind bulging curve of anterolateral margin; hepatic margin armed with small but prominent spine. Anterolateral margin behind cervical suture armed with 8 or 9 teeth and spines, first 3 or 4 shorter than remainder. Posterolateral margin with 3 or 4 unequal spines. General surface of carapace pitted and eroded, with granulated tubercles disposed as follows: 1 gastric, 1 genital, 2 cardiac, 2 on branchial ridge in line with lateral spine, and tendency to rows of tubercles on branchial regions. Rostrum tipped with long, narrow, obtuse tooth with denticle on each side, subacute basal tooth with short spine below and outside it. Supraorbital spine blunt, postorbital spine smaller but somewhat sharper; upper side of emargination on eye spined.

Chelipeds long, rough, armed with lacinated teeth and spine on both margins; merus with additional median row of spiniform tubercles on upper surface with largest spine at inner angle; hand with obsolete median row beneath. Meri of walking legs spinulose, also carpus and propodus of last pair; dactyls furred; tubercle on sternum at base of cheliped and each of first 3 walking legs.

Abdomen with large tubercle in middle of second to sixth abdominal segments and conical tubercle at extremity of segments 2 and 3; segments 3 to 5 fused in male. Lower surface of body granulate and tuberculate.

Measurements in mm.—Carapace: male, length 40, width 53; ovigerous female, length 35, width 47.

Variation.—Varies greatly in number and prominence of tubercles and teeth, and in constriction and ornamentation of the rostrum. Elevations of the carapace may bear spines or tubercles.

Color.—Purplish red with cross bands of buff on chelipeds and walking legs; palms pinkish brown (various authors).

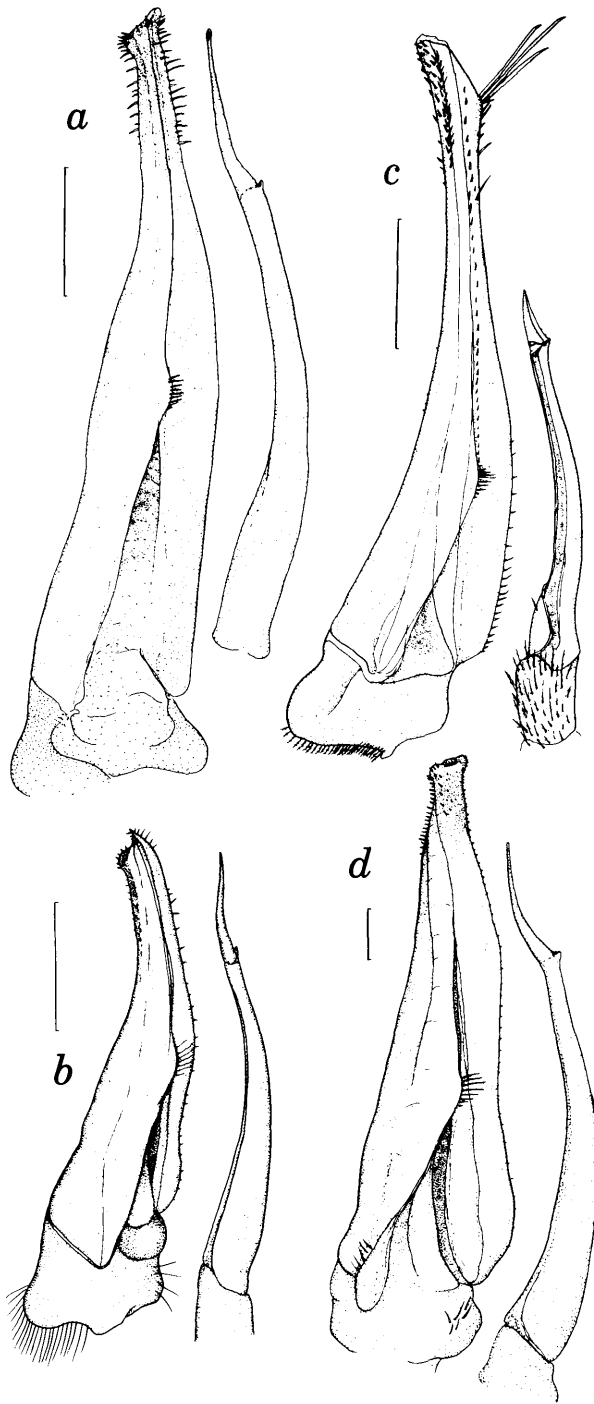


Fig. 280. Family Parthenopidae, first and second right pleopods of males in mesial view: a, *Parthenope (Parthenope) agona* (Stimpson); b, *P. (Platylambrus) fraterculus* (Stimpson); c, *P. (Platylambrus) granulata* (Kingsley); d, *P. (Platylambrus) pourtalesii* (Stimpson); 1 mm indicated (from Williams 1965).

Habitat.—Predominantly on sand or sandy mud bottoms (Rathbun 1925); 18 to 440 m.

Type-localities.—Off Conch Reef, French Reef, and American Shoal [southern Fla.], 73–214 m.

Known range.—Off Martha's Vineyard, Mass.; latitude of New Jersey southward; Gulf of Mexico through West Indies to Grenada.

Remarks.—Ovigerous females are known from Florida in July, North Carolina in December, and South Carolina in January (USNM).

Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but were dead after 17-h exposure (F. J. and W. B. Vernberg 1970).

Genus *Cryptopodia* H. Milne Edwards 1834

Garth 1958:470.

Cryptopodia concava Stimpson

Figs. 281, 286a

Cryptopodia concava Stimpson 1871a:137.—Rathbun 1925:553, pl. 202, figs. 3, 4; pl. 282, figs. 6–11.—Williams, McCloskey, and Gray 1968:64.—Coelho and Ramos 1972:206.—Powers 1977:67.
Cryptopodia concava Gore and Scotto 1979:13, figs. 4, 5H-P (erroneous spelling).

Recognition characters.—Surface smooth and shining. Carapace broadly triangular, dorsally presenting 3 concave faces sloping away from rounded gastric region, large lateral vaulted expansions scarcely concealing walking legs and projecting beyond base of abdomen. Anterolateral margin twice length of posterolateral, meeting at obtuse lateral angle; posterolateral margins slightly converging posteriorly; posterior margin straight in female, slightly emarginate in male; all margins cut into small teeth with denticulate distal edges, separated by closed fissures. Ridge from gastric region toward posterolateral margin granulate. Rostrum triangular and flattened; pterygostomian region smooth. Orbits small, nearly circular, with suture in superior margin; eyes small and retractile. Epistome well developed. Merus of third maxillipeds triangular, internal angle slightly truncate.

Cheliped with upper surface of merus and hand dilated toward middle; margins with few teeth analogous to those on carapace. Crests of walking legs denticulate.

Sternum very concave anteriorly; deep hollow fitting terminal segment of abdomen, strong dentate crest on each side.

Measurements in mm.—Carapace: male, length 8.1, width 10.9; female, length 8.6, width 11.6.

Variation.—A few larger individuals tend to have more denticulate distal edges on teeth of the carapace and chelipeds than smaller crabs in which the distal edges of these teeth are truncate.

Color.—Female with body and chelipeds translucent dirty white dorsally, few scattered small red-

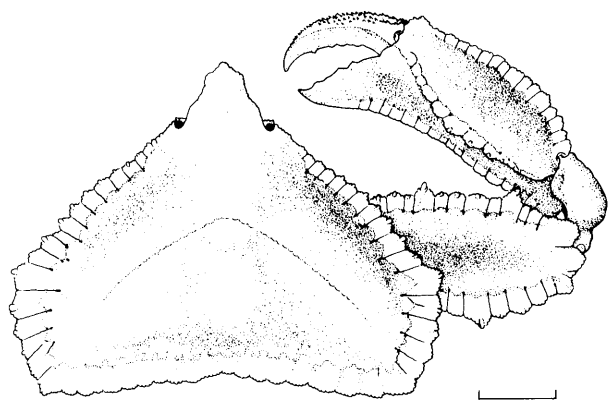


Fig. 281. *Cryptopodia concava* Stimpson. Male in dorsal view, walking legs hidden and left cheliped not shown, 2 mm indicated (UNC-IMS 2659).

dish spots ventrally at base of chelipeds and elsewhere on chelipeds and other limbs ventrally; faint suggestion of transverse pink band at midlength of fingers. Eggs bright orange (Williams, et al. 1968).

Habitat.—Sand and broken shell or coral, also mud; 7.3 to 73 m.

Type-locality.—Off Conch Reef [Fla.], 62.2 m.

Known range.—SE Cape Lookout, N. C.; central east Florida; S Cape San Blas, Fla., to St. Thomas; Ceará to Bahia, Brazil.

Remarks.—Ovigerous females are known from Florida in June, October and December.

Gore and Scotto (1979) gave a comprehensive review of the species along with details of its distribution in Florida.

Genus *Heterocrypta* Stimpson 1871

Garth 1958:473.—China 1966:255.

Heterocrypta granulata (Gibbes)

(Pentagon crab)

Figs. 282, 286b

Cryptopodia granulata Gibbes 1850:173.

Heterocrypta granulata.—Hay and Shore 1918:464, pl. 39, fig. 9.—Rathbun 1925:555, text-fig. 152, pl. 203, figs. 1–2; pl. 282, figs. 1–3.—Williams 1965:270, figs. 251–252E.—Coelho and Ramos 1972:206.—Felder 1973:45, pl. 6, fig. 6.—Powers 1977:67.—Gore and Scotto 1979:15, figs. 5A–D, 6, 7.

Recognition characters.—Carapace subtriangular, with wide clypeiform vaulted expansions, length $\frac{2}{3}$ width; general surface smooth, punctate; margins crenulate. Anterolateral margin nearly straight, with dorsal surface sloping upward from margin to

prominent, granulate branchial ridge running parallel with each side, these connected by short transverse ridge on gastric region and joined behind to posterior marginal ridge. Rostrum broad, blunt, deflexed, with rounded margins connected to gastric ridge by pair of granulate crests. Orbits small, nearly circular; eyes small, retractile. Cardiac region with large domelike elevation granulated at summit.

Chelipeds unequal, rather heavy, longer than width of carapace; margins of upper surface of merus, carpus, and hand expanded into irregular granulate or dentate crests; fingers short, agape in larger cheliped. Walking legs short, almost completely hidden beneath carapace.

Sternum and lower surface of abdomen coarsely granulate; male abdomen with third, fourth, and fifth segments fused, sixth segment with sharp proximal appressed spine with tip lying between 2 tubercles on fifth segment.

Measurements in mm.—Carapace: male, length 13, width 19; female, length 15, width 21.

Color.—Varying from light gray to nearly black, usually commingled so as to produce an irregular mottling or marbling (various authors).

Habitat.—This species is found on shingly bottoms, sometimes on oyster beds (Felder 1973). Its angular form and coloration bear so close a resemblance to fragments of shell among which it lives that it is extremely difficult to detect; 3.7 to 137 m.

Type-localities.—Near Kiawah Island, Sullivan's Island, and White Point Shoal, Charleston Harbor, S. C.

Known range.—Nantucket Sound, Mass., around peninsular Florida to southern Texas; through West Indies to Trinidad; Ceará to Bahia, Brazil.

Remarks.—Ovigerous females are found in the Beaufort, N. C., area throughout the summer, and are known from Florida in February (USNM), March, April, June, July, and October (Gore and

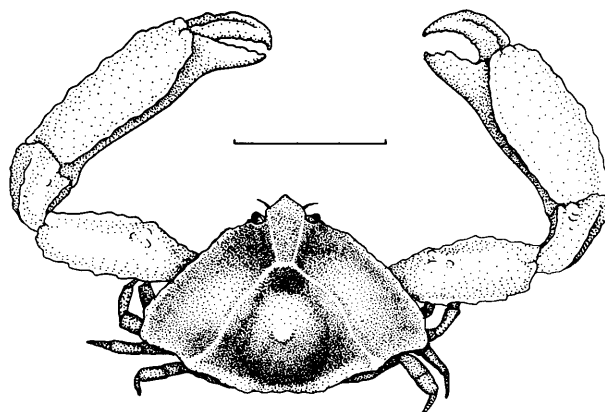


Fig. 282. *Heterocrypta granulata* (Gibbes). Male in dorsal view, 10 mm indicated (from Williams 1965).

Scotto 1979). These authors discussed the possible identity of *H. granulata* and *H. lapidea* Rathbun.

Genus *Mesorhoea* Stimpson 1871

Garth 1958:465.

Mesorhoea sexspinoso Stimpson

Figs. 283, 286c

Mesorhoea sexspinoso Stimpson 1871a:136 (spelling error, *sexspinoso*).—Rathbun 1925:547, pl. 200, text-fig. 150.—Williams, McCloskey, and Gray 1968:64, fig. 17.—Powers 1977:68.—Gore and Scotto 1979:30, figs. 5E-G, 13.

Recognition characters.—Carapace about equally produced in front of and behind lateral angles; surface punctate and inconspicuously pubescent. Protuberances of gastric, cardiac and branchial regions strongly angular, 3-sided, branchials forming projection on posterolateral margin; angles or ridges more or less crenulate. Lateral edges of gastric protuberance continued anteriorly toward front; cardiac protuberance more slender than others; surface between ridges more or less regularly concave. Rostrum short. Eyes small and retractile into deep sockets. Margins of carapace sublaminiiform and almost entire, normal crenulation indicated only by faint impressed lines and microscopic notches; anterolateral margin slightly convex at middle, terminating in tooth on either side (sometimes obtuse). Afferent channels deep, separated from subhepatic channels by prominent, thin, sharp, ciliated lamina and defined on inner side by ciliated outer edge of third maxillipeds.

Chelipeds short, somewhat pubescent along ridges and on inner surface; merus with margins crenulated with 6 or 7 small teeth on either edge; carpus flattened above with 2 strong crenulated

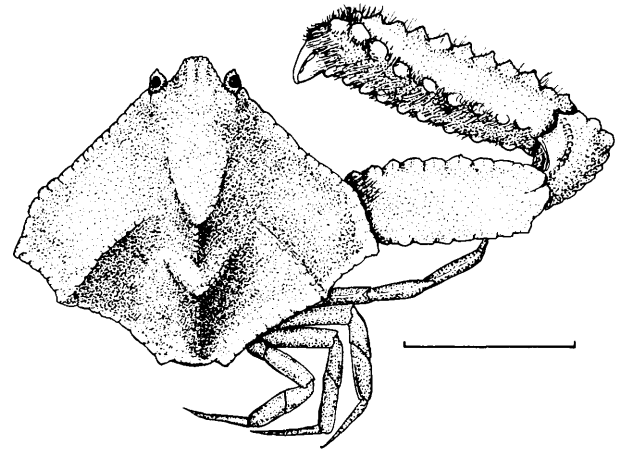


Fig. 283. *Mesorhoea sexspinoso* Stimpson. Female in dorsal view, legs of left side not shown, 5 mm indicated (from Williams, et al. 1968).

crests; hand with 9-toothed superior crest and 11-toothed outer margin; fingers small, dactyls at right angle to palm. Walking legs much compressed, carpus and propodus crested above, merus and propodus of last pair crested below.

Measurements in mm.—Carapace: male, length 10, width 12.5; female, length 9.5, width 12.5.

Variation.—Young individuals show a tendency to relatively more slender tipped protuberances than adults.

Habitat.—8 to 100 m.

Type-locality.—4 miles southwest of Loggerhead Key, Florida, 20 m.

Known range.—SE Cape Lookout, N. C.; off NW Florida, to Flanagan Passage, Virgin Islands.

Remarks.—Ovigerous females are known from Florida in January, August (USNM), and June (Gore and Scotto 1979).

Genus *Solenolambrus* Stimpson 1871

Garth 1958:458.

Key to Species

(Modified from Rathbun 1925)

1. Carapace with no teeth on posterior or posterolateral margins; dorsal protuberances rounded (except short branchial crests in some specimens). *S. tenellus*
- Carapace with 4 teeth on posterior and posterolateral margins; dorsal protuberances angular. *S. typicus*

Solenolambrus tenellus Stimpson

Figs. 284, 286d

Solenolambrus tenellus Stimpson 1871a:134.—Hay

and Shore 1918:463, pl. 39, fig. 8.—Rathbun 1925:541, pl. 194, figs. 3–4; pl. 279, figs. 5–9.—Chace 1940:54.—Williams 1965:270, fig. 250.—Powers 1977:70.—Gore and Scotto 1979:21, figs. 8, 9D-F, 10A.

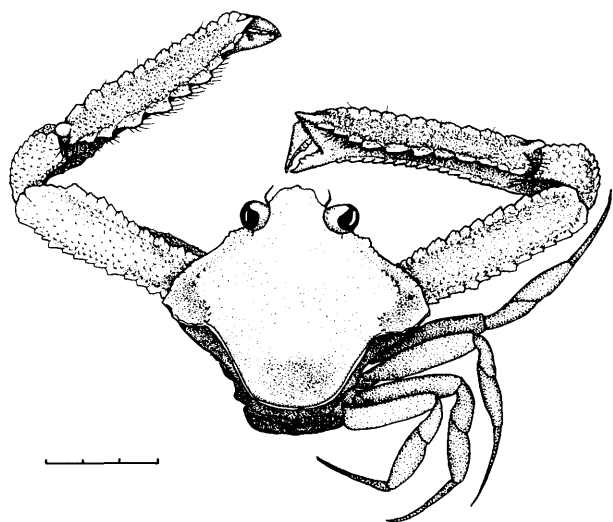


Fig. 284. *Solenolambrus tenellus* Stimpson. Female in dorsal view, walking legs of left side not shown, 3 mm indicated (from Williams 1965).

Recognition characters.—Small delicate species. Carapace but little broader than long and about equally produced in front of and behind line of lateral angles; surface punctate; protuberances of gastric and cardiac regions fairly well marked and often surmounted by tubercle near posterolateral margin but almost obsolete anteriorly. Anterolateral margins of carapace crenulated, 5 or 6 teeth on expanded and broadly rounded lateral angle being most prominent and defined chiefly by impressed lines on marginal shelf; hepatic region with 2 or 3 denticulate teeth. Posterolateral margin concave; branchial region often with short crest extending forward from margin broken into tubercles or ending in anterior tubercle, isolated tubercle on anterior slope; posterior margin convex, its lateral angles obtuse. Rostrum rather prominent, faintly tridentate at extremity, median tooth most prominent. External angle of orbit not prominent; eyes large with extremely minute tubercle at summit. Basal article of antenna approximately as long as next article. External maxilliped with ischium somewhat tuberculate near outer margin and extremity.

Chelipeds long, slender, general surface smooth, polished; edges denticulate. Merus with about 13 teeth on either edge, third tooth from distal end larger than others. Hand with 12 sharp forward-curving teeth on superior edge, terminal tooth above finger spiniform and considerably longer than others; outer margin with about 11 small teeth, inner with 19 or 20 minute teeth. Walking legs naked, compressed, without laminiform crests; merus of last pair slightly expanded below near base.

Abdomen and sternum of male coarsely pitted, otherwise smooth and glabrous.

Measurements in mm.—Carapace: male, length 6, width 6. Length of cheliped 16. Carapace: ovigerous female, length 5, width 6 (width 6.9, Gore and Scotto 1979).

Habitat.—5.5 to 366 m.

Type-localities.—Off Carysfort, Conch, and French reefs, 64 to 89.6 m [southern Fla.].

Known range.—Off Cape Lookout, N. C.; central east Florida southward; Gulf of Mexico, near Cape St. George, Fla., to Florida Keys; Bahamas; Barbados.

Remarks.—Ovigerous females have been reported in April from Cuba (Chace 1940), May from Barbados, May, June and August–November from Florida (Rathbun 1925; Gore and Scotto 1979), and questionably in August from North Carolina (an incompletely labeled specimen from Hay and Shore's material in UNC-IMS collection, and *Fish Hawk* records for 1902).

Solenolambrus typicus Stimpson

Figs. 285, 286e

Solenolambrus typicus Stimpson 1871a:133.—Rathbun 1925:537, text-fig. 148, pl. 192–193, pl. 279, figs. 1–4.—Chace 1940:53.—Williams, McCloskey, and Gray 1968:63.—W. E. Pequegnat 1970:184.—Powers 1977:70.—Gore and Scotto 1979:24, figs. 9A–C, 10B, 11, 12.

Recognition characters.—Small species. Carapace slightly broader than long; surface punctate; protuberances of gastric and cardiac regions triangularly pyramidal and acute with ridges at angles crenulated. Cardiac pyramid symmetrical, equal sided; gastric pyramid asymmetrical, its posterior ridge short and nearly vertical but with long, curved

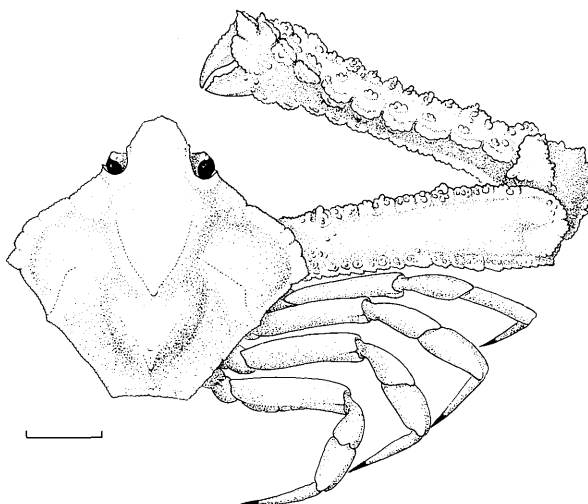


Fig. 285. *Solenolambrus typicus* Stimpson. Male in dorsal view, legs of left side not shown, 3 mm indicated (USNM 48885).

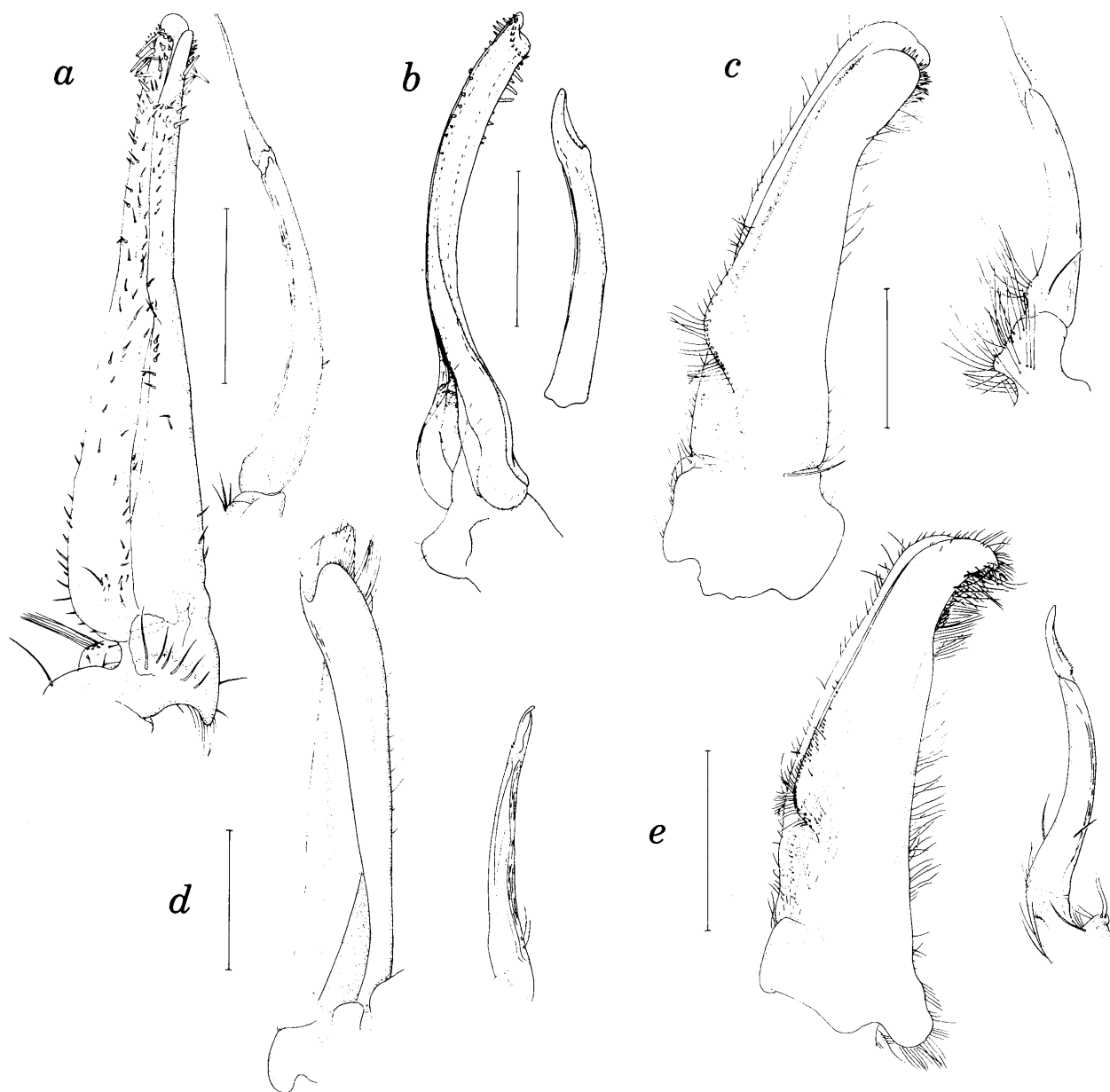


Fig. 286. Family Parthenopidae, first and second pleopods of males: *a*, *Cryptopodia concava* Stimpson, sternal view, UNC-IMS 659; *b*, *Heterocrypta granulata* (Gibbes), mesiosternal view (from Williams 1965); *c*, *Mesorhea sexspinosa* Stimpson, sternal view, USNM 72556; *d*, *Solenolambrus tenellus* Stimpson, mesiosternal view, USNM 18678; *e*, *S. typicus* Stimpson, sternal view, USNM 18677; 1 mm indicated.

anterior ridges enclosing somewhat convex anterior side gradually sloping toward front. Branchial ridges crenulated and bent at nearly right angle in middle. Each protuberance of carapace tending to be surmounted by small spine in male, more rounded in female. Margins more or less distinctly crenulated; anterolateral margin concave anteriorly, convex posteriorly and bearing suggestion of 3 weak teeth near often dentiform lateral angle; no more than 4 teeth on posterolateral and posterior margins; posterior margin straight. Rostrum rather prominent and faintly tridentate, median

tooth most prominent. Basal article of antenna somewhat longer than next article. Epistome of moderate length. External maxilliped tuberculate near outer margin and extremity.

Chelipeds long, slender, naked except for inconspicuous setae on crest of hand; merus with denticulate margins, surface smooth and glossy except for few tubercles near margin; carpus with 5 denticulate crests; hand trigonal, 10 strong teeth on inner crest, 12–14 small granulate teeth on outer margin, upper surface with 2 rows of tubercles, inner surface with 2 rows, outer with 3 rows and all

tubercles ornamented with 2–5 granules. Fingers very short, closed dactyl at right angle to palm. Walking legs compressed, smooth, crested above and merus of last pair crested below with proximal expansion.

Abdomen tuberculate at sides; sternum with few tubercles between bases of chelipeds.

Measurements in mm.—Carapace: male, length 10.8, width 11.6 (Rathbun 1925); ovigerous female, length 10.4, width 11.1.

Variation.—The two projections at ends of the posterior margin vary from prominent to inconspicuous teeth or spines. Chelipeds vary in roughness, those of some specimens having a merus with nearly smooth upper surface and a line of granules near the posterior edge, but on others the posterior half is quite granulate; rougher specimens have longer marginal teeth on the hand, especially on the upper crest.

Habitat.—Sand, shell, and coral fragments; 14.6 (?), 91 to 618 m.

Type-localities.—Off the Samboes and off Alligator Reef [southern Fla.], 146.3 to 201.2 m.

Known range.—SE Cape Lookout; western Gulf of Mexico off Corpus Christi, Tex., and N of Yucatan; Swan Island and Nicaragua Shelf; southern Florida through West Indies to Surinam and Brazil (Gore and Scotto 1979).

Remarks.—An ovigerous female from Florida (USNM) bears no collection date.

Section Cancridea

Superfamily Cancroidea

Family Cancridae

Carapace broadly oval or hexagonal. Last pair of legs not adapted for swimming. Antennules folding lengthwise. Antenna with flagellum more or less hairy.

Genus *Cancer* Linnaeus 1758

Rathbun 1930a:176.—Hemming 1958b:51.—Glaessner 1969:R509.—Nations 1975:30.—1979:153–187 (passim).—Bigford 1979:1.

Nations (1975; 1979) revised the genus *Cancer*, dividing it into 4 subgenera based primarily on shape of the carapace and the chelae, and reviewed its modern distribution as well as its geologic record which dates from the Miocene Epoch. The modern distribution is limited to waters ranging in temperature from about 1.3° to 25°C (Williams and Wigley 1977), i.e., to the temperate zones except along the northwestern coast of South America in the cold Humboldt Current, and regions of limited tropical submergence (Nations 1975; 1979).

Key to Species

1. Anterolateral teeth of carapace with denticulate margins; upper margin of palm denticulate; outer orbital tooth with pointed tip, not coalesced with adjacent anterolateral tooth in small juveniles *C. (Metacarcinus) borealis*
Anterolateral teeth of carapace with margins granulate; chelipeds granulate, not denticulate; outer orbital tooth with rounded tip, coalesced with adjacent anterolateral tooth in small juveniles *C. (Cancer) irroratus*

Cancer (Metacarcinus) borealis Stimpson

(Jonah crab; northern crab)

Fig. 287

Cancer borealis Stimpson 1859:50.—Hay and Shore 1918:434, pl. 35, fig. 2.—Rathbun 1930a:182, text-fig. 30.—Williams 1965:175, fig. 156.—Powers 1977:71.

Cancer (Metacarcinus) borealis.—Nations 1975:45, figs. 4, 38-2, 38-3.—1979:184 (by implication).

Recognition characters.—Carapace transversely oblong, approximately $\frac{2}{3}$ as long as wide, surface

granulate. Anterolateral margins divided into 9 quadrangular, crenate lobes or teeth, with margins minutely denticulate and with notches between teeth continued on carapace as short closed fissures. Front produced beyond inner orbital teeth and provided with 3 teeth, center one longest and depressed. Orbits circular, with 2 narrow fissures above and 2 below; suborbital lobe strongly produced.

Chelipeds nearly as long as second pair of legs, stout; carpus and hand with strong, granulose rugae; carpus with sharp spine at inner angle; hand smooth on inner face, heavily rugose on outer face, 2 rugae continued from hand on slightly deflexed

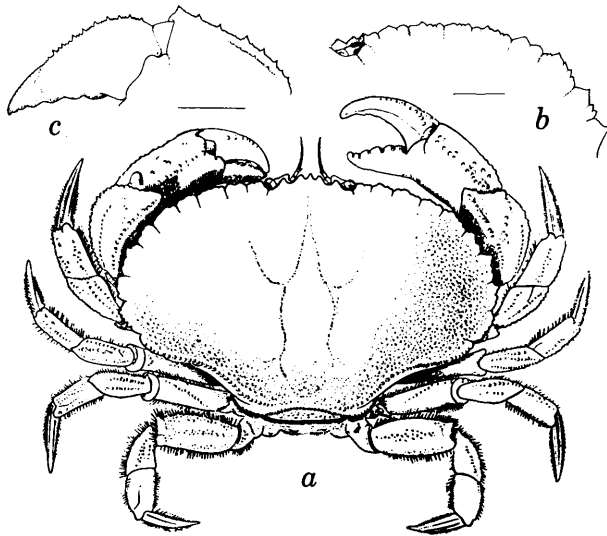


Fig. 287. *Cancer (Metacarcinus) borealis* Stimpson. a, Male in dorsal view, reduced (from Smith 1879); b, right anterolateral border; c, dactyl and upper border of chela (USNM 9446, from Williams 1974c); b-c, 1 cm indicated.

fixed finger; dactyl with rough upper surface, both fingers slaty black at tip. Walking legs short, fringed beneath, dactyls dark tipped.

Measurements in mm.—Carapace: male, length 90, width 143; ovigerous female, length 80, width 124.

Color.—Red above, yellowish beneath; carapace with 2 curved lines of yellowish spots and, behind middle, a figure somewhat resembling letter H; legs mottled and reticulated with yellow and red, more or less purplish.

Habitat.—See discussion under “Remarks.” Small to medium-sized individuals found near shore seasonally (especially in the south), whereas larger ones occur in deeper water; between tides among rocks to 800 m.

Type-locality.—Nova Scotia to Cape Cod.

Known range.—Nova Scotia to south of Tortugas, Fla.; Verrill (1908a) judged that a Bermuda record was probably mislabelled.

Remarks.—Recent studies treat aspects of the biology and ecology of *C. borealis*. Haefner (1977) showed, from samples trawled in March, April, June and October in the mid-Atlantic Bight, that gonad development in June is related to size. Gonads of most crabs ≤ 80 mm in carapace width were undeveloped or slightly developed. Mature gonads were seen only in crabs ≥ 100 mm in width. Testes and vasa deferentia of most males ≥ 150 mm in width were well developed, but no females were ripe. Reilly and Saila (1978), studying samples from commercial trawls in southern New England waters as well as stomach contents of predacious fishes and observations of SCUBA divers, found that growth

of the two sexes is similar up to 30–40 mm carapace width, but the rate then diverges, females showing less increment per molt than males. Growth does not exceed 15 mm during the first year. Females were judged to attain a maximum of 100 mm width in 8 years after 14 molts, and males were judged to attain a little under 130 mm width after 13–14 molts in 6–7 years. They found that females mature at carapace widths as low as 14–30 mm. Ovigerous females of 21 mm width were calculated to carry 4430 eggs, and 88-mm females to carry 330,400 eggs. Females with unripe, red-orange eggs were found from November to May, and those with ripe brown eggs from March to June; they thought the eggs may be carried for up to five months. The largest females molted in December, the largest males from January to March, and an additional smaller group of males 40–60 mm wide molted in May. Growth curves and age and mortality estimates were calculated. Jeffries (1966), working with both *C. borealis* and *irroratus* in Narragansett Bay, observed a major shedding period in May and June. Since *Cancer* mates when the female is in the soft condition (Snow and Nielsen 1966; Hartnoll 1969), the season from June to December would seem to be an active breeding period.

Sastry (1977b) worked out the larval development in laboratory culture, but did not record the times at which parent females from Narragansett Bay were taken by SCUBA divers. Larvae were reared from eggs isolated in compartmented plastic boxes in sea water of 30‰ salinity and held at constant temperatures between 10° and 25°C. First stage zoeae released at 20°C were segregated after hatching and reared at that temperature on a diet of *Artemia salina* nauplii. Five zoeal stages and a megalopa were described and illustrated. The larvae are identical to those of *C. irroratus* except for minor variation in number of setae on some appendages, but the physiological requirements differ. Under the above conditions, early stage eggs of *C. borealis* deteriorated, but the late-stage eggs hatched to release mostly prezoeae and first zoeae. Fish (1925) recorded larvae attributed to *C. borealis* in plankton of the Woods Hole region in September and October. Hillman (1964) found *Cancer* larvae in Narragansett Bay from May through July.

Jeffries (1966) found *C. borealis* on rocky areas in association with *Homarus americanus* whereas *C. irroratus* was found on sandy bottom, with little mixing of the two populations. *Cancer borealis* has proportionately heavier chelae than *C. irroratus*, is less prone to burying in sand when disturbed, and in experiments generally showed a lower walking and activity rate which Jeffries correlated with differences in serum phosphate concentrations possibly

related to level of energy metabolism. Comparison of walking ability in an experimental treadmill showed *C. irroratus* to react optimally at 14°–18°C, *borealis* at 6°–14°C, but endurance of the former was far above the latter. Jeffries correlated the experimental results with distribution records, concluding that spatial partitioning of the bottom prevents competition. However, Musick and McEachren (1972) found the species not to be mutually exclusive on the Continental Shelf from Cape Henlopen, Del., to Cape Hatteras, N. C., over an area where sand is predominant, with occasional patches of gravel, and slope sediments are mostly silt and clay. Both species were most abundant along the shelf edge, but probability of catching *C. borealis* was highest over silt clay or coarse canyon sediments. Scarratt and Lowe (1972) found *C. irroratus* also on rocky areas, but larger individuals often on sand, and fishermen in the same area found commercial-sized crabs on mud. Musick and McEachren (1972) judged *C. borealis* to be more stenothermal than *C. irroratus*, supporting Sastry's finding (see below). They also suggested that there may be inshore and offshore populations of *C. borealis*.

In that same area of sampling, males in Haefner's (1977) samples ranged from 12 to 175 mm in carapace width, females from 13 to 152 mm. He recognized four modal-size groups, with tendency for sizes to correlate positively with depth. The population had a contagious distribution within a depth range of 20 to 400 m, and was maximally abundant within 150 to 400 m at 8°–13.9°C.

Haefner (1977) recorded incidence of fouling organisms, predominant among which was the barnacle, *Poecilasma inaequilaterale*, attached to gills in the branchial chamber.

Cancer (Cancer) irroratus Say

(Rock crab)

Fig. 288

Cancer irroratus Say (in part) 1817:59, pl. 4, fig. 2.—Hay and Shore 1918:435, pl. 35, fig. 1.—Rathbun 1930a:180, text-fig. 29, pl. 85, fig. 1.—Williams 1965:175, fig. 155.—Bigford 1979a:1, fig. 1.

Cancer (Cancer) irroratus.—Nations 1975:45, figs. 4, 42–3, 42–4.—1979:185 (by implication).

Recognition characters.—Carapace approximately $\frac{2}{3}$ as long as wide, convex, granulated. Anterolateral border divided into 9 teeth with margins granulate, not denticulate as in *C. borealis*, and with

notches between teeth continued on carapace as short, closed fissures giving teeth a pentagonal character. Posterolateral border a granulated ridge with 1 tooth at outer end similar to those of anterolateral border but smaller. Front with 3 teeth, middle one exceeding others and depressed.

Chelipeds of moderate size, not so long as second pair of legs; carpus with granulated ridges and sharp spine at inner distal angle; hand nearly smooth on inner face, outer face with 4 or 5 granulated lines, 2 lower ones continued on slightly deflexed fixed finger, superior one cristate. Walking legs rather long and slender; merus of first and second pairs extending far beyond carapace. Abdomen of male broad, first, second, and third segments with transverse granulated ridge.

Measurements in mm.—Carapace: male, length 78, width 119; length 62, width 91; ovigerous female, length 44, width 67.

Color.—Yellowish, closely dotted with dark purplish brown, becoming reddish brown after death. Squires (1965a) noted that it is reddish to pale purple on a light yellow background.

Habitat.—See discussion under "Remarks." Small to medium-sized individuals found near shore seasonally, whereas larger ones occur in deeper water. This species, and the preceding one, have ranges extending south of the Carolinas only in deep water. Low water mark to 575 m.

Type-locality.—"Inhabits the ocean" [Atlantic coast of the United States].

Known range.—Labrador to off Miami, Fla.

Remarks.—*Cancer irroratus* has a fossil record ex-

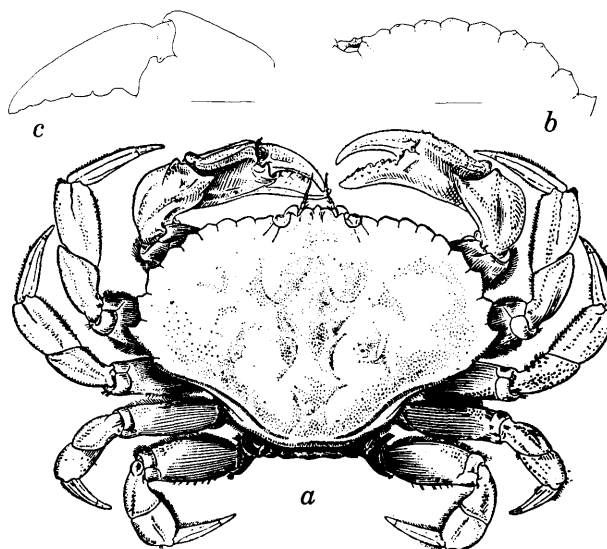


Fig. 288. *Cancer (Cancer) irroratus* Say. a, Male in dorsal view, reduced (from Rathbun 1884); b, right anterolateral border; c, dactyl and upper border of chela (USNM 13023, from Williams 1974c); b-c, 1 cm indicated.

tending from the Plio-Pleistocene to the present in North America (Nations 1975).

Bigford (1979a) summarized biological data more completely than can be done in space available here. Information on reproduction and development of *C. irroratus* is more extensive than that for *C. borealis*. Scarrett and Lowe (1972) reported mating in Northumberland Strait, near Prince Edward Island, from July to October, noting that males always mate with females 30–40 mm narrower than themselves, carrying them in a courtship embrace before, during and after molting, and copulating when the female is in the postmolt soft condition (also Hartnoll 1969, Elner and Staski 1978). Turner (1953, 1954) implied an earlier mating season in April–May for the Boston Harbor, Mass., area. Haefner (1976) gave detail from studies along the Middle Atlantic States, finding the species actively molting in April and June. Gonad development in June was related to size, that of males > 101 mm wide being well developed but that of males < 50 mm being undeveloped or in a very early stage of maturation; most females < 70 mm wide were in an early stage of ovarian development, but none with ripe ovaries were observed. Ovigerous females have been reported year round in Maine, peaking in August (Krouse 1972), but spawning there was judged to occur in late fall and early winter. Otherwise ovigerous females are known in January, February, April, and June in Virginia (Van Engel and Sandifer 1972; Haefner 1976), in March off Miami, Fla. (USNM), and August in Massachusetts (Rathbun 1930a). Musick and McEachren (1972) found ovigerous females only at depths < 30 m.

Sastry (1977a) described and figured five zoeal stages and a megalopa reared under laboratory conditions on a diet of *Artemia salina* nauplii. Eggs were removed from ovigerous females collected in Narragansett Bay (date not given), washed with sea water treated with Streptomycin and held in compartmented plastic boxes in 30‰ salinity seawater at 10°, 15°, and 20°C under a 14 h light–10 h dark regime. Eggs hatched directly into stage I zoeae, never into prezoae as did *C. borealis* from the same locality. The 15°C group survived best and they were described. Connolly (1923), reporting only four zoeal stages, may have missed an intermediate stage in plankton, and described a megalopa that does not agree with the reared one. Recent experiments (Sastry 1978) show that larvae cultured under daily cyclic temperatures (10°–20°, 15°–25°, 12.5°–17.5° and 17.5°–22.5°C) complete development to first crab stage at 10°–20°, 15°–25° and 12.5°–17.5°C and to megalopa at 17.5°–22.5°C, and that survival of all stages is enhanced at 10°–20°C cyclic tempera-

tures when compared with other constant and cyclic temperatures. Bigford (1979) found that the zoeal stages have positive phototaxis, but the extent of such movement decreases slightly as metamorphosis approaches; conversely, responses to gravity appear to change significantly as development proceeds from geonegative to rather abruptly geopositive behavior in zoeal stage V. This strong change results in a shift from planktonic to benthic habit.

Larvae from plankton were reported by: Fish (1925) from May to August at Woods Hole; Frost (1936) during summer around Newfoundland; Deevey (1960) from April to June in Delaware Bay; Hillman (1964) from late May to mid-July in Narragansett Bay near its mouth (*Cancer* sp.); Sage and Herman (1972) near Sandy Hook, N. J., in late spring; Scarrett and Lowe (1972) from June to September in Northumberland Strait with a peak in August and September; and Sandifer (1973d) occasionally at lower Chesapeake Bay stations in low concentrations, most abundantly off the mouth of the Bay in 23.3–32.3‰ salinity (mainly > 25‰) from May to July and September to October, with a peak in May and a smaller one in October, mainly in the temperature range 13°–21°C. There was little difference between surface and bottom densities. He (1975) felt that larvae of this species showed no distributional adaptations for retention in bays as do some other species more or less restricted to estuarine habitats.

Although *C. irroratus* is essentially a marine species as are other species of the genus, it does occur in lower reaches of estuaries, the movements being mainly seasonal (inshore during fall–winter–spring) among the younger segment of the population (Winget, et al. 1974; Ferreira, et al. 1979). Haefner and Van Engel (1975) found that male *C. irroratus* migrate into lower Chesapeake Bay in late fall, molt extensively in January, remain in papershell condition until late March and April, and leave the Bay in May. Crabs held in the laboratory confirmed the molting pattern observed in the field, which seems related to decreasing seawater temperatures, although rate of progression through the intermolt cycle is positively related to temperature. Crabs larger than 100 mm wide did not molt. Turner (1953, 1954) found that males in Massachusetts molt in November and March. The spring molters are soft in April and show a great growth increase in May. Haefner and Van Engel (1975) confirmed this, showing that most water uptake occurred between peeler and soft crab stages when progressive growth in length, width and weight resulted in increases of 18%–23%, 19%–27%, and 52%–82% respectively. In tank experiments, crabs

acclimated at 7°C approached isosmoticity near 28–30‰ salinity; crabs acclimated at 17.5°C were isosmotic near 24–26‰, but showed hyperregulation in salinity less than 20‰. Beers (1958), studying structure of the green gland in related *C. borealis*, concluded that its function is inefficient in salinities below 50‰ seawater, and hence limits the estuarine tolerance of the species.

In temperature tolerance experiments, F. J. and W. B. Vernberg (1970) found that animals collected from the Cape Hatteras area in February died after 1 h in water of 30°C, May animals died after 2 h at 32°C, but animals were unaffected by 48-h exposure to 10°C. Zoeae exposed to 4°C in 30‰ seawater survived for long periods with no harm, but zoeae at 20°C in 10‰ seawater were inactive after 1½ hr.

Distribution on the Continental Shelf is discussed in "Remarks" for *C. borealis*. Musick and McEachren (1972) suggested a continuous population of *C. irroratus* from southern New England to the Chesapeake Bight. Haefner (1976), in samples taken on the Continental Shelf in October, April, and June, found the species contagiously distributed in depths from 18 to 390 m with maximum density at 40–60 m in water of 6° to 9.9°C.

Mann (1973) showed that rock crabs are active predators on sea urchins but eat smaller sizes and less than the American lobster. Predatory fishes and crabs attracted to sclop dredge tracks within one hour of fishing have been observed at densities 3–30 times those observed outside the tracks (Caddy 1973); a photograph shows *C. irroratus* eating a lethally damaged scallop. Squires (1965a), noting its attraction to baited lobster traps, as have others, listed the food of *C. irroratus* as small *Littorina*, amphipods, *Crangon*, polychaetes and small pelecypods. He wrote that "dominated by the lobster, it

occupies fringe areas of the lobster grounds and makes forays into these grounds in search of food. Lobsters eat them and when stranded they are preyed upon by crows and gulls." *C. irroratus* is also preyed upon by fishes such as hake (Sikora, et al. 1972).

These and other aspects of the species' biology were reviewed by Saila and Pratt (1973), and parasites were reviewed by Sinderman and Rosenfield (1967). Haefner (1976) recorded incidence of fouling ectoparasites, *Alcyonidium* sp., and barnacles, *Octolasmis lowei*. *Gaffkya homari* is the causative agent of the fatal septicemic disease of lobsters. Cornick and Stewart (1968) showed that experimental infections with this agent from lobsters could cause significant numbers of crab deaths in a prolonged period at 15°C but that mean time to death is doubled at 10°C and is even longer at still lower temperatures. They postulated that at the latitude of Halifax, Nova Scotia, *C. irroratus* could serve as a reservoir of infection for lobsters, being relatively unaffected by it themselves during the prolonged cold season.

Section Brachyrhyncha

Superfamily Portunoidea

Family Portunidae

Carapace broad and flat, greatest width commonly marked by lateral spine; front dentate or lobate, orbits and eyestalks moderately large or elongate, anterolateral margin dentate; antennules folding obliquely or transversely, fifth legs mostly flattened, with leaf-shaped dactyl (Glaesner 1969).

Key to Subfamilies, Genera, and Some Species

1. Carapace with 5 teeth on anterolateral margin; lateral tooth equal to or not much larger than others 2
 Carapace with 9 anterolateral teeth, lateral tooth often much larger than others [Subfamily Portuninae] 3
2. Distal articles of fifth legs not paddlelike.
 [Subfamily Carcininae] *Carcinus maenas*
 Distal articles of fifth legs paddlelike [Subfamily Polybiinae] *Ovalipes*
3. Movable part of antenna not excluded from orbit. 4
 Movable part of antenna excluded from orbit by prolongation of basal article; anterolateral teeth alternately large and small *Cronius ruber*
4. Carpus of cheliped with mesiodistal spine; abdomen of male triangular . . 5
 Carpus of cheliped without mesiodistal spine; abdomen of male T-shaped *Callinectes*
5. Front with 2 bifurcated teeth between inner orbitals; fissures on orbital margin broadly open; color light brown, thickly covered over dorsal surface

with small white spots, reticulate pattern persisting in alcohol.

. *Arenaeus cribrarius*
Front with 4 separate teeth between inner orbitals (latter sometimes bifurcate);
fissures on orbital margin closed except for shallow notch; color varied
but never as above *Portunus*

Subfamily Carcininae

Carapace not very broad, anterolateral margins with 5 teeth (3–5 in extraterritorial species). Basal antennal article longer than broad. Legs 2–5 similarly constructed, though dactyl of fifth leg broadened and flattened. (After Christiansen 1969.)

Genus *Carcinus* Leach 1814

Christiansen 1969:49.—Hemming 1958b:107.—Manning and Holthuis 1981:75.

Carcinus maenas (Linnaeus)

(Shore crab; green crab)

Fig. 289

Cancer maenas Linnaeus 1758:627.

Carcinides maenas.—Rathbun 1930a:15, fig. 4.

Carcinus maenas.—Zariquey Alvarez 1968:354, fig. 115a, c.—Christiansen 1969:49, fig. 18.—Manning and Holthuis 1981: 75.

Recognition characters.—Carapace about $\frac{3}{4}$ as long as broad, regions well defined, surface finely and unevenly granular, especially in anterior half. Front with 3 broad, rounded teeth or lobes projecting moderately beyond orbits, middle one most advanced. Anterolateral border slightly arched and shorter than posterolateral, its 5 strong teeth directed forward. Superior orbital margin with single

notch about in middle, another in lower border near outer orbital tooth.

Chelipeds slightly unequal, nearly smooth except for 2 ridges (slightly granular in large individuals) on upper surface of hand; merus short; carpus with broad internal tooth or angle. Walking legs smooth and unarmed, second and third pairs longest, last pair shortest and more flattened than remaining legs with fringe of hairs on last 3 articles and dactyl acutely lanceolate. Rather broadly triangular abdomen of male with segments 3–5 fused, broad abdomen of mature female with segments free.

Measurements in mm.—Carapace: male, length 60, width 79 (Rathbun 1930a); female, length 60, width 77 (Christiansen 1969). Larger crabs are known in nature, one specimen from the Scilly Islands measured 92 mm, and widths of 132 mm have been induced experimentally (Carlisle 1957).

Color.—Usually multicolored with dorsal surface dark green, bluish green, grayish green or reddish, sometimes clear light sky blue, often mottled with white in juveniles; a row of lighter colored spots following cervical groove on each side and curving backward to posterolateral margins; yellowish white to darker (tile) color ventrally; legs varying from yellowish white to “tile” color or violet (Christiansen 1969; Crothers 1968; Rasmussen 1973). Provenzano (1960) noted 3% total or partial albinism in an adult population in Massachusetts. Larvae of albino adults also lacked pigment except for the eyes. Provenzano suggested that more than one gene may be responsible for the wide variation in degree of albinism. Hogarth (1975a) contrasted the highly polymorphic color pattern of juveniles with the typically drab adults, suggesting that among crabs in general a bold small pattern appears less conspicuous against a natural textured background but becomes conspicuous when the crab grows. He (1978) found loss of pattern with growth. Wald (1968) showed that the green crab has a visual system composed of at least two types of receptor with red and blue sensitivities presumably serving the function of color discrimination.

Habitat.—Usually in shallows less than 5 or 6 m but rarely to 200 m (Christiansen 1969). The species lives on a variety of bottoms. Naylor (1962) found small crabs (35 mm wide) present at low tide in all months; larger crabs tended to move up-

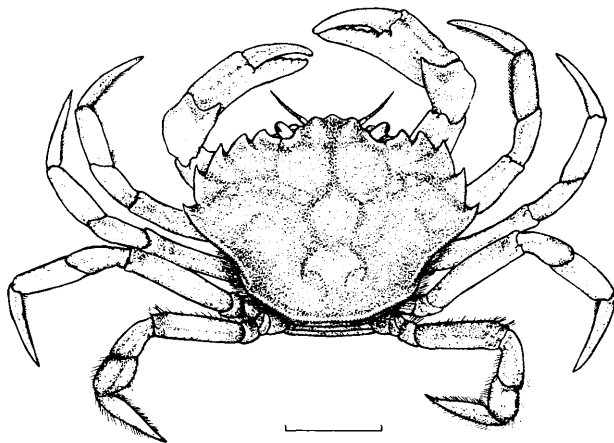


Fig. 289. *Carcinus maenas* (Linnaeus). Male in dorsal view from Oslofjord, Norway, 2 cm indicated (from Christiansen 1969).

shore with high tides in summer to remain stranded beneath stones at intervening low tides, but no such movements occurred in winter. Crothers (1969, 1970) found variation in population density associated with habitat, lower densities occurring on wave beaten, exposed shores and higher levels prevailing in protected bays with lower salinity. Muus (1967) described a peculiar construction of shallow hollows in sand. The salinity range usually tolerated is about 10–33‰, although in intertidal zones regularly flooded by fresh runoff the crabs may reside between tides in 1.4–3.2‰ salinity (Perkins, et al. 1969).

Type-locality.—Marstrand N of Goteborg, west coast of Sweden (Holthuis and Gottlieb 1958).

Known range.—Northumberland Strait near Pugwash and Merigomish, Nova Scotia, and St. Patrick's Channel, South Bay in central Cape Breton Island (Bousfield and Laubitz 1972) to Virginia; Iceland; Kvaenangen, Norway, just beyond 70°N, southward, including southwestern and rarely southern Baltic Sea, through North Sea and British Isles to Mauritania; Australia (Almaça 1960, 1962, 1963; Christiansen 1969; Manning and Holthuis' 1981). According to these authors, both the North American and Australian populations are probably the result of introductions, and reported occurrences other than the above represent either temporary introductions or misidentifications, but Boschma (1972) noted introductions, probably by transport on ships, in Maungmagan, Burma, also the Red Sea, Madagascar, India and Ceylon.

Remarks.—The literature on *C. maenas* and its close relative *C. aestuarii* (= *C. mediterraneus*, see Manning and Holthuis 1981) is probably even more extensive than that on the American blue crab, *Callinectes sapidus*. Broekhuysen's (1936) comprehensive work on the species in the Netherlands consolidated a great deal of earlier investigation and served as a baseline for elaborative studies. That together with Crothers's (1967, 1968, 1969, 1970) masterful interpretive summary and Clay's (1965) exhaustive review of literature of the species make further summary redundant. For convenience and recognition of a few additional papers, the following notes are included.

The green crab is an omnivore whose feeding is influenced by abundance, size, and kinds of food available (Ropes 1968). Pelecypods formed a dominant part of the diet of crabs 30 to 59 mm wide in Plum Island Sound, Mass.; crabs there opened and ate clams equal to their own width, only the largest clams resisting attack. Greater amounts of food in crabs caught during low tide and just after sunrise suggested that feeding is heaviest at night at high tide. Activity and feeding seemed reduced at water

temperatures below 7°C; low salinity apparently did not influence feeding. Ovigerous females were relatively inactive, thus less destructive of clams than non-ovigerous females; feeding was reduced among males during mating and in crabs preparing for molting or assuming a new hardened integument.

Animals hatched in spring from winter eggs may attain a carapace width of about 20 or more mm by fall of the first season; those developed from summer eggs will be much smaller but by the next spring will catch up to the first group because the young crabs molt frequently until reaching about 30-mm width after which they molt infrequently. Early estimates of mean increase in size per molt were $\frac{1}{3}$ – $\frac{1}{5}$ regardless of age and sex, but Hogarth (1975b) formulated instar number and growth for juveniles from observation and results of other research. Females are judged to live about 3 years attaining average widths of 36, 42 and 50 mm in yearly intervals while males are judged to attain ages of 3 or more years (some even 5) at slightly larger sizes with increasing age, 36, 42, 48, 56 mm annually, with a few even larger. Mature males tend to molt during May-June, females in July-September. Females may reach sexual maturity at 19–20 mm width (in one case an ovigerous dwarf measured 12.1 mm [Williams and Needham 1937]), and males at 25–30 mm may have spermatophores, but ability to copulate at this size is not proved.

Early molting of the males may be correlated with the fact that hard males mate with females that are in the soft condition (Hartnoll 1969), hence would molt before the latter. Mating resembles that described for *Callinectes sapidus*; it may last for hours and be repeated if the pair is separated (Cheung 1966a, and others). Reaction of males to a displaying female may vary from pairing to rejection with injury to the female, probably depending on physiological state of the male. A single mating can fertilize more than one batch of eggs but few soft females fail to mate. Spalding (1942) described functional morphology of the male and female reproductive systems. He considered the seemingly useless internal spermatophore of *Carcinus* to represent a holdover from affixed external spermatophores of *Macrura* and *Anomura*.

In Holland, the number of females ovigerous declines to near zero during the later summer-early fall molting period but abruptly thereafter rises to a level of 50%–60%. This number persists through winter until June when another brief drop occurs followed by some new egg production in July. These fluctuations correspond to phasing of maturity among females. Those that spawned in fall drop hatching eggs in the spring, molt, and then may cast a second clutch of eggs in summer. Overwin-

tering juveniles may attain maturity in spring and spawn after that in early summer, but in other geographic areas spawning varies. In the Baltic, berried females hide in deeper (8–10 m) more saline water until the larvae are hatched (Rasmussen 1959). The egg mass often contains a nemertine, probably *Carcinonemertes carcinophila*.

A debate has set forth alternate possibilities for the mechanism of attachment of eggs to the abdominal pleopods of ovigerous decapod crustaceans. Cheung (1966b) reviewed the evidence and partly on basis of experiments with *C. maenas* contended that in decapods no externally deposited membranes are formed around the egg at any stage. The outermost membrane really consists of 3 layers which are histochemically distinct from one another and cannot be equated with epicuticle. The outermost layer is derived from the vitelline membrane, the middle layer through solidification of a fluid exuded from the egg at spawning, and the inner layer formed by a highly PAS-positive substance (a histochemical test) from the egg. It is suggested that formation of this trichromatic membrane is initiated by fertilization. The funiculus (stalk) for attachment is formed of the outermost layer of the trichromatic membrane. The glue appears to be derived from the same substance which solidifies to form the middle layer. This is assumed to be liberated from the egg by being squeezed through layer 1 under pressure when the latter is being stretched and twisted during formation of the stalk. "Cement" glands are lacking in *Carcinus*, the mucuslike substance of *Macrura* is absent in *Brachyura*; hence the only conceivable source of the glue for the eggs, and perhaps also of the appropriate enzymes which Burkenroad (1947a) suggested, must be the egg itself. In any case, for eggs to be successfully attached to pleopods a female must bury herself in sand to form an enclosed cavity beneath her body in order that the extruded eggs can be forced against the pleopods.

A large female (46 mm wide) is estimated to have 185,000–200,000 eggs in a clutch. During the incubatory period females carry on characteristic preening and aerating movements about the egg mass. It was for this species that Bethe (1897) described the "Eierschutzreflex" for berried females which when intensely stimulated freeze into a huddled protective posture with the legs cradled around the egg mass. Ovigerous females of many *Brachyura* show this reflex. *Carcinus maenas* infested with *Sacculina carcini* also will show cleaning-aerating and migrating movements, feminized males reacting as if even a small-sized externa were an egg mass (Rasmussen 1959) and demonstrating the "Eierschutzreflex." Rasmussen found that ovigerous crabs in Danish waters leave littoral areas to hide in

deeper, more saline water until larvae are hatched, after which they return to molt and copulate with males that stay all summer in shallows of 0–1.5 m at a salinity of 19.54‰ (\bar{x}). Behavior of the parasitized crabs is similar and highly influenced by oxygen tension, low tension accelerating the movements in a conspicuous way. In aquaria, when *Sacculina externa* had stopped producing sexual products and a slight decaying commenced, the crabs stopped this behavior and in some cases tore and even ate the externa. This suggests that only a living externa can induce the behavior and that hormonal feminizing influences it.

Experimentally, eggs will develop in a salinity range of 25.8–26 to 40.3–50.4‰ at 10°C, or 41–53.1‰ at \bar{x} 16.3°C, and 20‰ at 15.7–17°C. Cold of 1.4°C in low salinity areas kills eggs; the animals usually migrate to avoid such extremes. Wear (1974), using *C. maenas* along with other species, showed that increasing egg size slows down rate of development and increases a constant factor (a) which reflects change in incubation period due to changes in temperature, thereby defining shifts along a development axis. Hence, among closely related forms increasing egg size (yolkiness) slows down rate of development and increases value of a . Moreover, the increasing temperatures of spring (March–June) can effect a 3-fold decrease in natural incubation time of a single species in one locality, depending on when eggs are incubated.

Upon hatching, development of *C. maenas* passes through a perhaps abnormal prezoal stage, 4 zoeal stages and a megalopa that were described from rearing and plankton by Williamson (1903, 1915) and Lebour (1928). Williams (1968) was the first to complete rearing of larvae in the laboratory with the aid of a variety of diets, but Rice and Ingle (1975) are the only recent workers to give detailed description of reared larval stages (at 15°C). Average duration of the zoeal stages in days was I 14.8, II 7.9, III 9.6, IV 10.0, and megalopa 15.4. Dries and Adelung (1976) found that food and temperature are the most important exogenous factors for larval rearing success. On a diet of *Artemia* nauplii, success of zoeae was best at 15°C, megalopae at 17.5°C. Larvae hatched in darkness.

In the western Atlantic, Deevey (1960) found larvae in Delaware Bay from June to August, and Hillman (1964) reported them in July–August and December in Narragansett Bay. Kurian (1956) reviewed records of larval occurrence in Europe showing variation with latitude. Larvae of *C. maenas* are present year round at Plymouth, England, but most abundant in spring and summer, while in the Sound off Norway they are present in summer with megalopae persisting until fall. Rasmussen (1973) found that eggs spawned later than May–July may

never develop to first crab off Denmark and that annual fluctuation in salinity-temperature governs success or failure of a year class in those waters. Experimentally, *C. maenas* zoeae show higher mortality in diluted sea water than megalopae, and molting of the latter into crabs is delayed or prevented by water of low salinity.

In the United States, the green crab has had an economic impact on the fishery for the soft clam, *Mya arenaria*. Decreases in the fishery, especially from clam farming, have been correlated with predation by the crab (Glude 1955). Marked increase in the soft clam fishery of New England has been linked to mortalities and declining abundance of the green crab associated with cold winters and a general cooling trend (Welch 1968).

A vast literature on physiology, genetics, growth, etc., resting disproportionately on studies of *C. maenas*, is beyond the scope of this account and more fittingly found in reviews such as Waterman (1960, 1961).

Subfamily Polybiinae

Carapace not broad, anterolateral margin with 3 to 5 teeth, some legs as long as chelipeds, fifth legs

paddle-shaped. (After Glaessner 1969.)

Holthuis (1968) reviewed the synonymy of this subfamily and gave notes on related subfamilies.

Genus *Ovalipes* Rathbun 1898

Rathbun 1898b:597.—Stephenson and Rees 1968:215.

Carapace relatively narrow but somewhat broader than long, deep dorsoventrally; anterolateral borders curved, bearing 5 teeth approximately equal in size and spacing; stridulating ridges on under surface of pterygostomian region. Front rather narrow, 3 teeth on margin between orbits; basal article of antennules dorsally visible. Chelipeds subequal, merus with boss on anterodistal margin; carpus with well-developed internal spine; palm with conspicuous inner and outer dorsal carina continued on dactyl, inner surface dorsally with dense row of hairs. Second, third, and fourth legs with long, sharp dactyl with grooved surfaces and carinate edges; propodus and carpus grooved and carinate on outer border. (Adapted from Stephenson and Rees 1968.)

Key to Species

1. Carapace yellowish gray, closely set with small annular spots of reddish purple; iridescent spots between each pair of anterolateral spines approximately alike in size and shape *O. ocellatus*
Carapace yellowish gray, without ocellated spots; iridescent spot between fourth and fifth anterolateral spines large and nearly semicircular in shape *O. stephensoni*

Ovalipes ocellatus (Herbst)

Fig. 290

Cancer ocellatus Herbst 1799:61, pl. 49, fig. 1.

Ovalipes ocellatus.—Williams 1965:160, fig. 143.—Stephenson and Rees 1968:241, pls. 37B, 40D, 41C, 42I, figs. 1I, 2H, 3H, 4H.—Williams 1974c:29, fig. 81.—Felder 1973:54.

Recognition characters.—Carapace about $\frac{1}{4}$ wider than long, convex, finely granulate except for longitudinal band of slightly enlarged granules in median line, and smooth area on posterior central part of adults. Median frontal tooth about twice as long as lateral ones. Orbit with shallow fissures above, often nearly closed in adults, open in young. Anterolateral teeth strong, acute, directed forward; inner suborbital angle projecting at least as far as median frontal tooth. Pterygostomian region with long, curved, stridulating ridge made up of ap-

proximately 50 close-set striae narrowing into tubercles at inner end of ridge, short complementary ridge on proximal end of inner margin of cheliped merus. Lobe at distal inner angle of merus of outer maxilliped longer than broad.

Chelipeds rather large; distal $\frac{3}{5}$ of anterior margin of merus with several small, blunt spines and dense fringe of hair; carpus finely but irregularly granular, with 2 spines, inner one very long; hand triangular in cross section, external border ridged and covered with fairly uniform small tubercles; fingers about as long as palm, tapering gradually, tips turned abruptly toward each other.

Abdomen of male narrow, sides nearly parallel; sixth segment nearly twice as long as seventh in midline, seventh segment subcircular; first pleopod of male broad and stout in proximal $\frac{2}{3}$, narrowing abruptly distally and with terminal part bent ventrolaterally in sinuous curve. Abdomen of adult female suboval and small compared to sternum.

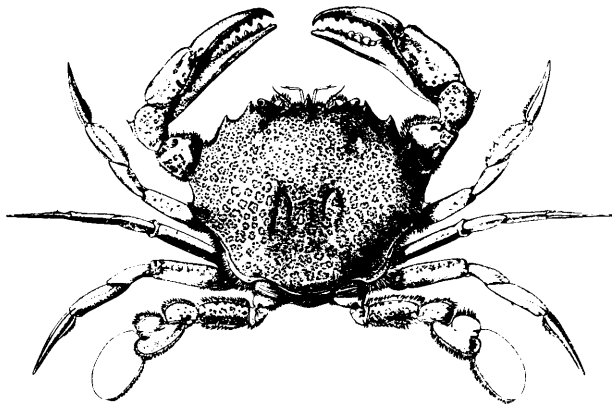


Fig. 290. *Ovalipes ocellatus* (Herbst). Male in dorsal view, approximately $\times 0.8$ (from Rathbun 1884).

Measurements in mm.—Width of carapace: male 87; female 60.

Variation.—Spines are more acute on young than old individuals; on some old adults the anterolateral spines are worn away leaving only rounded humps. The orbital fissure is nearly closed in adults but often open in juveniles. The width between the suborbital angles tends to increase relatively with age.

Color.—"Yellowish gray, closely set with small annular spots of reddish purple; carapace and chelipeds with a silvery or brassy iridescence; ground color of chelipeds and legs light brownish tending to orange and bluish; large irregular bluish purple spots on upper surface of chelipeds; large part of carpus including spine bluish; similar but lighter spots on proximal half of other legs; paddles greenish yellow, with deep yellow rim" (Rathbun 1930a, and others). An iridescent spot between each pair of anterolateral spines.

Habitat.—Common on a variety of bottoms, especially sand; surface to 95 m (Williams and Wigley 1977).

Type-locality.—Long Island near New York.

Known range.—Northumberland Strait, Prince Edward Island, Canada (Bousfield and Laubitz 1972), to Georgia. Records from Mississippi (Franks, et al. 1972) and the Texas coast (Whitten, et al. 1950) should be referred to *O. floridanus* Hay and Shore (Leary 1946 and 1967; Williams 1976; Park 1978).

Remarks.—The distinction between this species and *O. stephensoni* (= *guadulpensis*) was discussed by both Williams (1962) and, in detail, by Stephenson and Rees (1968) in their revision of the genus (see also Powers 1977). There is a distinct difference in color, and an apparent difference in habitat among the adults. Adults of *O. ocellatus* are usually found near shore (Musick and McEachren 1972) and in the Carolinas the young of both species are found

there, as pointed out by a number of authors. Occasional specimens are carried well into estuaries by currents (Mansueti 1962). Assessing lethal limits, F. J. and W. B. Vernberg (1970) found that animals from the Cape Hatteras region in October became inactivated after 1 h exposure to 35° water, recovered when returned to 25°C, but at the other extreme tolerated 4°C for prolonged periods without harm. Physiologically, *O. ocellatus* is a species with northern affinities (W. B. and F. J. Vernberg 1970). Ferreira, et al. (1979) found that the species enters New Haven, and Stamford, Conn., harbors during summer, reaches a peak in numbers in early fall, then leaves before the onset of winter.

Females mate in the soft stage (Bliss 1968; Hartnoll 1969). Ovigerous females have been noted in North Carolina with orange eggs in October and February and with black eggs in October and December (Dudley and Judy 1971). Costlow and Bookhout (1966a) reared larval stages in the laboratory, finding five zoeal stages and a megalopa. At 30°C larvae completed development to first crab in salinities of 25, 30 and 35‰. At 25°C larvae survived in 25 and 30‰ salinity, but did not develop beyond the megalopa at 35‰. Extra larval stages were not observed. Development required 26.1 to 27 days at 20°C, and approximately 18 days at 25°C. Rate of development was not affected by the limited range of salinities employed. Hillman (1964) found larvae in plankton on 27 June and 18 July in Narragansett Bay and Fish (1925) took them from late July until late October at Woods Hole. Sandifer (1973d; 1975) found them common around Cape Hatteras in November, but in an extensive plankton survey in the lower Chesapeake Bay region took only 39 zoeae, mostly late stages, in 25.26–32.34‰ salinity at 20°–26.2°C from June to October, most commonly in September and usually at the surface.

Pearse, et al. (1942) pointed out that *O. ocellatus* can bury itself completely in sand and respire by passing water into the gill cavity from anterior or lateral openings, then out through two posterior openings. An evidence for this is presence of the parasitic barnacle *Octolasmis mulleri* on the afferent side of the gills whereas in most hosts it is on the efferent side (Walker 1974). Gray (1957) correlated great activity of the species with large gill area and compared this with gill areas of other strictly aquatic crabs.

Stephenson and Rees (1968) suggested that the ancestral *Ovalipes* had a predisposition towards stridulation leading to the remarkable development of stridulatory apparatus in the genus. Stephenson (1969) expanded analysis of these functions by study of museum specimens, suggesting

that since both sexes possess the mechanisms, sound communication may be a method for attracting individuals into aggregations.

***Ovalipes stephensoni* Williams**

Fig. 291

Platyonichus ocellatus (var.).—Smith 1887:632.

Ovalipes ocellatus gadulpensis.—Rathbun 1930a:23 (part, the North Carolina and Georgia specimens).

Ovalipes gadulpensis.—Williams 1962:39–41.—1965:161.

Ovalipes gadulpensis (Form a).—Stephenson and Rees 1968:243, pls. 37C, 40E, 41D, 42J; figs. 1J, 2I, 4I.

Ovalipes stephensoni Williams 1976:208, figs. 1e, f, 2.

Recognition characters.—Closely resembling *O. ocellatus*, but differing in the following characters: dorsal aspect of carapace not covered with ocellated spots; body flatter; outer orbital and frontal teeth more acute, median frontal tooth acuminate; iridescent spot between fourth and fifth anterolateral spine larger than spots between first to fourth teeth and nearly semicircular in shape; dorsal sur-

face of palm and external ridge of palm with tubercles not uniform in size, giving a roughened appearance in individuals larger than 30 mm wide.

Measurements in mm.—Carapace: male, length 68, width 82; female, length 63, width 78.

Variation.—The distance between the suborbital angles tends to increase relatively with age.

Color.—General color of carapace light lavender-gray underlaid with dull yellow, some specimens darker or lighter, with regular pattern of lighter spots dull yellow, off-white, or bluish yellow to lavender yellow, rear border of carapace light blue; spine of carapace purplish red at base to red or purple subdistally, white at tips; carpus and merus of chelipeds somewhat same color as carapace except pink flesh colored at merocarpal joint and on hand; fingers white on inner surface, and with white teeth; large spine at internal angle of carpus and a few small but distinct spots on superoexternal surface of hand purple, large spine grading to lighter purple on body of carpus; anterior border of chela and first 3 pair of walking legs with longitudinal band of brownish purple, band extending to lower border of dactyl on chela; dactyls of first 3 walking legs and outer border of hand immediately below external ridge same color, sometimes darker on dactyl with teeth same color, distal tip of fixed fin-

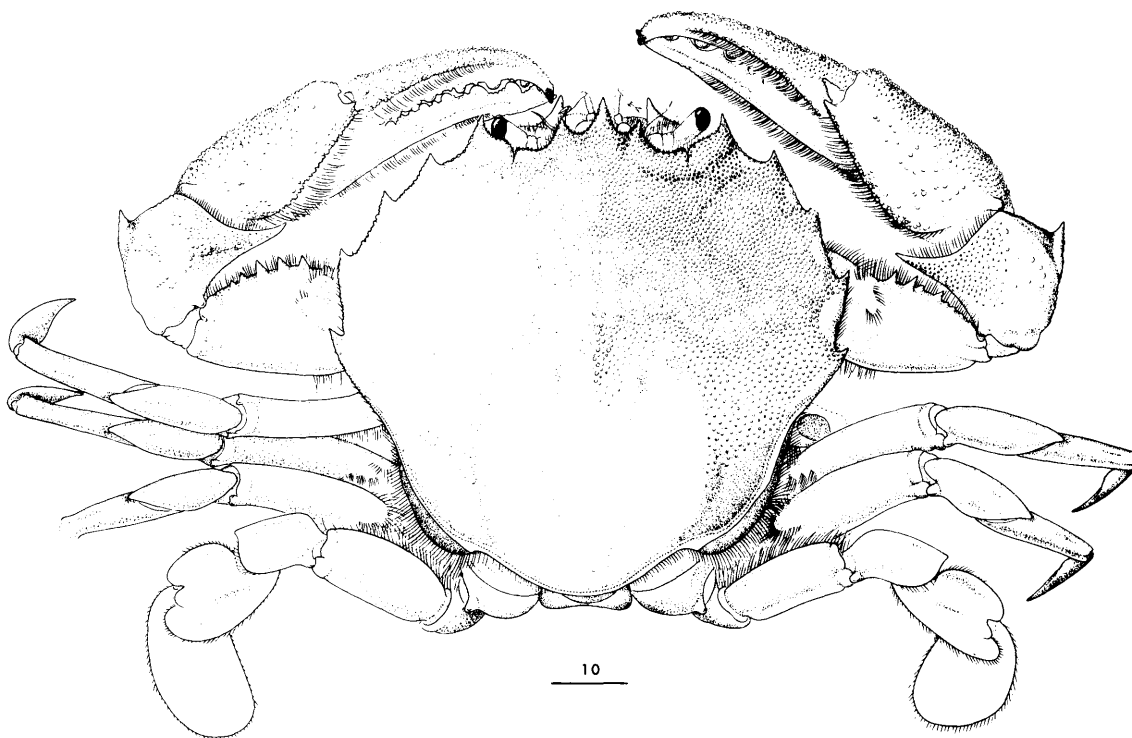


Fig. 291. *Ovalipes stephensoni* Williams. Male in dorsal view, 10 mm indicated (from Williams 1976).

ger similarly colored; blade of swimming leg yellowish; underparts light.

Iridescent spots between anterolateral teeth, on distal or dorsal surface of external carpal spine and along upper edge of hand, at superodistal corner of merus on first 3 walking legs and along dorsal edge of these legs distally, on dorsal surface of second abdominal segment; spot between fourth and fifth anterolateral spines nearly semicircular (Williams 1962; 1965).

Habitat.—On or over sandy bottom, surface to 227 m (Wenner and Read 1982).

Type-locality.—South of Beaufort Inlet, N. C., 31°11'N, 76°42'W, 35 m.

Known range.—Off Accomack County, Va., 37°31'N, to near Biscayne Bay, Fla.

Remarks.—This species and its twin, *O. floridanus* Hay and Shore (= *guadulpsensis* [Saussure] of various authors [Williams 1976]), are among the relatively few described examples of divergence of a marine Carolinian stock into two recognizable entities. The Gulf of Mexico species is much smoother than the Atlantic Carolinian one, but coloration and habitat seem similar.

Adults of *O. stephensoni* are found farther from shore than adults of *O. ocellatus* in the Carolinas, but the young of both species occur near shore as pointed out by a number of authors. Musick and McEachren (1972) thought that the difference may be related to temperature preferences; they captured *O. ocellatus* from 8° to 12°C and 11 to 22 m and *O. stephensoni* from 11° to 19°C and 18 to 49 m in the southern Chesapeake Bight. F. J. and W. B. Vernberg (1970) found that both of these species have similar tolerance to elevated temperature, but did not compare low temperature tolerance of *O. stephensoni* with the sustained low of 4°C survived by *O. ocellatus*.

Ovigerous females are reported from North Carolina in January and Florida in March.

Adaptations of *O. floridanus* (= *guadulpsensis*) for feeding and burrowing in sandy bottoms (Caine 1974) are parallel to those of *O. stephensoni*. The crabs are nocturnally active, walking with dactyls of walking legs penetrating the substrate, and are extremely aggressive with conspecifics or other portunids but not with other crabs. Burrowing by alternate thrusts, flexures and sweepings of several pairs of legs, the crabs squat at rest in sand at an angle of 60° where they breathe by reversed circulation, thus avoiding oxygen-deficient water from the substrate. Caine discussed the opportunistic carnivorous feeding habits and described the gastric armature.

Subfamily Portuninae

Carapace broad, anterolateral margin with up to 9 teeth, chelipeds very long; fifth legs flattened, paddle-shaped. (After Glaessner 1969.)

Genus *Arenaeus* Dana 1851

Rathbun 1930a:134.—Hemming 1958b:13.

Arenaeus cribrarius (Lamarck)

(Speckled crab, siri-capote (Brazil))

Fig. 292

Portunus cribrarius Lamarck 1818:259.

Arenaeus cribrarius.—Hay and Shore 1918:434, pl. 34, fig. 3.—Rathbun 1930a:134, pl. 58, figs. 2–3; pls. 59–60.—Williams 1965:173, fig. 153.—1974c:30, fig. 86 (key).—Coelho and Ramos 1972:188.—Taisoun 1973:52, photo 9, figs. 8A, 9A.—Felder 1973:55, pl. 8, fig. 4.—Powers 1977:74.

?*Arenaeus websteri* Jones 1968a:156, photograph p. 155.

Recognition characters.—Carapace more than twice as wide as long, finely granulate, produced on each side into strong spine. Front not so far advanced as outer orbital angles, with 6 teeth including inner orbitals, submesial pair of teeth at either side of central notch coalesced. Anterolateral teeth strong, somewhat acuminate, heavily ciliate beneath. Superior margin of orbit with 2 deep fissures divid-

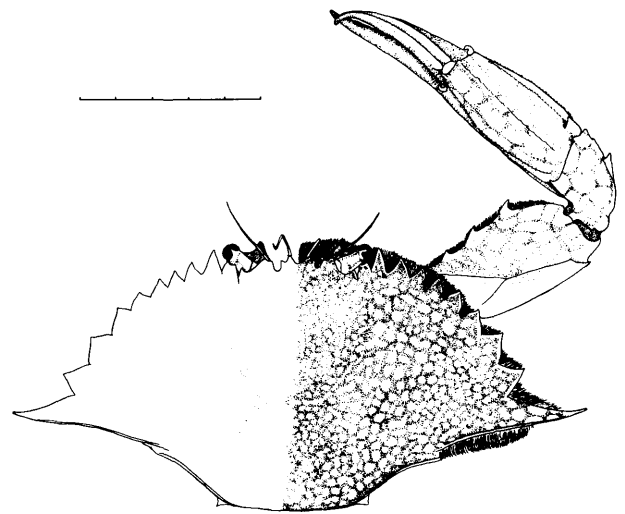


Fig. 292. *Arenaeus cribrarius* (Lamarck). Male in dorsal view, legs not shown except for right cheliped, color pattern of right side indicated, 5 cm indicated (from Williams 1965).

ing it into 3 lobes; inferior margin of orbit with wide external fissure, inner angle much advanced. Lower surface of carapace hairy.

Chelipeds of moderate size; merus with 3 spines on anterior border and short tuberculiform one near distal end of posterior border; carpus with inner and outer spine and lower lateral ridge flanked mesially by obsolescent row of tubercles; hand with 5 longitudinal granulose ridges and 2 spines, one at articulation with carpus and another above base of dactyl. Walking legs rather short and broad, densely fringed with short hairs. Swimming legs stout. Basal segment of abdomen produced on each side into strong, sharp, slightly upcurved spine.

Measurements in mm.—Carapace: male, length 65, width including lateral spines 142; mature female, length 54, width 116. Both males and females reach width of 153 (Camp, et al. 1977).

Color.—Light brown, light maroon, gray or olive brown thickly covered over dorsal surface with small, rounded, white to yellow spots; spots on dorsal surface of chelipeds somewhat larger; tips of walking legs yellow. Color pattern persisting in alcohol (various authors). Occasionally white with pinkish-brown reticulations (Jones 1968a).

Habitat.—This crab lives in rather shallow water along ocean beaches from the water line to 68 m and is well adapted to life in the waves and shifting sand (Dragovich and Kelly 1964; Dudley and Judy 1971; Fausto-Filho 1966a; Hoese 1972; Wass 1955). Hildebrand (1954) reported it as preferring the relatively shallow water of the white shrimp grounds in Texas, and Siebenaler (1952) regarded it as a "trash" form on the Florida east coast shrimp grounds. Pearse, et al. (1942) stated that where waves roll at the low-tide mark *A. cribrarius* may scurry across sand and burrow backward. In doing this, the crab flips sand forward away from the body with the chelipeds, waves the second to fourth legs rapidly from the median line laterally, and the fifth legs posteriorly and dorsally, thus sinking vertically into the sand. Often the crabs bury themselves completely. The heavy coat of hairlike setae on each side of the mouthparts keeps out sand, and with the chelipeds held close to the body a clear channel is left for currents from the branchial chamber. Ability to maintain strenuous activity in the breaker zone near shore may be partly explained also by the relatively large respiratory surface in this species (Gray 1957).

Type-locality.—Brazil.

Known range.—Vineyard Sound, Mass., to Santa Catarina, Brazil.

Remarks.—At a beach-seine sampling station in

the surf zone and an associated tidal pool in South Carolina, Anderson, et al. (1977) took 422 specimens of *A. cribrarius* over a two-year period. In water temperature of 11°–28.6°C at 27.5–35‰ salinity, the specimens taken measured 7 to 141 mm in carapace width. One of the most abundant organisms taken in the samples, the number of crabs was directly correlated with water temperature. Ovigerous females occurred as early as mid-June, and recently spawned ones as late as mid-September (see also Park 1978). Small individuals occurred from May through October.

Elsewhere, ovigerous females are known in May, July and August from Florida (Camp, et al. 1977), in August from North Carolina, and in September from Venezuela and Brazil. Many ovigerous females have been collected at night on sand shoals near Beaufort Inlet, N. C., at the edge of the surf zone in very shallow water (J. Costlow, personal communication).

Old crabs may bear the barnacle *Octolasmis mulieri* on the gills (Camp, et al. 1977).

The case of *Arenaeus websteri* Jones probably parallels that of *Callinectes humphreyi* Jones for which positive determination cannot be achieved because the dry holotype was destroyed by a bloodhound pup (see Williams 1974b:741). Differences between the eastern Pacific *A. mexicanus* and western Atlantic *A. cribrarius* are slight, and the possibility of a population of the latter becoming genetically isolated in Barbados seems remote. Light-colored crabs living on light-colored bottoms are common, and *A. websteri* is probably an albinistic phase of *A. cribrarius*. Limits of morphometric variation in *A. Cribrarius* probably encompass the dimensions of *A. websteri*.

Randall (1967) reported *A. cribrarius* from stomach contents of the porcupinefish, *Diodon hystrix*.

Genus *Callinectes* Stimpson 1860

Williams 1974b:719.

Portunid crabs lacking internal spine on carpus of chelipeds. Abdomen of male broad proximally, narrow distally, roughly T-shaped; third to fifth segments fused and tapering from broad third to distally narrow fifth; sixth narrow, elongate, telson ovate with acute tip. Abdomen of female exhibiting two forms: immature with abdomen triangular from fourth segment to tip of telson, segments fused; mature with abdomen broadly ovate, segments freely articulated, telson narrow, triangular. (After Williams 1974b.)

Key to Species Based on Carapace

(Excluding juveniles)

1. Front with 2 prominent, broad-based, triangular teeth between inner orbitals; each with or without rudimentary submesial tooth on mesial slope. *C. sapidus*
 Front with 4 teeth between inner orbitals, or 2 prominent teeth separated by space often bearing pair of rudimentary submesial teeth 2
2. Submesial pair of frontal teeth well developed and more than half as long as lateral pair (measuring from base of lateral notch between teeth). *C. bocourti*
 Frontal teeth decidedly unequal in size, submesial pair no more than half as long as lateral pair (measuring from base of lateral notch between teeth) 3
3. Carapace very smoothly granulate, lines of granules visible but barely perceptible to touch (except epibranchial line variably prominent). *C. similis*
 Carapace coarsely granulate, scattered granules and lines of granules quite evident to sight and touch 4
4. Anterolateral teeth (exclusive of outer orbital and lateral spine) lacking shoulders and swept forward 5
 Anterolateral teeth (exclusive of outer orbital and lateral spine) lacking shoulders, not swept forward 6
5. Anterolateral teeth well separated, all except first 3 and lateral spine with anterior margins concave; chelipeds with ridges finely granulated *C. larvatus*
 Anterolateral teeth adjacent, stout, anterior margins not noticeably concave, fifth tooth often largest; chelipeds with ridges coarsely granulated *C. exasperatus*
6. Submesial pair of frontal teeth absent or vestigial *C. ornatus*
 Submesial pair of frontal teeth never vestigial, but no more than half length of lateral pair *C. danae*

Key to Mature or Nearly Mature Males

(Based primarily on first pleopods)

1. Tips of first pleopods falling well short of suture between thoracic sternite VI and mesially expanded sternite VII 2
 First pleopods reaching to, almost to, or beyond suture between thoracic sternite VI and mesially expanded sternite VII 4
2. First pleopods well separated from each other, almost never touching or crossing; tips not lanceolate 3
 First pleopods overlapping each other, often crossing; tips lanceolate *C. ornatus*
3. First pleopods slender distally, nearly straight, tips bent slightly mesad *C. similis*
 First pleopods fairly stout distally, angled toward midline, then abruptly bent forward in a short slender terminal extension *C. larvatus*
4. Tips of first pleopods curved abruptly mesad. *C. exasperatus*
 Tips of first pleopods not curved abruptly mesad 5
5. First pleopods with tips never extending beyond abdominal locking tubercle on thoracic sternite V, slender distal part almost straight, minutely spined, tips almost always bent ventrolaterally. *C. danae*
 First pleopods with tips extending beyond abdominal locking tubercle on thoracic sternite V, slender part definitely curved or sinuous, variously

- spined, never bent ventrolaterally at tip. 6
6. Front with 2 prominent, broad based, triangular teeth between inner orbitals; each with or without rudimentary submesial tooth on mesial slope *C. sapidus*
- Front with 4 teeth between inner orbitals reaching nearly common level. *C. bocourti*

***Callinectes bocourti* A. Milne Edwards**

(Siri (Brazil))

Figs. 293f, 294

Cancer pelagicus.—De Geer 1778:427, pl. 26, figs. 8–11.

Callinectes Bocourti A. Milne Edwards 1879:226.

Callinectes bocourti.—Williams 1974b:766, figs. 12, 18j, 20m, 22j, 27.—Powers 1977:75.

Recognition characters.—Carapace bearing 4 frontal teeth with tips reaching nearly common level, lateral triangular pair obtuse with mesial side having flatter angle than lateral side, submesial pair narrower than laterals. Metagastric area with length and posterior width about equal, anterior width 2 times length. Anterolateral margins moderately arcuate, anterolateral teeth exclusive of outer orbital and lateral spine swept forward, anterior margin of teeth shorter than posterior margin, teeth in lateral half of row always acuminate. Surface of carapace dorsally smooth and glistening around perimeter (when wet) and on epibranchial surfaces; central part granulate, coarsest granules over mesobranchial and rear half of cardiac areas and lateral half of branchial lobes. Epibranchial line prominent and nearly continuous, sulci on central part of carapace deeply etched.

Chelipeds remarkably smooth except for usual spines and obsolescent granules on ridges; fingers of major chela heavily toothed, lower margin of fixed finger often decurved near base in adults.

Male abdomen and telson long, extending nearly to juncture between thoracic sternites III and IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching as far forward as in male, sixth segment nearly as long as fifth, its distal edge uniformly arched, telson elongate-triangular with inflated sides. First pleopods of male very long, often exceeding telson and crossed near tips; sinuously curved and overlapping in 2 places proximally, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercle and recurving gradually to termination near midline; armed distally with dorso-lateral band of large and small recurved spi-

nules. Gonopores of female asymmetrically ovate in outline with apex on long axis directed antero-mesad; aperture of each sloping from surface on mesial side under rounded, sinuous anterolateral border superior to low rounded eminence on posterior border.

Measurements in mm.—Largest male: carapace length 76, width at base of lateral spines 132, including lateral spines 156. Largest female: length 70, width at base of lateral spines 121, including lateral spines 146. The species characteristically reaches fairly large size.

Variation.—Williams (1974b) discussed variation in this species.

Color.—Complete color descriptions (Chace and Hobbs 1969; Taissoun 1969, 1972) and notes (Rathbun 1896a, 1930; Holthuis 1959) give a range of color variations. These can be broadly summarized as: Overall cast olive green with prominent reddish markings. Carapace olive, grayish green, greenish chestnut or forest green with variable purplish to red markings, especially on branchial, hepatic, cardiac, and gastric areas, individuals of large size sometimes being dark chestnut tinted blackish brown on gastric and metagastric areas, with an oblique spot on subbranchial region; anterolateral teeth olive green with brown to red tints and yellowish white tips. Chelipeds red to dark reddish brown above and whitish below with bluish tints, main colors being sharply separated on outer surface of palm; fingers red to reddish brown, a purplish cast on internal articulation of merus with carpus and this member with chela; tubercles, tips of fingers and spines on articles cream. Remaining legs reddish above with shades of maroon, yellow and olive green ventrally except distal articles scarlet to red or dark red distally; hairs olive-tan. Underparts of body mainly dirty white to purplish red with suffusion of blue marginally, first abdominal segment mainly reddish tan. Males tend to be reddish, females greenish.

Habitat.—Usually in shallow brackish waters ranging in salinity from nearly fresh (Norse 1978; 1978a) to nearly full marine concentrations over mud to sandy bottoms; mature females tend to move to saltier water after mating. Associated with *Callinectes sapidus* in many estuaries but seems more tolerant of stagnant, polluted situations (Chace and

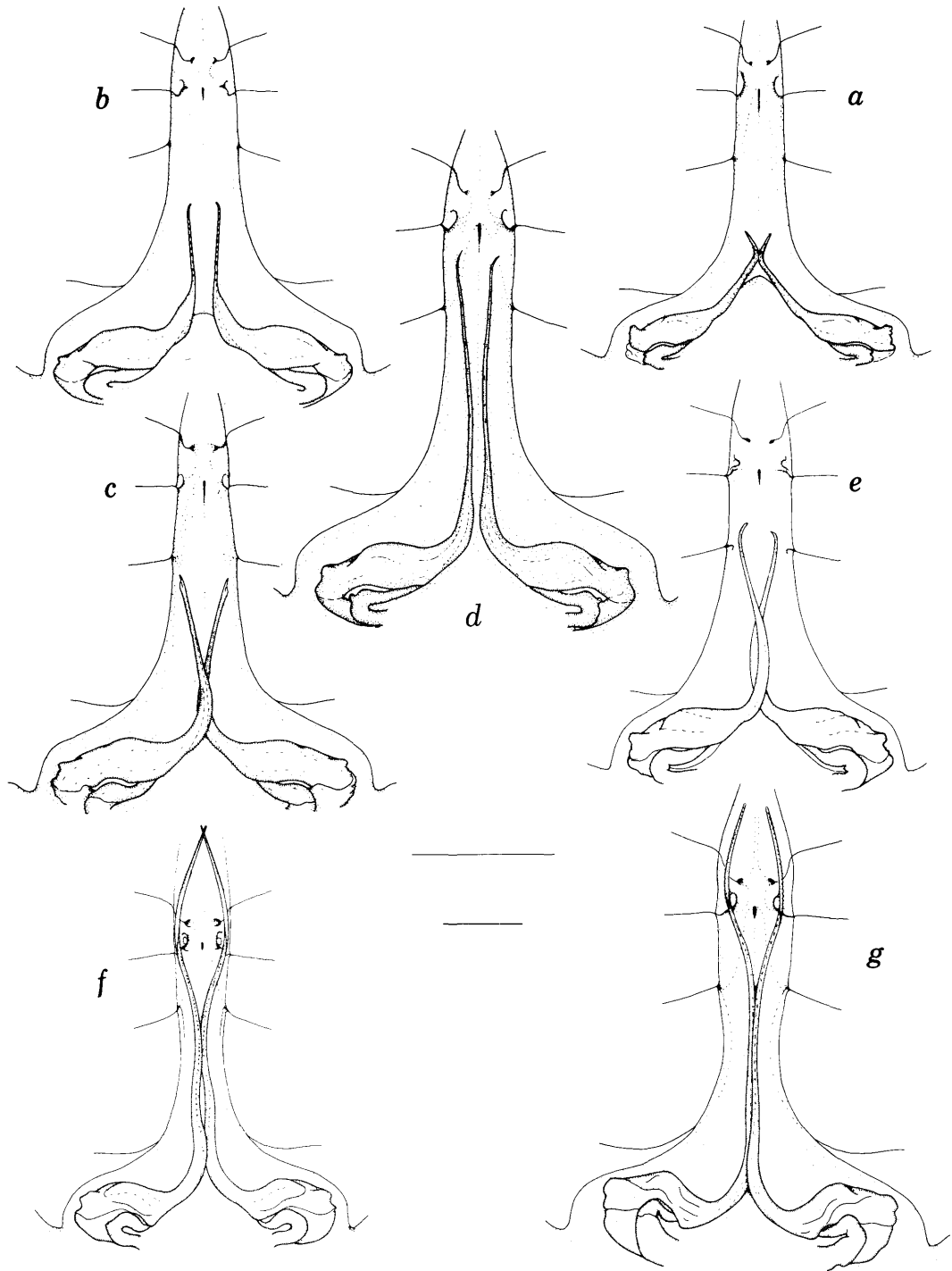


Fig. 293. *Callinectes*, male first pleopods in situ with abdomen removed; portions of sternites IV-VIII; a, *C. larvatus* Ordway; b, *C. similis* Williams; c, *C. ornatus* Ordway; d, *C. danae* Smith; e, *C. exasperatus* (Gerstaecker); f, *C. bocourti* A. Milne Edwards; g, *C. sapidus* Rathbun. Scales = 1 cm, g has lower magnification (from Williams 1974b).

Hobbs 1969; Taissoun 1969, 1972; Williams 1974b).

Type-locality.—Mullins River, 20 miles south of Belize, [British] Honduras.

Known range.—Jamaica and Belize to Santa Catarina, Brazil; occasional occurrences in Florida, Mississippi and North Carolina, USA (Williams

1974b; Perschbacher and Schwartz 1979; Williams and Williams 1981).

Remarks.—North American records may be explained by drift from the Caribbean, possible routes being suggested by drift bottles (Brucks 1971) and debris (Williams and Williams 1981).

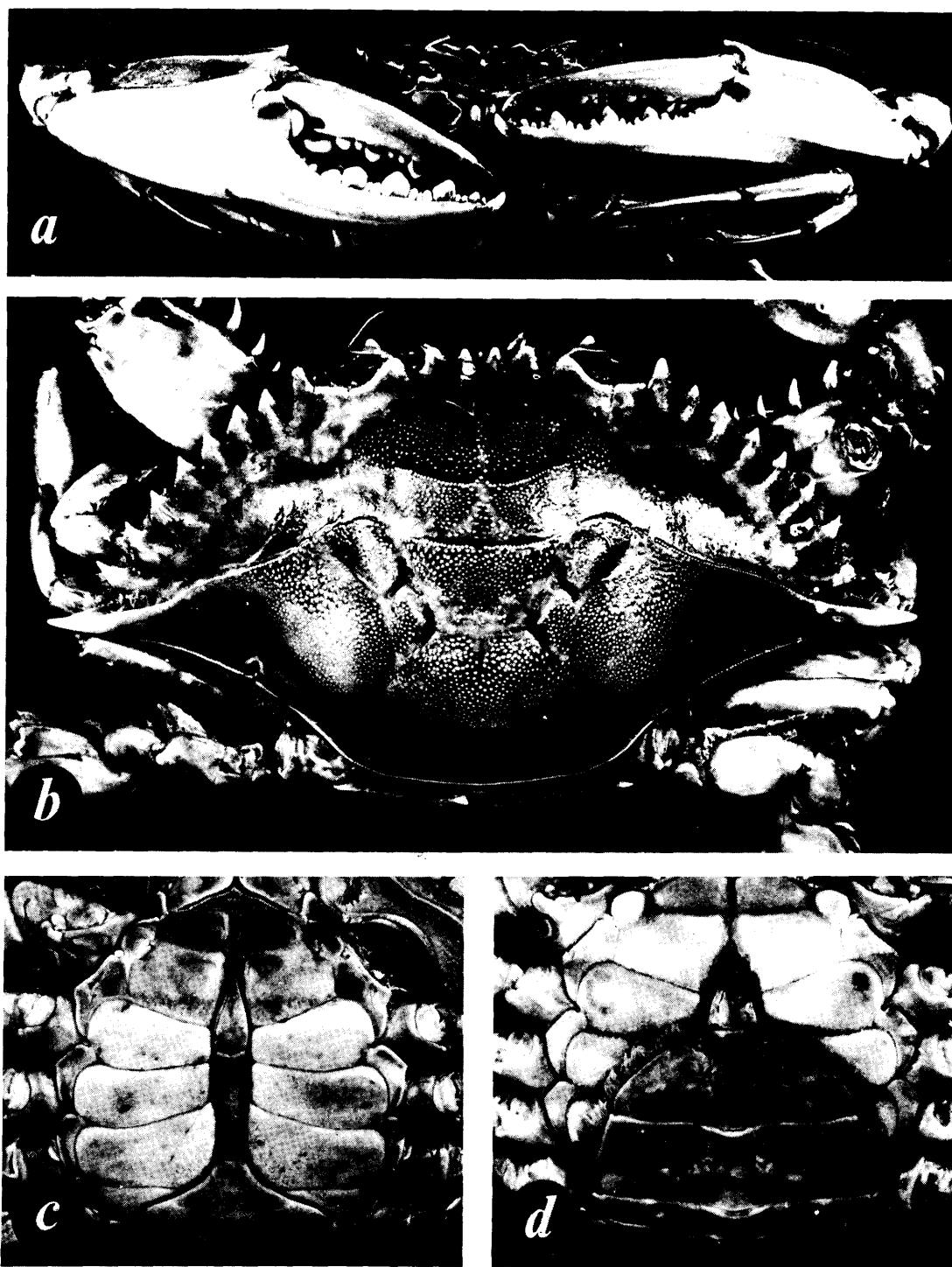


Fig. 294. *Callinectes bocourti* A. Milne Edwards. *a*, Male chelae in frontal view; *b*, carapace; abdomen and sternal area, *c*, male, *d*, female; *a*, *c* $\times 1$; *b* $\times 1.2$; *d* $\times 1.4$ (from Williams 1974b).

Ovigerous females are known nearly the year round in one part or another of the range, perhaps with seasonal peaks in abundance associated with latitude (Williams 1974b).

Though not so important economically as *C. sapidus*, fisheries for *C. bocourti* exist along the northern coast of South America (Williams 1974b).

Callinectes danae Smith 1869

Figs. 293*d*, 295

Callinectes Danae Smith 1869:7.

Callinectes danae.—Williams 1974b:746, figs. 7, 18*e*, 20*e-f*, 22*e*, 24.

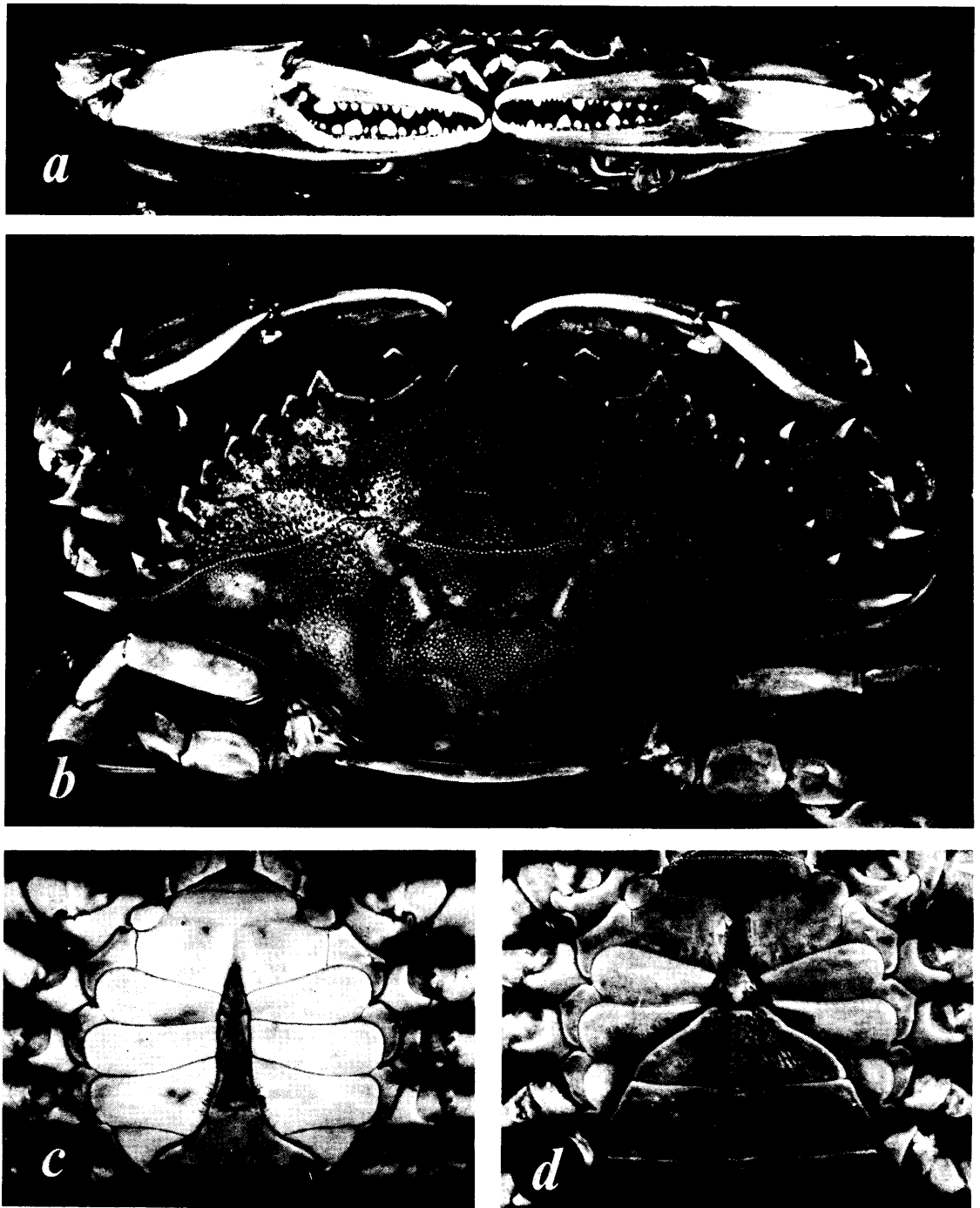


Fig. 295. *Callinectes danae* Smith. a, Male chelae in frontal view; b, carapace; abdomen and sternal area; c, male, d, female; a, $c \times 1$; b $\times 1.4$; d $\times 1.5$ (from Williams 1974b).

Recognition characters.—Carapace bearing 4 frontal teeth, submesial pair no more than half length of lateral pair. Metagastric area of adults with anterior width about 2–2.5 times length, posterior width about 1.5 times length. Anterolateral margins somewhat arched, teeth exclusive of outer orbital and lateral spine varying from often convex sided with subacute tips at orbital end of row to sharper

and more spiniform laterally, each with anterior margin shorter than posterior and separated from contiguous ones by narrow based rounded notches. Surface of carapace rather evenly and smoothly granulate, except granules more widely spaced on epibranchial region and near anterolateral border, most crowded on gastric, mesobranchial and cardiac regions; nearly smooth along frontoorbital,

posterolateral and posterior borders.

Chelipeds with granulate ridges, upper surface of carpus bearing slightly developed interrupted ridges trending longitudinally with axis of limb, ridges bearing obsolescent granules often better developed in males than in females, inferior lateral ridge terminating in strong lateral spine or teeth often followed by strong eminence. Male abdomen and telson reaching beyond suture between thoracic sternites IV and V; telson triangular, longer than broad with somewhat inflated sides; sixth segment of abdomen with sides nearly straight, diverging proximally, poorly calcified proximally except for variably indurated basal portion often connected to distal part by narrow central column. Mature female abdomen and telson reaching as far as in male, sixth segment shorter than fifth, telson triangular with slightly inflated sides. First pleopods of male reaching beyond midpoint of thoracic sternite VI, overlapping each other near base, or adjacent, and tapering to narrow membranous tips usually bent ventrolaterally; armed with scattered but mainly dorsal minute spinules and 2 to 4 subterminal, sternomesial, exceedingly slender elongate spinules. Gonopores of females broadly and irregularly ovate with apex on long axis directed anteromesad, aperture of each broadly open mesially, narrowing laterally, and sloping from surface on mesial side under curved and rounded superior border and rounded prominence on posterolateral border.

Measurements in mm.—Largest male: carapace length 58, width at base of lateral spines 104, including lateral spines 139. Largest female: length 48, width at base of lateral spines 84, including lateral spines 108.

Variation.—Williams (1974b) discussed variation in this species.

Color.—Live males from Cubatão River near Santos, São Paulo, Brazil: Carapace olive, becoming indigo on edges of lateral spines and outer anterolateral teeth in some individuals, more uniformly olive in others; teeth and spines on chela white tipped; a white patch in deepest part of depression above third walking leg. Cheliped with upper surface of palm, dactyl, part of carpus and spined edge of merus indigo to purple, and same color in splashes on inside of fingers, distally on merus and laterally on carpus. Flat outer dorsal surface of palm and upper surface of merus reticulate blue and olive (but many crabs predominantly olive on this part). Walking and swimming legs predominantly china to azure blue, grading to greenish and olive in darker parts. Lower edge of chelae grading from purple to china blue or azure individually. Chelipeds with inner face of palm,

outer face of palm and fingers, lower face of merus, as well as meri of remaining legs and ventral surface of cephalothorax, white.

Described above is a colorful male which should be called the "purple crab" if *C. sapidus* is called a "blue crab." Some individuals are duller and some have a reticulate pinkish-blue cast on the upper surface of chelipeds.

Color notes by Kretz and Bucherl (1940) and Taissoun (1969) emphasized the distal intense purple coloration of legs and grayish-blue carapace on adult males.

Habitat.—A common species in Brazil where it occurs from muddy estuaries in mangroves and algae-covered broken shell bottoms, to beaches and open ocean depths of 75 m. Specific limits of salinity tolerated are not well documented, but ranges indicated are from fresh to full sea water, and perhaps to hypersaline lagoons. Norse (1978; 1978a) regarded the species as more marine than estuarine. Kretz and Bucherl (1940) indicated that *C. danae* is the most abundant member of the genus along beaches from Santos to Rio de Janeiro where they worked. Park (1969) found the species only on or adjacent to the ocean side of islands in Biscayne Bay, usually on wave-beaten shores. He reported it absent from the Florida Keys.

Type-locality.—Recife [= Pernambuco, Estado de Pernambuco], Brazil.

Known range.—Bermuda; New Hanover County, N. C., near Cape Fear, rare (Perschbacher and Schwartz 1979); southern Florida and eastern side of Yucatan Peninsula to Estado de Santa Catarina, Brazil.

Remarks.—Records north of Florida may be explained by drift from the Caribbean (Williams and Williams 1981). A probable Pleistocene occurrence in Maryland is reported by Williams (1974b).

The spawning season probably extends the year round over the range as a whole (Williams 1974b).

Incidental reports of purchase in markets and capture on fishing vessels imply fairly general utilization of this species where it is abundant (Williams 1974b).

Callinectes exasperatus (Gerstaecker)

Figs. 293e, 296

Lupea exasperata Gerstaecker 1856:129.

Callinectes exasperatus.—Williams 1974b:757, figs. 9, 18g, 20i, 22g, 26.

Recognition characters.—Carapace bearing 4 well-developed frontal teeth, submesial pair narrower and slightly shorter than lateral pair. Metagastic

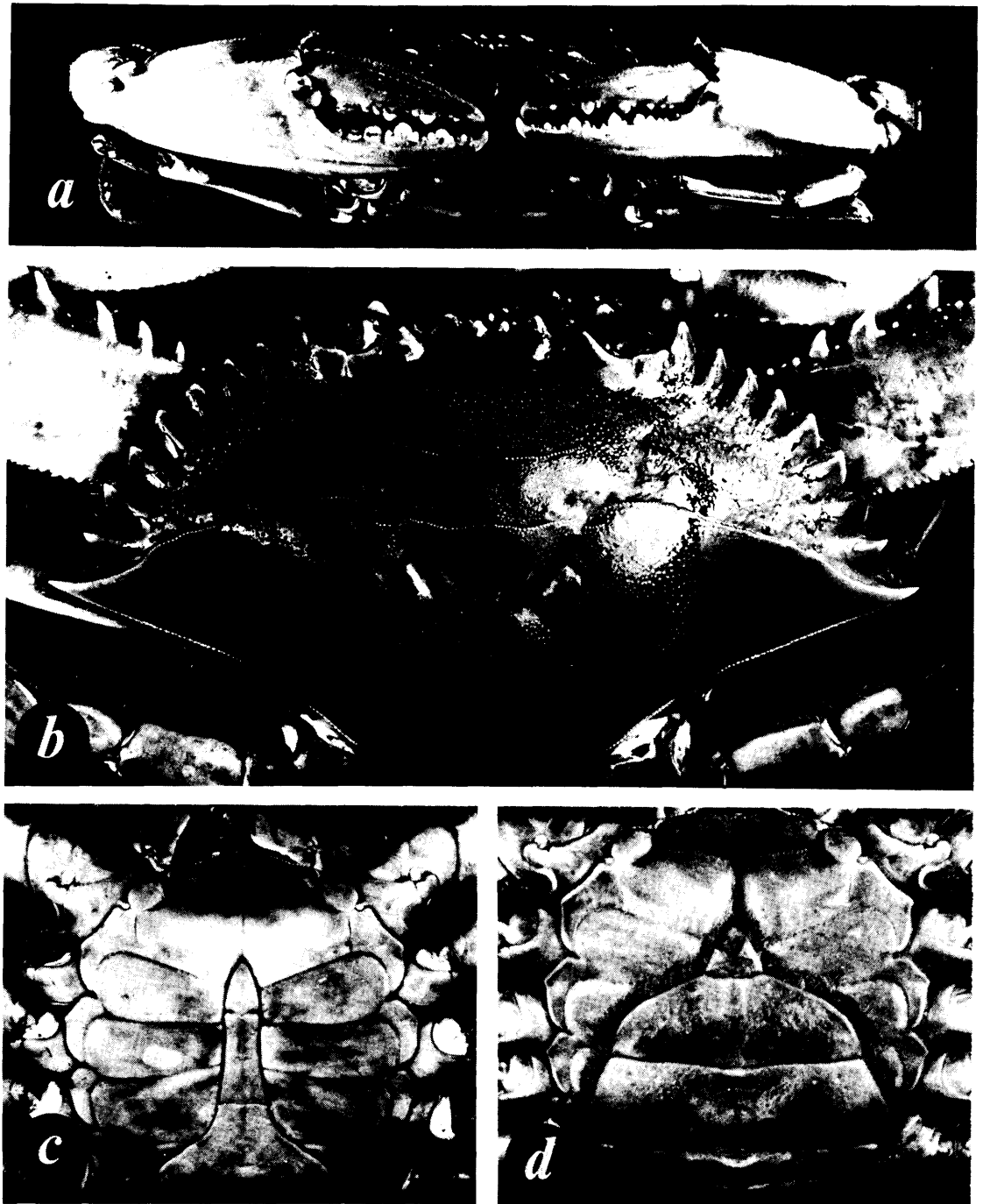


Fig. 296. *Callinectes exasperatus* (Gerstaecker). a, Male chelae in frontal view; b, carapace; abdomen and sternal area, c, male, d, female; a $\times 0.8$, b $\times 1.1$, c $\times 1$, d $\times 1.4$ (from Williams 1974b).

area with posterior width 1.2–1.3 times length, anterior width 2.3–2.5 times length. Anterolateral margins strongly arched with anterolateral teeth exclusive of outer orbital and lateral spine usually but not always curved forward; teeth progressively broader laterally with fifth tooth often largest. Lateral spine stout, usually less than twice length of preceding tooth. Surface of carapace conspicuously granulate with densest concentrations on central eminences, coarsest and most widely spaced

granules in front of epibranchial line separated by smooth surfaces. Central sulci on carapace definite but not deep; epibranchial line rather flatly arched, slightly sinuous.

Chelipeds robust, ridges and crests of all articles coarsely granulate; fingers of major chela strong but not markedly gaping.

Male abdomen and telson reaching along posterior quarter of thoracic sternite IV; telson lanceolate with sinuous inflated sides, length 1.5 times

basal width; basal portion of fused segments 3–4–5 truncate laterally. Mature female abdomen and telson reaching about same level as in male; telson triangular with inflated sides, length 1.2 times basal width; fifth segment longer than sixth. First pleopods of male reaching slightly beyond suture between thoracic sternites VI and VII, sinuously curved, overlapping in proximal half along midline then diverging distally, twisting on axis near tip and bending abruptly mesad; armed distally with scattered minute spinules, tip slightly broadened and opening posteromesially. Gonopores of female broadly and somewhat asymmetrically ovate in outline with orientation of long axis mainly in frontal plane but with apex directed anteromesad; aperture of each laterally elongate and sinuous, sloping from broadest area at surface on mesial side to narrower and deeper portion under rounded overhanging anterior border with prominent central projection and posterior border with elongate posterolateral eminence.

Measurements in mm.—Largest male: carapace length 67, width at base of lateral spines 114, including lateral spines 129. Largest female: length 59, width at base of lateral spines 101, including lateral spines 124.

Variation.—Williams (1974b) discussed variation in this species.

Color.—Carapace of adult male purplish red, more accented on proto-, meso-, and metagastric areas and at base of lateral spines and anterolateral teeth; branchial region and anterolateral teeth obscure maroon. Dorsal surface of all legs purplish red with intense orange red on articulations; inferior portion of merus, carpus, and fingers of chelipeds intense violet; internal and external portion of chelae as well as remaining ventral aspect of animal white with tints of soft purple (Taissoun 1969).

Habitat.—Primarily in shoal marine, estuarine, and perhaps fresh water, especially in association with mangroves and around river mouths from water's edge to recorded depths of about 7.5 m (Rankin 1900; Coelho 1967, 1970; Chace and Hobbs 1969; Taissoun 1979).

Type-locality.—Puerto Cabello, Venezuela.

Known range.—Duval County, E of Jacksonville, Fla. (rarely) (USNM), to Santa Catarina, Brazil; Veracruz, Mexico; Bermuda; also reported from extreme southern Texas.

Remarks.—*Callinectes exasperatus* has a number of distinctive features. It has the roughest appearing carapace and chelipeds of any species in the genus because the granulations are coarser and sharper than in others. The median epistomial tooth is more widely separated from the front than among the

congeners, perhaps a function of the vaulted carapace which contributes to the deep bodied form. Similar to *C. bocourti* in structure of frontal teeth, *C. exasperatus* has less prominent cardiac lobes and sulci bounding the metagastric area. The lateral spines are relatively shorter than among other species of the genus. A blunt anteromesial eminence on the carpus is pronounced. Narrowest width of the male abdomen is in the distal third of the sixth segment, the narrowed portion becoming increasingly distal with age together with progressive crossing of the pleopods.

Few dated collections contain ovigerous females: March, Puerto Rico and Guadeloupe; April, Barbuda and Panama; May, Jamaica; June, West Indies; August, Santa Catarina, Brazil. Other undated collections in museums are from Bermuda, southern Florida, Pernambuco and São Paulo, Brazil.

Callinectes larvatus Ordway

Figs. 293a, 297

Callinectes larvatus Ordway 1863:573 [8].—Manning and Holthuis 1981:93, fig. 20c, d.

Callinectes marginatus.—Williams 1974b:722 (part), figs. 3, 18b, 20a, 22b.—Felder 1973:59, pl. 8, fig. 9.—Powers 1977:77.

Recognition characters.—Carapace bearing 4 frontal teeth, submesial pair no more than half length of lateral pair. Central trapezoidal (metagastric) area short, anterior width about 2.4 times, posterior width about 1.5 times length. Anterolateral margins arched slightly; anterolateral teeth exclusive of outer orbital and lateral spine without shoulders, usually trending forward and anterior margins of all except first 2 concave, last 2 teeth spiniform. Lateral spine moderately long and slender. Surface coarsely granulate anterior to prominent epibranchial line and over mesobranchial regions, more finely and closely granulate on proto- and mesogastric areas, prominent branchial lobes, and especially on cardiac lobes; posterior and posterolateral margins smooth.

Chelipeds with smoothly granulate prominent ridges on propodi and reduced ones on carpi; fingers compressed but broadened dorsoventrally producing a pointed spatulate shape; major chela with usual enlarged proximal tooth on dactyl opposing molariform complex on fixed finger often with decurved lower margin.

Male abdomen and telson narrow, reaching slightly beyond suture between sternites IV and V; telson about 1.8 times longer than wide; sixth seg-

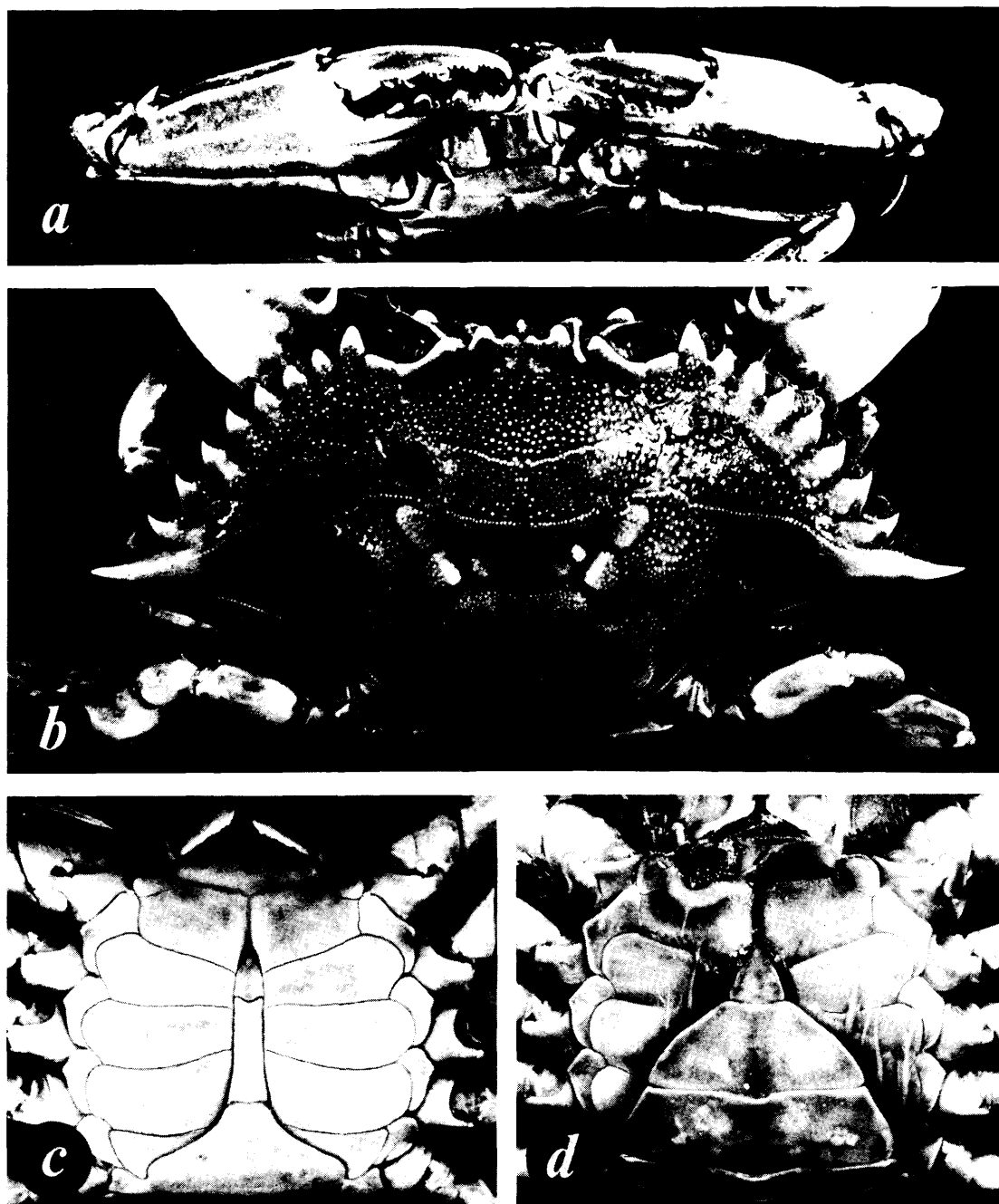


Fig. 297. *Callinectes larvatus* Ordway. a, Male chelae in frontal view; b, carapace; abdomen and sternal area, c, male, d, female; a \times 1, b \times 1.5, c \times 1.4, d \times 1.7 (from Williams 1974b).

ment nearly parallel-sided but somewhat broadened proximally. Mature female abdomen and telson reaching same level as in male, length slightly exceeding width (1.05 times); sixth segment longer than fifth. First pleopods of male short, reaching about midlength of sternite VII, approximating each other or occasionally overlapping at level of sharp distal curve, distal portion abruptly curved laterad, tapered to a rather sharp point, twisted $\frac{1}{4}$

turn on axis and, except for membranous spout-like tip, armed with minute scattered reflexed spinules tending to arrangement in rows, a few spinules proximal to flexure. Gonopores of female ovate with apex on long axis directed anteromesad, aperture of each with margin irregularly rounded and sinuous except on mesial side where it slopes from surface laterad under superior anterior border.

Measurements in mm.—Largest male: carapace length 67, width at base of lateral spines 118, including lateral spines 142. Largest female: length 59, width at base of lateral spines 82, including lateral spines 95. Mature size of females varies considerably, the smallest examined having a carapace length of 33 and width including lateral spines of 70.

Variation.—Williams (1974b) discussed variation in western Atlantic members of *C. larvatus* (= *C. marginatus*).

Color.—Carapace brown with areas of bluish black. Chelae brown above; fingers dark on external face except for tips and proximal portion, internal face dark in distal $\frac{2}{3}$; dark color of fingers retained in preservation.

A juvenile male collected by Elliott Norse at Pigeon Key, Fla., 6 August 1974, frozen and observed by me a few days later: mottled grayish tan over carapace and dorsal side of chelipeds. Fingers of chelae white tipped; central band of blue on both fingers running onto palm and becoming lighter as it grades into white; teeth maroon in center of row or white rimmed with maroon along "gum line"; distal and proximal teeth white, large proximal crushing tooth off-white.

Tiny male with essentially white chelae except for mottled dorsal side.

Habitat.—The species lives in a variety of shallow environments probably seldom exceeding 15 m but usually in depths of 5 m or less and often in intertidal pools. Most specimens have been collected by hand, seine, dip net, etc., from sand and mud flats, algae and grass flats, sandy beaches, rocky pools, eroded coral bases, oyster bars, shallows at edge of mangroves, and at the surface under lights at night (Williams 1974b)

Type-localities.—Key West, Florida; Tortugas; Bahama Islands; Haiti.

Known range.—Beaufort, N. C., through Caribbean Sea to south central Brazil off São Paulo; Bermuda. North Carolina records are rare (Williams 1974b; Perschbacher and Schwartz 1979).

Remarks.—The populations of *C. larvatus* and *C. marginatus* on each side of the Atlantic were judged indistinguishable by means of external morphological characters until Manning and Holthuis (1981) studied a large series of specimens and found differences in granulation of the carapace, depth of cervical groove behind the orbits, ventral inner orbital angle, and minute differences in the male pleopods.

Ovigerous females are recorded from December to July in various parts of the geographic range on both sides of the Atlantic. Specifically the records

are: St. Thomas, December and January; Grenadines and Cuba, March; Haiti, April; Jamaica, May; Colombia and Curaçao, June; Florida and Puerto Rico, July.

Callinectes ornatus Ordway

Figs. 293c, 298

Callinectes ornatus Ordway 1863:571.—Williams 1974b:739, figs. 6, 18d, 20d, 22d.—Felder 1973:58.—Powers 1977:77.

Recognition characters.—Carapace with lateral pair of frontal teeth prominent but submesial pair small, often almost completely rudimentary. Metagastric area of adults not deeply sculptured, anterior width about 2.8–2.9 times length, posterior width about 1.75 times length. Anterolateral margins broadly arched, teeth exclusive of outer orbital and lateral spine progressively more acuminate laterad; first 5 teeth with posterior margins longer than anterior margins, shouldered, distinctly separated by narrow based, rounded notches; last 2 teeth with margins approximately equal in length, separating notches broad, next to last tooth distinctly more acuminate than spiniform last one. Lateral spine trending forward. Surface of carapace with granulations most prominent on anterior half and on mesobranchial regions, granulations smaller and more closely crowded on meso-metagastric and cardiac regions, nearly smooth along postero-lateral and posterior borders.

Chelipeds with smoothly granulated ridges on chelae, carpus almost smooth dorsally, inferior lateral ridge terminating in a low tooth occasionally followed by an inconspicuous eminence. Major chela usually with strong basal tooth on dactyl and, especially in adult males, lower margin of propodal finger often decurved near base.

Male abdomen and telson reaching beyond suture between thoracic sternites IV and V, usually with distal portions recessed below plane of sternum in retracted position; telson slightly longer than broad with somewhat inflated sides; sixth segment of abdomen relatively narrow, sides slightly constricted, not parallel. Mature female abdomen and telson reaching as far forward as in male, telson as broad as long. First pleopods of male reaching almost to suture between thoracic sternites VI and VII, overlapping each other completely near base but diverging distally and tapering to usually lanceolate membranous tip; armed subterminally with short reflexed spinules quite visible at low magnification, somewhat more numerous and longer

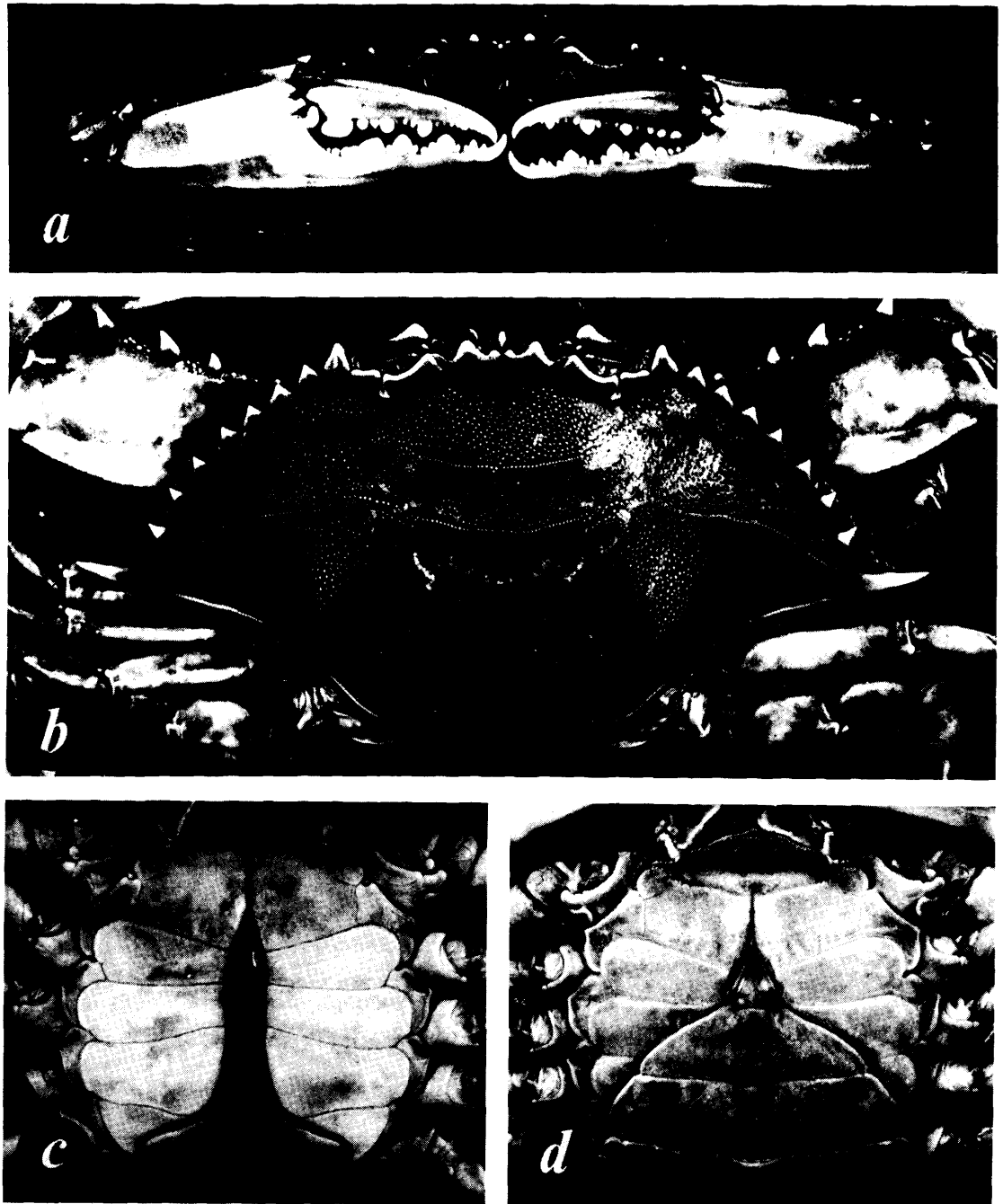


Fig. 298. *Callinectes ornatus* Ordway. a, Male chelae in frontal view; b, carapace; abdomen and sternal area, c, male, d, female; a \times 1; b, d \times 1.3; c \times 1.5 (from Williams 1974b).

distally than proximally with tendency to arrangement in rows near tip on ventral and mesial margin. Gonopores of females irregularly ovate with apex on long axis directed anteromesad; aperture of each irregularly and broadly lunate, sloping from surface on mesial side under rounded crenate anterior border and rounded eminence on posterior border.

Measurements in mm.—Largest male: carapace length 60, width at base of lateral spine 105, in-

cluding lateral spine 130. Two largest females: length 58, width at base of lateral spines 84, including lateral spines 107—length 69, width at base of lateral spines 83, including lateral spines 99. These two females demonstrate variability in mature form that is characteristic of all species in the genus.

Variation.—Williams (1974b) discussed variation in this species.

Color.—Color of this species varies. Three de-

scriptions follow:

(1) Adult males with carapace dull olive to dark brown, usually with a large, ill-defined, roundish spot of orange or orange red on each side posteriorly; lateral spines and anterolateral teeth maroon, light blue or whitish, white tipped. Eyestalks purple. Chelipeds proximally similar to carapace, spotted with blue or soft purple and with spines paler, joints red; inner surface of palm white but with a large bright red patch bordered with purple; fingers mostly purple, tipped with red. Walking legs bright blue above, with a band of scarlet at each joint and a patch of paler blue or green on posterior and lower side of each article; dactyls red or violet. Swimming legs similar in color but with red articular bands wider, a patch of orange or yellow on each article; dactyl with proximal blue band separated from distal scarlet band by an orange band. Abdomen light blue posteriorly. Females similar to males except upper surface of chela more violet; fingers with white or fuchsia colored teeth.

Many individuals less brilliantly colored, juveniles often dull or plain olive-yellow to greenish above. Some males more melanistic, exhibiting shades of dark brown and purple with accents of yellow and brownish red. Albinistic (or light hued) forms not uncommon (Verrill 1908a as condensed in Williams 1966; Taissoun 1969).

(2) Mature male with dorsal side of carapace a uniform light grayish green; anterolateral teeth and lateral spine white tipped. Chelipeds generally same color dorsally to somewhat grayer on upper surface of palm and dactyl, dorsal lateral ridge of palm darker gray; outer face of chelae white; inner surface of fingers dark blue with color running onto carpus, outlining mesiodorsal margin of palm (under shelflike ridge) and along anterior margin of merus; spines and teeth white. Tints of blue on legs. Swimming legs barred with alternate cross bands of light in central parts of articles and a tendency to light slate blue to gray at ends of articles, pale orange at articulations. Sternum white, and legs white to grayish distally. Some specimens more tan than grayish green, some tending toward pinkish gray. (Described a few days later from specimens brought to me frozen from Pigeon Key, Fla., 6 August 1974, by Elliott Norse.)

(3) Carapace almost uniformly light olive to suffused shades of flesh to pale orange or pale rust. Chelipeds light olive dorsally as on carapace, spines white, mesial margins dorsally rimmed with purple that spreads to spines and continues to tip of dactyl in males but ends at proximal half of dactyl in females; purple grading in tints of blue also along lower inner margin of hand and propodal finger of male, fading to white in center of palm; female

with no such lower border, but inner surface of palm with two longitudinal lines of blue separated by reticulate blue pattern on white background. Fingers white distally in females and teeth white. In males, fingers colored as outlined above, and teeth on inner surface blue and purple to magenta. Externally, hands of both sexes are light olive above but white below (a gradual change) with fingers white distally. Dactyls of walking legs rust to olive dorsally; propodus, carpus and merus slightly greenish to tannish blue. Fifth legs tannish to buff, barred with a broad transverse lighter band on proximal half of propodus and dactyl; these articles (especially the last) rust distally; propodus with a tinge of bluish near distal articulation. Venter white in males; females same with some transverse buff to magenta barring on segments of abdomen in adults. (Described 24 June 1975 from specimens taken at *Oregon II* Stn. 17696 off mouth of Amazon River, Brazil, and frozen by Bruce B. Collette, 12 May 1975.)

Gore (1977b) pointed out that dactyls of the swimming legs are a uniform golden brown or light tan, and the propodus is banded with translucent yellow proximally and dark bluish green distally.

Habitat.—Essentially a tropical species found mainly on sandy or muddy bottom from shore to about 75 m; the young have also been collected on shell and sponge bottoms. Occurrence in bays and river mouths (Holthuis 1959; Park 1969; Rouse 1970; in addition to collection data presented here), as well as entrapment in fresh water (Brues 1927), indicates tolerance of a broad range of salinity (recordings of 0–50‰ in temperatures ranging from 18°–31°C); nevertheless, most collections have come from waters of relatively high salinity (Norse 1978; 1978a). Taissoun (1969) reported occurrence in a temperature of 9°C, but this is perhaps a reference to *C. similis* which occurs in colder water.

Type-localities.—Charleston, South Carolina; Gonaives, Haiti; Cumana, Venezuela; Tortugas and Bahamas also listed in original description.

Known range.—Bermuda; Virginia, North and South Carolina through southern Florida; northwestern Yucatan to Estado de São Paulo, Brazil.

Remarks.—It is difficult to distinguish some juveniles, immature males, and adult females of *C. ornatus* from *C. danae* and *C. similis*. Width of the metagastric area approaches that of *C. similis* in some individuals. Borders of this area are more prominently defined than in *C. similis*, but become indistinct with age; in that condition they approach the smoothness of young *C. similis*.

The anterolateral teeth are more acuminate, forward pointing, and longer than in *C. similis*. The abdomen of males usually is recessed, but may be

flush with the sternum as in immature male *C. similis*, though never so broad as in *C. similis*.

Williams (1966), in restricting *C. ornatus*, noted that syntypes from Charleston, S. C., were from a locality representing an apparent extreme northern limit of geographic range. At that time no other specimens of *C. ornatus* were known from the Carolinas, but now material from the Cape Fear River estuary (Perschbacher and Schwartz 1979) and the Beaufort Inlet area of North Carolina has been taken on a number of occasions, as well as a few immature specimens from the mouth of the Chesapeake Bay in late summer (USNM). The records for *C. ornatus* from New Jersey represented by museum specimens all refer to *C. similis* (Williams 1974b). Large collections of this species from Bermuda were the basis for Verrill's (1908b) postulation that drifting larvae in currents could serve as colonizers for the islands.

The spawning season probably extends year round. Museum collections studied include ovigerous females as follows: January, Puerto Rico; April, Guyana, Rio de Janeiro, Brazil; May, São Paulo, Brazil; July, Rio de Janeiro, Brazil; August, Trinidad, Guyana, Surinam; September, Venezuela, the Guianas; October, North Carolina; December, St. Thomas, Rio de Janeiro, Brazil. Taisoun (1969) reported ovigerous females from the Golfo de Venezuela in January and May. Undated collections are recorded from southern Florida, Margarita I., Venezuela, and São Paulo, Brazil.

Callinectes sapidus Rathbun

(Blue crab)

Figs. 293g, 299

Callinectes sapidus Rathbun 1896a:352, pl. 12; pl. 24, fig. 1; pl. 25, fig. 1; pl. 27, fig. 1.—Fowler 1912:416, pls. 128–130.—Williams 1974b:778, figs. 1, 16, 17, 19d, 21, 23b-c.—Felder 1973:55, pl. 8, fig. 7.—Powers 1977:78.

Recognition characters.—Carapace bearing 2 broad either obtuse or acuminate, triangular frontal teeth with mesial slopes (incorporating pair of rudimentary submesial teeth) longer than lateral slopes. Metagastric area with posterior width approximately 1.2 times length, anterior width about 2 times length. Anterolateral margins slightly arched; anterolateral teeth exclusive of outer orbital and lateral spine obtuse to acuminate and directed outward more than forward. Much of surface smooth, with scattered granules, but granules concentrated locally on mesobranchial, posterior slope of car-

diac, and anterior portion of mesogastric areas; tendency to crowding of granules into transverse ridge at summit of cardiac and mesobranchial area in some individuals. Sculpturing of surface varying individually from low to raised relief. Lateral spines varying from rather stout, blunt and forward trending to slender, elongate and slightly backward trending. Epibranchial line nearly straight over branchial region, otherwise sinuously curved.

Propodus and carpus of cheliped with moderate finely granulate ridges, width of chelae similar, propodal finger of major hand occasionally with lower margin decurved proximally.

Male abdomen and telson reaching about midlength of thoracic sternite IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching about midlength of thoracic sternite IV; telson with inflated sides almost equilaterally triangular, fifth and sixth abdominal segments equal in length. First pleopods of male very long, reaching beyond suture between thoracic sternites IV and V but not exceeding telson; sinuously curved and overlapping proximally, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercle and recurving to termination near midline; armed distally with row of large and small reflexed spinules following ventral and lateral borders with twist of axis; tip membranous, flared portion suggesting an elongate quadrilateral in outline. Gonopores of female paraboloid in outline with apex on long axis directed anteromesad, aperture of each sloping from surface on mesial side under irregularly rounded and linearly wrinkled anterior border superior to bulbous posterolateral border.

Much of the following discussion is taken almost verbatim from Williams (1974b).

Measurements in mm.—Largest male: carapace length 91, width at base of lateral spines 168, including lateral spines 209. A male measuring 9 inches (227 mm) across the carapace was reported from Ingram Bay, mouth of Great Wicomico River, Northumberland Co., Va. (Anonymous 1975a). Largest female: length 75, width at base of lateral spines 143, including lateral spines 204. Mature size of females varies considerably, the smallest examined having a carapace length of 21, width at base of lateral spines 41, including lateral spines 55.

Pretzmann (1966) discussed a large immature female with acute spines: length 65, width 132.5. The largest immature female I have seen, also with fairly acute spines, reached a carapace length of 60, width at base of lateral spines 109, including lateral spines 135. Some others in material studied approached this size. All such specimens seen by

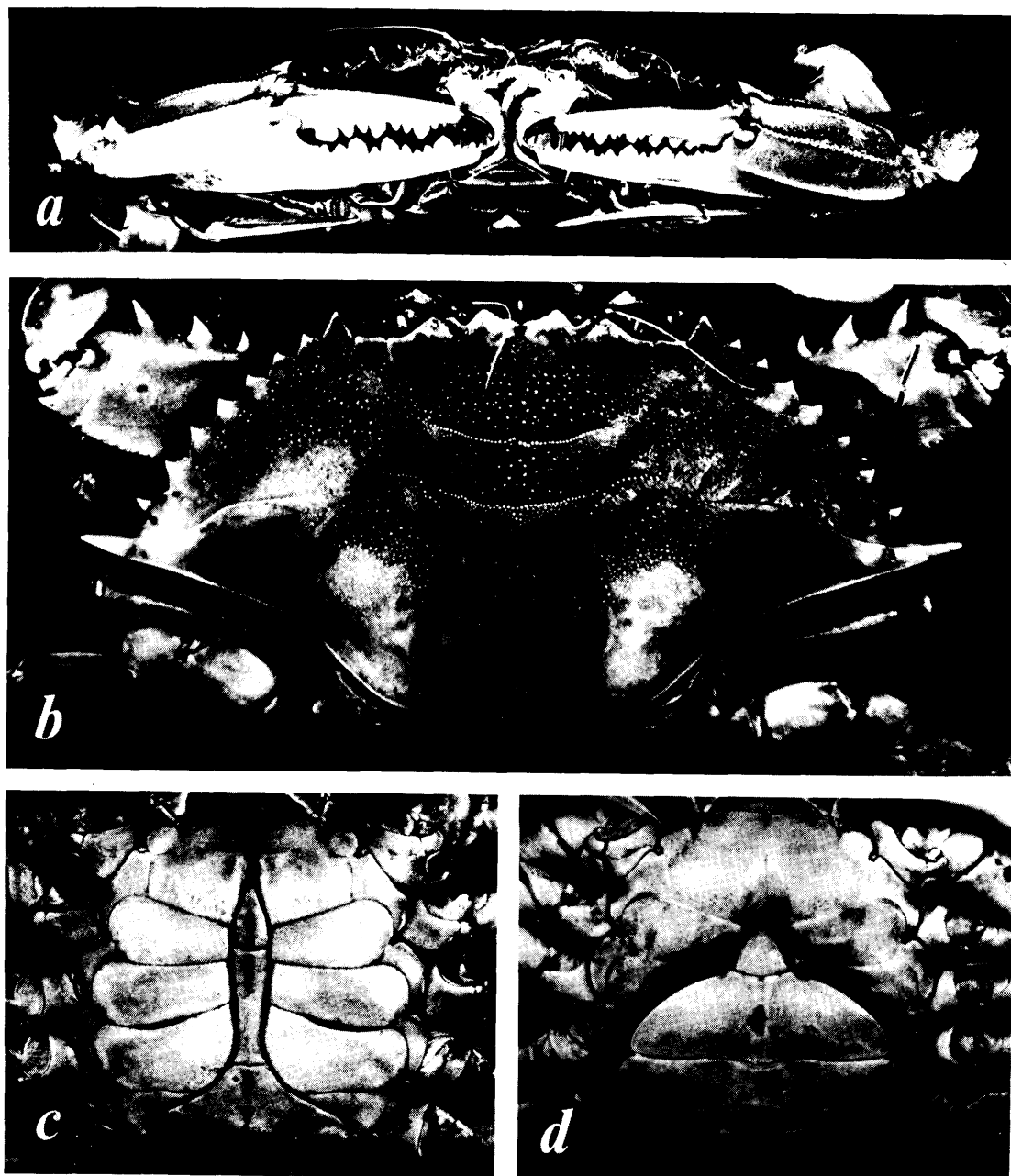


Fig. 299. *Callinectes sapidus* Rathbun. a, Male chelae in frontal view; b, carapace; abdomen and sternal area, c, male, d, female; a \times 0.8, b \times 1.3, c \times 0.6; d \times 0.85 (from Williams 1974b).

me are from the Gulf of Mexico and may represent parasitized individuals in which the maturation process has been altered.

Pullen and Trent (1970) developed regression equations for total weight and carapace width of *C. sapidus* from Galveston Bay, Tex. Male crabs were significantly heavier than females for a given carapace width.

Variation.—There are morphological variations in this species having far greater systematic interest than size and color. Study of many specimens from throughout the range of the species bears out

the conclusion of Chace and Hobbs (1969) that extreme variants “are so different from each other that they could easily be interpreted as distinct species,” but there is “no point of demarcation”—morphological, geographic, bathymetric—between the “typical” rather blunt-spined form predominating along the east coast of the United States and the acute-spined form named *C. sapidus acutidens* by Rathbun predominating from Florida southward.

Rathbun (1896a) characterized the “acutidens” form (paraphrasing) as being wider than the “typ-

ical" with all prominences more strongly marked, areolations separated by deeper depressions, granules more raised, gastric ridges stronger and more sinuous, a transverse granulate ridge on each cardiac lobe, frontal teeth narrower and more acute and bearing two small intervening teeth, anterolateral teeth broad at base and narrowing abruptly to long acuminate tips with margins granulate, lateral spines longer than in "typical" specimens of equal size, and ridges of chelipeds quite prominent and strongly granulate.

I thought for a time that a species distributed through approximately 85 degrees of latitude from North Temperate through Tropic to South Temperate zones might reflect responses to temperature in spination or other characters, "typical" structure being prevalent in the temperate zones and sharp spination in the tropics, the differences thereby justifying nomenclatural recognition. There is weak but inconsistent evidence for this pattern. Though "acutidens" individuals are uncommon outside the tropics, intermediates occur everywhere to some degree, and some "typical" individuals occur in the tropics. Genetic pooling or environmental response reflected in morphology seems poorly structured. I consider the whole *C. sapidus* complex to be a single species which has diverged into ill-defined populations in certain parts of its range. The "acutidens" form predominates over most of the latitudinal range, but there are variations. Among these are "typical" features that reach their most pronounced expression in the population along the east coast of the United States. Taxonomic thinking of biologists has been influenced by the form originally described, the North American variant which became the standard against which all comparisons were made. The variations are discussed in more detail by Williams (1974b).

Color.—Grayish, bluish, or brownish green of varying shades and tints dorsally on carapace and chelipeds; spines may have reddish tints, tubercles at articulations of legs orange, and legs varying blue and white with traces of red or brownish green. Males with propodi of chelae blue on inner and outer surfaces, fingers blue on inner and white on outer surfaces and tipped with red. Mature females with orange fingers on chelae tipped with purple. Underparts off-white with tints of yellow and pink.

Color variations other than those associated with sexual dimorphism and molt cycle are known. Albinos or partial albinos are in museum collections and have been reported both in systematic literature and elsewhere (Gowanloch 1952; Sims and Joyce 1965). Haefner (1961) reported an adult male lacking dorsal green coloration and bright blue and

scarlet markings on legs. Instead, the upper surface of the carapace was "robin egg blue" and the appendages were paler than usual, but the abdomen and underparts had normal color. A similar blue specimen was reported elsewhere (Anonymous 1950). Haefner also pictured a bilateral gray and brown colored specimen from the collection of L. Eugene Cronin. Williams (1974b) summarized important literature on coloration.

Habitat.—The blue crab is a coastal creature occurring on a variety of bottoms in freshwater, estuaries, and shallow ocean from the water's edge to approximately 90 m (Franks, et al. 1972) but mainly in the shallows to depths of 35 m. Biology of the species is better known than that of any other in the genus. Hatching in mouths of estuaries and shallow ocean, development of larvae progresses in the ocean (studied both in nature and the laboratory), followed by migration of megalopae and young crabs back into estuaries to mature into adults (summarized in Williams 1965, 1971; Tagatz 1968; Taissoun 1969; literature compilation, Tagatz and Hall 1971; Williams 1974b). It is probable that all species in the genus carry out their life histories on this model.

Tolerant of extremes, the species has been found from freshwater to hypersaline lagoons such as Laguna Madre de Tamaulipas, Mexico, where collections have been made in salinities ranging from 44 to 48‰ and unproductive portions of the lagoon range up to 117‰ (Hildebrand 1957), in temperatures ranging from 3° to 35°C, and in tertiary sewage treatment ponds in which mean daily O₂ tension dropped as low as . . . 08 mg/l in summer (Smith 1971). In Lebanon (eastern Mediterranean) it has been collected in winter in 39‰ salinity water at 17.5°C where there is no good place for estuarine development because streams are small, seasonal, and exceedingly foul in dry weather (George and Athanassiou 1965). In Marion Co., Fla., large males have been taken from salt springs in the St. Johns River over 180 miles from the sea. Invasion of fresh water is governed by adaptation to chlorinity. On the basis of experiment and observation Odum (1953) concluded that oligohaline (100–1000 p.p.m. Cl) and nearly oligohaline waters (25–1000 p.p.m. Cl) can be invaded to a considerable extent if the crabs are able to adjust slowly to the reduced chlorinity, as in natural invasions. Tagatz (1971) found that osmoregulatory ability of adult males and females is essentially the same, showing good hyperosmotic regulation in 5 and 50% sea water, but hyposmotic regulation in 100% sea water.

Type-locality.—East coast of United States.

Known range.—Occasionally Nova Scotia, Maine,

and northern Massachusetts to northern Argentina, including Bermuda and the Antilles; Øresund, Denmark; the Netherlands and adjacent North Sea; northwest and southwest France; Golfo di Genova; northern Adriatic; Aegean, western Black, and eastern Mediterranean Sea; Lake Hamana-ko, central Japan (T. Sakai, in litt.).

The extreme southern record by Ringuelet (1963) is substantiated by the figure in his paper. Records north of Cape Cod occur only during favorable warm periods (Scattergood 1960).

Holthuis (1961a, 1969), Holthuis and Gottlieb (1955, 1958), and Christiansen (1969) summarized the introduction of *C. sapidus* into Europe, and Bulgurkov (1968) extended the known range, recording an adult female taken in the western part of Varna Bay in Oct., 1967; Froglija (1972) and Maury (1975) added still other European records, and introduction to Japan was first noted in July, 1975 (T. Sakai, in litt.). From these accounts it seems that introduction over the world has resulted from transport of individuals (op. cit., and Wolff 1954a, 1954b). Banoub (1963) noted that presence in Egypt does not seem to have been recorded before 1940. When *C. sapidus* was first noticed there in Lake Manzilah, it was confused with *Portunus pelagicus* (Linnaeus), itself an immigrant to the area from the Indian Ocean via the Suez Canal, and this confusion has persisted in literature concerning both species. Banoub thought that *C. sapidus* may have migrated from Greece around the eastern Mediterranean to flourish in the brackish lakes of Egypt, reproducing the life pattern it exhibits in the Western Hemisphere.

Remarks.—The vast, growing literature on species such as *Callinectes sapidus* cannot be fully reviewed in a short digest such as this; therefore, the discussion is selective.

The fossil record for the genus *Callinectes* extends through the Eocene-Miocene of Brazil, Central America and the West Indies, and the Pleistocene of North America (Glaessner 1969), but in material seen by Rathbun and recently by Williams (1974b) only two specimens from the Pleistocene are certainly identifiable as *C. sapidus*, although some published records of Pleistocene occurrence are valid.

Though all species of *Callinectes* are consumed as human food, there is no doubt that *C. sapidus* is the most valuable in commercial fisheries, providing a highly acceptable, nutritious product worth several million dollars annually. Traditionally, the seat of this fishery in the United States has been Chesapeake Bay where records on the fishery have been kept for about a century. Pearson (1948), summarizing annual catch for this area from 1880 to 1942,

showed the annual catch to have increased from 9.5 million pounds in 1890 to a peak of 68.7 million pounds in 1930, but catch fluctuated before and after 1930 declining to 35.8 million by 1942 during World War II. Van Engel (1962) provided a history of the types of gear used in this fishery, and evolution from hand-dip trotline to the baited crab pot (trap) and dredge. Adoption of the baited pot and its spread to the Carolinas and elsewhere during the late 1950's, along with other methods of capture including incidental harvest of crabs from shrimp trawls, greatly expanded the catch. By the 1970's, the United States fishery had expanded to over 140 million pounds of hard crabs with a landed value of over 20 million dollars annually (5 year average 1971–75, Robinson 1977).

The species is harvested throughout its range either commercially or for home use. It is caught locally in Belize with hand nets (B. Kensley, personal communication), and Taissoun (1969, and personal communication) reported a growing industry in Venezuela. Banoub (1963) reported growth of an Egyptian fishery in lakes (poor flavor) and sea (good flavor), but remarked on losses from damage to nets and on the myriads of crabs having no local commercial value because Egyptians consider the meat unpalatable (Anonymous 1965). A developing fishery in northern Greece (Kinzelbach 1965) declined because of overfishing (Boschma 1972).

Because the blue crab supports such a large crab fishery, fluctuations in abundance (especially in the Chesapeake area) have been the subject of a number of investigations. Pearson (1948) concluded that the fluctuations appear to be associated with variable rates of survival in the first year of life. No correlation was found between relative abundance of female crabs and their progeny. Examination of data from 13 generations indicated that size of spawning stock did not determine size of population surviving to commercial age at the rate of fishing prevailing during the years studied. Pearson found evidence that excessively cold weather may reduce availability of immature and adult crabs either by direct mortality or by making crabs less available to the fishery immediately after the periods of cold weather. Heavy runoff in some wet years may lower salinity in the spawning areas enough to have an adverse effect on survival of young, but such limits are poorly understood.

During its life the blue crab leads a migratory existence. The migratory patterns have been studied in greatest detail in Chesapeake Bay but the pattern seen there appears to be true of other areas as well. Mating usually takes place in water of reduced salinity well up in estuaries. After this, the

females migrate downstream to areas of higher salinity near the mouths of estuaries where the eggs are laid and hatched, whereas the males tend to remain in the low-salinity areas for the remainder of their lives. For this reason, samples of adult crabs (or commercial catches) near the sea contain greater numbers of females, whereas those from the middle or upper reaches of bays contain larger percentages of males except at the breeding season. Once in the spawning areas, the females tend to remain for the duration of their lives or move a short way out to sea. Once hatched, the zoeae lead a planktonic existence until they transform to the megalopa stage. This stage also is planktonic, at least in part, for large numbers of megalopae enter estuaries in surface plankton, their abundance influenced to some degree by light, current or pressure (King 1971; More 1969; Naylor and Isaac 1973; Williams 1971). King (1971) found three waves of abundance in Texas, January-March, May-June, October, but there as elsewhere they occur all through the year. Migration either as megalopae or first crab stage leads up the estuary to the maturing grounds. Early recruits may reach these areas in their first summer, but the remainder may not reach them until early in the second year of life. In areas smaller than Chesapeake Bay, there may be a certain amount of overlap in mating and spawning grounds but the two areas tend to be distinct. In Chesapeake Bay, the spawning grounds are near the mouth of the Bay; in North Carolina and Louisiana, near the inlets and passes. In Texas, most females with eggs are found in the Gulf proper (Daugherty 1952; King 1971) but also in bays (More 1969).

In Chesapeake Bay, it has been demonstrated that crabs spawned in June of one year are mature about 14 months later and at that time mate. Most mating pairs are found in July, August, or September, though the mating season extends from May to October. At this time, females ready to molt into the mature stage (terminal molt) are carried about, cradled upright, under the males' bodies. Such pairs are called doublers. The male frees the female during the time she is actually casting the old exoskeleton, but when this is shed he grasps her again, this time with the ventral surfaces together, and completes the breeding act by introducing sperm via the copulatory stylets into the spermathecae. Copulation may last for several hours. When sperm transfer is complete, the female is allowed to resume an upright posture and is again carried under the male for a time until her shell hardens. Males may mate more than once and at any time during their last three intermolts (Van Engel 1958); females usually mate once, but the sperm supply may

serve to fertilize more than one mass of eggs. However, Abbe (1974) reported an already mature and mated female, carapace width 140 mm, caught in upper Chesapeake Bay doubled with a male; the female was undergoing a second terminal molt. Usually, a female mated in late summer casts the first batch of eggs the following spring at an age of approximately two years, but egg laying may be at any time from two to nine months after mating. A second spawning has been observed to occur later in summer among some individuals, and it is possible that a third may occur, possibly as late as the succeeding spring or at an age of three years. Three years is judged to be about the normal maximum age for this species and the animals are estimated to undergo some 18 to 20 or more molts before reaching maturity (Van Engel 1958).

Although most spawning occurs in spring and early summer, warm water helping to assure survival of larvae, females with egg masses have been found in North Carolina from mid-March to late November. Northward the season is somewhat shorter and to the south (United States) it is longer (Williams 1965).

Five stages in the reproductive cycle of mature females have been described (Hard 1942), and a number of authors have estimated the number of eggs per spawning at 700,000 to more than 2 million. Rare records of ovigerous females in museum collections suggest that at least some spawning occurs almost year round in the tropics, for example in the Golfo de Venezuela where ovigerous females are most abundant between April and September, reaching a sample maximum of 75% in July and August (Taissoun 1969). Also, in the northern part of Bahia del Tablazo, Venezuela, ovigerous females occur during all the year except between August and November, reaching a sample maximum of 95% in May. Absence of ovigerous females there in late summer and fall occurs because heavy rainfall and increasing river flow freshen the area, driving females downstream to areas of higher salinity, where increases of ovigerous females occur in the Golfo de Venezuela during August and September.

Churchill (1919) found that eggs hatch in about 15 days at 26.1°C and slightly faster at higher temperatures.

Among *Callinectes* species, larval development of only *C. sapidus* and *C. similis* has been described from hatching eggs and rearing in the laboratory. Costlow, Rees, and Bookhout (1959) and Costlow and Bookhout (1959) described seven zoeal stages, atypically an eighth, and a megalopa for *C. sapidus*. Larvae and megalopae of the two species are apparently almost identical, the stages being similar

to those of other portunids (Costlow and Bookhout, personal communication). The megalopae of *Callinectes* lack an internal carpal spine on the chelipeds whereas megalopae of *Portunus* have a well-developed spine on this member (Williams 1971), showing one of the generic distinctions at an early phase of development.

Costlow (1965, 1967) followed the early work on larvae with a series of experimental studies showing that development of *C. sapidus* is subject to variation both in staging and duration. Total development time of *C. sapidus* from hatching of egg to transformation of the megalopa to first crab stage has varied from 31 to 69 days in the laboratory in various combinations of salinity and temperature, but duration of individual stages is variable even in a single salinity-temperature combination. Development progresses at a comparable rate in salinities between 20.1 and 31.1‰ at 25°C. Above 31.1‰, development slows and below 20.1‰, larvae rarely complete the first molt. Larvae never went beyond the first zoeal stage when reared at 20°C and did not progress beyond the third zoeal stage when reared at 30°C.

The stages are constant enough that Cargo (1960), More (1969), Nichols and Keney (1963), King (1971), Pinschmidt (1964), Sandifer (1973d), Tagatz (1968), Van Engel (1958), and Williams (1971) were able to identify zoeae or megalopae from nearshore oceanic and estuarine plankton. Sandifer (1973d) found the first four larval stages and the megalopa, but mainly the stage I larva. In nature as in experiments, development time may be extended by environmental conditions. Kalber (1970) showed that the early zoeae are good osmoregulators but that the late zoeae lose this ability. The megalopa, a poor regulator at first, becomes a good one by the fifth day, overall physiological adaptations to salinity fitting distributional stresses encountered.

Investigators working with larval stages (reviewed in Sandifer 1973d; Williams 1971) suggest that larvae and megalopae can move considerable distances; zoeae have been found off St. Johns River, Fla., at stations up to 160 km, and megalopae in the same area up to 128 km from shore. In Chesapeake Bay and Pamlico Sound, N. C., megalopae have been found 170 and 100 km respectively from presumed points of entry to the estuarine systems. Most of this off- and onshore movement of larval stages appears to be a homeostatic developmental feature. Some dispersal of larvae at the fringes of *Callinectes* populations obviously occurs, but the wanderers are at competitive disadvantage in establishing temporary range extensions. Nevertheless, larval dispersal of *Callinectes* coupled with

movement of adults, usually judged to be minor except within an estuarine system (Fischler and Walburg 1962; Tagatz 1968), seems to assure genetic continuity over broad areas. In some areas such as west Florida there is evidence of longshore movement of adults (Leahy 1975).

Often considered a scavenger, which it certainly is, the normal diet of *C. sapidus* includes a variety of materials including fishes, benthic invertebrates and plant material (Darnell 1959; 1961; Dunnington 1956; Menzel and Hopkins 1956; Tagatz 1968). Individuals 100 mm in carapace width may feed on jellyfishes (Phillips, et al. 1969; Farr 1978). Odum and Heald (1972) found mainly an abundance of small mussels in stomach contents of individuals in a marsh in southwest Florida. Hamilton (1976) described feeding on *Littorina littorea* adhering to plant stems near the water line at high tide level. Virstein (1977), with use of exclusion experiments, showed that *C. sapidus* is a major predator on infauna in a shallow subtidal sand community in Chesapeake Bay. There (Orth 1977) the crabs obtain food either by thrusting chelae into sediment to obtain shallow, surface-dwelling animals or by digging holes 6–12 cm deep with chelae and walking legs to gather deeper dwelling animals. In excavating, they scoop up mud and sand with chelae and walking legs, carry sediment in the crook of the chelae, and thus form an inclined excavation, moving up and down as they dig. Sediment is loosened with the chelae and fifth legs. The rhizome mat underlying *Zostera* beds was found to prevent digging below 2 cm, but experimental removal of the rhizomes permits penetration. The crabs were also found to feed on epibiota on *Zostera* leaves, grabbing the leaves at the bases with chelae and passing the leaves through the mandibles. There are numerous notes on feeding and predation in the literature, recording such habits as feeding on oysters, clams, and tunicates.

In a study of gill area correlated with degree of activity and habit of several species of crabs, Gray (1957) found that the blue crab has a larger gill area per gram of body weight than the other portunids studied (*Ovalipes*, *Arenaeus*, and *Portunus* spp.), exceeding that of any crab studied among aquatic, intertidal, and land crabs in the Beaufort, N. C., area. The blue crab is notorious for its vigorous and pugnacious nature, and this anatomical feature gives one reason for such temperament.

Callinectes sapidus is fairly long-lived following its last molt, and thus affords a lodging place for parasites and commensals. Its gills and gill chambers may become clogged with clusters of a small stalked barnacle, *Octolasmis mulleri* (= *lowei*) (Causey 1961). Walker (1974) showed that this barnacle is present on gills of many crab species (12 species

in 10 genera) in Beaufort Inlet, N. C., but not on *C. sapidus* further upriver, indicating that salinity is probably a factor controlling incidence of the barnacle. Distribution of the barnacle on individual gills of *C. sapidus* was analyzed and factors affecting distribution discussed, chiefly cleaning action of epipods and respiratory flow of the crab. The cyprid larvae attach to blue crab gills a short distance in from the gill margin. Orientation of the larvae at settlement is a response to respiratory flow of water through the crab branchial chamber resulting in cirral nets of the young barnacles facing into the current (mostly efferent whereas in *Ovalipes ocellatus* they are on the afferent side, evidence of the burrowing habit). The crab's main protection is molting. After spawning the female blue crab has fulfilled her role in propagation and individual survival becomes less important for the species. Molting terminated, she gradually becomes debilitated under epizootic attack.

The barnacles *Balanus amphitrite* and *Chelonibia patula* attach to the carapace. The sacculinid parasite, *Loxothylacus texanus*, lives beneath the abdomen (Wass 1955). Hopkins (1947) discussed infestations of the parasitic nemertean *Cacrinonemertes carcinophila* on female blue crabs showing that only light-colored worms are found on the gills of mature females which have never spawned. Large red worms are found only on the gills of mature female crabs which have spawned at least once, or in the gills and egg masses of ovigerous females. Presence of large red nemerteans in the gills is a sure sign that the crab has spawned some time in the past.

The marine leech *Myzobdella lugubris* has been found to cling to *C. sapidus*, as well as other decapod crustaceans, and to deposit egg capsules on the exoskeleton, though it is not known to be parasitic on crustaceans (Daniels and Sawyer 1975; Sawyer, et al. 1975).

Further review of literature on parasites is beyond the scope of this account but some noteworthy references are: Adkins 1972; Bridgeman 1969; Christmas 1969; Colwell, et al. 1975; Heard 1970; Pauley, et al. 1975; Pearse 1932b, 1952b; Reinhard 1950a, 1950b, 1951; Rosen 1967; Sinderman and Rosenfield 1967; Sprague 1970; Umphlitt and McCrary 1975.

Agonistic behavior was well reviewed by Jachowski (1974) from observation of blue crabs in both field and laboratory. Most agonistic acts employ chelipeds as organs of expression as well as weapons. Such acts as cheliped extending, shielding, leaning, fending, embracing, poking, striking, grasping, and crouching are described and illustrated. Responses in an encounter varied with ori-

entation of the two individuals, the distance between them, their size and sex, as well as being influenced by presence of food. Vigorous combat was seen only when threats failed to deter crabs attracted to food, or among males when a sexually attractive female was held by another. Presentation of a model of an adult male to captives showed that responses differed with speed of approach, orientation, cheliped posture and distance of the model, and with size and sex of the crabs. Captives responded to the model more often when it approached rapidly, frontally, or with extended chelipeds than when it approached slowly, laterally, or with folded chelipeds. Females responded to the model more often than did males, and smaller crabs more often than larger ones. More frequent responders typically extended their chelipeds, crouched in the apparently submissive gesture or withdrew from the model. Teytaud (1971) found that pre-pubertal "red-sign" females showed a significantly greater intensity of response to visual stimulus (male or female model) combined with male odor than with either olfactory or visual stimuli alone, or visual stimuli in combination with odor from mature females. Male models in display postures elicited significantly greater responses than nondisplaying models when each was presented with male odor. Dunham (1978), in a review, felt that Teytaud's studies were among the better designed of their kind but that most available evidence for a sex pheromone in Crustacea remains doubtful. Jachowski (1963) also noted young blue crabs clinging to the umbrellas of *Chrysaora quinquecirrha* but not feeding on them.

The swimming behavior of *C. sapidus* has been studied by analysis of high-speed cinematographs (Spirito 1972).

Callinectes sapidus exhibits the usual cheliped laterality of brachyurans, having a crushing pincer on one side (usually right) and a cutting pincer on the other. Variations in this pattern were the subject of recent study (Hamilton, et al. 1976) in field and laboratory showing that the proportion of crabs with a right crusher decreases with size (age) from 100% in smallest crabs to 74% in largest crabs. Crabs with two cutters are not uncommon and apparently result from regeneration of a cutter regardless of which cheliped is autotomized. Only 0.4% of all crabs possessed two crushers. The authors discussed theories that account for these proportions, tending to agree with Przibram's (1931) idea that a cutter is always regenerated so the crab can attain a full-sized crusher in the least amount of time, the original cutter having to grow only a little and undergo change in dentition to become a crusher, while the regenerating crusher has to grow

only moderately before it becomes a normal-sized cutter. Learning adaptations to the new laterality would be necessary.

No attempt has been made to update review of early work on rhythm of color changes (Williams 1965).

Callinectes similis Williams

(Lesser blue crab, Gulf crab)

Figs. 293b, 300

Callinectes similis Williams 1966:87, figs. 3, 4E, F.—1974b:731, figs. 4, 18a, 20c, 22a.—Felder 1973:58, pl. 8, fig. 1.—Powers 1977:81.

Recognition characters.—Carapace with 4 frontal teeth, submesial pair small but definitely formed. Central trapezoidal (metagastric) area short and wide, anterior width about 2.75 times, posterior width about 1.6–1.7 times length. Anterolateral margins broadly arched; anterolateral teeth exclusive of outer orbital and lateral spine short and broad, tips of first 5 nearly rectangular, sixth and especially seventh acuminate; first 5 teeth with anterior margins shorter than posterior and separated by narrow based rounded notches. Lateral spine strong, slender, and curved forward. Surface of carapace even, lightly and quite uniformly granulate except smooth along posterolateral and posterior slopes, and nearly smooth along anterolateral and anterior margins, especially between teeth and along orbits; smooth areas with tendency to iridescence.

Chelipeds with very fine granulations on ridges; carpus bearing 2 obsolescent granulate ridges and suggestion of others, inferior lateral ridge terminating anteriorly in low tooth occasionally followed by low flattened eminence; chelae strong, not greatly dissimilar in size.

Male telson longer than wide; sixth segment of abdomen slightly sinuous-sided but broader at all levels than telson, proximal half slightly constricted laterally and less indurated than other parts, flush with sternum in retracted position. Mature female telson slightly wider than long. First pleopods of male reaching anteriorly $\frac{2}{3}$ length of sternite VII, or beyond; distal portion slender, extending straight to tips curved slightly mesad, armed with scattered minute reflexed spinules, most dense distally and laterally and largest distally. Gonopores of female narrowly ellipsoid with long axis in transverse plane; aperture of each with simple rounded borders except at mesial end where it slopes from surface laterad under superior anterior margin.

Measurements in mm.—Largest male: carapace length 55, width at base of lateral spines 97, including lateral spines 122. Largest female: length 45, width at base of lateral spines 76, including lateral spines 95. Franks, et al. (1972) reported an individual with carapace width 171.

Variation.—Williams (1974b) discussed variation in this species.

Color.—Adult male: "Carapace green dorsally, irregular areas of iridescence at bases of and between anterolateral teeth, and on posterior and posterolateral borders. Chelipeds and portions of legs similar in color or more tannish green dorsally, with iridescent areas on outer and upper edges of carpus and hands; chelae white on outer face, blue to fuchsia on inner surface, with fuchsia on tips of fingers and teeth of opposed edges. Lateral spines and some anterolateral teeth, as well as spines on chelipeds, white tipped. Walking legs grading from fuchsia distally through violet blue to light blue mottled with white proximally, pubescence on legs beige. Swimming legs variably mottled with white; all legs with stellate fuchsia markings at articulations. Underparts white and blue" (Williams 1965).

Ovigerous female: "Similar to male except with more violet blue on inner surface of chelae; fingers either with white teeth or fuchsia colored teeth. Legs with dactyls reddish orange grading abruptly to blue on propodi, pubescence brown to beige. Abdomen with iridescent areas" (Williams 1965).

Carapace of juveniles sometimes with a maculate light olive pattern.

Gore (1977a) gave great detail on color, pointing out that the dactyls of the swimming legs are a pale translucent blue and the propodi are olive drab on each end and banded with translucent blue mesially.

Habitat.—The species occurs in the oceanic littoral where it has been taken in salinities of 24.9–37.4‰ in temperatures of 13.2°–29.0°C at depths as great as 92 m (rarely to depths of 379 m off eastern Florida). It has usually been found most abundantly in salinities greater than 15‰. In all areas studied the species is associated with *C. sapidus*, often in large numbers (Williams 1974b, summary).

Type-locality.—2–3 mi. off beach between St. Johns River jetties and Jacksonville Beach, Fla.

Known range.—Off Delaware Bay to Key West, Fla.; northwestern Florida around Gulf of Mexico to off Campeche, Yucatan; also Isla de Providencia, Colombia (USNM); reported from northern Jamaica (Norse 1978).

Remarks.—This species closely resembles *C. danae* and *C. ornatus* with which it has often been confused. So far as known, only *C. sapidus* occurs with regularity in the same range along the Carolina-

Florida coast. Small to medium-sized individuals of these species are exceedingly difficult to distinguish.

Callinectes similis seems to be the Carolinian member of the complex. The few specimens from off Delaware Bay are all juveniles, suggesting that northern limits for this species, as for many others from the Carolinian Province, vary seasonally and are extended northward during favorable warm years.

Callinectes similis has the smoothest and most uniformly granulated carapace among these three, and the shortest, broadest anterolateral teeth. These teeth are not equilaterally triangular, having shorter anterior than posterior borders, and are directed more forward in the anterior portion than in the remainder of the row. Central teeth in the row have the anterior border extending almost straight laterad. The carapace of mature females has very little sculpture and remarkably uniform granulation

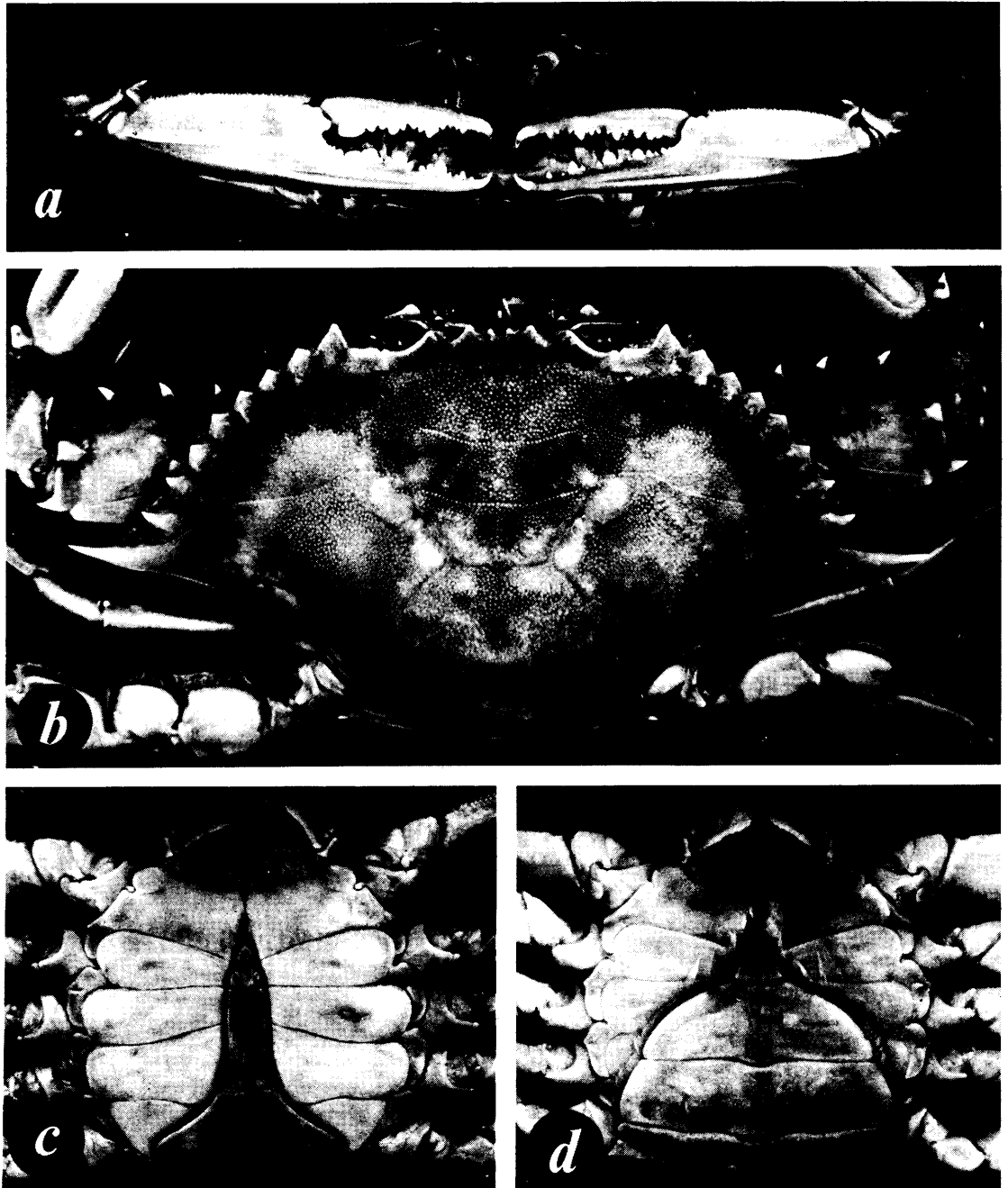


Fig. 300. *Callinectes similis* Williams. a, Male chelae in frontal view; b, carapace; abdomen and sternal area, c male, d, female; a \times 1, b \times 1.4, c \times 1.2, d \times 1.3 (from Williams 1974b).

overall. Granulations on the ridges of the chelipeds are among the finest of any species in the genus (Williams 1974b).

Published data on spawning in Texas and South and North Carolina summarized by Williams (1966) suggested a spring and fall spawning season for *C. similis*, and Tagatz (1967) found this true for north-eastern Florida as well where females spawn in the ocean from March to July, peaking in May when 75% of them are ovigerous, and again from October to November. Ovigerous females in the collection of the USNM indicate that these limits are somewhat broader elsewhere and may be correlated with temperature, for there are representatives from Louisiana and Texas in February and Campeche Banks in December.

From ovigerous females trawled in the vicinity of Beaufort Inlet, N. C., Bookhout and Costlow (1977) reared freshly hatched larvae to the first crab stage in filtered sea water of 30‰ salinity. Eight zoeal stages and a megalopa were described and illustrated, with particular reference to types of setae on the appendages. Comparison was made to stages of the congener *C. sapidus*, with updated information on development of the latter.

In studies on osmoregulatory ability, Engel (1977) found that *C. similis* is a poorer osmoregulator at low salinities (tested in 5, 20, and 35‰) than *C. sapidus*, the difference in osmoregulatory capacity corresponding well with their distribution in estuaries.

Overstreet and Heard (1978) found that red drum, *Sciaenops ocellata*, in Mississippi Sound consume a diet dominated by crustaceans, especially *C. similis*, although the diet changes with season and locality and contains far too many organisms to be listed in detail in this manual.

Genus *Cronius* Stimpson 1860

Rathbun 1930a:138.

Cronius ruber (Lamarck)

Fig. 301

Portunus ruber Lamarck 1818:260.

Cronius ruber.—Rathbun 1930a:139, pls. 62–63.—Monod 1956:189, figs. 218, 221.—Guniot-Dumortier 1960:514, fig. 15a,b.—Williams 1965:174, fig. 154.—Garth 1961:143.—1965:15.—Forest and Guinot 1966:61.—Jones 1968b:188.—Coelho and Ramos 1972:188.—Felder 1973:55, pl. 8, fig. 3.—Powers 1977:81.—Manning and Holthuis 1981:98, fig. 21a-b.

Recognition characters.—Carapace somewhat hexagonal, smooth but pubescent; sinuous transverse ridge extending between lateral spines, and another shorter, transverse, biarcuate ridge about halfway between this ridge and front. Front with 4 prominent teeth, not including inner orbitals; submesial pair of teeth most advanced; second pair more pointed and directed slightly laterad, separated from notched inner orbitals by deep cut. Orbit nearly circular, basal fixed article of antenna with spine below insertion of movable part. Anterolateral teeth unequal, alternating large and small; lateral spine not strikingly enlarged.

Chelipeds heavy; merus with 4 to 6 spines in front, and with small distal spine behind; carpus with granulate ridges on all surfaces, armed with 4 spines on superior surface, 2 on inner and 2 on outer border; fingers strongly ribbed.

Measurements in mm.—Carapace: male, length 50, width 79; female, length 59, width 92.

Color.—“Violet red or deep purple red more or less marbled with a lighter shade or white. Extremity of all spines black” (Rathbun 1930a).

Habitat.—Siebenaler (1952) reported *C. ruber* as a “trash” form on the Tortugas shrimping grounds, and Park (1969; 1978) judged it to be primarily resident on rocky or coral bottoms. Below low tide mark to 73 m; Fausto-Filho and Neto (1976) reported a maximum depth of 105 m. Manning and Holthuis (1981) summarized the findings of West African zoologists, characterizing *C. ruber* as a shallow-water species occurring on a variety of bottom types.

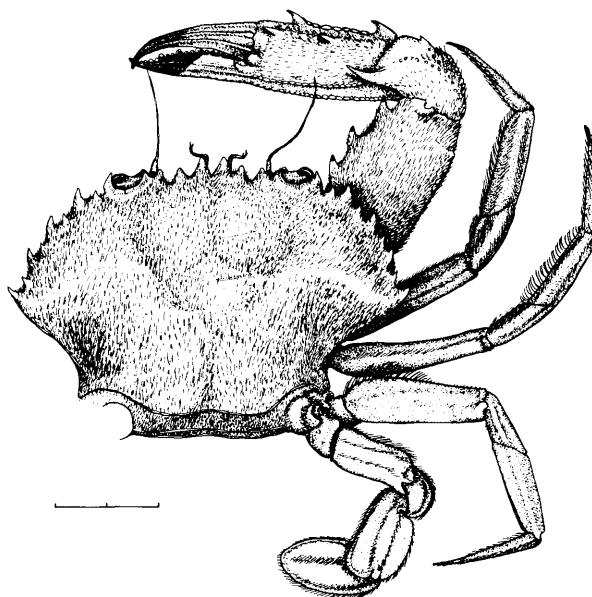


Fig. 301. *Cronius ruber* (Lamarck). Male in dorsal view, legs of left side not shown, 2 cm indicated (redrawn from Monod 1956 in Williams 1965).

Type-locality.—Brazil.

Known range.—Vicinity of Little Egg Inlet, N. J. (Milstein, et al. 1977); Rehoboth Bay, Del. (USNM); Virginia (rare, Van Engel and Sandifer 1972); South Carolina to Santa Catarina, Brazil; Baja California to Peru; Clipperton Is., Galapagos Is.; West Africa from Mauritania to Angola; Cape Verde, Principe, São Tome and Annobon I.

Remarks.—Rathbun (1930a) reported ovigerous females from Panama in March; Park (1978) found them mainly in March but a few in June-July; along West Africa they are reported in January, March, and September (Manning and Holthuis 1981).

The New Jersey record is based on a male (50 mm cl, USNM) taken 27 September 1974 from an engine block used as an anchor for an offshore epifauna study during the period January 1972 through December 1974. Depth of the anchor at time of collection was 12.2 m, water temperature 19.5°C, salinity 31‰ (C. B. Milstein, personal communication, and Milstein, et al. 1977).

Randall (1967) reported *C. ruber* from stomach

contents of the Nassau grouper, *Epinephelus striatus*, and mutton snapper, *Lutjanus analis*.

Genus *Portunus* Weber 1795

Rathbun 1930a:33.—Hemming 1958b:133.—Stephenson and Campbell 1960:75.

Carapace transverse, usually broad, depressed or slightly convex, surface often areolated. Front cut into 3–6 teeth exclusive of inner orbital angles. Anterolateral borders arched, longer than posterolateral, cut into 9 teeth including outer orbital, ninth may be enlarged. Chelipeds usually much longer and heavier than other legs; merus spined; inner and outer angles of carpus spiniform; palm prismatic, costate, usually spined; fingers strongly toothed and about as long as palm. Second to fifth legs compressed; last pair with merus and carpus short and broad, propodus and dactyl foliaceous and paddlelike. Abdomen of male triangular, 5-segmented, 3–5 fused.

Key to Species

(Adult or Subadult)

1. Carapace wide, anterolateral margins forming arc of a circle with center near posterior margin 2
Carapace narrow, anterolateral margins forming arc of a circle with center near middle of cardiac region 4
2. Interocular teeth 6 (including entire inner orbital angle) 3
Interocular teeth 8 (including bilobed inner orbital angle) *P. gibbesii*
3. Carapace convex, mostly smooth and glossy; palms of chelae swollen, only 1 spine on upper margin *P. sayi*
Carapace uneven, not smooth and glossy; 2 spines on upper margin of palm of chela (submesial teeth of front less advanced than laterals). *P. anceps*
4. Posterodistal margin of merus of fifth legs rounded and unarmed (tuft of setae sometimes covering minute serrations); 2 spines on upper margin of palm near articulation of dactyl 5
Posterodistal margin of merus of fifth legs armed with 1 or 2 spines, spinules, or both; 1 spine on upper margin of palm near articulation of dactyl. .6
5. Lateral spine of carapace similar to and very little larger than preceding spine or tooth; upper margin of dactyl on chela conspicuously fringed with long hairs *P. depressifrons*
Lateral spine of carapace much larger than preceding spine or tooth and directed more outward; upper margin of dactyl on chela with hair inconspicuous. *P. floridanus*
6. Chelipeds with mesiodorsal spine of carpus less than half length of palm. 7
Chelipeds with mesiodorsal spine of carpus greater than half length of palm *P. spinicarpus*
7. Interocular teeth 6; superoexternal surface of chela flat and iridescent (iridescence may be lost with preservation). *P. ordwayi*
Interocular teeth 8 (including bilobed inner orbital angles); superoexternal surface of chela ridged, not iridescent. *P. spinimanus*

***Portunus anceps* (Saussure)**

Fig. 302

Lupea anceps Saussure 1858:434, pl. 2, figs. 11-11b.*Portunus (Achelous) anceps*.—Hay and Shore 1918:431, pl. 33, fig. 8.*Portunus (Portunus) anceps*.—Rathbun 1930a:42, pl. 15.*Portunus anceps*.—Williams 1965:163, fig. 145.—

Coelho and Ramos 1972:186.—Powers 1977:82.

Recognition characters.—Carapace twice as wide as long, pubescent, and with several indistinct, arching, granulate, transverse ridges. Six frontal teeth including inner orbitals; inner orbitals blunt and considerably shorter than lateral pair of true frontal teeth; submesial teeth short, smaller than inner orbitals. Anterolateral teeth small, acute, directed forward, last one sharp, slender, and about as long as space occupied by 4 preceding teeth.

Chelipeds long; merus with 4 spines in front, a distal one behind; carpus ridged, with strong internal and a smaller external spine; most ridges of palm continuing on fingers, superointernal ridge more elevated than others, ending distally in 2 spines, one behind other.

Measurements in mm.—Carapace: male, length 13, width 26; female, length 15, width 29.

Color.—Mottled gray and yellowish white so as to imitate sand; first pair of legs red or yellow; chelipeds and other legs same color in part (Verrill 1908a).

Habitat.—This species lives on or near sandy shores in tropical waters, but is sometimes carried northward in the Gulf Stream to the North Carolina capes; it is occasionally found on mud or calcareous algae (Coelho and Ramos 1972); surface to 103 m but usually 0–20 m (Park 1978).

Type-locality.—Cuba.

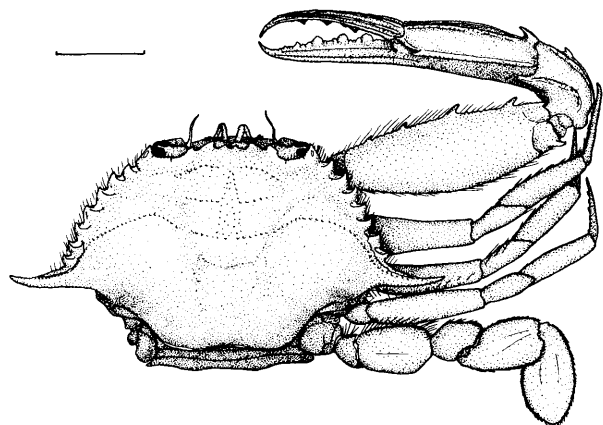


Fig. 302. *Portunus anceps* (Saussure). Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

Known range.—Cape Hatteras, N. C. (Park 1978), to Bahia, Brazil; Bermuda.

Remarks.—Ovigerous females are known from April in Florida (Camp, et al. 1977) to June in Cuba and October in North Carolina (Rathbun 1930a); Park (1978) reported them chiefly in July, but June–August, October and early December in the western Atlantic. He also reported a high population density whenever the species was taken.

Randall (1967) reported *P. anceps* from stomach contents of the spotted scorpionfish, *Scorpaena plumieri*.

***Portunus depressifrons* (Stimpson)**

Fig. 303

Amphitrite depressifrons Stimpson 1859:58.*Portunus (Achelous) depressifrons*.—Hay and Shore 1918:430, pl. 33, fig. 7.—Rathbun 1930a:84, pl. 41.*Portunus depressifrons*.—Williams 1965:166, fig. 149.—Powers 1977:83.

Recognition characters.—Carapace approximately 1.6 times as wide as long, uneven, pubescent, and with indistinct transverse ridges. Six frontal teeth including inner orbitals much broader than others, tips of all teeth about on a line. External orbital tooth strong, tip rounded; anterolateral teeth acute, turned forward, lateral tooth scarcely longer than one next anterior, teeth and intervals between them fringed with hairs.

Chelipeds trigonal, serratogranulate and pubes-

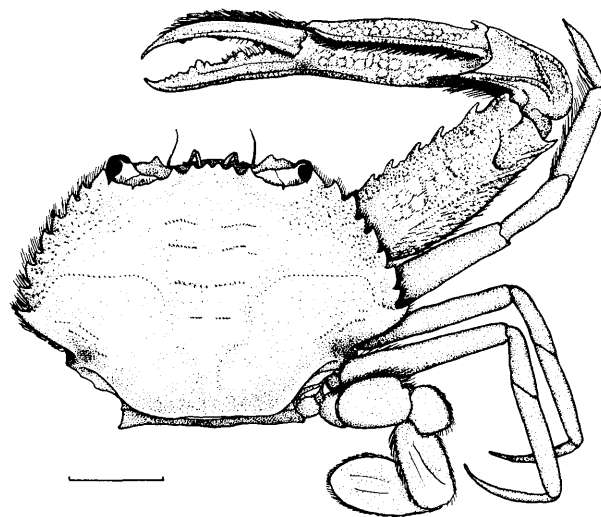


Fig. 303. *Portunus depressifrons* Stimpson. Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

cent; merus with 5 spines in front and distal one behind; carpus with 2 spines, outer much smaller than inner; hand compressed, much longer in immature males than females, upper margin raised into crest terminating distally in stout spine, smaller spine at carpal articulation; fingers flattened, dactyl with border of hairs on superior margin. Walking legs unusually long and slender, articles of first pair fringed with hairs. Swimming legs shorter than in most species of genus, posterodistal margin of merus rounded and unarmed.

Measurements in mm.—Carapace: male, length 30, width 47; female, length 29, width 47.

Color.—Carapace irregularly mottled with light and dark gray, closely imitating colors of sand; chelipeds and posterior legs similar though paler; first pair of walking legs bright purple or deep blue in larger individuals, with some of same color usually apparent on next 2 pairs, but color of first pair in striking contrast with rest of crab. Very young specimens observed do not show this distinction in color of legs (Verrill 1908a).

Habitat.—Abundant in shallow water on sandy bottoms of coves and inlets at Bermuda (Verrill 1908a). Park (1969) found the species everywhere in Biscayne Bay, Fla., except on hard packed bottom. Surface to 29 m, rarely 93 m.

Type-localities.—South Carolina and Florida Keys.

Known range.—Fort Macon, N. C. (Coues 1871; Kingsley 1878-79), through northwest Florida to Bay of Campeche and Caribbean Sea; Bermuda.

Remarks.—This crab has not been collected in the Carolinas for a century so far as known, the record there being Coues's, repeated by Kingsley. Absence from concentrated collections in the Carolinas suggests that the old record is questionable or the result of accidental drift in the Florida current. Park (1969) found this species to be second most abundant among portunids in Biscayne Bay, Fla., but Rouse (1970) found it rare in southwest Florida. The 93-m depth record is from off Bay County, northwest Florida.

A number of specimens in the USNM collection were taken from the stomachs of the gray snapper *Lutjanus* (= *Noemaenus*) *griseus*, the yellow goatfish *Mulloidichthys* (= *Upeneus*) *martinicus*, and other predaceous fishes.

Rathbun (1930a) reported ovigerous females in June from Florida, and in August from Florida and the Caribbean. More recently, egg-bearing females have been taken on Campeche Banks in late August, and Park (1978) summarized their occurrence in the western Atlantic as March, May-June, with a few in July-August; peak spawning was in May.

Park (1978) reviewed evidence for euryhalinity in this species.

Portunus floridanus Rathbun

Fig. 304

Portunus (*Achelous*) *floridanus* Rathbun 1930a:82, pl. 40.

Portunus floridanus.—Powers 1977:83.

Recognition characters.—Carapace narrow, without strong ridges but with extensive pattern formed by tracts of fine granules; branchial ridge short, starting well forward at gastric region, trending obliquely backward and forming an obtuse angle opposite seventh anterolateral tooth; pubescence short, inconspicuous; anterolateral teeth 2-7 small, spiniform and similar, sinuses U-shaped; lateral spine short, strong, larger than adjacent teeth, tip trending forward. Frontal teeth triangular, submesial pair much smaller and less advanced than broad, blunt lateral pair, not exceeding epistomial spine on almost same level. Eyes large; inner orbital obtuse, single conspicuous central fissure on upper orbital margin and almost obscured one lateral to it, outer orbital tooth narrow in dorsal view and advanced.

Chelipeds long, ridges appressed, granulate; merus with 3-5 spines on anterior border and small curved spine at distal end of posterior border; carpus ridged and finely granulate, small outer spine and broad inner spine larger than propodal spine at articulation; hand trigonal with distal and subdistal spine on upper crest. Merus of swimming leg longer than wide, armed distally along posterior margin with row of spinules.

Measurements in mm.—Carapace: male, length 23,

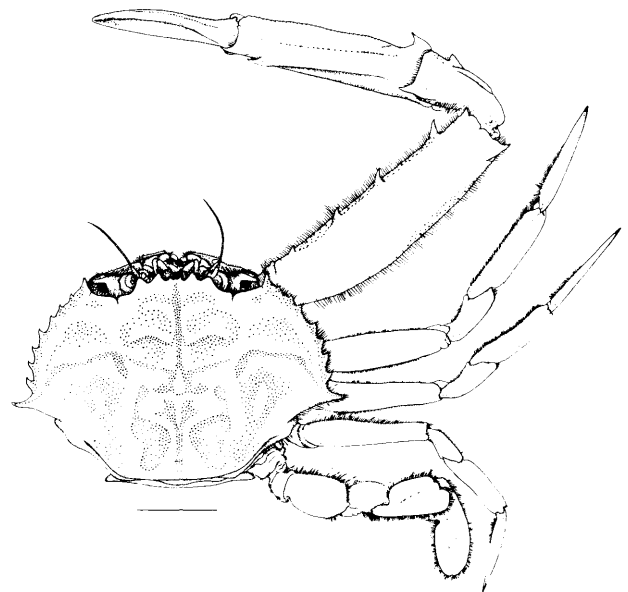


Fig. 304. *Portunus floridanus* Rathbun. Male in dorsal view, legs of left side not shown, 3 mm indicated (USNM 168179).

width 47; mature female, length 19.5, width 25 (occasionally 30).

Variation.—Rathbun (1930a) described the merus of the swimming leg as unarmed on the postero-distal extremity; however, the holotype shows clearly a row of spinules on the distal posterior edge. Specimens from over the range of distribution show this character in varying degree, the spinules being worn or obsolescent in some. In a lot of 5 males from east of Trinidad, this article varies from spinulate to nearly smooth.

Habitat.—Coral bottom reported from type-locality; hard bottom, but muddy sand or mud in some localities; 9 to 640 m, but most common 60–80 m (Park 1978).

Type-locality.—Off Key West, Fla., 24°25'45"N, 81°48'W.

Known range.—E Cape Lookout, N. C., to Honduras and Nicaragua, through West Indies and northern South America to Surinam.

Remarks.—Cain (1972) reported a range extension of *P. floridanus* to the *Lithothamnion* reef zone southeast of Cape Lookout, N. C., and other records are in the collection of the USNM.

The subspecies *P. (Achelous) floridanus isolamargaritensis* Türkay, 1968, from the island of Margarita off Venezuela was considered to be very near typical *P. floridanus*, distinguished by its having a row of spinules on the posterodistal margin of the merus of the swimming leg and a tooth and blunt lobe on the inner distal border of the merus of the cheliped. In *P. floridanus* the inner distal point of the merus of the cheliped is quite acute and might be interpreted as spinous. Adjacent to this is the raised lobelike condyle for articulation with the carpus. Türkay's type-specimen has not been seen by me, but it appears to differ little from typical *P. floridanus*, and it occurs within the distributional range of that species.

Ovigerous females are known off Surinam in March, North Carolina in April, and elsewhere in the western Atlantic in February (Park 1978).

***Portunus gibbesii* (Stimpson)**

Fig. 305

Lupa gibbesii Stimpson 1859:57.

Portunus gibbesii.—Hay and Shore 1918:428, pl. 33, fig. 1.—Williams 1965:164, fig. 146.—Taissoun 1973:48, figs. 6, 8E, 9C.—Felder 1973:60, pl. 8, fig. 16.—Powers 1977:83.

Portunus (Portunus) gibbesi.—Rathbun 1930a:49, pls. 16–17.

Recognition characters.—Carapace approximately

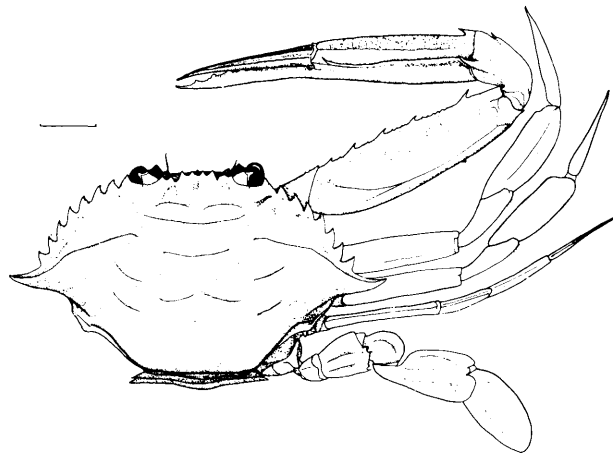


Fig. 305. *Portunus gibbesii* (Stimpson). Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

twice as wide as long, not tumid, thickly ornamented with tracts of small spherical granules, pubescent, and with naked, transverse ridges, 2 of which arise from lateral spines and arch toward gastric region. Eight frontal teeth including 2 slightly more advanced than lateral pair. External orbital tooth not much larger than teeth of anterolateral border; latter stout, acute, directed forward; last tooth or lateral spine, slender, sharp, curved slightly forward and about as long as space occupied by 3 preceding teeth. One or more small, naked, iridescent areas near anterolateral margin at base of teeth.

Chelipeds long, slender (especially in males); merus with 4–7 spines in front and 1 behind at distal end; carpus with large internal and smaller external spine; hand slender, ribbed on all surfaces; ribs continued on fingers and roughened by sharp-pointed, appressed tubercles; hand with 2 spines, 1 at articulation with carpus, another near distal end of superior rib; fingers nearly straight with incurved tips. Merus of swimming leg with row of spinules on posterodistal edge.

Measurements in mm.—Carapace: male, length 37, width 76; ovigerous female, length 35, width 66.

Variation.—Some individuals have elongate lateral spines and suggestion of a spine on the posterodistal margin of the merus of the swimming legs.

Color.—Brownish red, transverse ridges on carapace, spines and margins of chelipeds carmine red; front side of legs brilliantly iridescent by lantern light, iridescence evident to some extent in preserved specimens.

It has also been described as a beautiful iridescent purple and red swimming crab (Anonymous 1975).

Habitat.—Faunal surveys in shallow shelf waters of the Carolinian Province and Caribbean Sea show this to be a common and abundant crab. Hay and Shore (1918) noted its abundance in deeper channels of Beaufort Harbor, N. C., as have others since, and Park (1969) reported it most common on coarse bottoms of cuts and channels in Biscayne Bay, Fla. Further southwest, Tabb and Manning (1961) found it in Coot Bay when salinity was 28–32‰, feeding on massive concentrations of cyprinodont fishes driven from mangrove swamps by oxygen depletion, and they noted it elsewhere in salinities as high as 38‰. In the same region, Rouse (1970) said it was the most often collected portunid, migrating in large numbers during summer. Dragovich and Kelly (1964) found it in their Tampa Bay sampling area, and Wass (1955) recorded it as exceeding other portunids in Alligator Harbor. Franks, et al. (1972) found it nearly year round off Mississippi and noted its presence in lower Aransas Bay, Tex., while Hildebrand (1955) reported it as common on the Campeche Bank shrimping grounds but rare on the Texas coast. Holthuis (1959) and Taissoun (1973) made similar finds off Surinam and Venezuela. To the north off Virginia, Musick and McEachren (1972) found it in temperatures as low as 6°C, possibly left in cold water by the meandering Gulf Stream which was 18°C on bottom nearby. Park (1978) reported it from mainly mud, but also sand and shell substrates. Recorded depths are surface to 393 m.

Type-localities.—South Carolina and St. Augustine, Fla.

Known range.—Southern Massachusetts through Gulf of Mexico along coast to French Guiana, but reported absent from the Antilles (Park 1978).

Remarks.—*Portunus gibbesii* has been reported as fossil from the Pleistocene of Barbados (Collins and Morris 1976).

Ovigerous females are known to occur from February to November between North Carolina and Surinam. Off Beaufort Inlet, N. C., Dudley and Judy (1961) found larvae from May to September 1.6 km offshore at a depth of 1 m, from May to October at depths of 1–8 m, predominantly 1 m, 6.5 km offshore, and from May to October variably at 1–8 m depths 10–13 km offshore. Ovigerous females occurred there from May 1 to August, mainly in June.

Gray (1957) computed gill area per unit weight for *P. gibbesii* as intermediate among a number of swimming crabs studied. Camp, et al. (1977) reported young *P. gibbesii* (≤ 10 mm wide) settling in shallow water near Cape Canaveral, Fla., then migrating offshore as they grew to become most abundant in depths of 40–45 m. Park (1978), from

distribution records and sex ratios in samples (26% ♂; 16% of ♀ ovig.), concluded that the species is slightly euryhaline.

Portunus ordwayi (Stimpson)

Fig. 306

Achelous ordwayi Stimpson 1860a:224.

Portunus (Achelous) ordwayi.—Hay and Shore 1918:431, pl. 33, fig. 6.—Rathbun 1930a:71, pl. 33.

Portunus ordwayi.—Williams 1965:166, fig. 148.—Coelho and Ramos 1972: 186.—Powers 1977:84.

Recognition characters.—Carapace approximately 1.5 times as wide as long, uneven, elevations granulate and depressions pubescent, with a number of conspicuous, curving transverse ridges. Six frontal teeth including acuminate inner orbitals; true frontal teeth about equal in size, triangular, acute, middle pair advanced beyond others. Outer orbital tooth similar to remainder of anterolateral teeth which diminish slightly in size laterad to lateral spine, latter about as long as space occupied by 2 preceding teeth, tips of all acute and turned forward.

Chelipeds of moderate length; merus with 4–6 strong spines in front, single distal one behind; carpus ribbed, with strong internal and much smaller external spine; hand ribbed on all surfaces except for obliquely flat, iridescent, superior surface; superointernal ridge raised into crest terminating in strong, sharp, subdistal spine. Margins of carapace and chelipeds more or less fringed with silky hairs. Merus of swimming leg without posterodistal lobe but spinulose.

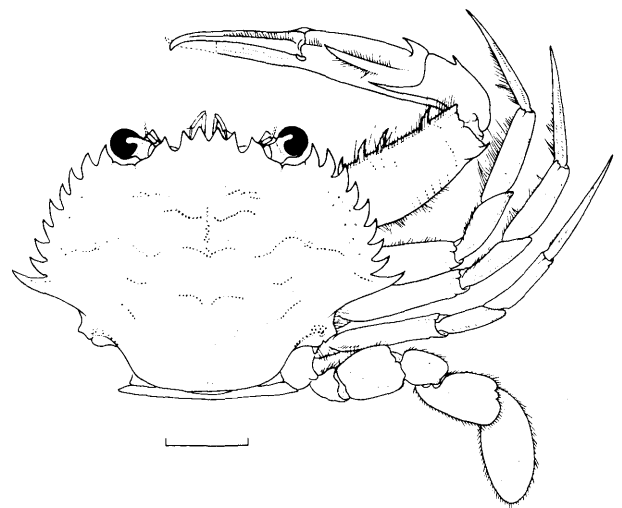


Fig. 306. *Portunus ordwayi* (Stimpson). Male in dorsal view, legs of left side not shown, 1 cm indicated (USNM 31048).

Measurements in mm.—Carapace: male, length 33, width 49; ovigerous female, length 32, width 50.

Color.—Carapace and legs reddish brown because of fine mottling with red, yellowish brown and gray; pale orange beneath, deeper orange on chelipeds and legs; chelae deep red brown above, finger with 2 cross bands of light orange red. Blue coloration also apparent near red and dark pigments; hairs on appendages deep red (Abramowitz 1935).

Habitat.—This is another of the tropical swimming crabs which move northward with warm water currents. It is reportedly associated with calcareous algae, occasionally fine material of organic origin (Coelho and Ramos 1972) and a variety of other soft substrates (Park 1978); surface to 106 m, occasionally 366 m.

Type-localities.—Key Biscayne and Tortugas, Fla.; St. Thomas [V. I.].

Known range.—Vineyard Sound, Mass.; North Carolina through Gulf of Mexico, West Indies and Caribbean Sea to near Rio de Janeiro, Brazil (Park 1978); Bermuda; Fernando de Noronha.

Remarks.—Ovigerous females are known from Florida in March and August, Ceará, Brazil, in March, Guyana in August, Honduras and Surinam in September, and Georgia-Florida in December. No ovigerous females have been found in the Antilles, indicating some degree of euryhalinity (Park 1978).

Park (1978) found this to be a fairly common species in samples of western Atlantic portunids, never abundant but associated with each of the three most abundant species, *P. spinicarpus*, *P. gibbesii* and *P. spinimanus*.

Specimens collected from a deep-water reef near Cape Lookout, N. C., in autumn died after 17-h exposure to temperature of 4°C (F. J. and W. B. Vernberg 1970).

Randall (1967) reported *P. ordwayi* from stomach contents of the spotted scorpionfish, *Scorpaena plumieri*, and porcupinefish, *Diodon hystrix*.

***Portunus sayi* (Gibbes)**

(Gulf weed crab)

Fig. 307

Lupa sayi Gibbes 1850:178.

Portunus sayi.—Hay and Shore 1918:428, pl. 33, fig.

2.—Williams 1965:163, fig. 144.—Zariquiey Alvarez 1968:384.—Felder 1973:59, pl. 8, fig. 12.—Powers 1977:84.

Portunus (Portunus) sayi. Rathbun 1930a:37, figs. 6–7, pl. 14.

Neptunus sayi.—Monod 1956:197.

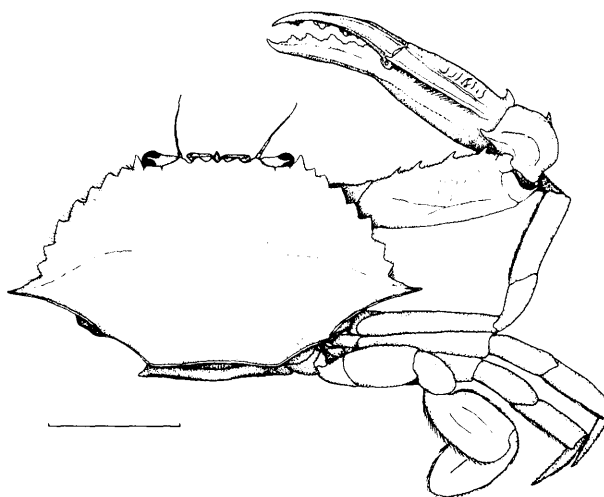


Fig. 307. *Portunus sayi* (Gibbes). Animal in dorsal view, legs of left side not shown, 2 cm indicated (from Williams 1965).

Recognition characters.—Carapace nearly twice as wide as long, somewhat tumid, smooth and polished to naked eye, finely granulate under magnification. Six frontal teeth including inner orbitals, 2 submesial teeth smaller but on line with lateral pair. External orbital tooth larger than those of anterolateral border except stout, acute lateral spine; remaining anterolateral teeth blunt, increasing slightly in size in middle of row.

Chelipeds of moderate length, somewhat larger in males than in females; merus with 3–4 stout, curved spines in front, none behind; carpus with 2 spines and noticeable ridge above lateral margin; hand with acute spine at articulation and smaller one near base of dactyl; external surface with 2 longitudinal ribs with lowermost extending on finger; superior surface with 3 ribs continuing on finger, innermost one with fringe of hair beneath.

Measurements in mm.—Carapace: male, length 31, width 61; ovigerous female, length 31, width 64 (length 40, width less lateral spines 63 [Milne Edwards and Bouvier 1900]).

Color.—Chocolate brown or purplish with cloudings of olive green or light brown and irregular white or flesh-colored spots; orange margins on spines of chelipeds.

Habitat.—Normally this is a pelagic form living among floating *Sargassum*, but it is occasionally carried into coastal areas by currents.

Type-locality.—South Carolina.

Known range.—North Atlantic Ocean from Nova Scotia through Gulf of Mexico to the Guianas; Bermuda; mid-Atlantic Ocean; Canary Islands and Morocco. The only record from Brazil is that of Gerstaecker for his *Lupea pudica* (= *sayi*), and modern collections have not confirmed this. Records

from Kerguelen Island and the south Indian Ocean need confirmation as do those from the western Mediterranean which Milne Edwards and Bouvier (1900) first reported, Bouvier later ambiguously accepted (1922), and finally disregarded (1940). These records were accepted by Zariquey Alvarez (1968) who also recorded the species from Cap Spartel, Morocco.

Remarks.—The numerous published records and notes on this species cannot be reviewed here. The species has a fossil record dating from the lower Miocene of North America (Rathbun 1935).

Ovigerous females are known from April to August in the southeastern United States and parts of the West Indies. They are also reported from Culebra in February, near Nantucket in September (Rathbun 1930a, in part) and off Morocco in June (Milne Edwards and Bouvier 1900). Park (1978) suggested that spawning sites are restricted to areas of attached *Sargassum*. Some of the larval stages were described by Lebour (1944) at Bermuda. Dudley and Judy (1971) found larvae attributed to this species from May to November off Beaufort Inlet, N. C.

***Portunus spinicarpus* (Stimpson)**

Fig. 308

Achelous spinicarpus Stimpson 1871a:148.

Portunus (Achelous) spinicarpus.—Hay and Shore 1918:429, pl. 33, fig. 3.—Rathbun 1930a:92 (part), pl. 45.

Portunus spinicarpus.—Williams 1965:167 (part), fig. 150.—Holthuis 1969a:415, fig. 1 (top).—Coelho and Ramos 1972:187.—Taissoun 1973:50, figs. 7, 8C, 9B.—Felder 1973:60, pl. 8, fig. 13.—Powers 1977:85.

Recognition characters.—Carapace about twice as wide as long; sculptured, with number of naked, rather coarsely granulate, arching, transverse ridges separated by finely granulate and pubescent surfaces. Six frontal teeth, including inner orbitals with sinuate but unnotched outer margins; true frontal teeth narrow, acute, separated by broad usually U-shaped notches, median pair considerably advanced beyond others. External orbital tooth acute, larger than neighboring teeth of anterolateral margin; latter varying somewhat in size, concave sided, acute; lateral spines slender, curving, more than half as long as anterolateral border; posterolateral angle sharp, margin slightly recurved.

Chelipeds long, slender; merus with 4 or 5 stout, curved spines in front, and single, similar distal spine behind. Carpus with 2 spines, outer small and weak, inner long, extending along side of hand to near base of dactyl. Hand with serratotuberculate

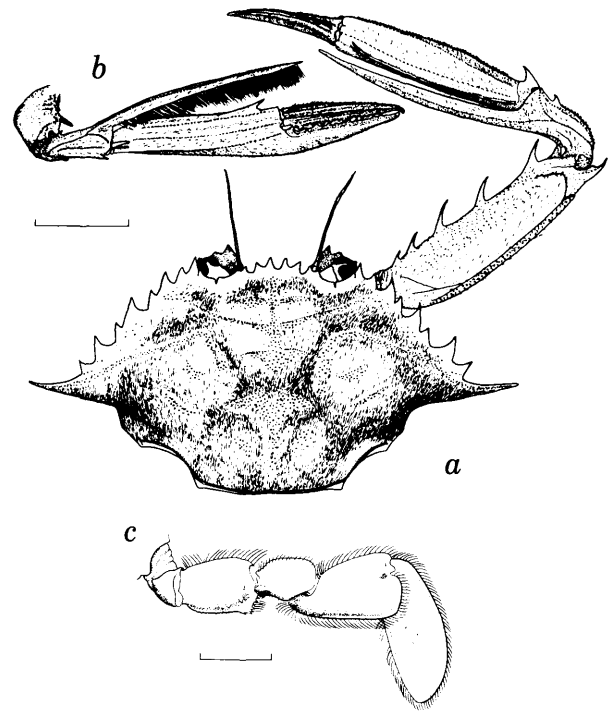


Fig. 308. *Portunus spinicarpus* (Stimpson). a, Male in dorsal view, legs not shown except for right cheliped; b, right chela in frontal view (from Williams 1965); c, right fifth leg; a-c, 5 mm indicated.

ridges prolonged on fingers, and 2 spines, one at carpal articulation, another on superior surface near base of dactyl.

Measurements in mm.—Carapace: male, length 34, width 64; female, length 32, width 58; ovigerous females, width 18–58 (Holthuis 1969a); occasionally larger.

Variation.—The internal carpal spine of the chelipeds may extend beyond midlength of the fingers in males but in females it does not reach beyond the superior spine of the palm. The lateral spine is relatively longer in young than in old individuals and changes in angle of projection with age, extending straight laterally or slightly backward in the young but curving slightly forward in adults (Rathbun 1930a).

Color.—Carapace grayish green marbled with short, curved reddish brown line and streaks; a dark median longitudinal line over cardiac and intestinal regions; epibranchial line dark red distally. Eyestalks with conspicuous red spot on anterior surface. Third maxillipeds with last 3 articles iridescent. Cheliped with merus very lightly spotted, a prominent dark or contrasting submarginal streak paralleling its outer margin and similar color on inside of anterior spines at their bases; carpus with long spines uninterruptedly red proximally fading to white intervals distally and fringed with long red

hairs, an inconspicuous streak on basal part of outer margin; outer surface of palm uncolored except for red spot at base of proximal spine, inner surface in females uncolored except for red proximal spot and a very distinct proximal red band on fingers, that of males with some long reddish hairs. Walking legs grayish green with pink dactyls. Swimming legs similar but with a distinct red spot distally on dactyl. Reddish color, especially on merus, tending to persist in alcohol (Holthuis 1969a).

Habitat.—On shrimping grounds in the western Gulf of Mexico, Hildebrand (1954) reported this form as found only along the seaward side in depths of 27 to 68 m. Coelho and Ramos (1972) reported it on mud and sand bottom; 9 to 550 m (Holthuis 1969).

Type-locality.—Straits of Florida S of Dry Tortugas, 24°23'N, 82°57'W to 24°24'N, 82°56'W (Holthuis 1969a, restricted).

Distribution.—ESE Oregon Inlet, N. C., 35°42'N, 74°54'30"W (Musick and McEachren 1972) to Santa Catarina, Brazil.

Remarks.—This species is very close to *P. binoculus* which Holthuis (1969a) distinguished from it in the West Indies and Caribbean Sea. The two occasionally occur together, and are more easily differentiated by color than by other characters whose variabilities overlap, such as acuteness of frontal spines and shape of the notches between them, or length of anterolateral processes on the third maxillipeds. Since *P. binoculus* usually has persistent red color spots on the two branchial lobes, and it has not been seen in a rather extensive set of samples from the Carolinian Province, no confusion in identity is likely to occur there. Treatment of these species in the older literature should be viewed with caution. Park (1978) found *P. spinicarpus* most often and in greatest density among samples of portunids from the western Atlantic.

Ovigerous females are known from January to October in the area stretching from North Carolina to Surinam, and in November in Florida and Texas, but Park (1978) found none in the Antilles. Bookhout and Costlow (1974) described seven zoeal stages and a megalopa from laboratory hatching and rearing, giving particular attention to types of setae on all appendages. They also gave great detail on kinds of spination in crab larvae and differentiated the larval stages of *P. spinicarpus* from those of *Callinectes sapidus*. Freshly hatched larvae were reared to megalopa in temperatures of 20° and 25°C in salinities of 30, 35, 40, and 45‰, but did not reach megalopa in 20 and 25‰. None survived to megalopa in this full range of salinity at either 15° or 30°C. Two percent of the larvae survived to first

crab stage at 20° and 25°C in 35‰ salinity water, but there was no survival in other combinations. Molting rates at 20°C and 35‰ were not only slower, but survival was consistently lower in each stage leading to megalopa in contrast to the 25°C–35‰ combination. At 20°C, 24% of larvae reached megalopa in a mean of 46.8 days, whereas at 25°C, 40% reached that stage in an average 38.3 days.

W. B. and F. J. Vernberg (1970) considered *P. spinicarpus* to be a species with metabolically tropical affinities. Assessing lethal limits, F. J. and W. B. Vernberg (1970a) found that animals from Cape Hatteras region in December died after 3-h exposure to 30°C; those collected from a deep water reef near Cape Lookout, N. C., in October died after 7-h exposure to 4°C.

Pearse (1932b) found the barnacle *Dichelaspis sinuata* on a number of individuals. Several small specimens, all apparent females, have been noted bearing one or two sacculinid parasites (Holthuis 1969a).

Portunus spinimanus Latreille

Fig. 309

Portunus spinimanus Latreille 1819:47.—Hay and Shore 1918:429, pl. 33, fig. 4.—Rathbun 1972:186.—Taissoun 1973:43, Foto 8, figs. 8B, 9E.—Felder 1973:59, pl. 8, fig. 15.—Powers 1977:85.

Portunus (Achelous) spinimanus.—Hay and Shore 1918:429, pl. 33, fig. 4.—Rathbun 1930a:62, text-fig. 10, pls. 26–28.

Recognition characters.—Carapace considerably less than twice as wide as long, finely granulate and pu-

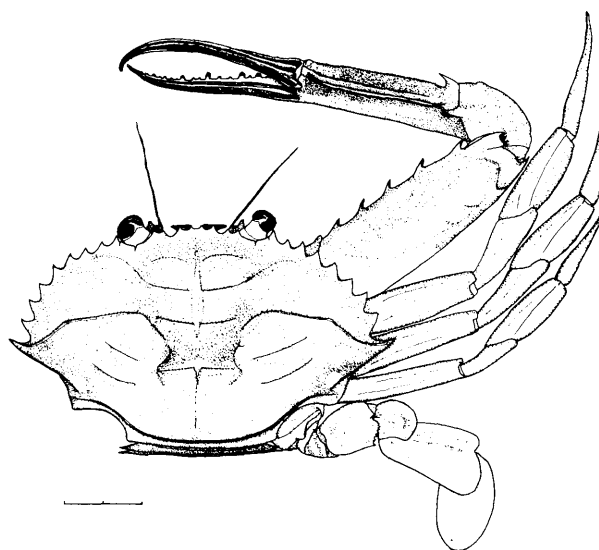


Fig. 309. *Portunus spinimanus* Latreille. Male in dorsal view, legs of left side not shown, 2 cm indicated (from Williams 1965).

bescent, with number of prominent, curved, coarsely granulate, transverse ridges. Eight frontal teeth, including inner orbitals, each notched at summit and presenting 2 points; submesial pair of teeth slightly narrower and more advanced than next lateral pair, all considerably more advanced than inner orbitals. Outer orbital tooth not much larger than those of anterolateral border; latter strong, acute or acuminate, about equal in size except lateral spine about twice as large as others and usually curved forward.

Chelipeds long, pubescent, serratogranulate all over; merus with 4, occasionally 5 strong, curved spines in front and 1 at distal end; carpus with 2 spines; inner one much stronger, and with 4 conspicuous ridges on upper surface; hand slender, all surfaces with ridges which extend on fingers; strong spine at carpal articulation and another near base of dactyl; fingers nearly straight, tips incurved.

Measurements in mm.—Carapace: male, length 65, width 110; ovigerous female, length 57, width 94.

Variation.—Large males have relatively much longer, thinner chelipeds and walking legs than large females.

Color.—Pubescence yellowish or reddish brown, ridges of carapace, spines of chelipeds, fingers and tips of legs reddish brown; anterolateral teeth reddish at base, white at tips; merus, carpus and hand of chelipeds with white blotches.

Habitat.—Common in water of inner continental shelf, occasionally in deeper channels or harbors such as Beaufort, N. C., *P. gibbesii* is often found in company with *P. spinimanus*, both in the Atlantic off the Carolinas and on the Campeche Banks (Hildebrand 1955). Park (1969) found *P. spinimanus* on open sand with light cover of *Diplanthera* or algae

in Biscayne Bay, and Olsen, et al. (1978) also reported concentrations on sand, but it is commonly on coral reefs in Florida and the Bahamas (Park 1978); on beach under *Sargassum*; surface to 91, occasionally 393 m.

Type-locality.—American waters, common in Brazil.

Known range.—New Jersey through Gulf of Mexico and West Indies to Santa Catarina, Brazil; Bermuda.

Remarks.—This species, which somewhat resembles *P. gibbesii*, can be readily distinguished from the latter by its narrowed, rounder form, and by the lack of iridescent patches on the carapace.

Ovigerous females are known virtually the year round in Florida (Camp, et al. 1977; Wass 1955; Williams 1965), May to October in North Carolina (Dudley and Judy 1971), February to May in the Virgin Islands (Olsen, et al. 1978), and otherwise from March to November in the region outside the United States from Bermuda to Rio de Janeiro (Holthuis 1959; Lebour 1950; Rathbun 1930a; Taissoun 1973; USNM). At Bermuda, Lebour found an ovigerous female among *Sargassum* and from the eggs reared larvae which she illustrated.

Gray (1957) computed gill area per unit weight for *P. spinimanus* as intermediate among a number of swimming crabs studied. Johnson (1964) studied histology of the reproductive system, comparing it with other decapods. Sikora, et al. (1972) listed *P. spinimanus* as a prey species of the hakes, *Urophycis regius* and *U. floridanus*. Camp, et al. (1977) found this to be one of the commonest decapod crustaceans in samples from nearshore east Florida waters in a salinity range of 32 to 39.3‰ at 19.2°–32°C, and Olsen, et al. (1978) judged it to be a potential fisheries resource in the Virgin Islands.

Superfamily Xanthoidea

Key to Families

(Amplified)

1. Carapace always nearly oval or hexagonal in dorsal view; frontoorbital width never more than $\frac{4}{5}$ greatest width of carapace; males without or with variable small part of sternite 8 visible between second abdominal segment and coxa of fifth leg (visible, e.g., in *Panopeus*, *Rhithropanopeus*, *Eurytium*); male opening coxal, genital duct not lying in sternal groove **Xanthidae**
- Carapace either subquadrate in dorsal view, or xanthoid as above in *Glyptoplax*, *Panoplax*, *Nanoplax* or *Speocarcinus*; frontoorbital width from about $\frac{1}{2}$ to $\frac{9}{10}$ greatest width of carapace; male with part of sternite 8 visible between second abdominal segment and coxa of fifth leg; male opening either coxal with genital duct extended and lying in sternal groove, or sternal with involution edges of groove covering genital duct **Goneplacidae**

Family Xanthidae

Crabs with body transversely oval or transversely hexagonal. Front broad, never produced in form of rostrum. Last pair of legs normal. Antennules folding obliquely or transversely. Male openings coxal. (Rathbun 1930a; Balss 1957.)

Containing more genera than any other brachyuran family, the family Xanthidae has been treated either as too complex to organize easily along natural lines (Rathbun 1930a; Monod 1956; Williams 1965; Glaessner 1969), separable into families and subfamilies (Ortmann 1893), or as separable into subfamilies (Balss 1957). Guinot (1971, summary of her previous papers) did not make more than preliminary subfamily groupings even though she discussed affinities of some provisional subfamilies, and in 1978 did subdivide the Xanthoidea into both families and subfamilies. The problem is compounded by relationship of these crabs to the family Goneplacidae, for the two families share certain characters which form a continuum that allows no clear distinction if reliance for separation is placed on these alone (Guinot 1971). For example, in one character that illustrates this relationship: males of the xanthid genus *Neopanope* show no part of sternite 8 visible between the second abdominal segment and the coxa of the fifth leg, whereas in *Panopeus* a small part is left uncovered, and in *Rhithropanopeus* a sizeable lateral piece is un-

covered; in males of the goneplacid genus *Cyrtoplax* (Caribbean-Pacific) a still broader part of sternite 8 is exposed, and in *Prionoplax* (oriental) the part exposed is equal in size to the readily visible part of sternite 7. In development of this character the families merge, yet presence or absence of a visible piece of sternite 8 lateral to the male second abdominal segment is the usual key difference used to separate the families. Guinot (1971) considered at least certain of the Goneplacidae to be an evolutionary grade not completely distinct from the Xanthidae. Still, the families, at least their representatives in the area considered here, are distinct enough to be separable with reasonable accuracy.

Because revisionary studies of the Xanthidae are still in progress, formal subdivision into subfamilies is not attempted here; the statements I made in 1965 still apply, but the arrangement of genera is somewhat different than used then. Because many of the genera occurring in the region contain a single species, the generic key is in large part also a key to species. Parts of the key have been adapted from Rathbun (1930a) and Ryan (1956).

Arrangement of the genera is not alphabetical but based on similarities and differences in the first pair of male pleopods. Though no attempt is made to divide the family into subfamilies, at least three well-marked groups appear, and perhaps one of these groups (Fig. 333) could be split into additional groups.

Key to Genera and Some Species of Xanthidae

1. Low anteroposterior ridges on endostome (palate or roof of mouth) absent or not reaching to anterior margin of buccal frame 2
 Low anteroposterior ridges on endostome (palate or roof of mouth) present and reaching to anterior margin of buccal frame 13
2. Frontoorbital width less than $\frac{1}{2}$ greatest width of carapace; body lobulate, granulate or eroded 3
 Frontoorbital width more than $\frac{1}{2}$ greatest width of carapace; body rough or smooth 4
3. Carapace and legs covered with nodules, granulate, often hairy
 *Paractaea rufopunctata nodosa*
 Carapace and legs with surface deeply and intricately eroded
 *Glyptoxanthus erosus*
4. Chelipeds with large notch clearly forming an open hole between carpus and palm when viewed frontally with cheliped fully pressed against body *Carpoporos papulosus*
 Chelipeds lacking notch forming an open hole between carpus and palm when viewed frontally with chelipeds fully pressed against body 5
5. Transverse groove between extreme edge of frontal margin and row of granules or nodules paralleling it above (under magnification) 6
 Front lacking such transverse groove, each half presenting but a single edge (under magnification) 8
6. Body covered with smooth, coarse lobules and tubercles, with tracts between obscured by feltlike covering of hairs *Allactaea lithostrota*

- Body smooth or rough but never pronouncedly as above 7
7. Carapace and chelipeds more or less roughened, granulate or spiny along anterolateral margin; marine species *Pseudomedeus*
Carapace not granulate but with low, transverse ridges on dorsum; chelipeds not roughened; estuarine species *Rhithropanopeus harrisi*
8. Anterolateral border with 4 or 5 easily discernible stout teeth or lobes, including outer orbital; first and second teeth more or less united; edges of teeth smooth or at most granular, tips may be acute but not spinelike; carapace may be granular but not nodose 9
Anterolateral border with 3–4, rarely 5 (*M. urinator*) spine-tipped or denticulate teeth, including outer orbital; second tooth obsolescent, fifth somewhat so (except in *M. urinator*); carapace more or less nodose *Micropanope*
9. Five anterolateral teeth including outer orbital. 10
Only 4 broad, low, lobular anterolateral teeth including outer orbital; carapace very convex longitudinally; front truncate; chelae elongate *Tetraxanthus rathbunae*
10. Dactyl of major chela lacking enlarged, terminally rounded tooth proximally on prehensile edge, but low, pointed tooth not much larger than other teeth may be present. 11
Dactyl of major chela with enlarged, terminally rounded tooth proximally on prehensile edge 12
11. External maxillipeds with red spot on internal face of ischium. *Eurypanopeus*
External maxillipeds without red spot on internal face of ischium *Neopanope sayi*
12. Third and fourth teeth of anterolateral border definitely swept forward, their lateral margins curved outward; external maxillipeds of males and some females with conspicuous red or orange spot on inner surface of ischium *Panopeus*
Third and fourth teeth of anterolateral border triangular and pointed outward or slightly forward, their lateral margins not conspicuously curved outward; external maxillipeds of both sexes lacking red or orange spot on inner surface of ischium *Hexapanopeus*
13. Antennae separated from orbits 14
Antennae not separated from orbits 15
14. Merus of external maxillipeds as long as broad, or nearly so; anterolateral spines strong and outstanding; large species. *Eriphia gonagra*
Merus of external maxillipeds twice as broad as long; carapace and chelipeds armed with slender, acute, often black spines; small species *Domecia acanthophora acanthophora*
15. Chelipeds smooth or nearly so 16
Chelipeds spiny 17
16. Fingers white; anterolateral teeth pointed or rounded, never large-sized. *Eurytium limosum*
Fingers black; anterolateral teeth broad, not pointed, with occasional exception of fifth tooth; attains large size. *Menippe mercenaria*
17. Carapace smooth, front definitely more than $\frac{1}{3}$ carapace width including lateral spines; eyes noticeably large *Melybia thalamita*
Carapace spiny or nodose, front less than $\frac{1}{3}$ carapace width including lateral spines; eyes not noticeably large 18
18. Carapace and chelipeds variably spiny, not nodose; with long plumose (clubbed) hairs, short hairs, or both *Pilumnus*
Carapace with patches of nodules along anterolateral border and extending backward from front; with close pile of short hair only; body massive *Lobopilumnus agassizii*

Genus *Paractaea* Guinot 1969

Guinot 1969:241.

Carapace oval, more or less swollen, covered dorsally with numerous lobules (prominent, widely separated, or flattened). Front convex or quite advanced. Anterolateral border cut into 4 lobes, probably from fusion of outer orbital and adjacent anterolateral lobe (*retusa* group), or 5 lobes (*rufopunctata* group). Legs often nodose or flanged, ornaments occasionally obsolescent. Orbits with well-developed infraorbital fissures. Basal antennal article applied against subfrontal prolongation, not united to latter at internal angle, barely penetrating orbital hiatus. Third maxillipeds almost parallel-sided, not separated in front, ischium a little widened and merus little wider than long; lacinia of first maxilliped leaving large part of endostome uncovered. First male pleopod thick, tip forming more or less flattened lobe; subapical hairs implanted linearly, mainly along one side. (Translation paraphrased from Guinot 1969.)

Paractaea rufopunctata nodosa (Stimpson)

Fig. 310

Actaea nodosa Stimpson 1860a:203 [75].

Actaea rufopunctata var. *nodosa* Miers 1886:122.

Actaea rufopunctata nodosa.—Rathbun 1930a:257, pl. 105, figs. 1–2.

Paractaea rufopunctata forma *nodosa*.—Guinot 1969:252, fig. 25.—Coelho and Ramos 1972:189.

Recognition characters.—Ovoid carapace with length not quite $\frac{3}{4}$ but more than $\frac{2}{3}$ width, surface broken by deep, broad grooves into numerous very complex lobules (about 27 excluding those along orbits and front) covered with closely packed vesicular granules; grooves filled with dense, short, and a few longer hairs. Front strongly deflexed, rather sharply bilobed. Swollen supraorbital margin cut by two fissures and separated from lower margin by fissure. Anterolateral border with 4 rounded lobules in addition to reduced outer orbital.

Chelipeds and walking legs with lobulation similar to carapace, edges fringed with coarse hair; lower outer surface of palm with granules arranged in rows; dactyls of walking legs furred, corneous tips grooved below.

Measurements in mm.—Carapace: male, length 14.3, width 20.8; female, length 16.4, width 25; ovigerous female, length 4.1, width 6.0.

Habitat.—Variety of bottoms from sand to broken shell and coral, sometimes associated with sponges; to 172 m.

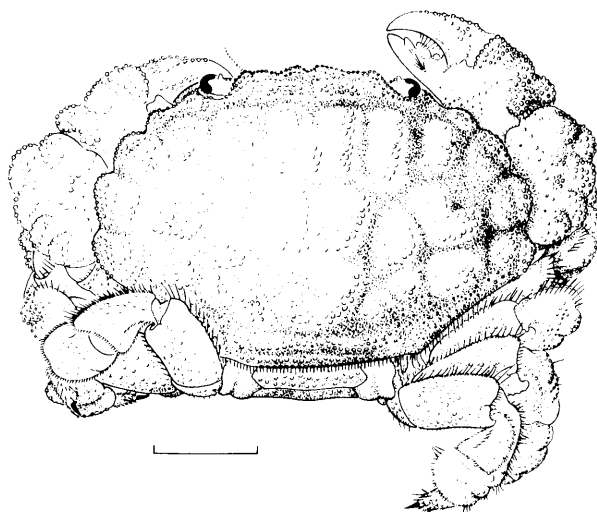


Fig. 310. *Paractaea rufopunctata* forma *nodosa* (Stimpson). Female in dorsal view, 5 mm indicated (USNM 15010).

Type-locality.—Tortugas, Florida.

Known range.—SE Cape Lookout, N. C. (34°12.2'N, 76°08'W, 90 m, to 34°12.27'N, 76°08'W, 50 m; 33°55.5'N, 76°28.4'W); off Mississippi River Delta through West Indies to Rio de Janeiro, Brazil; Ascension Island (USNM, UNC-IMS).

Remarks.—This crab has been treated as a form of *P. rufopunctata* by Guinot (1969) because its relation to other members of the *rufopunctata* complex in the eastern Atlantic and western Indian Ocean remains unclear. The fringe occurrences off North Carolina include an ovigerous female, indicating that breeding populations of a tropical species can occur where warm environment sustains them.

Genus *Allactaea* Williams 1974

Williams 1974a:19.

Allactaea lithostrota

Figs. 311, 331a

Allactaea lithostrota Williams 1974a:19, figs. 1–3.—Soto 1980:125, fig. 1A-B.

Recognition characters.—Conspicuously tuberculate. Carapace wider than long, arched anteroposteriorly, regions prominently indicated by smooth raised lobules arranged in characteristic radiating pattern emanating from urogastric region; tracts between lobules almost completely obscured by thick covering of club shaped hairs. Front divided by narrow U-shaped median notch, dorsally submarginal row of about 8 coalesced lobules extending

from this to each antennal notch resulting in transversely doubled appearance. Orbital margin thickened raised and smooth dorsally, fissures closed; eyestalks with 2 spiniform tubercles in corneal emargination and smaller tubercles at base of cornea. Anterior lateral border with 4 teeth exclusive of outer orbital reduced to anteriorly directed mammillary lobules; row of smaller intercalary teeth slightly below these on margin; hepatic and subbranchial region slightly tuberculate; row of tubercles on posterolateral border.

Chelipeds dissimilar, right larger than left; outer surfaces with spaces between lobules and tubercles covered with club-shaped hairs, inner surfaces smooth; merus with dorsal crest of sharp forward-curved spines; palm and carpus with distally directed lobules varying from sharpest along dorsal crest to flared at tip with narrower bases on external surface of carpus and outer dorsal part of palm, becoming smaller, sharper and tending to alignment in longitudinal rows on outer surface of palm; carpus with spiniform lobule at inner angle and another below it, anterior border with few small teeth hidden in hairs; fingers dark colored, moderately toothed, crest of tubercles at base of dactyl.

Measurements in mm.—Carapace: male, length 11.6, width 16.2; female, length 18.1, width 28.1.

Variation.—Lobules tend to be rather sharply pointed in juveniles, but grow progressively blunter as they increase in size, many of them finally becoming flattened knoblike expansions on somewhat restricted bases. Also, small lobules proliferate with increasing size. Clusters on front and mesial areas tend to be tripartite with an opening in the clusters directed forward and outward.

Habitat.—Offshore *Lithothamnion* reef off North Carolina; 50 to 640 m.

Type-locality.—Approximately SE Cape Lookout, N. C., 33°43'N, 76°40'W, 90 m, to 33°42.7'N, 76°40.2'W, 110 m, *Eastward* Stn. 1087.

Known range.—Near edge of continental shelf SE of Cape Lookout, N. C.; Florida Straits; off Cape Catoche, Yucatan; off Venezuela and Surinam

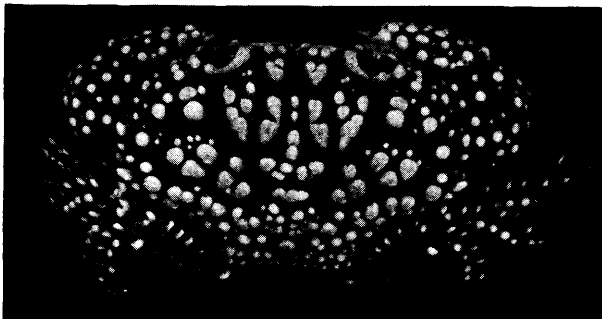


Fig. 311. *Allactaea lithostrota* Williams. Female in dorsal view, 10 mm indicated (from Williams 1974a).

(USNM); Bermuda (Markham and McDermott 1981).

Remarks.—Ovigerous females are known in July from North Carolina and Venezuela and October off Venezuela. Changes in carapace dimensions with growth were calculated by Soto (1980).

Genus *Glyptoxanthus* Milne Edwards 1879

Rathbun 1930a:263.—Guinot 1967b:554.

Glyptoxanthus erosus (Stimpson)

Figs. 312, 331b

Actaea erosa Stimpson 1859:51.

Glyptoxanthus erosus.—Rathbun 1930a:263, pl. 107.—

Williams 1965:185, figs. 167, 183A.—Guinot 1967b:556, fig. 30a, b.—1969:237–241.—Felder 1973:60, pl. 9, fig. 9.

Recognition characters.—Surface of body and legs covered with rough vermiculations, furrows or cavities between them narrow, making regular pattern and giving body an eroded appearance; elevations between furrows or cavities formed by masses of small granules crowded together producing rough surface in young and half-grown individuals, but variably worn smooth in old ones; margins of cavities with short pubescence. Carapace areolated, but divisions obscured to large extent by character of surface; lateral boundaries of gastric region and median suture from front to middle of gastric region deep. Front steeply inclined, median lobes evenly rounded, margins granulate. Ischium of third maxilliped with deep, longitudinal, central groove.

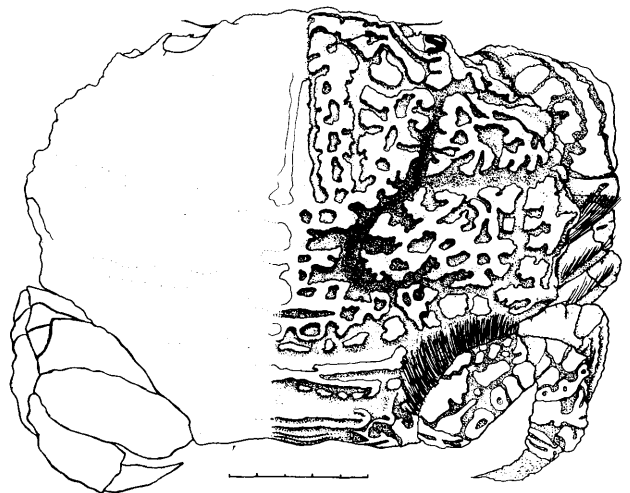


Fig. 312. *Glyptoxanthus erosus* (Stimpson). Animal in dorsal view, detail shown on right side, 5 mm indicated (from Williams 1965).

Chelae short and broad, upper surface divided by furrows into transverse tuberculate ridges, outer surface divided into longitudinal tuberculate ridges; fingers short, deeply grooved, even-toothed; dactyls tuberculate at base on upper side. Walking legs with hairy edges, dactyls pubescent.

Measurements in mm.—Carapace: male, length 39, width 54; female, length 47, width 67.

Color.—Rathbun (1930a) described a specimen in formalin as cream white with blotches and small spots of bright red, color especially persistent on walking legs, with dactyls red at base and yellowish distally.

Habitat.—The species has been taken from rocks and the alga *Halimeda* in shallow water, from coarse sand, and sponges and coral reefs in deeper water. Low-tide mark to 70–90 m (Cain 1972).

Type-locality.—Florida.

Known range.—Cape Lookout, N. C., southward; off Grand Isle, La., southeastward; Yucatan; through West Indies to Guadeloupe.

Remarks.—Ovigerous females have been taken off northeast Florida in January and North Carolina in September.

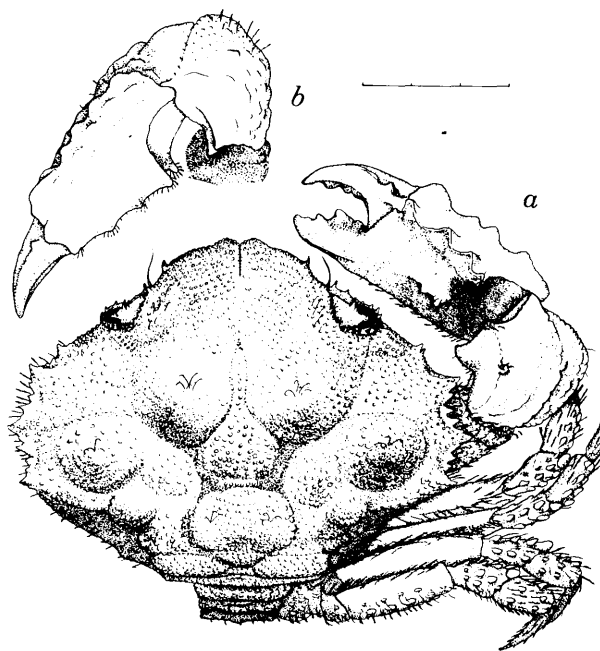


Fig. 313. *Carpaporus papulosus* Stimpson. *a*, Animal in dorsal view, legs of left side not shown; *b*, cheliped partially extended in frontal view; 3 mm indicated (from Williams 1965).

Genus *Carpaporus* Stimpson 1871

Rathbun 1930a:269.—Hemming 1958b:14.

Carpaporus papulosus Stimpson

Figs. 313, 331c

Carpaporus papulosus Stimpson 1871a:139.—Rathbun 1930a:269, pl. 110, figs. 3–6, pl. 111.—Williams 1965:186, figs. 168, 183B.

Recognition characters.—Carapace subhexagonal, nearly as long as broad, naked above; regions protuberant, somewhat wartlike and granulated, gastric and epibranchial regions prominent. Two or 3 small, spiniform lateral teeth, interspaces armed with denticles. Front strongly projecting at middle, bilobed, margin concave, inner end rectangular, outer end spiniform. Peduncle of eye granulated; orbit with margin granulate above. Exposed surface of third maxilliped with beadlike granules.

Chelipeds when retracted each having large hole between carpus and hand for passage of water to afferent branchial apertures; inner surface of hand

with 2 unequal peglike spines near middle forming a kind of filter in front of branchial opening; carpus and hand sculptured externally with granulated protuberances, arranged in 4 or 5 serial rows on hand; hand serrate above with 4 teeth partly joined; fingers stout, short. Walking legs hairy below.

Measurements in mm.—Carapace: male, length 14.6, width 18.3; female, length 12.4, width 15.3.

Habitat.—Variety of bottoms from sand to rock and coral; 32–113 m.

Type-localities.—Southwest of Tortugas and off Carysfort Reef, [Fla.].

Known range.—Between Capes Hatteras and Lookout, N. C.; Gulf of Mexico off Mobile Bay southeastward; Cape Catoche, Yucatan.

Remarks.—Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but were dead after 17-h exposure (F. J. and W. B. Vernberg 1970).

Genus *Pseudomedeus* Guinot 1968

Guinot 1968:726.—Williams 1978:547.

Key to Species

1. Median frontal notch V-shaped, usually narrow; margins of anterolateral teeth either spinous or with beadlike granules; carpus of chelipeds with strong internal spine, sometimes double *P. agassizii*

Median frontal notch U-shaped; margins of anterolateral teeth almost always smooth (rarely granulated); carpus of chelipeds with stout internal double spine *P. distinctus*

***Pseudomedaes agassizii* (A. Milne Edwards)**

Figs. 314, 331d

Leptodius agassizii A. Milne Edwards 1880:270, pl. 49, fig. 3.—Hay and Shore 1918:441, pl. 34, fig. 6.—Rathbun 1930a:307, pl. 141, figs. 4–5.—Williams 1965:192, figs. 174, 183H.

Medaeus latifrons Chace 1942a:83, pl. 25.

Medaeus agassizi var.—Monod 1956:309–310, figs. 381–382.

Pseudomedaes agassizi.—Guinot 1968:726, figs. 25, 58.—Felder 1973:67, pl. 9, fig. 11.

Pseudomedaes agassizii.—Williams 1978:551, fig. 3.

Recognition characters.—Carapace broad, sub-oval, flattened, finely granulate posteriorly but anteriorly ornamented with bead granules in transverse lines or clusters, scattered hairs along anterior margin of lines. Front little advanced, divided at middle by V-shaped notch; margin transversely grooved, appearing doubled, upper edge less pronounced than lower but hiding lower edge if viewed dorsally; both edges of front and orbital margin granulate. Of 5 anterolateral teeth only last 2 or 3 well developed, sharp, turned forward, anterior margins granulate; second tooth, and sometimes third, triangular, obtuse or rounded, first (outer orbital angle) represented by elevated mass of granules.

Chelipeds unequal; carpus strong with sharp internal spine, sometimes doubled, and with many irregular, granulate rugae above; each hand with

upper surface granulate and tuberculate, tending to arrangement in row on crest of palm; larger hand with strong blunt-tipped fingers; smaller with more slender, acute, and more conspicuously grooved fingers showing tendency to be spoon shaped at tips; fingers dark, color continued to oblique line on palm. Walking legs each ragged, stout; hairs along upper and lower crests of articles and spiny, especially on upper margin; dense pile on propodi and dactyls, prominent smooth outer condyles at articulation between them.

Measurements in mm.—Carapace: male, length 11.8, width 19.2; ovigerous female, length 19.5, width 31.

Variation.—Small specimens from near Beaufort, N. C., have the last anterolateral teeth well developed, but a series of specimens from Pensacola, Fla., in the USNM show that these spines may be reduced to two in larger individuals. There is considerable variation in depth of sculpturing dorsally on the anterior carapace and chelipeds.

Habitat.—Primarily from rock and other hard substrates with fouling growth of sponges, bryozoans, etc., but also on sand; 7.3 to 82 m (rarely to 221 m, Wenner and Read 1982).

Type-locality.—Florida reefs, 21.9 to 32.9 m.

Known range.—Cape Hatteras, N. C., to southern Texas. The species is not known to occur in the Virgin Islands as previously reported (Williams 1965). That record was based on specimens of *Cataleptodius* (= *Leptodius*) *floridanus* (Gibbes) in the USNM collection mistakenly identified as *P. agassizii* (see Williams 1978).

Remarks.—Ovigerous females are known from February to November in various parts of the range. From an ovigerous female collected near Cape Lookout, N. C., Costlow and Bookhout (1968) reared larval stages in the laboratory at 25°C in 35‰ salinity on a 14-h day. They described four zoeal stages and a megalopa typical of xanthid crabs.

Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but were dead after 17-h exposure (F. J. and W. B. Vernberg 1970).

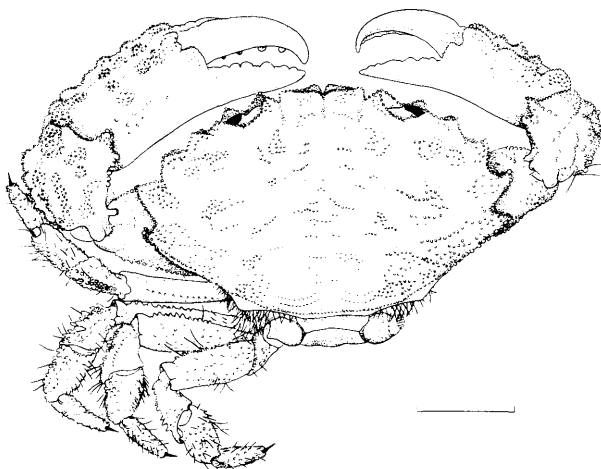


Fig. 314. *Pseudomedaes agassizii* (A. Milne Edwards). Male in dorsal view, walking legs of right side not shown, 5 mm indicated (USNM 18008).

***Pseudomedaes distinctus* (Rathbun)**

Figs. 315, 331e

Micropanope sculptipes.—A. Milne Edwards 1880:325, pl. 54, fig. 2–2c.—1880a:14.

Lophopanopeus distinctus Rathbun 1898b:272.—1930a:331, pl. 155, figs. 1–2.—Cerame Vivas and Gray 1966:263 (in faunal list).

Micropanope distinctus.—Menzies 1948:24 (new combination).

Pseudomeda distinctus.—Williams 1978:547, figs. 1, 2, 4b,

Recognition characters.—Carapace broad, regions well marked, lobulate and granulate on highest parts, with tendency to form transverse series; sparsely hairy. Front little advanced, deflexed, double edged, upper edge more coarsely granulate than lower, true margin; median notch broad, each lateral lobe with concave margin and obtuse angle at outer end. Orbital margin granulate; inner angle and outer suborbital angles prominent. Five anterolateral teeth, outer orbital angle (first) inconspicuous; second tooth low and broad, granulate subhepatic eminence below it; following 3 teeth subequal, last 2 with pointed tips and equally produced laterally in adults but fifth tooth less produced in young.

Chelipeds subequal, narrow, pubescent and covered with sharp granules; merus spinulose along upper margin; carpus with stout inner doubled spine, outer surface irregularly furrowed; palm with longitudinal furrow subdorsally on outer and inner surfaces, and another shallower furrow along dorsal surface (absent in larger adults); fingers

elongate, little or no gape, shallow teeth on opposed edges. Walking legs spined along crests of articles; pubescence dense and ragged, especially on distal articles.

Measurements in mm.—Carapace: male, length 19.4, width 30; female, length 10.8, width 16.8.

Color.—“Large adult; body mottled gray and reddish gray or light brown, longitudinally elongate spot in anterior extension of mesogastric area darkest; fingers light brown. Small specimen; body more darkly blotched, legs banded with brownish speckled bands of same color as blotches on body” (Williams 1978).

Habitat.—Has been found on hard substrate; 47.5 to 185 m.

Type-locality.—Gulf of Mexico, NW Dry Tortugas, 25°33'N, 84°21'W, 184.7 m.

Known range.—Off Cape Hatteras, N. C., 34°57'N, 75°19'W, through Straits of Florida to NW of Dry Tortugas; Puerto Rico; Barbados.

Remarks.—*Pseudomeda distinctus* is a problem species, as indicated by its synonymy. Williams (1978) placed it in *Pseudomeda* with two similar species but remarked that the three may eventually be placed in separate genera.

Genus *Rhithropanopeus* Rathbun 1898

Rathbun 1930a:455.—Hemming 1958b:37.

Rhithropanopeus harrisii (Gould)

Figs. 316–317, 331f

Pilumnus harrisii Gould 1841:326.

Rhithropanopeus harrisii.—Hay and Shore 1918:441, pl. 35, fig. 5.—Rathbun 1930a:456, pl. 183, figs. 7–8.—Williams 1965:187, figs. 169, 183C.—Christiansen 1969:81, fig. 23.—Felder 1973:67, pl. 9, fig. 14.

Recognition characters.—Carapace subquadrate, approximately as long as wide, much less convex from side to side than from front to back, sparsely pubescent toward anterolateral angles; protogastric regions with 2 transverse lines of granules; similar line from posterior lateral tooth to opposite one across mesogastric region. Front almost straight, slightly notched, with its margin transversely grooved, appearing double when viewed from front. Postorbital angle and first anterolateral tooth completely coalesced; first and second developed anterolateral teeth of about same size and perhaps larger than last tooth.

Chelipeds unequal and dissimilar; carpus scarcely grooved above and with moderately developed in-

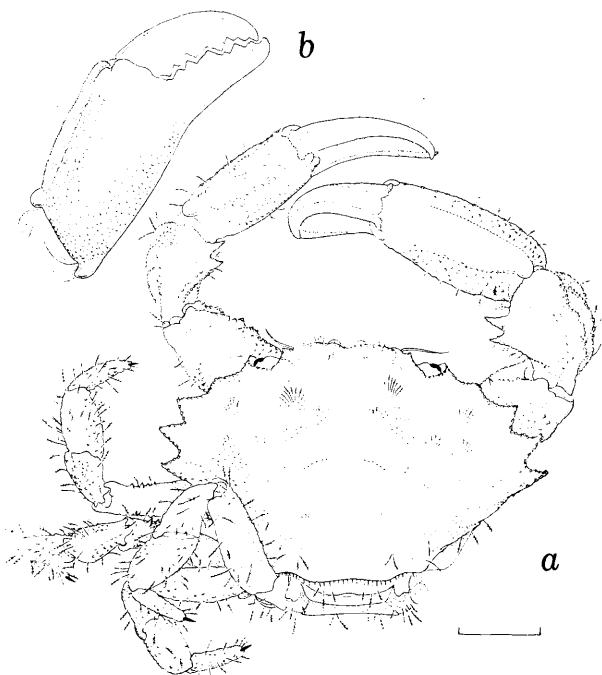


Fig. 315. *Pseudomeda distinctus* (Rathbun). a, Male in dorsal view, walking legs of right side not shown; b, major chela, external view; 5 mm indicated (from Williams 1978).

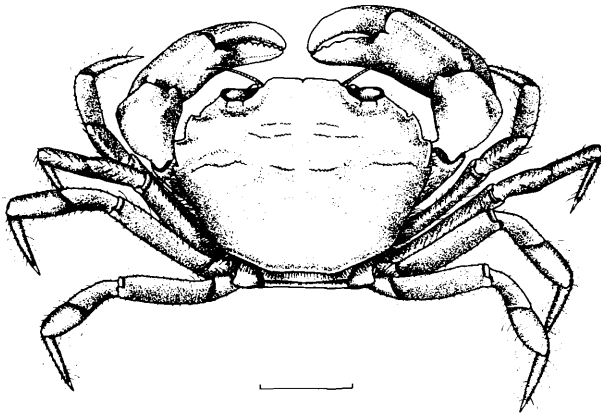


Fig. 316. *Rhithropanopeus harrisi* (Gould). Male in dorsal view, from Copenhagen, Denmark, 5 mm indicated (from Christiansen 1969).

ternal tooth; chelae indistinctly costate above. Major chela with short fixed finger and strongly curved dactyl. Minor chela with proportionately longer fixed finger and long straight dactyl. Walking legs long, slender, compressed, and somewhat hairy.

Measurements in mm.—Carapace: male, length 15.6, width 21.3; female, length 12.4, width 16.

Variation.—The chelipeds are nearly smooth in old individuals, but in juveniles the carpus is rough with lines and bunches of granules, its distal groove deep, the upper margin of palm with 2 granulate ridges, and the upper edge of the fingers granulate.

Color.—Brownish above, paler below; fingers light.

Habitat.—Ryan (1956) found this species distributed primarily in upper Chesapeake Bay and tributaries of the lower Bay in depths of about 0 to 9 m in a salinity range of fresh to 18.6‰, always associated with some kind of shelter—oyster bars, living and decaying vegetation, old cans, and other debris. Similar habitat is known for upper Delaware Bay (McDermott and Flower 1952) and the tributaries of the Neuse River estuary in North Carolina, as well as estuarine streams in southern Florida (Odum and Heald 1972). Surface to 36.6 m.

Type-locality.—Cambridge Marshes and Charles River, Mass.

Known range.—The original range of this species is presumed to be in fresh to estuarine waters from the southwestern Gulf of St. Lawrence, Canada, to Veracruz, Mexico. The species has been introduced on the west coast of the United States and in parts of Europe.

Remarks.—*Rhithropanopeus harrisi* thrives in a wide range of salinities, an attribute which helps to explain transport from its original range to two widely separated areas of the earth. One of these is the

west coast of the United States where it was reported in the San Francisco Bay area by Jones (1940) and Filice (1958), and at Coos Bay, Ore., by Ricketts and Calvin (1952). An older and wider introduction in Europe was reviewed by Buitendijk and Holthuis (1949) who considered the European form a separate subspecies (*R. h. tridentatus* (Maitland)). Originally confined to the old Dutch Zuider Zee, the species gradually diminished in abundance there with the closing of that inland sea in 1936 and in that year was first reported outside the Netherlands. In 1939 it was first reported in large numbers from southern Russia in the Dnestr River and Bug River estuaries, and according to fishermen there was first observed in 1936 but certainly not present before 1932. Gadzhiev (1936) and Turoboyski (1973) reviewed its occurrence in the Black Sea and Caspian Sea areas of eastern Europe, and Christiansen (1969) its presence in northwestern Europe (SW France, Normandy, Netherlands, Denmark, Germany, Poland) as well as in Bulgaria, Roumania and the U.S.S.R. Williams (1965) listed specimens from northeastern Brazil, but reexamination shows that occurrence to be an error. The remarks that follow apply only to the Western Hemisphere.

Osmotic capabilities of the adults consist of hyper-regulation of chloride and osmotic pressure in salinities up to 60%–70% that of sea water and a slight tendency to hypo-regulate in higher salinities (Smith 1967). There is a high rate of water turnover, but inward permeability decreases in the lower salinities.

Connolly (1925) stated that four zoeal stages and a megalopa comprise the larval and postlarval development of this species. These conclusions were based on study of plankton taken from the Miramichi River estuary, New Brunswick, Canada, in August. Chamberlain (1962) confirmed and supplemented Connolly's account with eggs taken from Chesapeake Bay and cultured in the laboratory. Duration of larval stages was twice as long when zoeae were fed copepod nauplii and algae as when fed nauplii alone. In an array of salinities and temperatures, development was found to proceed best at 6 to 10‰ salinity. Developmental time increased with decreasing temperature. Developmental times of larvae in nature were found to agree with results of laboratory culturing at similar salinities and temperatures. Mortality rates for zoeae in nature were found to be lower than expected. A relatively high rate was postulated for the megalopa or early crab stages. Presence of adult crabs in fresh water was deemed a result of migration after larval stages are complete. Hood (1962) also described a series of larval and postlarval stages from eggs hatched

and reared under laboratory conditions in Mississippi.

Christiansen and Costlow (1975) reared the species from hatching through the first or second crab stages under experimental conditions in 11 combinations of salinity and cyclic temperatures (5, 20, 35‰ S at 20°–25°, 25°–30°, 30°–35°C; 25‰ S at 20°–25°, 30°–35°C). Larvae survived to megalopa plus first crab in all combinations except 5‰ S at 30°–35°C. Best survival to megalopa (94%) and first crab (90%) occurred in 20‰ S at 20°–25°C. In all other combinations there was a reduction in survival to the first crab stage. Duration of larval stages was affected significantly by temperature whereas the effect of salinity on mean days from hatching to the first crab was not consistent in different temperatures cycles. Development to first crab was shortest in 20‰ salinity, 20°–25°C (22.6 and 21.6 days (\bar{x}) respectively). Megalopae reared in 35‰ salinity at all cycles of temperature, as well as larvae in 20 and 25‰ S, 30°–35°C, showed abnormality, with highest percentages occurring in 35‰ S, 30°–35°C. The authors concluded that larval development of *R. harrisii* is strongly influenced by environmental factors and not solely related to genetic differences.

Earlier Costlow, et al. (1966) had found that time of development in non-cycled temperatures was not significantly affected by salinities of 5–35‰. Survival to first crab occurred in 2.5 to 40‰ salinity; 60–90% of zoeae survived to megalopae in 15–25‰ salinity, but in lower and higher salinities there was reduction in percent survival to first crab. Duration of stages as well as mortality was affected by temperature. The authors suggested that the capacity to develop normally within this broad range of environments may have contributed to the wide distribution of this species.

Field studies fill out and corroborate this experimental evidence. Herman, et al. (1968) found zoeae

present from May to October in the Patuxent River, Md., with peak occurrence in June–July. Sandifer (1973d) found larvae common to abundant mostly at 0–10‰ salinity in the upper York and Pamunkey rivers tributary to lower Chesapeake Bay, and to lesser extent in the Bay proper. Zoeae first appeared in May, were most numerous in July–September, and nearly disappeared by October. Most occurred in a temperature range of 25°–29°C. All four zoeal stages were found in both surface and bottom samples, stage I comprising 55% of the total and being more numerous in bottom than surface samples. Numbers of larvae in surface samples decreased steadily with successive stages. Bousfield (1955) found the larvae in salinities <20‰ at the level of no net motion in the Miramichi estuary. Pinschmidt (1963) noted occurrence of larvae in the Newport River, N. C., roughly paralleling that in the York River, but most abundant at 31°C in a salinity range of 13–19‰. Herman (1968), Tagatz (1968), and Williams (1971) added supporting evidence for period of occurrence of larvae (as late as November in Florida), level of salinity, etc. Sandifer (1975) contended that stratification of larvae on bottom indicates retention of larvae in estuaries as the major means of recruitment for the species, and Wheeler and Epifanio (1978) showed that larval response to differences in hydrostatic pressure may be related to this type distribution. Cronin (1979) found that larvae of all stages maintain an average depth near the zone where net tidal flow is zero.

Ryan (1956) summarized life history data for *R. harrisii* in the Chesapeake Bay area. He collected ovigerous females from June to September. Though juveniles were found in all months of the year, they occurred most frequently in samples taken from July to October. Immature forms of undetermined sex ranged from 2.2 to 2.6 mm in width, immature males from 3.2 to 5.0 mm, and similar females from 3.3 to 5.7 mm in width. Ryan considered maturity to be reached the following summer at a carapace width of 4.5 mm for males and 4.4 to 5.5 mm in females.

Adults continue to grow and molt after maturity is reached. No concrete data on number of instars throughout life are available but it is estimated that there may be four instars between attainment of the 5 and 10 mm carapace widths.

Success of *R. harrisii* in the estuarine environment is emphasized by its role in the food web. Odum and Heald (1972) found more than 40 animals per m in an estuarine stream draining a *Juncus* marsh in south Florida. An omnivorous diet was dominated by mangrove leaf detritus. Crustaceans such as small amphipods and harpacticoid cope-

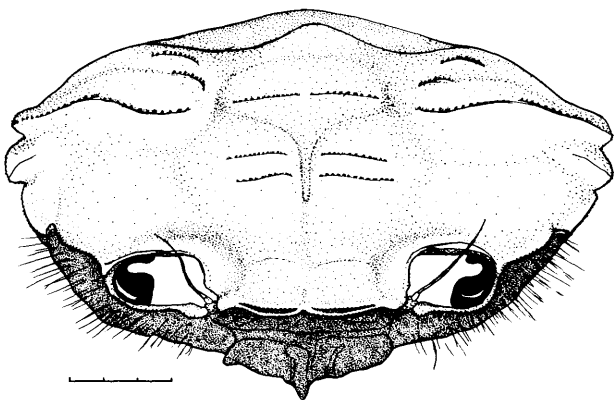


Fig. 317. *Rhithropanopeus harrisii* (Gould). Frontal aspect of body viewed from above, 3 mm indicated (from Williams 1965).

Pods were eaten more often by small crabs. Sikora, et al. (1972) found *R. harrisii* preyed on by two species of hake, *Urophycis regius* and *U. floridana*, in a Georgia estuary, and Heard (1975) reported it as forming a significant part of the diet of *Ictalurus catus*, the white catfish.

Boschma (1972) reviewed occurrence of specimens from the Gulf of Mexico bearing the parasite *Loxothylacus panopei*.

Rhithropanopeus harrisii has proved to be a hardy experimental animal from an environment of great interest to developmental and physiological ecologists. This circumstance is reflected by a flow of papers dealing with subjects beyond the scope of this sketch. A few of these are: Capen (1972), os-

moregulation; Christiansen, et al. (1977a, b), effects of hormone mimics on development; Costlow (1966), effect of eyestalk removal on development; Costlow and Sastry (1966), free amino acids in developmental stages; Forward (1976), shadow-sinking response of larvae; Gooch (1977), and Morgan, et al. (1978), allozyme genetics; Jones (1941) osmoregulation; Kalber and Costlow (1966; 1968), ontogeny of osmoregulation and its neurosecretory control; Rosenberg and Costlow (1976), effects of cadmium on development.

Genus *Micropanope* Stimpson 1871 (restr.)

Guinot 1967a:349.

Key to Species

1. Carapace with last anterolateral tooth obsolescent; legs spinulose *M. sculptipes*
Carapace with last anterolateral tooth small but easily discernible 2
2. Anterolateral teeth with granular margin; second tooth absent or fused with first (orbital) tooth; outer surface of hands rough with beadlike granules *M. nuttingi*
Anterolateral teeth with denticulate bases; second tooth present; outer surface of hands spiny *M. urinator*

Micropanope nuttingi (Rathbun)

Figs. 318, 331g

Xanthias nuttingi Rathbun 1898a:271, pl. 4, fig. 1.
Micropanope nuttingi.—Rathbun 1930a:450, fig. 74.—Williams 1965:194, figs. 177, 183J.—Coelho and Ramos 1972:192.—Felder 1973:66, pl. 9, fig. 22.

Recognition characters.—Carapace suboval, convex anteroposteriorly, nearly flat transversely; regions distinct, anterior half rough with squamous tubercles, especially in tract adjacent to margins. Front convex, bilobulate, with granulate margins separated by V-shaped sinus, outer angle of each lobe subrectangular. Anterolateral teeth with sharply granulate margins; second normal tooth united with small first tooth; 3 remaining teeth sharp pointed, posterior tooth smallest.

Chelipeds heavy, quite unequal; merus spinulose on upper edge; carpus covered with beadlike tubercles, deep distal groove, inner angular eminence tipped with spinule, second spinule below. Females with whole outer surface of both chelae tuberculate. Major chela of males with upper and approximately $\frac{2}{3}$ of outer surface beaded, tuberculate; lower $\frac{1}{3}$ and distal extremity smooth and shining; fingers broad, not gaping, brown with light

tips, color of fixed finger not continued on palm and ending in line with articulation of dactyl; dactyl with large basal tooth. Minor chela almost entirely tuberculate, growing less so toward distal and lower margins; upper margin with longitudinal

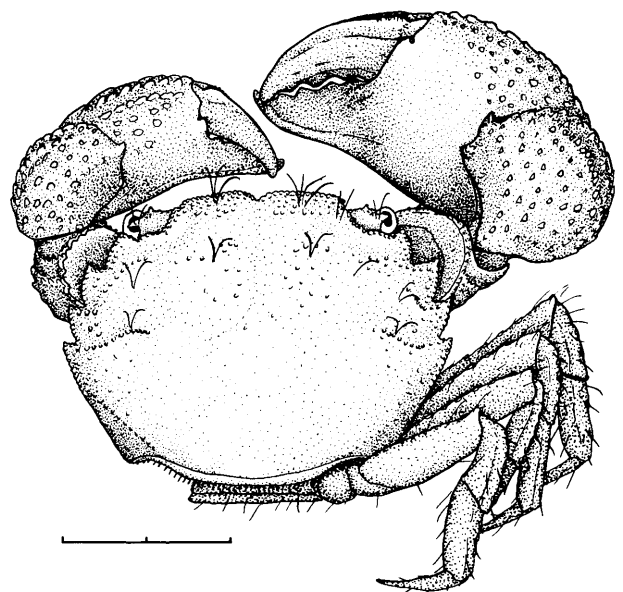


Fig. 318. *Micropanope nuttingi* (Rathbun). Animal in dorsal view, walking legs of left side not shown, 2 mm indicated (from Williams 1965).

groove, fingers deeply grooved. Upper margin of walking legs tuberculate or granulate.

Measurements in mm.—Carapace: male, length 4, width 6; female, length 3.8, width 6.3.

Color.—General overall color orange; carapace brown-orange with distinct red-orange granules anteriorly, anterolateral teeth white tipped, branchial region and posterolateral margins white, irregularly shaped white splotches behind each supraorbital margin parallel with third anterolateral tooth, 2 more at posterolateral margin of cardiac region, and 1 posteriorly on intestinal region; chelipeds bright orange becoming white ventrally, numerous bead granules bright red-orange, fingers salmon, distinct white spot at articulation of dactyl; walking legs irregularly orange-brown with distinct white patches posteriorly at articulation of merus and carpus, spinules on meri and spinules and granules on remaining articles red-orange (R. H. Gore, personal communication).

Habitat.—Has been taken from boulder-covered beach, from *Porites* clumps and *Halimeda* (USNM records); shallow water to 183 m.

Type-locality.—Bahama Banks.

Known range.—Cape Hatteras, N. C., through Gulf of Mexico and West Indies to Bahia, Brazil.

Remarks.—As Felder (1973) remarked, this species probably does not belong in the genus *Micropanope*, judging from the structure of the male first pleopods. Also, the third maxillipeds have the merus produced anterolaterally, the hands of some specimens (USNM 75811, male) have fingers bent downward at an angle with the palm, and the second abdominal segment of males has each posterolateral corner obliquely truncated to reveal a small portion of sternum. All of these features suggest goneplacid rather than xanthid affinities.

Ovigerous females are known from Puerto Rico in January and Florida in July.

***Micropanope sculptipes* Stimpson**

Fig. 319

Micropanope sculptipes Stimpson 1871a:140.—Rathbun 1930a:428, pl. 178, figs. 1–3.—Lunz 1937a:13.—Williams 1965:193, fig. 175.—Guinot 1967a:349, figs. 1, 4.—1971:1075 (listing).—Felder 1973:66, pl. 9, fig. 15.

Recognition characters.—Carapace naked, distinctly areolated; anterior and anterolateral regions somewhat roughened in front with small, sharp, toothlike tubercles partially disposed in lines. Anterolateral teeth sharp, denticulate, fifth (last) obsolescent, first and second almost entirely fused. Frontal lobes abruptly deflexed, with convex out-

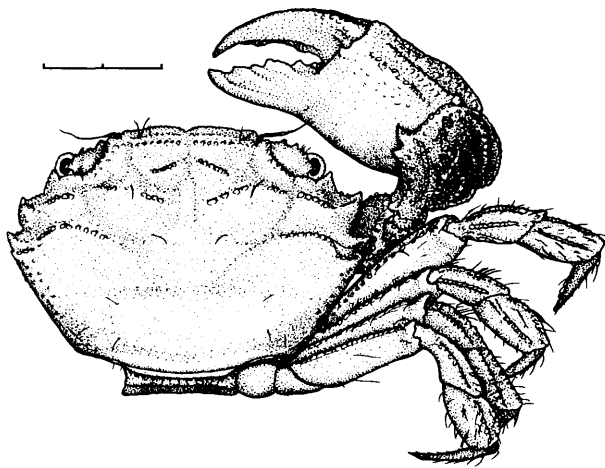


Fig. 319. *Micropanope sculptipes* Stimpson. Animal in dorsal view, legs of left side not shown, 2 mm indicated (from Williams 1965).

line; margin thin, minutely crenulate, with slight furrow above it. Small tubercle on subhepatic region below second anterolateral tooth.

Chelipeds granulate above; carpus with granules arranged more or less in raised reticulated rugae, inner margin denticulate and with sharp double spine; hands with double denticulate crest above and minute granules on outer surface showing tendency to arrangement in rows (becoming obsolete in distal lower half of major chela), upper part of inner surface granulate; fingers grooved, thin superior crest on dactyls. Walking legs with minute spines above forming rows on carpus, single row in young.

Measurements in mm.—Carapace: male, length 4.3, width 6.5; female ovigerous, length 4.1, width 6.0.

Habitat.—11 m (Wenner and Read 1982).

Type-localities.—Seven hauls in Florida Keys, 27.4 to 124 m.

Known range.—SE Cape Lookout, N. C., to Port Aransas, Tex; West Indies to Barbados.

Remarks.—Guinot (1967a; 1971) in preliminary studies restricted the genus *Micropanope* to *M. sculptipes* and *M. lobifrons* in the Western Atlantic.

Micropanope sculptipes has been taken in numerous samples from offshore reefs of North Carolina (Cerame-Vivas and Gray 1966). Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but were dead after 17-h exposure (F. J. and W. B. Vernberg 1970).

***Micropanope urinator* (A. Milne Edwards)**

Fig. 320

Pilumnus urinator A. Milne Edwards 1881:289, pl. 53, figs. 2–2b.

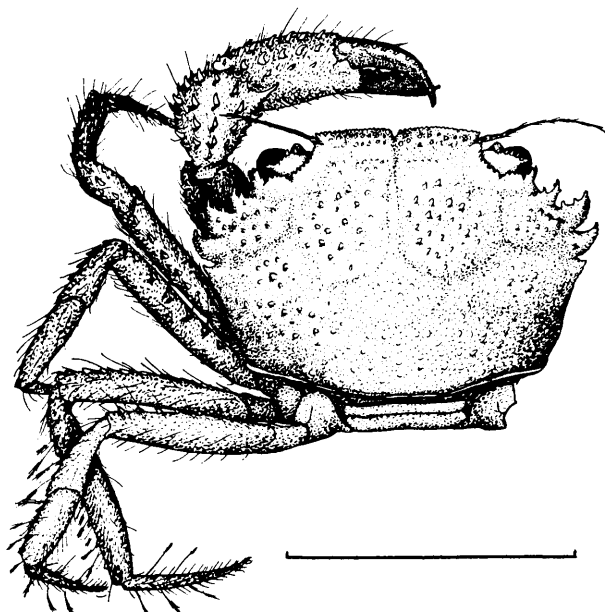


Fig. 320. *Micropanope urinator* (A. Milne Edwards). Male in dorsal view, legs of right side not shown, 5 mm indicated (from Williams, et al. 1968).

Micropanope urinator.—Rathbun 1930a:451, pl. 182, figs. 3, 4; pl. 183, figs. 1–3.—Williams, McCloskey, and Gray 1968:51, fig. 7.

Recognition characters.—Carapace broad, rough, regions plainly marked, granulate except in depressions, furred with thin, short pubescence. Frontal lobes slightly arcuate, edge finely denticulate, small median notch, outer angle subrectangular and edged with white granules. Orbital margin spinulose, diminishing to granules on mesiodorsal margin, interrupted laterally by broad sinus, somewhat larger on lower margin and continuing inward to large, triangular, granulated tooth. Five anterolateral spines including small outer orbital; second to fifth set in stouter denticulate bases; third and fourth largest, subequal, curved; first, second and fifth subequal, second curved, first and fifth straight.

Chelipeds spiny; merus with 2 curved spines dorsally; carpus heavily spined, longest spine at inner angle, second of equal size below it on minor cheliped; minor palm spinous over outer surface, major with spine changing to coarse granules distoventrally; fingers deeply grooved, especially on minor hand where accented by sharply granulate ridges. Walking legs rough on most surfaces; with long hairs below and on upper surface of distal 3 articles; dactyl long, slender, slightly curved, with acute brown horny tip.

Measurements in mm.—Carapace: male, length 7, width 10.

Color.—Preserved specimens have white-tipped spines, spinules and granules; body darker.

Habitat.—Hard substrates; 146 to 457 m.

Type-locality.—Near Santa Cruz [St. Croix], West Indies, 448 m.

Known range.—Off Capes Hatteras and Lookout, N. C.; Florida Keys to St. Croix, West Indies.

Genus *Tetraxanthus* Rathbun 1898

Rathbun 1930a:458.

Tetraxanthus rathbunae Chace

Fig. 321

Tetraxanthus bidentatus.—Rathbun 1898a:275.—1930a:458, pl. 184.

Tetraxanthus rathbunae Chace 1939a:52.—1940:37.—Coelho and Ramos 1972:192.

Tetraxanthus rathbuni W. E. Pequegnat 1970:173, 195.

Recognition characters.—Carapace subquadrate, smooth to naked eye but microscopically granulate; very convex anteroposteriorly, less so transversely; gastric and hepatic regions feebly indicated. Front advanced, nearly straight, median emargination very small. Orbit half as wide as front, dorsal fissures obsolescent; outer orbital angle small, triangular. Anterolateral border with 3 other lobes or teeth behind orbital; second very shallow and broad; third obtuse angled with short, nearly transverse anterior and rather convex, nearly lon-

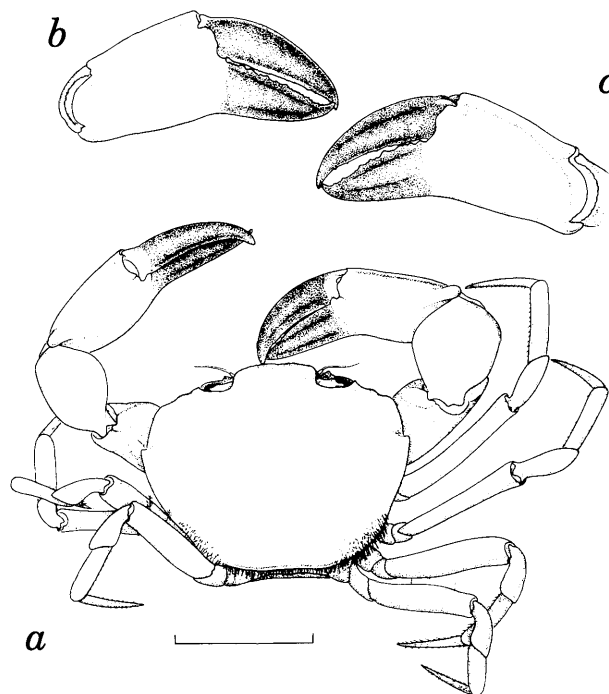


Fig. 321. *Tetraxanthus rathbunae* Chace. a, Male in dorsal view; b, right, c, left chela in external view; 1 cm indicated (USNM 92160).

gitudinal posterior margins; last lobe dentiform, short, elevated.

Chelipeds long, strong, smooth, unequal; especially in male; broad central lobe on upper margin of merus and mesial lobe at inner angle of carpus. Chelae elongate, increasing in width distally, margins convex; fingers long, deflexed, little or no gape; prehensile teeth uneven, largest one at base of major dactyl; dark color not covering finger tips or base of fixed finger. Walking legs slender, unarmed, pubescent distally.

Male abdomen with sixth segment free, broader than long, sides sinuous; telson broader than long, rounded and pubescent distally.

Measurements in mm.—Carapace: male, length 20, width 25; female, length 15.5, width 19.6.

Color.—Fingers red except for white tips (Henderson in Rathbun 1930).

Habitat.—Variety of bottoms; 27 to 430–476 m.

Type-locality.—Old Bahama Channel due N Punta Caldera, Camaguey Province, Cuba, 22°44'N, 78°41'W, 274–329 m.

Known range.—Off Cape Lookout, N. C., to Rio

de Janeiro, Brazil (Coelho and Ramos 1972), including Gulf of Mexico (W. E. Pequegnat 1970; USNM).

Remarks.—This crab seems to be primarily distributed on the upper continental slope, but it has been recorded a number of times from shallower depths. Ovigerous females are known from off Florida and Yucatan in January, Louisiana in June, and Veracruz in July.

Until now the species has been considered a xanthid, but has a number of features linking it to the Goneplacidae, suggesting that it is one of the transitional or evolutionary grades between these groups (Guinot 1969a, b; 1971) (smooth, granular ornamentation; long, slender walking legs; deflexed fingers; shape of male first pleopods; shape of male abdomen leaving a tiny section of sternite 8 visible between it and the fifth coxa).

Genus *Eurypanopeus* A. Milne Edwards 1881

Rathbun 1930a:403.

Key to Species

1. Fingers of both chelae with acute tips, not spooned *E. abbreviatus*
- Fingers of minor chela spoon-shaped at tip *E. depressus*

Eurypanopeus abbreviatus (Stimpson)

Figs. 322, 331i

Panopeus abbreviatus Stimpson 1860a:211.

Eurypanopeus abbreviatus.—Rathbun 1930a:404, text-fig. 63, pl. 172, figs. 1–2.—Williams 1965:94, fig. 178, 183K.—Coelho and Ramos 1973:191.—Felder 1973:68.

Recognition characters.—Carapace approximately $\frac{2}{3}$ broader than long, moderately convex in 2 directions, naked above, granulate and uneven on front and along anterolateral border, smooth and polished elsewhere; areolations slightly but distinctly indicated, a number of well-marked rugae among granules. Front deflexed, 4-lobed, median lobes prominent, separated by V-shaped notch. Anterolateral margin thin, divided into 4 lobes, first and second teeth coalesced, separated by slight concavity; third tooth obtuse; fourth with outer margin longitudinal or nearly so; fifth subtriangular, directed outward. Low granulate swelling below interval between first 2 teeth.

Chelipeds quite unequal in males; carpus with blunt internal tooth; fingers slender, pointed, widely gaping in major chela; fitting closely in minor, tips crossing in both; major dactyl with large basal tooth, color of fingers not extending on palm.

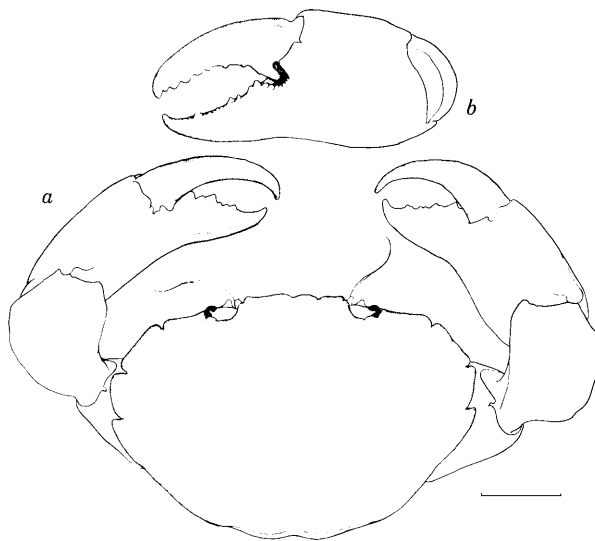


Fig. 322. *Eurypanopeus abbreviatus* (Stimpson). *a*, Male in dorsal view, walking legs not shown, front with anomalous notch to right of midline; *b*, right chela in external view; 5 mm indicated (from Williams 1965).

Measurements in mm.—Carapace: male, length 15.8, width 25; female, length 12.8, width 20.

Color.—Yellowish or brownish above, front margin of carapace and chelipeds roseate or tinged with bluish purple; fingers black with paler tips. Brazil-

ian specimens with a number of large dark spots on upper half chelipeds.

Habitat.—Specimens have been found near shore on oyster beds, under rocks, and among sponges and bryozoan growth; shore and shallow water to unknown depth.

Type-locality.—Barbados, British West Indies.

Known range.—South Carolina, through West Indies and Gulf of Mexico to Santa Catarina, Brazil.

Remarks.—Ovigerous females are known from April to November in the West Indies, and August to November in southern Brazil (Rathbun 1930a, in part). Ogawa and Rocha (1976) calculated that females of carapace length 6.0–10.5 mm bear 2,560 eggs (\bar{x}).

Eurypanopeus depressus (Smith)

(Flat mud crab)

Figs. 323, 331j

Panopeus depressus Smith 1869a:283.

Eurypanopeus depressus.—Hay and Shore 1918:437, pl. 34, fig. 4.—Rathbun 1930a:410, text-fig. 65, pl. 173, figs. 3–4.—Williams 1965:195, figs. 179, 183L.—Felder 1973:67, pl. 9, fig. 17.

Recognition characters.—Carapace transversely oval, approximately $\frac{3}{4}$ as long as wide, flattened posteriorly, slightly convex in anterior half; areolations well defined, finely granulate, with several pairs of transverse rows of granulations. Antero-lateral teeth 4, outer margins curved granulate; first 2 teeth coalesced to form broad lobe with slightly sinuate margin; third tooth blunt or spine tipped; fourth and fifth spine tipped, pointing obliquely upward and forward. Front nearly straight, median notch small or absent.

Chelipeds dissimilar and quite unequal. Smaller one more rugose than larger and with margin of fingers nearly straight and completely closing for considerable distance distally, opposed margins of tips thin edged and hollowed out—"spoon shaped." Larger cheliped with nearly smooth articles, hand heavy and inflated; dactyl strongly curved, obscurely toothed at base and meeting fixed finger only at tip; internal tooth of carpus tipped with small spinule; in unworn condition both fingers show indication of spoonlike flattening.

Measurements in mm.—Carapace: male, length 17.5, width 25; female, length 12.5, width 18.7.

Variation.—Ryan (1956) described a persistent, central, oval, blood-red spot or structure on the inner surface of the ischium of the third maxillipeds

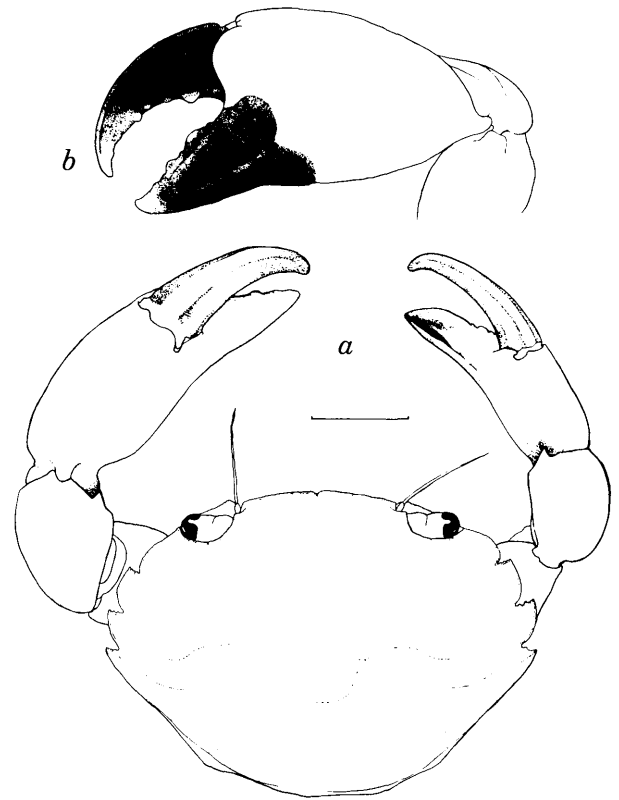


Fig. 323. *Eurypanopeus depressus* (Smith). a, Animal in dorsal view, walking legs not shown; b, major chela in external view; 5 mm indicated (from Williams 1965).

of both sexes. The spot is often $\frac{2}{3}$ the length of the article, with its surface raised slightly above the surface of the ischium. When pressure is applied, the hard spot cracks and is easily dissected out. A similar spot has been noted on *P. herbstii*.

The normal male abdomen is narrow, with the third, fourth, and fifth segments fused. A few (parasitized?) variant males have wide abdomens with seven segments, resembling females.

Color.—Mottled grayish olive or dark olive brown, especially on upper surfaces of chelipeds and anterior parts of carapace; fingers dark brown with dark color of fixed finger extended on palm; body and legs light colored underneath.

Habitat.—In Chesapeake Bay, Ryan (1956) found this species in greater abundance on oyster bars than any other species of mud crab, and evidence was presented showing a positive relationship between presence of oyster shells and this species. Others have noted a similar habitat preference (Lunz 1937a; Rouse 1970; Tabb and Manning 1961; Grizzle 1974). In the Bay, the depth range was 1.8 to 27 m (Cowles 1930, in part), and the salinity range 4.5 to 20.4‰. Elsewhere the species occurs from shore to 48 m.

Type-locality.—New Haven, Conn.

Known range.—Massachusetts Bay through Florida to southern Texas; Dutch West Indies; Uruguay; Bermuda (USNM).

Remarks.—Ryan (1956) gave much detail on the life history of this species in Chesapeake Bay. Oviparous females were collected there from June to September, but otherwise are known from April to November in Virginia, and year round in Florida, with isolated records elsewhere (Rathbun 1930a; Lunz 1937a; Ryan 1956; USNM). Zoeal stages were studied by Hyman (1925) from plankton tows made in the Beaufort, N. C., area, but Costlow and Bookhout (1961b) worked out the entire larval and postlarval history in the laboratory, illustrating four zoeal stages and a megalopa. Sandifer (1973d) found these larvae only three times during an extensive plankton survey in southern Chesapeake Bay (June and July), but reviewed larval findings of others: May to October in Newport River, N. C., mainly in salinities $>26\text{‰}$ (Pinschmitt 1963); in low concentrations outside Beaufort Inlet from May to October (Dudley and Judy 1971); May to October with peak in June-July in the Patuxent River, Md. (Herman, et al. 1968); and April to October with maximum in August in St. Johns River, Fla. (Tagatz 1968).

Ryan (1956) found that immature males from Chesapeake Bay range in carapace width from 3.2 to 6 mm, and females from 3.6 to 6.4 mm. He considered maturity to be attained at widths of 5.1 to 6 mm in males and 5.5 to 6.4 mm in females. Oviparous females observed ranged from 6 to 21 mm in width. The range of sizes suggested that growth and molting continue after maturity is reached. Maturity may be reached in the first summer after eggs have hatched.

Walton and Williams (1971) studied populations of *E. depressus* on artificial reefs in three small experimental estuarine ponds in North Carolina, finding the crab to be the most abundant xanthid following heavy seeding with estuarine plankton a year before. The crabs matured in the ponds, males reaching a mean carapace width of 20 mm, females 16 mm. When sampling began in late June, up to 50% of females were gravid in one pond. This percentage varied in samples from each pond during summer, once being as high as 100% in an estimated population of 276. There was general reduction of gravid females after the end of August.

Grant and McDonald (1979) showed that *E. depressus* loses tactile responses when it is experimentally desiccated to 30% loss of body water. Desiccation tolerance increased exponentially with size. Still, crabs are more abundant on exposed oyster reefs in high summer temperatures than in the cold of winter, and it is thought that moisture-seeking

behavior in interstices of the reefs as well as predator avoidance combine to protect intertidally exposed crabs from drying.

McDermott (1960) found that *E. depressus* is a predator on oyster spat in southern New Jersey but not so serious a pest as *P. herbstii*.

A population of *E. depressus* in the York River, Va., parasitized by a sacculinid, *Loxothylacus panopaei*, was first reported in 1966 by Van Engel, et al. The parasite, known from the Caribbean, Gulf of Mexico, southern California and British Colombia, and not found at that time in other areas of Chesapeake Bay or in other xanthids, was considered to be a recent introduction brought with live oysters from the Gulf of Mexico.

Genus *Neopanope* H. Milne Edwards 1800

Rathbun 1930a:366.

Neopanope sayi (Smith)

Figs. 324, 331k

Panopeus sayi Smith 1869a:284.

Neopanope texana sayi.—Hay and Shore 1918:438, pl. 34, fig. 8.—Rathbun 1930a:369, text-fig. 58, pl. 168, figs. 3–4.—Williams 1965:190, figs. 172, 183F.

Neopanope texana nigrodigita Rathbun 1934:3–4, illus.

Neopanope sayi.—Abele 1972:268, figs. 2B, C, D; 3D.

Recognition characters.—Carapace subhexagonal, length contained in width about 1.3 times, greatest width at fifth pair of anterolateral teeth, quite convex; carapace minutely granulate, and lightly pubescent especially near anterior and lateral regions. Five anterolateral teeth somewhat upturned, first 2 coalesced and separated by shallow sinus, third and fourth larger and directed forward, fifth smaller and directed somewhat outward; each of last 2 teeth with oblique ridge extending inward and backward. Front with small median notch, each half only slightly sinuate, with whole forming a much flattened curve extending from eye to eye.

Chelipeds unequal; merus armed with stout rectangular tooth on upper crest, carpus usually smooth, shallow groove parallel to distal margin and usually a strong spine on inner distal margin; dactyl of major chela about as long as palm, fingers armed with low, blunt teeth decreasing distally. Walking legs long and slender, dactyl of fifth leg as long as or shorter than propodus, its dorsal and ventral borders covered with thick pubescence.

Resembles *Eurypanopeus depressus*.

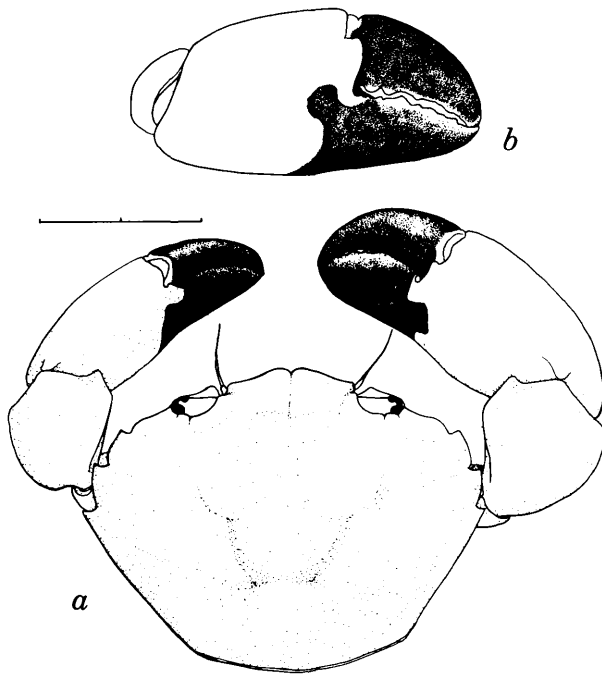


Fig. 324. *Neopanope sayi* (Smith). *a*, Male in dorsal view, walking legs not shown; *b*, major chela in external view; 1 cm indicated (from Williams 1965).

Measurements in mm.—Carapace: male, length 21.1, width 29.7; female, length 14.4, width 19.8.

Color.—Carapace a dark, slaty bluish green, brown or buff, with dark reddish-brown speckles on yellowish background, or bluish purple on gray background, especially on anterior portion of carapace and upper portion of chelae; outer face of chelae yellowish gray; fingers dark or black, color extending extensively on palm, tips light.

Habitat.—Most studies indicate greatest abundance on mud or oyster shell bottoms, though the species occurs in other situations such as sea grass beds as well (Marsh 1973), and, in the Chesapeake area, in a salinity range of 12.6 to 31.62‰. Low-tide mark to 46 m.

Type-localities.—New Haven, Conn., and Cape Cod Mass.

Known range.—Miscou Harbor, mouth of Chaleur Bay, New Brunswick, Prince Edward Island, and Cape Breton Island, Nova Scotia, Canada (Bousfield 1956, Bousfield and Laubitz 1972), to Florida Keys (Abele 1972). Introduced, Swansea, Wales (Naylor 1960).

Remarks.—Abele (1972) accorded *N. sayi* full specific rank, defining its range along the east coast of the United States and restricting that of *N. texana* (Stimpson) to the northern rim of the Gulf of Mexico.

Swartz (1978) described the reproductive systems of male and female *N. sayi*, and the sperma-

thecae and sperm plugs in some detail. From observations at Gloucester Point, Va., he found that pairs copulate in the hard condition, that there is evidence that copulation may occur more than once, and that males probably copulate as often as possible during the mating season. Females usually mate once and sometimes more often between successive spawnings, but they do not copulate after spawning the last egg mass in a given molt cycle nor during molt cycles in which they fail to spawn. There is no trans-molt retention of sperm, but there is sometimes trans-spawning retention which is not always sufficient to fertilize the next egg mass. Mating behavior is apparently integrated with molting and spawning cycles, and different from species that mate in the soft condition.

Swartz found that most reproduction occurs in the 24°–30°C range (April in South Carolina [Lunz 1937a] to October in Chesapeake Bay for ovigerous females). Mature females spawned fertile eggs 10–16 days after molting. Embryonic development lasts 9–10 days in the normal spawning season; mean interval between hatching one batch of eggs and spawning of the next batch is 2.9 days; mean duration from hatching of the last egg mass deposited in a molting cycle to time of molt is 5.3 days. Thus, mean duration of a molt interval, including one spawning, is 27.8 days; an additional spawning lengthens a molt cycle by 12.9 days. If a mature female did not spawn between successive molts, the intermolt interval was 14.9 days. If a female spawns more than once between molts, her seasonal fecundity is reduced even though she spends a greater part of the spawning season bearing eggs. Females have constant relative size increments at post-pubertal molts. The reduction in fecundity necessitated by molting is more than compensated for by a logarithmic increase in fecundity accompanying growth. This may explain why the observed mean number of intermolt spawnings is close to unity. An 8 mm female will molt four to five times during the first spawning season, increasing to a carapace width of 17.2 mm by September. She will have 1400 eggs in the first mature instar (8 mm), 2400 in the second (9.7 mm), 4000 in the third (11.7 mm), 6900 in the fourth (14.2 mm), and, if there is a fifth at the end of the season, 11,600 eggs (17.2 mm). The total for that season is 15–30,000 eggs (four or five instars). Assuming a maximum life span to end in the middle of the third summer, and production of two to three egg masses in the second spawning season, lifetime fecundity of a female would be ~100,000 eggs. Most females do not grow larger than 15 mm in width and produce fewer than 30,000 eggs before death.

Chamberlain (1957, 1961) discussed develop-

ment time for larval stages, finding four zoeal stages (sometimes preceded by a brief prezoal stage) and a megalopa. Development time varied with temperature (14 days at 30°C, 37 at 21°C) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, did moderately well on *Artemia* and algae, but did not transform at all when fed pure algae. Sulkin and Norman (1976) found rotifers to be an unbalanced diet for developing larvae. Ryan (1956) summarized the work of Hyman (1925) on zoeal and megalopal stages.

From plankton tows along a transect of York River, Va., and lower Chesapeake Bay to its mouth, Sandifer (1973d) found zoeae at all stations in the euhaline to mesohaline range (10.87–32.34‰ salinity), but mostly in the lower Bay near the mouth of the river with maximum concentrations in June and mainly in 20–25‰ salinities. Larvae were taken from June to October, mainly in a temperature range of 19.3° to 29.6°C in bottom samples. Elsewhere, occurrence in plankton conforms to length of warm season, June to September in Narragansett Bay (Hillman 1964), June to October in Delaware Bay (Deevey 1960), and March to November in St. Johns River, Fla. (Tagatz 1968). In the ocean, Dudley and Judy (1971) found zoeae from May to early October at 1–8 m depths as far as 10–13 km off Beaufort Inlet, N. C. Megalopae were found in June, August, and September. Sage and Herman (1972) found zoeae of *N. texana* (= *N. sayi*) in zooplankton of the Sandy Hook Bay area in midsummer with peak numbers in early July. Sandifer (1975) felt that *N. sayi* adults may occur outside estuaries, for 69% of the larvae of this species were in bottom samples and the last two larval stages were much more abundant in bottom than in surface samples; transport of zoeae and migration of megalopae in bottom water strata could tend to replenish the estuarine populations.

Ryan (1956) concluded that mature females range in carapace width from 6.1 to 18.7 mm. Swartz (1972) concluded that the largest young of the year reached a carapace width of 8–10 mm, occasionally 12 mm, by early November. By the following midsummer almost all of that year class were mature, but at the same time a scarcity of crabs 15–25 mm wide suggested that the previous year class

(now two years old) had nearly disappeared. Most mature females observed reached 18–18.9 mm carapace width, males 20–20.9 mm. Swartz (1976b) showed that females molt less often than males during vitellogenesis, and perhaps in the initial stage of egg brooding, hence never reach the size of mature males even though a few crabs may live into their third summer.

McDermott and Flower (1953) considered *N. sayi* to be the most abundant xanthid in Delaware Bay, but within the area studied it was more common on oyster beds than in littoral or low-salinity areas. They found (also McDermott 1960) that *N. sayi* readily preys on *Balanus improvisus*. Farther north, Landers (1954) reported the crab abundant in Narragansett Bay where it is a serious predator on young *Mercenaria mercenaria*. Ryan (1956) found the species widely distributed in Chesapeake Bay, but apparently not so abundant as in the more northern bays. Here it ranged in depth from 3.7 to 46 m (Rathbun 1930a, in part), depths similar to those reported by Sumner, et al. (1913a, b) for the Woods Hole region.

Parasites and microbial diseases of *N. texana* (broad sense) were reviewed by Sinderman and Rosenfield (1967). Two species of hake were observed to prey on this crab in Georgia (Sikora, et al. 1972).

Swartz (1972, 1976a, b) studied social behavior of *N. sayi*, showing it to be "more complicated than that usually reported for totally aquatic brachyurans. Ritualized visual displays, especially the Lateral Merus, are important in agonistic encounters. Fights are rare. During sexual interactions stereotyped periodic movements immediately after the male grabs the female may be responsible for the species, sexual, and mate discrimination. Behavior prior to the Grab resembles advanced agonistic encounters, which may explain why males almost always copulate with females smaller than themselves." Many details of reproductive biology too complex for summary here are given in these references.

Genus *Panopeus* H. Milne Edwards 1834

Rathbun 1930a:333.

Key to Species

1. Dark color of fixed finger continued more or less on outer surface of palm, especially in males; no distal groove on carpus of chelipeds . . . *P. herbstii*
 Dark color of fixed finger not continued on outer surface of palm; carpus of chelipeds with shallow groove parallel to distal margin
 of chelipeds with shallow groove parallel to distal margin *P. occidentalis*

***Panopeus herbstii* H. Milne Edwards**

(Common mud crab)

Figs. 325, 331I

Panopeus herbstii H. Milne Edwards 1834:403.—Hay and Shore 1918:437, pl. 34, fig. 9.—Rathbun 1930a:335, text-figs. 52–53, pl. 156, figs. 1–3; pl. 157, figs. 1–3.—Williams 1965:196, figs. 180, 183M.—Chace and Hobbs 1969:154, figs. 46c, 47.—Coelho and Ramos 1973:190.—Felder 1973:69, pl. 9, fig. 21.—Holthuis 1979:159.

Recognition characters.—Carapace approximately $\frac{2}{3}$ as long as wide, regions well marked, surface sparingly granulate. Anterolateral margins with 5 teeth; first 2 coalescent; third and fourth larger, prominent, and with arcuate outer margins and acute tips; fifth smaller, acute at tip and with outer margin nearly straight. Transverse ridge extending inward from fifth tooth, and shallow groove from fourth tooth. Front wide, not produced, with narrow median fissure; anterior margin of each half sinuous. Male abdomen with side of penultimate segment nearly parallel; terminal segment broader than long, rounded at tip.

Chelipeds heavy, finely granulate; carpus without groove on superior surface and with blunt internal spine; hands unequal and dissimilar, large one with dactyl curved and strongly toothed at base,

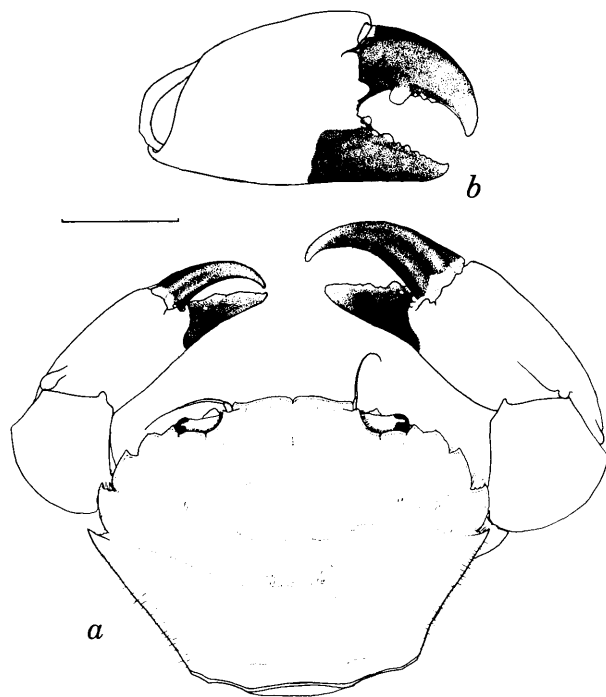


Fig. 325. *Panopeus herbstii* H. Milne Edwards. a, Animal in dorsal view, walking legs not shown; b, right chela in frontal view; 5 mm indicated (from Williams 1965).

dactyl of smaller more nearly straight; fingers dark, with color extending somewhat on palm.

Measurements in mm.—Carapace: male, length 43, width 62; female, length 36, width 53.

Variation.—Rathbun (1930a) separated this species into a number of forms on the basis of structural characteristics but considered these the result of response to environment rather than genetic differences. The forms are not always easily separated and are now being restudied by a number of workers.

Ryan (1956) described a persistent, central, oval, red spot or structure on the inner surface of the ischium of the third maxillipeds of both sexes. Mrs. Peggy Keney (personal communication) in a sample of 596 specimens from the Beaufort, N. C., area found this spot on 100% of males and 55% of females.

Habitat.—Depth distribution for the species ranges from the intertidal zone to 22 m. Ryan (1956) found the species to be rare in Chesapeake Bay in a salinity range of 13.95 to 19.04%. . . . Depth distribution was 3.7 to 11 m and at each collection spot the bottom was composed of soft mud with few oyster shells. In North and South Carolina, this is one of the most common estuarine crabs, found wherever the bottom is muddy or covered with shells or stones. In some localities along edges of the higher marshes, it is found in burrows, frequently associated with *Sesarma reticulatum* and *Uca minax*.

In the West Indies, collections have been made from mangrove roots, sponges, and coral reefs.

Type-locality.—Oyster beds of eastern United States.

Known range.—Boston, Mass., to State of Santa Catarina, Brazil; Bermuda.

Edmondson (1962) gave the first Hawaiian record for *P. herbstii* as December 1947 when a specimen was taken from fouling on a boat in Pearl Harbor. In 1953 numerous specimens were taken in Maunaloa Bay, Oahu, where the species appears to be well established. He thought its introduction doubtless came about through transport on the bottom of a ship in very recent times, and further stated that the species has long been seen on "west American shores."

Remarks.—The genus *Panopeus* has a fossil record dating from the Paleocene (Glaessner 1969), and *P. herbstii* was considered by Rathbun (1935) to date from the Miocene in North America.

Ovigerous females are known virtually the year round in Florida, through late spring and summer in the Carolinas, from February to September in various parts of the West Indies, and August to October in southern Brazil. Ryan (1956) gave cara-

pace widths of mature males as 8.3 to 37.3 mm and mature females as 21.6 to 27.8 mm in Chesapeake Bay.

Costlow and Bookhout (1961a) reviewed early descriptions of larvae and described and illustrated four zoeal and one megalopa stage reared in the laboratory. Costlow, et al. (1962) reared the larval stages under 12 different conditions of salinity and temperature. Eggs were maintained in salinities of 12.5, 20.1, 26.5, and 31.1‰, and all larvae hatched as first stage zoeae. Succeeding stages showed higher percentages of survival under different conditions, with shortest development time in the highest salinity. The lowest salinity tested did not permit development to be completed. In addition, low temperature affected duration of all larval stages and mortality of some stages. Larval development was completed to first crab in 48–52 days at 20°C., and 18–28 days at 30°C. From data, the effects of salinity and temperature on mortality of larval stages were projected by statistical methods over a wide range of combinations. They hypothesized that effect of temperature on successive larval stages limits the productive spawning period. Low temperatures favor the spring brood of larvae [in these latitudes], prolonging larval development until warmer water produces favorable conditions for the megalopal stage. Larvae hatched in fall are not so favored, therefore mortality in late zoeal and megalopal stages would be high.

Sandifer (1973d) found larvae of *P. herbstii* rather commonly in plankton samples from the Pamunkey River to off the mouth of Chesapeake Bay over a salinity range of 1.76 to 32.4‰, but less abundantly there than the larvae of any xanthid except *Eurypanopeus depressus*. Greatest numbers were taken in the lower York River where salinity was 15–25‰. Occurring from June to September, larvae were most abundant in July–August when temperature was 25°–28°C. All four zoeal stages were taken in surface and bottom samples but stages III and IV were rare. Stage I comprised 70% of the total and there was little difference between surface and bottom concentration of stages I and II.

Further south the spawning season is longer. Pinschmidt (1963) found larvae from May to September in the Newport River, N. C., with peak numbers from May to August at temperatures of 28°–31°C in salinities of 12–36‰. Dudley and Judy (1971) found *P. herbstii* larvae: 1.6 km off Beaufort, N. C., from May to November at 1–8 m depths and *Panopeus* sp. megalopae at 1–8 m in September and 8 m in October; 6.5 km offshore at depths of 1–8 m from May to August and at 8 m; July in 1–8 m, November at 1 m, and *Panopeus* sp. megalopae in October at 8 m. Sandifer (1973d) found zoeae near

Cape Lookout, N. C., in November. Tagatz (1968) observed *Panopeus* sp. larvae in St. Johns River, Fla., from April to November with greatest concentration in August.

In a study of the relationship of habitat to oxygen consumption by estuarine crabs, Ayers (1938) found *P. herbstii* to be intermediate in a scale of partial adaptation of the respiratory mechanisms to life in air. Teal (1959) found this species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, it was found in burrows, usually near the top, in air or water. Among various marsh crabs studied (see remarks, *Uca minax*) only *P. herbstii* was active at temperatures below 12°C. Respiration in this crab was most affected by reduced oxygen pressure among species tested, showing a rate reduction of 90% at 4 mm Hg.

Menzel and Nichy (1958) found that *P. herbstii* and *Menippe mercenaria* are the only xanthids large enough to kill significant numbers of adult oysters. McDermott (1960), studying predatory activities of xanthid crabs on oyster beds in New Jersey, found that *P. herbstii* destroyed 1- and 2-year-old oysters at a rate of 0.15 oysters per crab per day. The crab also preyed actively on oyster spat as well as barnacles (*Balanus improvisus*). He concluded that *P. herbstii* is potentially the most destructive of the five species of mud crabs occurring on New Jersey oyster beds. The species is also common on oyster beds in Delaware Bay, where it commonly cracks and eats small oysters and the barnacle *Balanus eburneus* (see McDermott and Fowler 1953). The toadfish was considered a common predator. Other predators are the hakes *Urophycis regius* and *U. floridanus* in Georgia estuaries (Sikora, et al. 1972).

Panopeus occidentalis Saussure

Figs. 326, 331m

Panopeus occidentalis Saussure 1857:502.—Rathbun 1930a:348, text-fig. 55; pl. 161, figs. 1–3.—Williams 1965:198, figs. 181, 183N.—Coelho and Ramos 1972:190.

Recognition characters.—Similar to *Panopeus herbstii*, but differing in having more convex carapace, especially in gastric region; front narrow, advanced; second anterolateral tooth usually narrower and separated by deeper sinus from first tooth, third to fifth teeth thicker, more prominent and widely separated, third blunt, forming almost right angle at tip; abdomen of male wider, sides of penultimate segment not parallel; narrowed toward proximal end.

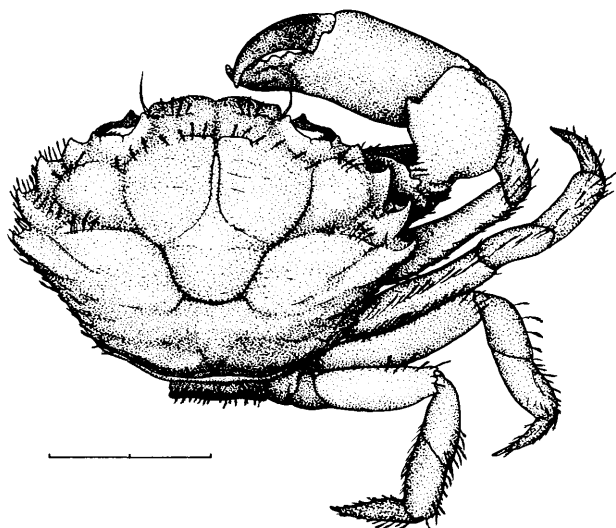


Fig. 326. *Panopeus occidentalis* Saussure. Animal in dorsal view, legs of left side not shown, 1 cm indicated (from Williams 1965).

Carpus of chelipeds with groove parallel to distal margin, sometimes rugose; dark color of fixed finger not continued on palm. Walking legs somewhat longer and more slender.

Measurements in mm.—Carapace: male, typical form, mean length 27.7, width 40.5; serrate form, mean length 19.9, width 27.5; ovigerous females, width 13.3 to 25.3 (de Oliveira 1940).

Variation.—There is considerable variation even in a single lot of specimens. The carapace may be smooth and shining, or with light, granulate, transverse lines; the second anterolateral tooth may be small, subacute, and similar to the first rather than broadly rounded and large; the female abdomen may have sides of the sixth segment parallel instead of converging slightly toward the proximal end. Variations in teeth of the anterolateral border were noted in 12% of females studied by de Oliveira (1940). In these the first, second, and third teeth of one side were depressed, giving the impression of but one sinuous tooth while those of the other side were normal.

This species, like *P. herbstii*, has been divided into two environmental forms (typical and serrate), and both occur in the Carolinian province (Rathbun 1930a).

Color.—Carapace dull yellow spotted with brown and red; legs yellow with brown maculations and

speckles on chelipeds; walking legs with brown or rose streaks. Color of Brazilian specimens (de Oliveira 1940): carapace dark yellow with red blotches or chocolate varying in tone; legs same color but spotted with reticulated points, points of fingers chocolate to almost black; body yellow ventrally, legs yellow to grayish; some rare specimens completely yellow.

Habitat.—This species has been found among rocks, mangrove roots, sponges, ascidians, and seaweed, and on pilings of piers along shore; shore to 18.2 m.

Type-locality.—Guadeloupe.

Known range.—North Carolina to State of Santa Catarina, Brazil; Bermuda.

Remarks.—In the vicinity of the Ilha Pinheiro, near Rio de Janeiro, Brazil, the species is primarily crepuscular or nocturnal, living chiefly in ditches, between and beneath stones, and among mangrove roots, often burrowing to a depth of 30 cm (de Oliveira 1940). That author found both sexes together except when the eggs were deposited; then females were not so often seen.

Molting individuals and copulating pairs were rarely found, the latter in November to December, on one occasion in water of 22‰ salinity at 22°C. Periods of egg deposition extended from January to May, and again from July to August (also September, Rathbun 1930a). Such females bore 3,000 to 70,000 eggs, depending on size. Females were observed to aerate and clean the eggs in water at low tide in the evening. Eggs in the laboratory hatched in about 15 days. Molting of females followed hatching of eggs. (Otherwise ovigerous females are known from January to July in the Caribbean area (USNM) and in winter in south-west Florida [Rouse 1970].)

In Brazil, young of the species were found throughout the year, as others have noted.

The species was believed to have few predators. Material from the gut consisted of varied plant and animal matter. In addition to the ecological discussion, de Oliveira gave observations on autotomy and its effect on movement and behavior.

Genus *Hexapanopeus* Rathbun 1898

Rathbun 1930a:383.

Key to Species

(After Felder 1973)

1. Carpus of cheliped roughened and irregular in contour but lacking distinct knoblike tubercles; less than 8 granulated lines on gastric, cardiac, and branchial regions of carapace *H. angustifrons*

Carpus of cheliped with about 10–15 irregular, coarsely granulate, knoblike tubercles; at least 8 distinct granulated lines on gastric, cardiac, and branchial regions of carapace *H. paulensis*

***Hexapanopeus angustifrons* (Benedict and Rathbun)**

(Narrow mud crab)

Figs. 327, 331n

Panopeus angustifrons Benedict and Rathbun 1891:373, pl. 22, fig. 3; pl. 24, fig. 18.

Hexapanopeus angustifrons.—Hay and Shore 1918:436, pl. 34, fig. 7.—Rathbun 1930a:384, pl. 169, figs. 1–2.—Williams 1965:188, figs. 170, 183D.—Felder 1973:70, pl. 9, fig. 24.

Recognition characters.—Carapace hexagonal, about $\frac{2}{3}$ to $\frac{3}{4}$ as long as wide, convex from front to back, regions fairly well marked, surface finely granulate. Anterolateral edge thin, upturned, and divided into 5 teeth, first 2 separated by well-defined sinus, third and fourth successively broader, fifth shorter, narrower, more distinctly directed outward; each of last 2 teeth with ridge extending obliquely inward and backward for distance twice length of teeth. Front narrow, produced, divided in half by prominent V-shaped notch; each half bilobate, with markedly sinuate anterior border forming broad inner and small, inconspicuous outer lobe.

Chelipeds strong, granulate, and finely rugose; merus with well-developed tooth on upper margin; carpus with moderately deep groove parallel

to distal margin, an obtuse tooth at inner angle, and with superior surface rough and more or less tuberculate. Hands unequal and dissimilar; palm usually with fairly strong ridge above and indication of one on outer surface, both ridges continued on fingers; fingers strong, slightly hooked at tips; dactyl of larger hand with strong tooth at base.

Measurements in mm.—Carapace: male, length 20, width 28; female, length 16.1, width 23. Ryan (1956) gave the range in carapace width of mature males as 9.7 to 28.9 mm and of mature females as 8.4 to 20.2 mm in Chesapeake Bay. Rathbun (1930a) considered specimens from Chesapeake Bay southward to average smaller than those from farther north.

Color.—Usually dark reddish brown or dark gray, sometimes uniform brownish yellow or light buff; females usually darker than males often more or less spotted; fingers black or dark brown at base, lighter at tips, color not continued on palm. Often a light yellow band along anterior border of carapace (Wass 1955, in part).

Habitat.—Results of faunal surveys show that this species occurs in salinities ranging from 9 to 53‰, usually 20's to low 30's, from nearshore regions of estuaries to the sublittoral region of the ocean (Cowles 1930; Rathbun 1930a; Lunz 1937a; Behre 1950; McDermott and Flower 1953; Wass 1955; Ryan 1956; Dragovich and Kelly 1964). It often occurs in shelly situations, but may be found on soft or sandy bottoms; near shore to 139 m.

Type-locality.—Long Island Sound.

Known range.—Vineyard Sound, Mass., to Port Aransas, Tex.; Bahamas; Jamaica.

Remarks.—Rouse (1970) found ovigerous females throughout the year in SW Florida, but scattered records indicate that the spawning season is limited to warmer months farther north. Chamberlain (1961) reported four zoeal stages and the megalopal stage in larval development of the species but did not describe them in detail. He found that larval development time varied with temperature (17 days at 30°C, 28 at 21°C) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, matured well on *Artemia* and algae, but did not transform at all when fed algae alone. Costlow and Bookhout (1966c) described and figured four zoeal stages and the megalopa from laboratory hatching and rearing in 30‰ salinity at 25°C on a diet of *Artemia salina* nauplii.

Zoeae of this species were the most common

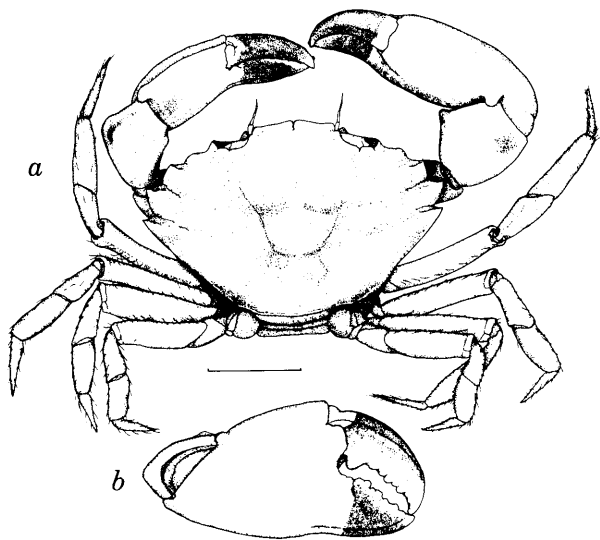


Fig. 327. *Hexapanopeus angustifrons* (Benedict and Rathbun). a, Animal in dorsal view; b, major chela in external view; 5 mm indicated (from Williams 1965).

xanthid larvae found in a plankton survey of lower Chesapeake Bay (Sandifer 1973d), mainly in salinities above 20‰ from June to October with peak abundance in August. Williams (1971) found the same pattern in a plankton survey of North Carolina inlets. Sandifer (1975) also found 58% of zoeae in bottom samples, later stages being much more abundant there than in surface samples, and felt that distribution of the species may thus be maintained by retention of larvae in estuarine circulation currents and megalopal migration.

Hexapanopeus angustifrons is preyed upon by two species of hake (*Urophycis regius* and *U. floridanus*) in Georgia estuaries (Sikora, et al. 1972).

Hexapanopeus paulensis Rathbun

Figs. 328, 331o

Hexapanopeus paulensis Rathbun 1930a:395, pl. 170, figs. 5–6.—Williams 1965:189, figs. 171, 183E.—Coelho and Ramos 1972:191.—Felder 1973:70, pl. 9, fig. 23.

Recognition characters.—Carapace hexagonal, approximately $\frac{2}{3}$ to $\frac{3}{4}$ as long as wide, convex, regions fairly well marked, surface with approximately 12 transverse granulated lines on gastric, cardiac, and branchial regions. First tooth of anterolateral border small; second larger, broad and shallow, with arcuate outer margin; third with nearly straight margin directed forward and inward; fourth and fifth acute and prominent; sometimes with small denticle between first, second, or third pairs of teeth. Front with edge thin, arcuate; small median, V-shaped notch; each half with small lobule at outer end. Inner suborbital angle large; raised line of granules on subhepatic region.

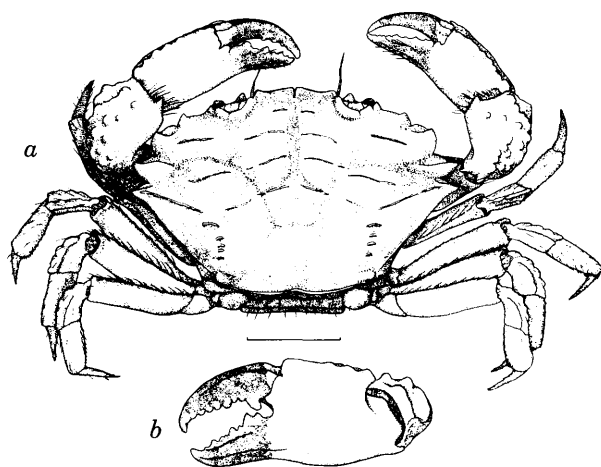


Fig. 328. *Hexapanopeus paulensis* Rathbun. a, Animal in dorsal view; b, major chela in external view; 5 mm indicated (from Williams 1965).

Chelipeds with carpus and upper part of palm roughened; carpus with approximately 15 tubercles above, an internal tooth, and below it a small tooth or denticle, distal groove deep. Hand with superior groove and another on outer surface below upper edge, ridges bordering groove with low tubercles; fingers deeply grooved, dark or horn colored, color continued somewhat on palm ending in oblique, scalloped line; tips light.

Measurements in mm.—Carapace: male, length 13, width 19.2; female, length 12, width 18.2.

Habitat.—Offshore marine waters on hard substrates among sponges, ascidians and bryozoans; also on sand and shell fragments; to 14+ m (Felder 1973).

Type-locality.—Santos, São Paulo, Brazil.

Known range.—South Carolina, through Gulf of Mexico to Uruguay (Milstein, et al. 1976).

Remarks.—This species has been reported from only a few widely separated areas. Rathbun (1930a) reported ovigerous females in September from Brazil.

Genus *Eurytium* Stimpson 1859

Rathbun 1930a:422.—Hemming 1958b:32.

According to Glaessner (1969) the genus has a fossil record dating from the Pleistocene of Panama.

Eurytium limosum (Say)

Figs. 329, 331p

Cancer limosa Say 1818:446.

Eurytium limosum.—Hay and Shore 1918:438, pl. 35, fig. 7.—Rathbun 1930a:423, pl. 176, figs. 1–2.—Williams 1965:199, figs. 182, 183.—Chace and Hobbs 1969:153, figs. 45, 46b.—Coelho and Ramos 1972:193.

Recognition characters.—Carapace broad, approximately 1.5 times as wide as long, quite convex from front to back, nearly plane from side to side; surface smooth to eye but finely granulate under magnification, granulations coarser near frontal and anterolateral margins. Front approximately $\frac{1}{4}$ width of carapace, divided into 2 lobes by median notch giving rise to shallow groove disappearing over gastric region. Orbital margins somewhat elevated; external orbital tooth coalesced with first tooth of anterolateral border, division between these teeth indicated by shallow indentation. Anterolateral teeth with raised margins, second and third teeth rounded at tip, fourth more prominent and subacute.

Chelipeds massive, unequal, and dissimilar, more

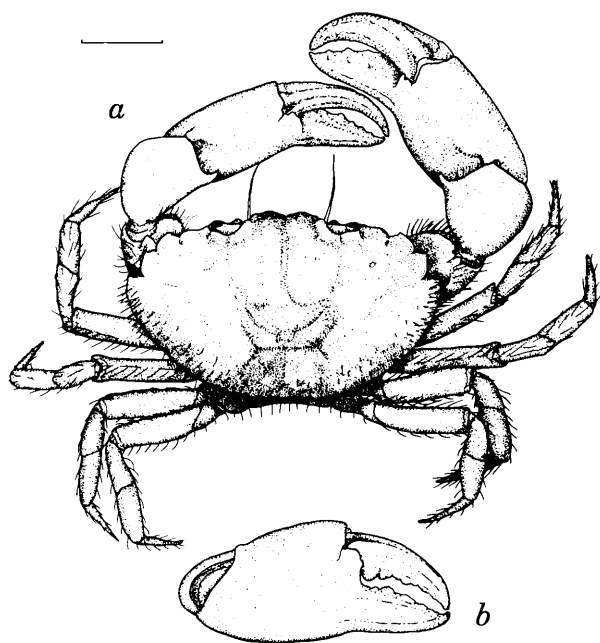


Fig. 329. *Eurytium limosum* (Say). a, Animal in dorsal view; b, major chela in external view; 1 cm indicated (from Williams 1965).

so in male than in female; merus with coarsely tuberculate superior border and distal spiniform tooth; carpus with narrow internal spine, not grooved; fingers pointed, deflexed, large basal tooth on major dactyl.

Measurements in mm.—Carapace: male, length 27, width 43; female, length 22, width 33.

Color.—Carapace brilliant purplish blue, dark gray, or black; carpus and hand bluish; proximal upper half of dactyl pink or purple; remainder of fingers porcelain white; lower part of chelipeds and carpal teeth yellow or orange; color of fingers not continued on palm.

Habitat.—This primarily tropical species lives mainly in muddy or marshy banks a bit below the high-tide mark in burrows partly filled with water, among stones at the high-tide mark, in burrows in sand, intertidally under stones, and on coral reefs (Rathbun 1930a; Rouse 1970; Tabb and Manning 1961). High-tide mark to 71 m.

Type-locality.—"Inhabits shores of the Northern States."

Known range.—South Carolina and Louisiana through West Indies and Caribbean Sea to São Paulo, Brazil; Bermuda. Behre (1950) and Hoese (1972) gave Louisiana records. According to Rathbun (1930a, citing DeKay), the species has been reported from New York, and specimens at the Philadelphia Academy are labelled as from New Jersey. Modern records do not extend this far north.

Remarks.—According to Rathbun (1935) this species has a fossil record in North America dating from the Miocene of North Carolina and Florida.

Teal (1959) found this species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, it was found in burrows, usually near the top, either in air or water. Respiration rates in water were higher than in air. The species showed internal regulation of metabolism in that it was independent of oxygen tension but not of temperature.

Ovigerous females are known from Panama in July (USNM) and Florida in August (Wass 1955).

Genus *Domecia* Eydoux and Souleyet 1842

Rathbun 1930a:553.—Hemming 1958b:144.—Guinot 1964:267.

Domecia acanthophora acanthophora (Desbonne and Schramm)

Figs. 330, 331q

Neleus acanthophorus Desbonne and Schramm 1867:35.

Domecia hispida.—Rathbun 1930a:554, pl. 227 (part, Atlantic localities only).—Pequegnat and Ray 1974:237, figs. 16, 17.

Domecia acanthophora forma *acanthophora.*—Guinot 1964:271, figs. 4, 5, 7, 8, 15.

Domecia acanthophora acanthophora.—Williams, McCloskey, and Gray 1968:52.—Manning and Holthuis 1981:122 (discussion).

Recognition characters.—Carapace somewhat transversely oval but much contracted posteriorly, anterior parts armed with spines; clothed with short,

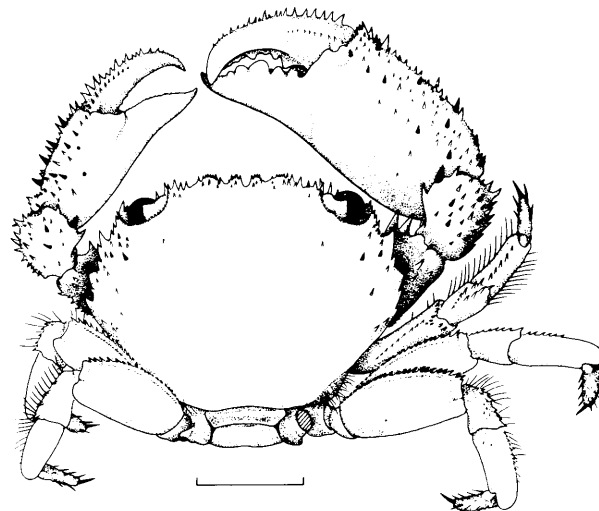


Fig. 330. *Domecia acanthophora acanthophora* (Desbonne and Schramm). Male in dorsal view, right fifth and left first and second walking legs missing, 3 mm indicated (USNM 24315).

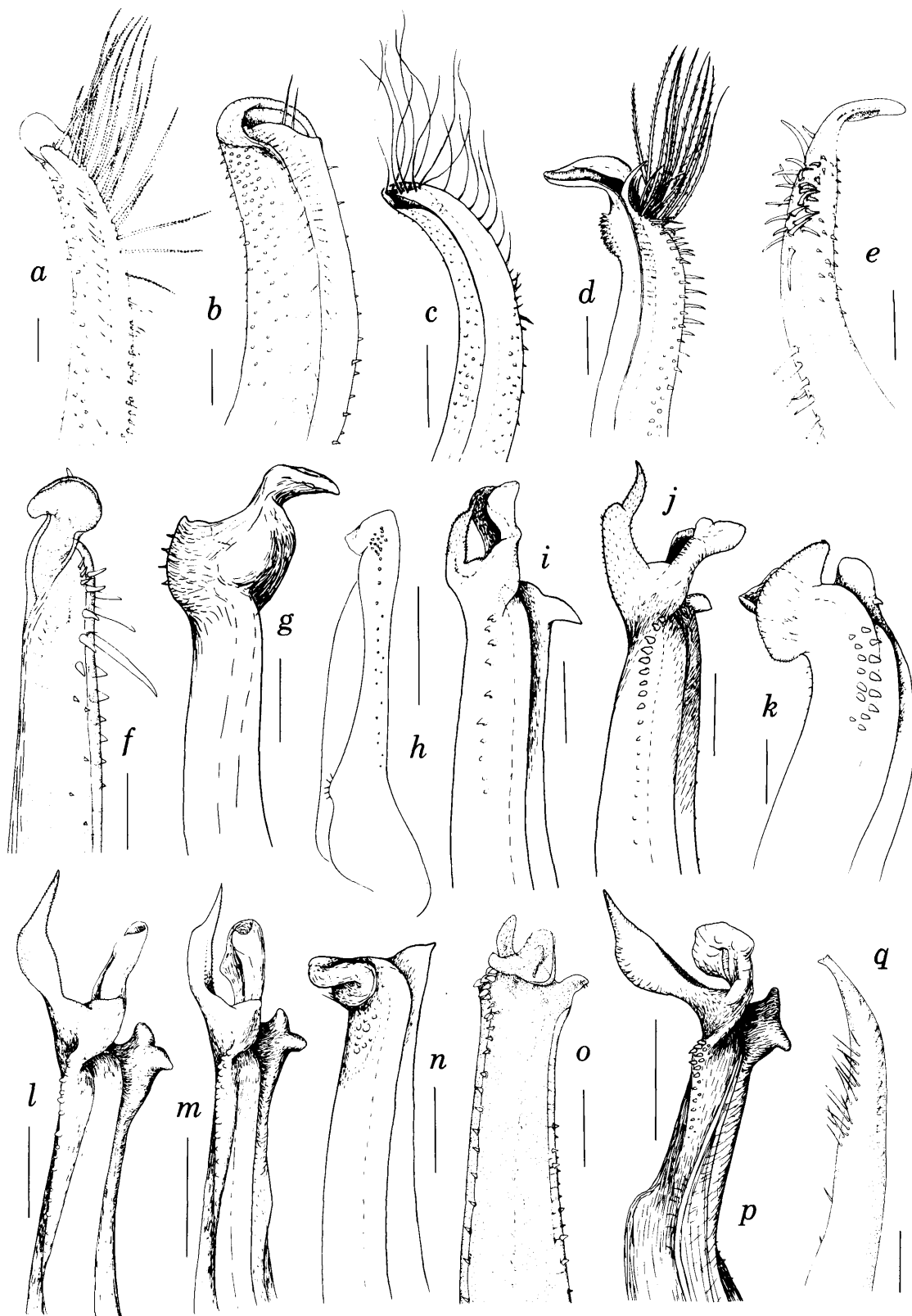


Fig. 331. Tips of right first pleopods of male Xanthidae, mesial view: *a*, *Allactaea lithostrota* Williams; *b*, *Glyptoxanthus erosus* (Stimpson); *c*, *Carpoporus papulosus* Stimpson; *d*, *Pseudomedaes agassizii* (A. Milne Edwards); *e*, *P. distinctus* (Rathbun); *f*, *Rhithropanopeus harrisii* (Gould); *g*, *Micropanope nuttingi* (Rathbun); *h*, *M. sculptipes* Stimpson; *i*, *Eurypanopeus abbreviatus* (Stimpson); *j*, *E. depressus* (Smith); *k*, *Neopanope sayi* (Smith); *l*, *Panopeus herbstii* H. Milne Edwards; *m*, *P. occidentalis* Saussure; *n*, *Hexapanopeus angustifrons* (Benedict and Rathbun); *o*, *H. paulensis* Rathbun; *p*, *Eurytium limosum* (Say); *q*, *Domecia acanthophora acanthophora* (Desbonne and Schramm); *a*, 0.1 mm; *b-f*, *i-k*, *n-o*, 0.25 mm; *g-h*, *l-m*, *p-q*, 0.5 mm indicated (*m* from Guinot 1967a; others from Williams 1965 except *a*, 1974a; *e*, 1978).

short, sparse, light-colored hairs and scattered longer ones. Frontoorbital border not much less than greatest breadth of carapace; front divided on each side into narrow submesial and broader lateral lobes with sharply spined margin, row of smaller, scattered spines behind lobes. Eyes large. Orbits at anterolateral angles; margins not fissured but denticulate above, spinous below; upper and lower inner angles broadly in contact or nearly so to exclude antennae from orbit. Anterolateral borders with 4 to 6 (including orbital angle) principal acute, dark-tipped spines, often smaller intercalated spines; scattered smaller dorsal spines just inside border and also behind frontoorbital border. Third maxilliped with merus remarkably broad and short, ornamented with median transverse patch of spines and few granules as well as on ischium distally. Anterior border of buccal cavity spined. Thoracic sternum terminating in moderately acute anterior point.

Chelipeds unequal; merus, carpus and palm studded with acute spines above and few proximally on inner surface on palm, crests of dactyl finely and closely spined. Walking legs moderately spined and hairy, meri rather broad, superior crest of merus on last leg spined throughout length.

Measurements in mm.—Carapace: male, length 7.5, width 10.8; ovigerous female, length 9.9, width 14.4; female, length 15 (Pequegnat and Ray 1974).

Variation.—There is slight variation in development of spines but the pattern of spination is constant.

Color.—Light yellowish red, front darker; spines blackish (Verrill in Rathbun 1930a).

Habitat.—Associated usually with coral, reef formations, and incrustations on pilings; to 55 m; occasionally in surface waters far from shore (32°N, 74°W).

Type-locality.—Guadeloupe.

Known range.—Bermuda; Cape Lookout Shoals, N. C., NW Gulf of Mexico through West Indies and Caribbean Sea to Alagoas, Brazil.

Remarks.—In her review of the genus, Guinot (1964) distinguished three species, the Pacific *D. hispida* and *glabra*, and Atlantic *acanthophora* which in turn was separated into western and eastern "forms. Guinot (1964) added *D. acanthophora* sensu lato to a number of species having ampho-Atlantic distribution (Monod 1956). Manning and Holthuis (1981) recognized the eastern and western populations of *D. acanthophora* as subspecies.

Ovigerous females are represented in the USNM collection in every month from December to August in various parts of the range.

Patton (1967; 1967a) discussed adaptations of *D.*

acanthophora to reef habitats, especially its association with *Acropora* which harbors numerous commensal decapods in the Indo-Pacific but apparently only this one in the Caribbean. The mouthparts of the species differ from those found in typical xanthids; the mandible is weakly calcified and the second maxilliped possesses rows of peculiar paddle-tipped spines on the distal margin of the dactyl. Most likely food for the crab seems to be organic detritus which it separates from the surrounding water.

Randall (1967) listed *D. a. acanthophora* (= *D. hispida*) from stomach contents of the longspine squirrel fish, *Holocentrus rufus*, dusky squirrelfish, *H. vexillarius*, and rock hind, *Epinephelus adscensionis*.

Genus *Eriphia* Latreille 1817

Rathbun 1930a:545.—China 1966:255.

Eriphia gonagra (Fabricius)

(Calico crab)

Figs. 332, 333a-c

Cancer gonagra Fabricius 1781:505.

Eriphia gonagra.—Hay and Shore 1918:439, pl. 35, fig. 6.—Rathbun 1930a:545, text-fig. 83, pl. 222.—Williams 1965:182, figs. 164A, B, C; 165.—Coelho and Ramos 1972:192.

Recognition characters.—Carapace approximately quadrate, about $\frac{1}{4}$ wider than long, flattened, with regions clearly marked off on anterior $\frac{2}{3}$; surface nearly smooth posteriorly but granulate anteriorly, and with 2 transverse lines of subspinous granules, 1 in front of epigastric lobes and another across protogastric and hepatic lobes. Front wide, almost straight, strongly deflexed, and divided into 4 lobes, both submesial lobes broader and more advanced than lateral ones, and with finely granulate border; lateral lobes (inner orbital lobes) forming mesiodorsal margin of orbits and in contact beneath with prolongation of infraorbital plate, thus completely excluding antenna from orbit. Anterolateral margins evenly arched, each with row of 5 spines including outer orbital, behind and inside these a few squamiform tubercles.

Chelipeds unequal, strong, swollen; hands covered with large, round, flattened, squamiform tubercles, more elevated on small than on large hand; carpus with less prominent tubercles; dactyls with squamiform tubercles above at base; major dactyl with large rounded tooth at base. Walking legs

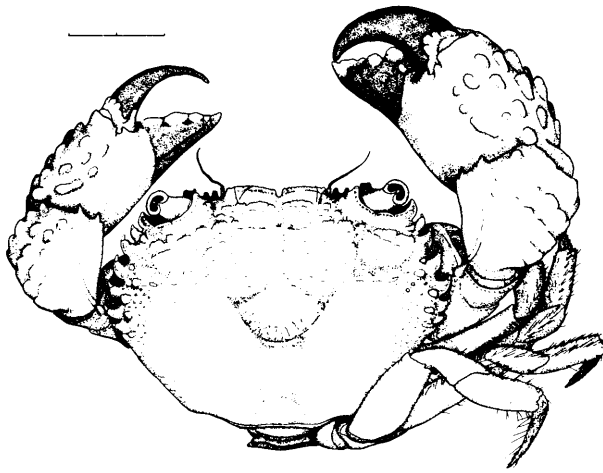


Fig. 332. *Eriphia gonagra* (Fabricius); Male in dorsal view, walking legs of left side not shown, 1 cm indicated (from Williams 1965).

rather slender, their distal 3 articles with fine stiff hairs.

Measurements in mm.—Carapace: male, length 34, width 48; female, length 30, width 34.

Color.—Gaily colored. Anterior half of carapace and a broad median stripe extending to posterior margin dark purplish brown, legs a lighter tint of same color; front margined with brownish orange. Sides of carapace, upper surface of chelipeds, dactyls, bases of legs, and a narrow band on distal margin of other articles, light yellow. Tubercles on upper half of chelipeds dark blue, on lower half yellow. Underparts of body and chelipeds white, fingers brown. Rathbun (1930a) gave another detailed color description.

Habitat.—The species has been found in a variety of situations: under flat rocks above the watermark, in seaweed, sponges, brackish ponds, tide pools, and on coral reefs. Shoreline to shallow water of uncertain limits.

Type-locality.—Jamaica.

Known range.—North Carolina to Patagonia; Bermuda.

Remarks.—Ovigerous females are known from March to September in various parts of the West Indies and southern Florida, in October from Santa Catarina, and February from Bahia, Brazil (Rathbun 1930a, in part). Lewis (1960) observed ovigerous females from March to June in Barbados. He regarded this as one of the commonest crabs of the intertidal region there.

Genus *Menippe* de Haan 1833

Rathbun 1930a:472.

Menippe mercenaria (Say)

(Stone crab)

Figs. 333d-e, 334

Cancer mercenaria Say 1818:448.

Menippe mercenaria.—Hay and Shore 1918:439, pl. 35, fig. 8.—Rathbun 1930a:472, text-fig. 78, pls. 191–193.—Williams 1965:183, figs. 164D, E, 166.—Felder 1973:64, pl. 9, figs. 2–3.

Recognition characters.—Carapace transversely oval, approximately $\frac{2}{3}$ as long as wide, convex, nearly smooth to unaided eye, minutely granulate and punctate. Anterolateral border divided into 4 lobes: first 2 wide, third wide but dentiform, fourth much narrower and dentiform. Front with median notch and broad trilobulate lobe on each side. Orbital border thick, fissures indistinct.

Chelipeds large and heavy, unequal, nearly smooth; inside surface of hands with patch of fine, oblique, parallel striae serving as a stridulating organ and adapted for playing against thick edge of second and third anterolateral teeth and outer suborbital tooth; dactyl of major chela with large basal tooth, and fixed finger with large subbasal tooth; fingers of minor chela with numerous small teeth. Walking legs stout, hairy distally.

Measurements in mm.—Carapace: male, length 91, width 129; female, length 79, width 116. This is the largest xanthid species in the area.

Color.—Juveniles dark purplish blue, very young always with a white spot on carpus. Older individuals become dark brownish red or less mottled and spotted with dusky gray; fingers dark; walking legs with reddish and yellow bands (Futch 1966).

Habitat.—Adult stone crabs burrow in mud flats just below low-tide mark, among rocks on jetties, on offshore reef areas, under rocks or coral heads, and among dead shells or grass clumps (Whitten, et al. 1950; Wass 1955; Powell and Gunter 1968; Costello, et al. 1979). Apparently colonial burrows beneath scattered clumps of oysters have been observed on mud flats in south Texas, but most were solitary (Powell and Gunter 1968). There was usually a conical depression at the entrance to each burrow where the crabs often rested, and a mound of mud and debris. No freshly broken oyster shell was noticed near burrows, but this has been seen by others there and in Louisiana (Menzel and Hopkins 1956). Size of burrow was not correlated with size of crab nor with amount of debris around the hole. Mouths of burrows were plugged in cold weather. Burrows of crabs between 44 and 73 mm wide dropped straight down for 25–60 cm; there they more or less leveled off or made several turns

before ending blindly with the crab resting sideways at the end with the minor chela toward the entrance. Larger crabs (90 mm or wider) occupied more or less horizontal burrows in the edge of shoals or banks that extended as much as 75 cm to end in a chamber where the occupant rested facing the entrance, much as described by earlier authors. McRae (1950) recorded a burrow extending 127 cm.

Crabs of less than 30 mm carapace width (juveniles) do not dig burrows (Powell and Gunter 1968), but live in deep channels, on grass flats, under shell fragments, in crevices among rocks, among oyster shells, around pilings, and even cling to buoys (Hay and Shore 1918; Lunz 1937a; McRae 1950; Wass 1955; Manning 1961; Costello, et al. 1979). Larger juveniles to subadults have often been observed on oyster reefs (Menzel and Nichy 1958).

In an unusual occurrence, Clark (1965) found a small *M. mercenaria* resting beneath the deformed and peaked posterior shield of a weakened hawks-bill turtle taken near Sarasota, Fla. The crab rested on a place eaten away through the carapace to the flesh.

The species is well adapted to salinity ranges near the mouths of estuaries and can survive extremes considerably lower or higher than than 35‰ (Karandevya and Silva Lee 1976).

Surface to 51 m.

Type-locality.—"The Southern States."

Known range.—Cape Lookout, N. C., to Yucatan, Mexico; Bahamas; Cuba; Jamaica.

Remarks.—Summary of literature for this species is selective. The genus *Menippe* has a fossil record dating from the Middle to Upper Eocene (Glaesner 1969), the thick, hard exoskeleton no doubt enhancing its chances of fossilization. The record for *M. mercenaria* dates from the Pleistocene (Rathbun 1935).

Reproduction in *M. mercenaria* has been a subject for active investigation during the past 20 years, although Binford (1912) first discussed spermatogenesis and fertilization in the species and gave notes on spawning habits in his often cited "unpublished" account. Savage (1971) observed and described mating of a male and female *M. mercenaria* held in an outdoor aquarium. A fresh molt of the female was found on the morning of May 31, 1970, and at 9:00 the following morning the pair was found mating, the male in superior position cradling the inverted female. By 1:30 p. m. the pair had separated and the female had righted herself. Among mating crabs observed in the field, males were always with freshly molted or presumed freshly molted females, coupled in the described posture.

Females in laboratory experiments have produced more than 10 broods of viable eggs within the same intermolt period without copulation taking place in intervals between production of the different broods (Cheung 1968). Eggs of all these broods were successfully attached to hairs of pleopods, and developed to hatch as normal zoeae. Moreover, females from the wild held in isolation through a molt were found to retain sperm through ecdysis, a special adaptation (late disposal of the old invaginating exoskeletal wall between sperm and new wall) enabling retention. Yang (1971) recorded 10 spawnings within one intermolt for a single female over a 120-day period, the interval between hatch of one brood and oviposition of the next being 2–3 days. Cheung (1969) also showed that ovarian development is closely correlated with water temperature, optimum being at 28°C. Seasonally, spawning built to a peak in August-Sep-

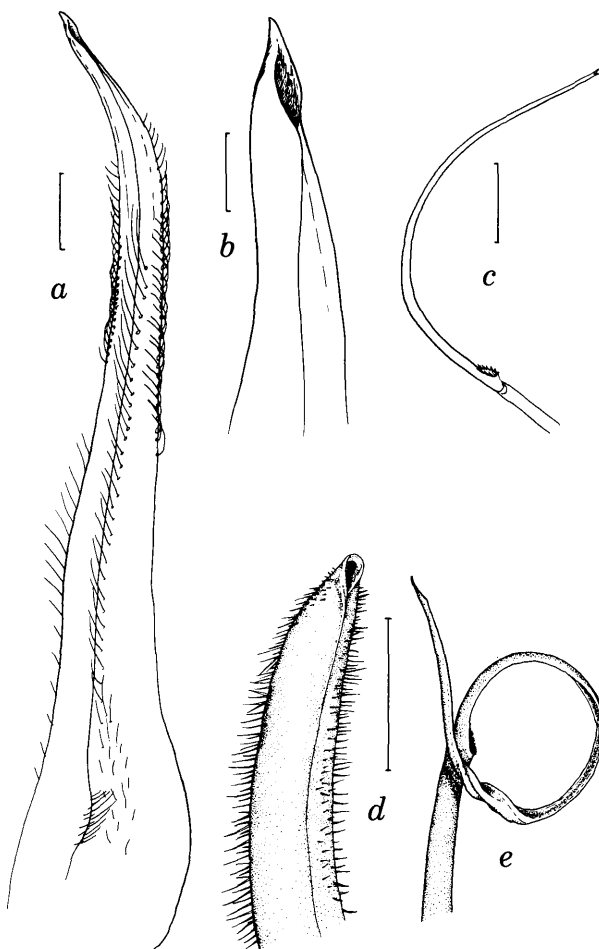


Fig. 333. Male first and second pleopods of *Eriphia gonagra* (Fabricius); a, entire first pleopod; b, tip of first pleopod; c, tip of second pleopod; and *Menippe mercenaria* (Say); d, tip of first pleopod; e, tip of second pleopod; a, c, 0.75 mm; b, 0.25 mm; d-e, 5 mm indicated (from Williams 1965).

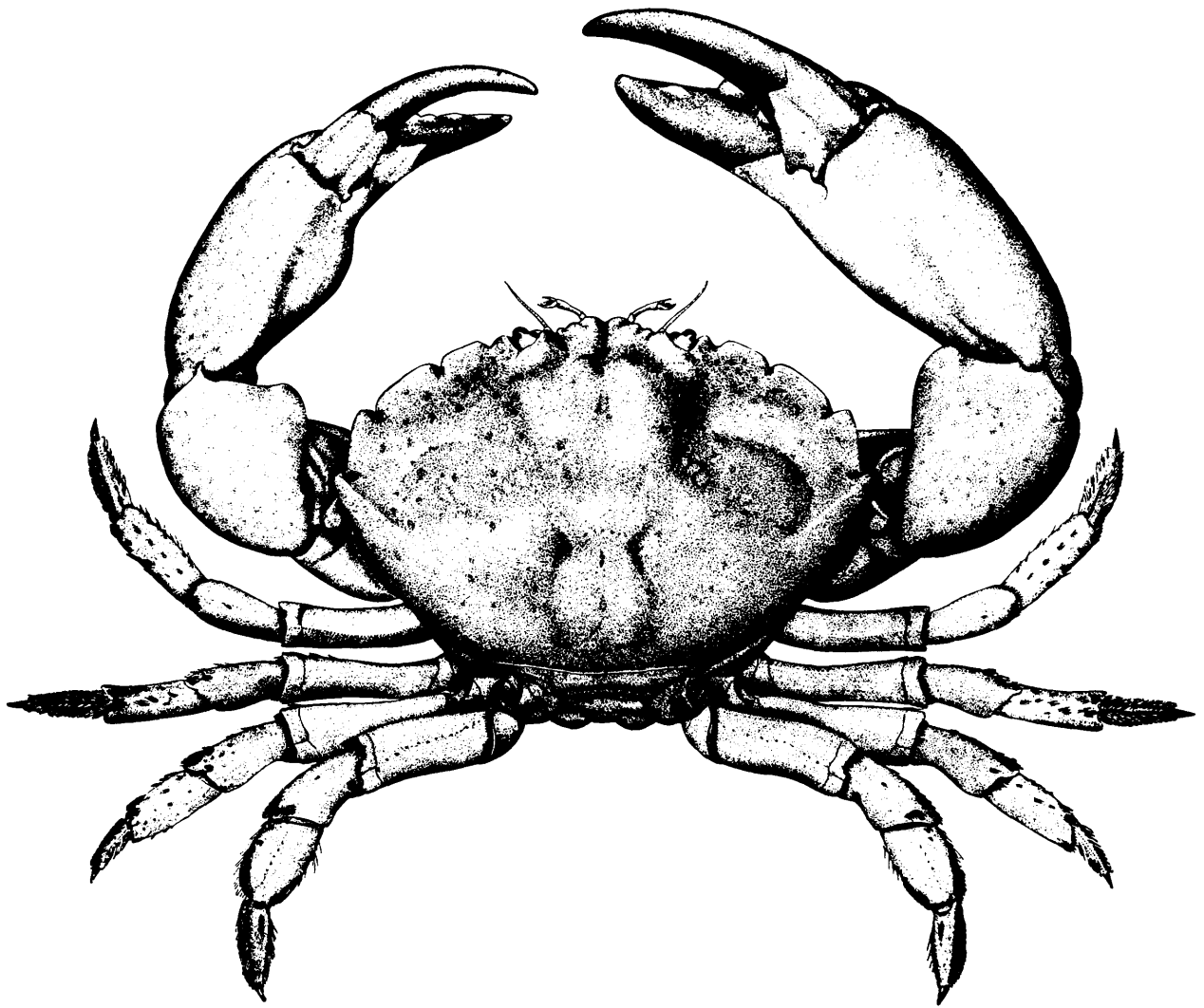


Fig. 334. *Menippe mercenaria* (Say). Male in dorsal view, approximately $\times 0.6$ (from Rathbun 1884).

tember in southern Florida, but dropped to a low in winter. Elsewhere, ovigerous females are known from May to August in North Carolina and in August in Texas (Powell and Gunter 1968).

Porter (1960) described development of larvae, hatched from an ovigerous female taken near Beaufort, N. C., that were reared individually in compartmented plastic boxes by feeding on *Artemia* nauplii. He found a prezoeal and 6 zoeal stages, but considered the prezoea and last zoeal stages to be atypical. Length of larval life was approximately 27 days under the conditions imposed. Ong and Costlow (1970), with much more sophisticated equipment, reared larvae hatched also from North Carolina females in 18 environments (6 salinities, 3 temperatures). Both of these factors were found to affect rate of development and survival. Optimal condition for development was about 30°C in a salinity range of 30 to 35‰, at which the megalopa was reached in 14 days and the first crab

in 21 days with survival of 60%–72%. Development was slower in 20‰ salinity than in 30–40‰, and markedly retarded in decreasing temperatures from 30° to 20°C. In all temperatures tested there was total mortality at 10‰ salinity. At 20°C, larvae developed only to the megalopa, but survival was less in 20–25‰ than in 30–40‰; survival was higher at 25° and 30°C. The authors felt that the stone crab might be a good subject for large-scale rearing experiments. Yang (1971) successfully reared mass cultures of larvae from ovigerous females captured in Biscayne Bay, Fla. Hatching took place in about 10 days at 29°–30°C. Duration of larval period was 14 days at 30.5°–32°C in 30‰ salinity in mass cultures, about 20–21 days in individual compartments, and included five zoeal stages and a megalopa. The results confirmed Porter's judgment regarding number of larval stages. Mass-cultured crabs fed beyond larval stages on mixtures of ground squid and fish, dried shrimp

shells, calcium phosphate, vitamin E, yeasts, marine protein concentrate and crushed oyster shells reached sexual maturity in a year (Yang 1972). In time, F2 progeny were produced from this culture. Yang and Krantz (1976) collated all of this information in a manual for "intensive" culture of the species. A related Caribbean species, *M. nodifrons*, has a similar larval development that is judged to represent the most primitive pattern in the Xanthidae (Scotto 1979).

Dudley and Judy (1971) found stone crab larvae in plankton 1.6 and 6.54 km off Beaufort Inlet, N. C., at 1–8 m depths from June to August; none were found 10–13 km offshore. Mootz and Epifanio (1974) determined an energy budget for larvae fed *Artemia salina* nauplii, finding that larval growth is exponential during zoeal stages but decreases during the megalopal stage even though consumption reaches a peak during this stage.

From study in the Aransas Pass, Tex., area (reviewed briefly here), Powell and Gunter (1968) found that the number of *M. mercenaria* increased from January to August, male to female ratios changing from 5:1 to 2.65:1 during that time. Only one ovigerous female was found, and they concluded that the breeding population lived outside the area of study.

Daily observations indicated that time of greatest activity was evening before dark, but the crabs were somewhat active both day and night. Behavior patterns in response to disturbance resembled those shown by other brachyurans. Stone crabs will usually push an intruder away with a quick lateral motion of the cheliped rather than attack with the chela. Ordinarily the crabs adopt passive means of defense, but the fingers of the chelae are powerful and if fastened upon a hard object can hardly be pried apart. Strength of this grip by one male on a hard object was so great that it crushed its own chela and bled to death. The crabs can hug objects tightly or clasp them with the legs; crabs that are held fast can autotomize appendages to gain freedom.

Sinclair (1977) observed agonistic behavior in experimental tanks and the field, during daylight or at night under red light in the laboratory or by flashlight in the field, and with the aid of SCUBA. Fights with extensive bilateral aggression were infrequent. There is a relatively high degree of ritualization. Dominance is correlated with size, males, and prior possession of a burrow, in which case a smaller individual can dominate one larger. Interactions between animals of different sizes or of different sexes are characterized by lower frequency of fights than encounters between animals of a similar size or of the same sex. During the period of observation, crabs were seen outside burrows only

twice, once by day and once at night. They are solitary except while mating, may be territorial, may move hundreds of feet to dig new burrows, but can live as closely as 1/m (Menzel and Hopkins 1956). Although the large chelae are easily capable of crushing a conspecific, such pressure is not applied during a grasp and vulnerable mouth and eye areas are rarely contacted.

Cheung (1976) confirmed by statistical study the earlier contention of Przibram (1931) that the pincer claw is a more primitive condition than the crusher. He showed that right or left crushers are identical functionally and structurally in a rather rigidly unvarying size range for best survival, but that the smaller pincers, owing to loss and regeneration, are not always structurally or functionally identical. Savage, et al. (1974) showed how sutural structures on proximal segments of the cheliped allow extraction of the larger diameter propodus-carpus during molting, briefly describing behavior of the molting crab with the aid of photographs. In molting, the proximal suture lines of the cheliped merus are fractured and simultaneously there is a forced expulsion of hemocoelic fluid from the chela (Hiatt 1948) allowing the larger distal elements to be withdrawn. Turgidity is regained following ecdysis. These authors also (1975) classified claws of crabs trapped in Florida by means of the pattern of striae on the inner surface of the palm: oblique unbroken = normal; randomly granular = early regenerated; dashed or elongated granules = later stage in regeneration; beaded oblique lines = still later stages of regeneration. From several thousand claws taken in the commercial fishery over several months they found that 90.5% were normal and most were major claws. Dashed patterns were conspicuously more numerous than granular patterns, and both were most commonly on minor claws. Frequency of natural claw loss was postulated to be 5.6% and mean calculated regeneration following commercial harvesting was 8.2% in November and 2.8% in April. The composite ratios of major to minor claws taken in the fishery permitted the formulation of a hypothesis that the largest crabs are caught early in the season and this population is gradually depleted to a point at which the fishery depends on smaller crabs to provide harvestable claws. In the laboratory, crabs with both claws removed regenerated new claws 70% of original size at the first succeeding molt.

Juvenile *M. mercenaria* carapace length and width increase in a constant relationship (Savage and McMahan 1968). Crabs grow to maturity in about two years and may live beyond this age, although Cheung (1973) suggested that males reach a terminal molt after which further growth and regen-

eration ceases. In Florida, harvest of 2-year-old or older crabs which presumably have spawned at least once is allowed (Costello, et al. 1979). In an extensive review of the species biology and economic role in fisheries, these authors showed that the Florida fishery extends to 30 miles (48 km) offshore in depths of up to 18 m or more off most of the west coast counties from Monroe to Franklin, but with 75% caught in the extreme southwestern corner of the Everglades-Florida Bay area, mostly in traps made of wooden slats. The largest commercial catch was during the 1977-78 season when 2.1 million pounds were landed and potential for still greater harvest remained. There have been local hand fisheries for stone crabs since the early settlement days.

Powell and Gunter (1968) judged stone crabs to have a strong influence on the life of sand and mud flats that are exposed by wind or lunar low tides, because their water-filled burrows are refuges for small aquatic organisms that cannot withstand drying. Commensals found in burrows include sea anemones, tube worms, bivalve and gastropod mollusks, barnacles, amphipods, caridean and brachyuran decapod crustaceans and fishes, to name a few.

Food of the juvenile and adult crabs included the above organisms as well. Menzel and Hopkins (1956) found the stone crab in Louisiana to be an active predator on oysters. The powerful crabs killed small and large oysters alike, predation being lowest in winter and highest in fall. Powell and Gunter (1968) thought that earlier estimates of predation of the crabs on oysters may be high and that other foods such as acorn barnacles are preferred, but there is no question that *M. mercenaria* preys on a variety of macroorganisms in its habitat. The animals expend from 45% to 82% of assimilated food energy for growth and reproduction (Sushchenya and Claro 1973).

Manning (1961) gave data on relative growth, showing that juveniles have a relatively broader front than adults. Both he and Wass (1955) pointed out the superficial resemblance of young *M. mercenaria* to *Panopeus herbstii* and *Eurytium limosum*, and Manning gave distinguishing characters for each species at comparable sizes. Further, the stridulating mechanism was shown not to be visible in small specimens and, indeed, stridulation itself had not been observed (Guinot-Dumortier and Dumortier, 1960) until its production by both juveniles and adults was seen and heard by Powell and Gunter (1968). Bender (1971) observed stridulation over 70 times. Two patterns were observed: (1) downward rasping of the striated ridges of one palm against the interocular teeth followed by circular waving of the cheliped 3-5 times in a manner similar to motions made by fiddler crabs, followed by similar movements of the opposite cheliped; (2) scraping of one cheliped up and down against the carapace for 15-second periods. Stridulation was observed in crabs (many females) of 3 to 10 cm carapace width. Function of the behavior was not determined.

In studies on the relationship of number and volume of gills to oxygen consumption, Pearse (1929) and Ayers (1938) found this form, along with other mud crabs, intermediate between the sluggish common spider crab and the more active, partially terrestrial, fiddler and ghost crabs. Pearse also found that *M. mercenaria* could withstand considerable dilution of its environment with fresh water. Gray (1957) found gill area per gram of weight to be intermediate in an array of species ranging from land to shallow-water habitats.

Genus *Pilumnus* Leach 1815

Rathbun 1930a:481.—Hemming 1958b:35.

Key to Species

1. Hairy covering of carapace not forming so thick a coat as to conceal surface beneath 2
 Hairy covering over whole carapace forming thick coat concealing surface beneath (hair sometimes worn off) 3
2. Two or more superhepatic spines *P. sayi*
 No superhepatic spines *P. dasypodus*
3. Chelipeds spinose above; transverse row of long hairs across front
 *P. floridanus*
 Chelipeds not spinose above; carapace tuberculate, but tubercles often sparse and low 4
4. Tubercles of carapace neither numerous nor prominent, upper margin of orbit not spinose *P. lacteus*

Tubercles on anterior half of carapace and upper surface of chelipeds numerous, upper margin of orbit with truncate spines (but occasionally these poorly developed) *P. pannosus*

***Pilumnus dasypodus* Kingsley**

Fig. 335, 340a

Pilumnus dasypodus Kingsley 1879:155.—Rathbun 1930a:493, pl. 200, figs. 5–6.—Williams 1965: 178, figs. 157C, 159.—Felder 1973:61, pl. 9, fig. 7.

Pilumnus desypodus.—Coelho and Ramos 1972:193.

Recognition characters.—Carapace thinly covered on anterior $\frac{2}{3}$ with long, fine hair and occasional stouter setae; upper surface of chelipeds and walking legs similarly clothed; small sharp granules on anterolateral region. Anterolateral border with 4 spines including small outer orbital; spines with bases conical, extremities long, slender, incurved. Orbital border with 3 or 4 spines above and about 7 below. Frontal lobes separated by median V- or U-shaped notch; margins furnished with short spines or sharp granules, with an outer tooth separated from remainder of margin by U-shaped notch.

Chelipeds unequal, spinose, and granulate except for smooth and naked lower distal $\frac{2}{3}$ of outer surface of major palm, spines and granules not arranged in rows on upper part of major palm; fingers of minor chela grooved on outside, dactyls with

rows of sharp granules and hairs at base. Walking legs hairy and spinose above.

Measurements in mm.—Carapace: male, length 11, width 15; ovigerous female, length 6.5, width 10.3.

Color.—Body and claws brownish-red, legs much lighter; fingers and extremities of spines brown (Milne Edwards in Rathbun 1930a).

Habitat.—This species has been taken from pilings, jetties, buoys, and offshore reefs (Lunz 1937a; Pearse and Williams 1951; Rathbun 1930a) including loggerhead sponge *Speciospongia vespara* (see Pearse 1934); 1 to 52 m.

Type-locality.—Key West, Fla.

Known range.—Off Cape Hatteras, N. C., through Gulf of Mexico, Caribbean Sea and West Indies to Santa Catarina, Brazil.

Remarks.—This species is not so common in the Carolinian area as *P. sayi*, and small specimens of the latter are not always easily distinguished from it. Rathbun (1930a) stated that "*dasypodus* is less heavily clothed with hair than *sayi* and less ragged looking. The front is more deflexed and less advanced, therefore appears wider. The spines and tubercles of the major palm in *sayi* are arranged more or less in rows and these rows have a tendency to encroach on the lower distal half; in *dasypodus* there are seldom any definite rows and the lower distal two-thirds or one-half in both sexes is smooth and bare. The immovable finger of the major chela in *dasypodus* is a little longer than in *sayi*."

Ovigerous females are known year-round in the West Indies (USNM), December to May in south Florida (Rouse 1970) as well as in summer (Camp, et al. 1977, in part), and April through August in the Carolinas (Lunz 1937a).

From ovigerous females taken in August on a jetty near the mouth of Charleston Harbor, S. C., Sandifer (1974a) reared four zoeal stages and a megalopa on a diet of *Artemia* nauplii under constant light at 28°C in artificial seawater of 35‰ salinity. Development to megalopa required a minimum of 11–12 days under these conditions. Bookhout and Costlow (1979) reared four zoeal stages and a megalopa from ovigerous females taken on heads of a scleractinian coral, *Oculina arbuscula*, off Cape Lookout, N. C., in filtered seawater of 30‰ at constant 25°C on the same diet. Similar comments in both studies compared larval differences between *P. dasypodus* and *sayi*, and contrasted developmental stages of these species with those of

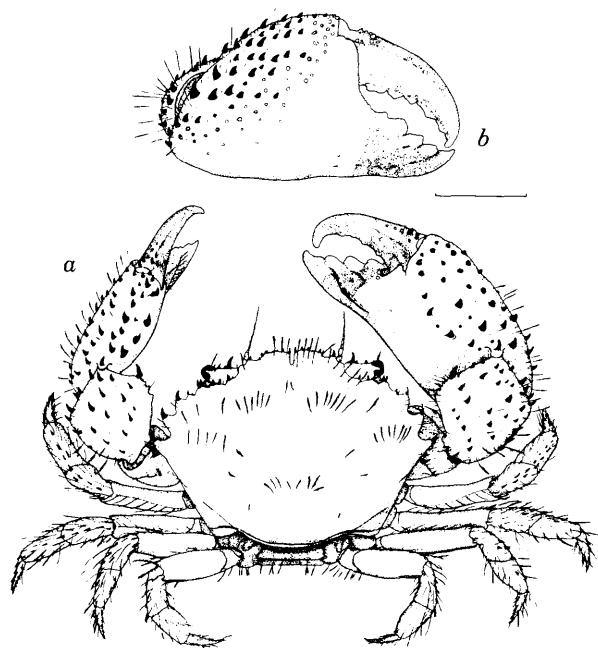


Fig. 335. *Pilumnus dasypodus* Kingsley. a, Male in dorsal view; b, major chela in external view; 5 mm indicated (from Williams 1965).

other xanthids. McCloskey (1970) discussed association of this crab with *Oculina arbuscula* in the Carolinas. Gore, et al. (1976; 1978) characterized a population of *P. dasypodus* on sabellariid reefs along east Florida as moderately abundant but fluctuating in density from year to year. Stomach analyses showed that the species is omnivorous, a facultative predator-scavenger that also consumes diatoms and algae.

***Pilumnus floridanus* Stimpson**

Figs. 336, 340b

Pilumnus floridanus Stimpson 1871a:141.—Rathbun 1930a:507, pl. 205, figs. 3–4.—Williams 1965:179, figs. 157D, 160.—Coelho and Ramos 1972:193.—Felder 1973:61, pl. 9, fig. 8.—Pequegnat and Ray 1974:238, figs. 23, 24.

Recognition characters.—Carapace covered with dense, short pubescence thinning behind, and with few longer clavate hairs, conspicuous transverse series of these crossing frontal region. Anterolateral margin with 4 somewhat conical spines; small subhepatic spine between outer orbital and second spine; hepatic region slightly roughened but with no spines. Frontal lobes almost bare, edge slightly oblique, minutely crenate, with median triangular notch and rounded lateral notches; tooth at outer

angle minute, deflexed. Orbital margin essentially unarmed above, with 8 to 10 spinules below.

Chelipeds spinose above; merus with 2 spines near distal end on upper surface; carpus armed over entire exposed surface; spines on hand becoming pointed tubercles on outer surface. Male with large hand smooth and bare on outer lower half or less of surface, smooth part more restricted in female. Walking legs spined above.

Measurements in mm.—A small species. Carapace: male, length 8.5, width 12.8; female, length 6.3, width 9.

Habitat.—In North Carolina this species has been taken from an offshore reef (Pearse and Williams 1951) and found in sponges. Rathbun (1930a) and Felder (1973) listed it from rocks, grass, and a variety of primarily hard bottoms. Low-tide mark to about 146 m.

Type-locality.—Tortugas, [Fla.].

Known range.—Off Cape Lookout, N. C., through Gulf of Mexico, and Yucatan Channel, to Honduras; through West Indies to Bahia, Brazil.

Remarks.—This species is not common north of Florida. Ovigerous females are known from March to August in Florida (Rathbun 1930a, in part) and they have been taken in February in North Carolina.

***Pilumnus lacteus* Stimpson**

(Small hairy crab)

Figs. 337, 340c

Pilumnus lacteus Stimpson 1871a:142.—Hay and Shore 1918:440, pl. 35, fig. 3.—Rathbun 1930a:511, pl. 205, figs. 1–2.—Williams 1965:180, figs. 157E, 161.

Recognition characters.—Carapace about $\frac{3}{4}$ as long as wide, covered with short velvetlike pubescence easily rubbed off (and often is), nearly smooth, sparse tubercles almost invisible through hairy coating; usually a row of 5 tubercles paralleling anterolateral and orbital margins, others scattered. Anterolateral margins with 4 anteriorly directed teeth, first or outer orbital small; small subhepatic spine between latter and second tooth. Front depressed, deeply notched in middle, and with smaller notch near eye. Orbital margin occasionally a bit uneven but not tuberculate.

Chelipeds dissimilar in size but otherwise nearly alike, stout, velveted, sparsely long setose and somewhat tuberculate above, but naked and polished below and on ventral half or $\frac{2}{3}$ of both inner and outer surfaces of chelae; merus with 2 similar

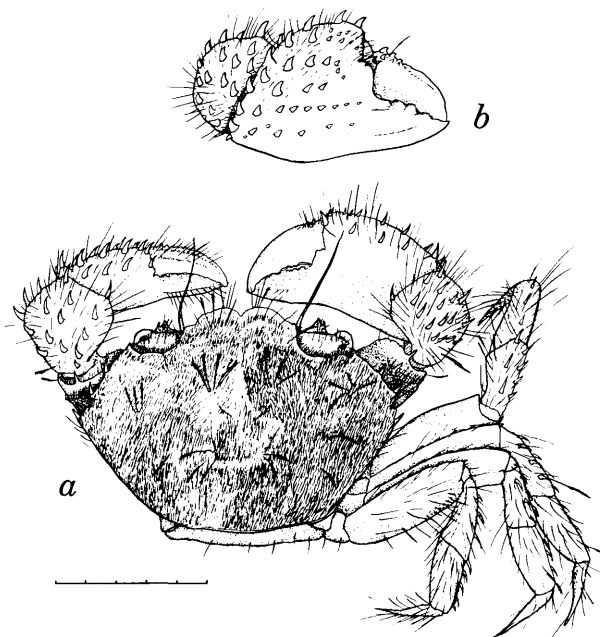


Fig. 336. *Pilumnus floridanus* Stimpson. a, Animal in dorsal view, walking legs of left side not shown; b, major chela in external view; 5 mm indicated (from Williams 1965).

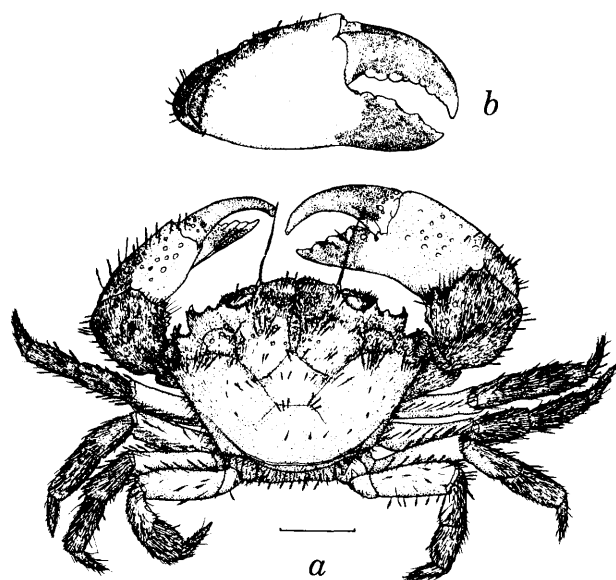


Fig. 337. *Pilumnus lacteus* Stimpson. a, Animal in dorsal view; b, major chela in external view; 5 mm indicated (from Williams 1965).

curved spines on upper margin distally; carpus with stout spine on inner angle.

Measurements in mm.—Carapace: male, length 12, width 15; female, length 7.5, width 11.1.

Color.—Gray or pinkish, with plumose hairs whitish or cream colored; hands and tips of legs light red. Small black under-hairs on anterior $\frac{1}{3}$ of carapace (Rouse 1970).

Habitat.—This crab may be found on wharf pilings or in seaweed. It has been taken from buoys both in sounds and at sea in South Carolina (Lunz 1937a). Rathbun (1930a), Tabb and Manning (1961) and Rouse (1970) reported it from a variety of situations farther south. Near low-tide mark to about 32 m (Wenner and Read 1982).

Type-localities.—Cruz del Padre, Cuba, and Key West, Fla.

Known range.—Near Beaufort, N. C., to Florida; Cuba.

Remarks.—Ovigerous females are known year-round in southern Florida (Rouse 1970) where this is the commonest of three species of *Pilumnus* associated with sponges in salinities ranging from 15 to 45‰. They are reported also in May from Cuba (Rathbun 1930a) and South Carolina (Lunz 1937a).

Pilumnus pannosus Rathbun

Figs. 338, 340d

Pilumnus pannosus Rathbun 1896b:142.—Rathbun 1930a:514, figs. 4–5.—Williams 1965:181, figs. 157F, 162.—Felder 1973:64, pl. 9, fig. 12.

Recognition characters.—Carapace about $\frac{3}{4}$ as long as wide, almost entirely covered with unevenly distributed, soft, thick, velvety pubescence, with scattered longer club-shaped setae giving ragged appearance. Anterior half of carapace and upper surface of chelipeds and legs dotted with beadlike tubercles; these tubercles and anterior lobulations of carapace showing through pubescence. Antero-lateral margin with 4 triangular spines (outer orbital small) having slender forward-projecting tips; subheptic spine between first and second tooth well developed. Frontal lobes (when well formed) broadly subtriangular, granulate on margin, separated by V-shaped notch; outer tooth of front almost triangular, acute (blunt at tip in some specimens). Upper margin of orbit with truncate teeth covered by pubescence, lower margin with row of short, stout, truncate teeth or tubercles.

Chelipeds with upper surface tuberculate but usually large; part of outer surface smooth and naked; small hand with outer surface often rough with rows of spines; dactyls with a few tubercles near articulation. Male with shallow grooves on fingers, female with well-defined grooves on minor fingers and fixed major finger. Walking legs pubescent, fringed with club-shaped setae mixed with long fine hair.

Measurements in mm.—Carapace: male, length 9, width 12; female, length 11.6, width 16.5.

Color.—Carapace under pubescence and bare part of palms bright red (Milne Edwards in Rathbun 1930a). Tan, red tubercles, dark fingers on orange-brown hands.

Habitat.—Pearse and Williams (1951) listed this species as taken from a submerged rock reef, and

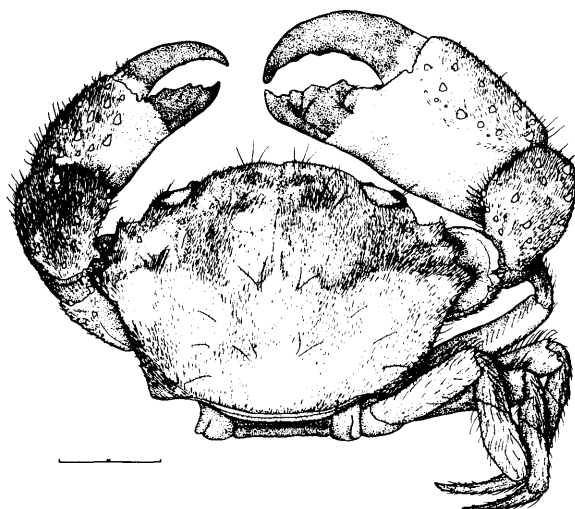


Fig. 338. *Pilumnus pannosus* Rathbun. Male in dorsal view, walking legs of left side not shown, 2 mm indicated (from Williams 1965).

Rathbun (1930a) listed it from similar situations as well as from sponges and corals. About 1 to 20 m.

Type-locality.—Key West, Fla.

Known range.—Bogue Sound off Beaufort, N. C., to Port Aransas, Tex.; West Indies to Virgin Islands.

Remarks.—Rathbun (1930a) listed ovigerous females in December and January from Florida, and they are known from April to August between South Carolina and Cuba.

Pilumnus sayi Rathbun

(Hairy crab)

Figs. 339, 340e

Cancer aculeatus Say 1818:449.

Pilumnus sayi Rathbun 1897b:15.—Hay and Shore 1918:440, pl. 35, fig. 4.—Rathbun 1930a:484, pl. 200, figs. 1–2; pl. 201, figs. 4–7.—Williams 1965:177, figs. 157A, B, 158.—Felder 1973:61, pl. 9, fig. 6.

Recognition characters.—Carapace about $\frac{3}{4}$ as long as wide, anterior half semicircular, strongly deflexed, sparsely covered with long filiform and

plumose hairs. Anterolateral border with 4 marginal spines including outer orbital; 2 curved spines on hepatic region with sometimes 1, 2, or 3 supplementary spines; 1 long spine and sometimes spiniform tubercles between first and second marginal spines below margin. Orbit armed with 3 long spines above, and 4 long and 2 to 4 short spines below. Front advanced, deeply notched in center, less so on each side, armed with about 4 spines on each side.

Superior surfaces of chelipeds and walking legs with many filiform and plumose hairs; carpal and propodal articles most thickly covered and with several strong spines as well. Chelipeds large, unequal; carpus with 15 or 20 erect dark spines; spines of hand strong and acute above but becoming smaller on external surface, spines tending to arrangement in rows on large hand; fingers ribbed, dark, and with obtuse teeth; dactyl spiny above at base.

Measurements in mm.—Carapace: male, length 23, width 32; female, length 20, width 28.

Variation.—The specimen taken on Frying Pan Shoal off North Carolina (Charleston Museum No. 38.228) reported by Lunz (1939) appears to be an aberrant specimen of *Pilumnus sayi* rather than *P. marshi*. The specimen lacks superhepatic spines on the carapace but otherwise more nearly resembles *P. sayi* than any other western Atlantic species of *Pilumnus*. Reduced superhepatic spines are not unusual.

Color.—Grayish brown irregularly suffused with red or purple on body and legs; spines black, horn color, or purple; fingers of chelae black or brownish purple.

Habitat.—This species is fairly common from the Carolinas southward, and is often taken on shelly bottom. It has been taken from wharf piles, buoys (Lunz 1937a), the sponge *Stematumenia strobilina* (see Pearse 1934), and from offshore reefs (Pearse and Williams 1951; Cain 1972). From low-water mark to 90 m.

Type-locality.—Georgia and east Florida.

Known range.—North Carolina through Gulf of Mexico and West Indies to Curaçao.

Remarks.—Ovigerous females occur in the Carolinas from May to August, and in Florida perhaps year round (Gore, et al. 1978; Rouse 1970; Wass 1955). Chamberlain (1961) reported four zoeal stages and a megalopa in the larval development of the species, but did not describe the stages in detail. He found that larval development time varied with temperature (18 days at 30°C, 28 at 21°C) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, did moderately well on

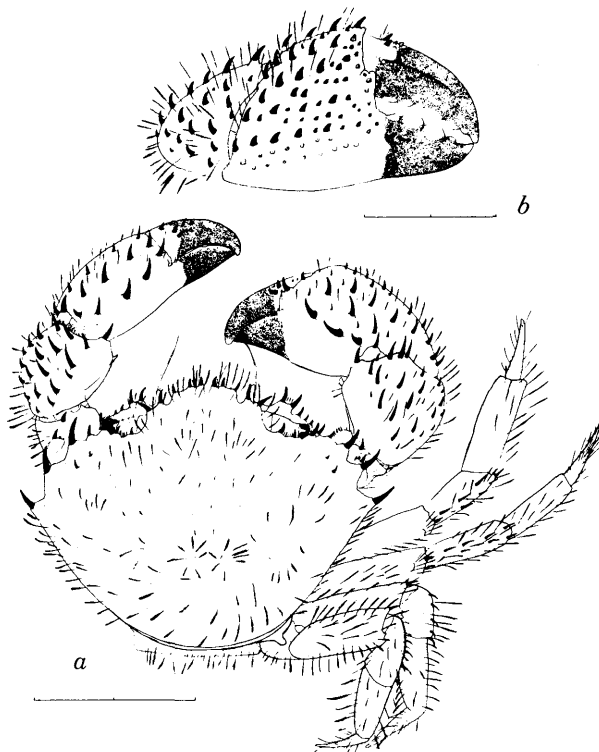


Fig. 339. *Pilumnus sayi* Rathbun. a, Male in dorsal view, walking legs of left side not shown; b, major chela in external view; 1 cm indicated (from Williams 1965).

Artemia and algae, but did not transform at all when fed algae alone. Amplifying these experiments, McDonald and Lang (1976) found that larvae reared at 20°C took twice as long to develop to crab stage II and exhibited higher mortality during metamorphosis from megalopa to crab stage I than larvae reared at 25°C. Mortality in the latter peaked at an earlier time in development. The difference in development time under the two conditions reflects tropical affinities of the species. Comparisons of the larval development of *P. sayi* and *dasyopodus* were given by Sandifer (1974a) and Bookhout and Costlow (1979).

Dudley and Judy (1971) found larvae in plankton at 1–8 m depth 1.6 km off Beaufort, N. C., from July to September, and from June to August 6.5 km offshore where they were more abundant at 8-m than at 1-m depth. None were found at stations 10–13 km from shore.

Genus *Lobopilumnus* A. Milne Edwards 1880

Rathbun 1930a:525.

Lobopilumnus agassizii (Stimpson)

Figs. 340g, 341

Pilumnus agassizii Stimpson 1871a:142.

Lobopilumnus agassizii.—Hay and Shore 1918:441, pl. 34, fig. 5.—Rathbun 1930a:526, pl. 211.—Williams 1965:181, figs. 157G, 163.

Recognition characters.—Regions of carapace protuberant, surface pubescent, except naked and thickly granulate on anterior and anterolateral regions; depressions between regions broad, occupying as much area as regions themselves. Front consisting of 2 large lobate masses deeply separated from each other and from orbits. Orbital region protuberant and granulate, margin crenulated with granules, with 2 fissures above and 2 very narrow ones below. Anterolateral margin with 3 triangular, spine-tipped teeth of moderate, equal size; subhepatic tooth distinct.

Chelipeds short, stout; carpus rough, tubercles thickly studded with forwardly directed granules, confluent laterally forming transverse ridges; superior and outer surfaces of hands covered with small prominent mammiliform tubercles, arranged largely in rows on outer surfaces and having apices directed forward. Walking legs pubescent and hairy, carpal and propodal articles with minute spines above.

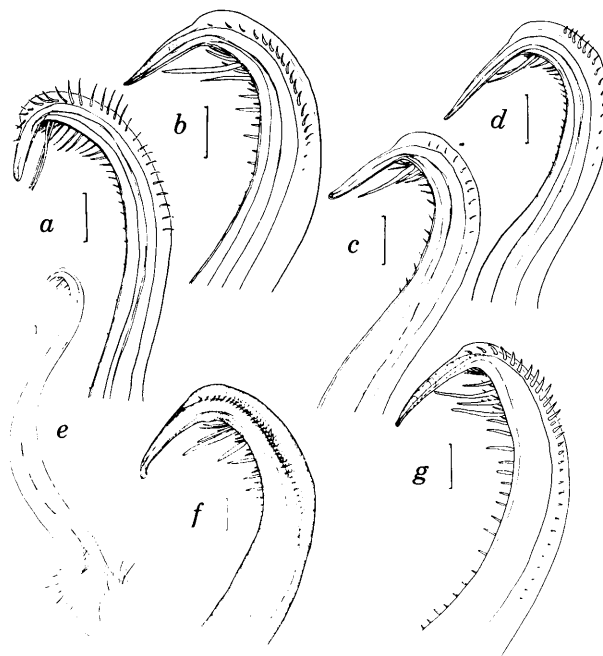


Fig. 340. Male first pleopods in mesial view: a, *Pilumnus dasyopodus* Kingsley, tip; b, *P. floridanus* Stimpson, tip; c, *P. lacteus* Stimpson, tip; d, *P. pannosus* Rathbun, tip; *P. sayi*, e, entire pleopod, f, tip in detail; g, *Lobopilumnus agassizii* (Stimpson), tip; a–g, 0.125 mm indicated (from Williams 1965).

Measurements in mm.—Carapace: female from North Carolina, length 16, width 21; male from Florida, length 23, width 31; female, length 20, width 27.

Variation.—Rathbun (1930a) stated that this species is variable as to the number and prominence of regions on the carapace, and she recognized four environmental forms within the species. Because only one specimen has ever been reported from North Carolina, and this is no longer extant, it is not possible to assign a form or forms to this area.

Color.—Gray above with granules and knobs yellowish red and reddish brown; legs white or with whitish spots (Schmitt in Rathbun 1930a).

Habitat.—In Bermuda, Verrill (1908a) found the carapace and legs of this species often thickly covered, sometimes almost concealed, by a coating of calcareous mud and sand adhering to hairs on the back. He found it most frequently under stones and dead corals at low tide. Pearse (1934) reported this crab from loggerhead sponge *Speciospongia vespara*. Low-tide mark to 51 m.

Type-locality.—Typical form: East and Middle Keys, Tortugas, Fla.

Known range.—North Carolina; eastern Gulf of Mexico; Yucatan; Cuba; Venezuela and Trinidad; Bermuda.

Remarks.—Ovigerous females are known from

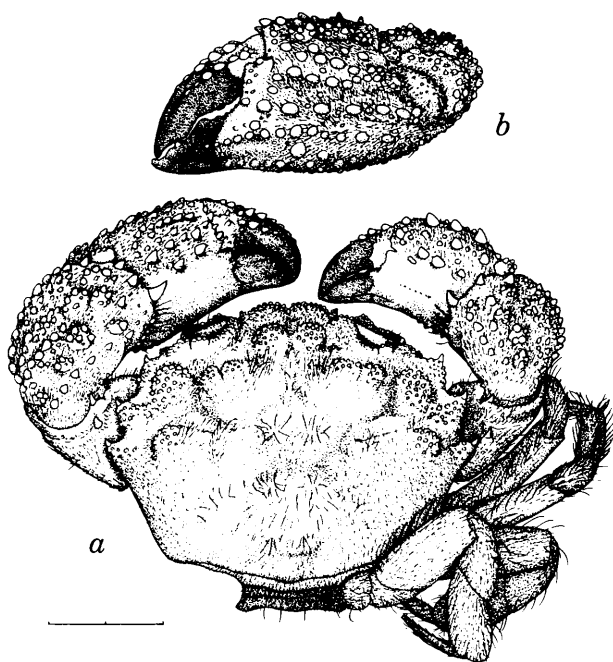


Fig. 341. *Lobopilumnus agassizii* (Stimpson). *a*, Male in dorsal view, walking legs of left side not shown; *b*, major chela in external view; 1 cm indicated (from Williams 1965).

February to July in Florida and Cuba (Rathbun 1930a, in part).

Genus *Melybia* Stimpson 1871

Rathbun 1930a:561.

Melybia thalamita Stimpson

Fig. 342

Melybia thalamita Stimpson 1871a:144.—Rathbun 1930a:562.—Coelho and Ramos 1972:194.—Powers 1977:96.

Recognition characters.—Surface finely granulate and covered with short, thin pubescence. Carapace subelliptical, slightly convex, regions faintly marked. Frontoorbital width about $\frac{5}{6}$ greatest width of carapace; front about $\frac{2}{3}$ width of carapace, depressed, divided by median V-shaped notch and separated by notch from inner orbital angle. Large orbits filled by stout eyes with cluster of spinules on anterior surface of stalk; orbital margin minutely crenulate, 2 notches above with space between arcuate, inner angle subtriangular. Antero-lateral margin short, bearing 4 spiniform acuminate teeth, first (outer orbital angle) and fourth small, middle 2 teeth larger, first occasionally bifid, but absent in juveniles. External maxillipeds broadly separated and densely hairy mesially.

Chelipeds unequal, long and strong, reaching far beyond carapace; merus armed with spines on upper and inner margins; carpus slightly spinulose above and laterally, 3 strong spines along inner margin; palm with double row of spines above; fingers $\frac{1}{4}$ – $\frac{2}{3}$ length of palm, heavy, broad, compressed, grooved, prehensile edges shallowly toothed; dactyl with superior carina roughened proximally. Walking legs long and slender, tapered and flattened, with sparse, long hairs; merus with superior row of spines and spine (sometimes smaller second) near distal end of lower margin in first 3 pairs; dactyl nearly length of propodus, spiny.

Measurements in mm.—Carapace: male, length 7.25, width 11.3; ovigerous female, length 4.9, width 7.3.

Variation.—Some specimens are smooth (Rathbun 1930a), old males may lack the distal lower spines on the merus of walking legs 1–3 (USNM 99731), and still others may have supernumerary spines as noted above.

Habitat.—Under *Sargassum*, coral and broken shell; beach to about 80 m, but also as deep as 368 m.

Type-localities.—Off French Reef, 27.4 m, and west of Tortugas [southern Fla.], 64–76.8 m.

Known range.—About 30 mi. SSE Cape Lookout, N. C. (34°11'N, 76°09'W); SW of Mississippi River Delta, through West Indies to Bahia, Brazil.

Remarks.—Ovigerous specimens are known from Puerto Rico in February, Barbados in March, and Florida in July.

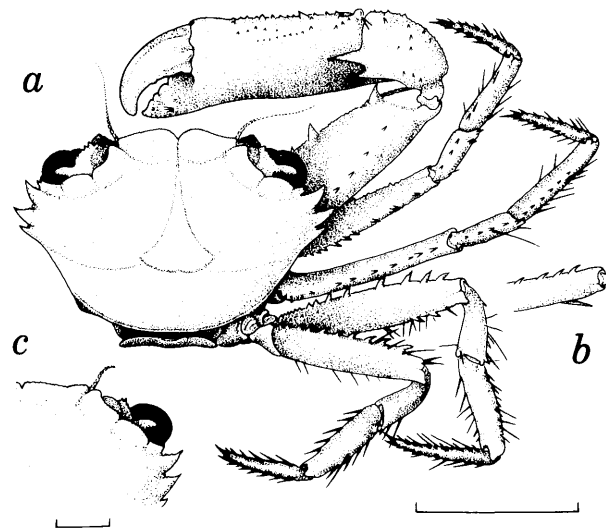


Fig. 342. *Melybia thalamita* Stimpson. *a*, Male in dorsal view, legs of left side not shown; *b*, distal end merus of first walking leg; *c*, portion of female in dorsal view; *a*–*b*, 5 mm, *c*, 1 mm indicated (USNM 7774).

Family Goneplacidae Dana 1852

Carapace usually quadrate. Orbit indistinctly divided into 2 hollows. Inner antennular septum a thin plate. Palp of third maxilliped articulating on or near anteromesial corner of merus; exognath of normal form and not concealed. Male genital openings either on sternum or, if coxal, with genital duct extending into groove on sternum. Marine forms, not sharply separated from the Xanthidae. (After Balss 1957.)

Guinot (1969a, b, c) tentatively regrouped a number of goneplacid genera into subfamilies that

are more restricted than the groupings set forth by Balss (1957) or listed by Serène (1968). The family is still not completely revised, and Guinot's preliminary work emphasizes Balss's statement that the Xanthidae and Goneplacidae merge. Her studies show this transition partly through changes in the male genital apparatus; the subfamilies as they stand now are based largely on structure of the male pleopods. Since a subfamily key based mainly on cryptic male characters has limited utility in a faunistic handbook, I list the subfamilies recognized by Guinot that are pertinent to this study, with the similarly pertinent genera of each, and give a key to the few species considered here.

Key to Subfamilies, Genera, and Species

1. Carapace xanthoid, anterior margin consisting of front, orbits, and anterior part of arched, toothed, anterolateral border 2
 Carapace subquadrate, anterior margin almost completely occupied by front and elongate orbits 5
2. Posterolateral borders obviously convergent; eyestalks rather thick and not conspicuously hairy 3
 Posterolateral borders imperceptibly convergent (almost parallel); eyestalks tapering to reduced cornea and conspicuously hairy
 [Pseudorhombilinae] *Speocarcinus carolinensis*
3. Front prominent and almost straight, with small median notch; usually 4 anterolateral teeth, second tooth largest; carpus of chelipeds smooth.
 [Eucratopsinae] *Glyptoplax smithii*
 Front with lobes convex; usually 5 anterolateral teeth; carpus of chelipeds roughened with rugae or lines of granules 4
4. Anterolateral teeth with smooth margins, first 2 coalesced, third largest, obtuse, with strongly curved lateral margin
 [Eucratopsinae] *Panoplax depressa*
 Anterolateral teeth with granular margins, first 2 low and coalesced, third and fourth strong and acute
 [Pseudorhombilinae] *Nanoplax xanthiformis*
5. Two anterolateral spines including outer orbital 6
 Three anterolateral spines including outer orbital
 [Euryplacinae] *Euryplax nitida*
6. Chelipeds with conspicuous tufts of dense hair
 [Euryplacinae] *Frevillea hirsuta*
 Chelipeds without conspicuous tufts of dense hair
 [Goneplacinae] *Goneplax sigsbei*

Subfamily Euryplacinae

Front with outer lobe more or less developed; strong projection extending ventrad to rest on basal antennal article. Orbit closed by antennal article or ventral projection from outer frontal lobe, or remaining open. Male abdomen basically triangular with segments 4–7 slender and progressively narrowed. Sternites much broadened, variable part of

sternite 8 visible at level of second abdominal segment. Genital opening of male either on coxa of fifth legs with genital duct tending to lie in sternal groove, or on sternum with genital duct passing mesially from coxa through involute groove between sternites 7 and 8 to emerge where groove flares. Male first pleopod long, rather slender, tapering to filiform tip, bearing small tubercles along length; second pleopod short. (Adapted from Guinot 1969b.)

Genus *Euryplax* Stimpson 1859

Rathbun 1918b:34.—Hemming 1958b:32.—Guinot 1969b:512.

Euryplax nitida Stimpson

Fig. 343

Euryplax nitida Stimpson 1859:60.—Rathbun 1918b:34, fig. 11, pl. 7.—Williams 1965:202, fig. 185.—Guinot 1969b:512, figs. 39, 41, 47, 56–57.—Felder 1973:70, pl. 10, fig. 1.

Recognition characters.—Carapace smooth and shining, convex, noticeably broader than long. Front with interantennal margin nearly straight but deeply notched on each side at insertion of antenna; wide ventral extension from front lateral to antenna overlapped by narrower infraorbital expansion from ventral side to close orbit. Anterolateral margin converging anteriorly, less than half as long as posterolateral margin and armed with 3 strong teeth including outer orbital, carapace widest at level of third tooth.

Merus of chelipeds in male with deep round pit at anterior distal corner of lower surface, pit surrounded by fringe of long hairs and with sharp curved spine near distal end of upper surface; carpus with inner surface pilose and bearing sharp spine. Walking legs slender.

Male abdomen basically triangular, concave sides of distal segments tapering to rather narrowly rounded telson; first segment barely visible, second widest and meeting coxa of fifth legs at each

side by leaving triangular, posterolateral corner of sternite 8 exposed between it and third abdominal segment at each side; exposed part of sternite 8 with involute edge meeting counterpart of sternite 7 to form short, closed groove housing genital duct opening sternally. Male first pleopods stout proximally but tapering to slender, darkened tip grooved mesially and bearing minute, sharp tubercles near tip.

Measurements in mm.—Carapace: male, length 15, width 25; female, length 15, width 24.

Variation.—Females have more nearly equal chelipeds lacking the meral pit with surrounding hair.

Color.—Distal half of fingers white (Rathbun 1918b).

Habitat.—Sandy shell, grass and mud bottoms; 3.5 to 90 m (Rathbun 1918b).

Type-locality.—Florida Keys.

Known range.—Off Beaufort, N. C., to Heald Bank, Tex. (USNM); West Indies to St. Thomas; Bermuda; specimen from “Bresil, Dertero” [sic] (= Florianopolis?) figured by Guinot (1969b).

Remarks.—Ovigerous females have been taken in June from southern Florida.

Randall (1969) reported *E. nitida* from stomach contents of the longspine squirrelfish, *Holocentrus rufus*.

Genus *Frevillea* A. Milne Edwards 1880

A. Milne Edwards 1880:15.—Guinot 1969b:513.

Frevillea hirsuta (Borradaile)

Fig. 344

Goneplax hirsuta Borradaile 1916:99, fig. 11.—Rathbun 1918b:28, fig. 7.—Williams 1965:201, fig. 184.

Frevillea hirsuta.—Guinot 1969b:513.—Coelho and Ramos 1972:194.

Recognition characters.—Carapace finely granulate, approximately $\frac{2}{3}$ as long as broad, greatest width between tips of outer orbital spines; regions faintly marked except for H-shaped depression in middle. Sides converging backward from prominent, sharp outer orbital spines each followed by sharp spine close behind. Front almost straight, with low prominence in broad, shallow median notch. Frontoorbital notch turned toward base of orbit, orbital hiatus open. Orbital margin sinuous, sloping backward, width of orbit and front nearly equal; ocular peduncles enlarged with globular cornea fully visible ventrally; infraorbital tooth present. Remarkably large basal antennular article lodged

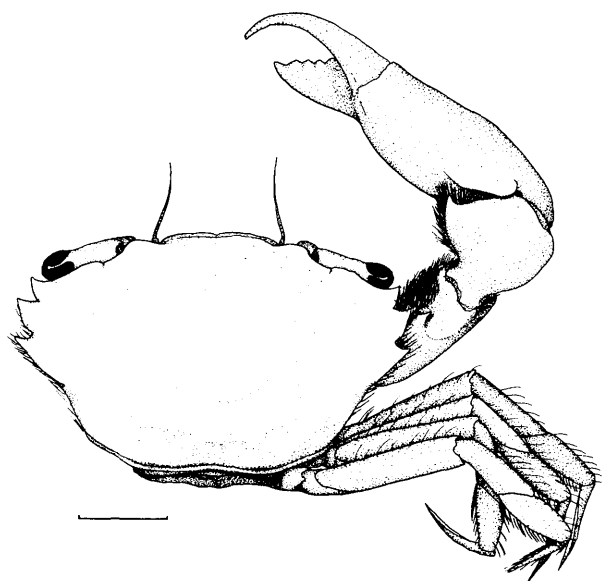


Fig. 343. *Euryplax nitida* Stimpson. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

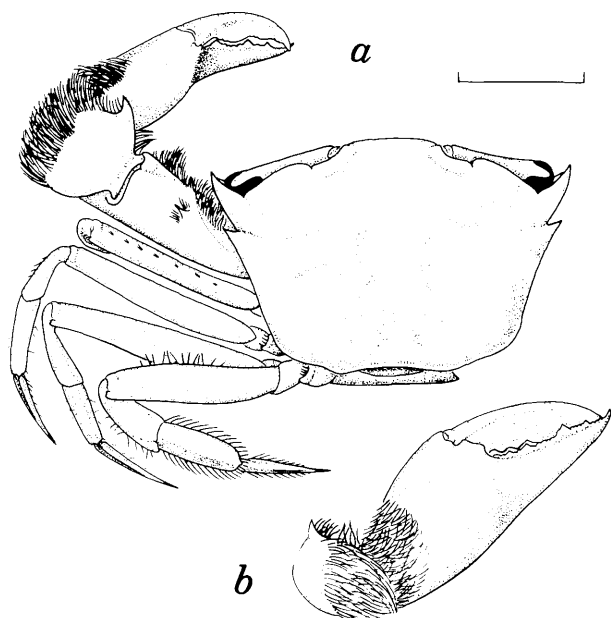


Fig. 344. *Frevillea hirsuta* (Borradaile). a, Male in dorsal view, legs of right side not shown; b, right chela and carpus in external view, 1 cm indicated (USNM 92361).

in more or less transverse fossa; following articles folding transversely and covering base of antenna.

Chelipeds almost equal; merus about $\frac{2}{3}$ length of carapace, deep, with spine a little beyond middle of upper edge; carpus broader than long, with stout internal spine. Hand longer than remainder of limb; fingers about equal to palm, irregularly toothed, not gaping; external base of hand and distal half of carpus with long dense tuft of hair, fringe of similar hairs along inner side of merus. Walking legs slender, meri smooth or fringed with light pubescence, distal articles fringed with hairs.

Male abdomen basically triangular, concave sides of distal segment tapering to rather narrowly rounded telson; first segment barely visible; second meeting coxa of fifth legs at each side but leaving tiny, uncovered posterolateral part of sternite 8 at each side between it and broader third abdominal segment. Lateral adjacent parts of sternites 7 and 8 separated by broad groove containing genital duct emerging from coxa of fifth leg. Male first pleopods stout proximally but tapering to slender tip, and bearing minute, sharp tubercles.

Measurements in mm.—Carapace: male, length 22, width 33; ovigerous female, length 19.3, width 29.

Habitat.—73 to 155 m.

Known range.—North Carolina to Rio de Janeiro, Brazil.

Remarks.—Ovigerous females have been taken in the Gulf of Mexico off Yucatan in January and Florida in June (USNM).

Subfamily Goneplacinae

Carapace subquadrate, widest between postorbital angles because of width of front and elongate orbits. Male genital openings on coxa of fifth leg but genital duct lying in groove between sternites 7 and 8. Male first pleopod stout along all of length, tapered toward apex; second pleopod longer than first.

Genus *Goneplax* Leach

Rathbun 1918b:25.—Hemming 1958b:32.—Guinot 1969b:520.

Goneplax sigsbei (A. Milne Edwards)

Fig. 345

Frevillea sigsbei A. Milne Edwards 1880:16.

Goneplax sigsbei.—Rathbun 1918b:26, pl. 4, figs. 2, 4.—Williams, McCloskey, and Gray 1968:54, fig. 10.—Guinot 1969b:520, figs. 63, 68, 71, 72.

Recognition characters.—Carapace subrectangular, broader than long; moderately convex, regions faintly indicated; anterolateral angles acute, outer orbital spine directed obliquely forward, second spine smaller, angled more outward; lateral borders posteriorly convergent. Frontoorbital complex occupying whole anterior border of carapace; front equal to or shorter than either orbit; slight depression behind orbital margin; eyestalks long, cornea enlarged. Antennules folding transversely, almost covering short basal article of antenna at either side, antennal flagellum in orbital hiatus. Buccal area anteriorly widened, well separated from prominent epistome.

Chelipeds with merus projecting well beyond carapace, occasionally with small tooth at middle of outer margin; carpus with small, blunt tooth at inner angle; palm with longitudinal groove on outer surface just above lower margin and more oblique shorter groove on inner surface; fixed finger much broader than dactyl, shallow irregular teeth on prehensile edges. First 3 walking legs with slender dactyls longer than propodi, distal 3 articles of reduced last leg relatively broader than in preceding legs.

Abdomen of male rather broadly triangular, sides concave, all segments free, second segment broadest; small lateral part of sternite 8 uncovered between abdominal segments 2 and 3. Genital duct emerging from male opening on coxa of last leg, lying in groove between sternites 7 and 8. Male first

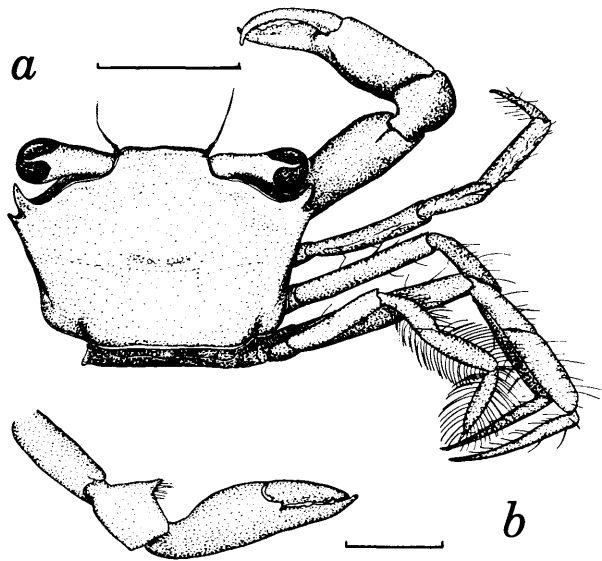


Fig. 345. *Goneplax sigsbei* (A. Milne Edwards). *a*, Male in dorsal view, legs of left side not shown; *b*, cheliped of immature specimen showing carpal spine; *a*, 5 mm, *b*, 1 mm indicated (from Williams, et al. 1968).

pleopod stout but tapered toward tip; slender second pleopod longer than first.

Measurements in mm.—Carapace: male, length 7.5, width 11.5; ovigerous female, length 10, width 12.5 (Williams, et al. 1968).

Habitat.—137 (Wenner and Read 1982) to 300 m.

Type-locality.—Grenada.

Known range.—E Cape Fear, N. C., 33°56'N, 76°26'W to 33° 55.3'N, 76°28.8'W, 130–120 m, Eastward Stn. 3213; Grenada, 11°27'N, 62°11'W, and 11°25'N, 62°04'15"W (Williams, et al. 1968).

Subfamily Eucratopsinae (= Prionoplacinae)

Carapace xanthoid, greatest width not at outer orbital corner; tendency to elongation of orbits and development of ocular peduncles. Sternum broadened behind chelipeds. Lateral part of sternite 8 variable, well covered by basal abdominal segments or broader and well exposed between edge of abdomen and coxa of fifth leg. Male genital openings coxal, with genital ducts extending onto sternum in a groove, or sternal, with ducts passing through involute sternal groove. Male first pleopods moderately stout, usually terminating in foliaceous lobe flanked by 2 processes, reminiscent of *Panopeus*. (Adapted from Guinot 1969a.)

Genus *Glyptoplax* Smith 1870

Rathbun 1918b:48.—Hemming 1958b:32.—Guinot 1969a:258.

Glyptoplax smithii A. Milne Edwards

Fig. 346

Glyptoplax smithii A. Milne Edwards 1880:336, pl. 61, figs. 4, 4a-d.—Rathbun 1918b:51, pl. 14, figs. 3–4; pl. 158, figs. 7–10.—A. Milne Edwards and Bouvier 1923:328, pl. 5, fig. 5.—Williams, McCloskey, and Gray 1968:55, fig. 11.
Glyptoplax smithi?—Guinot 1969a:359, fig. 24a-c.

Recognition characters.—Carapace xanthoid in form, narrow, hexagonal, slightly convex, distinctly areolated, slightly granulate anteriorly and in patches on areoles. Front prominent, lobes squared, somewhat deflexed, separated by tiny median notch and from inner orbital angle. Eyes of moderate size, median lobe on anterior margin of stalk. Anterolateral border usually with 4 teeth, rarely 5, tooth following outer orbital either completely obsolete or reduced; second of first 3 teeth present largest, last tooth much smaller. Basal antennal article just touching front, flagellum in orbital hiatus. Mouth area divergent anteriorly.

Chelipeds rather large; merus with superior granulate crest ending in tubercle or obsolescent spine; carpus occasionally nodulous as well as granulated, low internal spine or blunt projection; palm deep distally, lobe projecting inward from proximal upper margin; fixed finger of minor hand slightly deflexed, major less so and with large tooth at base of prehensile tooth row; fingers dark brown.

Male abdomen with broadest, conspicuous first segment reaching nearly to coxa of fifth leg at each side, its dorsal surface transversely grooved and granular, especially on slightly elevated lateral parts; second segment somewhat rectangular, much narrower than first, visible part of sternite 8 between it and coxa of fifth leg; segments 3–5 fused, sides slightly concave, posterolateral corner well rounded. Exposed lateral part of sternite 8 with involute anterior edge meeting counterpart from sternite 7 to form short, closed groove housing genital duct opening sternally. Male first pleopod fairly stout, terminating in 3 projections, opposite, divergent slender and obtuse projections exceeded by central, folded, membranous hood; shaft with tracts of spinules.

Measurements in mm.—Carapace, male, length 5.6, width 7.1; ovigerous female, length 4.75, width 6.5.

Variation.—In most individuals there are 4 prominent anterolateral teeth, but in a very few there is indication of the suppressed second tooth, and in others all of the teeth are poorly developed. Terminal elements of the male first pleopod are

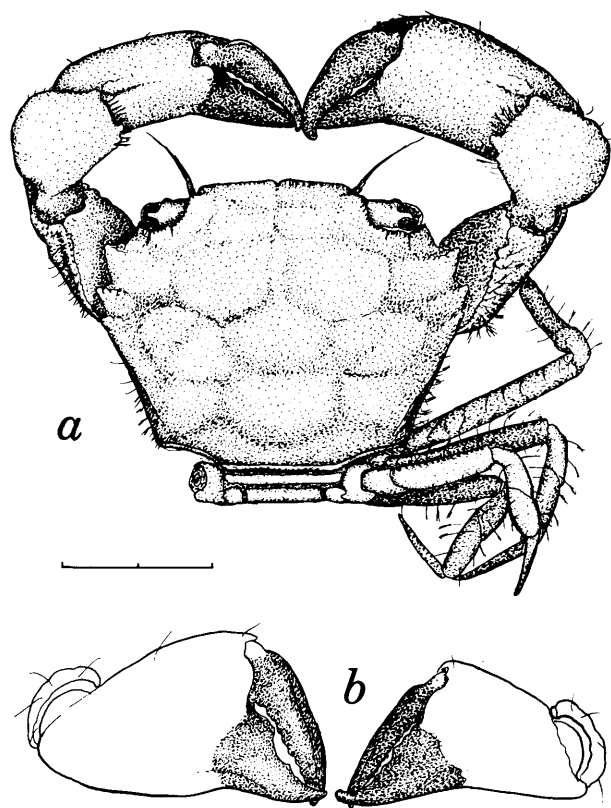


Fig. 346. *Glyptoplax smithii* A. Milne Edwards. *a*, Male in dorsal view, walking legs of left side not shown; *b*, chelipeds of same in frontal view; 2 mm indicated (from Williams, et al. 1968).

subject to some variation in size and folding of the central hood.

Habitat.—24 to 110 m.

Type-locality.—Reefs west of Florida, 23.8 m.

Known range.—From Cape Hatteras, N. C., to Gulf of Mexico and Yucatan Channel.

Remarks.—Guinot (1969a) pointed out differences between this species and *G. pugnax* Smith, the type-species of the genus, namely in male first pleopods and the visible part of sternite 8, suggesting that the two species probably do not belong in the same genus. Though these differences exist, the two are constructed on the same general plan, and I let the generic placement stand.

Ovigerous females are known from off North Carolina in January, May, and November, and off Yucatan in January.

Genus *Panoplax* Stimpson

Rathbun 1918b:47.—Guinot 1969a:264.

Panoplax depressa Stimpson

Fig. 347

Panoplax depressa Stimpson 1871:151.—Rathbun

1918b:47.—Guinot 1969a:264, figs. 3, 28a, b.
Eucratoplax elata A. Milne Edwards 1880.
Eucratopsis elata? A. Milne Edwards and Bouvier 1923:341, pl. 7, figs. 4, 5.
Micropanope levimanus Chace 1940:35; figs. 13, 14.
Micropanope laevimanus.—Guinot 1969a:265, figs. 29a, b.

Recognition characters.—Carapace depressed, arcuate anteriorly, much broader than long; finely punctate, granulate along anterolateral teeth and orbital margins, 2 oblique epigastric lobes. Frontal lobes convex, deflexed, well separated from inner orbital angles, margin often flanked by transverse, submarginal row of hairs. Orbit as wide as frontal lobe, frontoorbital margin $\frac{2}{3}$ width of carapace; superior orbital margin with 2 notches; eyes moderate. Anterolateral border with 5 teeth; outer orbital tooth separated from shallow second tooth by shallow sinus; third tooth large, blunt, outer margin strongly arcuate; fourth triangular, acute, located at greatest carapace width; fifth reduced, usually not projecting beyond general outline. Posterolateral margins moderately converging.

Chelipeds with merus and carpus granulate toward margins; merus dentate on upper margin; carpus oblong, stout tooth at inner angle and few tubercles below it, anterior transverse groove; palms smooth and rounded, punctate; fingers not gaping, prehensile teeth low and broad, color not extending on palm. Walking legs with meri roughened, distal articles hairy, carpi and propodi broadened, especially on last leg.

Abdomen of male broadest at segment 1; posterolateral corner of sternite 8 conspicuous lateral to abdominal segment 2 and wedged between lateral parts of segments 1 and 3; segments 3–5 fused, basically triangular but concave laterally. Exposed lateral part of sternite 8 with involute anterior edge meeting counterpart from sternite 7 to form short, closed groove housing genital duct opening sternally. Male first pleopods gently curved, tapering to twisted tip terminating in membranous, irregular, minutely spinulate lobe; tiny, short spines on shaft distally.

Measurements in mm.—Carapace: male, length 7.5, width 10.9; female, length 8.2, width 12.7.

Variation.—Granulation of the carapace and chelipeds is most distinct in larger males; the carpus of the chelipeds is occasionally rugose distally. Acuteness of the third and fourth anterolateral teeth varies from acute to obtuse; in juveniles to subadults these teeth may be spine tipped. The terminal lobe of the male first pleopod is mostly elon-

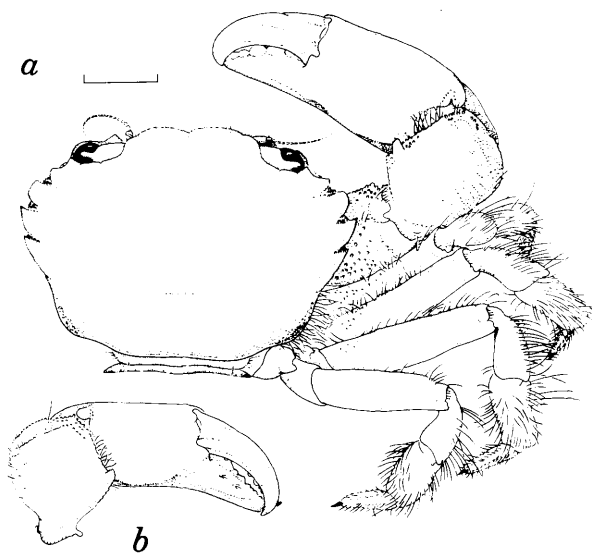


Fig. 347. *Panoplax depressa* Stimpson. a, Male in dorsal view, legs of left side not shown; b, same, left chela and carpus in dorsal view; 2 mm indicated (USNM 24556).

gate but occasionally shorter, as noted by Guinot (1969a, figs. 29a, b, c), and rarely somewhat folded distally. This last may be an artifact of preservation. The fused male abdominal segment 3–5 becomes more concave sided as the body broadens with age.

Habitat.—Recorded from coral rock, 5 to 95 m.

Type-locality.—East and Middle Keys, Tortugas, [Fla.], 9.1. to 12.8m.

Known range.—SE of Cape Lookout, N. C.; off Jacksonville and Cape San Blas, Fla., through West Indies to Barbados.

Remarks.—Guinot (1969a) suggested the above synonymy for this species on the basis of preliminary study. Following examination of a series of identified material in the USNM and type-material of *Eucratoplax elata* and *M. levimanus*, I agree with her analysis.

Ovigerous females are known from Puerto Rico in March and Dry Tortugas in July.

Subfamily Pseudorhombilinae

Carapace xanthoid, anterolateral border arched and armed with 5 teeth. Male with lateral part of sternite 8 variably covered by basal abdominal segments but always exposed between edge of abdomen and coxa of fifth legs; adjacent exposed edges of sternites 7 and 8 involute, forming tube housing genital duct opening sternally. Male first pleopods strong, twisted and often ornamented with spinules following twist of shaft, terminated by rolled lobe; second pleopod short. (Adapted from Guinot 1969c.)

Genus *Nanoplax* Guinot 1967

Guinot 1967:362.

Nanoplax xanthiformis (A. Milne Edwards)

Fig. 348

Panopeus xanthiformis A. Milne Edwards 1881:353, pl. 53, figs. 4–4b.

Micropanope xanthiformis.—Rathbun 1930a:442, pl. 180, figs. 7–8.—Lunz 1937:13.—Williams 1965: 193, figs. 176, 183I.

Nanoplax xanthiformis.—Guinot 1967a:362, fig. 16.—Coelho and Ramos 1972:192.

Recognition characters.—Carapace much broader than long, hexagonal, convex anteroposteriorly; regions well defined, depressed coarse granulations on anterior and anterolateral portions, oblique ridge parallel to margin on hepatic region. Front slightly deflexed, shallow, lobes separated by shallow notch; margin sinuous, outer corner rectangular. Anterolateral margin arched, bearing 5 teeth with sharply granulate margins; first small; second small, lobiform, and separated from preceding by slight notch; third strong and triangular; fourth more spiniform; fifth small and pointed.

Chelipeds rather strong, unequal, rugose with coarser granules than on carapace; merus with row of spines above; carpus with prominent anterior groove, strong internal spine and often a smaller spine or spiniform tubercle below it; major hand slightly roughened on upper and proximal parts; minor hand rougher on outer surface; fingers deeply grooved, major dactyl with large basal tooth. Walking legs elongate, merus with row of spines above, other legs spinulose.

Male abdomen rather short; third segment concealing sternum, narrower second segment with posterolateral corner obliquely truncate revealing small portion of sternum; first pleopod strong, tightly twisted on long axis, opening apical.

Measurements in mm.—Carapace: male, length 9.9, width 14.5; female, length 8.1, width 11.2.

Variation.—There is considerable individual difference in roughness of chelipeds; the major hand, especially, is relatively smoother in older individuals.

Color.—"Anterior portion of carapace light yellowish orange. Fingers of major chela brownish black, of minor chela black. Spines and tubercles of both chelipeds light salmon" (Rathbun 1930a).

Habitat.—Various types of bottom in deeper water; 11 (Wenner and Read 1982) to 340 m.

Type-locality.—Off Grenada, 168.3 m.

Known range.—Cape Hatteras, N. C.; through

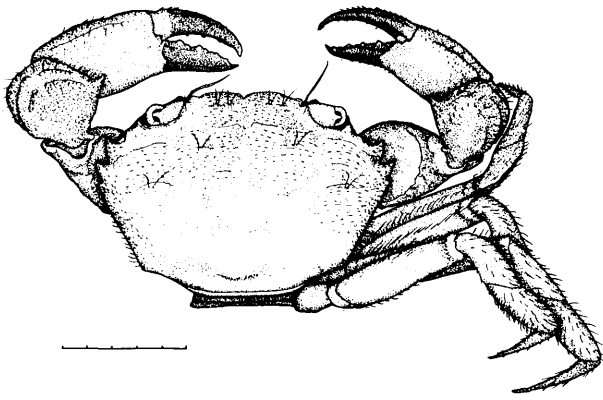


Fig. 348. *Nanoplax xanthiformis* (A. Milne Edwards). Animal in dorsal view, walking legs of left side not shown, 5 mm indicated (from Williams 1965).

Gulf of Mexico and West Indies to Cabo Frio, Rio de Janeiro, Brazil.

Remarks.—Ovigerous females are known in June, August, and November from Florida, and in October from North Carolina (Rathbun 1930a, in part; Camp, et al. 1977).

Guinot (1967a; 1971) placed *Nanoplax* in both the Xanthidae and the Goneplacidae, leaving its status uncertain.

Genus *Speocarcinus* Stimpson 1859

Rathbun 1918b:38.—Hemming 1958b:37.—Guinot 1969c:706.

Speocarcinus carolinensis Stimpson

Fig. 349

Speocarcinus carolinensis Stimpson 1859:59, pl. 1, figs. 1–3.—Rathbun 1918b:39, pl. 8, pl. 159, fig. 6.—Williams 1965:202, fig. 186.—Guinot 1969c:707, figs. 119–122, pl. 4, fig. 1.

Speocarcinus carolinensis Fausto-Filho and Neto 1976:69.

Recognition characters.—Carapace convex longitudinally, gastrocardiac and mesogastric regions faintly outlined; surface punctate, obscurely granulate near margin, faintly rugose, varyingly pubescent; anterior and anterolateral margins beaded. Front straight, projecting and deflexed, $\frac{1}{4}$ width of carapace, median notch. Orbital margin with faint lobe between dorsal fissures; infraorbital tooth pointed; ocular peduncles hairy, narrowing from thickened base to cornea, not filling orbit. Anterolateral border with 5 teeth including outer orbital; second tooth rounded and poorly separated from first by shallow concavity, third lobiform but pointed,

fourth more acute and directed forward; fifth smaller, acute and directed slightly more laterad. Posterolateral margin almost parallel. Third maxillipeds divergent anteriorly.

Chelipeds strong, short, unequal; -merus with strong spine on upper border; carpus granulate internally and with blunt internal spine; hands with outer surface smooth, microscopically granulate, 2 rows of small tubercles on upper surface (often most prominent on minor), diminishingly continued on dactyls; fingers with low, irregular teeth on prehensile edges, stronger on major hand with stout tooth at base of dactyl. Walking legs with hairy margins, tapered to very slender dactyls.

Male with large part of sternite 8 exposed lateral to abdominal segments 1 and 2; abdominal segments 3–5 fused, broadest at base, concave sided. Exposed lateral part of sternite 8 with involute anterior edge meeting adjacent counterpart of sternite 7 to form closed groove housing genital duct opening sternally. Male first pleopods rather slender, twisted and tapering to terminal lobe bent mesially at right angle to shaft; second pleopods short.

Measurements in mm.—Carapace: male, length 23, width 29; female, length 17, width 27 (most individuals smaller).

Habitat.—Burrows of worms, *Squilla*, *Callinassa*, and other crustaceans in mud (Stimpson in Rathbun 1918b); near low-tide mark to 149 m (150 m according to Fausto-Filho and Neto 1976).

Type-locality.—Charleston Harbor, S. C.

Known range.—S Cape Hatteras, N. C., 35°3.5'N, 75°25.7'W, through West Indies to Amapá, Brazil.

Remarks.—Guinot (1969c) regarded *S. carolinensis* as recognized until that time to be a composite

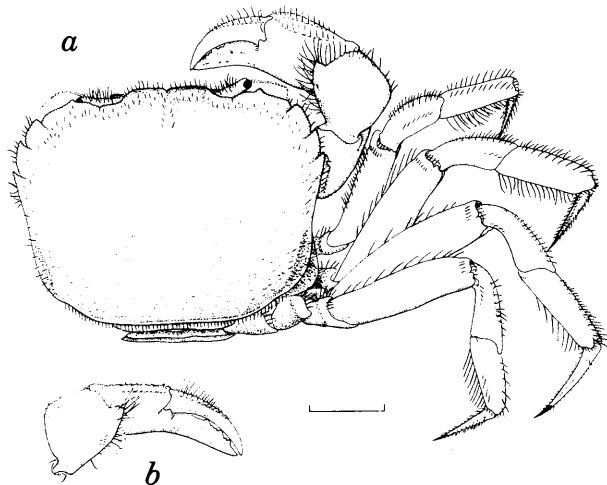


Fig. 349. *Speocarcinus carolinensis* Stimpson. a, Female in dorsal view, legs of left side not shown; b, same, left chela and carpus in dorsal view; 5 mm indicated (USNM 45951).

species. She restricted *S. carolinensis*, recognized specimens from off Texas in the Gulf of Mexico, and Surinam, as *S. lobatus* Guinot, and described a probable third species from Puerto Rico.

An ovigerous female is known from North Carolina in August.

Superfamily Pinnotheroidea

Family Pinnotheridae

Carapace often somewhat membranous. Anterolateral margins entire or very slightly dentate.

Front, orbits, and eyestalks very small, cornea often rudimentary. Buccal cavity usually wide, often semicircular in outline. Merus of third maxilliped never quadrate, and never with palp distinctly at anterointernal angle; ischium small, absent, or fused with merus and directed obliquely inward (Rathbun 1918b).

Small crabs living as commensals or parasites in bivalve mollusks, ascidians, worm tubes, and on or in echinoderms. Free-living or migratory stages are occasionally taken in open water.

Key to Genera

1. Dactyls of walking legs simple, acute 2
Dactyls of first, second and third walking legs bifurcate *Dissodactylus*
2. Third walking leg longer and stronger than other walking legs, often considerably so *Pinnixa*
Third walking leg little, if any, longer than other walking legs 3
3. Walking legs diminishing in size from distinctly largest first to smallest last leg; carapace about twice as broad as long, oval, flattened and rather firm; buccal mass subtriangular *Parapinnixa*
Walking legs similar shaped, second and third nearly equal in length; carapace suborbicular, or flattened and firm in small stages 4
4. Buccal mass subquadrate; carapace somewhat orbicular and either smooth and membranous or firm and covered with short pile *Pinnotheres*
Buccal mass subtriangular; carapace firm, smooth *Pinnaxodes*

Subfamily Pinnotherinae

Carapace usually not markedly transverse. Ischium of external maxillipeds either rudimentary or indistinguishably fused with merus to form single piece, usually oblique, occasionally nearly trans-

verse; palp not so large as merus-ischium (Rathbun 1918b).

Genus *Dissodactylus* Smith 1870

Rathbun 1918b:114.—Hemming 1958b:31.

Key to Species

1. Dactyls of walking legs 1–3 bifurcated less than halfway to base
. *D. crinitichelis*
Dactyls of walking legs 1–3 bifurcated halfway to base *D. mellitae*

Dissodactylus crinitichelis Moreira

Fig. 350

Dissodactylus crinitichelis Moreira 1901:37, pl. 3, figs. 1–4.—Rodrigues [da] Costa 1971:260.—Coelho and Ramos 1972:196.—Schmitt, McCain, and Davidson 1973:17.—Powers 1977:120.

Dissodactylus encopei Rathbun 1901:22, fig. 5a-e.—1918b:119, text-figs. 67a-e, pl. 27, figs. 1–4.—Williams, McCloskey, and Gray 1968:56, fig. 12.

Recognition characters.—Carapace about 1.4 times

wider than long, posterior width little less than greatest width. Dorsal surface nearly naked and polished, strongly convex longitudinally, slightly so transversely. Anterolateral margins and front smoothly arched, former marked by slightly raised line continued somewhat mesioposteriad on carapace beyond rounded lateral angles. Posterolateral margins slightly convergent, posterior margin sinuous. Ventrolateral margins of carapace and margin of female abdomen clothed with soft hair. Outer maxillipeds very small; inner distal angle of propodus fitting against thickened, hairy inner angle of

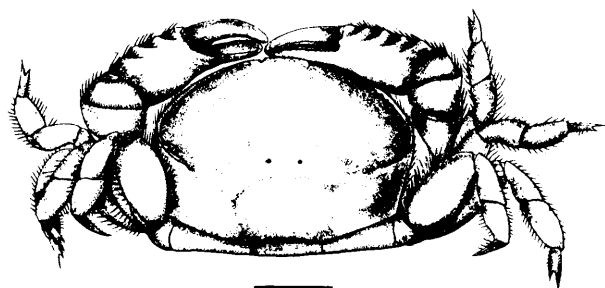


Fig. 350. *Dissodactylus crinitichelis* Moreira. Male in dorsal view, 2 mm indicated (from Moreira 1901).

merus; merus-ischium subspatulate, curved; propodus about as long as carpus, widening distally, truncate and bearing short, stumpy dactyl at distal, inner angle.

Chelipeds short, stout, upper and outer surfaces of propodus and carpus crossed by oblique rugae fringed with hair; hand elongate, subcylindrical, upper margin nearly straight, lower margin sinuous; fingers deflexed, grooved edges meeting when closed, tips acute, crossing, tooth at base of dactyl fitting in sinus of fixed finger. Walking legs lightly fringed with long hair, dactyls 1–3 curved, bifurcate less than halfway to base and acuminate; that of last leg straight, styliform.

Male abdomen with segments 1–2 fused and very slightly constricted at middle, segments 3–6 fused, sides slightly convex, telson equilaterally triangular; female with all segments free, 3–6 nearly equal in width, triangular telson broad and short.

Measurements in mm.—Carapace: male, length 4.6, width 6.6; female, length 5, width 9 (Rathbun 1901).

Habitat.—Fine white sand, coral and broken shell bottoms; sea grass (*Halodule*); commensal in various parts of its range on the echinoids *Encope emarginata*, *E. michelini*, and *Clypeaster subdepressus*; to 52 m (summarized by Schmitt, et al. 1973; Powers 1977).

Type-locality.—Estado de Rio Grande do Sul, Brazil.

Known range.—Southeast of Cape Lookout, N. C.; off northwest Florida; Caribbean Sea and South America to Rio de la Plata, Argentina (Coelho and Ramos 1972).

Remarks.—Ovigerous females are known from west Florida in March, Barbados in June, and Jamaica in September (USNM).

Dissodactylus mellitae (Rathbun)

Fig. 351

Echinophilis mellitae Rathbun 1900a:590.

Dissodactylus mellitae.—Rathbun 1918b:117, text-fig.

66, pl. 28, figs. 7–8.—Hay and Shore 1918:444, pl. 36, fig. 1.—Williams 1965:209, fig. 192.—Schmitt, McCain, and Davidson 1973:18.—Powers 1977:120.

Recognition characters.—Minute. Carapace about $\frac{1}{4}$ wider than long, slightly wider at lateral angles than posteriorly, dorsal surface convex, smooth and polished except anterior parts slightly pubescent. Edge of front concave, fringed with short hairs. Anterolateral borders arcuate, with fine raised rim curving inward on carapace at lateral angles and continuing mesioposteriorly for some distance; posterior margin sinuous. Orbits opening mesially, eyes small. Outer maxilliped with fused, spatulate merus and ischium; outer edge of carpus arcuate; propodus quadrate.

Chelipeds short and stout; hand longer than other articles combined, cylindrical, upper and outer faces bearing few impressed, short, oblique lines with short appressed hairs extending distally; fingers considerably shorter than palm, bent inward and curved, opposable margins with tufts of short bristles; carpus with distal fringe of short hairs and an impressed line similar to those of chelae; merus short and stout, lower surface with oblique lines. First, second, and third walking legs stout, margins fringed with short hairs, dactyls bifurcated halfway to base; fourth walking legs with styliform dactyls, fringed with long hairs on margins.

Abdomen of male with first and second, and third to fifth segments partially fused, margins convex; telson subtriangular with convex sides. Abdomen of females with first segment linear, second to fourth fused; telson broadly triangular, half as wide as sixth segment, sides sinuous.

Measurements in mm.—Carapace: male, length 2.9, width 3.5; ovigerous females, length 3.3, width 4.5.

Color.—Light, with scanty dark mottlings which persist in alcohol and are then of purplish color (Rathbun 1918b).

Habitat.—This species clings to the outside of the keyhole urchin *Mellita quinquesperforata* and the sand dollars *Echinarachnius parma* and *Encope michelini*. The crabs are easily overlooked because as the sand dollars are lifted from the water, the small crabs may move about and drop off. Shallow water to 124 m (Wenner and Read 1982).

Type-locality.—Pensacola, Fla., on *Mellita quinquesperforata*.

Known range.—Western part of Vineyard Sound, Mass., to Charleston, S. C.; Hutchinson Island, east Florida (Camp, et al. 1977); western Florida; off Galveston, Tex. (Rogers 1968).

Remarks.—Hyman (1924a) described the first zoeal stage of this crab, comparing it to the zoea of

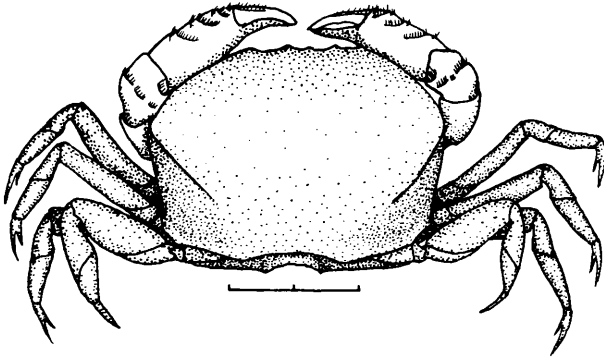


Fig. 351. *Dissodactylus mellitae* (Rathbun). Animal in dorsal view, 2 mm indicated (from Williams 1965).

Pinnotheres maculatus, and reported it as common in plankton tows in the Beaufort, N. C., area in summer. Dudley and Judy (1971) found the larvae in low concentrations off Beaufort Inlet from May to October. Ovigerous females occur there during summer, and are reported from Narraganset Bay in August (Rathbun 1918b), and in Florida from July to October (Wass 1955, in part). Sandifer (1973d) found larvae tentatively identified as *D. mellitae* only twice in plankton near the mouth of

Chesapeake Bay in July and August, and Tagatz (1968) found them once in May in St. Johns River, Fla.

Dissodactylus mellitae reacts positively to host-factor of *Mellita quinquiesperforata* and also to *Encope michilini* when it is conditioned to the latter for a day or two before testing (Gray, et al. 1968). It is possible that the crab may be conditioned to any flat sand dollar, but it does not react to other echinoderms in experiments. Rate of flow of scent-bearing streams was an important factor in orienting and directing the crabs toward a host, the stronger of unequal currents being more effective. In nature, crabs dislodged from a host are seldom far from other sand dollars and can search randomly for host-factor streams. When a crab locates a host it pounces on it and scurries to the oral side. Incidence of crabs on *Mellita* in the Beaufort, N. C., area varies from 9% to 88% (\bar{x} = 33%) in surveys, with a mean of 1.22 crabs per host.

Genus *Pinnotheres* Bosc [1802]

Rathbun 1918b:62.—Hemming 1958b:36.—Schmitt, McCain, and Davidson 1973:36

Key to Species

Key to Hard-stage Males and Females

1. Carapace with striking pattern of light spots on dark background of pubescence. *P. maculatus*
- No striking color pattern *P. ostreum*

Key to Posthard Females (and Male *P. maculatus*)

1. Carapace nearly naked 2
- Carapace covered with short, deciduous pubescence *P. maculatus*
2. Third maxilliped lacking dactyl on propodus; host mollusk *Chama congregata*, little corrugated jewel box *P. chamae*
- Third maxilliped with dactyl inserted behind middle of propodus; host mollusk *Crassostrea virginica*, American oyster *P. ostreum*

Pinnotheres chamae Roberts

Fig. 352

Pinnotheres chamae Roberts 1975:238, figs. 1–2.—1975a:243–252 (passim), figs. 1–5.

Recognition characters.—Mature female: Carapace suborbicular, widest posteriorly; smooth non-pubescent, regions undefined. Front narrow, covering eyes in dorsal view; lateral margin with dense row of plumose setae. Antennules folding beneath

carapace, short 4-segmented outer ramus bearing numerous long aesthetascs, inner 2-segmented ramus bearing 2 short terminal setae and 2 subterminal setae. Antennae originating in orbits, 5-segmented. Buccal mass roughly quadrangular but crescentic in outline, much broader than long; ischium and merus of external maxilliped united; carpus or first article of palp densely setose, terminal propodus smaller.

Chelipeds symmetrical, elongate, slender; propodus setose on inner surface, palm swollen at in-

sertion of dactyl; tips of both fingers calcareous and hooked almost at right angle; prehensile edges closing closely, tip of dactyl crossing inside slightly longer fixed finger; more slender dactyl with 2 or 3 small proximal teeth and larger tooth fitting between teeth on fixed finger; latter bearing 2 teeth proximally, distal one serrate. Walking legs slender, similar in length, last leg originating slightly dorsal to preceding leg; slender tips of dactyls curved sharply inward, first 3 legs with dactyls bearing scattered short setae, that of fourth with dense row of long plumose setae on inner margin.

Abdomen wider than carapace, third and fourth segments widest.

Male unknown.

Measurements in mm.—Carapace of female: length 4.3–6.8, width 3.6–5.9 (Roberts 1975).

Color.—Ivory or cream; eyes brown, ovaries bright orange (Roberts 1975).

Habitat.—"Commensal with *Chama congregata* attached to coral nodules" (Roberts 1975).

Type-locality.—North Carolina coast.

Known range.—Known only from type-locality.

Remarks.—The above data from Roberts (1975) were taken from the holotype and seven paratype females.

Roberts (1975a) reared and described larval stages

that developed from eggs on six of these females. The females were placed individually in finger bowls containing 200 ml of filtered water of 31‰ salinity at 25°C and maintained with daily changes of water until the eggs hatched. Adults were not fed. After hatching, zoeae from a single female were placed individually in plastic compartmented boxes with 50 ml of filtered water of 31‰ salinity, at temperatures of 23.5°–28°C (\bar{x} = 25.3°C) over a culture period of 22 days. A mixture of post-trochophore larvae of *Arenicola marina* obtained from egg masses held in filtered seawater for 24 h, and *Artemia* nauplii were provided as food. In addition, a mass culture was established in a large finger bowl containing 1 liter of like water and fed the same food. All larvae were examined daily as they were transferred to clean water.

Three zoeal instars and one megalopa were observed, described and illustrated. Intermolt durations were: zoea I, 3.2 days; II, 3.7 days; III, 3.7 days; megalopa, 1.5 days. The first crab stages were also described. In summarizing knowledge of the morphology of two groups of *Pinnotheres* larvae, those with carapace spines and those without, Roberts pointed out that *P. chamae* and *P. ostreum* among American species lack spines but *P. maculatus* is spined.

Pinnotheres maculatus Say

(Mussel crab)

Fig. 353

Pinnotheres maculatus Say 1818:450.—Rathbun 1918b:74, text-figs. 35–36, pl. 17, figs. 3–6.—Hay and Shore 1918:443, pl. 35, fig. 10.—Williams 1965:206, fig. 190.—Coelho and Ramos 1972:195.—Felder 1973:74, pl. 10, figs. 10–11.—Schmitt, McCain, and Davidson 1973:53.—Fenucci 1975:167, pl. 3, figs. A, N.—Powers 1977:123.

Recognition characters.—Mature female: Carapace suborbicular, somewhat broader than long, thick and firm but not hard, convex, smooth; surface uneven, covered with short, dense, fragile, woolly hairs. Gastrocardic area higher than, and separated by depression from, branchiohepatic area. Front slightly advanced, approximately $\frac{1}{3}$ width of carapace, subtruncate in dorsal view, slightly bilobed. Orbits small, subcircular, eyes spherical. Antenna longer than width of orbits; antennules large, obliquely transverse. Buccal mass roughly quadrangular, crescentic, much broader than long; ischium and merus of external maxilliped united;

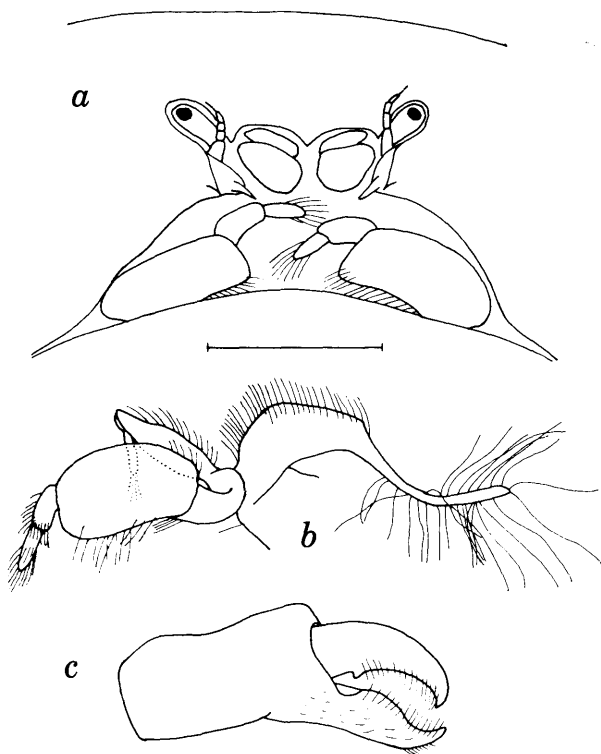


Fig. 352. *Pinnotheres chamae* Roberts. Female; a, Ocular and buccal regions in frontal view; b, third maxilliped; c, chela; 1 mm indicated (from Roberts 1975).

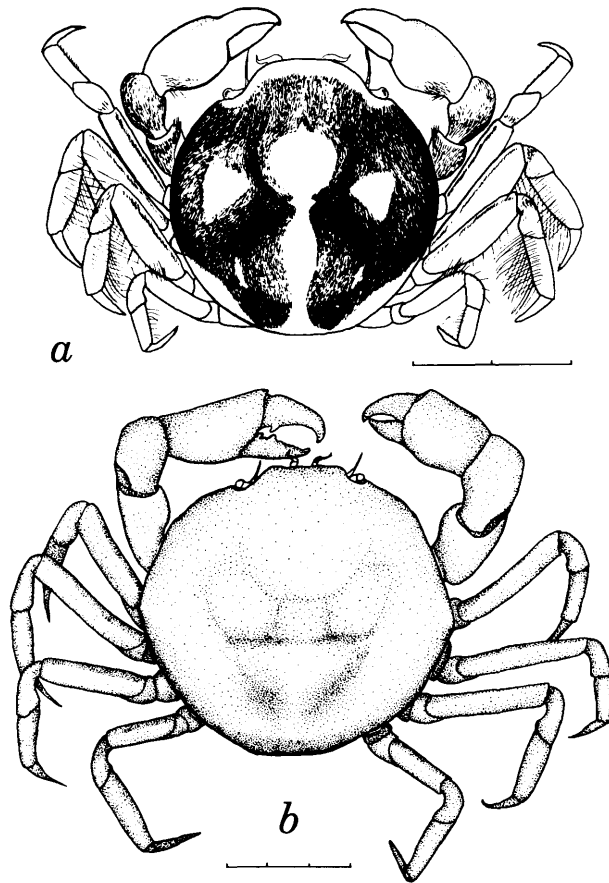


Fig. 353. *Pinnotheres maculatus* Say. *a*, Male in dorsal view, 2 mm indicated; *b*, female in dorsal view, 3 mm indicated (from Williams 1965).

propodus larger than carpus; dactyl narrow, curved, spatulate, attached near middle of propodus, and reaching to near extremity of propodus.

Chelipeds moderately stout, articles subcylindrical and more or less pubescent; carpus elongate; palm thick, blunt edged, increasing in size distally; fingers stout, fitting closely together with tips hooking past each other, fixed finger nearly horizontal, dactyl with tooth near base fitting into sinus with tooth at either side on fixed finger. Walking legs slender, hairy above and below; second pair longest, shorter than chelipeds; first 3 dactyls falcate, shorter than propodi; last leg shortest, turned forward and upward, with long dactyl equaling propodus.

Abdomen large, extending to bases of legs.

Measurements in mm.—Carapace: length 13.7, width 14.3.

Color.—Obscure brown.

Recognition characters.—Mature male: Carapace flat, subcircular, diameter about half as great as female, somewhat longer than wide, harder than female. Regions superficially defined more by color than by structural prominence, light areas mostly

elevated, usually allowing pubescence to wear; gastric, cardiac, and branchial regions separated by broad, shallow, confluent indentations. Front broad, prominent, depressed, slightly bilobed, approximately $\frac{1}{3}$ width of carapace. Orbits subcircular, eyes large. Antennae somewhat longer than width of orbit.

Chelipeds shorter than in female, hands stouter. Walking legs wider, especially propodal articles of first 3 legs; posterior surface overlaid with thin fringe of hairs attached near upper margin; last leg relatively shorter than in female, not reaching propodus of third, dactyl more nearly like third than in female.

Abdomen at middle approximately $\frac{1}{3}$ width of sternum, gradually narrowing from third to seventh segment, sides of third convex, of seventh obtusely rounded; sutures between segments of abdomen and sternum with narrow lines of dark pubescence.

Measurements in mm.—Carapace: length 9.1, width 8.7.

Color.—Striking, light dorsal color pattern of bare spots on background of dark pubescence consisting of median stripe constricted in middle and behind, a subtriangular spot on each side in front of middle, and a linear spot on each side behind. Chelipeds with dark pubescence on inner and upper surface of carpus, a bit on upper surface of merus and inner side of palm proximally, otherwise scattered flecks on hands and walking legs.

Variation.—Young females resemble dark-colored males except in shape of the abdomen and the character of its appendages. Such females are free swimming and range upward in length to 5.2 mm. More mature females, light colored and commensal or parasitic in habit, range from 3.3 mm in length upward. In such small and medium-sized females the long hair on the legs persists.

Some males resemble mature females in coloration and structure of legs, ranging in length from about 4 mm upward. Such males are commensal or parasitic in habit.

Individuals vary in stoutness of chelae, and in length and curvature of dactyls on the second legs. Normally this dactyl is like the dactyls on the first and third legs, but may be straightened and longer, and may occur on one or both sides of an individual and in different individuals in the same lot.

Habitat.—Mature males or females are commensal or parasitic in *Argopecten irradians concentricus*, *A. gibbus*, *Anomia simplex*, *Atrina serrata*, *A. rigida*, *Mytilus edulis*, *Modiolus modiolus*, *M. tulipa*, *Mya arenaria*, *Chlamys magellanica*, *C. tehuelcha*, *Ostrea puelchana* and a number of other bivalves, plus tubes of *Chaetopterus variopedatus*, from *Molgula robusta*,

the pharynx of *Bostrichobranchus pilularis*, on *Asterias vulgaris* (see Schmitt, et al. 1973; Fenuccci 1975), and in *Laevicardium murtoni* (see Cooley 1978). The free-swimming stages have been found in bays, sands and ocean from surface to 45.7 m.

Type-locality.—Given as—"inhabits the muricated *Pinna* of our coast."

Known range.—Off Martha's Vineyard, Mass., to Golfo San Matias, Argentina (Fenuccci 1975).

Remarks.—Ovigerous females have been found through most of the range of distribution. They have been reported in January from St. Thomas, March from Jamaica, May to November from Florida, June to January from North Carolina, July to September from Massachusetts and Rhode Island, and in June in Brazil (Rathbun 1918b and USNM).

Larval stages reared under experimental conditions in finger bowls of filtered seawater of 30‰ salinity at 25°C, and fed *Artemia salina* nauplii, passed through five zoeal stages and a megalopa (Costlow and Bookhout 1966b). Megalopae were segregated one to a bowl to avoid cannibalism. Morphological differences from other pinnotherid larvae were given both for the local fauna and that of other areas. In lower Chesapeake Bay and York River, Va., Sandifer (1973b, 1975) found the larvae from June to October over a salinity range of 10.91 to 32.34‰ at 20° to 28.1°C, peaking in August and September in a salinity range between 20 and 25‰, except for one specimen taken in February in the mouth of the Bay. The zoeae were common but never abundant, all stages being represented, but stage I was most numerous. Bottom samples contained 77% of all *P. maculatus* collected from the layer in which upstream drift is thought to favor retention in the estuary. He reviewed other studies on planktonic larvae of the species: common at Woods Hole from July to November (Fish 1925); July to October in Delaware Bay (Deevey 1960) and in low concentrations in Delaware River in summer (Cronin, et al. 1962); abundant in Narragansett Bay from June to September with peak in mid-bay in August (Hillman 1964); lower St. Johns River, Fla., in low densities (<1/m) from May to November (Tagatz 1968); off Cape Lookout, N. C., in November; and off Beaufort Inlet, N. C., from May to November (Dudley and Judy 1971), but never numerous.

Welsh (1932) found the swimming velocity of *P. maculatus* larvae to be greatly influenced by temperature and light intensity. The larvae are sensitive to only a small range of light intensity. At temperatures between 20° and 25°C the maximum velocity of swimming is attained at intensities between 10 and 25 meter-candles. When series of measurements were made to determine the effec-

tive light at different constant temperatures, it was found that, besides a marked effect on general activity, there was a change in the relationship of velocity to intensity; slopes of curves showing these relationships changed, and the maximum possible velocity of swimming for each temperature was reached earlier at the higher temperatures.

As in *P. ostreum*, the hard stage is found in both males and females, and though both swim actively, the males predominate in open water. An invasive stage may precede the relatively large hard stage as in *P. ostreum*. Unlike *P. ostreum* males, at least some *P. maculatus* males apparently live beyond the hard stage, for larger, somewhat globose males, resembling females in adaptation to parasitic or commensal life, occur in some hosts (see variation above).

Kruczynski (1973) found that distribution of *P. maculatus* living in the bay scallop, *Argopecten irradians concentricus*, fell into three areas in long, narrow, shallow Bogue Sound, N. C. (east, middle and west). Mature females were found only in the east and west ends of the sound near inlets but never really abundant (10% incidence in host); other crab stages were more abundant in these areas, but in reduced numbers also in the mid-sound scallop beds. Paradoxically, scallop density was highest in the mid-sound beds. The low percentage of infection in the sound as a whole may be controlled by a scallop fishery which diminishes crab incidence by harvest, but this does not explain why more crabs live near the inlets. Kruczynski explained this as follows: "larvae are swept to all reaches of the sound by tidal currents but survive best [in high salinity] near inlets. Scallops are invaded in great numbers in fall and early winter. Heavy rains at this time reinforce the salinity gradient in Bogue Sound. Many pre-swarmer and swarmer are lost because of scallop harvesting. Swarmer receive an external cue and begin a migration on ebb tides, becoming concentrated near inlets, or use tides to maintain near-inlet position. Copulation takes place and inseminated females seek a definitive host in the area where copulation occurs." Salinity thus seems a controlling element even though the host species tolerates a wide range throughout the sound. Experiment by others has shown that *P. maculatus* is a poor osmoregulator, surviving best in 20–30‰ salinity at 25°C.

More crabs infected *Mytilus edulis* growing subtidally on a piling at Woods Hole than were found in mussels in intertidal areas (Kruczynski 1974). This study demonstrated no correlation between salinity and temperature and presence of crabs, and no significant difference in mean shell height of mussels with and without adult female *P. maculatus*.

However, the crabs may choose subtidal hosts to assure a more constant environment than mussels in the intertidal would afford. Also, the longer the host is open, the more chance for entry by swarming young crabs.

Entry behavior of crabs into host scallops is related to scallop reaction to touch, attraction of crabs to excurrent water from scallops, sense of touch among invasive crabs, and phototactic responses of crabs (Eidemiller 1969). In sequence, the scallop mantle gapes apart at the point where the crab's legs touch it, the scallop then opens to its fullest [presumably the normal gape], closes abruptly but not completely as the margins usually do not make contact, and reopens within five seconds. The mantle seems most sensitive in the region of short guard tentacles. As long as a crab remains on the mantle the scallop continues to open and shut.

Kruczynski (1975) showed that adult female *P. maculatus* accumulate radioactivity when living in bay and calico scallops, *Argopecten irradians concentricus* and *A. gibbus*, fed *Nitzschia closterium* labelled with ^{14}C and in blue mussels, *Mytilus edulis*, fed *Thalassiosira pseudonana* under laboratory conditions. Crabs also accumulated radioactivity when kept in fingerbowls with labelled *N. closterium*. This demonstration strengthened the argument for the crabs being the causative agent for stunting in host scallops under natural and experimental conditions, but it was not determined whether the accumulation activity came from ingestion of phytoplankton, feces, pseudofeces, molluscan tissue or from water. Crabs without chelae in dishes did not pick up the radioactivity.

Caine (1975a), with a different approach, showed that both hard free-living and soft commensal phases of the mussel crabs feed on fine particulate matter, but the methods of food acquisition differ. Free-living forms acquire food while swimming (setae on carpus, merus and dactyls of second and third walking legs filter water), but commensal crabs obtain food from the host. Ossicles of the gastric mill are similar in the two forms, but the commensal phase has four pairs of setae on the posterior margin of the urocardiac ossicle which are thought to aid in manipulation of mucus strands ingested from the bivalve host. Crabs from plankton, quiet bottom water and bivalves did not burrow when freed but were secretive; swimming by dorsoventral movements of the first through fourth walking legs in metachronal waves from posterior to anterior produced an upward and forward motion. Only the fourth pair of walking legs is modified for feeding in commensals. The grasping surface of the dactyl and propodus are acutely inclined distally while the opposite side of the dactyl is finely

serrate. Anteroventral scraping movements of this leg pull mucus from ctenidia of host for transfer to the setose margin of the maxillipeds. In great detail, Caine described this set of movements and similar feeding of the free-living stages by filtering water with the second and third walking legs, scraping with the fourth, and transfer to the chelipeds as above. Detail was also given on movement of food through the stomach and associated structures.

Wells and Wells (1966) described what might be considered a hyperparasitic bopyrid, *Dactylokepon hunterae*, from *P. maculatus* in *Argopecten gibbus* dredged off Core Banks, N. C.

Pinnotheres ostreum Say

(Oyster crab)

Figs. 354–356

Pinnotheres ostreum Say 1817:67, pl. 4, fig. 5.—Rathbun 1918b:66, text-fig. 30; pl. 15, figs. 3–6.—Hay and Shore 1918:443, pl. 35, fig. 9.—Williams 1965:203, figs. 187, 188A-B, 189.—Coelho and Ramos 1972:195.—Felder 1973:75, pl. 10, figs. 12–14.—Schmitt, McCain, and Davidson 1973:61.—Powell 1977:124.

Pinnotheres depressum Say 1817:68.

Pinnotheres depressus.—Rathbun 1918b:79, pl. 17, figs. 1–2.

Recognition characters.—Mature female: Carapace subcircular in outline; surface glabrous for most part, smooth, shining, membranous, yielding to touch, convex from front to back and with broad, shallow, longitudinal depression each side of cardiac and gastric areas. Lateral margins thick and bluntly rounded; posterior margin broad. Front

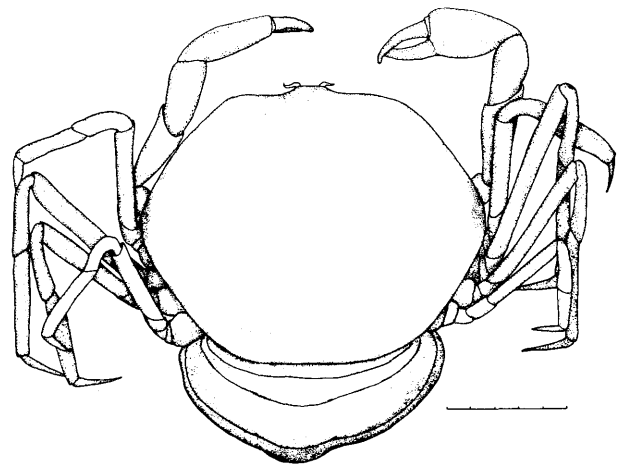


Fig. 354. *Pinnotheres ostreum* Say. Mature female in dorsal view, 5 mm indicated (from Williams 1965).

rounded, slightly produced, covering and concealing eyes. Orbits small, subcircular, anteriorly placed. Antennule large; antenna small, flagellum not so long as diameter of orbit. Buccal mass roughly quadrangular in outline but bent into broad crescentic arch, short anteroposteriorly. Outer maxilliped with ischium and merus fused; carpus or first article of palp short, oblong; propodus elongate, end rounded; dactyl inserted behind middle of propodus, minute, slender.

Chelipeds small, merus and carpus rather slender. Palm somewhat flattened inside, swollen outside, strongly widened from proximal toward distal end, then narrowed; width across base of fingers less than greatest width of palm; fingers, especially fixed one, stout, not gaping, tips hooked past each other, minute teeth on opposed edges, a larger tooth near base of each, fixed finger horizontal. Walking legs slender, subcylindrical; last 2 articles with thin fringe of hair; second and third legs about equal in length, first legs slightly stouter, last pair turned backward and upward.

Abdomen large, extending beyond carapace in all directions.

Measurements in mm.—Carapace: width, ranging from 4 to 15 (Christensen and McDermott 1958).

Color.—Whitish or salmon pink.

Recognition characters.—Mature male and hard-stage female: Carapace well calcified, flat dorsally, subcircular in outline, with truncate front more advanced than in mature female. Posterior margin straight; lateral margin thin, rather sharply bent from dorsal side, margin marked by raised band of short, dense hair. Eyes well developed. Buccal mass crescentic, arched, transversely broad but short anteroposteriorly; cavity completely closed by external maxillipeds formed as in mature female.

Chelipeds stout, merus and carpus not slender as in mature female. Palm slightly flattened inside, swollen outside and shaped as in mature female, both margins convex. Hand with bands of pubescence on upper and outer surface of palm, and outer surface of fixed finger. Fingers stout, especially fixed finger, with tips hooked past each other when closed; dactyl with small tooth proximally, tooth fitting between 2 protuberances on fixed finger when closed; both fingers with stiff hairs on gripping edges. Walking legs flattened, posterior margins thickened, and with plumose swimming hairs on second and third pairs.

Measurements in mm.—Carapace: male, width 1.4 to 4.6; female, width 1.3 to 2.7 (Christensen and McDermott 1958).

Color.—Dark or medium-dark brown with 2 large, distinct, almost circular, pale white spots on both carapace and sternum; dorsal spots on branchial

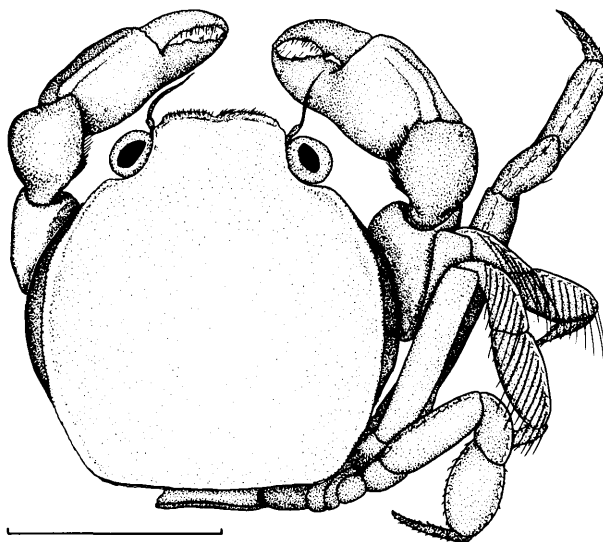


Fig. 355. *Pinnothereos ostreum* Say. Male in dorsal view, walking legs of left side not shown, 1 mm indicated (from Williams 1965).

regions, ventral spots flanking abdomen and mesial to first pair of legs; color and spots persistent in alcohol.

Habitat.—Parasitic [or commensal] chiefly in the oyster, *Crassostrea virginica*, also in *Pecten* spp. and *Anomia simplex* (see Christensen and McDermott 1958), in *Mytilus edulis* (see McDermott 1961), and in *Modiolus demissus* (see Sandifer and Van Engel 1970). Also occasionally found in *Chaetopterus* tubes (Gray 1961).

Type-locality.—“United States” (see Schmitt, et al. 1973); these authors mentioned six probable syntypes from the United States and Virginia in the British Museum (Natural History) and that, according to DeKay (1844), Say’s specimen was from New Jersey.

Known range.—Salem, Mass., to Santa Catarina, Brazil.

Remarks.—Say’s *P. depressus* appears almost certainly to be the hard-stage male as described above and discussed below.

The works of Hyman (1924a), Stauber (1945), Sandoz and Hopkins (1947), Christensen and McDermott (1958), and Beach (1969), together have made knowledge of the biology and life history of *P. ostreum* the most complete for any species of *Pinnothereos* in the world. The serious student should refer to these thorough works, for they can be summarized only in barest outline here. The complex life cycle of this species encompasses many developmental stages, as well as a striking sexual dimorphism in the mature animals, which, together with structural specializations and mode of existence, demonstrate a beautiful accommodation to an unusual habitat.

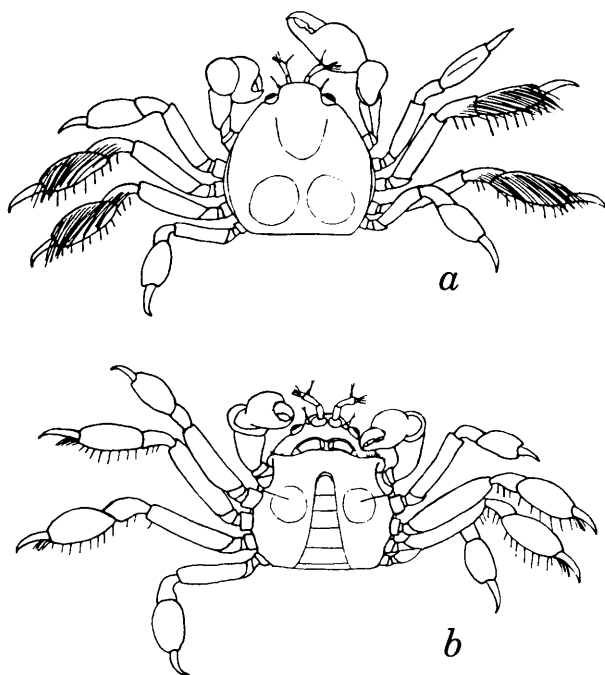


Fig. 356. *Pinnothereus ostreum* Say. a, Crab stage I female in dorsal view; b, same, ventral view; approximately $\times 9$ (from Stauber 1945).

The larval stages include four zoeae followed by a megalopa. The first two zoeal stages were described by Hyman (1924a), and a description of all these stages (partial for fourth zoeal stage) was given by Sandoz and Hopkins (1947). In general, the zoeae and megalopa have no dorsal or lateral spines on the carapace. Time of development from hatching to molting of the megalopa to first crab stage is 25 days.

Sandifer (1973d, 1975) collected planktonic larvae of *P. ostreum* from lower Chesapeake Bay and York River, Va., in salinities of 3.94 to 31.86‰ from June to October, with a peak in the lower York in July. Stage I zoeae dominated the samples, mostly at the bottom where upstream drift tends to hold them in the estuary. He (1973d) summarized the findings of others: Deevey (1960) in Delaware Bay, Pinschmidt (1964) from May to October in Newport River, N. C., at somewhat higher salinities, and Tagatz (1968) from St. Johns River, Fla., from April to November. Dudley and Judy (1971) also collected larvae up to 13 km off Beaufort, N. C., from June to October. From the first crab stage on, development was summarized by Christensen and McDermott (1958:154). The first crab stage, actually the stage which invades oysters, was called the invasive stage by these authors. It was described by Sandoz and Hopkins (1947) and in many respects is similar to the later hard stage in its flattened shape, legs adapted for swimming, and characteristic color marking (carapace width, 0.59–0.73 mm).

In Delaware Bay, few invasions take place before August 1. The peak of oyster setting there is in July; spat will have grown to size sufficient to harbor one or more crabs by the peak of the crab invasions in September. Invasions as early as June are reported for North Carolina (Beach 1969). Though invasive stages in oysters are found all winter, growth and development stop about the first of November when water temperatures begin to drop below 15°C. Surprisingly small spat may be invaded. Two crabs were found in an oyster 4.2 mm long, and in larger spat up to seven crabs were found in a single specimen. The crabs prefer to invade spat or yearling oysters rather than older ones (76.7, 54.6, and 21.5, being respective infestation percentages for a given year class of crabs), but survival rate of crabs is better in yearlings and older oysters. Beach (1969), from studies in North Carolina, thought that salinities below 10–15‰ prevent settlement of invasive stages in some areas and that swift currents may suppress it in others through lack of easy access to the host and lack of sufficient food. High salinity near areas of high organic content seemed to invite the highest rates of invasion, but there the host might suffer greater mortalities as a result of multiple infection. Infection was greatest around the low-tide mark as opposed to intertidally.

Following the invasive stage are two ill-defined stages designated as prehard. These stages, described by Christensen and McDermott (1958), are soft and resemble later posthard stages of the females (carapace width: male, 1.4–4.6; female, 0.75–2.7 mm). The legs are rounded and not adapted for swimming. These stages are found in all parts of the water-conducting system of infested oysters. In the region of Delaware Bay, most young crabs reach the prehard stages before growth ceases in fall and they overwinter in these stages. Development resumes when temperatures rise above 15°C.

The hard stage, formerly regarded as the invasive stage, is characterized above. On the average, males are larger than females, as they are in the preceding stages. The form of this stage resembles that of the invasive stage, and males of this stage swim freely. This is the copulatory stage (Hartnoll 1969), and the males normally die in this stage.

The succeeding female stages, described by Stauber (1945), resemble the adult female, and are found only in the host on the gills. Stage II (the hard stage was designated as stage I by Stauber) has a thin flexible carapace but a narrow abdomen contained wholly in the sternal groove (carapace width, 1.3–3.1 mm). Stage III has an abdomen extending beyond the depression in the sternum (carapace width, 2.6–4.4 mm). Stage IV has a relatively wide abdomen reaching the coxae of the legs

in most cases (carapace width, 3.6–8.9 mm). Stage V is the adult female described above.

The posthard stages are passed through rapidly. In Delaware Bay by mid-July, 62% of the females have developed from the overwintering stage to maturity. By mid-August, 95% are mature and more than half are ovigerous; thus, *P. ostreum* reaches maturity within its first year. Males live one year or less, but females continue to grow after they have hatched their first batch of eggs and may live to an age of two or three years, though many probably die after they have hatched their eggs in the second summer. In the second or third year, females may become ovigerous as early as mid-June, and ovigerous yearlings may occur as late as mid-October. Farther south the breeding season is more extended, and ovigerous females have been collected near Ocracoke, N. C., as early as mid-April.

Ovigerous females measuring 9.4 and 10.8 mm in width carried 7,957 and 9,456 eggs respectively. It is not known how long a female carries eggs, but it is believed to be three to five weeks. The females produce only one batch of eggs the first year but in a second or third year may produce twice (also Beach 1969).

Except for the brief free-swimming periods in the invasive hard stages, the crabs lead a parasitic existence. Stauber (1945) and Christensen and McDermott (1958) found that the crab feeds on food filtered from water by the host by picking food strings from the margins of the gills with its chelipeds. The crab also will catch newly formed mucus-food masses with its walking legs and then reach beneath the abdomen with its chelipeds, comb the legs, and pass the food on to the mouth. The method of feeding for young crabs not on the gills is unknown, but they may filter food with the mouthparts. Posthard stages are found only on the

gills, indicating that feeding on the food-laden mucus alone can insure adequate energy supplies for rapid growth and egg production. Growth of females is positively correlated with size of host and probably related to food supply and amount of water pumping by the host.

The ordinary feeding activities are harmful to the host (Stauber 1945), particularly causing gill erosion of two types, local erosion of one or more demibranchs, and an extensive shortening of demibranchs from the anterior end of gills to a point ventral to the adductor muscle. Christensen and McDermott (1958) noted that this erosion is a progressive process and nearly all infested oysters show some gill damage, some few older oysters having hardly any gill tissue left. Usually, however, only presence of a mature crab over a long time will noticeably affect growth of an oyster in normal environmental circumstances.

Genus *Parapinnixa* Holmes 1894

Rathbun 1918b:107.—Schmitt, McCain, and Davidson 1973:30.

Carapace calcified, much broader than long; anterior margin nearly straight, front depressed. Orbits nearly round. Antennules folded obliquely or transversely, fossettes communicating with each other beneath front. Buccal area small, broadly subtriangular. External maxillipeds with ischium rudimentary; merus large, subtriangular; palp 3-jointed, terminal article joined to distal end of preceding one. First walking leg largest, others successively diminishing in length, last very small. Abdomen of female small, not covering sternum. (From Rathbun 1918b.)

Key to Species

1. Carapace less than twice as wide as long *P. bouvieri*
Carapace more than twice as wide as long. *P. hendersoni*

Parapinnixa bouvieri Rathbun

Fig. 357

Parapinnixa bouvieri Rathbun 1918b:111, text-fig. 60, pl. 25, figs. 4–10.—1933:83, fig. 75.—Williams 1965:208, fig. 191.—Schmitt, McCain, and Davidson 1973:31.—Powell 1977:122.

Recognition characters.—Minute. Carapace smooth, shining, not more than twice as wide as long, longitudinally very convex transversely, sides arcuate; widest part with thin pubescent margin on lower

edge; anterior margin nearly straight, a row of 4 distinct pits behind margin. Frontoorbital width about $\frac{1}{3}$ carapace width. Front broadly triangular, deflexed, tip invisible in dorsal view, edge emarginate and pubescent; a pubescent groove running parallel to and immediately behind front terminating in orbital margins. Orbits circular, filled by eyes, cornea black, visible from above. Antennular cavities large, not wholly separated from each other or from orbits, extending laterally beyond minute antennae. Outer maxilliped subtriangular when folded in place, 2 free corners rounded, longitudinal side

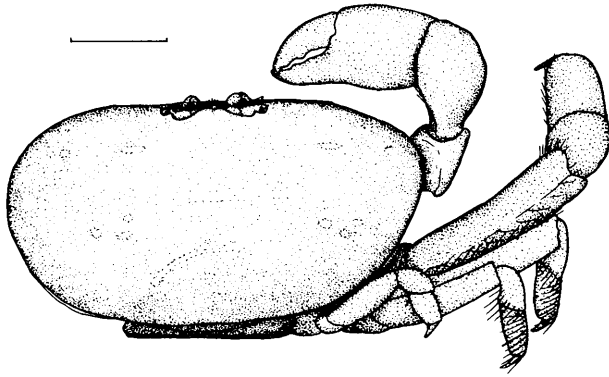


Fig. 357. *Parapinnixa bouvieri* Rathbun. Ovigerous female in dorsal view, legs of left side not shown, 1 mm indicated (from Williams 1965).

approximately $\frac{2}{3}$ as long as posterior side; ischium and merus fused, obliquely truncate distally leaving first joint of palp exposed; propodus elongate, distally tapering; dactyl small, suboval, both articles folding under merus.

Chelipeds short, stout, merus especially, partly hairy inside; palms thick, hairy outside; lower margin convex; fixed finger subtriangular, broad at base, small tooth on gripping edge near tip; dactyl with small basal tooth, remainder of edge finely and irregularly denticulate. Walking legs with edges more or less pubescent, second and third pairs with line of long hairs applied to posterior surface of carpus and propodus; first leg thick, merus not reaching laterally beyond carpus of cheliped; second and third leg about equal; fourth small, not exceeding merus of third; dactyls of second and third legs longer and more slender than of first and fourth.

Male abdomen with sides gradually convergent, seventh segment not more than 1.5 times as long as wide; female abdomen with sides of triangular part straight.

Measurements in mm.—Carapace: female, length 1.6, width 3.1; male, length 2, width 3.5.

Habitat.—Approximately 3.5 to 73 m.

Type-locality.—Off Cape Catoche, Yucatan, [Mexico], 22°08'30"N, 86°53'30"W, 45.7 m, Albartross Stn. 2362.

Known range.—Off Charleston, S. C.; south of Tortugas, Fla.; Puerto Rico; and type-locality.

Remarks.—Ovigerous females have been taken in Florida in August. The ovigerous specimen taken in Puerto Rico (no date) was found among ventral spines of a rose sea urchin (J. A. Rivero, USNM).

Parapinnixa hendersoni Rathbun

Fig. 358

Parapinnixa hendersoni Rathbun 1918b:109, text-fig.

59, pl. 26, figs. 1–5.—Righi 1967:99, figs. 7, 8.—Coelho and Ramos 1972:197.—Schmitt, McCain, and Davidson 1973:32.—Powell 1977:122.

Recognition characters.—Resembling *P. bouvieri* except as follows: Carapace more than twice as wide as long. Shallow pit to either side and one in mid-line of raised transverse area behind frontal margin; posterior to this a pubescent groove.

Chelipeds with palms thick, protuberant inside at middle, partly hairy inside, hairy outside at juncture of fingers and along 2 bands leading toward carpus; fingers stout, not gaping, tips hooked and overlapping; dactyl with granulate, pubescent crest and shallow, nearly hidden basal tooth fitting in basal excavation on fixed finger. Walking legs with dactyls similar, falcate, fitting closely in groove on propodus when flexed.

Abdomen of male covering nearly all of sternal width basally, third segment widest, rounded laterally, fourth partly invaginated in third, sides concave from fourth to angle near base of telson, latter long with rounded tip; female widest at third segment, subtriangular with concave sides beyond that, telson almost equilaterally triangular with blunt tip, margin fringed with long hairs; genital opening exposed at either side of telson.

Measurements in mm.—Carapace: male, length 4, width 8.3; female, length 3.5, width 8 (Rathbun 1918b).

Variation.—A juvenile male from North Carolina (UNC-IMS 2124) has an upper and lower row of remote granules on the external surface of the palm; above the upper row are a few similar, scattered granules, and the upper and lower crests of the

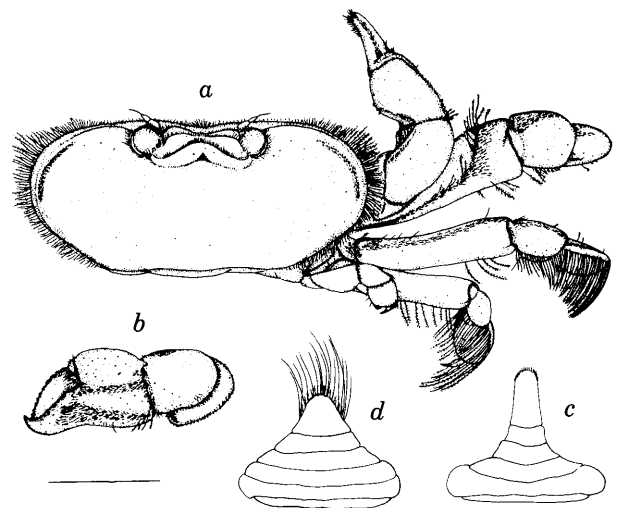


Fig. 358. *Parapinnixa hendersoni* Rathbun. Male: a, dorsal view, legs of left side not shown; b, left chela, external view; c, abdomen; d, female, abdomen; 3 mm indicated (USNM, Biscayne Bay, Fla).

merus are beaded. None of the larger specimens show these granules, although the dactyl of both adults and this tiny male has a granulate crest.

Color.—Small brownish pigment spots in alcohol (Rathbun 1918b).

Habitat.—Free swimming in surface plankton at night (Rathbun 1918b); surface to 84 m.

Type-locality.—Los Arroyos, Cuba.

Known range.—SE Cape Lookout, N. C. (UNC-IMS 2124 and 2448, 34°29'N, 76°13'W, 33 m; USNM 101505, 34°34'N, 75°50'W, 64 m); off Tampa Bay, Fla., through West Indies to Curaçao (USNM); Maranhão to Bahia, Brazil (Coelho and Ramos 1972).

Remarks.—The specimens from North Carolina are so small that they are questionably included in *P. hendersoni*. Whether the granular features on the palm of the chela are lost during growth or represent a character on an undescribed species is unknown. More material from the same area should help to resolve this question.

Genus *Pinnaxodes* Heller 1865

Rathbun 1918b:174.—Schmitt, McCain, and Davidson 1973:33.

Pinnaxodes floridensis Wells and Wells

Fig. 359

Pinnaxodes floridensis Wells and Wells 1961:269, figs.

1A-F, 2A-G.—Schmitt, McCain, and Davidson 1973:34.

Recognition characters.—Carapace convex, suborbicular, slightly wider than long, widest anterior to midpoint, moderately calcified, smooth, minutely punctate. Males with front usually somewhat produced and orbits visible in dorsal view; females with front usually deflexed and orbits often concealed in dorsal view. Lateral margins indistinct, rounded. Buccal mass subtriangular; line of long hairs extending lateral to buccal cavity. Outer maxilliped broad, with large palp; mesial edge of merus bearing distinct angle at midpoint; propodus larger than carpus, spatulate, about twice as long as wide; dactyl $\frac{2}{3}$ length of propodus, spatulate, articulated proximally on flexor surface of propodus and slightly exceeding it; both terminal articles with long hairs.

Chelipeds slightly asymmetrical, moderately long, smooth, minutely punctate; carpus slightly swollen; palm elongate, subcylindrical, swollen proximally but dorsoventrally broadening distally, line of hairs on low mesioventral crest extending along palm and fixed finger; fingers tapering, gaping

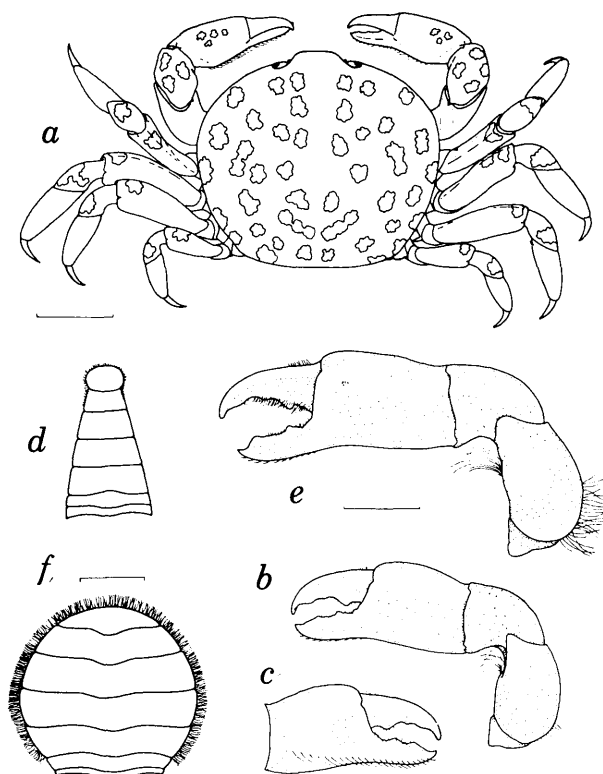


Fig. 359. *Pinnaxodes floridensis* Wells and Wells. Male: *a*, dorsal view showing color pattern in outline; *b*, left cheliped, outer view; *c*, chela, inner view showing line of hair; *d*, outline of abdomen. Female: *e*, left cheliped, outer view; *f*, outline of adult abdomen. Scales: *a* = 3 mm; *b*-*c*, *e* = 2 mm; *d*, *f* = 4 mm (from Wells and Wells 1961).

through most of length, distal shearing edges crossing at tips, somewhat spooned and with hairy internal crest; dactyl curved inward, basal tooth on cutting edge and an inconspicuous dorsal tuft of hair near articulation; fixed finger deflexed, small sinus and tooth on cutting edge. Walking legs moderately short and stout, second pair longest but shorter than chelipeds; last pair shortest; propodi elongate; dactyls curved, corneous at tip; merus with line of hair along dorsal crest and posterior ventral margin, continued also on propodi and dactyls.

Abdomen of male narrow triangular, with rounded telson; of mature female broad, subcircular and fringed with hair, telson broad and rounded distally; of immature female broadly triangular with narrow telson.

Measurements in mm.—Carapace: male, length 8.0, width 9.0; ovigerous female, length 9.5, width 11.0 (Wells and Wells 1961).

Variation.—Wells and Wells (1961) analyzed morphometric variations. In addition to sexual dimorphism mentioned above, mature females are generally wider than males; the carapace of immature females closely resembles the male form.

In males there are often distinct shallow grooves or depressions in the cardiac region, and the transition from dorsal to lateral surfaces is often marked by a low anterolateral ridge. The separation of merus and ischium on the third maxillipeds is complete in males, but in females the suture line between these articles extends only $\frac{2}{3}$ the width of the limb.

Color.—Many small red spots on white ground color dorsally, less developed ventrally, distributed in an imperfectly symmetrical pattern; typically, a distal spot of color on carpus of walking legs and on merus of external maxillipeds (Wells and Wells 1961).

Habitat.—Adults in cloaca and respiratory tree of *Holothuria princeps*, juveniles in anterior part of digestive system; shore (washed up in storm) to 38 m (Wenner and Read 1982).

Type-locality.—"Outer beach near Fort Walton Beach, Florida."

Known range.—Off North Carolina (USNM) to Georgia; northwest Florida.

Remarks.—Nearly all that is known of this species was given by Wells and Wells (1961); Patton (1967) and others have reviewed their findings. The original description and morphometric and reproductive analyses were based on a large number of specimens associated with the host holothurians that were either beached (on February 28, 1960) or stranded in shallow water following a severe storm. Sixty-one percent of the sea cucumbers examined contained these crabs. Female crabs outnumbered males 4:1. Females were present in a wide range of sizes and reproductive stages, juvenile, immature, mature and ovigerous, and some immature females contained sperm in the spermathecae. Wells

and Wells concluded that oviposition occurs over an extended time and that the crabs are filter feeders.

Subfamily Pinnothereliinae

Carapace transverse, usually broadly so. Ischium of external maxilliped usually distinct from merus, though smaller and sometimes imperfectly united with it. Merus longitudinal or somewhat oblique; palp of good size, sometimes as large as merus-ischium (Rathbun 1918b).

Genus *Pinnixa* White 1846

Rathbun 1918b:128.—Hemming 1958b:35.—Schmitt, McCain, and Davidson 1973:101.

Carapace much wider than long; integument usually firm; front narrow, nearly transverse, with median groove. Orbit broadly ovate or nearly circular, with wide inner hiatus partly occupied by basal antennal article. Antennules transversely or obliquely folded in wide fossettes open to each other beneath front. Eyestalks very short. Epistome transversely broadened. Ischium of maxillipeds small, merus large, distal part of outer margin convex; palp articulated to summit of merus, its third article arising on inner side of second article near base. Chelipeds moderate; hand large, compressed. Second walking leg larger than first, third largest, fourth shorter than third and relatively stouter than first and second. Abdomen of both sexes 7-segmented, narrower at base than last sternal segment. (Adapted from Rathbun 1918b.)

Key to Species

(By Richard E. Dowds)

1. Posterior part of carapace with conspicuous, sharp, transverse ridge extending uninterruptedly from side to side *P. cristata*
Posterior part of carapace without transverse ridge, or with ridge falling well short of lateral margin of carapace 2
2. Chela with inner margin of dactyl not smoothly bent 90° at $\frac{1}{4}$ to $\frac{1}{2}$ distance from its proximal end when flexed 3
Chela with inner margin of dactyl smoothly bent about 90° at $\frac{1}{4}$ to $\frac{1}{2}$ distance from its proximal end (adult male with dactyl flexed) 8
3. Fixed finger of chela with prehensile edge variously toothed, merging with lower margin at tip 4
Fixed finger of chela with prehensile edge and lower margin connected distally by subterminal, oblique margin (female and juvenile male) . . 8
4. Prehensile edge of fixed finger horizontal or inclined at less than 30° angle 5
Prehensile edge of fixed finger inclined at more than 40° angle (juvenile male) 8

5. Third walking leg with greatest length of merus more than twice greatest width, posterodistal end of ischium prolonged into stout curved spine (may be lacking in juvenile) *P. retinens*
Third walking leg with greatest length of merus less than twice greatest width, ischium lacking stout curved spine 6
6. Outer surface of chela with numerous scattered granules and long hairs above mid-horizontal row of granules; upper margin of dactyl bearing numerous long hairs *P. floridana*
Outer surface of chela with few, if any, granules; few short hairs (mainly on fixed finger and upper margin of dactyl) 7
7. Third walking leg with posterior surface of merus not deeply excavate behind smoothly beaded posterior margin *P. cylindrica*
Third walking leg with posterior surface of merus deeply excavate behind nearly entire length of laminate and strongly beaded or tuberculate posterior margin *P. lunzi*
8. Third walking leg with greatest length of propodus less than twice its greatest width *P. chaetoptera*
Third walking leg with greatest length of propodus twice or more than twice its greatest width. 9
9. Third walking leg with inferoposterior margin of merus coarsely granulated or toothed (may be concealed by hair). juvenile *P. chaetoptera*
Third walking leg with inferoposterior margin of merus finely toothed or granular. *P. sayana*

Pinnixa chaetoptera Stimpson

Fig. 360

Pinnixa chaetoptera Stimpson 1860a:235.—Rathbun 1918b:151, text-figs. 93–94, pl. 33, figs. 3–6.—Hay and Shore 1918:445, pl. 36, fig. 4.—Williams 1965:210, fig. 194A–C.—1974:57, fig. 104A–D (key).—Righi 1967:100, figs. 1–6.—Felder 1973:74, pl. 10, fig. 8.—Schmitt, McCain, and Davidson 1973:104.—Powers 1977:125.

Recognition characters.—Carapace transversely oval, somewhat more than twice as wide as long, more swollen in female than in male, surface uneven, sides densely pubescent. Front narrow, with deep median groove; epistome partly exposed in dorsal view. Regions well defined by pubescent grooves; cardiac region with acute transverse crest broadly interrupted in middle forming 2 dentiform prominences, more conspicuous in male than in female; subbranchial region advanced, forming prominent shoulder with granulated edge. Posterior margin concave.

Chelipeds stout, smooth, pubescent. Hand in adult male with perpendicular, distal palmar edge bearing prominent, rounded tooth near base of short, deflected fixed finger; dactyl smoothly curved about 90° ¼ to ½ distance from its proximal end, almost vertical when closed, forming oval gape with tips of fingers meeting. Hand of female relatively smaller, fixed finger having shorter upper and longer lower margins connected distally by subter-

minial, obliquely cusped margin; dactyl with tooth at basal ⅓ of length, longer than in male, prehensile edge of fingers crenulate, agape proximal to cutting portion when closed with tips crossing each other. First and second pairs of walking legs slender, propodi with distal V-shaped row of spinules on lower border; dactyls with 1 or more short rows of spinules. Third pair longer and much stouter, conspicuously pubescent, and with inferoposterior margins of ischium, merus, and propodus dentate; fourth pair like third but smaller, with minute spinules on dactyls.

Male abdomen with sixth segment slightly constricted laterally at middle; telson semicircular.

Measurements in mm.—Carapace: male, length 5.9, width 13.8; female, length 6.4, width 14.

Variation.—In small crabs, third walking legs have teeth on the inferoposterior margin of the merus large and few in number (as few as 8), but with increasing age they become relatively short, more numerous (up to 30), and increasingly concealed by hair. Chelae of male *P. chaetoptera* and *P. sayana* change with age. In very young males (carapace width less than about 3.5 mm) the chela is similar to that of young females. As males grow, the chela passes through intermediate forms in which the upper and terminal margins of the fixed finger merge to form a single steepening margin, and the dactyl becomes more bent and loses the tooth located about midway along its inner margin. By the time the carapace width reaches about 7 mm in *P. chaetoptera* or 4.5 mm in *P. sayana*, the

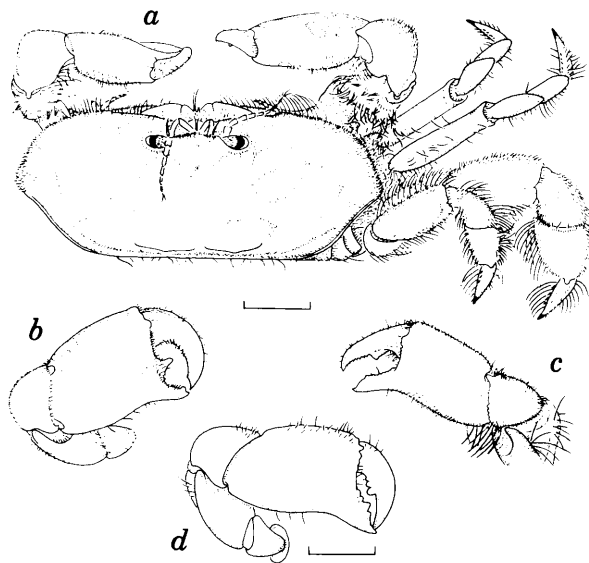


Fig. 360. *Pinnixa chaetopterana* Stimpson. a, Male in dorsal view, walking legs of left side not shown; b, male right chela and carpus, external view; c, female left chela and carpus, external view; d, juvenile male cheliped external view of chela; a-c, 2 mm; d, 0.5 mm indicated (USNM 57302).

chela has almost fully achieved the adult male form (R. E. Dowds, personal communication).

Wass (1955) pointed out that larger and smaller forms of *P. chaetopterana* occur on the northern Gulf of Mexico coast.

Color.—Nearly white, but usually much obscured by brown or blackish hairs and by dirt accumulated in them; eggs bluish (various authors).

Habitat.—The large form of this crab lives commensally with the worms *Chaetopterus variopedatus* and *Amphitrite ornata*, and is seldom found outside their tubes. The small form lives in the upper portion of *Callianassa jamaicensis* burrows (Biffar 1971a:650) on the northern Gulf coast (Chace in Wass 1955). Frankenberg and Leiper (1977) reported *P. chaetopterana* as dominant from June through November in grab samples from near-shore fine sand habitat in Georgia, apparently associated with the also dominant *Callianassa atlantica*. Intertidal to 15.5 m.

Type-locality.—Charleston Harbor, S. C., on muddy or clayey shores in tubes of *Chaetopterus variopedatus* [= *pergametaceus*].

Known range.—Wellfleet, Mass., to Rio Grande do Sul, Brazil.

Remarks.—Ovigerous females have been reported from Beaufort, N. C., between April (Gray 1961) and late October (Enders 1905), from Florida in October (Wass 1955) and February (Gray 1961), from southern Massachusetts in July and August (Pearse 1913; Rathbun 1918b), and from São Paulo, Brazil in August (Righi 1967). Other-

wise they are known from South Carolina in February. Faxon (1879) and Hyman (1924a) described the first zoeal stage.

Sandifer (1973d) reported *P. chaetopterana* larvae as common (97.6/kl) in lower Chesapeake Bay, being most abundant near the bottom, with zoeae I-III more common than IV-V. Larvae were collected in salinities of 20.3–32.34‰ in temperatures of 19.8–28.1°C from July to October, but few were taken below 23°C and most were in the 24–27°C range. He summarized other scattered reports of larvae: June to October in Narragansett Bay where they were most abundant in August (Hillman 1969); June to late October at Woods Hole (Fish 1925); and July to September in Delaware Bay (Deevey 1960). Other records, year-round in St. Johns River, Fla. (Tagatz 1968), and May to November near Beaufort, N. C., (Dudley and Judy 1971) were given for genus only. Subadults have been taken in surface mero-plankton from March to November in Bogue Sound, N. C., at the UNC-IMS pier, Morehead City.

Some habits of this crab were observed by Pearse (1913) at Woods Hole, Mass. The species is strongly thigmotactic. Crabs placed on sand in an aquarium usually buried themselves, but soon explored the surface and entered and remained in glass tubes left lying on the sand. In experiments, crabs found a buried, artificial “*Chaetopterus* tube” by accident. Adult crabs could enter or leave this tube. The crabs moved either forward or sideways on sand. The third walking leg was the chief locomotor organ, but in tubes the crabs braced themselves with all the legs.

Crabs placed in standing water in an artificial worm tube were able to exist for 8 days before leaving the tube for better aerated water. The crabs’ respiratory currents were feeble and inconstant in direction and force. Crabs were usually fouled with encrusting organisms and they took no trouble to clean their bodies except for mouthparts, eyes, and antennae. They fed by extending the fringed external maxillipeds and sweeping them toward the mouth, filtering small particles from the water, then cleaning the fringe with other mouthparts.

Gray (1961, see also account for *Polyonyx gibbesi*) described *Pinnixa chaetopterana* as primarily a mud crab and a facultative commensal of *Chaetopterus*. He found that the crabs readily enter and leave the tubes of the host, and if diameter of the parchment chimney of the worm tube is too small, the crab cuts a hole at the base of the chimney to make an entrance or exit.

Davenport and Hickok (1960), from choice experiments in an experimental trough designed to provide mixing streams from point sources, determined that *P. chaetopterana* shows marked reaction

to host-factor from *Chaetopterus* and *Amphitrite*, but not from *Nereis* or *Arenicola*. The crab shows marked akinesis when it first encounters host-factor, after which a klinokinetic response occurs. Intensity of the latter is proportional to the concentration of host-factor; with rise in concentration there is an increase in rate of random turning. There was also a tendency for the crabs to remain within the pool of host-factor in the experimental trough, not tending to transgress the steep gradients at its boundaries. However, there is no experimental evidence that the animals tend to be displaced toward the source of host-factor, and rheotactic responses are not present. Evidence indicates that the host-factor is a protein.

Pinnixa cristata Rathbun

Fig. 361

Pinnixa cristata Rathbun 1900a:589.—1918b:134, text-fig. 78, pl. 29, figs. 8–9.—Hay and Shore 1918:446, pl. 36, fig. 5.—Williams 1965:210, fig. 193.—Felder 1973:74, pl. 10, fig. 6.—Schmitt, McCain, and Davidson 1973:106.—Powers 1977:126.

Recognition characters.—Carapace short, surface punctate, wrinkled, and microscopically granulate, slightly pubescent at extreme outer corners; high, sharp, almost straight ridge extending without a break entirely across carapace somewhat in front of posterior border; deep furrow behind gastric region. Front deflexed, not advanced. Orbit no wider than half of front. Anterolateral margin with low raised crest stopping short of hepatic region; posterior margin wide, concave.

Chelipeds rather stout; palm oblong with upper and lower margins convex, surface covered with reticulate pattern of fine granulations. Male with distal palmar margin almost perpendicular and bearing median, truncate tooth nearly obscured by hair; fixed finger short, deflexed, truncate; dactyl

smoothly bent at approximately right angle at proximal $\frac{1}{3}$ – $\frac{1}{2}$ of length, gaping. Female with fixed finger short, deflexed, subtruncate, gripping edge with truncate, subbasal tooth; dactyl smoothly bent at approximately right angle at proximal $\frac{1}{3}$ of length, gaping, tips of fingers slightly notched and partly crossed when closed. Walking legs somewhat longer than in related species, sparsely hairy along margins only, third walking leg strongest; dactyls slender, slightly curved on first 3, straight on last walking legs.

Measurements in mm.—Carapace: male, length 3.5, width 9.1; female, length 4, width 11.

Color.—Two distinct color patterns are often found in the same area at the same time near Beaufort, N. C. First: predominantly yellowish-orange to tan, occasionally spots of gray or black on carapace and legs; abdomen and sternum often mottled gray overall. Second: nearly entire crab dark gray to black except for translucent white on dactyls and distal ends of propodi on walking legs; dactyls of chelae may be same light color and their propodi mottled with white spots. Intermediates are also found. The dark phase turns yellow-orange in 70% ethanol, and that color, as in the first phase, persists (R. E. Dowds, personal communication).

Habitat.—“Intertidal beaches and shallow sand and muddy-sand bottoms in brackish to marine waters; usually commensal with callianassids or other burrowers” (Felder 1973; also Pearse, et al. 1942).

Type-locality.—Beaufort, N. C.

Known range.—Beaufort, N. C., to Edisto Island, S. C.; Grande Isle, La., to Long Lake, Blackjack Peninsula, Aransas County, Tex. (Hedgpeth 1950, USNM).

Remarks.—This species has been taken from the mouth of the fish *Galeichthys felis* in Louisiana.

The anterolateral crest in many males and some females is elevated very little and in a few cases is barely discernible (R. E. Dowds, personal communication).

Pinnixa cylindrica (Say)

Fig. 362

Pinnotheres cylindricum Say 1818:452.

Pinnixa cylindrica.—Rathbun 1918b:159, text-fig. 99, pl. 35, figs. 5, 8.—Hay and Shore 1918:446, pl. 36, fig. 2.—Williams 1965:213, fig. 197.—Schmitt, McCain, and Davidson 1973:106.—Powers 1977:126.

Recognition characters.—Carapace smooth polished, with punctations small and scarce in middle

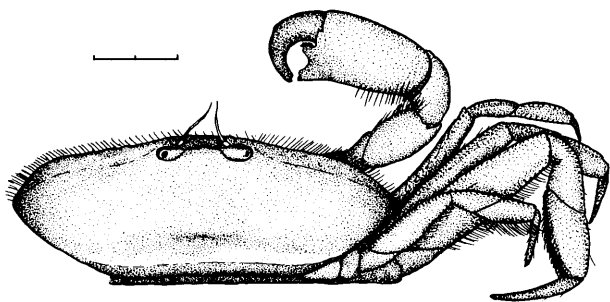


Fig. 361. *Pinnixa cristata* Rathbun. Male in dorsal view, legs of left side not shown, 2 mm indicated (from Williams 1965).

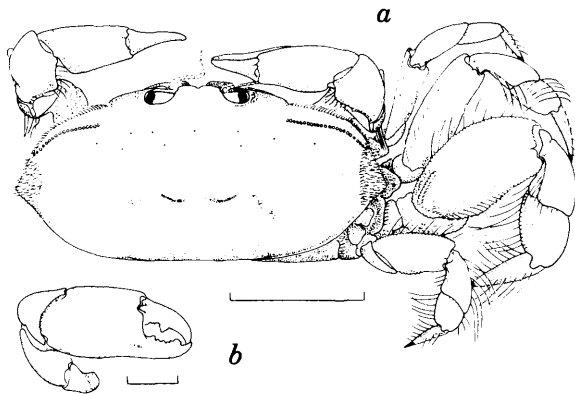


Fig. 362. *Pinnixa cylindrica* (Say). Male: a, dorsal view, walking legs of left side not shown; b, right cheliped, external view of chela; a, 5 mm; b, 2 mm indicated (USNM 102840).

third, large and more numerous elsewhere; pubescent at extreme outer corners; depressed in middle; anterior cardiac region separated from gastric and branchial regions by a groove. Anterolateral portions with sharp, granulate crest not reaching cervical suture, shoulder above lateral angle lacking blunt prominence; middle of cardiac region crossed by transverse (sometimes inconspicuous) ridge; posterior border short, somewhat concave. Front not prominent, bilobed, with submarginal groove.

Chelipeds moderately stout, smooth, punctate; hands suboval, approximately 1.5 times as long as wide, fingers horizontal, subequal in length, tips strongly hooked, overlapping when closed, leaving a gape; fixed finger with tooth near tip; dactyl with tooth near middle; finely milled crest running from tip of fixed finger backward and upward approximately $\frac{2}{3}$ length of palm on outer surface. First walking leg slender, reaching to propodus of second; second stouter, reaching to middle of dactyl of third; third leg stoutest, merus 1.6 times as long as wide, distally narrowed, upper and lower margins finely granulate; fourth short; dactyls nearly straight, that of fourth leg convex posteriorly, slightly concave anteriorly.

Abdomen of male with sixth segment constricted laterally, constriction narrower than telson.

Measurements in mm.—Carapace: male, length 7, width 14; ovigerous female, length 9.5, width 21.5.

Color.—Yellowish gray, light to dark brown, or sometimes grayish, and mottled with dark gray and/or white. Rhythmic chromatophore changes as well as genetic differences may control observed variations (McDermott 1963).

Habitat.—The species lives in burrows of *Arenicola cristata* (Wass 1955; McDermott 1963), and possibly with other large annelids; shallow water to 36.6 m.

Type-locality.—Jekyll Island, Ga.

Known range.—North Falmouth, Mass., to Pen-

sacola, Fla. (Cooley 1978), including Dry Tortugas.

Remarks.—McDermott (1963) summarized existing knowledge of the habits of this species and added numerous ecological observations. He reported the crab for the first time from New Jersey, finding it associated with 76% of the lugworms collected during summer. Crabs and worms were collected by manual digging. With one exception, single crabs were found on worms.

Of 18 female crabs found in July, 16 were ovigerous. One captive female produced eggs on July 7 and liberated zoeae "around" August 5. Crabs which liberated zoeae when collected produced new sponges of eggs which were in late stages of development approximately 30 days later. McDermott judged that this species produces at least 2 egg masses in a breeding season. Molting between broods did not occur in the laboratory.

Associates of *P. cylindrica* were found to be a peritrich ciliate, *Zoothamnium* sp., attached little boat shells, *Crepidula convexa*, and colonies of the bryozoan, *Triticella elongata*.

A few larvae attributed to *P. cylindrica* (zoeal stages I, II, III, and V) were reported from the mouth of Chesapeake Bay from July to October in salinities of 27.28–31.19‰ at 19.8°–26.2°C, nearly all in bottom samples (Sandifer 1973d), and subadults have been taken in surface meroplankton in September at the UNC-IMS pier, Bogue Sound, Morehead City, N. C.

Pinnixa floridana Rathbun

Fig. 363

Pinnixa floridana Rathbun 1918b:138, text-fig. 82, pl. 30, figs. 4–7.—Williams, McCloskey, and Gray 1968:57, fig. 13.—Schmitt, McCain, and Davidson 1973:110.—Powers 1977:126.

Recognition characters.—Carapace suboblong, narrower in male than in female, anterolateral angle forming slight shoulder; surface smooth, punctate; cardiac region elevated but without ridge, gastroducardiac groove shallow; anterolateral walls steep, sharp milled crest along margin up to cervical suture, male with anterolateral wall steeper and shoulder more prominent than in female; posterior margin concave. Front truncate, not advanced. Orbits inclined anterolaterally in dorsal view.

Chelipeds weak, hairy; chelae tapering distally. Hand of female with denticulate upper margin, row of granules near lower margin continued somewhat on fixed finger, another horizontal row of granules near middle of palm and scattered granules and long hairs above that as well as on dactyl; fingers nearly horizontal, few small teeth on pre-

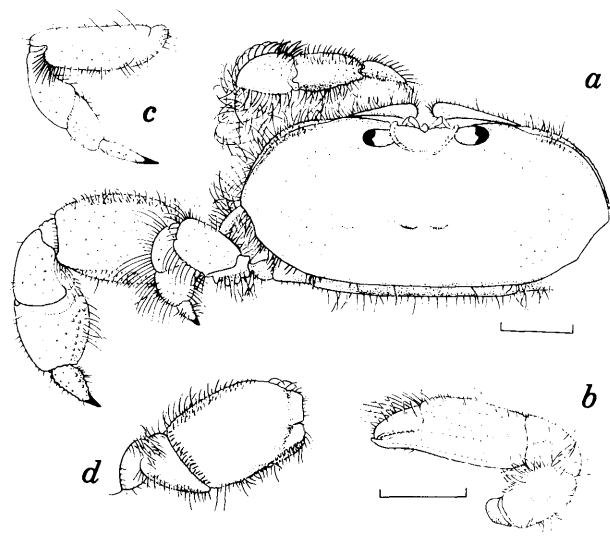


Fig. 363. *Pinnixa floridana* Rathbun. Female: a, dorsal view, legs of right side not shown; b, left cheliped, external view of chela; c, left walking leg, dissociated; d, third walking leg, merus and ischium in anterior view; a-d, 1 mm indicated (USNM 173017).

hensile edges, not gaping, tips hooked, dactyl with 2 rows of sharp granules. Hand of male with palm proportionately wider, fixed finger somewhat shorter, fingers gaping slightly. First walking leg narrower than second, reaching middle of second dactyl; second leg reaching middle of propodus of third; third leg very wide, lower margin denticulate, merus and propodus tapering rapidly toward dactyl; fourth leg not exceeding merus of third, wide in proportion; dactyls of all legs straight or nearly so.

Line of hair at distal end of second abdominal segment continued along sternum; telson of male abdomen broadened, truncate, arched at sides, margin hairy.

Measurements in mm.—Carapace: male, length 2.4, width 4.4; female, length 3.5, width 8; ovigerous female, length 1.8, width 4.3.

Habitat.—Commensal with compound ascidian growing at base of *Eugorgia virgulata* [*Leptogorgia virgulata*] washed ashore at Alligator Point, Fla., and under rocks (Wass 1955, amended by Schmitt, et al. 1973); perhaps living in *Diopatra cuprea* tubes (Williams, et al. 1968); to about 55 m.

Type-localities.—Marco, Fla., also Sarasota Bay.

Known range.—SE off Cape Lookout, N. C.; Hutchinson Island, east central Florida (Camp, et al. 1977); west coast of Florida.

Pinnixa lunzi Glassell

Figs. 364–365

Pinnixa lunzi Glassell 1937:3, figs. 1.8.—Williams 1965:214, figs. 198, 199A-E.—Felder 1973:71,

pl. 10, fig. 4.—Schmitt, McCain, and Davidson 1973:114.—Powers 1977:127.

Recognition characters.—Carapace slightly more than twice as wide as long, punctate, regions indicated, borders flanged, with shoulder formed near wide lateral angle; anterior border with fringe of long setae, and variable setae elsewhere on carapace and margin of limbs. Front prominent, bilobed, truncate, upturned over antennules. Gastric and cardiac regions separated by depression connecting with deeper depression on each side of these regions; beaded ridge on anterolateral slope, especially pronounced in smaller specimens; prominent cardiac ridge extending transversely almost across carapace with abrupt slope from crest of ridge to posterior border.

Chelipeds stout; hands of male shorter and stouter than in female, appearing disproportionately small in female; palm with margins subparallel in female, widest at base of dactyl in male; in both sexes fingers gaping, fixed finger horizontal, armed with row of small teeth, distal tooth largest; dactyl stout, curved, armed with median lobe. Walking legs stout. First 2 lightly crested with setae on merus; carpus crested with sharp beaded rim; propodus armed with row of fine, sharp, brown spinules; dactyls contorted, sharp pointed, fluted, with rows of small, sharp, forward-pointing spinules on crests. Third leg large; merus with 2 separated, upper, crenulate margins, lower border tuberculate, posterior surface with deep, pubescent concavity, smooth within; ischium at lower distal end extending well past base of merus and with meral concavity continued on posterior face, lower border tuberculate; carpus and propodus together equal in length to upper length of merus; dactyl stout, nearly straight, without minute spinules. Fourth leg similar to third but smaller, merus with lower border tuberculate, dactyl slightly upturned at tip.

Male abdomen with telson semioval, sides not wider than concave-sided sixth segment; third, fourth, and fifth segments partially fused.

Measurements in mm.—Carapace: male, length 9, width 21; female, length 9, width 21.

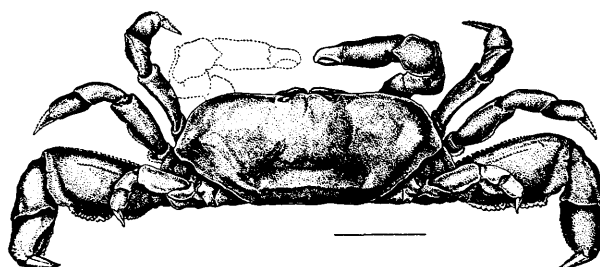


Fig. 364. *Pinnixa lunzi* Glassell. Male holotype in dorsal view, 7 mm indicated (from Glassell 1937).

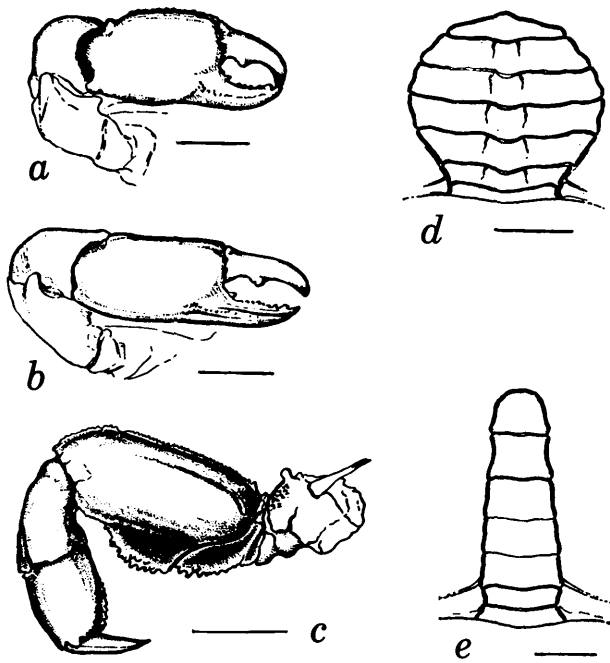


Fig. 365. *Pinnixa lunzi* Glassell. a, Male right chela; b, female right chela; c, female left third walking leg; abdomen, d, female, e, male; a-b, e, 3 mm; c, 4 mm; d, 6 mm indicated (from Glassell 1937).

Color.—In alcohol, a muddy bluish brown; legs, abdomen, and chelipeds ivory.

Habitat.—Beach under drift material to mud-shell bottom and fine silts and coarse sand-shell around offshore ridges or reefs; in burrow of echinuran *Thalassema hartmani* and probably other shallow burrowers (see remarks below); shore to 26 m.

Type-locality.—Isle of Palms (about 15 mi. north-east of Charleston, S. C.), washed on beach under drift material.

Known range.—Off Delmarva Peninsula, Va., North and South Carolina, Georgia; off Mississippi River delta and Seven and One-Half Fathom Reef off Texas near 26°51'N, 96°18'W.

Remarks.—Since its discovery in beach drift, this crab has been reported in a number of associations. Boesch (1971) found it off Virginia in grab samples from medium to coarse sand-shell ridges parallel to shore, separated by troughs of fine sand. There it was associated with the polychaetes *Clymenella torquata* and *Pherusa affinis*, the coelenterate *Ceriantheopsis americanus*, amphipod *Ampelisca vadorum*, sipunculid *Golfingia margaritacea*, and holothurian *Caudina arenata*. Boesch also reported the occurrence with *Thalassema* in burrows in Georgia. Woodward dug a male from a burrow in a normally subtidal sand flat back of Long Beach, Brunswick County, N. C. (USNM). Boothe (1977) reported an adult male in dredge samples from

mud-shell bottom in the Ashepoo River system (18‰ salinity) along with non-burrowing invertebrates. Felder (1973) reported Mississippi delta specimens and (1973a) a specimen from the stomach of a red snapper, *Lutjanus campechanus*, on a Texas reef. The fish was judged to have eaten this crab in the immediate vicinity shortly before it was collected. Reef temperature records varied from 14.8 to 26.3° C with salinities of 28.1 to 39.9‰. Other food items in snappers from this area indicate that they prey on crustaceans that are swimmers, vagrants, or shallow burrowers in substrates surrounding the reef. Boesch (1971) had earlier deduced that *P. lunzi* is a facultative commensal capable of existence for periods without a host.

Pinnixa retinens Rathbun

Fig. 366

Pinnixa retinens Rathbun 1918b:139, text-figs. 83–84, pl. 41, figs. 1–2.—Williams 1965:196, fig. 196A–D.—Felder 1973:74, pl. 10, fig. 7.—Schmitt, McCain, and Davidson 1973:118.—Powers 1977:127.

Recognition characters.—Carapace nearly twice as wide as long, almost flat, except sloping toward toward margins; regions indicated. Anterolateral margin marked by sharp, granulate ridge reaching to subhepatic sulcus, usually no cardiac ridge; posterior margin preceded by subparallel groove. Outer maxilliped with obliquely spatuliform dactyl attached to middle of inner margin of propodus.

Legs setose. Chelipeds small, approximately as long as first leg; hand flattened, with lower margin straight, suboblong, marginate below; fingers long, slender (especially females), subequal, hardly gaping; dactyl with tooth at proximal third of gripping edge. First and second walking legs similar; second little longer, dactyls slightly curved, long, pointed. Third walking leg stout, exceeding second by length of dactyl and half of propodus; lower edge of ischium, merus, and propodus armed with stout spinules; greatest length of merus more than twice its greatest width; posterodistal end of ischium prolonged in stout, curved spine with point directed upward and backward; dactyl more curved than in first and second legs, pointed. Last leg extending to distal end of third merus; dactyl stout, nearly straight, tip curved slightly upward.

Abdomen constricted at base of second segment, widest between second and third, and tapering to base of telson; telson wider than long; anterior and posterior margins of sternal segment granulate.

Measurements in mm.—Carapace: male, length 4,

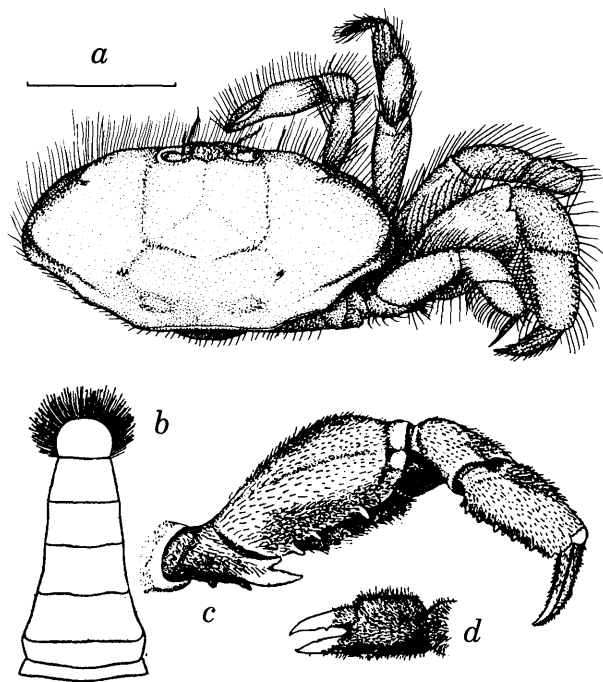


Fig. 366. *Pinnixa retinens* Rathbun. a, Female in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965); male, b, abdomen; c, third walking leg, lower side; d, left chela; b-d, holotype approximately $\times 9$ (from Rathbun 1918b).

width 7; ovigerous female, length 6, width 12.

Variation.—Juveniles may lack the posterodistal ischial spine on the third walking leg.

Habitat.—An ovigerous female was taken from the burrow of *Upogebia affinis* at Alligator Harbor, Fla., in June (Wass 1955). Small specimens have been taken from mud bottom in Chesapeake Bay (Wass, personal communication). Near low-tide mark to 36.6 m.

Type-locality.—Chesapeake Bay, off Poplar Island, Md., 36.6 m, soft bottom.

Known range.—Delaware Bay (Watling and Maurer 1976); Little River Inlet, S. C., Alligator Harbor, Fla.; Aransas area of Texas coast (USNM).

Remarks.—*Pinnixa retinens* is common in Chesapeake Bay (Van Engel and Sandifer 1972). Wass (1955) found an ovigerous female in a burrow of the mud shrimp, *Upogebia affinis*, in Alligator Harbor, Fla., in June, and Boothe (1977) reported it along with the possible host worm *Abarenicola* sp., with other associates, from Little River Inlet, S. C.

Pinnixa sayana Stimpson

Fig. 367

Pinnixa sayana Stimpson 1860a:236.—Rathbun 1918b:156, text-fig. 98, pl. 34, figs. 2–4.—Hay and Shore 1918:446, pl. 36, fig. 3.—Williams

1965:212, fig. 195.—Righi 1967:102, figs. 9–14.—Coelho and Ramos 1972:196.—Felder 1973:74, pl. 10, fig. 9a, b.—Schmitt, McCain, and Davidson 1973:119.—Powers 1977:128.

Recognition characters.—Carapace similar to *P. chaetoptera* but less hairy, less inflated anterolaterally, and with front more produced; smooth, polished, lightly pubescent on sides, depressed at middle; low, ill-defined, transverse ridge parallel with and close to posterior margin extending about $\frac{1}{3}$ width of carapace. Front narrow, with deep median groove, produced to cover epistome in dorsal view. Anterolateral slope crossed by beaded crest most pronounced in lateral $\frac{2}{3}$.

Chelipeds with hands stout, compressed, basically similar to *P. chaetoptera* but those of female with straighter fingers; female (and juveniles) with fixed finger having shorter upper and longer lower margins connected distally by subterminal, obliquely cusped margin; male with perpendicular palmar edge bearing prominent truncate tooth near base of short, deflected fixed finger, dactyl strongly curved about $90^\circ \frac{1}{4}$ to $\frac{1}{2}$ distance from its proximal end. Walking legs long and slender; smooth; first walking leg reaching propodus of second; second and third leg same length; fourth reaching beyond middle of carpus of third; merus of third leg approximately 3.5 times as long as wide, propodus twice or more than twice its greatest width; inferoposterior margin of merus finely toothed or granular; dactyls of first 2 legs slightly curved, of third straight, posterior edge of last dactyl slightly convex.

Measurements in mm.—Carapace: male, length 5, width 10; female, length 4.3, width 8.7 mm.

Variation.—Females differ from males in that the cardiac ridge is lower and less sharp, the fingers do not gape, the fixed finger is longer and less bent, and the dactyl on the chela is more oblique. Growth changes in chelae of *P. sayana* are compared with changes in *P. chaetoptera* in the account for that species.

Color.—Almost white, but lightly stained with brown.

Habitat.—The species has been found free in the water, has been dug out of mud (not found in the tubes of *Arenicola cristata*); shore to 47.5 m (Schmitt, et al. 1973), 75 m (Coelho and Ramos 1972).

Type-locality.—Mouth of Beaufort Harbor, N. C., 10.97 m, sandy mud.

Known range.—Vineyard Sound, Mass., to Beaufort, N. C.; Hutchinson Island, east central Florida (Camp, et al. 1977), Sarasota Bay, Fla., to Grand Isle, La.; Amapá, Pará, Pernambuco, São Paulo, Brazil.

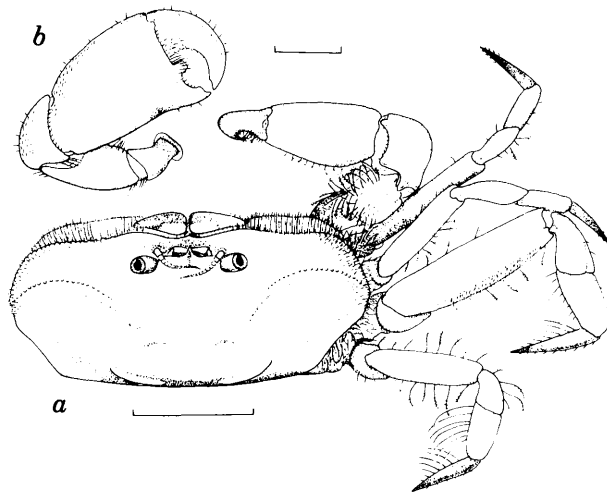


Fig. 367. *Pinnixa sayana* Stimpson. Male: a, dorsal view, legs of left side not shown; b, right chela, external view; 1 mm indicated (USNM 173396).

Remarks.—Ovigerous females have been reported in August from Narragansett Bay, R. I. (Rathbun 1918b), are known in September from Louisiana, and in January-February from São Paulo, Brazil (Righi 1967). The last zoeal stage of a *Pinnixa* commonly found off the New England coast and described by Faxon (1879), was tentatively referred to this species by Smith (1880a). Both Faxon and Smith found the first crab stage to follow immediately the last zoeal stage. These stages in development of *P. sayana* were summarized and illustrated by Hyman (1924a).

Sandifer (1973d) reported all 5 zoeal stages of *P.*

sayana from the middle York River, Va., to the mouth of Chesapeake Bay, being most abundant in bottom samples with stage III dominating. Larvae were collected in salinity of 18.1–32.34‰ (mainly in 20–30) in temperatures of 19.8°–27.9°C from June to October, with a peak in September. He also found the larvae in the Cape Hatteras region in November and summarized other scattered reports of larvae: June to October in Narragansett Bay (Hillman 1964); July to September at Woods Hole (Fish 1925); July to October in Delaware Bay (Deevey 1960); and August to December in Pamlico and Neuse Rivers, N. C. (Williams and Deubler 1968). Subadults have been taken in surface meroplankton in October at the UNC-IMS pier, Bogue Sound, Morehead City, N. C.

Superfamily Grapsoidea

Family Grapsidae

Front quite wide; carapace usually quadrilateral, with lateral borders either straight or slightly arched and orbits at or near anterolateral angles. Buccal cavern square; generally a gap, often large and rhomboidal, between external maxillipeds. Male openings sternal. Palp of external maxillipeds articulating either at anteroexternal angle or at middle of anterior border of merus, exognath either slender or broad. Interantennular septum broad. Division of orbit into two fossae accented (Rathbun 1918b).

Key to Subfamilies, Genera, and Some Species

1. Antennules folding beneath front of carapace in usual way. 3
 Antennules visible dorsally in deep clefts in front of carapace
 [subfamily Plagusinae] 2
2. Carapace broader than long *Plagusia depressa*
 Carapace longer than broad *Percnon gibbesi*
3. Third maxillipeds without hairy, oblique ridge. 4
 Third maxillipeds with oblique, hairy ridge crossing ischium
 [subfamily Sesarinae] *Sesarma*
4. Lower border of orbit continuing downward toward buccal cavern
 [subfamily Grapsinae] 5
 Lower border of orbit not continuing downward toward buccal cavern but
 supplemented by remote suborbital crest in line with anterior border of
 epistome [subfamily Varuninae] *Euchiropsus americanus*
5. Carapace decidedly broader than long *Pachygrapsus transversus*
 Carapace about as long as broad; legs strongly fringed with hairs.
 *Planes minutus*

Subfamily Grapsinae

Front usually strongly deflexed. Lower border of orbit running downward toward buccal cavern.

Antennal flagellum very short. External maxillipeds usually separated by wide rhomboidal gap, merus not traversed by oblique hairy crest; palp articulating at or near anteroexternal angle of

merus; exognath narrow and exposed throughout. Male abdomen filling all space between last pair of legs (Rathbun 1918b).

Genus *Pachygrapsus* Randall 1840

Rathbun 1918b:240.—Manning and Holthuis 1981:233 (synonymy).

Pachygrapsus transversus (Gibbes)

(Mottled shore crab)

Fig. 368

Grapsus transversus Gibbes 1850:181.

Pachygrapsus transversus.—Rathbun 1918b:244, pl. 61, figs. 2–3.—Hay and Shore 1918:447, pl. 36, fig. 9.—Williams 1965:217, fig. 202.—Forest and Guinot 1966:91.—Christiansen 1969:92, fig. 38.—Chace and Hobbs 1969:169, fig. 52k.—Coelho and Ramos 1972:201.—Felder 1973:79, pl. 11, figs. 5, 10.—Powers 1977:130.—Manning and Holthuis 1981:234.

Recognition characters.—Usually a small species. Carapace anteriorly rectangular, about $\frac{1}{4}$ broader than long, depressed, polished, with fine transverse plications, except oblique ones on branchial regions. Sides slightly arched, strongly converging posteriorly and armed with well-marked tooth behind orbital angle. Front slightly more than half as wide as carapace, edge sinuous and granulate, upper surface with 4 low elevations. Orbits oblique, approximately $\frac{2}{5}$ width of front, lower border denticulate.

Chelipeds equal, much stouter than other legs, 1.6 times longer than carapace in male, finely granulate; inner edge of merus produced in lami-

nate, toothed expansion. Meri of all legs and carpus of cheliped transversely striated; latter with blunt internal tooth; upper surface of palm with marginal line, oblique striae on inner and lower side, an oblique line on outer surface near lower edge; fingers narrowly gaping except for large triangular tooth near middle of fixed finger. Merus of walking legs with posterodistal angle dentate; first and fourth walking legs subequal, last 3 articles bristly and thorny. Female with conspicuous feathery hairs on carpus and propodus of first walking legs.

Male abdomen with telson broadly triangular.

Measurements in mm.—Carapace: male, length 16.9, width 21.2 (freshly molted and slightly shrunken, Nicteroy, Brazil); ovigerous female, length 13.0, width 16.7 (Balboa, Panama); male, length 21.7, width 26.4; female, length 15.4, width 19.5 (Port Said, Egypt) (USNM).

Color.—Variable; ground color almost black, olive green, yellowish, yellowish brown or dull gray, covered by irregular mottlings of dark brown, reddish or dark olive; usually darkest anteriorly with transverse ridges edged with greenish gray, reddish or dark brown; chelae often plain or reddish brown, tips light; walking legs brown or blackish with gray spots (various authors).

Habitat.—Mainly intertidal among rocks, also on pilings, roots of mangroves, and sandy shores.

Type-locality.—Key West, [Fla.].

Known range.—Cape Lookout, N. C., to Montevideo, Uruguay; Bermuda; Mediterranean Sea to northern Angola; eastern Pacific from California to Peru, Galapagos Islands. The species has been carried to higher latitudes than it normally inhabits by transport on ships' bottoms, and, as Verrill (1908b) suggested, the range may have been greatly extended by commerce in modern times.

Remarks.—Ovigerous females are known virtually year-round from various part of the normal range: Caribbean Sea—western Gulf of Mexico, February–August (Rathbun 1918b; Rickner 1977); year-round, eastern Florida (Gore, et al. 1978); Bermuda, April–July (Verrill 1908a) but the species is common there from April to October (Lebour 1944); North Carolina, August–September; Galapagos Islands, Egypt, July; west Africa, March, May–October, December (Manning and Holthuis 1981); Brazil, August–February; Ecuador, September. Females taken off northern Brazil bore 9,222 (\bar{x}) ova (carapace length 6.0–15.5 mm) (Ogawa and Rocha 1976). Lebour (1944) illustrated some of the larval stages reared from eggs hatched at Bermuda. Dudley and Judy (1971) found the larvae numerous near Beaufort Inlet, N. C., in June, but rare in October.

Pearse (1932b) reported the protozoan *Epistylis*,

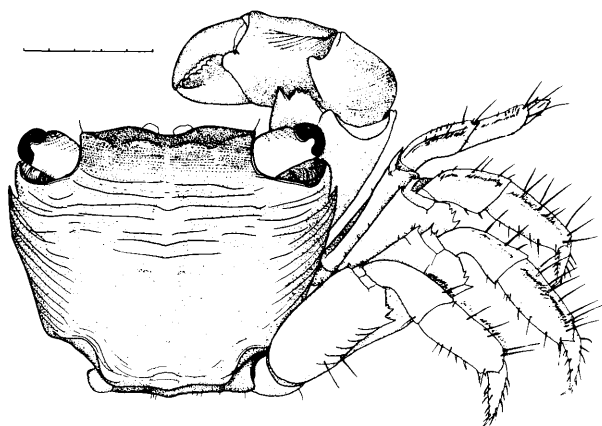


Fig. 368. *Pachygrapsus transversus* (Gibbes). Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

and Verill (1908a) the isopod *Leidya distorta* in the gill cavities of this crab.

Gore, et al. (1978) found *P. transversus* to be the third most abundant decapod on a sabellariid reef off eastern Florida where its feeding role was that of an omnivore-scavenger.

Genus *Planes* Bowdich 1825

Rathbun 1918b:253.—Chace 1951.—Hemming 1958b:36.—Manning and Holthuis 1981:235 (synonymy).

Planes minutus (Linnaeus)

(Gulf weed crab; turtle crab; Columbus crab)

Fig. 369

Cancer minutus Linnaeus 1758:625.

Planes minutus.—Hay and Shore 1918:448, pl. 36, fig. 6.—Chace 1951:81, figs. 1a, 2a, d, g, j, k, l, 3a-h.—Holthuis 1959:240.—1977:160.—Williams 1965:218, fig. 203.—Christiansen 1969:94, fig. 39.—Coelho and Ramos 1972:201.—Manning and Holthuis 1981:235.

Recognition characters.—Carapace approximately as wide as long, subquadrate in young, trapezoidal in medium-sized, laterally convex in old individuals, convex dorsally, smooth, but with faint oblique lines on outer part of branchial region. Front approximately half as wide as carapace, decurved, usually slightly emarginate in middle, edges minutely denticulate or smooth. Eyes large; orbits large, lower margin granulate, tooth at inner angle equilateral, subacute, outer angle spiniform, small sinus behind it.

Chelipeds large and heavy; merus and ischium with thin serrate crest along inner margin termi-

nating in 2 or 3 spines at distal end of merus; carpus with strong blunt spine on inner face; hands inflated and smooth except for small, sharp granules near lower margin; fixed finger bent downward, especially in males, dactyl curved, both with blunt teeth throughout length. Walking legs long, slender, and flattened; second and third legs subequal, fourth legs shortest; meri occasionally with inconspicuous anterior subterminal tooth and few posterior denticles; last 3 articles thorny and with dense fringe of hair on anterior edge.

Abdomen of male rather broadly triangular; telson rather narrowly triangular, approximately as long as basal width.

Measurements in mm.—Carapace: male, length 19, width 19. Length of large series reported by Chace (1951) 3.7 to 19.

Color.—Extremely variable; irregularly mottled or blotched with light greenish yellow or pale yellow on darker olive-green ground color; or reddish-fawn color, more or less blotched with dark brown, and usually with small white spot on each side or one large white spot on front of carapace (various authors).

Crozier (1918) observed no color change in a mahogany-colored *P. minutus* placed for a day on a lighter background. Hitchcock (1941) found three types of chromatophores in *P. minutus*: white, black, and yellow. The most prominent chromatophore is white. Color adaptation to different background is slow and though the chromatophores are responsive to such changes, extracellular pigment in the hypodermis and exoskeleton prevents the animal from effecting an immediate change in appearance. Hitchcock concluded that the pattern of the individual crab is probably genetic. Chace (1951) remarked that in view of these findings, the apparent color of any individual can be changed only at the time of molting.

Habitat.—These crabs are more abundant on *Sargassum* in the Sargasso Sea than elsewhere, but throughout their range they depend on flotsam or on floating or swimming organisms to which they cling (Chace 1951).

Type-locality.—On sargasso and other submarine sea plants on the north side of Jamaica (Sloane in Holthuis 1959).

Known range.—"Northern Atlantic Ocean south of the line connecting Newfoundland with the south coast of England and the southern North Sea" (Holthuis 1959; also Oord and Holthuis 1959), including the Mediterranean Sea, south to 11°05'N, exclusive of the Gulf of Mexico (Chace 1951). The authors regarded occurrences outside this region as doubtful, although Chace found the species at one locality in the Indian Ocean at 90° E on the

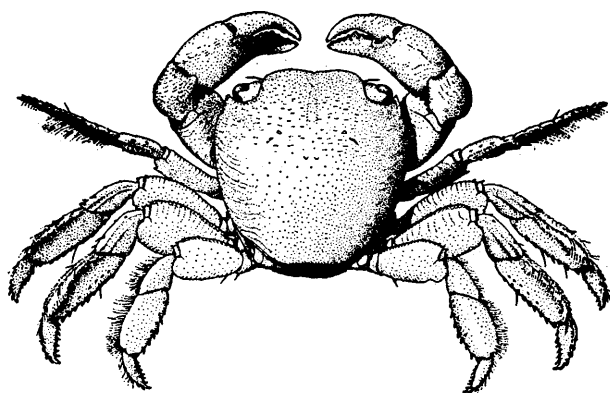


Fig. 369. *Planes minutus* (Linnaeus). Male in dorsal view, approximately $\times 2$ (from Chace 1951).

equator and Holthuis recorded a specimen from Surinam. Fausto-Filho (1968) reported the species from Ceará, as did Coelho and Ramos (1972) from Pernambuco, Brazil, in floating debris, placing the southern range limit at 5°S, but both Chace and Holthuis were uncertain about records south of 11°05'N.

Remarks.—The genus *Planes* was thoroughly reviewed by Chace (1951), and the serious student should consult this paper. Chace included remarks on relative growth, stating that:

"The carapace length-width relationship remains fairly constant with a slight tendency toward narrowing, from the smallest immature specimens examined to a carapace length of about 11 mm. At this stage the carapace seems to become somewhat narrower rather abruptly and continues to become narrower at a slightly more rapid rate than during the younger stages. A similar, but even more striking, trend is noticed in the relative shortening of the walking legs."

Chace conjectured that specimens larger than about 11 mm are found on flotsam and turtles rather than on *Sargassum*, and that the shorter legs may be more adapted to this existence than to life on floating weed. It is also possible that these sizes represent different taxonomic forms, but Chace deferred such a designation until a time when more material is available for study.

Both Hyman (1924b) and Lebour (1944) illustrated some larval stages of *Planes minutus*. In the region of the Carolinas, ovigerous females have been taken virtually throughout the year.

Subfamily Varuninae

Front moderately or little deflexed, sometimes sublaminar. Branchial region with downward-sloping posterolateral portion set off from rest of region by more or less distinctly marked line. Sub-orbital crest, supplementing defective lower border of orbit, rather distant from orbit and usually running in a line with anterior border of epistome. Antennal flagellum usually of good length. External maxillipeds moderately or slightly gaping, without oblique hairy crest; palp articulating with middle of anterior border or near anteroexternal angle of merus; exognath in American genera rather narrow, sometimes partly concealed. Male abdomen rarely covering all space between last pair of legs (Rathbun 1918b).

Genus *Euchirograpsus* H. Milne Edwards 1853

Rathbun 1918b:281.—Hemming 1958b:31.—Türkay 1975:104.

Euchirograpsus americanus A. Milne Edwards

Fig. 370

Euchirograpsus americanus A. Milne Edwards 1880:18.—Rathbun 1918b:282, text-fig. 144, pl. 74 (part).—Hay and Shore 1918:448, pl. 36, fig. 7.—Williams 1965:220, fig. 204 (except Pacific material).—Türkay 1975:114, figs. 6–7, 16b, 20a, b, 24.

Recognition characters.—Carapace slightly broader than long; sides nearly straight and parallel, flattened posteriorly, sloping gently down toward sides and front; surface covered with granules and short, soft hair. Front somewhat produced, lamellate, with narrow median notch. Eyes large; orbits large, small blunt tooth at inner angle; upper margin oblique, sinuous; outer angle spiniform, behind it 3 smaller spines on lateral margin; lower margin of orbit denticulate. Third article of antennae hollowed out on inner side.

Chelipeds stout, 1.5 times as long as carapace; merus with surface crossed by fine granulated line, margins spinose, a superior subdistal spine; carpus with inner distal margin spinulose; palm with 3 spinulose ridges above, outer ridge near lower edge, and another less distinct through middle; fingers slender, grooved, pointed, gripping edges with low, irregular teeth fitting together. Walking legs slender, compressed, hairy; second pair over twice length of carapace; all meri crossed by fine granulated lines, and with superior, subdistal spines; flexor surface of all meri except last with inner distal spine, all with outer distal spine, and first with another spine proximal to it; dactyls armed with long spines.

Measurements in mm.—Carapace: male, length 15.1, width 16.3; female, length 15.1, width 16.5.

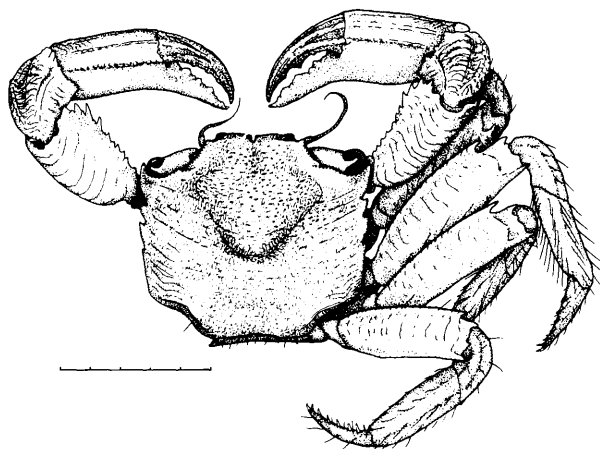


Fig. 370. *Euchirograpsus americanus* H. Milne Edwards. Animal in dorsal view, walking legs of left side not shown, 5 mm indicated (from Williams 1965).

Color.—Yellowish gray, arranged in marblings on carapace and in alternately light and dark bands on legs, or light brown with 5 or 6 bands of red on legs (various authors).

Habitat.—31 to 508 m.

Type-locality.—Barbados, 126.2 m, Blake Stn. 278.

Known range.—Off Oregon Inlet, N. C., Florida through West Indies, and Colombia to Venezuela.

Remarks.—Türkay (1975), in his generic revision, split a genus that had contained two species into a group of six species. Two of these occur in the western Atlantic, *E. americanus* having essentially the Atlantic distribution formerly attributed to it but not occurring in the Galapagos Islands, and between the Bahamas–east Florida and the Yucatan peninsula.

The northernmost record for *E. americanus* is the shallowest, represented by an ovigerous female taken in February (Cerame-Vivas, et al. 1963). Ovigerous females are otherwise known in Florida from March to September.

Subfamily Plagusinae

Front cut into lobes or teeth by antennular clefts visible in dorsal view. Lower border of orbit curving down into line with prominent anterior border of buccal cavity. External maxillipeds neither completely closing buccal cavity nor leaving wide rhomboidal gap, not crossed by an oblique hairy crest; palp articulating near anteroexternal angle of merus, often no flagellum on exposed exognath. Antennal flagella short. Male abdomen filling all space between last pair of legs (Rathbun 1918b).

Genus *Percnon* Gistel 1848

Rathbun 1918b:337.—Hemming 1958b:35.—Manning and Holthuis 1981:237 (synonymy).

Percnon gibbesi (H. Milne Edwards)

(Spray crab)

Fig. 371

Acanthopus Gibbesi H. Milne Edwards 1853:180.

Percnon gibbesi.—Rathbun 1918b:337.—Schmitt 1939:24.—Garth 1965:34.—Williams 1965:224.—

Fausto-Filho 1975:82.—Powers 1977:131.—Manning and Holthuis 1981:238.

Percnon ?gibbesi.—Fausto-Filho 1974:15.

Recognition characters.—Carapace thin, disclike, longer than wide, covered with small short bristles

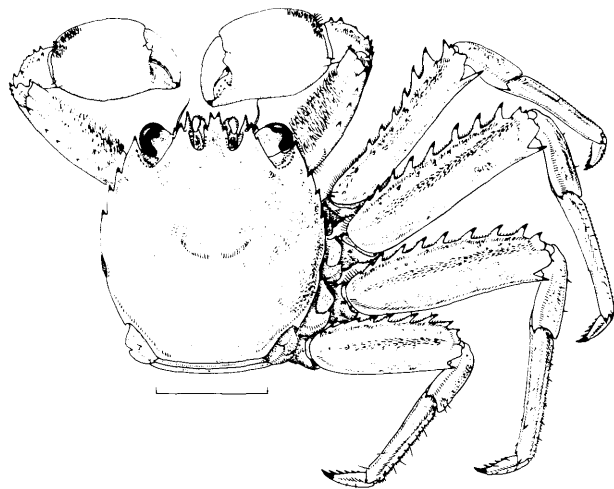


Fig. 371. *Percnon gibbesi* H. Milne Edwards. Male in dorsal view, walking legs of left side not shown, 1 cm indicated (USNM 151485).

except for bare raised patches; dorsal surface with few low tubercles. Front deeply cut by antennular furrows; part between antennules narrow and extended in form of rostrum armed with 2 erect spines on each side distally, and row of inconspicuous spinules just within and parallel to each margin proximally. Eyes large, cornea reniform. Inner margin of orbit bearing 3 spines, 2 distal spines prominent; outer half of upper orbital border more or less serrate. Anterolateral border of carapace with 4 acute spines, counting large spine on outer orbital angle; second spine on outer orbital angle; second spine in series with its lateral margin shorter than that of third spine.

Chelipeds varying in size with age and sex, small in females but large and unequal in adult males; merus and carpus armed with spines, merus in males with dense patch of feathered hairs along dorsomesial side, patch lacking in females; palm nearly smooth, oval and somewhat compressed, upper surface with ill-defined, proximal groove extending $\frac{1}{3}$ length and flanked by usually 2 proximomesial spines, pubescence filling groove continued behind proximal spines to small triangular zone on inner surface; fingers short, blunt, with tips concave on opposed surfaces. Merus of each walking leg with large, nearly uniform spines on anterior margin, upper surface covered with short bristles similar to carapace, longer along margins; flexor margin ending in distal spine; merus of first 2 legs with second row of spinules parallel with anterior border, row indistinct on third merus and absent on fourth.

Measurements in mm.—Carapace: male, length 30, width 28; female, length 33, width 34 (Garth 1946).

Color.—Carapace and meri of walking legs brown

or mottled above; usually a median longitudinal stripe of white or pale blue; legs banded with reddish, brown, and light pink distally; eyestalks and chelae orange; ventral side of body pale blue with legs pale pink (Garth 1946; Verrill 1908a). Greenish or light green, central light blue longitudinal band dorsally (Fausto-Filho 1974).

Habitat.—The usual habitat for this species is the underside of rocks at the low-tide level (Verrill 1908a), or in the surf at knee to hip depth, where it is extremely difficult to capture because of its propensity for rapidly keeping to the underside of turned objects (Garth 1946).

Type-locality.—Antilles.

Known range.—Fort Macon, N. C.; southern Florida and Bahamas to Brazil; Bermuda; Azores to Angola; Cape San Lucas, Lower California, to Chile; Galapagos Islands.

Remarks.—Rathbun (1918b) and Schmitt (1939) separated *P. gibbesi* from *P. planissimum* (Herbst) as, with some reservations, did Crosnier (1965), Garth (1965), Williams (1965) and Fausto-Filho (1974, 1975), but Forest and Guinot (1961; 1966) and Coelho and Ramos (1972) united them as *P. planissimum*. Admittedly, the species are close (carapace, male abdomen and pleopods identical; see Crosnier 1965; Fausto-Filho 1974), but they can be separated on the basis of cheliped characters. The palm of *P. gibbesi* has a small proximal, triangular, pilose zone on the internal surface and a pilose groove on the proximal $\frac{1}{4}$ – $\frac{1}{3}$ of the inner dorsal surface; this groove is noticeably shorter in *P. planissimum*, and the internal pilose zone is almost absent (Crosnier 1965; Garth 1965). As Garth observed, in material available for study the two forms are clearly separable, although study of a more complete series may show these characters to vary in a regular and continuous manner over the geographic range.

Ovigerous females are known from May to September in the Gulf of Mexico-Caribbean-Bahamian-Bermuda region (Rickner 1977; USNM). Muraokoa (1967) described the megalopa of *P. planissimum* taken from Sagami Bay, Japan.

Juveniles in the rocky sublittoral of Colombia were observed exclusively in the immediate vicinity of *Diadema antillarum*, apparently using the long urchin spines as protection against predation, for when the urchins were removed the associated crabs were eaten by fishes (Schmalfuss 1976). Schmalfuss hypothesized that the dimorphically ornate, larger chelipeds of male *P. gibbesi* are used in courtship or copulation and that the elaborate pattern of rows and fields of feathered hairs on the walking legs and dorsal surface of the carapace serve a purpose in suspension feeding. He noted that the

brush of hairs on the antennule displays a conspicuous yellowish color when the antennule is flicked up and down in quick strokes, following which it is brushed through the maxillipeds. He interpreted antennular motion as either a lure to attract small fish which are caught and eaten or as an active filter, considering these possibilities to be compatible.

Randall (1967) reported *P. gibbesi* from stomach contents of the coney, *Cephalopholis fulva*, rock hind, *Epinephelus adscensionis*, soapfish, *Rypticus saponaceus*, schoolmaster, *Lutjanus apodus*, puddingwife, *Halichoeres radiatus*, porcupine fish, *Diodon hystrix*, and longlure frogfish, *Antennarius multiocellatus*.

Genus *Plagusia* Latreille 1804

Rathbun 1918b:331.—Monod 1956:455.—China 1966:257.—Manning and Holthuis 1981:238 (synonymy).

Plagusia depressa (Fabricius)

Fig. 372

Cancer depressus Fabricius 1775:406.

Plagusia depressa.—Rathbun 1918b:332, text-fig. 154, pl. 101.—Monod 1956:455, figs. 614–617.—Williams 1965:223, fig. 207.—Forest and Guinot 1966:93.—Chace and Hobbs 1969:192, figs. 62r–t, 63.—Felder 1973:75, pl. 11, fig. 5.—Fausto-Filho 1974:15.—Powers 1977:131.—Manning and Holthuis 1981: 239.

Recognition characters.—Carapace subhexagonal, wider than long, depressed, covered with short, plumose hairs forming scalelike pattern around flattened tubercles and elsewhere; regions distinct, front of gastric region with series of approximately 6 prominent, acute tubercles arranged in an arc. Indefinite front broad, with deep median furrow and deep notches for antennules; spiniform tubercle on each side between median furrow and antennular notch. Eyes with cornea slightly narrower than eyestalks; orbits deep; outer orbital angle produced into strong, curved spine followed on anterolateral margin by 3 similar spines of diminishing size; lower orbital margin produced, armed with 2 teeth slanting toward anterolateral angle of mouth area. Epistome prominent beyond anterior border of carapace and cut into central and 2 or more lateral lobes on each side.

Chelipeds of adult male moderately heavy, subequal, approximately as long as carapace; in female slender, $\frac{3}{4}$ as long as carapace; merus with 3 small spines above at distal end; carpus rugose, inner tooth triangular; palm and dactyl (male) with

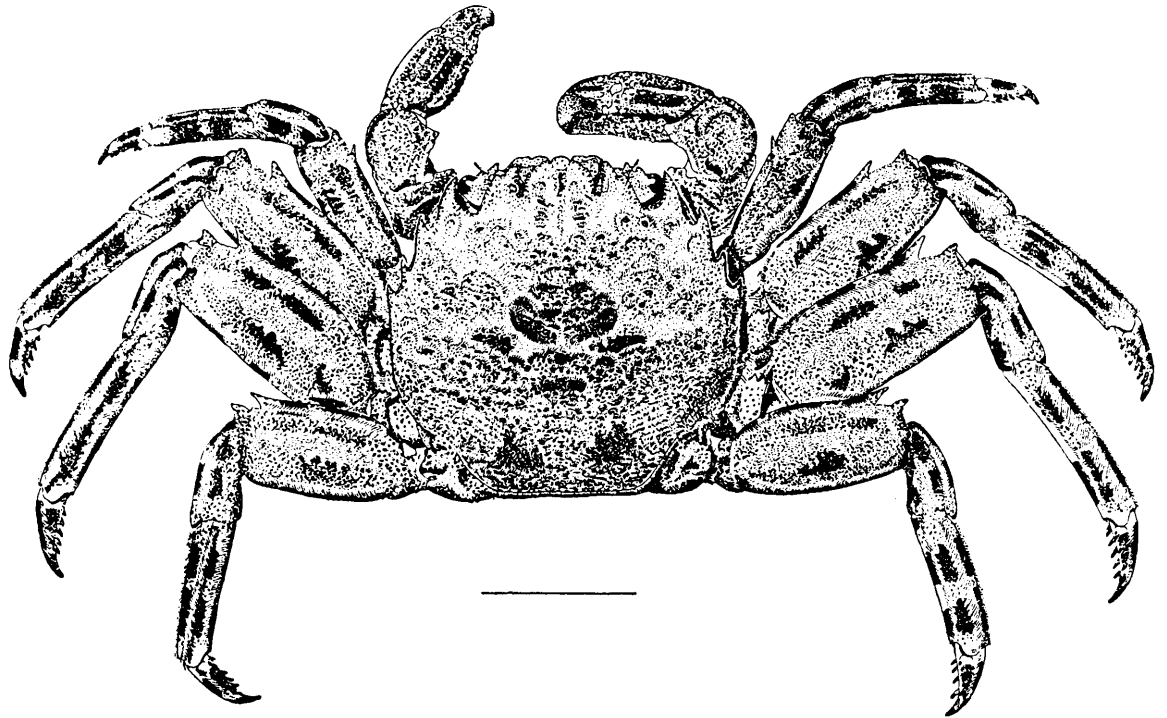


Fig. 372. *Plagusia depressa* (Fabricius). Male in dorsal view, 20 mm indicated (from Chace and Hobbs 1969).

tubercles arranged in 3 longitudinal ribs separated by setose furrows, outer surface smooth, inner surface with scattered small tubercles; fingers blunt, spoon tipped with corneous edges. Walking legs strong, somewhat flattened, increasing in size from first to third, fourth shorter than second; second and third legs with dentate crest above on coxae; meri with subterminal spine on anterior border; distal 3 articles with dense strip of long hair; dactyls with 2 rows of strong spines on flexor side.

Measurements in mm.—Carapace: male, length 50, width 53; female, length 59, width 62.

Color.—Light reddish, dotted with blood red, tubercles bordered with blackish hairs having gray extremities; blood-red spots on legs; underside of body yellowish (Latreille in Rathbun 1918b). Light to dark blue green (Fausto-Filho 1974). "Carapace olive tan with brown to black tubercles and dark brown or black areas dorsally." Chelipeds with white basal articles; merus, carpus and chela pinkish with purple spots and stripes, fingers white distally. Walking legs olive with purple spots and stripes, dactyls white to olive with purple band and corneous tips. Underparts white, including third maxillipeds (Chace and Hobbs 1969).

Habitat.—Found among rocks, on jetties, in tide pools, and thought to be transported on ships' hulls.

Type-locality.—"In mari mediterraneo" (erroneous).

Known range.—Beaufort, N. C., through Gulf of Mexico and West Indies to Pernambuco, Brazil; Bermuda; Azores; Madeira; Morocco to northern Angola; St. Helena Island (Chace 1966). Felder (1973) and Haburay (1975) considered the species uncommon in the Gulf of Mexico.

Remarks.—Chace (1966) compared male gonopods of the species of *Plagusia*, pointing out that *P. depressa* from the Atlantic is probably a distinct species.

Ovigerous females are known from samples collected in April to August in the main part of the range, and February at St. Helena Island (USNM). Muraoka (1965) described the megalopa of the Pacific *P. depressa tuberculata* in plankton taken in early autumn from Sagami Bay, Japan.

Subfamily Sesarminae

Front strongly deflexed. Lower border of orbit commonly running downward toward angle of buccal cavern. Side walls of carapace finely reticulated with granules and hairs or hairs only. External maxillipeds separated by wide rhomboidal gap, an oblique hairy crest traversing them from point near anteroexternal angle of ischium to point near anterointernal angle of merus; palp articulating either at summit or near anteroexternal angle of

merus; exognath slender and either partly or almost entirely concealed. Male abdomen either filling or not quite filling all space between last pair of legs (Rathbun 1918b).

Genus *Sesarma* Say 1817

Rathbun 1918b:284.—Manning and Holthuis 1981:241.

Key to Species

1. Lateral margin of carapace straight; distal articles of first 3 walking legs with long hairs but not densely pubescent; body nearly flat *S. (Chiromantes) cinereum*
- Lateral margin of carapace sinuous; last 3 articles of first 3 walking legs densely pubescent; body strongly convex *S. (S.) reticulatum*

Sesarma (Chiromantes) cinereum (Bosc)

(Wharf crab; wood crab; friendly crab; square-backed fiddler)

Fig. 373

Grapsus cinereus Bosc [1802]:204, pl. 5, fig. 1.

Sesarma cinerea.—Hay and Shore 1918:449, pl. 36, fig. 11.

Sesarma (Holometopus) cinereum.—Rathbun 1918b:300, text-fig. 149, pl. 83.—Abele 1973:377, fig. 1B, H.—Powers 1977:133.

Sesarma (Holometopus) cinerum [sic].—Williams 1965:222, fig. 206.

Sesarma cinereum.—Felder 1973:78, pl. 11, fig. 6.

Sesarma (Chiromantes) cinereum.—Manning and Holthuis 1981:242 (implication).

Recognition characters.—Carapace rectangular, nearly uniform in width throughout; regions well marked; surface nearly smooth, punctate, rough with squamiform tubercles toward front; supra-frontal lobes well marked, inner pair widest. Front 4 times as wide as high, widening below, somewhat 4-lobed in dorsal view, lower edge sinuous. Outer orbital angle acute. Lower surface of carapace covered with fine net of geniculate hairs.

Chelipeds heavy; merus and carpus covered with short transverse lines of scabrous granules; merus with upper edge sharp, inner edge irregularly dentate with triangular laminar expansion on distal half; carpus with inner angle rounded. Palm nearly twice as high as upper length; outer surface covered with scabrous granules arranged in parallel lines near upper margin; inner face coarsely granulate, with short prominent ridge near distal end; fingers gaping narrowly, largest tooth at middle of fixed finger. Walking legs rather narrow, meri with superior subdistal spine; third pair of legs over twice as long as carapace.

Abdomen of males broadly triangular; telson much narrower than sixth segment.

Measurements in mm.—Carapace: male, length 18, width 20; female, length 20, width 23; ovigerous

females, width 9.2–20.2 (Seiple 1979).

Color.—Brown varying toward olive.

Habitat.—Supralittoral zones of marshes characterized by high salinity (\bar{x} = 27.9%) and sandy substrates (Seiple 1979). Found actively crawling about on wharves and stone jetties or resting in shallow burrows above tidemark along shores. The crabs have often been found on vessels along the coast hiding anywhere out of sight or reach and coming forth at night to feed.

Type-locality.—"La Caroline."

Known range.—Magothy River, Chesapeake Bay, Md., to Palm Beach, E Fla.; Collier County, W. Fla., to Veracruz Mexico (Abele 1973). Older records from the West Indies and elsewhere are erroneous.

Remarks.—Ovigerous females occur from mid-April to November in North Carolina, also reported May-June in Mexico (Rickner 1977), and have been found along the Potomac River in January (USNM). Females in North Carolina produce 4–6 egg batches in close synchrony with lunar phases, each female carrying her eggs approximately one lunar month, with peak reproductive activity occurring from April to June (Seiple 1979). Hyman (1924b) briefly described the first zoeal stage. Costlow and Bookhout (1960) described four

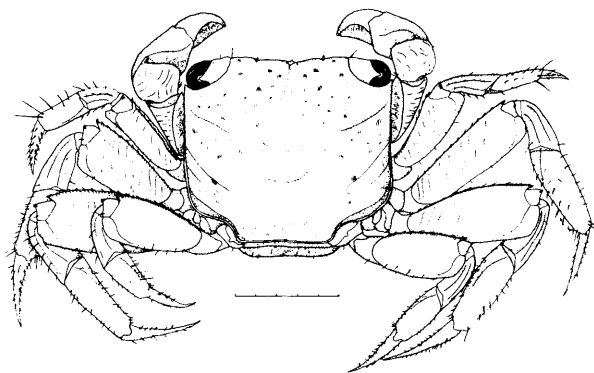


Fig. 373. *Sesarma (Chiromantes) cinereum* (Bosc). Animal in dorsal view, 5 mm indicated (from Williams 1965).

zoeal stages and the megalopa from 1,200 zoeae reared on *Artemia* nauplii and *Arbacia* eggs under constant conditions of temperature, salinity, and light. Costlow, et al. (1960) found that optimum salinities exist for each larval stage, but development proceeds best in the 20–26.7‰ salinity range (among those tested). Temperature was found to have more effect on length of larval development than on mortality, with higher temperature speeding development. No “extra stages” were observed. The authors concluded that salinity is the chief physical factor confining *S. cinereum* to estuaries. No allozyme genetic variation is shown in life-history stages (Gooch 1971).

Records of the larvae from plankton vary with site of sampling. Pinschmidt (1963), in Newport River near Beaufort, N. C., found stage I and II zoeae in low concentration from June to September in water of 19° to 13°C and 7 to 36‰ salinity, but most numerous in August at 25° to 31°C. Sandifer (1973d) found the larvae rarely in York and Pamunkey rivers Va., in June and August, the three samples being from bottom water or 24.8° to 26.6°C in 11.9 to 19.64‰ salinity. Dudley and Judy (1971) found larvae of the genus *Sesarma* more abundant inshore (1.6 km) than offshore (6.5 km) from June to September off Beaufort Inlet, N. C., and more numerous at 8-m depth than at the surface. Tagatz (1968) found larvae of the genus *Sesarma* the second most abundant form in St. Johns River, Fla., in samples taken from April to October, with greatest number in August.

Sesarma cinereum feeds on *Spartina* shoots (Seiple 1979). The species can survive for a considerable period of time in dilutions of sea water and also shows considerable resistance to desiccation (Pearse 1929). Oler (1941) maintained captive specimens from a Maryland tidal river in a house basement for about a year. The animals burrowed in mud in an aquarium where the only moisture provided was tap water. Vegetable matter was fed at irregular intervals. After several months, the larger animals ate the smaller ones, presumably at the time of ecdysis. Duncker (1934), in Germany, secured three live females identified as *S. cinereum* (see Abele 1973) which had been transported by chance in a cargo of logs from the West Indies. The animals were kept alive in a glass jar with damp peat and a container for a source of fresh water. One lived 4 years and 72 days from date of captivity. The crabs were fed shredded beef or fish and commercial fish food plus *Collembola* that appeared in the jar. All eating was done on land. Some regeneration of lost appendages occurred, and the longest lived specimen molted four times, molting always taking place in water. To the author's surprise, eggs were re-

leased six times (about 4,700 to 13,400 per mass) always in water, the longest lived female producing five of these batches. Larvae hatched from all but one of the egg masses, but survived only a short time. Duncker concluded that one mating was effective for three years or more. Incubation lasted approximately 30 days. The female ate eggs that protruded over the edge of the abdomen. Duncker considered that the crabs acted more like land than aquatic animals, each individual having its own burrow.

Teal (1959) implied the same conclusion, for in experiments under water *S. cinereum* was relatively inactive, thus holding its oxygen consumption down. There was some evidence for thermal acclimation of metabolism, but more evidence for acclimation by selection of microclimate. Gray (1957) also emphasized the terrestrial habits of the species but showed that its relative gill area is nearly double that of the similar species, *Ocypode quadrata*.

Sesarma (Sesarma) reticulatum (Say)

Fig. 374

Ocypode reticulatus Say 1817:73, pl. 4, fig. 6.

Sesarma reticulata.—Hay and Shore 1918:448, pl. 36, fig. 12.

Sesarma (Sesarma) reticulatum.—Rathbun 1918b:290, pl. 77.—Williams 1965:221, fig. 205.—Abele 1973:380, fig. 1E.—Powers 1977:136.

Sesarma reticulatum.—Felder 1973:78, pl. 11, fig. 7.

Recognition characters.—Carapace about $\frac{4}{5}$ as long as broad, convex, regions distinct, surface punctate and with scattered clumps of setae above and in front; sides concave behind widest point, convergent at orbital angles. Posterolateral regions obliquely striated and setose; inferolateral and frontal regions with irregular rows of tubercles bearing short, curved hairs. Dorsal portion of carapace overhanging sides; beneath projecting shelf a line of cilia. Lower surface of carapace covered with fine net of geniculate hairs. Front broad, slightly sinuate above basal articles of antennae. Eyestalks short and stout, set in deep oval orbits; deep gap below outer orbital angle leading into system of grooves opening into notch at anterolateral angle of buccal cavern. External maxillipeds separated by wide rhomboidal gap largely filled by hairy fringe, and obliquely traversed by conspicuous line of hairs from point behind anteroexternal angle of ischium to anterointernal angle of merus.

Chelipeds stout, subequal in male; merus and carpus lightly rugose; merus with obtuse subterminal tooth above, both lower margins denticu-

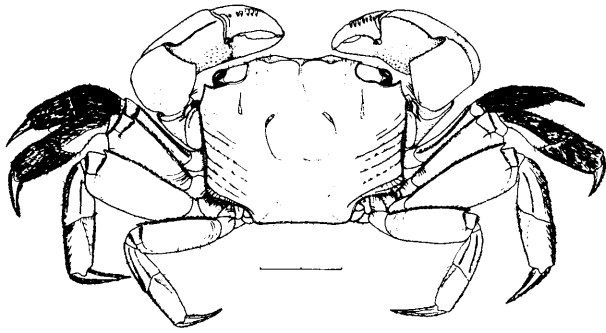


Fig. 374. *Sesarma (Sesarma) reticulatum* (Say). Animal in dorsal view, 1 cm indicated (from Williams 1965).

late; carpus with inner angle rounded. Palm almost smooth, in male slightly higher than midlength, upper edge with single granulate line, inner surface with short irregular ridge of tubercles near distal end; dactyl with 7 of 9 depressed spinules above on basal $\frac{2}{3}$; fingers agape, enlarged tooth near each end. Palm of female half again as high as midlength, fingers slightly agape. Third pair of walking legs approximately twice as long as carapace, last 3 articles densely pubescent.

Measurements in mm.—Carapace: male, length 23; width 28.

Color.—Carapace dark olive, nearly black or purple; dark plum-colored or bluish-black speckles crowded on grayish background, grayish color showing little except on posterior part; upper part of chelipeds similarly colored but brighter, greater part of palm yellowish, tips of fingers white or yellowish; upper part of legs as carapace; under parts grayish (various authors).

Habitat.—Burrows in muddy salt marshes with mean salinity of 16.2‰ (Seiple 1979).

Type-locality.—Muddy salt marshes [east coast of United States].

Known range.—Woods Hole, Mass., to Volusia County, E Florida; Sarasota, W Florida, to Calhoun County, Tex. (Abele 1973, and personal communication).

Remarks.—Ovigerous females are reported from Massachusetts in July, and mid-April to mid-September at Beaufort, N. C., with peak reproduction in April-June (Seiple 1979). Females produce 2–3 egg masses per season, carrying each batch approximately 45 days. Crichton (1960) found 8,000 to 10,000 eggs per egg mass. Hyman (1924b) described the first zoeal stage, comparing it with *S. cinereum*. Costlow and Bookhout (1962a) described the complete larval development of three zoeal stages and a megalopa, comparing these to similar stages they had described for *S. cinereum*. They concluded that photoperiod has no observable ef-

fect on development. Costlow (1966) discussed effects of eyestalk extirpation on larval development, showing that removal of both eyestalks results in acceleration of metamorphosis in megalopae but not in zoeae, suggesting that the X-organ-sinus gland complex is a phased storage organ for more than one endocrine substance which regulates rate of development. No allozyme genetic variation is shown in life history-stages (Gooch 1977).

Sandifer (1973d) took larvae of *S. reticulatum* in the York and Pamunkey rivers, but never abundantly, in a salinity range of 2.04 to 20.24‰. Few larvae occurred below 10‰ salinity, most being between 15 and 20‰, but there was one occurrence off the mouth of Chesapeake Bay. The larvae appeared in June, increased in July-August, and disappeared by October, living in a temperature range of 22.8° to 27.9°C. Stage I made up 73% of the larvae taken, and > 80% of all taken were at the bottom. Sandifer (1975) regarded this depth distribution as an adaptation for retention in estuaries. Pinschmidt (1963) found the same trends.

Foskett (1977) found that larvae are hyperosmotic over the salinity range 10 to 35‰ and hypertonic in salinities above that throughout zoeal stages and the early megalopa. He felt that this trend may serve to increase density of the larvae, helping to promote retention within the estuary. Hyperregulation may also act to provide turgor pressure insuring integrity of the thin larval cuticle, but the rapid molting cycles do not affect blood osmotic concentrations. Foskett also noted that adults hyperregulate in salinities up to 27.5‰ and hypo-regulate in salinities above that, acquiring the adult regulatory pattern during early juvenile crab stages.

Crichton (1960, 1974) in Delaware, with the aid of rubber casts, found that the species digs burrows which may have several openings leading at a gentle slope to a depth of 7.5–10 cm where a series of more or less level corridors curve, twist, and often interconnect. Each corridor usually leads to a vertical shaft as much as 0.75 m deep, usually filled with water. Burrows are communal, containing a male or two and several females. Crichton found that this species will eat fiddler crabs (the burrows occasionally intersect) when it can capture them; however, the usual diet is *Spartina*, the crabs often cutting swaths through this marsh grass. From experiments it was deduced that 42% of energy harvested by *Sesarma* is passed directly to the marsh surface in fecal deposits. Burrowing action of the crab tills the land, increases erosion, and turns over the cord grass more rapidly than the annual decay cycle could do it unaided. The role of this crab among macroinvertebrates in marsh ecosystems was further discussed by Day, et al. (1973) and Subrah-

manyam, et al. (1976), and analysis of its burrowing habits by Allen and Curran (1974).

Teal (1959) found the species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, the crabs were in burrows, usually near the top, in air or water. Respiration rates were higher in water than in air. Teal and Carey (1967) additionally found that *S. reticulatum* can regulate its metabolism down to 6% atmosphere; however, marsh crabs do not encounter low oxygen conditions in air, only in burrows in water. There, during periods of submergence, the respiration rate may decline with decreasing oxygen pressure, and below critical pressures the crabs must convert metabolism to fermentation. Lactic acid is probably formed from glycogen, to be oxidized at the next period of emergence. Gray (1957) found the gill area of *S. reticulatum* to be relatively low as compared with other species living in a similar habitat (*Uca pugnax* and *minax*). He found *S. reticulatum* to be more robust but less active than

the close relative *S. cinereum*.

Humes (1941) described a harpacticoid copepod (*Cancrincola plumipes*) from the gill chambers of this crab.

Superfamily Ocypodoidea

Family Ocypodidae

Palp of external maxillipeds coarse, articulating at or near anteroexternal angle of merus; exognath generally slender and often somewhat concealed. Front usually of moderate width, and often a somewhat deflexed narrow lobe. Orbits occupying entire anterior border of carapace outside front, and with their outer wall often defective. Buccal cavity usually large and somewhat narrowed anteriorly, external maxillipeds often, but not always, completely closing it. Abdomen of male narrow. Male openings sternal. (Rathbun 1918b.)

Subfamily Ocypodinae

Key to Genera and Species

(Modified in part after Felder 1973)

1. Stout eyestalk with conspicuous, enlarged, club-shaped cornea; chelipeds of both sexes well developed and somewhat unequal . . . ***Ocypode quadrata***
Slender eyestalk with cornea not conspicuously enlarged; chelipeds of male very unequal, of female equal and quite small. . . . [*Uca*; for males, include cheliped characters in rest of key; for females, ignore them] . . . 2
2. Major palm with oblique tuberculate ridge on inner surface extending from lower margin to carpal cavity (males); merus of last legs with upper margin curved; 75 or fewer spoon-tipped hairs on inner meral surface of second maxilliped. 3
Major palm without oblique tuberculate ridge on inner surface extending from lower margin to carpal cavity (males); merus of last legs with upper margin straight; more than 100 spoon-tipped hairs on inner meral surface of second maxilliped. ***U. pugilator***
3. Joints of major cheliped bordered by red patches, especially near condyles of carpus and merus (fresh male specimens); merus of second and third walking legs with sparse ventral rows of stiff hairs or bristles, as long as on carpus and propodus; 0–20 (usually 0–15) spoon-tipped hairs on inner meral surface of second maxilliped ***U. minax***
Joints of major cheliped bordered by yellow or yellow-brown color (fresh male specimens); merus of second and third walking legs ventrally with patch, row, or paired rows of dense velvety pubescence as well as sparse rows of stiff hairs on ventral edge (mainly distal half); 0–75, (usually 15–60) spoon-tipped hairs on inner meral surface of second maxilliped ***U. pugnax***

Genus *Ocypode* Weber 1795

Ocypode quadrata (Fabricius)

(Ghost crab; sand crab)

Rathbun 1918b:366.—Monod 1956:390.—China 1966:256.

Fig. 375

Cancer quadratus Fabricius 1787:315.

Ocypode albicans.—Rathbun 1918b:367, pls. 127–128.—Hay and Shore 1918:450, pl. 37, fig. 1.—Guinot-Dumortier 1960:515, figs. 16a-c.

Ocypode quadrata.—Holthuis 1959:259.—Williams 1965:225, fig. 208.—Chace and Hobbs 1969:204, figs. 68–69.—Coelho and Ramos 1972:198.—Felder 1973:82, pl. 12, figs. 5, 8.—Powers 1977:140.

Recognition characters.—Carapace quadrilateral, convex above from front to back, sides nearly vertical; dorsal region finely granulate on middle and posterior parts, coarsely granulate toward sides, center of carapace with well-marked H-shaped depression. Front and side margins raised, beaded, or serrulate, lateral margin continued into prominent, acute angle at outer corner of orbit; similar but lower ridge extending upward and forward from base of third walking leg. Orbits large and open, extending all along anterior margin on either side of narrow front, both upper and lower margins crested and dentate. Eyestalks large, club-shaped, cornea covering over half of distal article. Front narrow, deflexed; antennules and antennae much reduced, flagellum of antennules hidden beneath front.

Chelipeds in both sexes, and in young, unequal, well developed, rough; merus serrulate above, toothed on lower margins; carpus with sharp spines at inner angle; hands coarsely scabrotuberculate, margins of palm and fingers dentate, fingers pointed. Large hand with vertical stridulating ridge of tubercles on inner surface near base of dactyl that plays against smooth, distal, anteroventral ridge of ischium. Walking legs almost smooth, fringed with long, stiff, yellow hair, third pair longest, fourth shortest; meri of first 3 pairs broadened; propodi of these legs with longitudinal brushes of hair on anterior surface; dactyls of all legs fluted, depressions hairy. A hair-fringed breathing slit on ventral surface between basal articles of third and fourth walking legs.

Measurements in mm.—Carapace: male, length 44, width 50.

Color.—Gray, pepper-and-salt, grayish white, pale yellow, straw color, or yellowish white imitating color of beaches; sometimes light amber and often iridescent; yellow markings below and on legs; young mottled gray and brown (various authors). A brown phase was reported from black beaches of Dominica (Chace and Hobbs 1969). Cowles (1908) noticed that the ghost crab exhibits color changes. The crabs are generally dark in subdued light and in direct sunlight if temperature is not above 35°C. Above 35°C, the crabs are light colored regardless of light intensity. In absence of light, the crabs are

light colored regardless of temperature.

Habitat.—This species, the most terrestrial of the decapod crustaceans in the region, lives in abundance along the ocean beaches and sometimes on harbor beaches. The crabs construct burrows 0.6 to 1.2 m (2 to 4 ft) in depth from near the high-tide line to distances up to ¼ mi from the ocean.

Type-locality.—Jamaica.

Known range.—Block Island, R. I., to Santa Catarina, Brazil (megalopae have been taken at Woods Hole); Bermuda; Fernando de Noronha.

Remarks.—Perhaps because of their mode of life, ghost crabs have left a fragmentary fossil record. Rathbun (1935) recorded *O. quadrata* questionably from the Pleistocene of Florida, but Glaessner (1969) listed it only by genus. Hayasaka (1935) compared the “sandstone pipes” commonly found in certain Tertiary sandstones of Formosa to plaster casts of burrows made by the Formosan *O. ceratophthalma* and found them to be much alike. Burrows of the modern Formosan and eastern North America species are similar.

Habitats of *O. quadrata* have been treated in a number of scholarly and popular works, but the serious student is referred especially to Cowles (1908), Milne and Milne (1946), and Haley (1969, 1972). A popular account of some value, except for the concluding conjectures, was given by Phillips (1940). Only a brief summary from various authors can be given here.

Mating and spawning seasons of the species are correlated with temperature, hence vary in length to some degree with latitude. Early accounts state that spawning in the Carolinas appears to extend from April to July (Coues 1871), agreeing with that

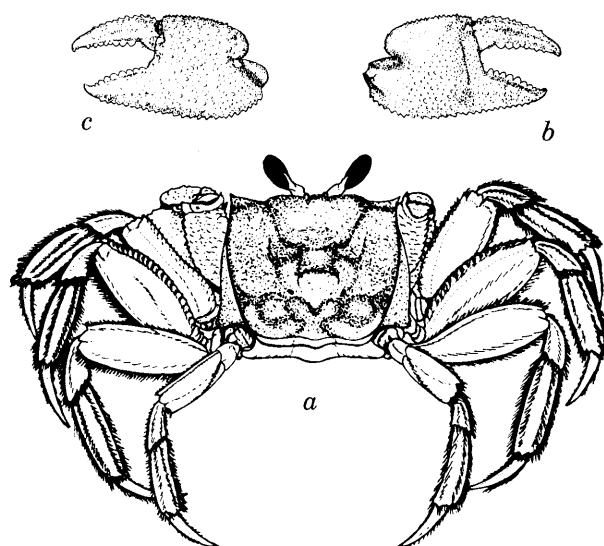


Fig. 375. *Ocypode quadrata* (Fabricius). a, Female in dorsal view, reduced (from Gmitter and Wotton 1953); major chela of male, b, outer view, c, inner view, reduced (from Crane 1941).

seen in New Jersey (Milne and Milne 1946) and at Tortugas, Fla. (Cowles 1908), but Haley (1972) stated that the crabs are inactive in Texas for only about three months a year when temperature is below 16°C. Mated females with ripening eggs found even before the active spring period indicate initiation of oogenesis in winter and retention of sperm during winter. Copulation probably occurs throughout the year, but in two peaks in spring and summer. Hughes (1973) stated that although mated pairs were occasionally dug from burrows in Costa Rica, burrows are not essential for mating nor do all matings occur at night (Henning and Klaassen 1973). Males in captivity usually rush females on sight; when mating occurs the pair have ventral sides juxtaposed for about 25 min, the male in vertical position with eyes pointed up and the passive female with eyes mostly retracted, a contrast to mating of most hard shell brachyurans in which the female is uppermost. Males in Texas enter puberty at about 24 mm carapace width (Haley 1969); first pleopods show puberty-related changes (also Hartnoll 1974), having grown at a constantly changing rate until the animal reaches about 25 mm width after which growth is isometric. Females maintain isometric growth except for a distinct change in the abdomen in which the fifth segment becomes widest; they enter puberty at 26 mm carapace width and are incapable of copulation below that size.

Ovigerous females differ in behavior from other individuals in that they wade in water more freely, run along on the bottom, and at intervals when the water is quiet open the abdomen out, flip upside down, extend the mouthparts, rotate the legs, and, thus, force water through the egg mass. Such females will run quickly to water when disturbed (Milne and Milne 1946).

From ovigerous females collected in evening or at night on the beach near the waterline, Diaz and Costlow (1972) obtained eggs that hatched and developed through larval stages. The eggs usually hatched on the night of collection, frequently on the way to the laboratory. Five zoeal stages were identified and described from rearing in water of 35‰ salinity at 25°C in a photoperiod of 12 light–12 dark h. The megalopa appeared in a minimum of 34 days following hatching. Prezoeae observed in a few broods lived only a few hours and did not molt to succeeding stages. There was high mortality in zoeal stages IV and V; less than 10% of all reared larvae reached the megalopa. The megalopa was first described by Say (1817) as *Monolepis inermis*. Smith (1873a, 1873b, 1880b) recognized the true status of the form and pointed out that though it is carried as far north as Vineyard Sound by the

Gulf Stream, that area is apparently too cold to support an adult population.

Haley (1972) outlined the life history, assuming that in a development time of 60 days the first crab stage should appear on the beach in July and late October (two Texas broods). A May brood could attain puberty in March of the following year with an instar period of 35 days for each of 7 molts. An August brood could attain puberty by the following July at the same rate. These two groups could thus represent the influx of new females in spring and summer. A female spawned in May develops to first crab in June and matures by April of the following year; in August these females make up the younger part of the spawning postpubertal females, the older ones spawning a second time after spring ovulation. By April of the third year these are the older part of the spawning females. They may or may not ovulate that summer and probably do not survive the following winter. A summer brood that reaches 7 mm carapace width in October overwinters as juveniles, mates in July, and spawns in August. These comprise the younger postpubertal females in spring and are the older postpubertal females spawning a second time that summer. A female probably ovulates no more than four times during a life span of nearly three years.

Burrows of *O. quadrata* show conspicuous zonation. The young crabs are found close to shore. Burrows of the young are near the water, extend to water level and are covered by high tides for a time, whereas older crabs burrow farther from water; the latter seldom are deep enough to reach water level. Hill and Hunter (1973) and Frey and Mayou (1970, 1971) observed that variation in shape, diameter, length, density and orientation of burrows could be used to differentiate subenvironments of beach-foredune areas. Burrows are of three general types: (1) a short vertical burrow made by young crabs, (2) a burrow sloped downward at about 45° away from the shoreline, often with branches, one of which may extend upward almost to the surface (or open to form a U-shaped tube), and (3) burrows higher on the beach or in dunes, much like the second type but without the vertical side branch. In fall in New Jersey the burrows have been found farther from water and far deeper than any studied earlier in the year, and it is presumed that various sizes of crabs hibernate in these. Hill and Hunter (1973) pointed out that burrows have different form in different latitudes.

Fisher and Tevesz (1979) observed that carapace width is approximately equal to burrow diameter. Adults along North Carolina outer banks were found to be more evenly spaced than would be expected under a Poisson distribution, but juveniles

had clumped distribution. The authors felt that the difference may reflect territorial behavior, adults defending larger areas of the stable beach environment than juveniles limited to a small area near the swash zone. The latter are poorer burrowers, and more subject to predation and dessication than adults. Beach disturbances reduce adult to juvenile ratios and abundance of adult crabs.

Burrow making is primarily an occupation of daylight hours. The crabs cease feeding on the wet beach toward dawn. Those feeding on a fish carcass often burrow within an inch or two of the carcass. Young crabs near water make new burrows, older ones range inland and build burrows or occupy old holes, renovation perhaps being more common than new construction (Hill and Hunter 1973). Sand is brought to the mouth of the burrow and dropped or spread near the opening in a fan-shaped area. Toward noon, openings to burrows are plugged with damp sand, thus concealing the burrow. Toward evening, the crabs begin to emerge again, and by 10 p.m. the whole population is usually on the beach.

Ghost crabs traditionally have been considered as scavengers and predators (or cannibals) that tend to feed most actively along the drift line, looking for beached fish or refuse and small bits of food buried in the top layer of sand. Wolcott (1978), however, showed that scavenged material accounted for less than 10% of their food on North Carolina beaches. More than 90% of the diet was live prey, the mole crab, *Emerita talpoida*, and coquina clam, *Donax variabilis*, in equal weights making up most of this. Because of higher caloric content, the mole crab provides about 60% of the energy, the clam only 25%. Estimates indicated that the crabs consumed most of the production of the two prey species. The ghost crabs are the top carnivores on the beaches, having little competition. Fales (1976) also reported their feeding on mole crabs, and Sprunt (1948) considered them to be a major predator on tern chicks at Dry Tortugas, Fla.

The crabs go into the water at intervals to moisten the gills, retaining a small amount of water in the branchial chamber (Edney 1960), and the young do this more frequently than adults. When undisturbed, individuals do not actually enter water but will stop a few inches from the waterline with one side presented to the water, the legs of the other side anchored in sand, and wait for a wave to wash over them, after which they return to the higher parts of the beach. If disturbed, the crabs will run into the water, then leave it as soon as possible. These crabs do not swim but walk on the bottom or are rolled about by waves; they can survive for a limited time if forced to remain submerged.

The crabs also take up moisture from damp substrate through setae at the base of the second and third walking legs which conduct it into the branchial chambers (Bliss 1963). *Ocypode quadrata* will die in 20 h in an atmosphere of 30°C at 78% relative humidity if water lost by transpiration is not replaced (Bliss 1968).

Flemister and Flemister (1951) and Flemister (1958) showed that when *O. quadrata* is confined in water, oxygen consumption is elevated, but elevated least when chloride ion concentration of the water equals that of the blood. Lower or higher ion concentration of the water raises the respiration rate. They demonstrated that the animals normally have blood hypotonic to sea water. In sea water containing less 120 or more than 160 millimoles of chloride per liter, the internal concentration is not maintained but tends to rise or fall depending on which end of this range the animal experiences. The antennal gland, aided by the gill membranes, functions in regulation of internal chloride ion concentration. Gifford (1962) found that *O. quadrata* can regulate major ions in its body fluid in all salinities tested (14–197‰ seawater) at temperatures between 12 and 25°C but that this ability is lowered above that temperature range, especially in high salinity.

The general relationship of habitat to oxygen consumption and general activity among certain decapods has been a subject of study of Ayers (1938), Pearse (1929), Vernberg (1956), and Gray (1957) in the Beaufort, N. C., area *Ocypode quadrata* was of prime interest because of its terrestrial adaptation combined with great activity. Of all the crabs studied there, the ghost crab possesses the highest rate of oxygen consumption both for the whole animal and for gill tissue alone. This is more striking when it is emphasized that *O. quadrata* has a reduced number of gills (though it has accessory respiratory tissues in the gill cavity) and the gill area per gram of weight in this species is by far the lowest among 16 species studied in near-shore, intertidal, and above-tide zones. However, air contains proportionately more oxygen than does water (Bliss 1968).

The eyes of *O. quadrata* are so large and prominent that it seems as if the crab can see exceptionally well. Experiment has shown that the eyes are primarily sensitive to large changes in intensity of light. The crabs do not tend to avoid strong light, but try to hide if lights are suddenly shut off or if an object on the beach is suddenly moved (Wolcott 1978). The eyes apparently aid in the search for food, but actual detection of food is by taste or smell.

Locomotion is accomplished by all eight walking

legs. Usually the crabs walk sideways or obliquely. If hotly pursued, they will run in another manner, holding the last pair of legs clear of the ground. Usually the crabs walk or run toward the side with the small chela, but they can also walk forward, or sometimes approach food by walking slowly backward.

When two crabs meet, they raise themselves on their legs, facing each other, chelipeds held apart with the tips pointing downward or downward and forward (Schöne 1968). After standing for a time, the encounter may end with one of the pair lowering or flattening itself; this sometimes happens when the "winner" is in a more elevated position. Fights are usually formalized; wild fights are rarely observed.

Ocypode quadrata produces three sounds: bubbling, rapping and rasping. These were detected in the burrow in early morning after the night's foraging (Horch and Salmon 1964, Salmon and Horch 1972). Rapping is done by animals when disturbed alone; rasping [stridulation] has been detected after one crab was thrust into the burrow of another; bubbling is produced by lone animals in burrows. The species responds to both airborne and substrate-borne sound through a single receptor (Barth's myochordotonal organ), but is most sensitive to substrate vibration.

Genus *Uca* Leach 1814

(Fiddler crabs or calling crabs)

Rathbun 1918b:374.—Monod 1956:399.—Crane 1975:15.

Differing from all other brachyuran genera in enormous size of male major cheliped without stridulating ridge on ischium; minor cheliped of male and both chelipeds of female minute.

In her exhaustive monograph on fiddler crabs of the world, Crane (1975) distilled years of study into a compendium of information on systematics, zoogeography, ecology, functional morphology, behavior, phylogeny, and evolution of the group. She recognized 79 species, clustering them into a number of subgenera and subdividing many into subspecies, but while this monograph was in press for years Bott (1973a, b) published two short papers on *Uca* that produced a profound effect on taxonomy of the group. His first paper created a nomenclatural problem (questioning the type-species of *Uca*) still unresolved by the Commission on Zoological Nomenclature, and the second, by erection of 10 new genera, preoccupied most of Crane's subgenera. Von Hagen (1976, 1980) recognized that

attempts to follow either Bott's new set of genera or Crane's subgeneric system might result in chaos. Since evolutionary patterns in the group are only beginning to be understood, he recommended that workers "adhere to the familiar use of plain *Uca*" until expert opinion resolves the systematic problems. I gladly follow his simplification. The three species treated here are so universally recognized in the biological literature as *Uca minax* (LeConte 1855), *U. pugilator* (Bosc 1801 or 1802), and *U. pugnax* (Smith 1870) that no confusion should result from ignoring the rules of nomenclature in this case.

The following summary and species accounts are intended only as a convenient abstract of Crane's work, with a few notes on other papers. Any careful worker should refer to her masterful treatment. Moreover, fiddler crabs have been the subjects of a multitude of studies on general ecology, thermal relations, molting, reproduction, biochemistry and physiology, osmoregulation, radiation sensitivity, response to pollution, circadian activity, color change, etc., that are beyond the scope of this brief account. Much of the literature is listed by Powers (1977).

Much biological information on the three *Uca* species can be grouped as in Williams and Duke (1979), and I selectively quote or paraphrase their account here. *Uca* species live in an environmental borderland along the edges of estuaries, habitually staying away from the sea proper. The crabs are behaviorally terrestrial but physiologically aquatic (Herrnkind 1968b), orienting themselves within their narrow environment on the strand between water and land by means of visual cues, and able to return to it even if displaced several meters into either open water or to land beyond the beach. They exhibit endogenous rhythms in activity and color changes that are associated with local tidal schedule as well as diel cycles (Barnwell 1968). All are burrowers, some retreating into more or less impermanent burrows during periods of inundation and emerging during low water stands. Of species discussed here, *U. minax*, the largest, lives on muddy banks of marsh creeks and among *Spartina*, *Salicornia*, and freshwater herbs in marshes threaded by brackish to freshwater streams under tidal influence (Miller and Maurer 1973). *Uca pugnax*, medium sized, frequents salt marshes and sheltered shores on mud to sandy mud substrate. *Uca pugilator*, smallest of the three, lives on sheltered shores with sandy to sand-mud substrates more or less free from vegetation and often mixed with scattered shells and stones but with muddy surfaces for feeding nearby. The food of all consists largely of minute particulate matter, algae, bacteria, detritus, etc., from the surface of the substrate which is

scraped up by the small chelipeds and passed to the mouth for separation of accepted organic and rejected inorganic components by various mouthparts, the rejectamenta being left behind as trails of rounded pellets (Schwartz and Safir 1915; Miller 1961), but feeding underwater has been observed for *U. pugnax* and *minax*, and the latter will kill and consume either of the other two species (Teal 1958). Males, having only one small chela, feed twice as long as females, animals of each sex otherwise having equal metabolic responses (Valiela, et al. 1974).

Life histories of the three species are similar. Crane (1975) discussed courtship and mating in great detail indicating that males attract females by waving display and sound production, i.e., drumming the major hand against the substrate either on the surface or in burrows (Salmon and Horch 1972), and that copulation in the hard condition (Hartnoll 1969) takes place in the burrow of the male, or, in *U. pugilator* and *pugnax*, on the surface at night, and even underwater in captivity (Herrnkind 1968a). Apparently the huge claw of males is reserved for display (threat, attraction, etc.), not for handling females. Both sexes show a periodicity in gametogenesis (Young 1974). Courtship and mating are influenced by temperature, with some evidence of latitudinal adaptation (Crane 1975). Near New York, for example, *U. minax* fed and moved above ground during low tide in mid-June but did not display when air temperature during the preceding night fell below 21°C even though daytime temperature then regularly reached above 29°C. On Cape Cod in early June, several *U. pugilator* waved at low intensities on a sunny day when air temperature was 19°C and the previous nighttime low had been 10°C. Maximum breeding activity for that population was in mid-June followed by notably less activity in July even though temperature was higher then. Never was the activity on Cape Cod equivalent to that seen in more southern populations. Spawning following mating, therefore, is most extended at low latitudes.

Uca minax (LeConte)

(Red-jointed fiddler; brackish water fiddler)

Fig. 377a

Gelasimus minax Le Conte 1855:403.

Uca minax.—Rathbun 1918b:389, pl. 137.—Hay and Shore 1918:451, pl. 37, fig. 3.—Williams 1965:227, figs. 209A, 210B.—Felder 1973:85, pl. 12, fig. 12.—Powers 1977:143.

Uca (Minuca) minax.—Crane 1975:176, pl. 25, figs. E-H; text-figs. 67D, 81K, 100.

Recognition characters.—Carapace subquadrilateral, approximately 1.3 times as wide as long, widest behind outer orbital angles, convex in both directions, finely granulate, except somewhat coarsely so near anterolateral angles; shallow H-shaped depression near center of carapace, and horizontal depression behind orbit. Lateral margins nearly vertical; anterolateral angles slightly produced, continued backward and inward as low, well-defined ridge, and above orbits as low revolute ridge. Front greater than $\frac{1}{3}$ frontoorbital width, broadly convex. Orbits large, open, eyebrow 5 times as wide as deep, lower margin dentate eyestalks long, slender. Antennules and antennae small, flagellum of antennules hardly visible. Merus of second maxilliped with usually 0–15 exceedingly slender spoon-shaped hairs on inner surface of merus.

Chelipeds in male very unequal, in female equal and of small size. Large chela with upper surface of merus sparingly granulate, inner edge denticulate, outer edge granulate; carpus tuberculate. Upper and outer face of large hand in male with tubercles diminishing to granules on lower face, ridged above; inner surface with oblique row of granules from lower margin to carpal cavity, short curved row leading down from ridge on upper margin, area between ridges tuberculate and with tuberculate ridge running along fixed finger from tip to internal distal border of palm. Fingers strong, widely gaping, cutting edges tuberculate; fixed finger with few larger teeth at irregular intervals, truncate at tip; dactyl longer and curving downward past tip of opposed finger. Walking legs strong, sparsely hairy, meri slightly wrinkled.

Measurements in mm.—Carapace: male, length 25, width 38; female, length 22, width 30.

Color.—Chestnut brown, becoming gray in front; chelipeds with red spots at articulations; hands ivory white; legs olive or grayish brown. Crane (1975) gave color as: lightest color of carapace grayish white to dull yellowish white, frontal and eyebrow regions sometimes dull orange; middle of cardiac region sometimes with red spot, major cheliped grayish orange to dull yellowish orange except narrow edging of red usually near articulations of articles, especially between carpus and hand.

Habitat.—This species occurs in marshes at some distance from water of high salinity. It is usually found on muddy substrates where flooding with freshwater occurs (Teal 1958), or on mud and sand substrate (Gray 1942), is often found in association with marsh phanerogams (Kerwin 1971), and has also been observed at the edge of low woodlands (Teal 1959). Whiting and Morshiri (1974) found that *U. minax* prefers substrates with high organic content, hence high energy value, but low oxygen

content, which explains the species' adaptation to withstanding low oxygen tensions. Experiments indicated that at high population densities the crabs reduce intraspecific encounters and competition by burrowing and subsequently covering their burrows. The crabs dig 2–5 cm diameter burrows (Allen and Curran 1974) to various depths, but the maximum is about 60 cm (2 ft); the openings are often considerably above high-tide level, and the bottoms reach to ground-water level. The burrows are only wide enough to accommodate the occupant. Usually only one crab lives in a burrow, though at times two females may occupy a single burrow, and burrows of females sometimes communicate with those of males, the connection being made by the female (Gray 1942). Young crabs are sometimes found in the burrows of females, never in those of males.

Type-locality.—Beesleys Point, N. J.

Known range.—Buzzards Bay (Wareham and southwestern Cape Cod), Mass., to northeast Florida, and from the area of Yankeetown, northwest Fla., to Louisiana, and on to Matagorda Bay, Tex., if Von Hagen's (1976) analysis treating *U. rapax longisignalis* Salmon and Atsides 1968 as a synonym is accepted. Heard (1977) agreed with the latter authors that the Gulf coast form is distinct.

Remarks.—The red-jointed fiddler has lived in freshwater for more than three weeks under experimental conditions (Teal 1958), and when offered choice of fresh or seawater chose freshwater. In choice of substrate experiments (mud or sand) it chose mud either above or underwater, but dug few burrows when competitive *Uca* species were present, an observation not confirmed by Whiting and Moshiri (1974).

Miller (1961) compared the mouthparts of *U. minax* to those of the more specialized Carolinian *Ucas*. He found that it prefers to feed in low areas of the *Spartina* marshes well up in estuaries where mud is fluid.

Teal (1959) found *U. minax* to have the lowest rate of oxygen consumption among a number of marsh crab species (*U. pugnax* and *pugilator*, *Sesarma cinereum* and *reticulatum*, *Eurytium limosum*, and *Panopeus herbstii*). He (also Vernberg 1959) showed that this species in all probability does not acclimate respiratory rate to change in temperature. Temperatures experienced in nature had no effect on survival (Teal 1958), but below 20°C the crabs are inactive (Gray 1942; Teal 1959). Gray found that *U. minax* overwinters in burrows just below the frost line. Gill area/g body weight in *U. minax* is lowest among the U. S. east coast *Uca* species (Gray 1957).

Sexual display of males is discussed by Crane (1975). In display, the males rear back on the last two or three walking legs so that the carapace is vertical. The major cheliped is extended diagonally up to about half of maximum extension. This position may be held for minutes, then the cheliped may be fully extended swiftly and smoothly, and finally brought back to the half-extended position in a series of jerks. This movement may be repeated about four times rather slowly. The small cheliped is moved asynchronously in similar motions.

Spawning occurs in summer. In Chesapeake Bay, ovigerous females are most abundant in July; none are known to occur before July or after the first week in September, and about the same length of breeding season is found in the Beaufort, N. C., area. Gray (1942) presented evidence for two spawnings per season. The act of egg laying has not been studied in minute detail, but Gray (1942) observed egg deposition among captive females held in aquaria. Completion of spawning was usually accomplished in a day but sometimes took as long as three days, depending on temperature. Hyman (1920) and others have dug ovigerous females from burrows. Freshly laid eggs were yellow or pale orange in color, but the color changed with development through purplish-black to an ashy gray color, at which stage the larvae emerged (see also Hyman 1920). Estimated egg counts on a number of ovigerous females ranged from 10,000 to 300,000, depending on size of the individual. Newly laid eggs measured about 0.09 mm in diameter but increased to about 0.27 mm at the time of hatching. Both Hyman (1920) and Gray (1942) observed that the females entered water in order to let the eggs hatch. Time of hatching extended from about 7:00 to 10:00 p.m., and the hatching of an egg mass required slightly less than an hour.

The first zoeal stage of *U. minax* is the smallest among these three species of *Uca*. (Larval stages are discussed in the remarks on *U. pugilator*). Sandifer (1975) found larvae of what was presumed to be this species mostly far upstream in the York River, Va., in an area inhabited almost exclusively by *U. minax*. It seemed to him unlikely that these early larvae would develop in such low salinity, but that they would be swept downstream to develop in marsh habitats (zoea I was abundant at the surface, II–IV were somewhat more abundant near bottom, V and the megalopa were abundant near bottom (bearing out Hyman's [1920] findings near Beaufort, N. C.) where the later stages concentrated in bottom strata would be brought back upstream by retention and migration.

***Uca pugilator* (Bosc [1802])**

(Sand fiddler)

Figs. 376, 377c

Ocypoda pugilator Bosc [1802]:197.*Uca pugilator*.—Rathbun 1918b:400, pl. 141; pl. 160, fig. 2.—Hay and Shore 1918:452, pl. 37, fig. 2.—Williams 1965:232, figs. 209C, D; 211.—Felder 1973:83, 85).—Powers 1977:145.*Uca (Celuca) pugilator*.—Crane 1975:223, pl. 29, figs. E-H; text figs. 37K, 69F, 101.

Recognition characters.—Carapace subquadrilateral, up to 1.5 times as wide as long, widest behind outer orbital angles, very convex, smooth; shallow H-shaped depression near center of carapace and narrow, flattened shelf behind orbit. Lateral margin strongly curved outward behind orbit, continued backward and inward as low, well-defined ridge across entire frontoorbital width. Front more than $\frac{1}{3}$ of frontoorbital width, broadly rounded below. Orbits large, open, upper margin slightly sinuous, lower margin dentate. Eyestalks long, slender. Antennule and antenna small. Merus of second maxillipeds with 150 to 200 spoon-tipped hairs arranged in about 10 rows on inner side.

Chelipeds in male very unequal, in females equal and small. Merus of large chela with short, granulated, rugose lines above and isolated dark hairs proximally, nearly smooth outside, lower margins granulate; merus of small chelipeds with scattered hairs. Carpus and outer surface of large hand with tubercles diminishing to granules on lower face of hand. Inner surface of palm without oblique tuberculate ridge as in *U. minax* and *U. pugnax*, but with tuberculate ridge running along fixed finger from tip proximally on internal distal border; surface granulate, granules coarser on thickest part of palm. Fingers strong, gaping; fixed finger with largest tubercles just behind middle and near truncate tip, inferior surface convex; dactyl evenly

denticulate and with irregularly placed large tubercles, strongly curving downward past tip of opposed finger. Walking legs narrow, last pair with upper surface of merus straight.

Measurements in mm.—Carapace: male, length 17, width 26; female, length 14, width 19.

Color.—Display whitening conspicuously present but fleeting in both sexes, usually yellowish white. Displaying males with fleeting purplish violet patch on cardiac region, sometimes pink and confined to gastric region in southern populations; major cheliped buff to yellowish white, base of chela often pale orange. Carapace in non-displaying phases variously marked in semi-reticular patterns of brown, or completely brown with small gold or light brown spots. Eyestalks buff or grayish white. Third maxillipeds white. Minor cheliped with hand white; walking legs white but anterior side of merus of first sometimes purplish brown or reddish purple (Crane 1975).

Habitat.—This species occurs in countless numbers on sandy and muddy beaches bordering marshes and along banks of tidal creeks. The crabs also occur farther from water in sandy situations of the *Salicornia-Distichlis* marsh and at times in *Juncus* marsh where the soil is sandy (Teal 1958). They burrow much as does *U. pugnax*, and populations of the two are often intermingled (Pearse 1914), though *U. pugilator* prefers sandier situations (Hyman 1922). Dembowski (1926) found that choice of a place to burrow depends upon many factors, among them phototaxis and thigmotaxis. Burrows may have any shape but are unbranched and usually dug at an angle to the surface of the ground, length of the burrow depending in part on amount of moisture in the ground. Digging by males is done with legs on the side opposite the large claw. The crabs plug the opening as soon as they feel the water level rising in the burrow with the tide, and do this by pulling in the edges of the burrows and by ramming sand up from below.

Type-locality.—"Caroline."

Known range.—Cape Cod, Mass.; (rare on the north shore) southward around the tip of peninsular Florida to near Pensacola (Heard 1982); single occurrences are on record from Old Providence Island, the Bahamas, and Santo Domingo (Crane 1975). Heard (1977, 1982) stated that another species whose range overlaps *U. pugilator*, *U. panacea* Novak and Salmon 1974, is distributed from west Florida to Texas.

Remarks.—Ovigerous female *U. pugilator* have been reported from early July to mid-August on Long Island (Schwartz and Safir 1915), March to midsummer in Virginia (Williams 1965), April to

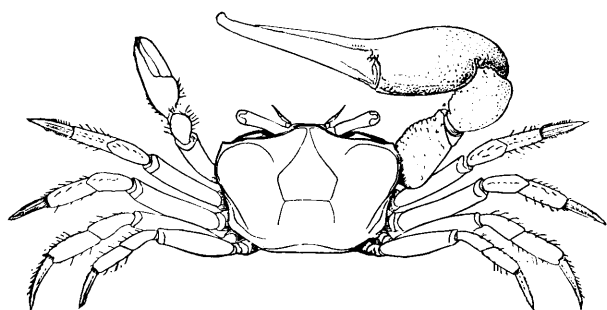


Fig. 376. *Uca pugilator* (Bosc). Male in dorsal view, about natural size (from Rathbun 1884).

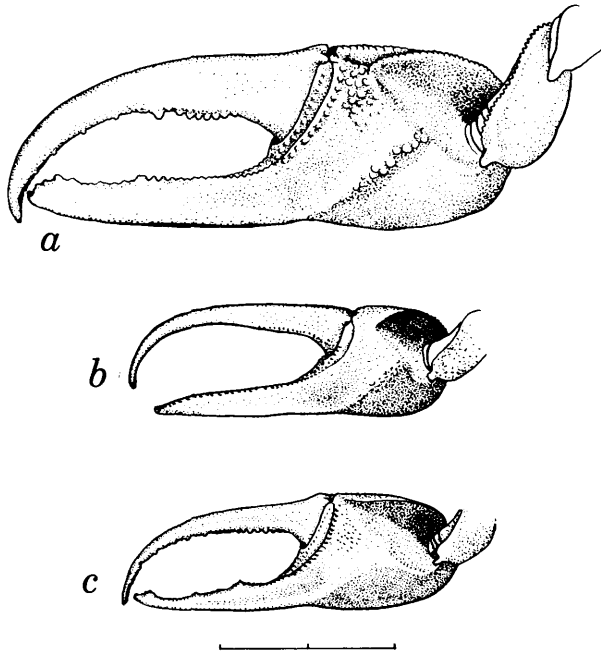


Fig. 377. Major chela of male, view of inner side: a, *Uca minax* (LeConte); b, *U. pugnax* (Smith); c, *U. pugilator* (Bosc); 1 cm indicated.

October near Miami, Fla. (Herrnkind 1968a), and Hedgpeth (1950) reported zoeae taken in a plankton net on May 20 at Long Lake, Tex. Females enter the water to let eggs hatch.

Representative of all *Uca* species discussed here, *U. pugilator* has five zoeal stages and a megalopa, each major subdivision of larval life lasting 3–4 weeks for a total development time of 6–8 weeks (Hyman 1920; Herrnkind 1968a). Gray (1942) described a transitory prezoal stage. The larvae are predatory, capturing prey (*Artemia* nauplii, etc.) on or between the telson spines by violent flapping of the abdomen, whereupon flexure of the body brings food to the mouth. The megalopa swims at first but gradually adopts a benthic existence. Zoeae of the three species have not been distinguished in plankton, but Sandifer (1973d) found zoeae of *Uca* sp. to be the most commonly collected and abundant decapod larvae in lower Chesapeake Bay, concentrations of $> 100/m$ not being unusual. The zoeae were taken over a salinity range of 0.06 to 32.34‰ at temperatures of 19.4° to 30.8°C, but most numerous in the York and Pamunkey rivers tributary to the Bay, mainly at salinities $< 5‰$ at 26° to 30°C. Larvae first appeared in June, peaked in July and disappeared in October. All of the zoeal stages were collected but stage I was most numerous, predominantly at the surface. Stage V was more numerous in bottom than in surface samples. Hyman (1920, 1922) found the first two zoeal stages most abundant at the surface, the third probably at in-

termediate depths, and the fourth and fifth zoeae usually on the bottom. Sandifer (1973d) found that the work of others (reviewed) reflected his findings with allowance for latitudinal variation, although workers in the Beaufort, N. C., area found larvae at higher salinities (Pinschmidt 1963, Dudley and Judy 1971). DeCoursey (1976) demonstrated that stage I zoeae have a distinct tidal rhythm of vertical movement.

Christy (1978) proposed that mating, incubation, hatching, and larval development in *U. pugilator* are so synchronized that male display reaches peaks at spring tides, and mating occurs in male burrows where females remain during the entire incubation period of about two weeks, emerging to release hatching larvae at neap tides. Ensuing larval development is so timed that the megalopae will be ready to metamorphose when they are swept into the estuary on spring tides. There are thus two breeding populations allied with new and full moon tidal phases. Non-breeding males and females, or displaying males, constitute the feeding droves that emerge at each low tide. DeCoursey (1979) extended this concept of periodicity by demonstrating that clutches of 1,500 to 94,000 eggs of *U. pugilator*, *pugnax* and *minax* hatch over the course of about two hours (ca. 104, 108, 104 min. respectively) in phase with time of nocturnal high tide. Females aid hatching by vigorous abdominal contractions. Ovigerous females isolated in laboratory aquaria for several days release zoeae synchronously with those in the wild. DeCoursey thought that such timing may minimize exposure of females to predation at time of releasing their young as well as placing early zoeae in favorable tidal currents.

The first two crab stages following metamorphosis are relatively weak and adapted to clinging, but following them the crab starts to assume the familiar structural and behavioral characteristics of the species, burrowing during high tides first in the wet intertidal area and later along the strand near or above the high-tide line (Herrnkind 1972). From that refuge the population emerges between high tides to carry on its activities in droves on the exposed intertidal surfaces. Rhythmic activities in such an environment follow naturally, but their behavioral complexities lie mainly beyond the purview of this paper (see Crane 1975). An example of internal rhythms is that of blood glucose level tied to the diurnal cycle, high in late afternoon, low in early morning. Example levels measured in mg % are: 5:30 a.m., 7.86; 1:30 p.m., 8.06; 5:30 p.m., 15.41 (Dean and Vernberg 1965).

Testing salinity tolerance, Teal (1958) found that 50% of *U. pugilator* died after 3.5 days in freshwa-

ter, but over 50% survived more than 10 days in seawater of 7‰ salinity. Given a choice of freshwater or seawater of 30‰ salinity, the crabs chose seawater but preferences of females were less strong than males, as was true of *U. pugnax*. He concluded that this species lies between *U. minax* and *U. pugnax* in its tolerance of freshwater and can survive soakings of the *Salicornia* marsh with rain between spring tides. Regulation of water and salt enables both *U. pugilator* and *pugnax* to maintain serum hypotonic to external media in 100% and 175% seawater under experimental conditions (Green, et al. 1959). Gill fluids in such crabs are more concentrated than the sera, and stomach fluid and urine are more concentrated than the external medium. Chief sites of water and electrolyte entrance are the stomach and gills. Chief sites of regulation are the antennary glands and gills, with some regulation by the stomach and probably the mid-gut gland.

Teal (1958) also concluded that *U. pugilator* cannot feed properly where sand is absent because in choice of substrate experiments (sand or mud above or underwater) it burrowed in sand above water and when restricted to an unfavorable low muddy marsh did not survive. In company of either of the other species, *U. pugilator* reduced its burrows in sand above water by 50%. Miller (1961) considered *U. pugilator* to have the most specialized mouthparts among Carolinian *Uca* species.

Respiration rates are higher underwater than in air (Teal 1959), probably due to increased activity necessary to aerate the gills. Like *Sesarma*, this species and *U. pugnax* can regulate their metabolism in air under experimental conditions down to 1% or 2% atmospheres (8–15 mm Hg), but low oxygen pressures are encountered in nature only in burrows in water and there the crabs, like *Sesarma*, can go into oxygen debt until emergence at the next low tide.

Latitudinal effects of temperature are manifest in metabolic response. Rate of metabolism in a Massachusetts population was higher at 1.4°C than in a Florida population, but at 15°C the difference was not significant. The northern population was less sensitive to temperature change and more resistant to low temperature than the Florida population (Démusy 1957). Edwards (1950) earlier had shown metabolic differences in the populations at 20°C. Teal (1959) found that crabs from Georgia showed no adjustment to respiration for temperature acclimation above 25°C, but that below 20°C there was some evidence of acclimation though not so well developed as in *U. pugnax*. Summer temperatures of 45°C on open *Distichlis-Salicornia* flats in Georgia prevent *U. pugilator* from permanently occupying these areas (Teal 1958). Metabolic activ-

ity in *Uca* of the temperate zone exhibits a seasonal cycle and this cyclic change must be taken into account in comparing physiologic activity of relatives at different latitudes. Metabolic response of fiddler crabs has real significance in their distribution (Vernberg 1959), manifesting itself to some degree even in the larval stages (Vernberg and Costlow 1966a).

Beyond respiratory responses, there is a significantly larger number of cells per unit volume and a higher titer of blood protein in *U. pugilator* at 30°C than at 10°C. Clotting times significantly lengthened in the 10°C crabs (Dean and Vernberg 1966). These physiological effects are associated with activity levels mediated by temperature.

The subject of intersexuality and relative growth was reopened by Darby (1935) as a result of examination of some 9,000 specimens of *U. pugilator* collected at Beaufort, N. C. Among these, 12 females were obtained with two fiddles, but no female was found with one large chela. These 12 specimens had fully widened, typically female abdomens and were always found feeding with the males in contrast to the other small-clawed females which stayed close to their holes. Darby termed these female-to-male intersexes. A male-to-female intersex, that is, a crab with a typical male abdomen and normal reproductive appendages, yet with small claws, was found only once at Charleston, S. C. Because feeding is accomplished with the small claw, it is not surprising that perfectly symmetrical large-clawed adults do not, or rarely, occur. Darby, thus, refuted the arguments of Huxley (1924) and Rathbun (1921) that females with narrow abdomens represented merely extremes in the normal variation curve for female abdomen growth, and supported the contention of Morgan (1921) that these were truly intersexes.

Vernberg and Costlow (1966b) demonstrated, from laboratory studies of *U. pugilator* and *rapax*, that young crabs with two large chelae are not uncommon (presumably males). Removal of one chela during the symmetrical period of development did not appear to influence subsequent formation of the large chela. Once asymmetry was established, differentiation of the chelae appeared to be fixed and removal of the large chela did not influence future development of handedness. At no time did the remaining small cheliped develop into large cheliped in absence of the large hand, which agreed with the findings of Morgan (1923). Miller (1973) contended that developing gonopods and enlargement of one chela in males occurs at the same time in an early postlarval stage, that growth of the major propodus is initially greatest in the palm but that a shift to an approximate doubling of the

growth rate of the fixed finger leads to elongation of the fingers while the rate for the palm remains constant. The resulting asymmetry also involves the first and second pair of walking legs on the major side.

Waving display (Crane 1975) in male *U. pugilator* is lateral circular but reverse in direction to that in other species. The cheliped is raised in front, still partly flexed, then extended outward, brought down and folded inward. There is a slight pause at the wave's highest point. In northern populations there is a jerk midway to the highest reach. The minor chela makes weak corresponding gestures and fingers of both chelae are nearly closed throughout. Waves are made at the rate of about one per second. The carapace is raised and lowered during each wave. At moments of extreme excitement, the major cheliped may be rapped against the substrate (Salmon 1971) or vibrated in the flexed position without touching the ground (Dembowski 1926, Burkenroad 1947b). Salmon, et al. (1977) demonstrated that *U. pugilator* and *minax* can detect both airborne (sound) and vibrational stimuli in substrate but are more sensitive to the latter, apparently detecting it through myochordotonal organs in the walking legs. Only sound carried through substrate was judged of importance for intraspecific communication. The female follows the male down the burrow after the drumming (Crane 1975).

Salmon, et al. (1978) studied display and burrow construction of *U. pugilator* and *panacea* in a mixed population in western Florida. There, *U. pugilator* is more abundant on clean sand whereas the latter is more abundant on wet muddy sand. Males of *U. panacea* display from burrows which descend 90 from a raised sand lip, whereas those of *pugilator* display to one side of funnel-shaped domes constructed to one side of openings to gently sloping burrows. No conspecific copulations were ever observed outside burrows at the surface in daytime, but five such interspecific matings that lasted about one hour were observed. Experiment and observation showed that the male courts the female with waving (visual) and rapping (acoustic) displays. Interspecific differences in these behaviors are statistically significant and geographic variations in the patterns are not a function of environmental factors such as temperature. Experimental hybrid matings (males of both species occasionally succeed in forced mating with females of the other species) result in fewer clutches of eggs than conspecific matings under the same conditions, and the larvae are less viable.

Intraspecific aggressive encounters between males of *U. pugilator* and *pugnax* were studied near Beau-

fort, N. C. (Hyatt and Salmon 1978). Most fights are between Residents (owning burrows) and Wanderers seeking to displace them; less commonly fighting occurs between Residents occupying adjacent burrows. In over 400 fights observed in each species, Wanderers were rarely successful in displacing Residents of the same size or larger, but they won a small percentage of fights when they were larger than the Residents. *Uca pugilator* Wanderers challenge Residents that are slightly smaller than themselves, but there was no evidence for size selection in *U. pugnax*. Combat duration and number of acts were not related to temperature, time of day, or time in relation to low tide, but incidence of fighting increases in early afternoon, most occurring within 1–3 h after low tide. The authors defined a series of 11 combat-act protocols and three fight categories. Differences between species were observed in length of fights and temperature. It was thought that the energy expended in reconstruction of impermanent burrows in sand near water at each change of the tide tends to engender strong defense of newly constructed shelters in *U. pugilator*, whereas more permanent burrows in mud banks where secondary choices are abundant and loss is not great lead to more passive defense in *U. pugnax*.

Uca pugnax (Smith)

(Mud fiddler)

Fig. 377b

Gelasimus pugnax Smith 1870:131, pl. 2, fig. 1; pl. 4, figs. 2–2d.

Uca pugnax.—Rathbun 1918b:395, pl. 139.—Hay and Shore 1918:451, pl. 37, fig. 4.—Tashian and Vernberg 1958:89.—Williams 1965:229, figs. 209B, 210A.

Uca (Minuca) pugnax pugnax.—Crane 1975:200, 203, pl. 27, figs. E–H, text-figs. 39H, 46J, 67E, 81J, 100.

Recognition characters.—Carapace subquadrilateral, approximately 1.5 to 1.75 times as wide as long, widest behind outer orbital angles, very convex anteroposteriorly, lower edge of front and upper margin of orbit invisible in dorsal view, smooth. A shallow H-shaped depression near center of carapace, pit on branchial region in line with gastrocardiac sulcus, and pit behind middle of orbit. Anterolateral angles slightly produced, each continued backward and inward as low, well-defined ridge, and across entire frontoorbital width. Front about $\frac{3}{4}$ of frontoorbital width, margin regularly arched. Or-

bits large, open, upper margin sinuous and oblique, lower margin dentate. Eyestalks long, slender. Antennule and antenna small. Merus of second maxilliped with 0–75 spoon-tipped hairs.

Chelipeds in male very unequal, in female equal and of small size. Large cheliped of male rough; merus with granulate rugose lines outside, lower margins granulated. Carpus and palm tuberculate outside; inner surface of palm with oblique row of granules leading from lower margin to carpal cavity; short row leading down from ridge on proximal half of upper margin; area between crests coarsely granulate or tuberculate and with tuberculate ridge running along finger from tip to internal distal border of palm. Fingers long, slender, widely gaping; fixed finger usually with 1 large tooth near middle, inferior border nearly straight, tip sometimes depressed, truncate; dactyl evenly denticulate and with irregularly placed large tubercles, strongly curving downward past tip of opposed finger. Walking legs with carpal and propodal articles hairy.

Measurements in mm.—Carapace: male, length 15, width 23; female, length 13, width 18.

Variation.—There is a tendency toward decrease in size in the southern extremity of the range (Tashian and Vernberg 1958).

Color.—Males usually brown, sometimes whitening to pale gray at least on branchial regions, but display whitening poorly or not at all developed; anterior part of carapace, eyestalks and anterior parts of third maxillipeds often blue to blue-green (turquoise), but often slight in southern extreme of range. Major cheliped dull yellowish orange to yellowish white, sometimes light brownish or yellowish, fingers white or nearly so; minor chela white; walking legs dark and banded. Females similar (Crane 1975).

Habitat.—The mud fiddler's name derives from its preference for a muddy marsh environment, often well shaded (Schwartz and Safir 1915), but it is perhaps somewhat excluded from areas where there is an abundance of halophyte roots or where substrate is too fluid to support burrows (Kraeuter and Wolf 1974). Results of salinity tolerance experiments are consistent with this type of distribution (Teal 1958): 50% of *U. pugnax* placed in freshwater died within 1.5 days, whereas 50% mortality occurred after three days in seawater of 7‰ salinity. Given a choice of freshwater or seawater of 30‰ salinity, the crabs chose seawater.

Given a choice of sand or mud substrate above or under water, *U. pugnax* burrowed only in mud without any reference to water level, and competitive species of *Uca* had no significant effect on numbers of burrows dug. When restricted to the

relatively high *Salicornia-Distichlis* marsh, *U. pugnax* survived less well than *U. pugilator*.

Burrows can extend to depths of 60 cm; the crabs dig most actively when the tide is falling, and often hasten to plug burrows when the tide is rising to cover the burrow mouths (Pearse 1914). Pearse found the maximum number of burrows about 60 cm below high-tide mark, and often the burrows had mud towers at the mouths when the beach was littered with debris. Crane (1943, 1975) observed "shelter building" in this species to be in its most rudimentary form among the *Ucas*. She found that in a mixed population of *U. pugnax* and *pugilator*, *U. pugnax* always chose the side of any surface irregularity for a hole entrance in preference to flat ground. Teal (1958) reported burrows on Georgia Sea Islands to be in situations similar to those observed by Pearse, on low levees bordering tidal creeks or farther from creeks in firm, marshy ground sometimes covered only at spring tides. Extreme variation in the number of crabs within the same general habitat (short, medium or tall *Spartina*) indicates that a clumped distribution is characteristic of crab populations there (Wolf, et al. 1975), a condition perhaps related to several factors as suggested by Teal. Where mixed populations of *U. pugnax* occur in Georgia, the number of burrows dug by each is less than would be predicted for populations of either alone (Aspey 1978).

Type-locality.—New Haven, [Conn.].

Known range.—Provincetown, Mass., to Daytona Beach, Fla. *Uca longisignalis* Salmon and Atsaides 1968 is now recognized as the Gulf of Mexico counterpart (Heard 1982).

Remarks.—According to Rathbun (1935), the fossil record for *U. pugnax* extends into the Pleistocene of New Jersey and Delaware, but Glaessner (1969) did not list it.

Waving display of male *U. pugnax* is weakly circular, almost straight at low intensity (Crane 1975). Jerks are almost always distinguishable but weak, 3 to 14 on rise of the cheliped and 1 to 7 on its descent. There is a variable pause at the highest point of the wave. The minor cheliped makes roughly corresponding motions. The body is held raised throughout a series of waves, with one or more walking legs kicked out during display. At times of high intensity, males will bob or curtsy between waves, with the major cheliped held flexed during this movement which is usually accompanied by stamping of the walking legs. Salmon and Atsaides (1968) found that males produce sounds at night by movements of the walking legs. Females attracted by waving, stamping or sounds follow the males into their burrows for mating.

Ovigerous females have been observed near

Woods Hole, Mass., from July 4 to July 15 (Pearse 1914). Farther south the spawning season is more extended, from early July to mid-August in New Jersey (Crane 1943), as early as May 21 at Long Lake, Tex. (Hedgpeth 1950), and in April in northeastern Florida (USNM records). On Long Island, N. Y., the peak of spawning occurs in August (Schwartz and Safir 1915). Crane (1943) thought it likely that in the region near New York two breeding times occur, one in July and the other in August.

The larval and postlarval stages are discussed in the remarks on *U. pugilator*. Hyman (1920) secured ovigerous females for hatching of eggs by digging them from burrows. He found the first zoea of *U. pugnax* to resemble closely that of *U. pugilator* except for smaller size of the former.

Uca pugnax exhibits one of the most highly developed thermal adaptabilities among marsh crabs tested (Teal 1959), and its abundance may be explained in part by its ability to regulate its metabolism over a wide range of temperature. At normal habitat temperatures, *U. pugnax* (= *rapax*) from Trinidad showed a higher metabolic rate than *U. pugnax* from localities in the United States (Tashian 1956). Tashian found that there is a decrease in sensitivity to temperature change from southern to northern populations, along with an increase in tolerance to low temperature. Teal (1958) found that temperatures experienced in nature are not limiting factors in distribution of *U. pugnax* in Georgia, though high temperatures near a lethal level occur at times in summer. Vernberg (1959), Vernberg and Tashian (1959), and Miller and Vernberg (1968) reinforced this conclusion, showing that *U. pugnax* exhibits a marked tendency to demonstrate seasonal thermal acclimation. Brett (1960) showed that the daily oxygen-consumption cycle is considerably modified by locomotion of the crabs. Gray (1957) found gill area per gram of weight in *U. pugnax* to be the lowest among *Uca* species along the U. S. east coast.

Crane (1943) observed hibernating *U. pugnax* in New Jersey, where the burrows were weathered open along the muddy banks of small creeks and could only have been submerged at spring tides. In March at air temperatures of 1.7° to 5.5°C, the immobile crabs were found from the burrow mouths to about 10 cm below the surface. Slight warming in the hand or in the sun elicited fairly rapid movement. Respiration rates for *U. pugnax* are higher underwater than in air (Teal 1959), probably because of increased activity necessary to ventilate the gills.

In another vein, Passano (1960) found an inverse correlation between temperature and proec-

dysis duration in *U. pugnax*. Surprisingly, at some temperature between 15° and 22°C proecydysis fails to proceed normally, though these animals experience much lower temperatures throughout their range. It was suggested that the northern limits of the species are influenced by the inability of larvae to molt in cold water; hence, adults cannot appear there.

Rhythmic cycles have received much attention in experiments with *Uca* species that are well summarized in studies by Barnwell (1966, especially 1968, and 1968a) and can only be touched upon here. Fiddler crabs inhabiting the intertidal zone must adapt activity to both day-night and tidal cycles. The tidal cycle imposes on them a rhythmic alternation between terrestrial and marine periods of existence. At the same time they are influenced by the day-night cycle, since they exhibit specific diurnal and nocturnal habits. Moreover, the interaction of daily and tidal rhythms may give rise to semimonthly variation in activity. It is now well established that persistent daily and tidal rhythms in physiological processes underlie rhythmic variations in behavior of crabs in the field. Rhythmic patterns recorded in the laboratory are found to be closely correlated with tidal conditions in the field. Persistent patterns can be modified by transplanting crabs to intertidal zones of other coasts where they are exposed to tidal cycles which differ from those in the original habitat. Experiments which have established these generalizations have involved not only *U. pugnax*, but also *U. pugilator* and *minax*.

Wheeler (1978) linked rhythmic patterns to larval development of *U. pugnax*, showing that larvae in Delaware are normally hatched in synchrony with the lunar cycle, with peaks at 15-day intervals at new and full moon. Zoeal stages were passed through in 15 days at 25°C in water of 25‰ salinity. Megalopae lived a mean of 12.5 days before metamorphosing to first crab. It was concluded that zoeae hatched on new or full moon would develop into megalopae during the next spring tide and metamorphose to first crab in approximately one lunar month. The pattern was thought to facilitate substrate selection at high spring tides.

Primarily because of the tremendous asymmetry in chelipeds of male fiddler crabs, *Uca* became an object of studies on relative growth. (In some of these papers no clear species designation was made.) In fiddler crabs [*Uca pugnax*] the percentage weight of the chela alters throughout life from 2% (the value retained by the female) to 65% (Huxley 1927). In the related larger species, *U. minax*, since allometric growth continues longer, the chela may weigh over ¾ of the remainder of the body (77%). In-

creasing relative size of the chela is associated with an increasing asymmetry of the central nervous system. Thus, such animals have no fixed form, for the proportions of parts are changing throughout postlarval life. On this basis, Huxley challenged Morgan's (1923) statement that females with intermediate-width abdomens (subject also to allometric growth, Huxley 1924) were actually intersexual female types. Tazelaar (1933) explored the subtleties of relative growth in *U. pugnax* in detail, finding that walking legs near the great chela and near the wide abdomen of females also reflect relative growth influences.

Miller (1961) in his well-illustrated study considered *U. pugnax* to be intermediate in development of spoon-shaped hairs on the mouthparts and, therefore, more ubiquitous in choice of feeding substrates than its congeners in the Carolinas. Great detail is given in this study.

Heard (1970) reported trematodes and cestodes from the three U. S. east coast *Uca* species, and (1975) showed that *U. minax* is a major food item of the white catfish, *Ictalurus catus*.

Superfamily Uncertain

Family Palicidae

Carapace broadly transverse, subquadrilateral. Anterolateral margins dentate. Frontoorbital width great, front dentate. Orbits and eyes large. Buccal cavity quadrate, outer maxillipeds not covering it; ischium of third maxillipeds strongly produced forward on inner side; merus small, subtriangular, with notch on inner distal side for articulation of palp. Afferent channels to gills opening at bases of chelipeds, efferent channels at anteroexternal angles of buccal cavity.

Chelipeds of moderate size, often unequal in male, usually tuberculate or granulate. Next 3 pairs of legs long, slender, and rough; last pair either very short and slender, subdorsal, smooth, or similar in position and ornamentation to other legs, and near size of first walking leg. Abdomen of male much narrower than sternum. Genital ducts of female

opening sternally, apparently near mesial end of fifth sternite (near second legs). (Rathbun 1918b.)

Because position of the family Palicidae in a superfamily is uncertain, Glaessner (1969) placed the group at the end of the list, as here. Placement by Faxon (1895) and Bouvier (1898) was near the Dorippidae, and near the Pinnotheridae (as Cymopoliidae) by Monod (1956) and Rathbun (1918b) who followed Alcock and Borradaile.

Genus *Palicus* Phillipi 1838

Rathbun 1918b:183.—Holthuis and Gottlieb 1958:104.

Carapace more or less depressed, broader than long, subquadrate to heptagonal, more or less covered with granules and symmetrical tubercles or rugosities with tendency to arrangement in transverse series. Front broadly triangular, horizontal, usually lobed or toothed. Anterolateral border straight or slightly curved, and lobed or toothed. Eyes large, constricted in middle, bearing 2 or more lobiform protuberances. Orbits deep, upper border cut by 2 or 3 clefts, lower border usually with 2 clefts. Antennules folding transversely; interantennular septum narrow; enlarged basal antennal article in orbital hiatus, flagellum well developed. Epistome ill defined. Buccal cavity square, lobelike prolongation of pterygostomian region at its anterolateral corner overlapping inner lobe of orbit and sometimes horizontal, sometimes bent down in vertical plane, and, in some species, deflexed in young but horizontal in adults. External maxillipeds often not meeting in middle, oblique merus much smaller and narrower than ischium; distomesial corner of ischium; and distolateral corner of merus produced; palp articulating in distal marginal concavity of merus.

Chelipeds short, usually slender in female, right often greatly enlarged in male. Second and third ambulatory legs largest, second usually longer than third, first similar but smaller, fourth weak, sometimes filiform and elevated above third. Abdominal segments free in both sexes. (Rathbun 1918b.)

Key to Species

1. Last sternal segment without posterolateral laminate crest conspicuous in dorsal view 2
 Last sternal segment bearing posterolateral laminate crest conspicuous in dorsal view *P. sica*
2. First 2 anterolateral teeth with rounded tips, teeth set apart by rounded sinuses; frontal margin almost straight or shallowly notched between low, rounded, submesial frontal lobes and inner orbital lobe . . . *P. alternatus*
 First 2 anterolateral teeth with acute tips and somewhat serrated sides, teeth

set apart by V-shaped sinuses; frontal margin conspicuously sinuous between somewhat prominent submesial frontal lobes and inner orbital lobe, notch for antennal article rather broad *P. faxoni*

***Palicus alternatus* Rathbun**

Fig. 378

Palicus alternatus Rathbun 1897a:95.—Williams 1965:215, fig. 200.—Powers 1977:118.

Cymopolia alternata.—Rathbun 1918b:188, text-fig. 117, pls. 42–43.

Recognition characters.—Elevations of carapace covered with small tubercles composed of single or a few granules. Front broadly triangular, notched at middle, with 4 submesial lobes or teeth, outer teeth less advanced than inner and broadly rounded. Orbits deep with upper border cut into teeth; middle tooth broad, obliquely truncate, bounded on each side by a V-shaped fissure; next tooth separated from outer tooth by shallow sinus; outer tooth directed forward or a little outward, tip curved inward. First 2 anterolateral teeth broad, dentiform with rounded tips, well separated; third tooth close to second, rudimentary or in form of small tubercle. Outer suborbital lobe nearly straight; inner lobe divided into 2 parts with inner angle produced in acute tooth beneath obtusely and often downturned pterygostomial lobe. Posterior margin bordered above by thin, sinuous, elevated ridge broken into variable number of unequal transverse tubercles with usually some granules interspersed.

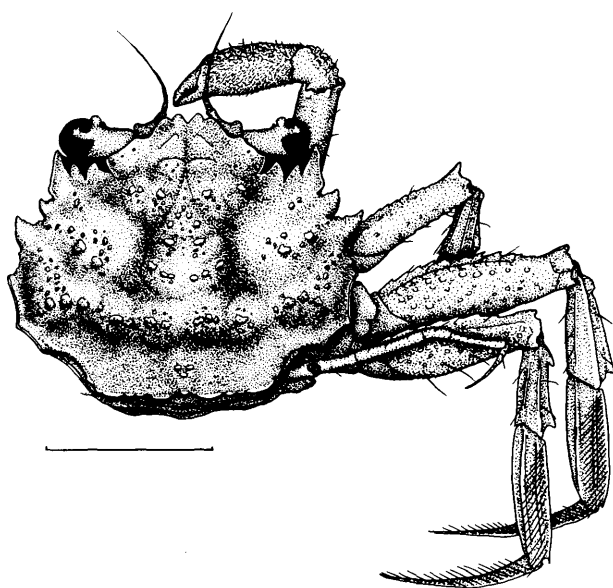


Fig. 378. *Palicus alternatus* Rathbun. Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

Chelipeds of male occurring in 2 forms. In one form, chelipeds very unequal; on right side large and heavy, on left, slender and weak, both tuberculate and pubescent; carpus with outer, laminate, lobed crest; hand surmounted by less pronounced double crest. Right hand very thick, width at distal end often equaling $\frac{1}{2}$ length of carapace; fixed finger short, wide; dactyl strongly bent down, overlapping opposed finger and leaving narrow gape. Left hand somewhat over $\frac{1}{3}$ width of right, fingers long and narrow. In second, weaker form males, right hand about twice depth of left; fingers long and slender. Females with chelipeds more nearly equal.

First 3 walking legs flattened, second longer than others. First reaching middle of propodus of second, with posterior margin of propodus and proximal half of dactyl hairy in male; third reaching middle of dactyl of second, fourth slender, much shorter than third. Meri rough with squamous tubercles; with shallow, single longitudinal groove on anterior surface, 2 on upper surface; first 3 meri with superodistal lobe, subtriangular on first, subrectangular on second and third, lobe exceeding article on first, equal to article on second, not reaching end of article on third. Carpus with rounded, anterior proximal lobe; anterior subdistal lobe low and rounded on first leg, triangular on second and third legs. Propodus with anterior margin convex, posterior margin straight.

Abdominal appendages of first form of male stout and twisted, tip bilobed, inner lobe thinner and longer than outer; second form of male with appendages weaker, not twisted, and tip less spreading.

Measurements in mm.—Carapace: male, length 7.1, width 11.9; female, length 13.1, width 16.2, but ovigerous at much smaller size.

Variation.—The species shows great variation in structure. In some individuals the carapace is wider behind in proportion to its length than in typical individuals, and the sides are less parallel. There is no consistency in relative size of the anterolateral teeth, for in some the first is largest and all teeth point forward, but in others the second tooth is largest and points slightly outward. In some individuals the anterodistal tooth on the merus of the second and third legs is more produced than in typical specimens, and there is variation in the length-width proportions of the propodus of the second leg. Details of lobulation on the front and

lower margin of the eye are also subject to variation.

Habitat.—The species has been taken from a variety of fine and coarse bottoms (Rathbun 1918b); 7.3 to 285 m (SCMRRI).

Type-locality.—29°11'30"N, 85°29'00"W, 47.6 m (south of Cape San Blas, Fla.).

Known range.—Cape Hatteras to SE Cape Fear, N. C.; Gulf of Mexico along west coast of Florida from Cape San Blas to Key West.

Remarks.—Ovigerous females have been reported in Florida from January to August, and from North Carolina in October (Rathbun 1918b, USNM).

Palicus faxoni Rathbun

Fig. 379

Palicus faxoni Rathbun 1897a:96.—Williams 1965:216, fig. 201.—Coelho and Ramos 1972:198.—Powers 1977:118.

Cymopolia faxoni.—Rathbun 1918b:194, text-fig. 120, pl. 45, figs. 2–3.

Recognition characters.—Carapace broader than long, sides converging anteriorly; adult female quite convex, surface hairy, and with numerous tubercles and granules. Front broadly triangular; 4 submesial frontal lobes well marked, outer pair not much wider than inner, median emargination deeper than wide with end often rounded, lateral emargination shallow. Eyes large; orbits deep, with upper border cut into teeth by V-shaped sinuses, middle and outer teeth triangular, subacute, middle one equilateral, outer one narrow and separated from outer orbital tooth by shallower sinus; outer orbital tooth directed forward, tip oblique, its lateral margin nearly straight. Lateral border with 2 sharp-pointed, slightly serrated teeth, second smaller, outer borders convex, inner concave. Lower margin of orbit oblique, bilobed; inner lobe in advance of outer, obscurely divided, outer part rounded, inner part a small acute tooth somewhat obscured by ventrally bent, pterygostomian lobe, sharp pointed at tip; outer lobe slightly convex. Posterior margin preceded by tuberculate ridge.

Chelipeds in both sexes somewhat unequal, right hand approximately twice as wide as left. Walking legs short and broad; first 3 meral articles with large, flat, acute distal spine, posterior distal tooth of merus sharp; carpal lobes prominent, distal one of second and third legs acute; propodus of second and third legs widening distally, dactyls wide, posterior margin sinuous.

Measurements in mm.—Carapace: male, length

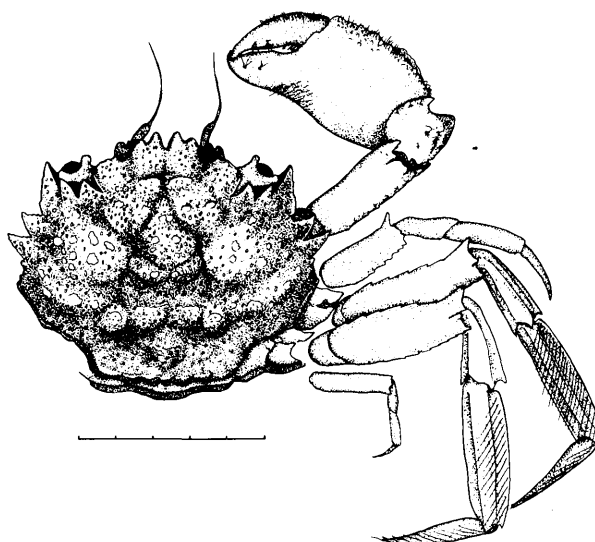


Fig. 379. *Palicus faxoni* Rathbun. Male in dorsal view, legs of left side not shown; cheliped, second and third walking legs detached; first and fourth walking legs from female in Rathbun (1918b); 5 mm indicated (from Williams 1965).

12.5, width 15.1; female, length 10, width 11.

Habitat.—Sand; 59 to 190 m.

Type-locality.—Off Cape Hatteras, N. C., 89.6 m.

Known range.—Off Cape Hatteras, N. C., to near Cape Canaveral, Fla.; off Yucatan, Mexico; near Quita Sueño Banks; SW St. Christopher; off Cabo Frio, Rio de Janeiro.

Remarks.—Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but were dead after 17-h exposure (F. J. and W. B. Vernberg 1970).

Palicus sica (A. Milne Edwards)

Fig. 380

Cymopolia sica A. Milne Edwards 1880:29 (part).—Chace 1940:49.

Palicus sicus.—A. Milne Edwards and Bouvier 1902:56, pl. 10, figs. 7–11; pl. 11, fig. 9.—W. E. Pequegnat 1970:198.

Palicus sica.—Powers 1977:119.

Recognition characters.—Carapace rather evenly but not strikingly convex, regions not deeply marked, granules of different sizes, sometimes clustered to form tubercles. Front broad, moderately prominent, submesial teeth small, median sinus a narrow V, sinuses between submesial teeth shallow, rounded and wider. Orbit with upper marginal lobes shallow, rounded, separated by rather shallow V-shaped sinuses, outer lobe nar-

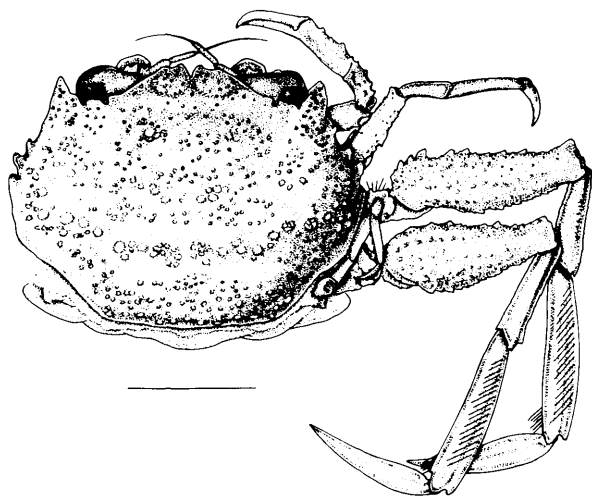


Fig. 380. *Palicus sica* (A. Milne Edwards). Female in dorsal view, legs of left side not shown, 5 mm indicated (USNM 17892).

row, outer orbital tooth projecting forward. Three anterolateral teeth small, second and third largest. Sinuous line of tubercles above posterior margin. Lower orbital margin oblique; outer lobe somewhat rectangular, inner lobe with 3 distal crenulations, inner angle subacute. Pterygostomian lobe broad, obtuse, covering all but tip of inner orbital lobe in ventral view.

Chelipeds slender and equal in both sexes. Second and third walking legs with rounded, dorsal plates on coxae; merus coarsely spinulose, especially along anterior margins, anterodistal angle subacute, almost rectangular; carpus long and narrow, anterior lobes low; propodus widening distally; dactyl with flexor margin sinuous, feathered setae along both margins of propodus and extensor margin of dactyl; first legs short, slender, merus slightly roughened, distal angle obtuse.

Last sternal segment with laminate crest projecting behind third and fourth walking legs. Abdominal segments of female carinate, first with shallow, granulate, posterolateral lobes, second with prominent median lobe, third invisible from dorsal view; abdomen of male wide, sides of third to fifth segments nearly straight.

Measurements in mm.—Carapace: male, length 6.8, width 10 (Milne Edwards and Bouvier 1902); female, length 9.8, width 13.5 (Rathbun 1918b).

Color.—Carapace light brown with slightly bluish cast; eyestalks reddish-brown; walking legs with some tubercles on meri salmon, sides of carpi and upper edge of propodi with faint dashes of brownish or salmon (Rathbun 1918b).

Habitat.—Sand, mud, shell and coral bottoms; 12.8 to 391 (481 + ?) m (W. E. Pequegnat 1970 in part).

Type-locality.—Barbados, 150 m, Blake Stn. 293.

Known range.—Off Charleston, S. C., to NNE Cape Canaveral, Fla; west coast of Florida through West Indies to Barbados and Grenada.

Remarks.—The specific name (*sica*) is a noun in apposition (Powell 1977). Ovigerous females are known from the Gulf of Mexico in March (USNM) and July (W. E. Pequegnat 1970), near Quita Sueño Bank in June, and north of Cuba in November (USNM).

Extralimital Species

The following list includes species having doubtful position in the regional fauna. Some range primarily in deep water, occurring incidentally on the continental shelf. Others have a range limited to shallow waters from beyond the immediate region. Species listed by name only have range limits given by Williams and Wigley (1977).

Family Penaeidae

Hymenopenaeus robustus Smith.

Family Hippolytidae

Bythocaris nana Smith.

Caridion gordonii (Bate).

Family Pandalidae

Parapandalus willisi L. H. Pequegnat.

Plesionika martia (A. Milne Edwards).

Plesionika tenuipes (Smith). Western Atlantic from Rhode Island to southern Florida; Gulf of Mexico. 159 to 476 m (L. H. Pequegnat 1970).

Family Paguridae

Catapagurus gracilis (Smith).

Catapagurus sharreri A. Milne Edwards.

Family Majidae

Mithrax (*Mithrax*) *cornutus* Saussure. Off Cape Canaveral, Fla.; Mississippi Delta through Florida Straits to Bahia, Brazil; shallow reef flats to 600 m.

Notolopas lamellatus Stimpson. A single female was erroneously recorded by Rathbun (1925) from "Off Beaufort, N. C., Fish Hawk." This eastern Pacific species was included with Atlantic material through a mistake in cataloguing.

Family Portunidae

Bathynectes longispina Stimpson. Martha's Vineyard, Mass., to off Mississippi Delta, southward to off Goajara Peninsula, Colombia; Bermuda; usually beyond edge of continental shelf; rarely as shallow as 7.3 m (Lewis 1976, 1977; Manning and Holthuis 1981; Roberts 1969).

Family Geryonidae

Geryon quinquedens Smith. Red crab. Gulf of Maine southward in western Atlantic, possibly to Argentina (Scelzo and Valentini 1974). Continental slope except for marginal occurrences at outer edge of continental shelf (Haefner 1977a; Rathbun 1937; Schroeder 1959; Wigley, et al. 1975).

Family Pinnotheridae

Parapinnixa beaufortensis Rathbun. Williams (1965) listed this form among extralimital and indeterminate species. The only specimen known is the holotype from fishing grounds, 20 mi. off Beaufort Inlet, N. C. Rathbun (1918b) doubtfully referred this form to the genus *Parapinnixa* and believed that it was a postlarval stage of an unknown species because of small size, relatively large eyes, hairiness of legs and carapace, and thin gripping edges of the fingers, suggesting that in another molt or two, gaping fingers might emerge. Williams thought that it might be a young *Palicus*, but shape of the external maxillipeds as well as the successively diminished ambulatory legs with hairy fringes strongly suggest pinnixid affinities.

Family Palicidae

Palicus gracilis (Smith).

A large amount of unidentified material is in existing collections and some of this contains undescribed species. It is expected that oceanographic research in the eastern United States will soon add to knowledge of decapod crustaceans in the region.

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