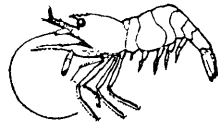
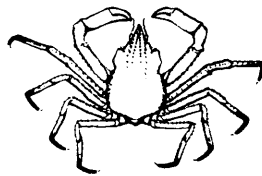


SHRIMPS, LOBSTERS, AND CRABS
OF THE ATLANTIC COAST
OF THE EASTERN UNITED STATES,
MAINE TO FLORIDA



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

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.

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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, *Pseudoscheles 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					Canadian Maritime Provinces and G. of Maine to—	G. Bank and Cape Cod thru G. Mex. and Carib. to S. Am.		
		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.	Cape Cod thru G. Mex. and Carib.		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						1EM		1	
Axiidae	3						1L 2NC			
Laomedidae	1									1NC
Upogebiidae	1							1		
Paguridae	31				1		2V 2WM			2F
Lithodidae	1				1					
Galatheidae	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									
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.)

Middle Atl. to S. Am.	Middle Atl. to G. Mex. and Carib.	Middle Atl. to G. Mex.	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 E 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	1	2	3				1	1			
	1	1	1	1	1		3				
							1		1		1
	1	1	2	2					1		
			2	2					4	2	3
2			1				6		1	1	
1			1				1		1		
1			1	2			2	2	3		2
							1	1			
			2				1			1	
								1			
3	1		1			2	1	5	4(1F)	2	5(1G–FS, 1GM)
		1	2	1		1		1	1EM	1	
		1					2		2		
			2			1		1			1GM
									1		1C
			1				2(1C)				1C
	1		1	2(1EM)			1		1		
1			1	1			2			1	1
1			5	4EM		1	2	2	2		
				1			5(2C)	5	8(2EM)	1	3(1GM)
					1		1		3		1
4	1	1FS	3					2	1		3
			4	3(2C)	2	1	5	1	3(1C)	2	3
			2		1	1	1		1		1C
		2							1GM	2(1NC)	3(1G, 1GM, 1C)
	1	1					3				
			1			1					1C
15	7	10	33	16	6	8	41	22	40	14	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

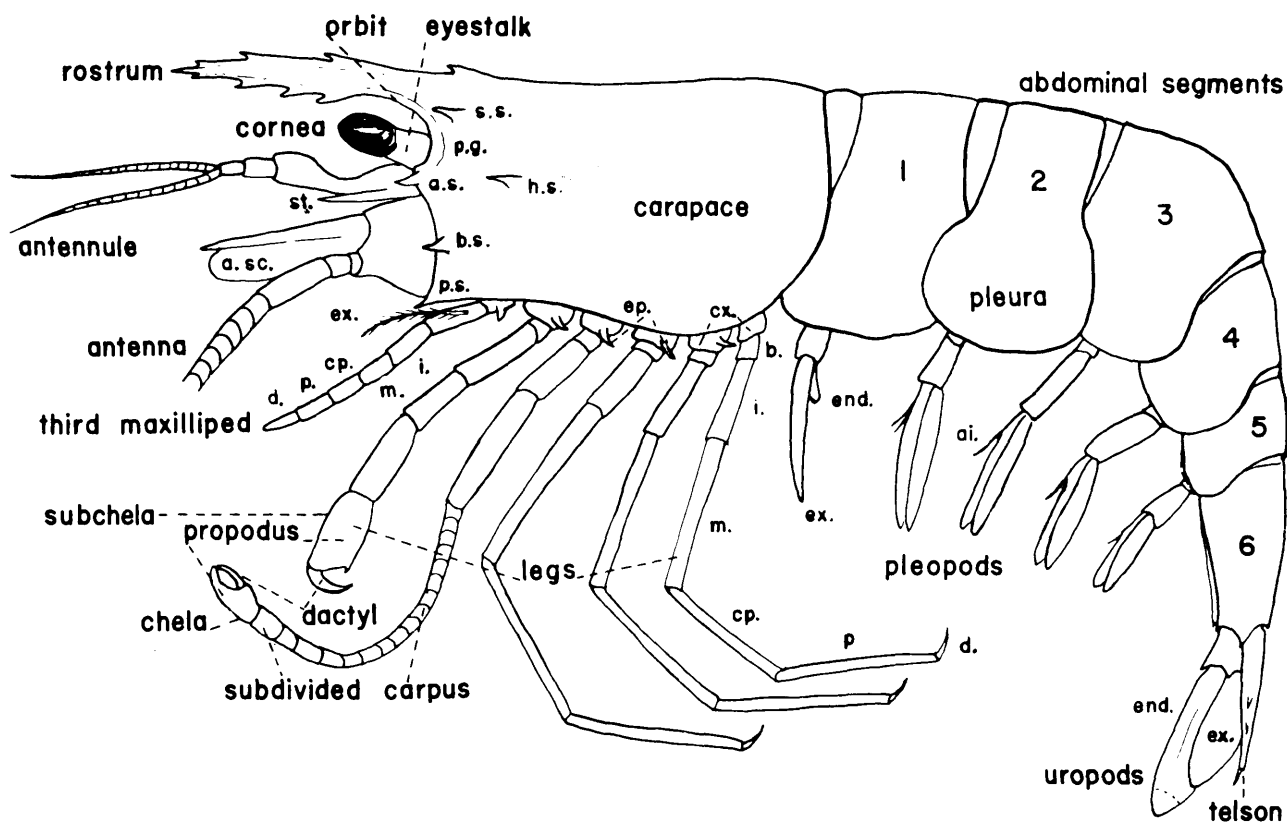


Fig. 2. Schematic drawing of shrimp in lateral view: ai, appendix interna; as, antennal spine; asc, antennal scale; b, basis; bs, branchiostegal spine; cp, carpus; cx, coxa; d, dactyl; end, endopod; ep, epipod; ex, exopod; hs, hepatic spine; i, ischium; m, merus; p, propodus; pg, postorbital groove;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

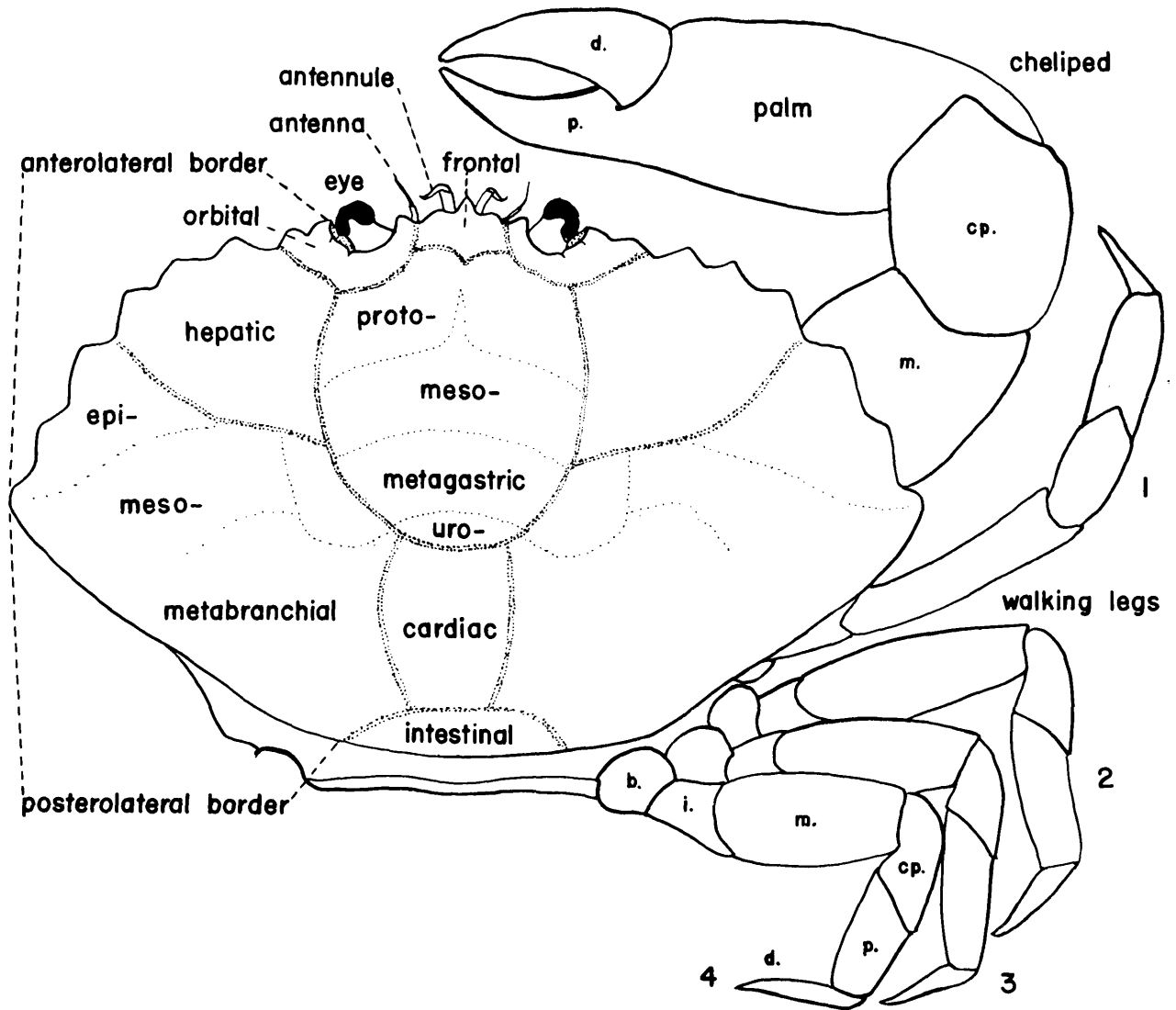


Fig. 3. Schematic drawing of brachyuran crab in dorsal view; areas of carapace indicated; legs of right side only shown; b, basis; cp, carpus; d, dactyl; i, ischium; m, merus; p, propodus.

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.

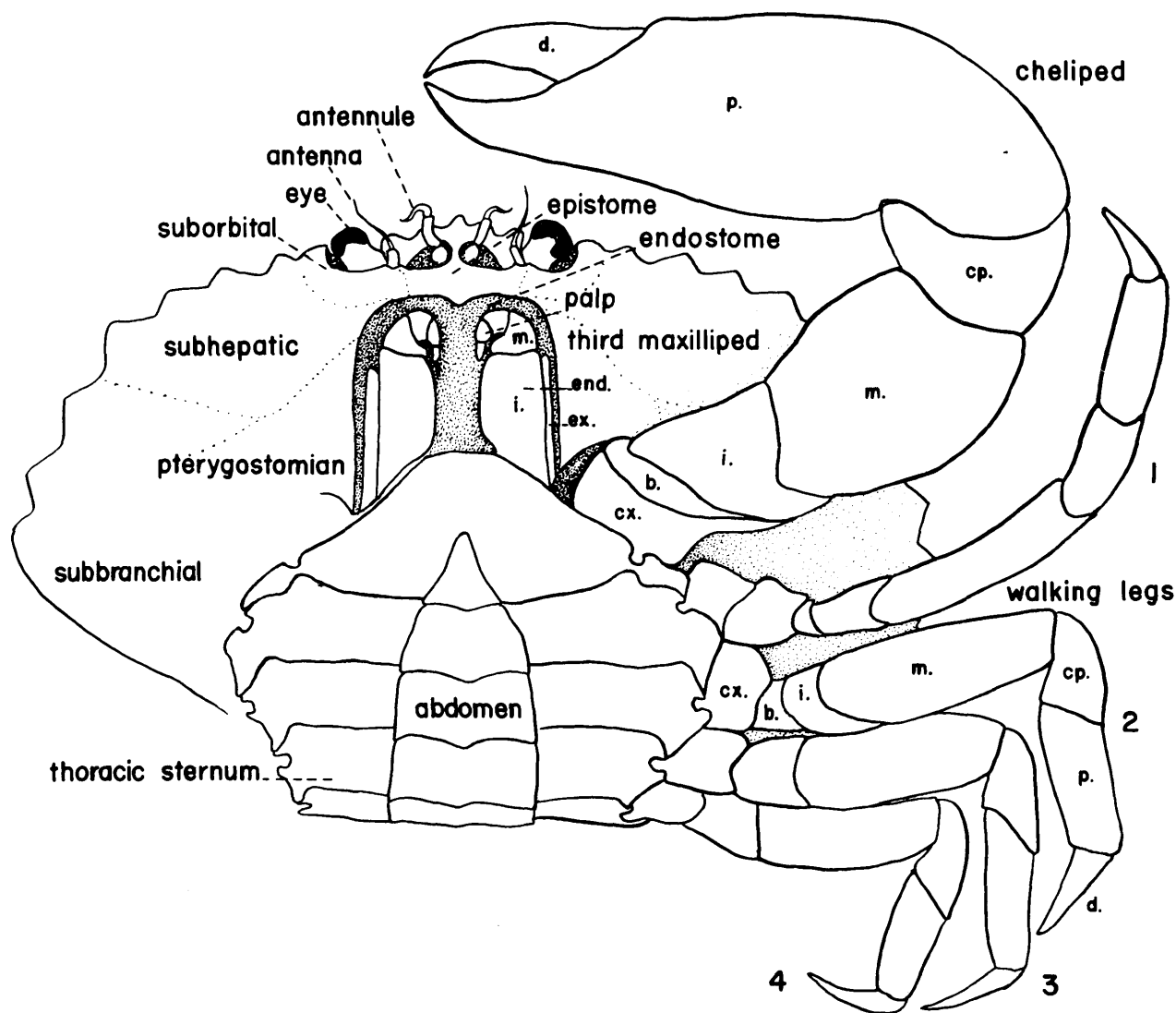


Fig. 4. Schematic drawing of brachyuran crab in ventral view; areas of carapace indicated; legs of left side only shown; b, basis; cp, carpus; cx, coxa; d, dactyl; end, endognath; ex, exognath; i, ischium; m, merus; p, propodus.

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 (propodite).—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 Bresiloidea] 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. Eystalks short, usually covered by carapace; first legs stronger than second Family **Alpheidae**
 Eystalks medium length or long, not covered by carapace; first legs not stronger than second 16
16. Rostrum small or wanting; eystalks long, slender; first 2 pairs of legs subequal Family **Ogyrididae**
 Rostrum well developed; eystalks 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 **Grapsidae**

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

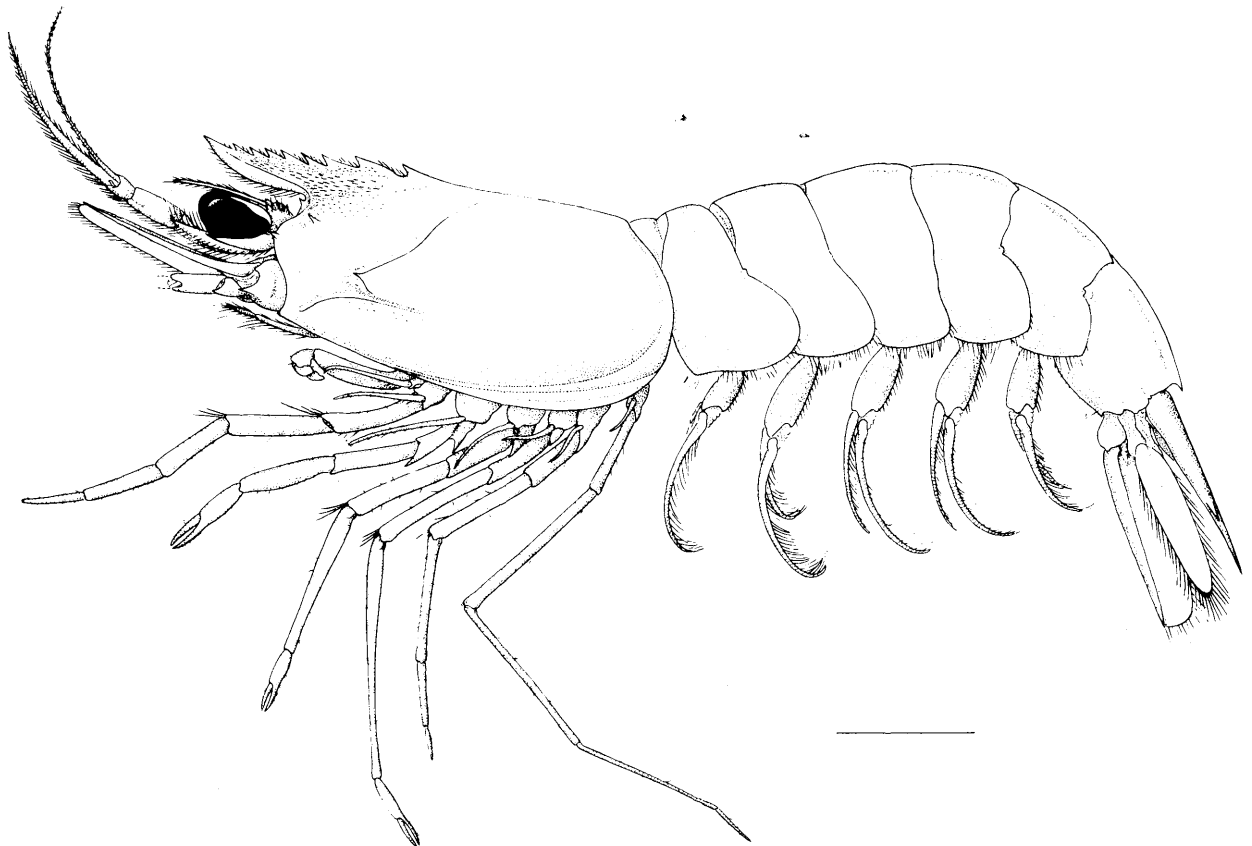


Fig. 5. *Mesopenaeus tropicalis* (Bouvier). Female in lateral view, 10 mm indicated (from Pérez Farfante 1977).

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.

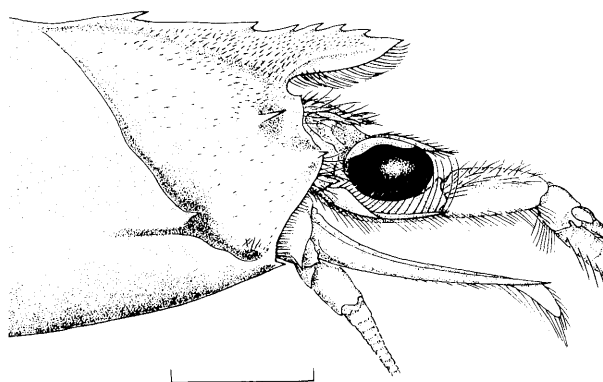


Fig. 6. *Solenocera atlantidis* Burkenroad. Female, anterior region of body in lateral view, 5 mm indicated (from Pérez Farfante and Bullis 1973).

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 Cananea, 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 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).

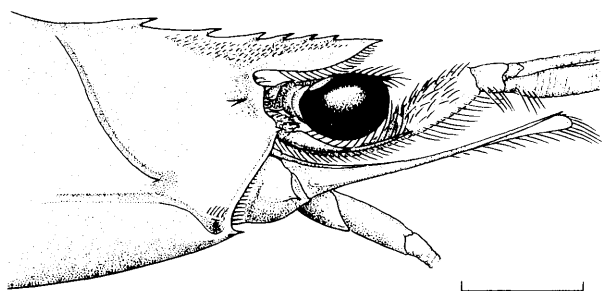


Fig. 7. *Solenocera necopina* Burkenroad. Female, anterior region of body in lateral view, 5 mm indicated (from Pérez Farfante and Bullis 1973).

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

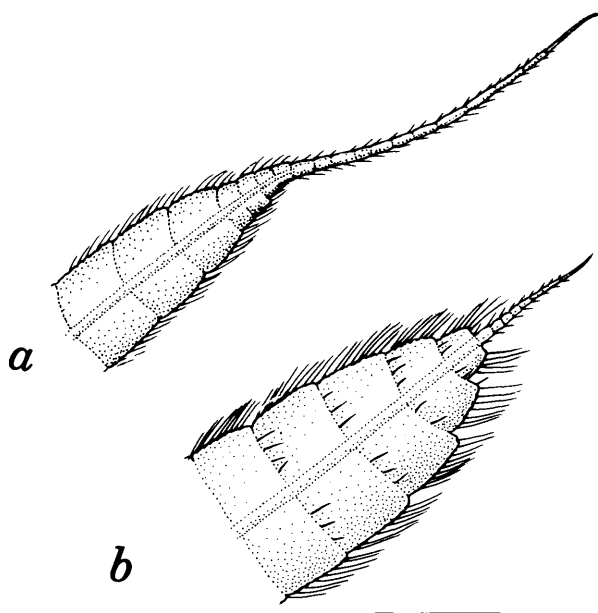


Fig. 8. *Solenocera vioscai* Burkenroad. Distalmost portion of antennular flagella: a, dorsal flagellum; b, ventral flagellum, 1 mm indicated (from Pérez Farfante and Bullis 1973).

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 (Farfantepeneaus) 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 (Farfantepeneaus) 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-

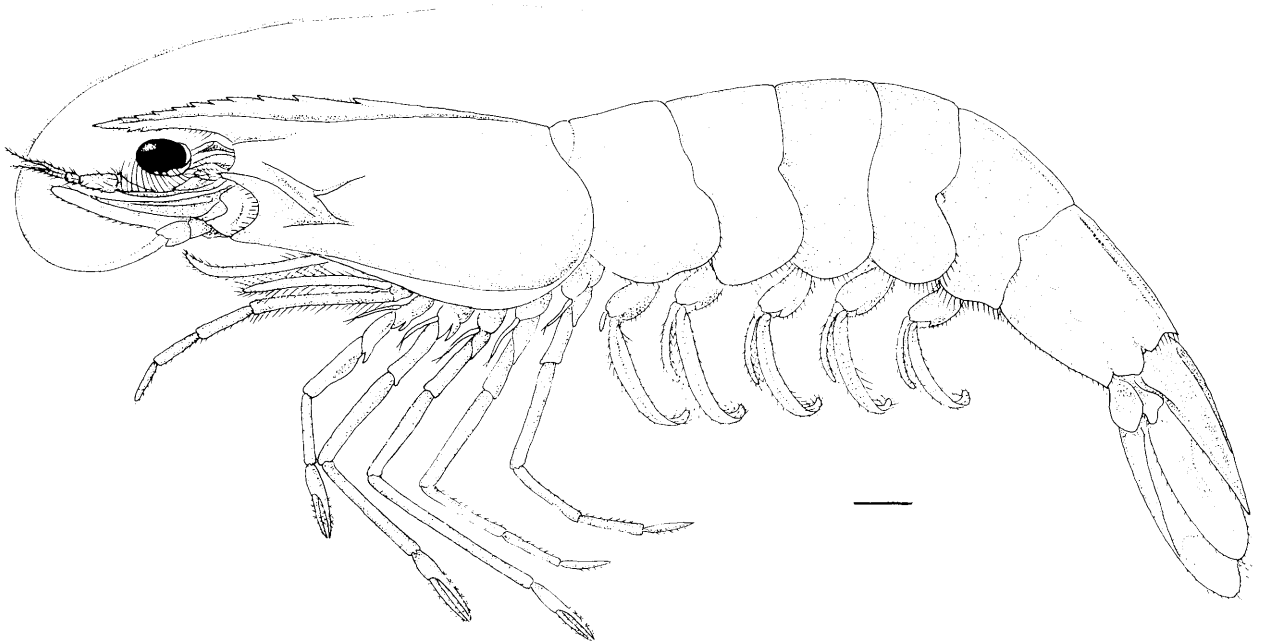


Fig. 9. *Penaeus (Farfantepeneaus) aztecus* Ives. Female in lateral view, 1 cm indicated (from Pérez Farfante 1978).

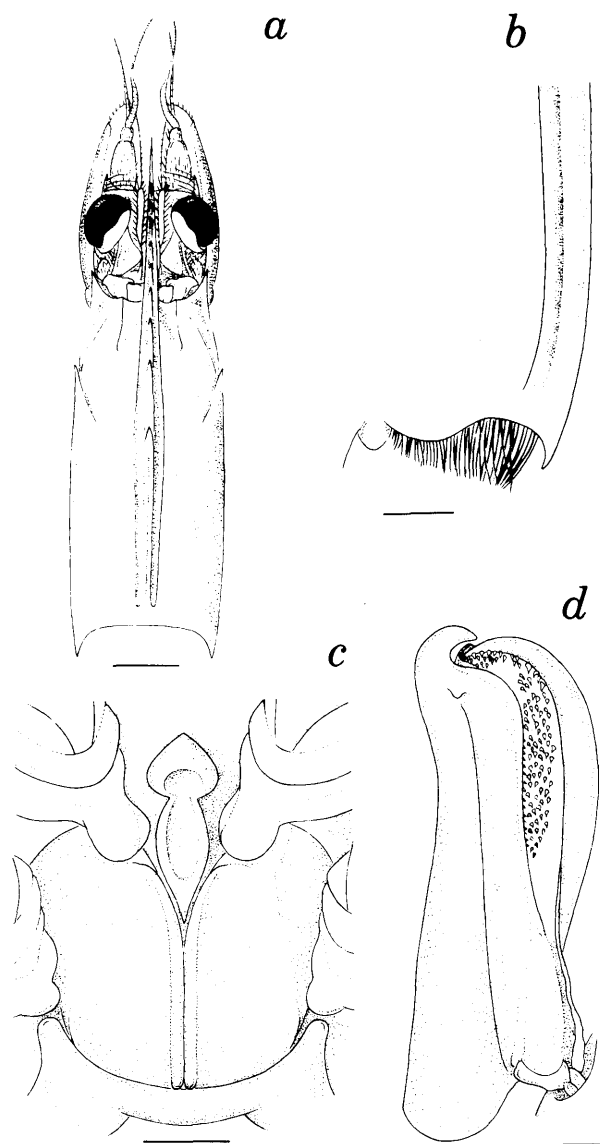


Fig. 10. *Penaeus (Farfantepeneaus) aztecus* Ives. a, Carapace in dorsal view; b, sixth abdominal segment in lateral view; c, thelycum of female; d, petasma of male; a, 10 mm; b-d, 2 mm indicated (from Pérez Farfante 1978).

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 Par-rack (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 post-larvae 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 post-larvae 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 post-larval 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).

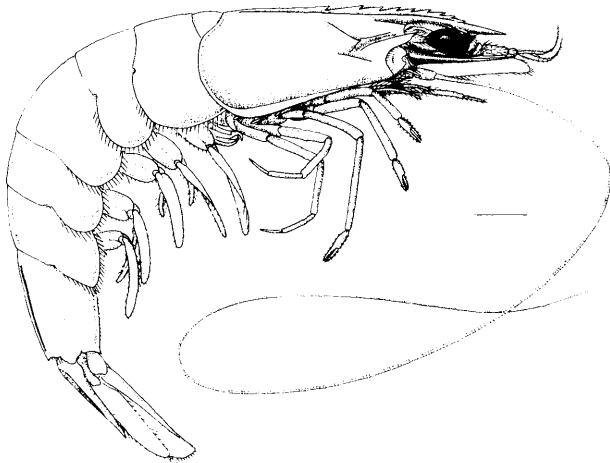


Fig. 11. *Penaeus (Farfantepenaeus) brasiliensis* Latreille. Male in lateral view, 1 cm indicated (adapted from Pérez Farfante 1978).

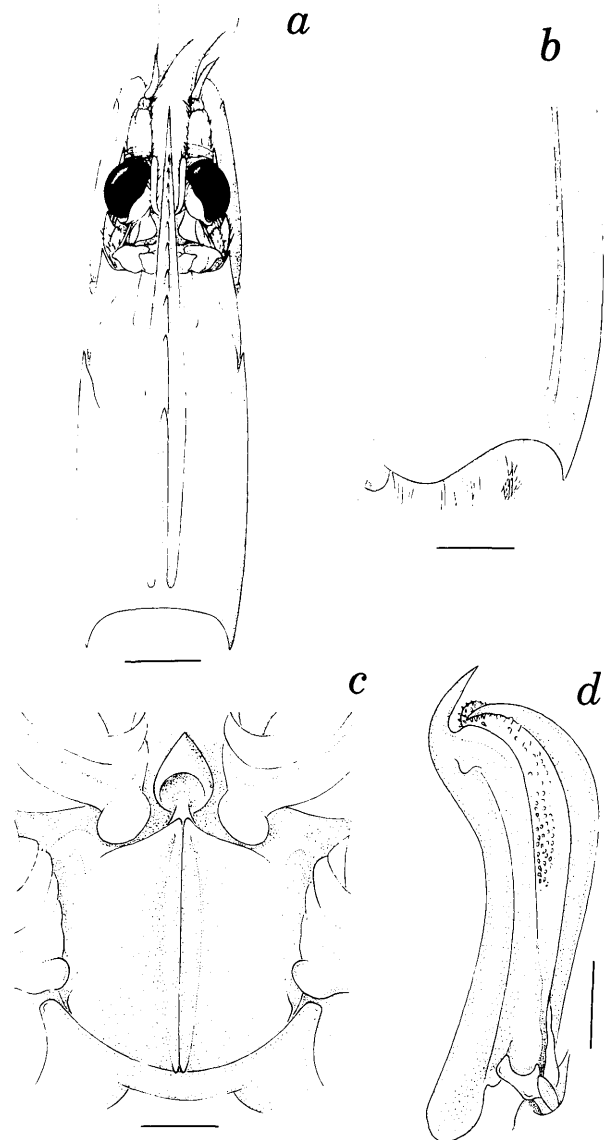


Fig. 12. *Penaeus (Farfantepenaeus) brasiliensis* Latreille. *a*, Carapace in dorsal view; *b*, sixth abdominal segment in lateral view; *c*, thelycum of female; *d*, petasma of male; *a*, 10 mm; *b-d*, 2 mm indicated (from Pérez Farfante 1978).

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

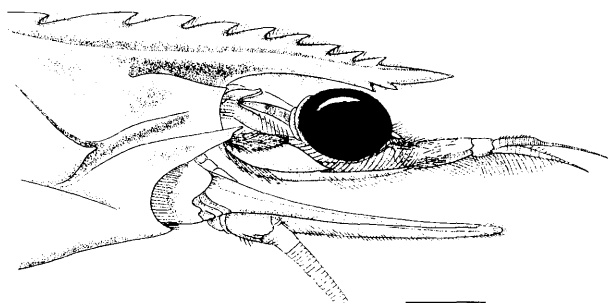


Fig. 13. *Penaeus (Farfantepenaeus) duorarum* Burkenroad. Female, anterior region of body in lateral view, 5 mm indicated (from Pérez Farfante 1978).

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).

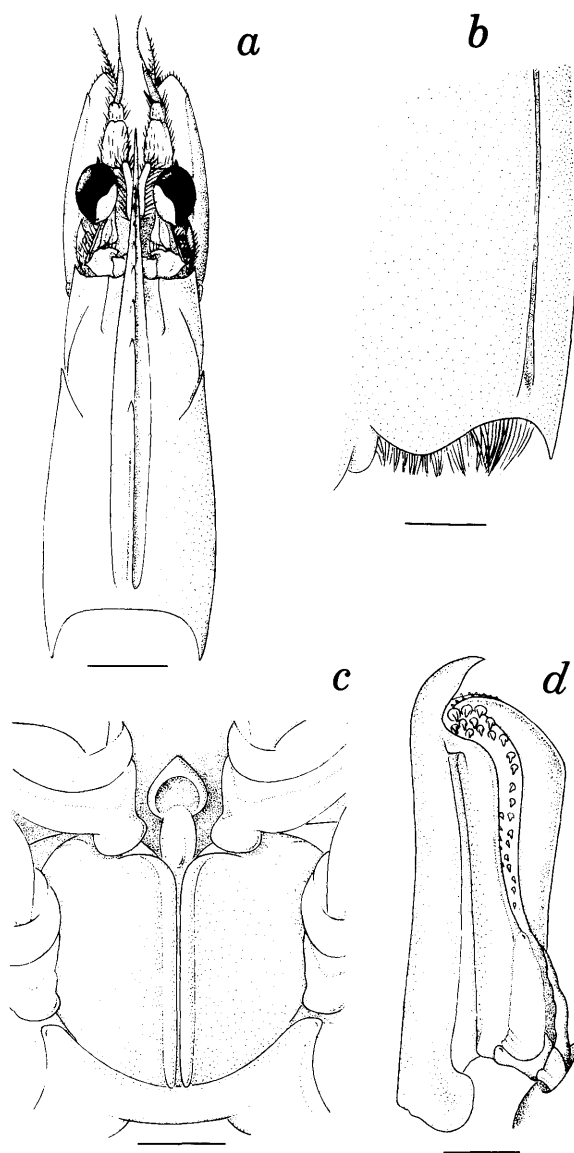


Fig. 14. *Penaeus (Farfantepenaeus) duorarum* Burkenroad. a, Carapace in dorsal view; b, sixth abdominal segment in lateral view; c, thelycum of female; d, petasma of male; a, 10 mm; b-d, 2 mm indicated (from Pérez Farfante 1978).

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 Rehrer 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 dorsoventrally 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.

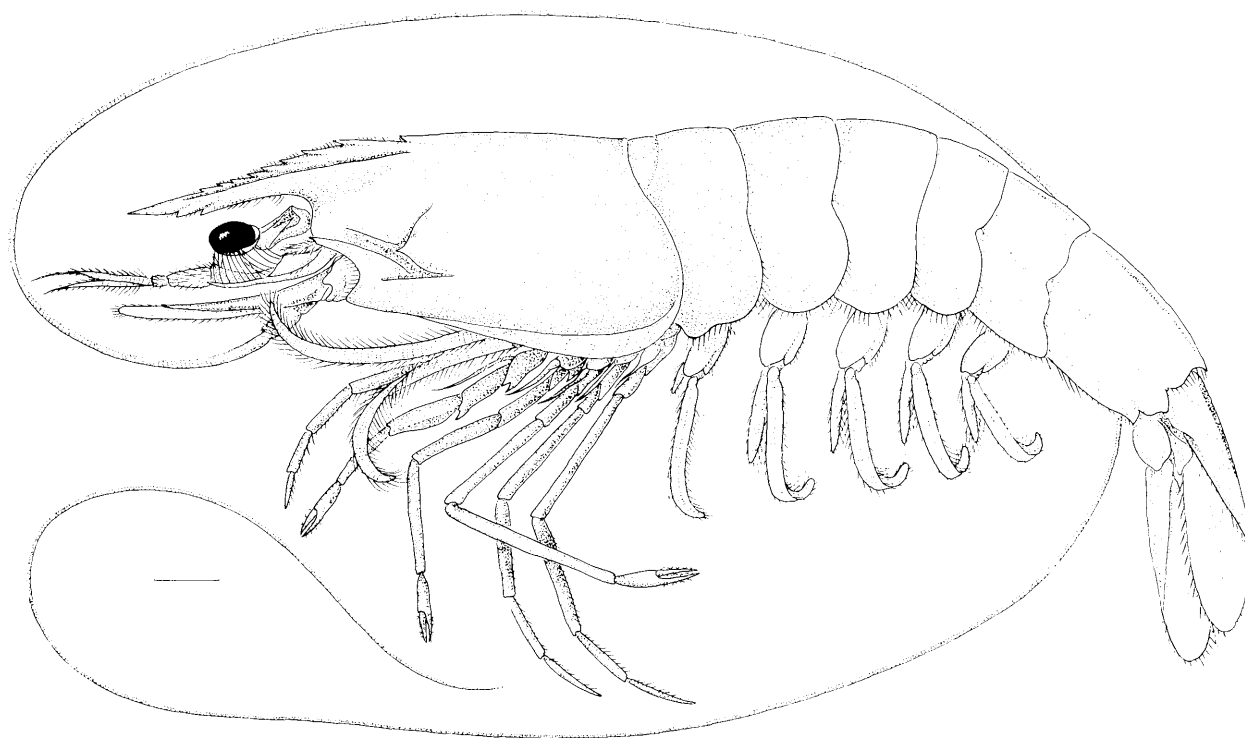


Fig. 15. *Penaeus (Litopenaeus) setiferus* (Linnaeus). Female in lateral view, 1 cm indicated (from Pérez Farfante 1978).

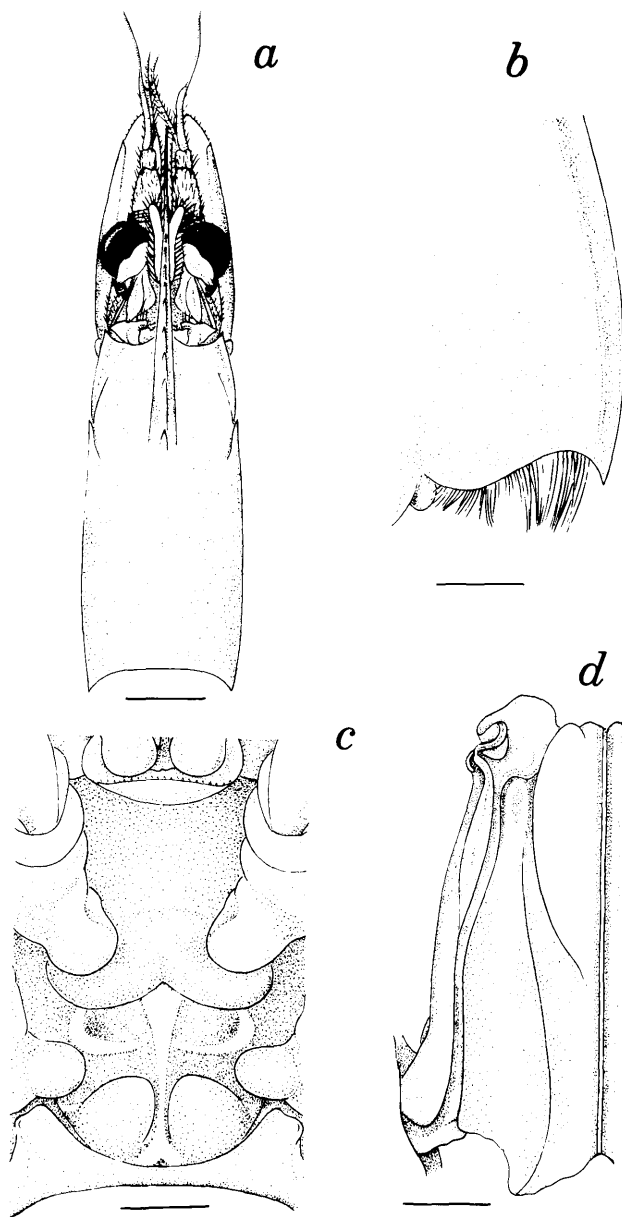


Fig. 16. *Penaeus (Litopenaeus) setiferus* (Linnaeus). *a*, Carapace in dorsal view; *b*, sixth abdominal segment in lateral view; *c*, thelycum of female; *d*, petasma of male; *a*, 10 mm; *b-d*, 2 mm indicated (from Pérez Farfante 1978).

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 hypoosmotic 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

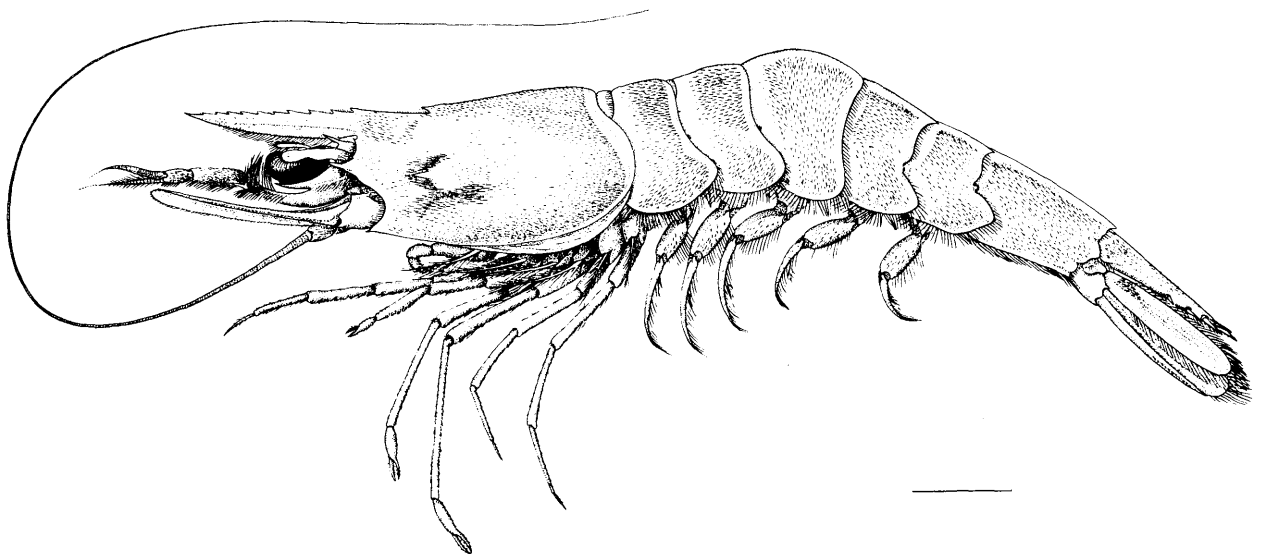


Fig. 17. *Metapenaeopsis goodei* (Smith). Female in lateral view, 5 mm indicated (from Pérez Farfante 1971).

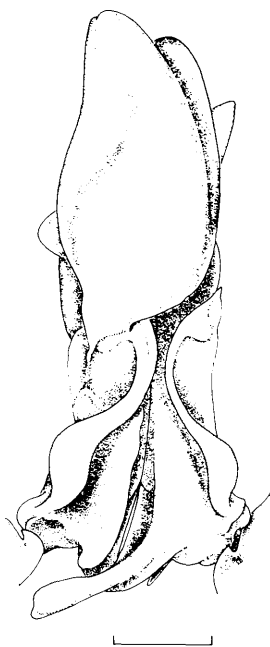


Fig. 18. *Metapenaeopsis goodei* (Smith). Petasma of male, ventral view, 1 mm indicated (from Pérez Farfante 1971).

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 Sombrero Island; Surinam; off Ceará, São Paulo, and Santa Catarina, Brazil (Mistakidis and Neiva 1964, 1966; Fausto-Filho 1966b, 1967a; Iwai 1973).

Remarks.—*Trachypenaeus 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

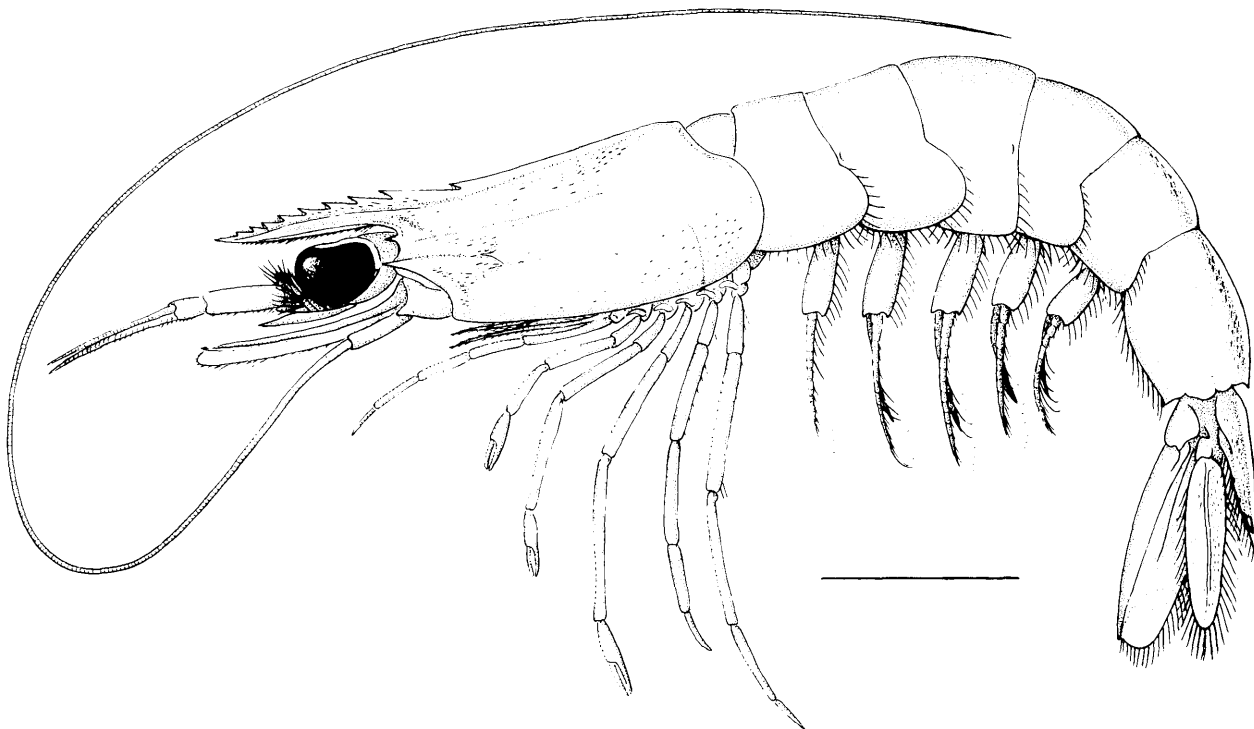


Fig. 20. *Trachypenaeus constrictus* (Stimpson). Female in lateral view, 2 cm indicated (from Pérez Farfante 1978).

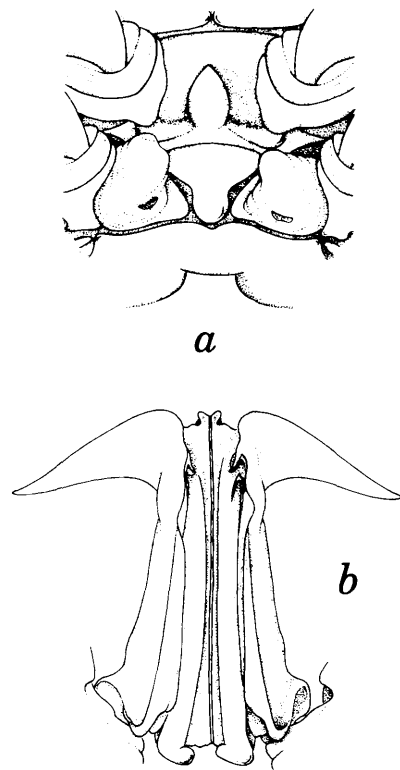


Fig. 21. *Trachypenaeus constrictus* (Stimpson). a, Thelycum of female; b, petasma of male (from Pérez Farfante 1978).

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 protozoae 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 protozoae, 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 protozoal 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.

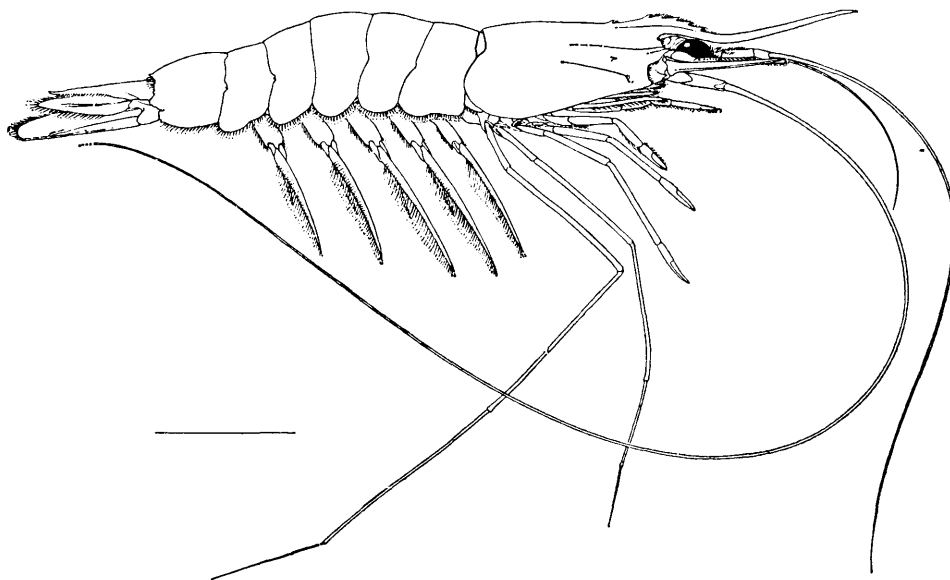


Fig. 22. *Xiphopenaeus kroyeri* (Heller). Female in lateral view, 2 cm indicated (from Chace and Hobbs 1969).

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

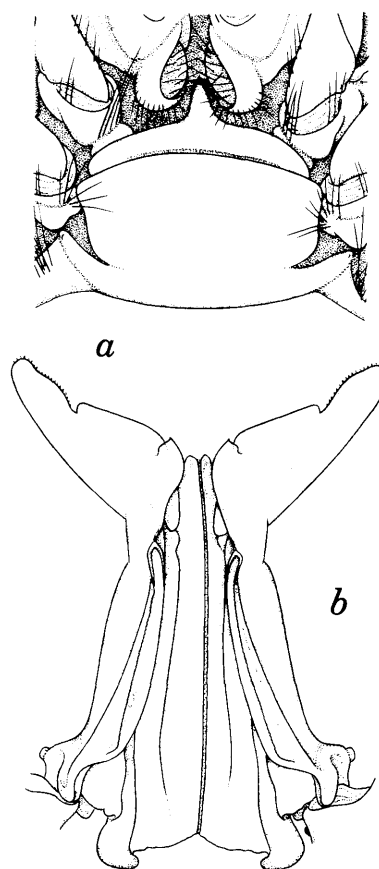


Fig. 23. *Xiphopenaeus kroyeri* (Heller). *a*, Thelycum of female; *b*, petasma of male (from Pérez Farfante 1978).

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 unirra-

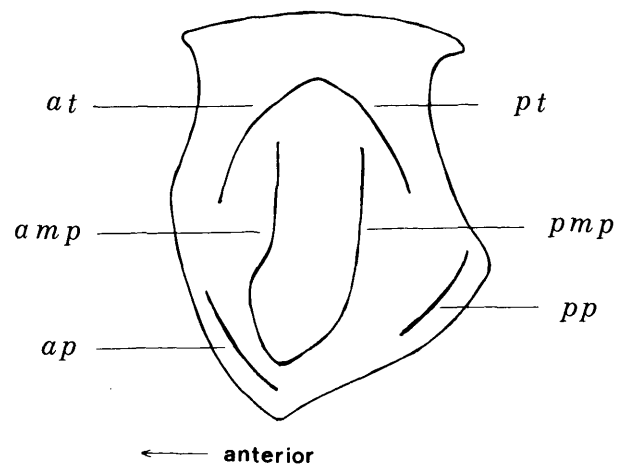


Fig. 24. Schematic lateral view of *Sicyonia* abdominal segment showing grooves: *at*, anterior tergal; *amp*, anteromedian pleural; *ap*, anterior pleural; *pt*, posterior tergal; *pmp*, posteromedian pleural; *pp*, posterior pleural (from Cobb, et al. 1973).

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.

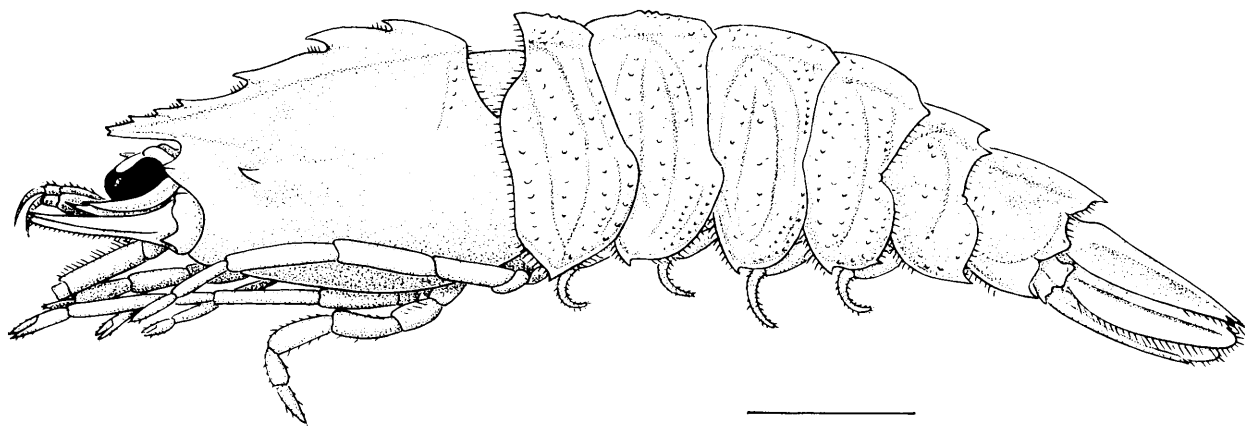


Fig. 25. *Sicyonia brevirostris* Stimpson. Male in lateral view, 10 mm indicated (from Cobb, et al. 1973).

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-

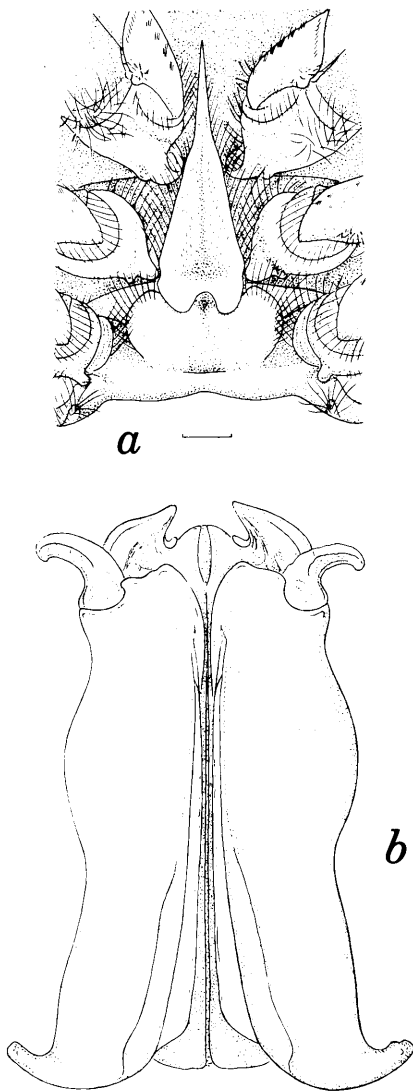


Fig. 26. *Sicyonia brevirostris* Stimpson. *a*, Thelycum of female (from Pérez Farfante 1978); *b*, petasma of male (from Williams 1965); *a*, 2 mm, *b*, 1 mm indicated.

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*.

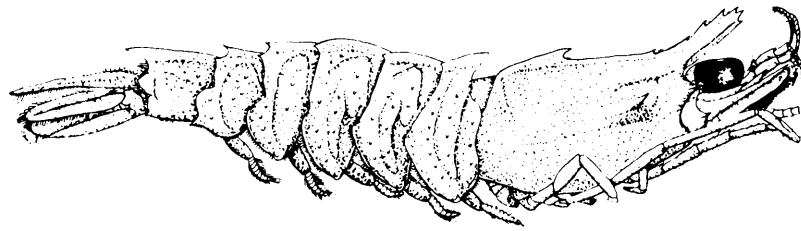


Fig. 27. *Sicyonia burkenroadi* Cobb. Female in lateral view, 5 mm indicated (from Cobb 1971).

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

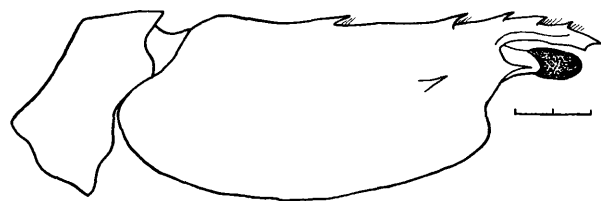


Fig. 28. *Sicyonia dorsalis* Kingsley. Carapace and first abdominal segment in lateral view, 2 mm indicated (from Lunz 1945).

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

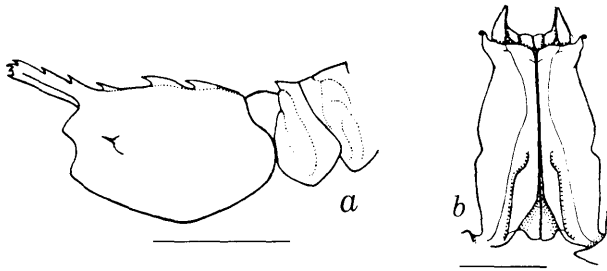


Fig. 29. *Sicyonia laevigata* Stimpson. *a*, Carapace and first two abdominal segments in lateral view, 5 mm indicated; *b*, petasma of male in ventral view, 0.5 mm indicated (from Burkenroad 1934a).

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

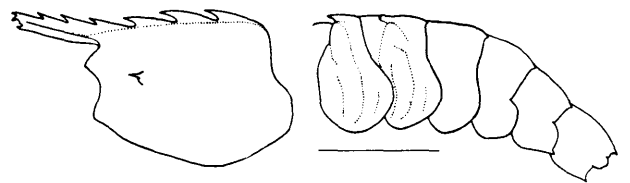


Fig. 30. *Sicyonia parri* (Burkenroad). Carapace and abdomen in lateral view, 5 mm indicated (from Burkenroad 1934a).

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 simpsoni Bouvier

Fig. 31

Sicyonia simpsoni 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 simpsoni.—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-

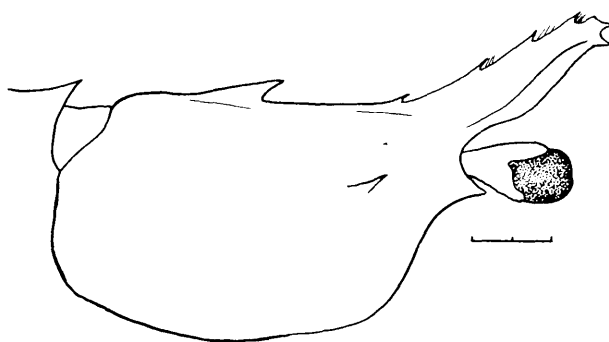


Fig. 31. *Sicyonia simpsoni* Bouvier. Carapace and part of first abdominal segment in lateral view, 2 mm indicated (from Lunz 1945).

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. simpsoni* 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-

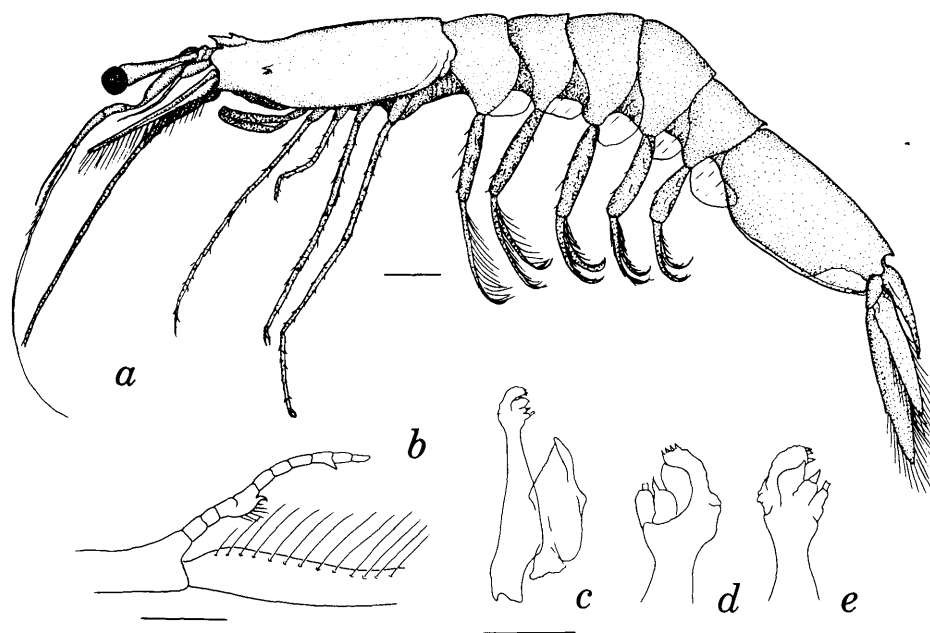


Fig. 33. *Acetes americanus carolinae* Hansen. *a*, Female in lateral view; *b*, clasper on antennule of male (from Williams 1965); *c*, petasma of male; *d-e*, capitulum of same (from Omori 1975); *a*, 1 mm; *b*, 0.1 mm; *c*, 0.5 mm; *d-e*, 0.2 mm indicated.

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 clasper, 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

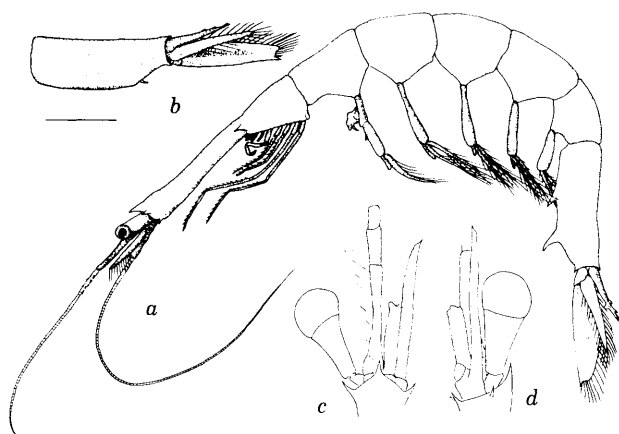


Fig. 34. *Lucifer faxoni* Borradaile. a, Male in lateral view; b, sixth abdominal segment and tail fan of female in lateral view (from Williams 1965); a-b, 1 mm indicated; c, anterior end of male head; d, same, lateral (from Bowman 1967).

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 protozoae, 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;

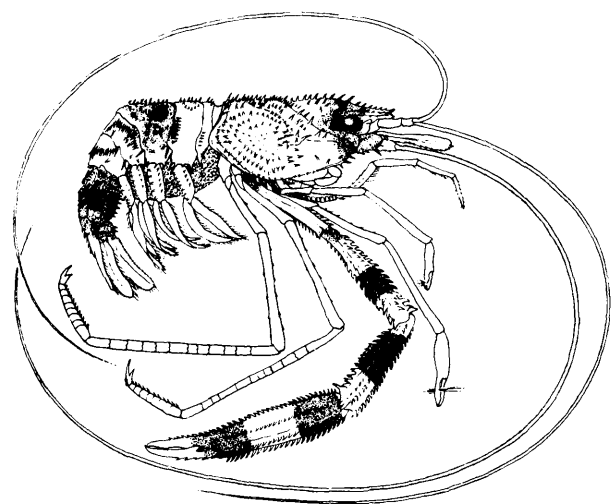


Fig. 35. *Stenopus hispidus* (Olivier). Female in lateral view (from Limbaugh, et al. 1961).

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

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

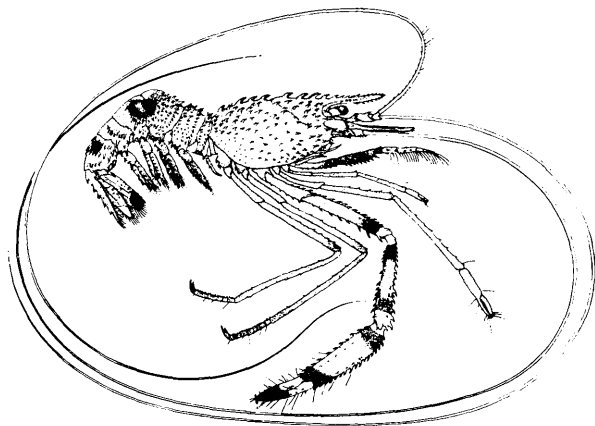


Fig. 36. *Stenopus scutellatus* Rankin. Animal in lateral view (from Limbaugh, et al. 1961).

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. Eystalks 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

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

Superfamily Pasiphaeoidea

Family Pasiphaeidae

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 dorso-laterally 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

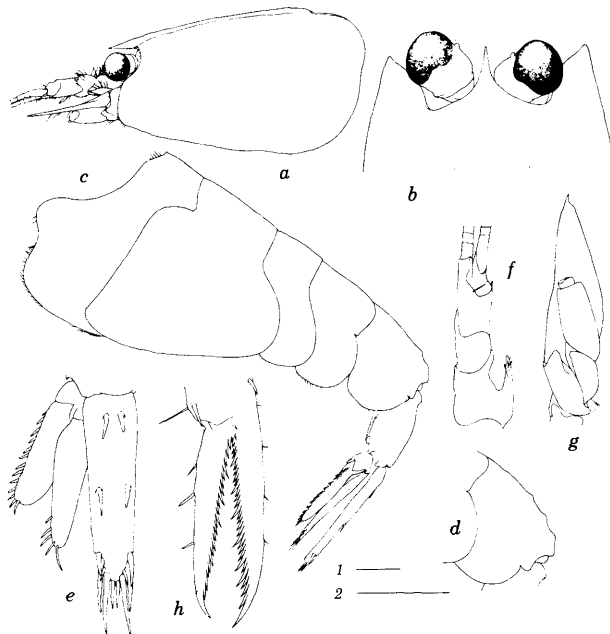


Fig. 37. *Leptochela (Leptochela) papulata* Chace. a, Carapace and anterior appendages, lateral view; b, anterior part of carapace and eyes, dorsal view; c, abdomen, lateral view; d, fifth abdominal segment; e, telson and left uropod; f, right antennule, dorsal view; g, right antenna, ventral view; h, 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).

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-

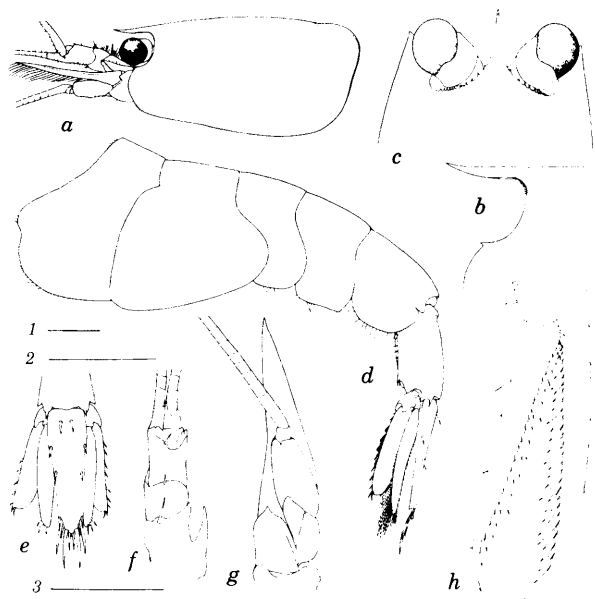


Fig. 38. *Leptochela (Leptochela) serratorbita* Bate. a, Carapace and anterior appendages, lateral view; b, orbital region; c, anterior part of carapace and eyes, dorsal view; d, abdomen, lateral view; e, telson and uropods; f, right antennule, dorsal view; g, right antenna, ventral view; h, fingers 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

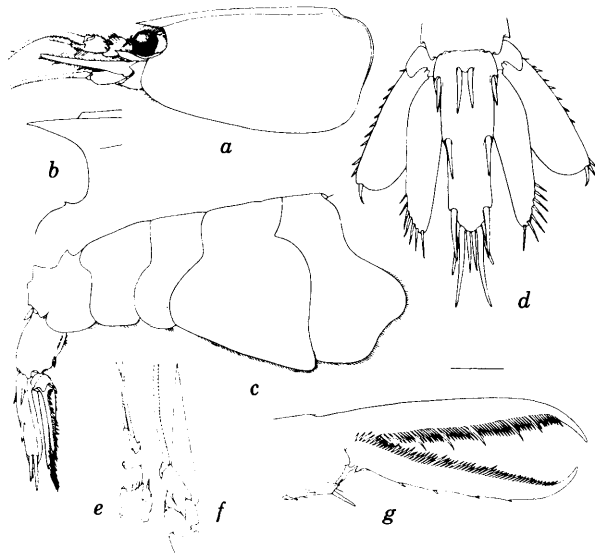


Fig. 39. *Leptochela (Proboloura) carinata* Ortmann. a, Carapace and anterior appendages, lateral view; b, orbital region; c, abdomen, lateral view; d, telson and uropods; e, right antennule, dorsal view; f, right antenna, ventral view; g, fingers of right first leg. Scales: a, c, e-f=2 mm; b, d=1 mm, 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 1/8 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

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

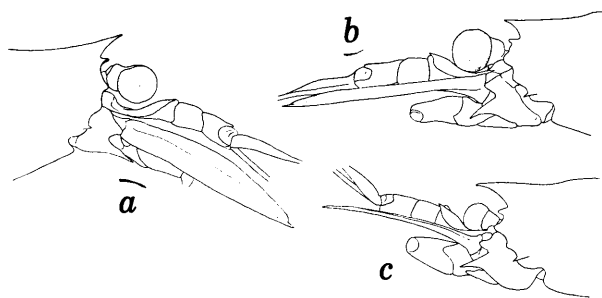


Fig. 40. *Pasiphaea multidentata* Esmark. Anterior part of body in lateral view, ovigerous females. *a*, *b* from Norway; *c* from Mediterranean coast of Spain (from Sivertsen and Holthuis 1956).

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 Disciadiidae, 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

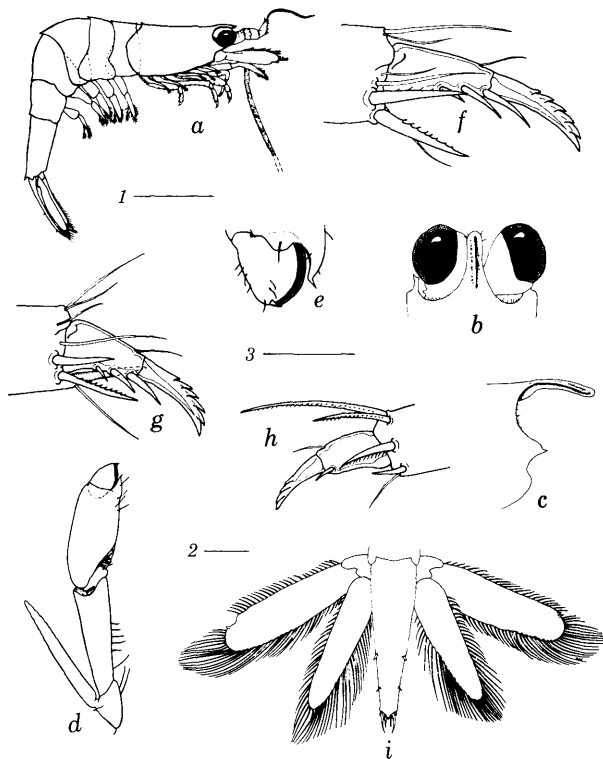


Fig. 41. *Discias atlanticus* Gurney. Female: a, lateral view; b, eyes and anterior carapace, dorsal; c, anterior carapace, lateral; i, tail fan (from Gore and Wilson 1979); d, cheliped, first leg; e, same, distal end, scale not given (from Gurney 1939); f-h, dactyl of third-fifth legs (from Bruce 1975).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

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