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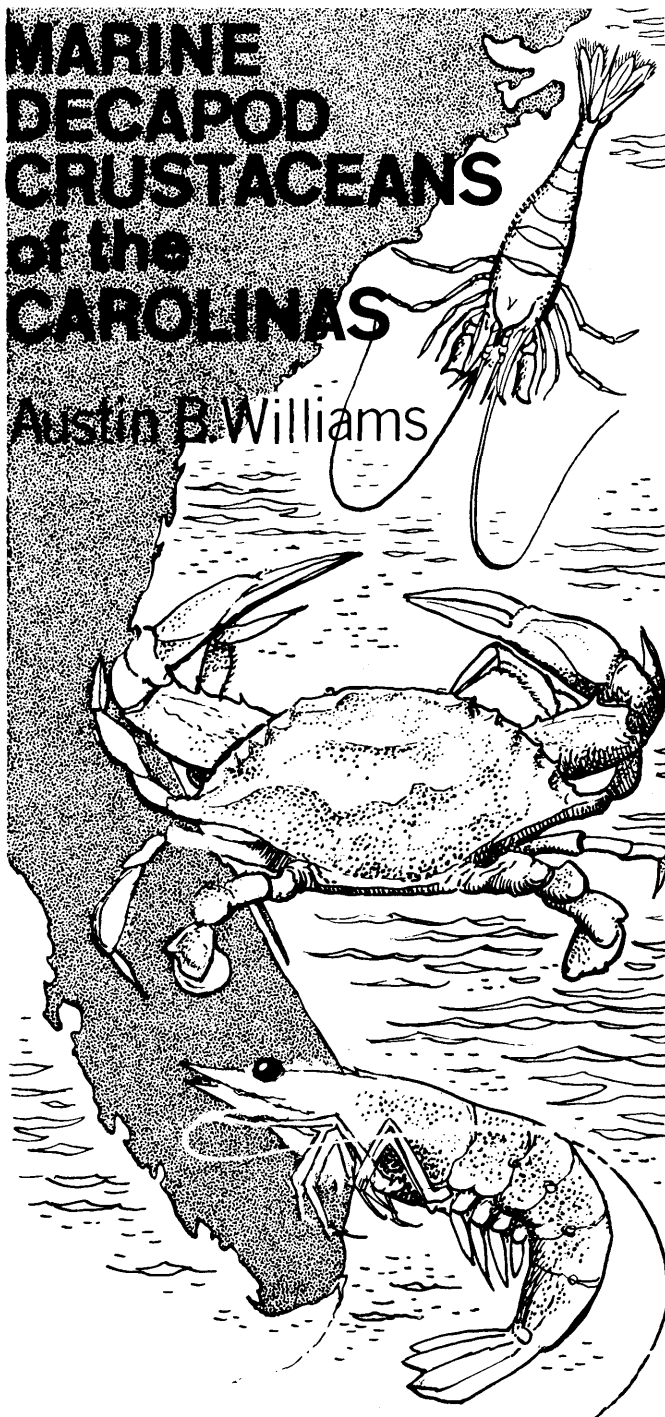
J. Martin

MARINE
DECAPOD
CRUSTACEANS
of the
CAROLINAS

Austin B. Williams

Williams, 1962

J. M. Crane



F I S H E R Y
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Created in 1849, the United States Department of the Interior—a department of conservation—is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

As the Nation's principal conservation agency, the Department works to assure that nonrenewable resources are developed and used wisely, that park and recreational resources are conserved for the future, and that renewable resources make their full contribution to the progress, prosperity, and security of the United States—now and in the future.

PREFACE

This is a revision of the first definitive handbook on marine decapod crustaceans of southeastern North America by Hay and Shore (1918).

The junior author, Clarence A. Shore (1873-1933), conceived the idea of the handbook while teaching in the medical school of the University of North Carolina at Chapel Hill. Shore entered the university in 1897, majored in biology, and earned the B.S. degree in 1901 and the M.S. in 1902. He 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. In 1904 Shore began 3 years of study compiling descriptions and photographs of most of the decapod crustaceans known to occur in the region. He did not complete the work, however, for he left the field of marine biology to enter the field of medicine (Cooper, 1933, 1940; Wilson, 1933).

William Perry Hay (1871-1947), who graduated from Butler University in 1891, taught from

1892 to 1934 in schools and colleges in the Washington, D.C., area. He had a great interest in natural history, especially herpetology and carcinology, and published a number of papers in both fields (Needham, 1947). Hay took up Shore's uncompleted project in 1912, but found so much new data available that the original had to be revised. Thus the work was published 14 years after it was initiated.

The introduction to that book included a history of the project, a review of earlier work in the region, statements on affinities of the fauna, some ecological remarks, a few comments on arrangements of the hierarchy, and acknowledgments. Since 1918 knowledge has increased. Taxonomists have changed names and the faunal list has been expanded, although certain groups that Hay and Shore treated have been deleted in this revision. For these reasons, the general introduction which follows is a combination of those authors' comments and my own.

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MARINE DECAPOD CRUSTACEANS OF THE CAROLINAS

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INTRODUCTION

Knowledge of the crustacean fauna of the Carolinas has grown slowly over many decades. Early in the last century, Thomas Say described species from the Carolinas, and in the middle 1800's Professor L. R. Gibbes, who maintained a private collection in Charleston, S.C., described species from the Carolinas. William Stimpson (1860b), who visited Beaufort, N.C., in company with T. N. Gill, gave a list of 38 species of decapod crustaceans which he collected there. Elliott Coues (1871), at that time an Army surgeon stationed at Fort Macon, N.C., recorded 27 species of decapods from the Beaufort area, 8 of which were additions to Stimpson's list. Seven years later, Coues and Yarrow (1878) gave a list of six species, two of which had not appeared previously. An appendix to the same paper by J. S. Kingsley included 51 species from the Beaufort area, and 3 of these were additions to the fauna. A year later, Kingsley (1879) contributed eight more new records.

The collection which was the subject of Kingsley's report had been made by Professor H. E. Webster, of Union College. It was later transferred, in part at least, to the U.S. National Museum, and supplied the types of *Lepidopa websteri* Benedict and *Pinnixa cristata* Rathbun, both collected near Beaufort, N.C.

Professor W. K. Brooks and his students, of the Johns Hopkins University, studied crustaceans at Beaufort at intervals from 1880 to 1903. They

contributed information on habits and development, but only one or two new species were added to the faunal list.

Shore's manuscript included 87 species, but he omitted 8 which had been listed by the writers already mentioned. He had added 33 species, making a total of 95 species for the region.

Following this, exploratory work on offshore fishing banks by the *Fish Hawk* in the summers of 1914 and 1915, energetic shore and shallow-water collecting by parties from the Bureau of Fisheries laboratory at Beaufort, and inclusion of freshwater species from the region, enabled Hay to add 57 species to Shore's list. These, plus description of a new species by Rathbun, brought the total number known from Beaufort, N.C., in 1918 to 153 species.

The authors pointed out that some of these species had not yet been reported from the area, though from distribution elsewhere they might be expected. Also, some of the species were considered more properly to be deep-sea forms, rather than strictly members of the Beaufort fauna, although they had been found on the continental shelf not far distant.

In the year the handbook appeared, Mary J. Rathbun brought out the first in a series of four monographs on recent crabs of the Western Hemisphere, and, thus, began a new advance in knowledge of Carolinian crustaceans, later furthered by major revisions of the Penaeidae by Burkenroad, revisions of Hippolytidae, Palaemonidae and Scyllaridae by Holthuis, Galatheididae by

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Chace, Paguridae by Wass, Thalassinidea by de Man, Oxyrhyncha by Garth, and the Porcellanidae by Haig. Schmitt's treatment of the Macrura and Anomura of the Puerto Rican area, as well as his contributions on the Hippidae and the genera *Callianassa* and *Upogebia*, and Verrill's completion of the work on Bermudan decapods added breadth to knowledge of distribution as well as taxonomic stability. Closer at hand, the studies of Lunz in South Carolina yielded similar results. To this list of scholars could be added the names of Borradaile, Glassell, and Provenzano, who described new forms from the Carolinian province. The works of these and other authors are given in detail in the text to follow.

Apart from these primarily systematic studies, a growing number of ecological studies have been published during the past 45 years. Such results are not usually cited in systematic handbooks, but because this one is directed primarily to students and ecologists who are often newcomers to the area, brief summaries have been attempted. The review of literature, though not complete, is exhaustive enough to lead to most of the published material.

Actually, few species have been studied in detail. Of these, almost all are littoral species easily accessible to the investigator by virtue of their abundant numbers and ecological niches. Beyond this, a few species of commercial value such as *Callinectes sapidus* and *Penaeus* spp. have been studied in detail. It is fair to say that ecological studies are scarcely started.

SYSTEMATIC DISCUSSION

This is a review of published material. Arrangement of families and genera follows that adopted by the most recent reviser of each group. Important diagnostic characters of families and genera have been incorporated in keys and are often repeated, in part, in species descriptions. Brief diagnoses of families are included to aid in identification. Diagnoses of genera are not included, with some exceptions, for these exist in the literature. Such treatment leads to repetition but gives more complete descriptive accounts for individual species.

The general key to suborders, sections, superfamilies, and families serves as a rough index, and an attempt has been made to arrange it

"phylogenetically". Other keys to subfamilies, genera, and species are either combined or separate depending on number of genera or species involved, and these keys are scattered throughout the text.

There is a tendency in carcinology to assume a specialized background on the part of readers, and beginners 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 terminology in various suborders and sections lacks 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 it is based on functional morphology, the shrimps tending to have five pairs of legs functionally adapted to walking, but most crabs only four. Because many shrimps do not walk, legs in this group herein have been called "legs," the term "walking legs" being reserved for crabs. Hopefully, the use of explanatory figures adapted from existing works, together with the glossary, will resolve most of such difficulties.

In the species accounts, no attempt has been made to include complete synonymies. A great deal of spadework by recent specialists has made abbreviation of synonymies desirable and practical; therefore, most are restricted to citation of original description, Hay and Shore (where applicable), and work of the most recent reviser.

Many descriptions which Hay and Shore wrote have been paraphrased, and many measurements, descriptions of color, and ecological notes have been included essentially unchanged. When available, more recent information has been used, and for this I have depended heavily on Rathbun (1918b, 1925, 1930a, 1937), Schmitt (1935a), and Holthuis (1951a, 1952, 1959) for key characters, color notes, and depth and latitudinal ranges. For these works, specific citations in the text have often been excluded for the sake of brevity.

ZOOGEOGRAPHIC CONSIDERATIONS

Though the original title implied a local list, the handbook included an assemblage that is quite widespread. Hay and Shore justly termed it a virtual descriptive list of decapod crustaceans of the Middle Atlantic coast, in large measure filling but continuing in part from northwestern Florida the gap between various lists of New England, New York, and New Jersey crustaceans, and the Puerto Rican list (Rathbun, 1901). The assemblage treated, both by Hay and Shore (in the original) and this revised version, has a latitudinal range extending primarily from Cape Hatteras, N.C., to northeastern Florida (fig. 1), to Texas; it is encompassed in a more generalized assemblage sometimes recognized as the Carolinian province (Hedgpeth, 1953). Primarily Antillean in its affinities, the Carolinian province is distinct from the Virginian province to the north and this fact has been emphasized by numerous authors.

Bathymetric limits included in this revised handbook are altered somewhat from the original. Species which occur from the heads of estuaries to the 100-fathom contour are included. Freshwater decapods, included in the original, have been excluded because they never occur in the marine environment. Species that occur only beyond the 100-fathom line more properly belong to a deep-sea fauna that ranges far beyond the Carolinian province, and are not included.

Arbitrary limits are difficult to establish. Judgments undoubtedly will differ as to what is extralimital and what is not. For some species with uncertain distributional limits, a list of extralimital species has been included.

An analysis of the decapod crustacean element in the Carolinian fauna is given by family in table 1. Here, categories chosen for limits in geographic range are used broadly, especially at their southern extremities. For economy of space, the term "South America" can mean either the northern or southern Atlantic shores of the continent, but details are given in the species accounts. Our interest here centers primarily on the eastern coast of North America, and on natural boundaries or barriers that exist on this stretch of coast.

It is apparent that a small number (6.8 percent) of Carolinian decapods are northern in affinity, extending to southern Florida in one case (*Cancer*

borealis). To this group, Cape Cod is no barrier, but to another group (12.7 percent) it is a barrier to northward extension into upper New England and the Maritime Provinces of Canada.

Totals are given for species extending northward to the Middle Atlantic States (9.1 percent). Many of these records are for accidental or seasonal occurrence; *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.

Cape Hatteras is a barrier to northward distribution of shallow-water forms. Here, warm water of the Gulf Stream meets the cold Labrador Current to be deflected seaward (Hutchins, 1947), and 27.7 percent of the decapods are apparently unable to bridge the narrow transition zone to colder water.

Cape Lookout, surprisingly, seems to be a greater barrier to northward extension of range among Antillean species (31.4 percent) than Cape Hatteras. This barrier may be real, or it may be that faunal limits fluctuate between these capes as a consequence of natural events. More likely is the fact that far more collecting has been done near Cape Lookout than at Cape Hatteras because of the nearness of marine laboratories to the former.

Species showing distributions reaching northward only to Charleston, S.C., (4.5 percent) are probably southern species with accidental records at that latitude, for there is no apparent barrier to dispersal in that area. Eastern and western Atlantic forms are equally small in number (4.5 percent).

Cosmopolitan species (1.8 percent) are few, as are endemic species (1.4 percent).

Aside from the above patterns of distribution, a number of species ranging along the Atlantic coast and the Gulf coast to Texas have a disjunct distribution in peninsular Florida. The number of these species is conservatively estimated, from literature records, at 10 percent 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 by emergence of peninsular Florida, but with the two areas being climatically equivalent

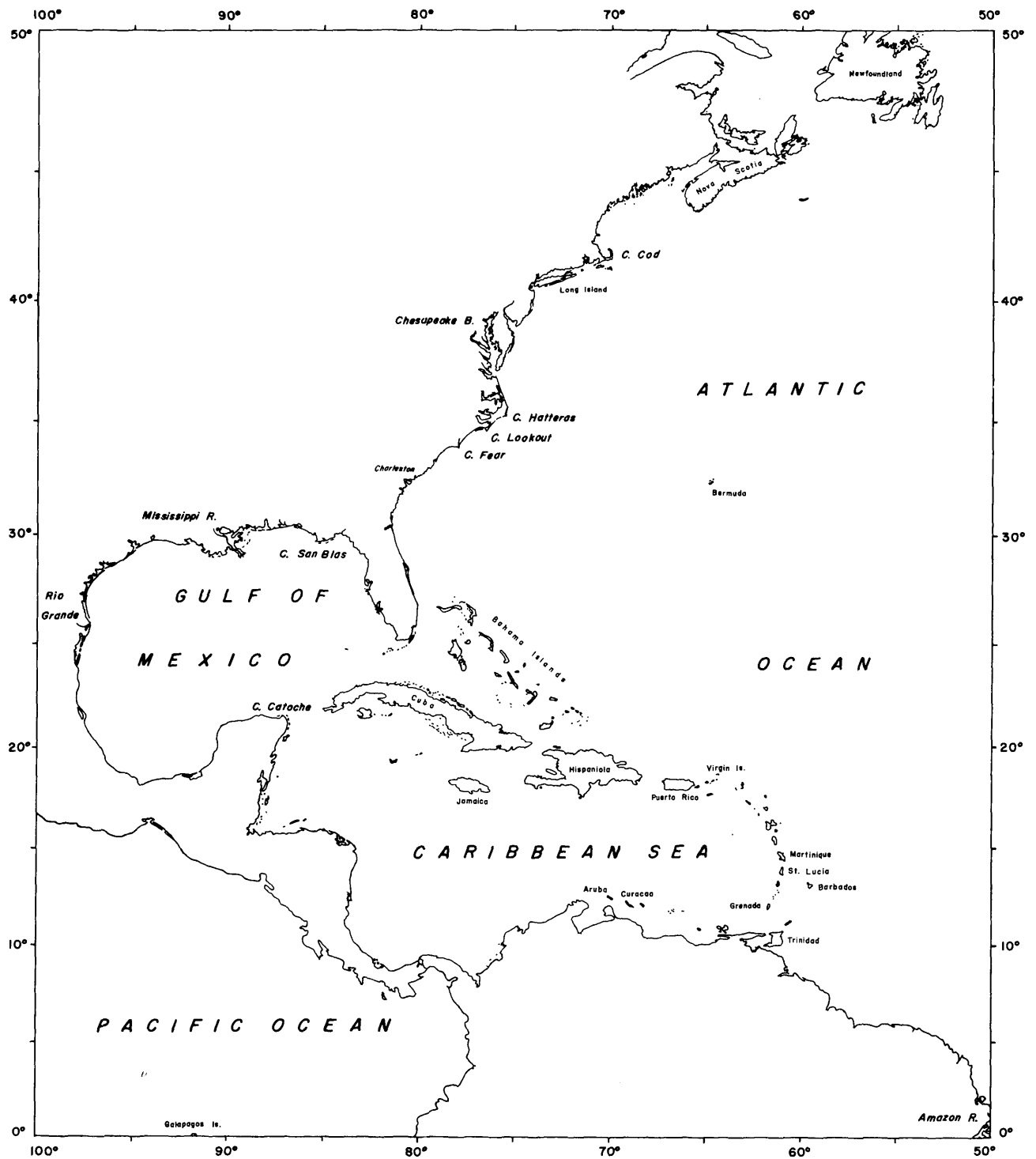


FIGURE 1.—Area of western North Atlantic Ocean, including portions of eastern North America, Middle America, and northern South America, covering centers of distribution for most species treated in this handbook.

(Hutchins, 1947). It is also clear, from families represented in this group, that many are relatively sedentary, at least as adults.

MATERIALS STUDIED

Materials studied at the U.S. National Museum (USNM) include recent records resulting from exploratory work by the vessels *Pelican*, *Albatross III*, *Combat*, *Oregon*, and *Silver Bay*, as well as records of collections by private individuals. Specimens studied were from the USNM, the Charleston Museum, Charleston, and Bears Bluff Laboratories, Wadmalaw Island, S.C., The University of North Carolina Institute of Fisheries Research (IFR), and various collections provided by Duke University Marine Laboratory and the U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C. Remnants of Hay and Shore's collections were also examined and are now housed at the IFR.

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.

EXTRALIMITAL AND INDETERMINATE SPECIES

The following list includes species having doubtful position in the Carolinian fauna. Some range primarily in deep water, occurring incidentally on the Continental Shelf. Others have a range limited to shallow waters distant from the Carolinas. Some are included because Hay and Shore mentioned them, and the remainder have a doubtful taxonomic status.

Penaeopsis megalops (Smith). North Carolina, through Gulf of Mexico to Surinam; 150–200+ fathoms.

Sicyonia sp. (Lunz, 1945). A distinct specimen from Beaufort River, near Parris Island, S.C., has been described but not named (Charleston Museum No. 35.131.5(a)).

Hippolyte coerulescens (Fabr.). Central Atlantic Ocean, Bermuda, North Carolina to

Florida, Azores, Canary and Cape Verde Islands, Gulf of Guinea and S. Angola, doubtful from Cape Horn region (Sivertsen and Holthuis, 1956). A single mutilated male from Sneads Ferry, N.C., is in the U.S. National Museum.

Homarus americanus H. Milne Edwards. Labrador to North Carolina; shallow water to 100+ fathoms. The American lobster is not normally found south of Cape Hatteras, but lobsters are frequently taken off Cape Henry, Va. For instance, one 5½-lb. and two 8–10-lb. lobsters were taken by the trawler *Ensign* approximately 45 miles E.N.E. Oregon Inlet, N.C., at 38–45 fathoms, January 21, 1963. In December 1958, an American lobster was caught in a crab pot near Cedar Island, N.C. Mr. Clayton Fulcher, Atlantic, N.C., reported that he tried to get the specimen, but this prize was eaten by the fisherman's family. Hay and Shore (1918) cited one doubtful occurrence of the lobster near Beaufort, N.C.

Munida longipes H. Milne Edwards. South Carolina to Curaçao; 154–338 fathoms (Schmitt, 1935a).

Pagurus cokeri Hay. South of Cape Lookout, N.C., to eastern Gulf of Mexico; approximately 150–200 fathoms.

Catapagurus sharreri Milne Edwards. Between Capes Hatteras and Lookout, N.C., to Barbados; 87–221 fathoms.

Latreillia elegans Roux. Both sides of North Atlantic Ocean, Mediterranean Sea, Natal; 70–200 fathoms (Rathbun, 1937).

Portunus ventralis (Milne Edwards). Georgia or Florida to Brazil; surface and near shore (Rathbun, 1930a).

Portunus sebae (Milne Edwards). Hay and Shore (1918) cited reports of this species in the Carolinas. Gulf of Mexico and Florida Straits to Brazil, Bermuda; surface to 15 fathoms.

Callinectes danae Smith. Status of this species on the southeastern coast of the United States needs clarification for there is no clear distinction there between it and *C. ornatus*. Indian River Inlet, Fla. to Brazil; shallow water to a few fathoms.

Parapinnixa hendersoni Rathbun. This species is questionably recorded from lat. 34°34' N. long. 75°50' W., southeast of Cape Lookout, N.C., 35

TABLE 1.—*Geographic ranges of decapod crustaceans*

[Lower portion of table shows combined totals of species with ranges limited by natural

Families	Number of species	North of Cape Cod to Florida, Gulf of Mexico, West Indies and South America	Cape Cod to east Gulf of Mexico and West Indies	Cape Cod to west Gulf of Mexico and South America	Middle Atlantic States to west Gulf and Caribbean	Middle Atlantic States to South America	Hatteras to east Gulf of Mexico, West Indies, and South America	Hatteras through Gulf of Mexico and West Indies to South America	Hatteras to west Gulf of Mexico
Penaeidae	17				1	3	2	4	2
Pasiphaeidae	1						1		
Palaemonidae	14	1		2		1	1	1	1
Gnathophyllidae	1								
Alpheidae	10	1						5	
Ogyrididae	2					2			
Hippolytidae	8			2	1	1			
Processidae	1								
Pandalidae	1								
Crangonidae	1	1							
Palinuridae	1							1	
Scyllaridae	4							1	
Galatheidae	2								1
Porcellanidae	8			2	1			3	
Callinassidae	3	1							
Paguridae	21	1	1	1		1	5		1
Albuneidae	3								1
Hippidae	2			1					
Raninidae	1								
Dromiidae	3							1	1
Homolidae	1								
Leucosiidae	6				1		1		
Calappidae	9			1	1		1	3	
Portunidae	13	2		3		2		3	
Cancriidae	2	2							
Xanthidae	24	3		2	1		3	6	
Goneplacidae	3							1	
Pinnotheridae	10	1	2	3	1				
Palicidae	2							1	1
Grapsidae	6	1		1	1				
Ocypodidae	4	1		3					
Majidae	30		3		1		5	2	
Parthenopidae	6			1		1	2		
Total	220	15	6	22	11	9	21	32	8
		North Cape Cod-South	Cape Cod-South		Middle Atlantic-South		Hatteras-South		
Combined total		15	28		20		61		
Percent total	99.9	6.8	12.7		9.1		27.7		

fathoms (U.S. National Museum). Cuba, Gulf of Mexico; 30-35 fathoms.

Parapinnixa beaufortensis Rathbun. The only specimen of this species known is the holotype from fishing grounds, 20 miles off Beaufort Inlet, N.C. Rathbun (1918b) doubtfully referred this form to the genus *Parapinnixa* and believed that it was a postlarval stage of an unknown species because of small size, relatively large eyes, hairiness of legs and carapace, and thin gripping edges of the fingers suggesting that in another molt or two gaping fingers might emerge. I believe that it may be a young *Palicus*.

Notolopas lamellatus Stimpson. Rathbun (1930a) gave one occurrence of an ovigerous female off Beaufort, N.C. Sonora, Mexico, to Ecuador (Garth, 1958).

A large amount of unidentified material is in existing collections and some of this contains undescribed species. It is expected that the increase in oceanographic research in Southeastern United States will soon add to knowledge of decapod crustaceans in the area.

GLOSSARY

Many of the structures listed alphabetically and defined are shown schematically on figures

occurring in the Carolinas, arranged by family

barriers. Numbers marked with an asterisk duplicate numbers in adjacent columns]

Eastern and western Atlantic	Pacific	Cosmopolitan	Endemic	Disjunct at Florida Peninsula	Lookout to east Gulf of Mexico and West Indies	Lookout to east Gulf of Mexico, West Indies, and South America	Lookout through Gulf of Mexico, West Indies, and South America	Charleston to West Indies, Texas or South America
1 + *1	*1	1		*1	1	1	1	
1	*1	2	1	0	2	1	1	
	*2			0	1	1	2	
2			1 (restr.)	*1			1	1
	*1			0	1			
				0				
	*1			0	1	2		
				0			1	
				0	1			1
				*2		1	1	
				*4	2	5	2	2
1				*1			1	
				*2				1
				0	1			
1				0		1		
				0	3	1		
				0	2			1
1				0	1			1
				0				
				0	2	1	6	
			1	0			2	
				*5	1		1	
2	*1	1		*1				
				*2				
1				0	4	6	5	3
				0		2		
10 + *1	*7	4	3	*23	23	22	24	10
East and west Atlantic		Cosmopolitan	Endemic		Lookout-South			Charleston-South
10 + *1		4	3		69			10
4. 5		1. 8	1. 4	*10. 5	31. 4			4. 5

2, 3, and 4. Other terms not listed are shown on these figures.

Acicle.—Antennal scale which is reduced to a spine.

Afferent channels.—Openings through which water passes to the gills. In brachyuran crabs, usually opening behind the 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 and lateral spine, exclusive of outer orbital teeth.

Apodeme.—Any cuticular ingrowth of body wall.

Appendix interna.—Small separate branch on medial side of pleopodal endopodite tipped with hooks which interlock with opposite member in swimming.

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

Arthrobranchiae.—Gills attached to articular

membrane between the coxa of an appendage and the body wall.

Basis (basipodite).—Second article (from the body) of a leg or maxilliped. Sixth segment from distal end of the 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 the thoracic somites, but overhanging on each side as a covering for chamber in which the gills are concealed.

Buccal cavity.—Cavity on ventral surface of body in which the mouthparts are situated; it is bounded anteriorly by the epistome, laterally by the free edges of the carapace.

Carina.—A keellike ridge or prominence.

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

Cervical groove.—Complex groove or series of grooves running across carapace. It is transverse at the middle, then turns obliquely forward (and outward in brachyurans) to the anterolateral margin.

Chela.—Arrangement of the distal two articles of a crustacean limb by which the terminal element is opposed to the element which precedes it, so that the appendage is adapted for grasping.

In a true chela, the elements are shaped as fingers which close against each other.

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

Chelipeds.—Pair or pairs of thoracic legs immediately behind the maxillipeds. They bear chelae, or pincer-claws, and are often stouter, sometimes much stouter, than the succeeding walking legs.

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

Dactyl (dactylus or dactylopodite).—Terminal or distal article of a leg or maxilliped. The dactyl is the movable finger of a cheliped.

Efferent channels.—Channels through which water passes from the gills. These open at the sides of the endostome, except in the superfamily

Oxystomata in which they open at the middle of the endostome.

Endognath.—Inner or principal branch of a maxilliped.

Endopodite.—Medial ramus of a biramous appendage.

Endostome.—Part of the epistome which forms the palate in brachyurans and is usually separated from the epistome proper by a transverse ridge.

Epibranchial (epibranchial region).—Portion of the porcellanid (crab) carapace which is situated behind the orbit and above the metabranchial region. The region situated between the cervical groove and the *linea anomurica*. There is often a strong spine on the region, referred to as the epibranchial spine.

Epigastric lobes.—Anterior lobes or subregions of the gastric region.

Epimere.—A lateral part of the wall of body somites situated between the tergum and the insertion of appendages.

Epipodite.—Outgrowth of the first seven thoracic coxae.

Epistome.—The antennal sternum is mainly represented by the epistome, a plate of varying shape, lying between the labrum and the bases of the antennae. In Natantia the epistome is comparatively narrow, and on each side is separated from the lateral portions of the carapace by the exhalant branchial channels. In most of the Reptantia, the epistome is broad and comes in contact with the carapace on each side; in the Brachyura, it becomes firmly united with the carapace. In this way, there is defined, more or less distinctly, a buccal frame within which lie the mouth parts, and which in most Brachyura is closed by the operculiform third maxillipeds. The sides of this buccal frame are formed by the free anterolateral margins of the carapace.

Exognath.—Outer or secondary branch of a maxilliped.

Exopodite.—Lateral ramus of a biramous appendage.

Fingers (digits).—Narrow scissorlike blades of the claw end of a cheliped, with the movable finger being the dactyl, and the immovable finger the terminal part of the propodus.

Front.—Frontal portion of carapace; that portion of the carapace of a crab which lies between the orbits.

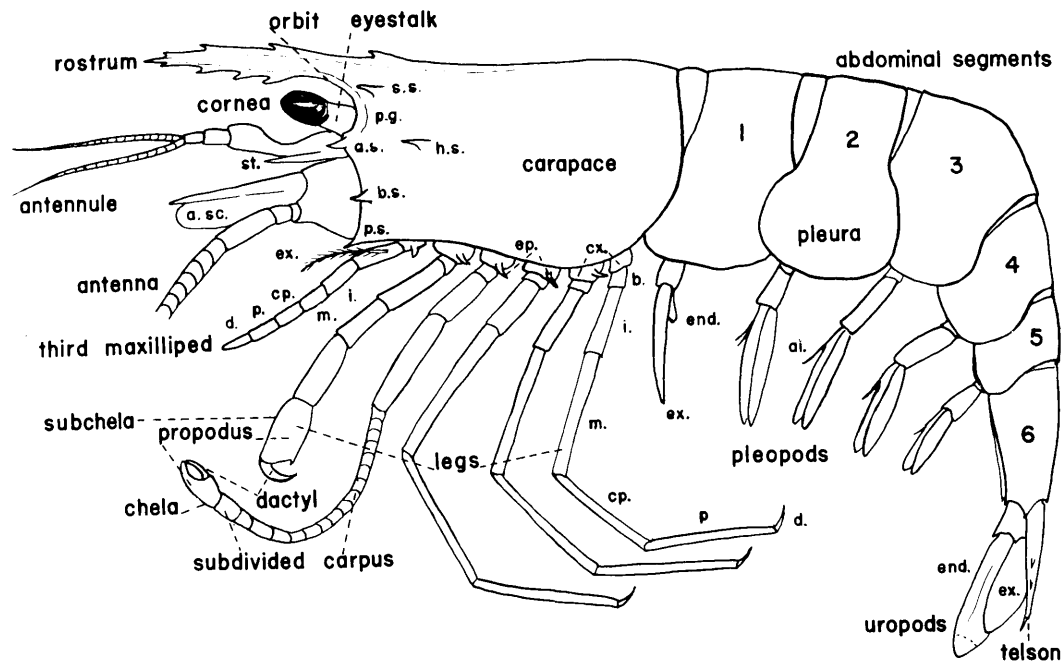


FIGURE 2.—Schematic drawing of shrimp in lateral view; ai., appendix interna; a.s., antennal spine; a. sc., antennal scale; b., basis; b.s., branchiostegal spine; cp., carpus; cx., coxa; d., dactyl; end., endopod; ep., epipod; ex., exopod; h.s., hepatic spine; i., ischium; m., merus; p., propodus; p.g., postorbital groove; p.s., pterygostomial spine; s.s., supraorbital spine; st., stylocerite. (Modified after Holthuis, 1955; Schmitt, 1921.)

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

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

Genital region.—See urogastric lobe.

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

Hepatic region.—A 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 Natania (fig. 2).

Ischium (ischiopodite).—Fifth article of a leg or maxilliped from the distal end. It is usually the first large article of the maxilliped.

Merus (meropodite).—Fourth article from the distal end of a leg or maxilliped. It is sometimes called the arm of a cheliped.

Mesogastric lobe.—Lobe or subregion which is the median division of the gastric region, pentagonal in form, and with a long, narrow, anterior prolongation.

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

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

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

Orbit.—Cavity in the carapace containing the eye.

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

Palate.—Roof of buccal cavity in crabs.

Palm.—Proximal portion of propodus of chela.

Petasma.—Endopodite of the first pleopods in male Penaeidae. It takes the form of a complicated membranous plate bearing coupling hooks medially which interlock with the member of the

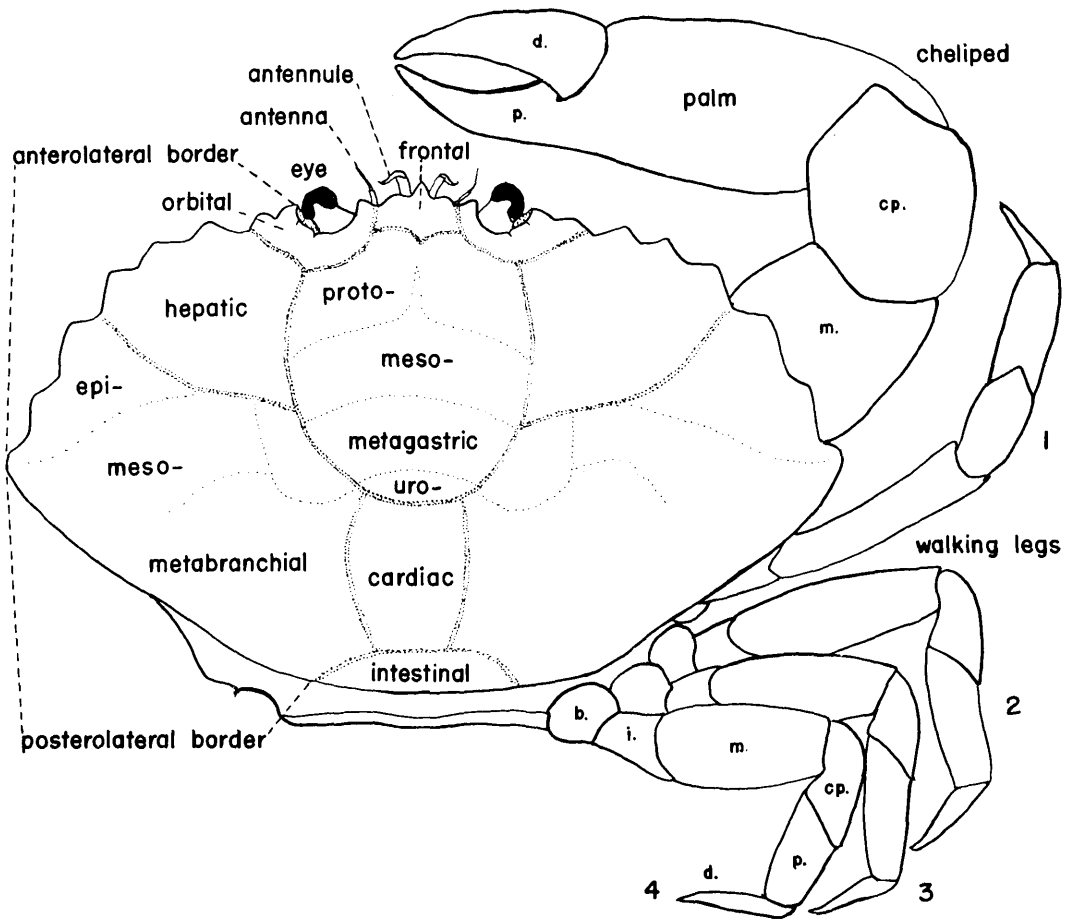


FIGURE 3.—Schematic drawing of brachyuran crab in dorsal view; areas of carapace indicated; legs of right side only shown; b., basis; cp., carpus; d., dactyl; i., ischium; m., merus; p., propodus.

opposite side. The petasma may terminate distally in various combinations of complex-shaped lobes. According to position, these have been termed: distolateral, distoventral, and distomedian. Additional complex processes may also be present.

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

Podobranchia.—Gills attached to the coxa of an appendage.

Postorbital groove.—Groove on carapace behind orbit and more or less parallel to margin of orbit (fig. 2).

Propodus (protopodite).—Second article from the distal end of a leg or maxilliped. In a cheliped, the propodus consists of a palmar portion and a narrower, immovable finger.

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

Protogastric lobe.—Lobes or subregions which are the anterolateral lobes of the gastric region.

Protopodite.—Peduncle of an appendage; in unmodified form, it consists of one coxal and one 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 Natantia.

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

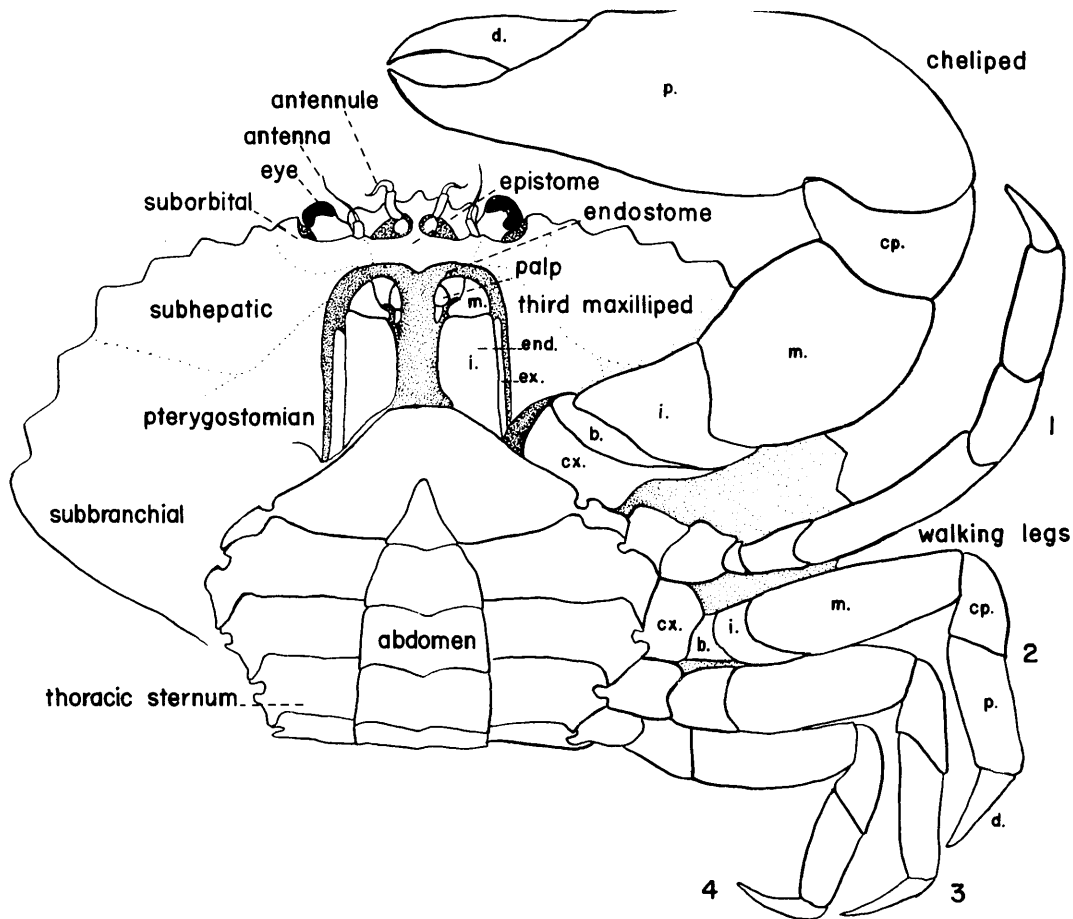


FIGURE 4.—Schematic drawing of brachyuran crab in ventral view; areas of carapace indicated; legs of left side only shown; b., basis; cp., carpus; cx., coxa; d., dactyl; end., endognath; ex., exognath; i., ischium; m., merus; p., propodus.

Scaphocerite.—Antennal scale (fig. 2).

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

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

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

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

Telson.—Terminal somite of the abdomen except in the Brachyura.

Tergite.—Dorsal plate of a segment.

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

to last thoracic somites.

Urogastric lobe.—Posteromedian lobe or sub-region of the gastric region; sometimes called the genital region.

ORDER DECAPODA

Caridoid facies either retained or greatly modified. Exopodite of maxilla (scaphognathite or bailer) large. First three 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 pleuro-branchia); rarely absent. Young rarely hatched in nauplius stage (Calman, 1909).

Systematic and Ecological Discussion

Suborder Natantia

Body almost always laterally compressed. Rostrum usually compressed and serrated. First abdominal segment not much smaller than rest. Antennules generally with stylocerite; antennal scale generally large and lamellar. Legs usually slender, except sometimes a stout chelate limb or pair, which may be any one of first three pairs; with basipodite and ischiopodite very rarely coalesced and with only one fixed point in carpopodal articulation (with some doubtful exceptions); sometimes with exopodites; podobranchiae hardly ever present on first three and never on last two pairs; male genital apertures in articular membrane. Pleopods always present in full number, well developed, used for swimming (Calman, 1909).

Section Penaeidea

Pleura of second abdominal segment not overlapping those of first segment. Antennules generally with stylocerite. Mandibular palps straight. First maxillipeds without expansion at base of exopodite, endopodite long; second maxillipeds with terminal articles normal; third maxillipeds with seven articles. Third legs chelate (except when much reduced), not stouter than first pair. First pleopods of male bearing sexual apparatus (Calman, 1909).

Family Penaeidae

Body somewhat or considerably compressed. Rostrum usually well developed, laterally compressed, often with teeth. Eyes moderate or greatly elongate. Antennules with two flagella; basal article of peduncle hollowed out dorsally for eye, with stylocerite on basal outer margin. Mandible with incisor process and palp of one or two articles. First three pairs of legs similar, chelate, slender, increasing in length posteriorly; fourth and fifth legs well developed, simple (Schmitt, 1921).

Remarks.—For most species treated in this handbook information on natural history is included in the separate species accounts. In the

case of parasites found in certain penaeids, such citation has proved too cumbersome. Parasites in this group have been studied only recently. Host specificity and life cycles of the parasites are imperfectly known and identification of some forms is uncertain. The interested student is referred to a review of most of the known parasites given by Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959), and Iversen and Manning (1959).

Spelling of the name *Penaeus* and related generic names has unfortunately not been uniform. Gunter (1957) reviewed these circumstances and re-emphasized that under the International Code, original spelling must be observed. He included a list of the genera of Penaeidae.

KEY TO SUBFAMILIES IN THE CAROLINAS

- a. Postorbital spine present.....Solenocerinae (p. 14).
- aa. Postorbital spine absent.
 - b. Carapace without a median dentate crest, except occasionally over eyes.....Penaeinae (p. 17).
 - bb. Carapace with a median dentate crest extending nearly or entirely to posterior margin
Sicyoninae (p. 32).

Subfamily Solenocerinae

Carapace with postorbital spine, cervical groove extending nearly or quite to dorsum. Ocular peduncle with a distinct tubercle, a scale at external angle of ocular somite. Antennular peduncle with an enlarged ciliated protuberance on inner proximal margin of basal article. First chelipeds with tuft of setae on propodus in both sexes. Coxae from second maxillipeds to fifth legs with weakly forked epipodites. A functional filamentose anterior arthrobranch on 13th somite (4th leg); pleurobranches behind 9th somite (3d maxilliped). Exopodites on maxillipeds and legs. Pleopods, except first pair, biramous. Telson with well-developed terminal point and a pair of sub-terminal fixed spines (Burkenroad, 1934b).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

- a. Antennular flagella hollowed out medially, channellike in structure.....*Solenocera atlantidis* (p. 15).
- aa. Antennular flagella not hollowed out medially nor channellike in structure
Hymenopenaeus tropicalis (p. 15).

Genus *Solenocera* Lucas, 1849

Burkenroad, 1934b, p. 64.—1936, p. 120.—1939, p. 6.

Solenocera atlantidis Burkenroad

Figure 5

Solenocera atlantidis Burkenroad, 1939, p. 10.

Recognition characters.—Body compressed, carapace deeper than broad; integument thin, smooth; sides of rostrum and area near base of rostrum covered with short hairs; carapace with small pterygostomial spine meeting frontal margin at right angle, spine sometimes doubled; postorbital and hepatic spines well developed; antennal angle acute, more or less toothlike, often not greatly produced; orbital angle with a distinct spine on margin; cervical groove reaching middorsal line; branchiocardiac groove prominent. Rostrum not reaching distal edge of eye; lower margin unarmed, convex; with five to seven, usually six, dorsal teeth not counting dagger-shaped tip, two behind, one above orbital margin, posterior tooth slightly remote from others. Postrostral carina not continued beyond crossing of cervical groove. Antennular flagella slender, about half as long as body; lower flagellum broader than upper at hollowed basal portion. Antennal scale extending no more than one-tenth its length beyond antennular peduncle.

Coxa of fifth legs with strong tooth on anteromedial margin in both sexes.

Abdomen with last three segments carinate; third to fifth segments cleft posterodorsally at midline; sixth segment with a spine at middorsal posterior and posterolateral corners and a toothlike projection at middle of distolateral edge. Telson short, broad, lateral spines large. Exopods of uropods with no spine at distolateral corner.

Measurements.—Length of body: large male, 37 mm.; large female, 56 mm.

Variations.—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.—Mud, shell, and coral bottoms; 10 to 180 fathoms.

Type locality.—Gulf of Mexico off Alabama (*Atlantis* station 2813, roughly lat. 30° N. long. 88° W.), 19 fathoms.

Known range.—Cape Hatteras, N.C., to near Campeche, Mexico; Surinam (Hildebrand, 1955; Holthuis, 1959).

Remarks.—Females with well-ripened ovaries have been taken in March off Alabama (Burkenroad, 1939).

Genus *Hymenopenaeus* Smith, 1882

Burkenroad, 1936, p. 102.

Hymenopenaeus tropicalis (Bouvier)

Figures 6-7

Parartemesia tropicalis Bouvier, 1905, p. 749.

Haliporus tropicalis: Bouvier, 1906, p. 4.—Milne Edwards and Bouvier, 1909, p. 247, pl. 3, figs. 1-9, text-figs. 45-54.

Hymenopenaeus tropicalis: Burkenroad, 1936, p. 102.

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

Recognition characters.—Body robust, laterally compressed; integument thin, polished, except finely setose at sides of rostrum and area near base of rostrum; carapace deeper than broad with antennal, hepatic, and postorbital spines well developed, a small stout spine on orbital margin; cervical groove extending nearly to middorsal line; branchiocardiac groove extending from near anterolateral corner to level of base of first legs. 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 about to distal edge of eye, straight or slightly upturned at tip, lower edge convex, unarmed, ciliated. Prosartema prominent, hairy, extending to or beyond middle of second segment of antennular peduncle. Antennular flagella somewhat flattened, upper ramus about one-third diameter of lower at base. Antennal flagella about three times body length.

Female with projections on coxae of last three pairs of legs, first pair posteromedial and blunt pointed; second pair medial, bladelike, with thin, styliiform posterior projection; third pair medial, broad, bladelike, partially covering thelycum. Thelycum setose, posterior lateral lobes united; 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

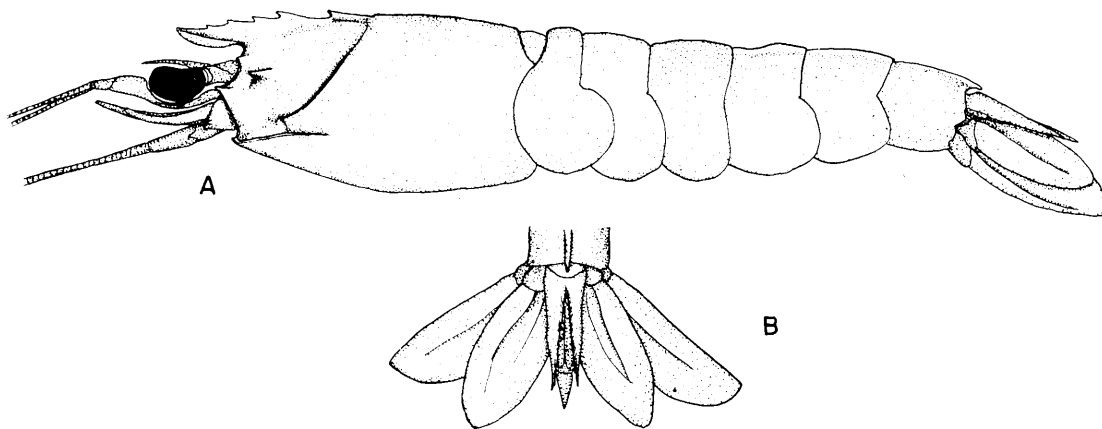


FIGURE 5.—*Solenocera atlantidis* Burkenroad. A, animal in lateral view; B, uropods and telson in dorsal view; A-B $\times 2.5$.

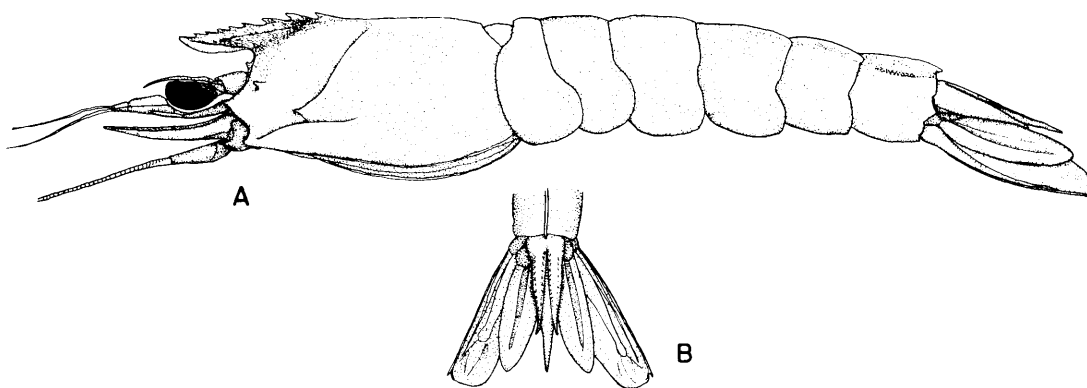


FIGURE 6.—*Hymenopenaeus tropicalis* (Bouvier). A, animal in lateral view; B, uropods and telson in dorsal view; A-B $\times 1.25$.

posteriorly; segments three to five variably cleft posterodorsally; sixth segment with a small mid-dorsal posterior spine, a spine at posterolateral corners, and a toothlike projection at middle of distolateral edge. Telson tapering to a strong point flanked on each side by a strong, fixed, subterminal spine; middorsal groove bifurcated at midlength, forks ending medial to base of fixed spines. Exopods of uropods with small spine at distolateral corner. Male with large, membranous, complexly folded petasma; tips of petasma reaching base of second legs.

Measurements.—Length of body: large male, 56 mm.; large female, 92 mm.

Color.—Red.

Habitat.—Seventeen to 200 fathoms, rarely deeper; usually inside 100-fathom curve.

Type locality.—Florida Bank (Gulf of Mexico), lat. $26^{\circ}31'$ N. long. $85^{\circ}03'$ W.

Known range.—Cape Hatteras, N.C., to Gulf of Mexico, off Alabama.

Remarks.—Burkenroad considered it likely (in Anderson and Lindner, 1945) that *Solenocera*

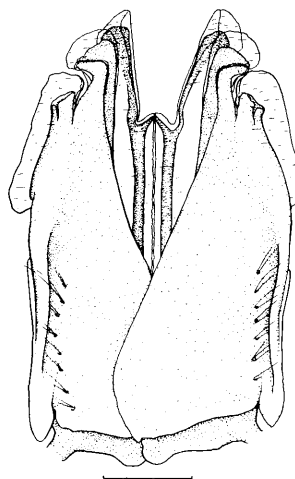


FIGURE 7.—*Hymenopenaeus tropicalis* (Bouvier). Petasma of male in ventral view, 1 mm. indicated.

weymouthi Linder and Anderson was identical with *Hymenopenaeus tropicalis* (Bouvier). Comparison of a number of specimens of both forms leads me to regard them as identical. Prominence of the coxal projections on the last three pairs of legs in females varies with age. Those illustrated by Lindner and Anderson appear not so well developed as in fully matured *H. tropicalis* females.

Subfamily Penaeinae

Carapace without postorbital spine; cervical groove not extending to dorsum. Ocular somite without a greatly produced pair of median pro-

jections, but with a more or less conspicuous pair of projections from lateral portions; ocular peduncles with some inconspicuous vestiges of a median tubercle. Proximomedian margin of antennular peduncle produced as an elongate scale. First chelipeds with tuft of setae on propodus in both sexes. No podobranchs behind eighth somite (second maxillipeds). No epipodites behind 12th somite (3d legs); epipodites usually forked. No filamentous anterior arthrobranch on 13th somite (4th leg). Pleopods, except first pair, biramous. Telson with well-developed terminal spine (Burkenroad, 1934b).

KEY TO GENERA AND SPECIES (PARTIAL) IN THE CAROLINAS

- a. Rostrum with ventral teeth.....*Penaeus* (p. 17).
- aa. Rostrum without ventral teeth.
 - b. Telson with subterminal pair of fixed spines.
 - c. Carapace with longitudinal and transverse sutures present; body nearly smooth
Parapenaeus longirostris (p. 27).
 - cc. Carapace without longitudinal and transverse sutures; body pubescent.....*Penacopsis goodei* (p. 29).
 - bb. Telson with no subterminal pair of fixed spines.
 - c. Rostrum slender, sinuous, as long as or longer than carapace, with basal thin, high crest armed with five teeth plus an isolated epigastric tooth.....*Xiphopenaeus kroyeri* (p. 30).
 - cc. Rostrum not slender and sinuous, about half length of carapace, dorsal teeth evenly spaced
Trachypenaeus constrictus (p. 31).

KEYS TO SPECIES IN THE CAROLINAS

Genus *Penaeus* Fabricius, 1798

Burkenrod, 1934b.—Hemming, 1958b.

Adults

(Based on keys by Anderson and Lindner, 1945, and Voss, 1955)

- a. Lateral rostral grooves not extending beyond base of rostrum.....*setiferus* (p. 18).
- aa. Lateral rostral grooves reaching almost to posterior margin of carapace.
 - b. Petasma of male with external edge of distoventral lobe armed with 2 to 12, usually 4 to 7, spinules; teeth of internal edge of lobe long and sharp in close-set group of 6 to 16. Thelycum of female with anteromedian corners of lateral plates moderately gaping, not covering carina of posteromedian part of median plate on 13th body somite (4th legs).....*duorarum* (p. 21).
 - bb. Petasma of male with external edge of distoventral lobe smooth, incurved, teeth of internal edge of lobe small, in close-set group. Thelycum of female with anteromedian corners of lateral plates widely gaping, exposing forked carina of posteromedian plate on 13th body somite (4th legs).....*aztecus* (p. 24).

JUVENILES BETWEEN 17 AND 47 MM. TOTAL LENGTH, LIVE OR FRESHLY PRESERVED

(Williams, 1953)

- a. Lateral rostral grooves not reaching almost to posterior margin of carapace; rostrum prominent and slightly upturned at tip in individuals above 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.....*setiferus* (p. 18).
- aa. Lateral rostral grooves reaching almost to posterior margin of carapace (shallow in 17 mm. individuals). 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.
 - b. Rostrum usually not upturned at tip. 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)
duorarum (p. 21).
 - bb. Rostrum usually slightly upturned and attenuate at tip. Chromatophores brown and olive-green; uropods with reddish-brown to brown areas distally.....*aztecus* (p. 24).

Penaeus setiferus (Linn.). White shrimp

Figures 8-9

? *Cancer setiferus* Linnaeus [in part]. 1767, p. 1054.
Penaeus setiferus: Hay and Shore, 1918, p. 378, pl. 25, fig. 5.—
Burkenroad, 1939, p. 17 (rev.).—Holthuis, 1962, pp. 115-118.
Penaeus fluviatilis: Gunter, 1962a, b, pp. 107-114; 118-121.

Recognition characters.—Integument thin, polished, translucent. Carapace with a high median carina continuous anteriorly with rostrum and extending back about two-thirds length of carapace; not grooved posteriorly, with lateral grooves terminating near posterior tooth in rostral series; armed with 9 or 10 sharp teeth dorsally, anterior 6 teeth on rostrum proper; postocular crest absent. Rostrum with tip long, slender, unarmed, up-curved distally, apex sometimes depressed, first dorsal tooth near distal edge of eye, ventral edge armed with two teeth. Antennal spine surmounting lateral carina extending upward short distance from hepatic spine. Medial antennular flagellum of adult male dorsoventrally flattened and armed dorsally with two sizes of teeth.

Anterolateral marginal ridges of last thoracic sternite of female extending conspicuously medially near middle of segment making an interrupted crescentic transverse ridge with concavity directed forward; posterior portion of sternite with conspicuous pair of fleshy protuberances. Posterior

margin of 12th sternite with pair of posteromedial convexities extending almost level with median portion of margin.

Abdomen with fourth to sixth segments carinate; carina of sixth segment with a groove on each side. Telson with deep median groove and an acuminate tip. Ventral margin of pleura of first abdominal segment almost straight. Petasma of male with diagonal ridge across face of distolateral lobe.

Measurements.—Length of body: large male, 182 mm.; large female, 197 mm.

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 17 fathoms off Atlantic coast; rarely to 43 fathoms in Gulf of Mexico (Springer and Bullis, 1952).

Type locality.—Off Matanzas Inlet, Fla.

Known range.—Fire Island, N.Y., to Cape Canaveral, Fla.; Gulf of Mexico from Pensacola, Fla., to Campeche, Mexico; Cuba; Jamaica.

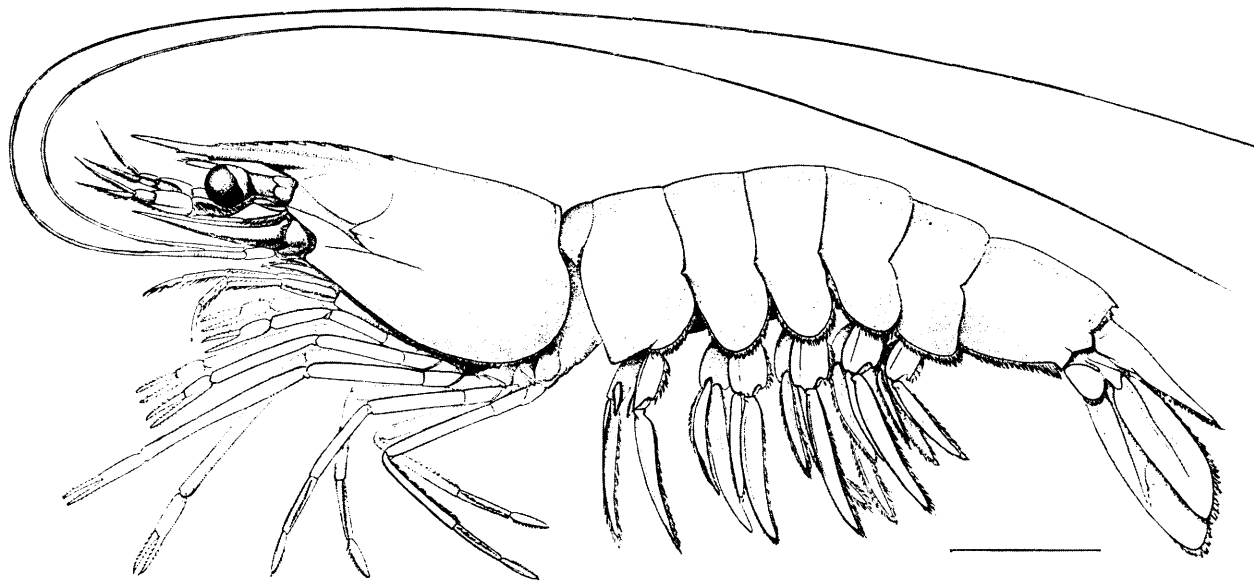


FIGURE 8.—*Penaeus setiferus* (Linnaeus). Animal in lateral view; approximately 25 mm. indicated (after Rathbun, 1884).

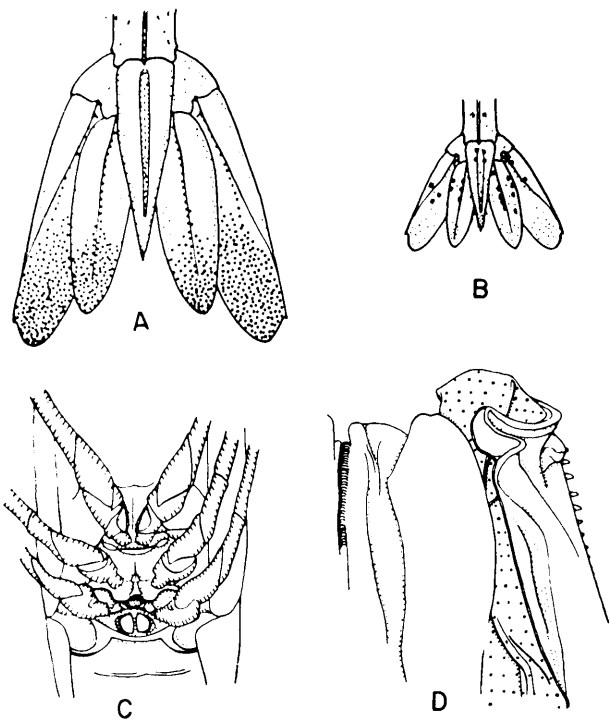


FIGURE 9.—*Penaeus setiferus* (Linnaeus). Chromatophore distribution in tail fan (semidiagrammatic) of A, 17 mm. juvenile, B, 32 mm. juvenile; A–B approximately $\times 5$ (after Williams, 1953). C, thelycum of adult female; D, petasma of adult male, ventral view, distal portion of left half (after Burkenroad, 1934b).

Remarks.—Of the shrimps occurring in the Carolinas, *P. setiferus* has been studied most extensively. This has resulted from the fact that 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 fishing effort to expand greatly, concern over the possibility of depleting the resource led the U.S. Fish and Wildlife Service to initiate a research program on various aspects of the biology of this species. At that time, *P. setiferus* composed over 95 percent of the commercial catch (Lindner and Anderson, 1956). A voluminous literature, scholarly and popular, has accumulated in the ensuing 30 years, and though it would be presumptuous to attempt a complete review of this work here, the chief results of studies can be outlined. (An exhaustive bibliography has been compiled by Chin and Allen, 1959).

Recently (see synonymy) usage of the name *setiferus* for the white shrimp in North America has been questioned. The well-established name *setiferus* would seem best retained here.

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.

One of the latest studies to be published should be cited at the outset. Young (1959) in his exhaustive morphological study of *P. setiferus* reiterated the generalized structure of the Penaeidae. This work is profusely illustrated and the text illuminates details which have often been 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. The genital armature, of great taxonomic value, is treated briefly, and here the student must look to the works of Burkenroad (1934b, 1939) for details.

In 1956, Lindner and Anderson summarized work of the U.S. Bureau of 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.

Spawning of the white shrimp in the Carolinas probably begins in May and extends into September (Lindner and Anderson, 1956; Williams, 1955a); farther south in the Gulf of Mexico the season probably extends from March to September or October. Gunter (1950) suggested two periods of spawning (spring and fall) for Texas waters, but in the Carolinas there is probably only one.

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 period of time (Lindner and Anderson, 1956); the developing stage is judged to last a month or less. The succeeding yellow stage persists for 1 to 2 months, and the ripe, olive-drab colored ovaries 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. A large female is estimated to produce a half million to a million eggs at a single spawning (Anderson, King, and Lindner, 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 aging by this method. It is possible, but not proved, that a shrimp can spawn more than once in a season. Occurrence of ripe females suggests that spawning in Louisiana takes place offshore in depths greater than 4.5 fathoms, probably between 5 and 17 fathoms. Heegaard (1953) reported occurrence of spawning 6 or more miles from shore in from 10- to 15-fathom water in Texas. The exact location of spawning grounds off the Carolinas remains unknown.

Developmental stages of the white shrimp were elaborated 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, three protozoal, two mysis, and a series of postlarval stages were described. Pearson thought it likely that though the larvae are more or less at the mercy of currents in the environment, 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 2 or 3 weeks.

Heegaard (1953), studying wild populations of larval white shrimp, and Johnson and Fielding (1956), studying populations 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 history 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 post-larva (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).

Once in estuaries on so-called "nursery grounds" the young grow rapidly. Williams (1955a) estimated an average increase in length of 36 mm. per month (1.2 mm. per day), and other estimates of similar nature have been made (Gunter, 1956; Loesch, 1957). 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 they 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 portion of the range may live to be about 2 years old. Mature females attain a larger size than mature males. 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 subadults back to sea, tagging experiments have indicated that *P. setiferus* may make coastwise migrations of considerable length. In their ana-

lysis 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 miles from the point of release. The greatest counter movement was from Cape Canaveral, Fla., in January, to South Carolina 168 days later, a distance of 260 miles.

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, 1955a). 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 2 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).

In recent years the 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).

Penaeus duorarum Burkenroad. Pink, spotted, brown spotted, or grooved shrimp

Figures 10-11

Penaeus brasiliensis: Hay and Shore [in part], 1918, p. 377, pl. 25, fig. 6.

Penaeus duorarum Burkenroad, 1939, p. 31, figs. 18, 19, 23, 25-27 (rev.).

Recognition characters.—Integument thin, polished, translucent. Carapace with a median carina continuous anteriorly with rostrum and extending nearly to posterior border of carapace, flanked on each side by a broad, rounded groove; posterior half of carina with a median longitudinal groove; anterior half arcuate, highest above orbit and with 9 or 10 sharp teeth; posterior tooth remote from others, anterior 6 or 7 on rostrum proper. Lower margin of rostrum with two to three teeth (occasionally one); 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. A subhorizontal suture below hepatic spine, and a groove extending from near hepatic spine to near base of ocular peduncle. An orbital ridge behind eye.

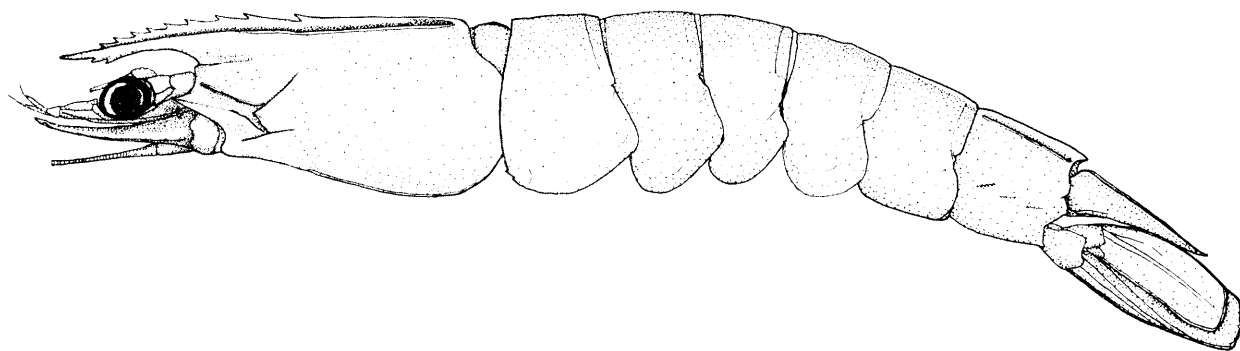


FIGURE 10.—*Penaeus duorarum* Burkenroad. Animal in lateral view with part of appendages removed, "Form A" from North Carolina; natural size.

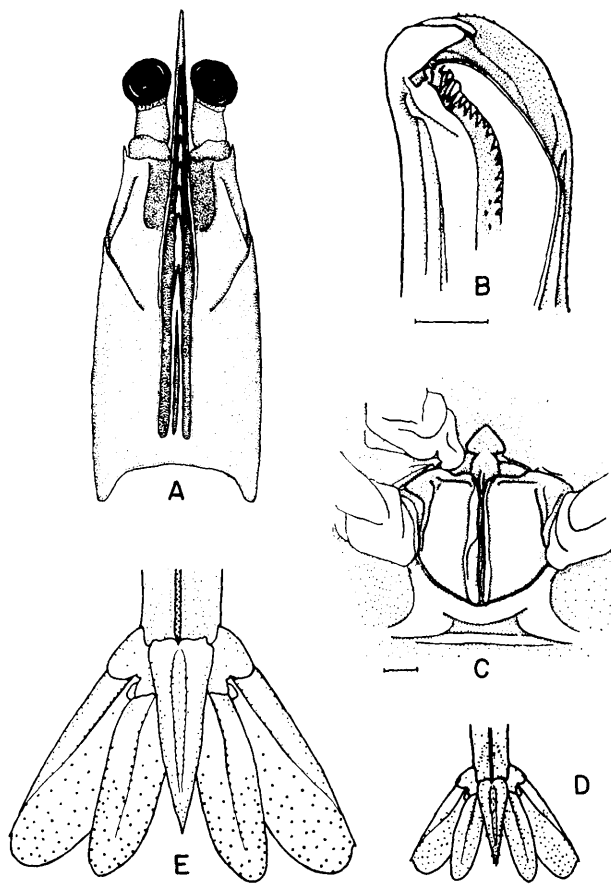


FIGURE 11.—*Penaeus duorarum* Burkenroad. A, carapace and eyes of animal in dorsal view, "Form A" from North Carolina, natural size; B, petasma of adult male, distal portion, view from right side; C, thelycum of adult female; B-C, 1 mm. indicated (after Burkenroad, 1939). Chromatophore distribution in tail fan (semi-diagrammatic) of D, 17 mm. juvenile, E, 32 mm. juvenile; D-E, approximately $\times 5$ (after Williams, 1953).

Female with thelycum composed of two broad lateral plates, and a median plate. Posteromedian part of median plate of adult with a well-developed, short, longitudinal carina extending anteriorly toward roughly semicircular, concave anterior portion. Lateral plates produced medially to meet in midline, except variably divergent at anteromedian corners, thus exposing carina of median plate.

Abdomen with segments four to six carinate, carina of sixth ending posteriorly in a spine and flanked on each side by a narrow groove. Telson with deep median groove and an acuminate tip.

Petasma of male with distal ends of distoventral lobes curved medially, not projecting free of distolateral lobes; external edge of distoventral lobes with a series of 2 to 12, usually 4 to 7, small spinules; median or attached edge of distoventral lobes with a compact group of 6 to 16 large, long, sharp, curved spines; fold of distolateral lobe rather small and armed inconspicuously if at all.

Measurements.—Length of body: large male, 167 mm.; large female, 210 mm.

Variations.—Burkenroad (1939) divided the species into two "Forms," "A" and "B."

In "Form A" the dorsolateral grooves of the sixth abdominal segment usually are almost or entirely closed, though they may be open to a width of one-third the distance from their dorsal lip to the midline.

In "Form B" the dorsolateral grooves of the sixth abdominal segment are broadly open, their width being from one-half to more than equal the distance from their dorsal lip to the midline.

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.—Juveniles and young adults from estuaries or oceanic water near shore 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 usually red (Broad, 1950) or lacking entirely. Detailed coloration of the young has been given by Williams (1953).

Habitat.—Estuaries and inner oceanic littoral, predominantly on sand, shell-sand or coral-mud bottom from water's edge to 28 fathoms; rarely 40 to 200 fathoms (U.S. Fish and Wildlife Service, 1960).

Type locality.—Off Alabama (*Atlantis* station 2813, roughly lat. 30° N. long. 88° W.), 19 fathoms.

Known range.—Chesapeake Bay through Gulf of Mexico and West Indies to Brazil; Bermuda; West Africa, from Mauritania to Angola.

“Form A,” Chesapeake Bay to Campeche, Mexico; Bermuda. “Form B,” Cuba through West Indies to Brazil; West Africa.

Remarks.—*Penaeus duorarum*, one of the western Atlantic littoral penaeids extensively utilized for food, is caught in commercial quantities throughout much of its geographic range (North Carolina to Nicaragua and perhaps Brazil (Lindner, 1957)). Distribution of this species is by no means uniform, consequently the fisheries are concentrated at diverse points, some of these being North Carolina, Key West, Fla., and Campeche Banks, Mexico, with the latter two being by far the largest. 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 Florida, have greatly enhanced our 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, 1955a) 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. There is strong evidence that this population is endemic.

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, Ingle, Woodburn, Hutton, and Jones, 1961). Cummings indicated that multiple spawning probably occurs. Eldred, Ingle, Woodburn, Hutton, and Jones (1961) postulated that mating behavior is possibly

related to migratory behavior and that spawning is initiated at minimal bottom temperatures of 23.9° C. (see also Cummings, 1961). They suggested that annual temperature ranges within certain poorly understood, but not fatal, limits may have a controlling influence on population size in the following year.

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 2 to 3 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.

Postlarvae of *P. duorarum* have been distinguished from those of *P. aztecus* by Williams (1959), and more fully described by Dobkin (1961). The recruitment period in North Carolina, extending from late May to November, agrees well with the occurrence of ripe adults in the fishery prior to and during the early part of this period, and it also suggests that movement and development time of larvae is about the same as that found in *P. setiferus* (i.e., 2 or 3 weeks). Bearden (1961) found a few postlarval *P. duorarum* from May through September in South Carolina.

Once on the nursery grounds in estuaries, the young undergo rapid growth. Williams (1955a) 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, Ingle, Woodburn, Hutton, and Jones (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, Ingle, Woodburn, Hutton, and Jones (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 live a year or longer. Adult females attain a larger size than adult males (various authors).

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 complicated in different parts of the species' range. In North Carolina, and perhaps elsewhere (Iversen and Idyll, 1960; Eldred, Ingle, Woodburn, Hutton, and Jones, 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 (4° C.) 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.

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, 1955b).

Tagging experiments to determine movements of this species have been restricted to waters off southern Florida. 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.

Distribution of *P. duorarum* may be limited by the same factors that influence *P. setiferus*; i.e.,

salinity, temperature, and substrate. Hildebrand (1954, 1955) and Springer and Bullis (1954) emphasized the fact that *P. duorarum* fisheries are located in areas where the bottom is composed of calcareous muds and sands or mixtures of mud and sand. (This species usually burrows in the substrate in the daytime and is most active at night (various authors).) 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.

The fact that *P. duorarum* alone, of the three commercially abundant species of shrimps, 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. Preliminary 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). Eldred, Ingle, Woodburn, Hutton, and Jones (1961) considered that the depth to which the species may burrow in cold weather (6 inches) may protect it from sudden cold snaps.

Penaeus aztecus Ives. Brown or grooved shrimp

Figure 12

Penaeus brasiliensis aztecus Ives [in part], 1891, p. 190.

Penaeus brasiliensis: Hay and Shore [in part], 1918, p. 377.

Penaeus aztecus: Burkenroad, 1939, p. 34, figs. 20, 21, 24, 28–33 (rev.).

Recognition characters.—Integument thin, polished, translucent. Carapace with a median carina continuous anteriorly with rostrum and extending nearly to posterior border of carapace, flanked on each side by a broad, rounded groove; posterior half of carina with a median longitudinal groove; anterior half arcuate, highest above orbit and with 9 or 10 sharp teeth; pos-

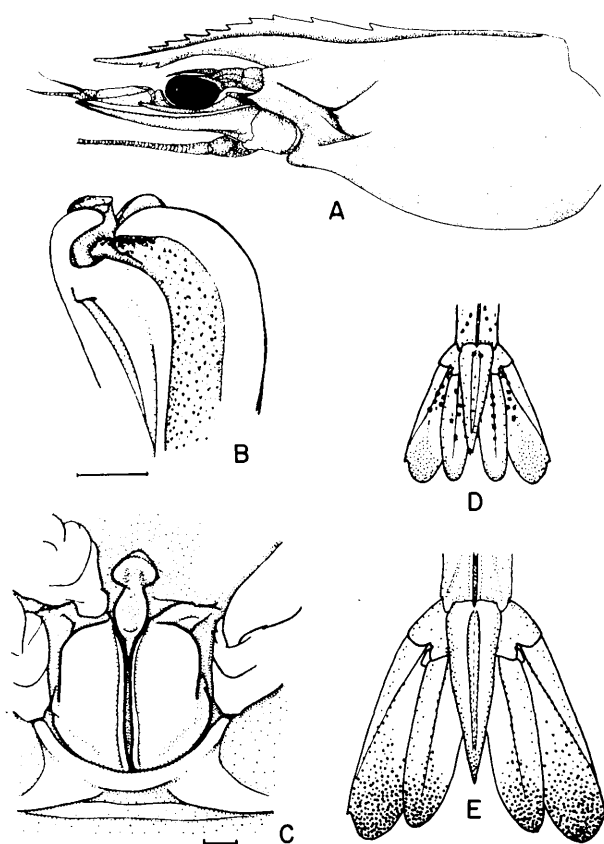


FIGURE 12.—*Penaeus aztecus* Ives. A, anterior portion of animal in lateral view, "Form A" from North Carolina, natural size; B, petasma of adult male, distal portion, view from right side; C, thelycum of adult female; B-C, 1 mm. indicated (after Burkenroad, 1939). Chromatophore distribution in tail fan (semidiagrammatic) of D, 17 mm. juvenile, E, 32 mm. juvenile; D-E, approximately $\times 5$ (after Williams, 1953).

terior tooth remote from others, anterior 6 or 7 on rostrum proper. Lower margin of rostrum with two or three 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. A subhorizontal suture below hepatic spine, and a groove extending from near hepatic spine to near base of ocular peduncle. An orbital ridge behind eye.

Female with thelycum composed of two broad lateral plates and a median plate. Posteromedian part of median plate variably ovate-acuminate in

outline with tip raised into a short posterior carina diverging anteriorly into raised margins. Ventral surface concave; broad anterior end of posterior part merging into concave, triangular or semi-circular anterior portion. Lateral plates produced medially to meet in midline except diverging to expose median plate.

Abdomen with segments four to six carinate, carina of sixth flanked on each side by a narrow groove. Telson with deep median groove and an acuminate tip. Petasma of male with distoventral lobes not projecting free of distolateral lobes; with several compact series of short, crowded spines near distal ends; a fold of free margin of distolateral lobe beyond end of distoventral lobe bearing moderate spinose armature.

Measurements.—Length of body: large male, 162 mm.; large female, 211 mm.

Variations.—Burkenroad (1939) divided this species into "Forms," "A," "B," and "C." The chief differences are summarized here.

In "Form A," the grooves lateral to the dorsal carina are well defined posteriorly and are distinctly broader than the carina. The carina is distinctly and continuously grooved. The dorsolateral grooves of the sixth abdominal segment are broadly open, their width "being from three-fourths to equal the interval between their dorsal lip and the midline."

In "Form B," the grooves lateral to the dorsal carina are usually much narrower than the carina and tend to be ill defined posteriorly. The dorsolateral grooves of the sixth abdominal segment "range up to one-half as broad as the interval between their dorsal lip and the midline, and the dorsal lip is frequently low and ill defined."

In "Form C," the grooves lateral to the dorsal carina are much as in "Form A," but the carinal groove is shallow and frequently interrupted by plane intervals. The dorsolateral grooves of the sixth abdominal segment are extremely narrow, "their width less than a third of the interval between their dorsal lip and the midline, and are sometimes entirely closed."

The rostrum is relatively shorter and deeper in old individuals than in young ones. In unworn adults, it reaches to or beyond the middle of the third antennular article. In young adults, it may reach the end of the antennal scale. The rostrum

in *P. aztecus* is more sinuous and slender than in *P. duorarum*.

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. Individuals from deeper water are light orange (Burkenroad, 1939). The tail fan is darkened distally and in adults is edged with purple to reddish purple. Detailed coloration of the young has been given by Williams (1953).

Habitat.—Estuarine and oceanic littoral, predominantly on mud bottom from water's edge to 45 fathoms; rarely to 89 fathoms.

Type locality.—Veracruz, Mexico.

Known range.—New Jersey (occasionally to Marthas Vineyard, Mass.) through Gulf of Mexico and West Indies to Uruguay.

"Form A," New Jersey to Campeche, Mexico.

"Form B," Florida through West Indies; Panama to Rio de Janeiro, Brazil.

"Form C," Pernambuco, Brazil, to Montevideo, Uruguay.

Remarks.—*Penaeus aztecus*, the third of the littoral penaeids abundant enough to be utilized profitably for food, is also fished commercially throughout much of its range (North Carolina to Brazil), and total landings for this species now outstrip the other two combined. When the U.S. Bureau of Fisheries began research on the natural history of *P. setiferus* in the 1930's, few grooved shrimp were sold, but with the advent of increased market, larger trawlers, and discovery of large concentrations of both *P. duorarum* and *P. aztecus* in different localities than had formerly been fished, the latter species were extensively utilized. Conversely, in recent years it is also possible that there has been a decline in abundance of *P. setiferus* throughout much of its range (various authors). Tremendous quantities of *P. aztecus* are now landed in the western Gulf of Mexico.

Prior to Burkenroad's revision (1939) of the grooved shrimps of the western Atlantic, three currently recognized species were lumped under the name *P. brasiliensis*. Biological data taken prior to that time on these species, never so extensive as those for *P. setiferus*, cannot now be assigned with certainty to any single species.

However, taking into consideration the locations where research was done, as well as modern knowledge of species distributions, it is probable that most of those data on grooved shrimps apply to *P. aztecus* (see also Pearson, 1939).

Maturation of gonads in *P. aztecus* probably parallels the process as understood in *P. setiferus*, although few data are recorded on this subject. Broad (1950) described maturing ovaries found in August as opaque white, yellow, tan, or gray in color. Burkenroad (1939), working in Louisiana, noted that whereas the proportion of males to females in *P. aztecus* near shore was about 1 to 1, this ratio progressively changed in samples farther from shore, in deeper water, to a ratio of 1 to 2 in water 50–70 fathoms deep. Moreover, the females in deep water were much larger than the males, a characteristic shown also by the related *P. setiferus* and *P. duorarum* and young adult populations of all three species inshore. Burkenroad attributed the size disparity of these large offshore individuals to greater length of life among females. Knowledge that impregnated females occurred only beyond 10 fathoms, 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.

Williams (1959) favorably assessed Pearson's (1939) determination of *P. brasiliensis* (unfortunately misspelled "*braziliensis*," in Williams) 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. Postlarvae of the latter 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 collections of juveniles (Williams, 1955a) 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 mid-winter 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.

Gunter (1950) found young brown shrimp in Texas bays most common in spring and fall with low abundance in late summer and winter.

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*.

Young *P. aztecus* enter estuaries as postlarvae, migrate to shallow, often low-salinity water, and undergo a remarkably rapid growth in the warmer months. In North Carolina, the juveniles increase in mean length by an estimated 46 mm. per month (1.5 mm. per day, Williams, 1955a). 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 seasons 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, b). The growing bait fisheries for estuarine shrimp in recent years have given impetus to studies in Alabama and Texas. Additional information on migration (Loesch, 1957) and studies on length-weight relationships (Chin, 1960) have resulted from this work.

Again, distribution of *P. aztecus* is usually thought of as limited by such factors as salinity, temperature, and substrate. Hildebrand (1954, 1955) and Springer and Bullis (1954) stated that the commercial fishery for this species in the Gulf of Mexico was 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 ob-

servations on habitat along the coast of North Carolina and in the Gulf of Mexico.

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

Genus *Parapenaeus* Smith, 1886

Burkenroad, 1934b, p. 107.

Parapenaeus longirostris (Lucas)

Figures 13-15

Penaeus longirostris Lucas, 1849, p. 46, pl. 4, fig. 6.

Parapenaeus politus: Hay and Shore, 1918, p. 379, pl. 25, fig. 7.

Parapenaeus longirostris: Burkenroad, 1934b, p. 108 (rev.).—1939, p. 53.

Recognition characters.—Integument smooth, not setose. Carapace with a low carina extending almost to posterior margin and bearing a 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 seven teeth diminishing in size anteriorly; ventral margin heavily ciliated. Hepatic, antennal, and branchiostegal spines well developed; later spine placed a little behind margin of carapace. A rectangular toothlike eminence at orbital angle. A 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 a spine on ventromedian margin distally.

Thelycum of female composed externally of a triangular plate with obtuse apex on 13th somite (base of 4th leg); 14th sternite raised anteriorly, with low relief posteriorly; lateral ridges with nearly straight but divergent medial borders separated by nearly plane, broad medial groove; lateral border of ridges ornately curved to fit contour of adjacent coxae and 13th sternite.



FIGURE 13.—*Parapenaeus longirostris* (Lucas). Anterior portion of animal in lateral view, $\times 3$.

in *P. aztecus* is more sinuous and slender than in *P. duorarum*.

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. Individuals from deeper water are light orange (Burkenroad, 1939). The tail fan is darkened distally and in adults is edged with purple to reddish purple. Detailed coloration of the young has been given by Williams (1953).

Habitat.—Estuarine and oceanic littoral, predominantly on mud bottom from water's edge to 45 fathoms; rarely to 89 fathoms.

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"Form A," New Jersey to Campeche, Mexico.

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Remarks.—*Penaeus aztecus*, the third of the littoral penaeids abundant enough to be utilized profitably for food, is also fished commercially throughout much of its range (North Carolina to Brazil), and total landings for this species now outstrip the other two combined. When the U.S. Bureau of Fisheries began research on the natural history of *P. setiferus* in the 1930's, few grooved shrimp were sold, but with the advent of increased market, larger trawlers, and discovery of large concentrations of both *P. duorarum* and *P. aztecus* in different localities than had formerly been fished, the latter species were extensively utilized. Conversely, in recent years it is also possible that there has been a decline in abundance of *P. setiferus* throughout much of its range (various authors). Tremendous quantities of *P. aztecus* are now landed in the western Gulf of Mexico.

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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.

Gunter (1950) found young brown shrimp in Texas bays most common in spring and fall with low abundance in late summer and winter.

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*.

Young *P. aztecus* enter estuaries as postlarvae, migrate to shallow, often low-salinity water, and undergo a remarkably rapid growth in the warmer months. In North Carolina, the juveniles increase in mean length by an estimated 46 mm. per month (1.5 mm. per day, Williams, 1955a). 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 seasons 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, b). The growing bait fisheries for estuarine shrimp in recent years have given impetus to studies in Alabama and Texas. Additional information on migration (Loesch, 1957) and studies on length-weight relationships (Chin, 1960) have resulted from this work.

Again, distribution of *P. aztecus* is usually thought of as limited by such factors as salinity, temperature, and substrate. Hildebrand (1954, 1955) and Springer and Bullis (1954) stated that the commercial fishery for this species in the Gulf of Mexico was 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 ob-

servations 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. duorarum*.

Genus *Parapenaeus* Smith, 1886

Burkenroad, 1934b, p. 107.

Parapenaeus longirostris (Lucas)

Figures 13-15

Penaeus longirostris Lucas, 1849, p. 46, pl. 4, fig. 6.

Parapenaeus politus: Hay and Shore, 1918, p. 379, pl. 25, fig. 7.

Parapenaeus longirostris: Burkenroad, 1934b, p. 108 (rev.)—1939, p. 53.

Recognition characters.—Integument smooth, not setose. Carapace with a low carina extending almost to posterior margin and bearing a 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 seven teeth diminishing in size anteriorly; ventral margin heavily ciliated. Hepatic, antennal, and branchiostegal spines well developed; later spine placed a little behind margin of carapace. A rectangular toothlike eminence at orbital angle. A 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 a spine on ventromedian margin distally.

Thelycum of female composed externally of a triangular plate with obtuse apex on 13th somite (base of 4th leg); 14th sternite raised anteriorly, with low relief posteriorly; lateral ridges with nearly straight but divergent medial borders separated by nearly plane, broad medial groove; lateral border of ridges ornately curved to fit contour of adjacent coxae and 13th sternite.



FIGURE 13.—*Parapenaeus longirostris* (Lucas). Anterior portion of animal in lateral view, $\times 3$.

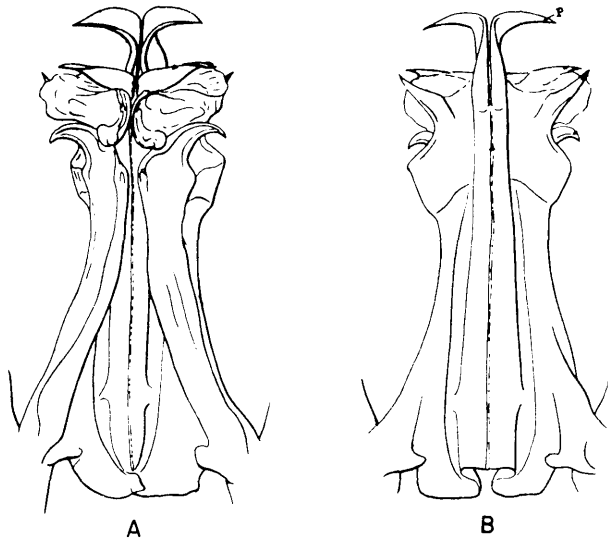


FIGURE 14.—*Parapenaeus longirostris* (Lucas). Petasma of male. A, ventral view; B, sternal view (after Heldt, 1938).

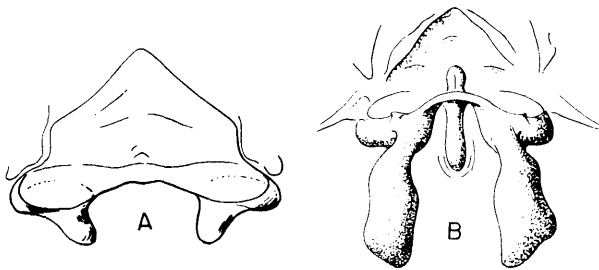


FIGURE 15.—*Parapenaeus longirostris* (Lucas). Thelyceum of female; A, external plate of somite 13; B, internal structure showing sacs extending into somite 14 (after Heldt, 1938).

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

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

Measurements.—Western Atlantic population: length of body, 104 mm. Mediterranean population: length of body, 165 mm.

Variations.—European examples of the species attain a greater size than do American forms. The length of the rostrum varies 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 exopod and distal half of endopod deep red (Burkenroad, 1934b).

Habitat.—Soft mud or muddy sand bottom (Heldt, 1954); 15 to 180 fathoms or more in western Atlantic (Burkenroad, 1934b, 1939); 20 to 250 fathoms in Mediterranean (Heldt, 1954, 1955).

Type locality.—Algiers and Cap-Matifou, Algeria.

Known range.—Marthas Vineyard, Mass., to Gulf of Mexico off Florida, Louisiana, and Yucatan; Gulf of Paria off Venezuela; coast of Portugal to Morocco; Mediterranean Sea from Spain to Asia Minor.

Remarks.—Though this species occurs on both sides of the Atlantic, it has been studied in detail chiefly in the European portion of its range. The European population is composed of larger individuals than the American population (Burkenroad, 1934b) and because of its size and abundance is commercially exploited off the coast of Tunisia (Heldt, 1954). The American population is also quite abundant in the northern Gulf of Mexico (Burkenroad, 1939).

It is possible that this species lives beyond the 100-fathom depth off the Carolinas, but because it is known to move into shallower water in parts of its range it is included here. Heldt (1938) stated that the depth distribution starts at about 30 fathoms, but usually extends from 55 to 200 and more fathoms. She described characteristic features of what she termed the "fonds à *Parapenaeus*" in the Mediterranean Sea (1954).

The developmental stages of this species have been treated in detail by Heldt (1938) from the Mediterranean and in somewhat lesser detail by Pearson (1939) from the northern Gulf of Mexico.

Heldt described cleavage stages of the egg, formation of the embryo, 8 naupliar, 3 protozoal, 14 mysis stages, and the first postlarval stage. Pearson found protozoal, mysis, and postlarval stages principally during July off South West Pass, La.; and usually a complete set of larval stages was 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.

Genus *Penaeopsis* Bate, 1881

Bate, 1881, p. 182.

Penaeopsis goodei (Smith)

Figures 16-17

Parapenaeus goodei Smith, 1885, p. 176.

Penaeopsis goodei: Verrill, 1922, p. 44, pl. 15, figs. 1A-1Aiv; pl. 16, fig. 3.—Burkenroad, 1934a, p. 15, figs. 2, 3 (rev.).

Recognition characters.—Carapace and abdomen covered with rather stiff, plumose hairs. Carapace 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 8 to 10 teeth in front of orbital margin; a sharp gastric tooth behind rostral carina. Antennal, hepatic, and branchiostegal spines well developed; a rectangular toothlike eminence at orbital angle; grooves inconspicuous. Eyes large, reniform, flattened above. Antennular flagella subequal in length and about as long as second article of peduncle. Antennal scale reaching to 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. A small distal spine on ventral side of ischium of first leg. A pair of long, slender spines arising from sternum between second legs.

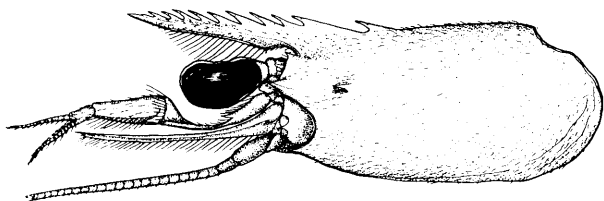


FIGURE 16.—*Penaeopsis goodei* (Smith). Anterior portion of animal in lateral view.



FIGURE 17.—*Penaeopsis goodei* (Smith). A, petasma of male in ventral view, approximately $\times 9.5$; B, petasma in ventral view, distal portion with right external piece removed, approximately $\times 14$ (after Burkenroad, 1934a).

The lycum of female composed of an anterior flattened oval portion with a slender anterior median spine on 13th somite (between 4th leg), and a short broad, posterior portion on 14th somite connected to preceding structure by a less elevated median prominence flanked by an irregular bulbous enlargement on each side. Petasma of male exceedingly complicated and asymmetrical; left side irregularly folded longitudinally, projecting proximally in a curved process beyond right half and to right of median line, and extending distally in an irregular process; right side enlarged distally and divided into several irregularly curved processes projecting beyond left appendage, and partially covered posteriorly by a thin spoon-shaped lamella arising at their bases.

Abdomen with third to sixth segments carinate dorsally; carina of fourth and fifth narrowly cleft at posterior margin. Telson considerably longer than sixth segment; rounded and obscurely grooved above; regularly tapered; armed with a long spiniform process at each side of acute tip, and three pairs of movably articulated spines in front of lateral spines, posterior ones largest.

Measurements.—Length of carapace including rostrum: male, 19 mm.; female, 21 mm.

Habitat.—Surface to 180 fathoms.

Type locality.—Bermuda.

Known range.—Between Capes Hatteras and Lookout, N.C., through Caribbean Sea and West Indies to Surinam; Bermuda.

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 2d and 26th days of the lunar month.

Genus *Xiphopeneus* Smith, 1869

Burkenroad, 1934b, p. 102.

Xiphopeneus kroyeri (Heller)

Figures 18-20

Peneus kroyeri Heller, 1962, p. 425, fig. 51.

Xiphopeneus kroyeri: Burkenroad, 1934b, p. 103, fig. 12 (rev.).—Schmitt, 1935a, p. 132, fig. 5.—Holthuis, 1959, p. 70, fig. 7.

Recognition characters.—Carapace and abdomen smooth. Rostrum laterally compressed, sinuous, armed with usually five dorsal teeth at base, styliform tip greatly elongated beyond antennal scales and varyingly elevated. Carapace with a single epigastric tooth behind rostral series on rounded postrostral carina extending from base of rostrum to near posterior border; no transverse suture in adults; anterior cervical groove reaching anterior margin and continuous 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 50 percent length of antenna. Exopodites of second and third maxillipeds slender.

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

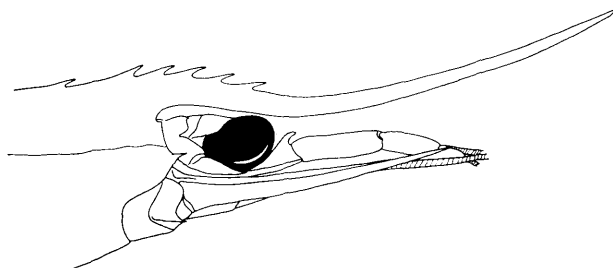


FIGURE 18.—*Xiphopeneus kroyeri* (Heller). Anterior part of animal in lateral view, approximately $\times 3.2$ after Holthuis, 1959).

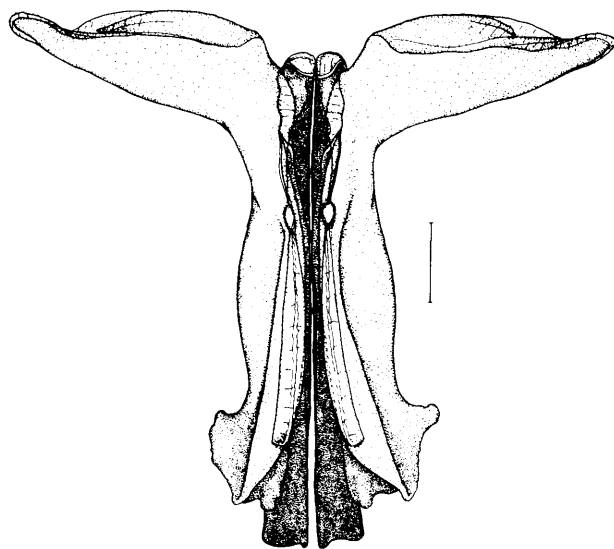


FIGURE 19.—*Xiphopeneus kroyeri* (Heller). Petasma of adult male, ventral view, 1 mm. indicated.



FIGURE 20.—*Xiphopeneus kroyeri* (Heller). Thelycum of female, filled sperm sacs showing through abdominal integument (after Burkenroad, 1934b).

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

Measurements.—Length of body: 127 mm.

Variations.—The rostrum is somewhat longer in 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 portion of estuaries (Gunter, 1950; Holthuis, 1959), from 2.5 to 20 fathoms, rarely to 24 fathoms (Burkenroad, 1939; Gunter, 1950).

Type locality.—Rio de Janeiro, Brazil.

Known range.—Between Capes Hatteras and Lookout, N.C., through Gulf of Mexico and Caribbean Sea to near Santos, São Paulo, Brazil; Pacific coast variety (*X. riveti*, see Burkenroad, 1934b) from Mexico to northern Peru.

Remarks.—This species is of commercial importance in the southern United States (Weymouth, Lindner, and Anderson, 1933; Hildebrand, 1954), and of great importance in South America (Lindner, 1957; Higman, 1959), especially along the northeast coast where it dominates the near-shore fishery and the young dominate the coastal nursery areas, perhaps offering serious competition to other penaeids.

No detailed study of the ecology of this species has been made. Burkenroad (1949) observed ripe or nearly ripe females off North Carolina in May, and Gunter (1950) found them along the Texas coast in June. Vieira (1947), in a study on maturation, found mature females off São Paulo, Brazil, from November to January.

Gunter (1950) studied a population ranging in size from 28 to 127 mm. total length. He found a population mode of 38 mm. total length in October but no definite modes in other months. The species was most abundant in fall. Gunter pointed out that the species does not customarily live in bays, even though it lives in shallow water close to the Texas shore. The young may enter the lower end of Texas bays (21.2–30.7 ‰), but most individuals were found in the Gulf of Mexico in a salinity range 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, the penetration into these areas is greatest in dry seasons. Both Lindner

and Holthuis gave data on the fisheries and processing methods.

Genus *Trachypeneus* Alcock, 1901

Burkenroad, 1934b, p. 94.

Trachypeneus constrictus (Stimpson)

Figure 21

Penaeus constrictus Stimpson, 1871b, p. 135.

Trachypeneus constrictus: Hay and Shore, 1918, p. 378, pl. 25, fig. 9.—Schmitt, 1935a, p. 131.

Recognition characters.—Dorsal region of carapace with fine, short, appressed setae; branchial region of carapace and last two abdominal segments variably pubescent; abdomen smooth proximally. Carapace carinate except for short stretch near posterior border; a spine behind base of rostrum; antennal and hepatic spines well developed; a rectangular toothlike eminence at orbital angle; lateral groove extending about three-fifths 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 bearing usually seven to nine 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.

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

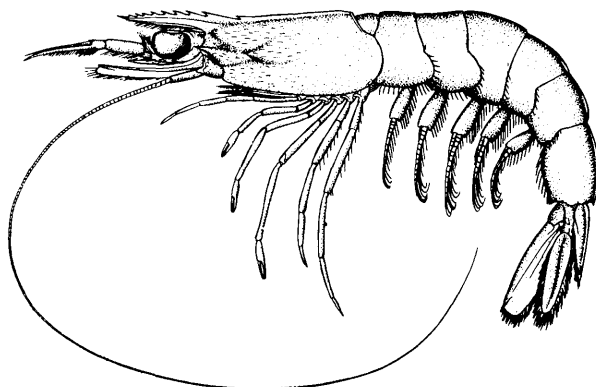


FIGURE 21.—*Trachypeneus constrictus* (Stimpson). Animal in lateral view, approximately $\times 1.5$ (after Verrill, 1922).

Thelycum of female with anterior margin of median plate and lips of transverse groove evenly rounded, notched in middle; lateral flaps 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 surfaces pubescent. Sternal elevation between coxae of fifth leg of male with lateral margins indented setting off posterior portion from broad anterior basal portion; petasma with distolateral corners greatly produced as hornlike projections.

Measurements.—Length of body: 92 mm.

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

Habitat.—Primarily sand or mud and shell bottom in high-salinity water; shallow water to 30 fathoms.

Type locality.—Beaufort, N.C.

Known range.—Tangier Sound, Chesapeake Bay, to Texas; Bermuda; Puerto Rico and Sombrero Island; Surinam.

Remarks.—Eldred (1959) reported *T. constrictus* as common in the Tortugas area of Florida where, along with its near relative, *T. similis*, it makes up about 7 percent of the annual commercial catch. It probably contributes more to catches in deeper water than to catches in the area sampled. Gunter (1950) stated that *T. constrictus* was rarely taken in coastal bays of Texas, being largely confined to water above 30‰. In littoral waters, ripe females were taken in September and small specimens (about 29 mm. total length) in March.

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.

The early developmental stages of *T. constrictus* were treated by Pearson (1939). All larval and postlarval stages were pieced together by successful rearing techniques coupled with plankton catches at St. Augustine Inlet, Fla. Descriptions were given of the egg (from the two-cell stage onward), five naupliar, three protozoal, two mysis, and early postlarval stages. A year-round spawning season is indicated, 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 being taken also in winter. Pearson found developmental stages of this species more abundant than those of related species in shallow oceanic water; in estuarine water the postlarvae were rare. He attributed this rarity and the comparative scarcity of adults in commercial catches to the burrowing habits of postlarvae and adults, as observed in the laboratory. Somewhat contrary to Pearson's findings, the juvenile stages of this species have been caught commonly in surface plankton tows made with a coarse-mesh net on nightly flood tides in Bogue Sound near Beaufort Inlet, N.C. These collections have been made in summer and fall (mid-June to mid-November) when salinities ranged from 28 to 36‰.

Subfamily Sicyoninae

Body more or less sculptured and rigid, with prominent, often more or less interrupted dorsal carina. Carapace with or without spine at antennal angle. Lateral section of ocular somite developed into elongated stylet. Basal antennular article lacking enlarged ciliated protuberance (proartema) on inner proximal margin. No pleurobranches behind ninth somite (third maxilliped). Fourteenth somite (fifth legs) without gills. Pleopods lacking endopods except in modified form on first and second pleopods of male (modified after Burkenroad, 1934b).

Burkenroad (1934b) pointed out that the subfamily Sicyoninae is an extremely uniform group. Unlike other penaeids, sexual maturity may be attained at a quite small size. "Differences between small and large individuals of any species are slight and chiefly affect 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 increases in strength and extent with growth." The thelycum, and corresponding male genital sternites, are less varied than among other penaeid groups, and, consequently, are not so serviceable in distinguishing species. The serious student is referred to Burkenroad (1934b, pp. 70-76) for full discussion of these characters.

Genus *Sicyonia* Milne Edwards, 1830

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

The generic name *Sicyonia* has had a complex nomenclatural history, and was reviewed in detail

by Burkenroad (1945) and Hall (1956). The name *Sicyonia* H. Milne Edwards, 1830, has been validated under Plenary Powers of the International Commission on Zoological Nomenclature (Opinion 382; Hemming, 1958b).

KEY TO SPECIES IN THE CAROLINAS

(Modified after Lunz, 1945)

- a. Antennal angle not armed with a definite spine; ischium of first leg armed with a spine.
 - b. Rostrum (excluding tip) with two dorsal teeth before posterior margin of orbit; carina of carapace with three teeth, first tooth smallest.....*laevigata* (p. 33).
 - bb. Rostrum (excluding tip) with three dorsal teeth; carina of carapace with three evenly spaced, subequal teeth.....*parri* (p. 34).
- aa. Antennal angle armed with definite spine (sometimes blunt); ischium of first leg unarmed.
 - b. Three or four teeth on carina of carapace behind orbital margin, three large; carina high; rostrum extending beyond midpoint of cornea, with two dorsal teeth (excluding tip).....*brevirostris* (p. 35).
 - bb. Two or three teeth on carina of carapace behind orbital margin, two large and behind hepatic spine; rostrum not extending beyond midpoint of cornea, with one or two dorsal teeth (excluding tip).....*typica* (p. 36).
 - bbb. Two teeth on carina of carapace behind orbital margin, one behind hepatic spine; rostrum with three dorsal teeth (excluding tip).
 - c. Fourth abdominal segment with anterior and posterior ends of ventral margin of pleura spined or angular.....*dorsalis* (p. 37).
 - cc. Fourth abdominal segment with posterior end of ventral margin of pleura rounded.....*stimpsoni* (p. 38).

Sicyonia laevigata Stimpson

Figures 22-23

Sicyonia laevigata Stimpson, 1871b, p. 131.—Hay and Shore, 1918, p. 379, pl. 25, fig. 1.

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

Recognition characters.—Integument rather firm, finely granulate and more or less sculptured. Rostrum elevated at angle of about 20 degrees, about half as long as carapace; armed dorsally with two teeth not counting tip; terminal portion divided into four teeth; notch between median pair shallower than dorsal and ventral notches; often two short, stout, asymmetrically placed, mobile spines distally above ventral margin. Postrostral carina with three 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 two teeth closer together; carina sometimes nearly obliterated anterior to each tooth. Antennal angle unarmed but not rounded. Ocular stylets short.

Abdominal segments marked by tergal carinae deeply notched behind on first to fifth segments. First abdominal segment with carina produced into an elevated anterior tooth; marked laterally by two grooves, a long posteromedian and short anteromedian groove obliterated a short distance

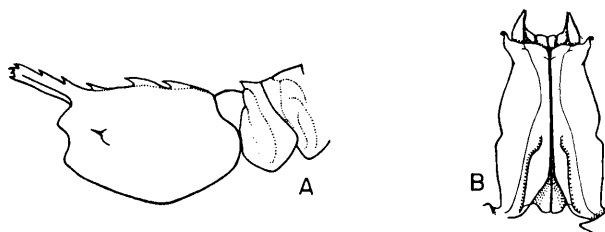


FIGURE 22.—*Sicyonia laevigata* Stimpson. A, carapace and first two abdominal segments in lateral view, approximately $\times 3$; B, petasma of male in ventral view, approximately $\times 20.5$ (A-B after Burkenroad, 1934a).

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; a short, shallow anteromedian pleural and a posteromedian pleural groove turning sharply anteriorly somewhat above middle of lateral surface. Second segment with carina narrowly and deeply cleft above juncture of tergal groove. Fourth and fifth segments with posterior tergal groove, and an anterior groove, obliterated for interval below short dorsal section; reappearing farther ventrad. Sixth segment with a posteromedian pleural, anterior tergal and a longitudinal groove; carina ending in a strong posterior tooth. Ventral pleural margins rounded except for a posterior tooth on fifth and sixth segments.

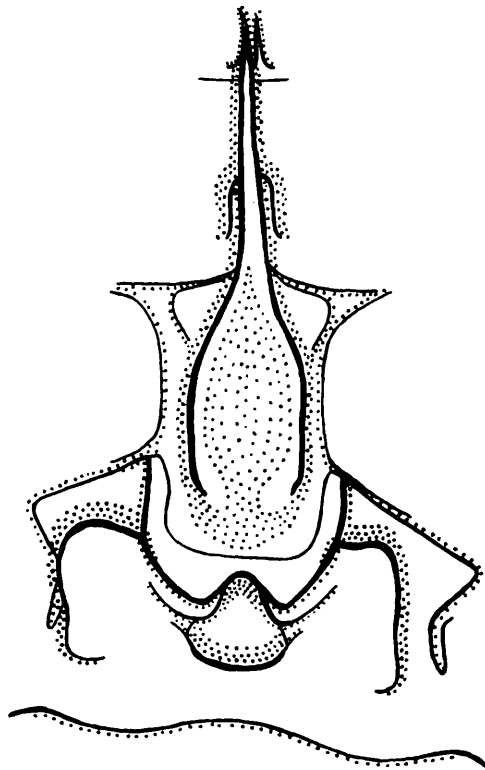


FIGURE 23.—*Sicyonia laevigata* Stimpson. Thelycum of female, $\times 10.4$ (after Burkenroad, 1934a).

Telson ending in a strong point flanked by a pair of shorter blunt spines; sometimes with a pair of mobile lateral spines distal to basal shoulders.

Petasma of male with distolateral projections extending straight distally. Thelycum most conspicuously marked by elongate plate arising on 13th somite (between 4th legs), with slender tip extending to level of 11th somite (2d legs).

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

Variations.—The angle of elevation of the rostrum varies with age. Nearly horizontal among the young, it rises to as much as 35 degrees in older individuals. The usual angle is somewhat in excess of 20 degrees. The number of carinal teeth on the carapace may be reduced to two (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 49 fathoms.

Type locality.—Charleston, S.C.

Known range.—Cape Hatteras, N.C., to northwest Florida; through West Indies to Colombia; Pacific coast of Panama.

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

Sicyonia parri (Burkenroad)

Figure 24

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

Recognition characters.—Resembling *S. laevigata*; integument rather firm, almost smooth and more or less sculptured. Rostrum elevated at angle of about 15 degrees, armed dorsally with three teeth not counting tip; terminal portion bearing three teeth with rudiment of another between lower teeth. Postrostral carina armed with three large, subequal teeth, anterior one slightly advanced beyond level of hepatic spine.

Abdominal segments marked by tergal carinae notched behind on first to fifth segments. First abdominal segment with carina produced into an elevated anterior tooth, marked laterally with a short anteromedian groove as in *S. laevigata*, but reappearing below obliteration and continuing conspicuously to ventral margin, not connected to posteromedian pleural groove ventrally. Second segment with carina cleft above juncture of tergal grooves. First four segments each with a shallow but perceptible posterior pleural groove. Fourth segment with dorsal and ventral positions of anterior tergal groove separated by narrow area of obliteration.

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

Measurements.—Length of body: female, 25 mm.

Habitat.—Shallow water to 14 fathoms.

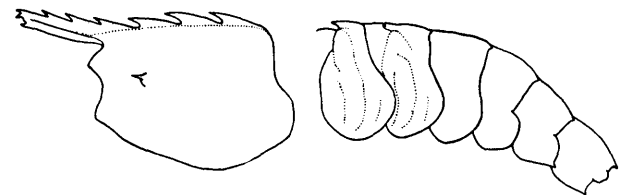


FIGURE 24.—*Sicyonia parri* (Burkenroad). Carapace and abdomen in lateral view, approximately $\times 3$ (after Burkenroad, 1934a).

Type locality.—Crooked Island, Bahamas.

Known range.—Beaufort, N.C.; Florida; West Indies to Curaçao.

Sicyonia brevirostris Stimpson

Figures 25–26

Sicyonia brevirostris Stimpson, 1871b, p. 132.—Hay and Shore, 1918, p. 380, pl. 25, figs. 2, 4.

Eusicyonia brevirostris: Burkenroad, 1934a, p. 84 (rev.).—Lunz, 1945, p. 6, fig. 3.

Recognition characters.—Integument firm, much sculptured, especially abdomen; abdomen with scattered tubercles, and whole body with covering of short, fine hairs. Rostrum short, elevated, slender, narrowing considerably to tip; extending beyond midpoint of cornea; armed dorsally with two (occasionally three) teeth not counting tip; terminal portion divided into two or three teeth with ventral tooth projecting distally farther than dorsal tooth. High postrostral carina with three or four teeth behind orbital margin. Antennal angle armed with a small spine. Hepatic spine well developed. Ocular stylets long.

Abdominal segments marked by prominent tergal carinae deeply notched behind on first to fifth segments. First abdominal segment with carina produced into an elevated anterior tooth; marked laterally by four grooves, an anteromedian and posteromedian pleural, a posterior pleural and posterior tergal. Second and third segments grooved with two tergals, two median pleurals extending far dorsad, and a posterior pleural. Fourth segment grooved with two tergals and one pleural; fifth with two tergals. Sixth segment with a posteromedian pleural, anterior tergal, and a longitudinal groove. Fifth and sixth segments each with carinal tooth directed posteriorly. Pleura of first four segments armed with an anterior ventral angle; angle produced



FIGURE 25.—*Sicyonia brevirostris* Stimpson. Carapace and first two abdominal segments in lateral view, 5 mm. indicated (after Lunz, 1945).

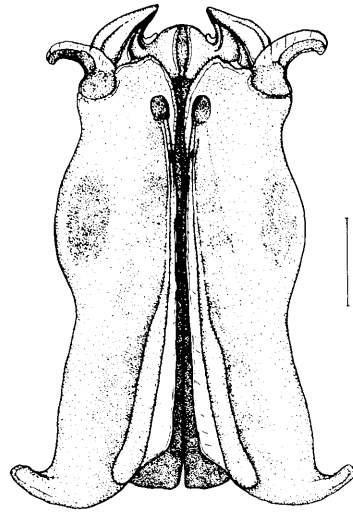


FIGURE 26.—*Sicyonia brevirostris* Stimpson. Petasma of adult male, ventral view, 1 mm. indicated.

into blunt, outward pointing spine on third and fourth, sometimes also on second segment. Last three segments armed with posterior ventral tooth. Telson ending in a strong point flanked by a shorter pair of subterminal, often obsolescent, spines.

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

Measurements.—Length of body: males and females 153 mm.

Variations.—This species exhibits considerable variation in degree of elevation of the rostrum (5–45 degrees). 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 may be located behind the orbital margin and appear as part of the carapace series, in which case there are four teeth on the carapace and two on the rostrum (exclusive of tip); or, this tooth may be located anterior to the orbital margin and appear as part of the rostral series, in which case there are three teeth on the rostrum and three on the carapace.

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 tipped median spines. Burkenroad (1939) gave a somewhat different and more detailed color description.

Habitat.—Common in offshore littoral of the Carolinas; on white shell sand on Campeche Banks; shallow water to over 100 fathoms in Carolinas (Broad, 1950), rarely to 180 fathoms.

Type locality.—Cuba.

Known range.—Off Norfolk, Va., through Bahamas and Gulf of Mexico to Yucatan, Mexico; Pacific coast of southern Mexico.

Remarks.—This large sicyonine shrimp is fairly common in North Carolina and has had a limited commercial usage. Formerly thought to be rare in South Carolina (Lunz, 1945), it is now found to be widely distributed out to the 50-fathom curve (Lunz, 1957). Eldred (1959) reported few *S. brevirostris* in the Tortugas controlled area off Florida. Hildebrand (1954) found the species to be fairly abundant on the Campeche fishing grounds where the bottom is white shell sand. On the Texas brown shrimp grounds and Campeche Banks, the species is rare in depths of 15–25 fathoms where *S. dorsalis* predominates on mud bottom. In deeper water and on mud bottom, 31–45 fathoms, it is more abundant. It is also common in shallow water at 6–10 fathoms. Hildebrand suggested a distribution in two zones separated by an intermediate zone where *S. dorsalis* predominates, or possibly the deeper zone of *S. brevirostris* over mud represents strays. On Campeche Banks, *S. brevirostris*, *dorsalis*, and *typica* have been taken together.

Lunz (1957) reported natural history notes on *S. brevirostris* in South Carolina based on 169 successful 30-minute hauls with a 20-foot experimental trawl. He found the species most abundant in depths of 35–40 fathoms. Catches at night were larger than those made in daytime. Though available throughout the year, largest catches were made in December. Meager data on maturity of gonads indicated spring and fall spawning seasons.

***Sicyonia typica* (Boeck)**

Figure 27

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

Synhimantiles typica Boeck, 1864, p. 189.—Danielssen and Boeck, 1872, p. 192, figs. 1–14.—Sars, 1883, pp. 8, 49.

Sicyonia edwardsii Miers, 1881, p. 367.—Milne Edwards and Bouvier, 1909, p. 251, pl. 8, figs. 1–3 (not fig. 4) (rev.).—Hay and Shore, 1918, p. 380. Schmitt, 1935a, p. 133 (not fig. 6).—Lunz, 1945, p. 7, fig. 4.

Sicyonia typica: Burkenroad, 1945, p. 2 (rev.).—Holthuis, 1959, p. 77.

Recognition characters.—Integument rather firm, more or less sculptured and covered with a short, thick pubescence more evident dorsally than ventrally, especially on abdomen. Rostrum extending halfway along eye, directed obliquely upward, armed dorsally with one or two small teeth not counting tip. Postrostral carina with two or three teeth, last two placed behind level of hepatic spine (third tooth, if present, may look like part of rostral series). Antennal angle armed with a short, often blunt, tooth.

Abdominal segments marked by tergal carinae deeply notched behind on first to fifth segments; first segment with carina produced into an elevated anterior tooth; fifth segment with carina ending posteriorly in a low tooth; sixth segment with carina produced into a posteriorly directed tooth. Pleura of first four segments with a ventrally directed acute tooth on distal margin (character apparent only in large adults). Fifth and sixth segments with tooth at posterolateral corner of pleura, that of fifth often small and rectangular. Abdominal grooves deep and well defined. First segment with posteromedian and anteromedian grooves connected ventrally. Second segment with anterior and posterior tergal grooves connected dorsally; anterior and median pleural 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.—Length of body: 74 mm.

Variations.—Position of the posterior rostral tooth is variable. In some individuals this tooth



FIGURE 27.—*Sicyonia typica* (Boeck). Carapace and first abdominal segment in lateral view, 1 mm. indicated (after Lunz, 1945).

is located behind the orbital margin, thus appearing as one of the carinal series on the carapace (Lunz, 1945).

Color.—Blue spots in tail prominent in life; bright red blotch surrounding rostrum (note by W. L. Schmitt in U.S. National Museum records).

Habitat.—Between tide marks to 37 fathoms.

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

Known range.—Beaufort, N.C.; east and west Florida; Gulf of Campeche; Cuba through West Indies to Rio de Janeiro, Brazil.

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

There remains some doubt that this species occurs in North Carolina, though Lunz (1945) stated that it does. If so, it is not common.

Sicyonia dorsalis Kingsley

Figure 28

Sicyonia dorsalis Kingsley, 1878b, p. 97.—Hay and Shore, 1918, p. 380, pl. 25, fig. 3.

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

Recognition characters.—Body small, 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 sloping upward to near dorsal margin; armed dorsally with three teeth not counting tip, posterior tooth in front of orbital margin and placed variable distance from anterior carinal tooth of carapace; tip appearing bifurcate, dorsal tooth greatly enlarged, ventral tooth reduced to blunt angle.

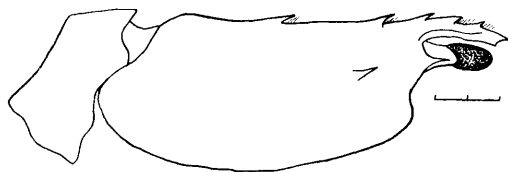


FIGURE 28.—*Sicyonia dorsalis* Kingsley. Carapace and first abdominal segment in lateral view. 2 mm. indicated (after Lunz, 1945).

Postrostral carina with two teeth, anterior tooth before level of hepatic spine, posterior tooth near midpoint. Antennal angle armed with a spine.

Abdominal segments with conspicuous tergal carinae; margins of notches at posterior ends of carinae on segments three to five sometimes produced into long slender spines. First abdominal segment with tergal carina produced into an elevated anterior tooth; anteroventral margin of pleura concave (or at least straight in young) and with an anterior angle in addition to one in middle of ventral edge, posterior angle sometimes produced into a dentiform projection. Second abdominal segment with tergal and pleural grooves connected as an uninterrupted groove extending full depth of segment. Ventral margins of pleura in segments three and four each with both anterior and posterior angle, anterior sometimes sharp, posterior sometimes armed with strong curved spine. Fifth segment with posterior spine only. Tergal carina of sixth segment extended into a posterior spine.

Petasma of male with distoventral lobe forked.

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

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

Habitat.—Common on mud bottom (Hildebrand, 1954), or mud and shells (Holthuis, 1959); from 3 to 88 fathoms, rarely to 230 fathoms.

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

Known range.—Cape Hatteras, N.C., to Texas; Colombia to French Guiana.

Remarks.—Hildebrand (1954, 1955) listed this species as third in abundance on the brown shrimp grounds in Texas but less common on Campeche Banks. It is most common in 15–25 fathoms but ranges shoreward to depths of 6.5 fathoms, and small specimens were occasionally taken in the mouths of bays. 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.

Sicyonia stimpsoni Bouvier

Figure 29

Sicyonia stimpsoni Bouvier, 1905, p. 748.—Holthuis, 1959, p. 75.

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

Eusicyonia stimpsoni: Burkenroad, 1934b, p. 121 (notes).—1939, p. 57.

Eusicyonia edwardsii: Schmitt, 1935a, p. 133, fig. 6.

Recognition characters.—Rostrum usually elevated at considerable angle, extending variable distance beyond eye; with three dorsal teeth not counting tip, posterior tooth in front of orbital margin separated by a variable distance from anterior carinal tooth of carapace; tip often appearing bifurcate but a third ventral tooth present behind or below level of anterior cleft; a slight ridge on lateral surface running parallel with ventral margin. Postrostral carina with two teeth, anterior tooth before level of hepatic spine, posterior tooth behind midpoint; sometimes rudiment of a third tooth appearing as a minute crest-like swelling with truncated anterior edge a little in front of posterior tooth. Antennal angle armed with a spine.

Abdominal segments with conspicuous tergal carinae. First segment with carina produced into an elevated anterior tooth. Margins of dorsal notches at posterior ends of segments three to five produced as short angular projections. A tooth at posterior end of fourth to sixth segments. Segments one to four with a ventral spine on pleura; segments five and six with spine at posteroventral corner. Second abdominal segment with pleural groove curving forward midlaterally, not connected to short tergal groove curving downward and backward.



FIGURE 29.—*Sicyonia stimpsoni* Bouvier. Carapace and portion of first abdominal segment in lateral view, 2 mm. indicated (after Lunz, 1945).

Petasma of male with distoventral lobe not forked.

Measurements.—Length of body: male, 44 mm.; female, 60 mm.

Variations.—Pleural spines may be absent in young individuals.

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.

Habitat.—Found on predominantly mud and shell bottom in Surinam (Holthuis, 1959); shallow water to 230 fathoms.

Type locality.—Off Barbados, British West Indies, lat. 13°03'05'' N. long. 59°36'18'' W., depth 103 fathoms.

Known range.—Cape Hatteras, N.C., to Campeche Gulf; West Indies to French Guiana.

Remarks.—Among species of *Sicyonia* occurring in the Carolinas, the only detailed description of development is that given by Pearson (1939) for this species. Eggs attributed to this species were taken in inlets, and larval development (reconstructed from plankton) proceeded 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.

Family Sergestidae

Penaeidea with last two pairs of legs reduced in size or lost; gills few or lost.

KEY TO SUBFAMILIES AND SPECIES IN THE CAROLINAS

a. Head not greatly elongated; gills present

Sergestinae; *Acetes americanus carolinae* (p. 39).

aa. Head greatly elongated; gills absent

Luciferinae; *Lucifer faxoni* (p. 40).

Subfamily **Sergestinae**

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 a short base. No protuberance on peduncle of first pleopod (after Hansen, 1922).

Genus *Acetes* Milne Edwards, 1830

Burkenroad, 1934a, p. 99.—1934b, p. 126.

Acetes americanus carolinae Hansen

Figures 30–31

Acetes americanus Ortmann, 1893, p. 39, pl. 2, fig. 2.

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

Acetes americanus carolinae: Holthuis, 1959, p. 49, fig. 1, a–c (rev.).

Recognition characters.—Body small. Integument thin, smooth, polished. Carapace with rostrum elevated, short; a single tooth behind acute tip. A 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 article, lower flagellum much shorter and more slender than upper, upper hairy ventrally near base; in males, curved lower flagellum forming clasping organ, basal four annulations thicker than distal annuli, third and fourth armed dorsally with a 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.

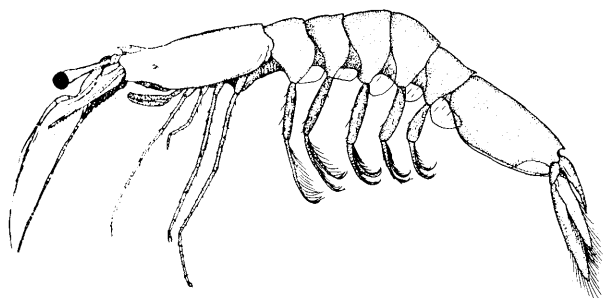


FIGURE 30.—*Acetes americanus carolinae* Hansen. Female in lateral view, $\times 4.8$.

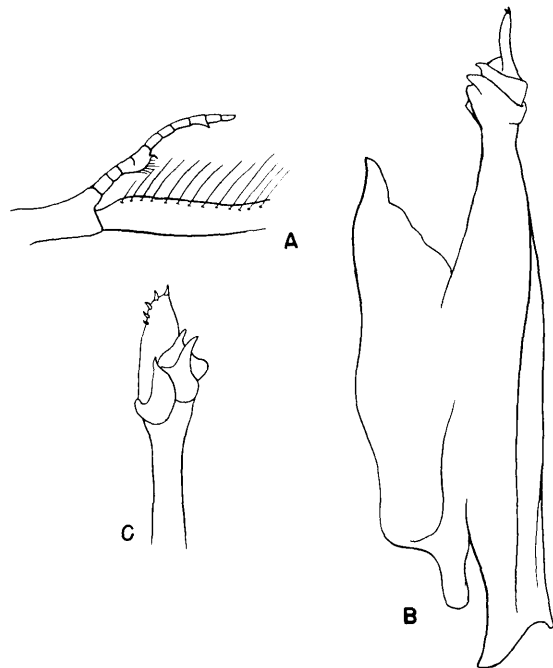


FIGURE 31.—*Acetes americanus carolinae* Hansen.

A, clasping organ on antennule of male $\times 50$; B, petasma of male, right side in posterior view $\times 90$; C, tip of petasma, anterior view of right side $\times 90$.

Sixth segment of abdomen with convex ventral margin bifurcated caudally. Exopod of uropod about 4.5 times longer than broad; proximal three-fifths of outer margin smooth, ending in a 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 four thick, short spines, and three other shorter lateral lobes each produced into an acute point. 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 a protuberance; sternite immediately behind third legs bearing two curved projections forming a U-shaped thelycum.

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

Variations.—Holthuis (1948, 1959) followed Burkenroad (1934a) in considering the known species of *Acetes* from the western Atlantic with one tooth behind the tip of the rostrum to be all

A. americanus. Burkenroad recognized four subspecies: *A. americanus americanus* Ortmann, Brazil; *A. a. limonensis* Burkenroad, Panama; *A. a. louisianensis* Burkenroad, Louisiana; *A. a. carolinae* Hansen, North Carolina. Holthuis considered these to be clinal variants, with the northern and southern representatives differing most widely from each other. Females of the four doubtfully valid subspecies differ in depth of the concavity in the middle of the posterior segment of the genital sternite. This structure is deeper than broad in Carolinian specimens, but becomes shallower in progressively more southern forms. Holthuis suggested that the extreme northern and southern forms might deserve to retain subspecific rank.

Color.—Nearly transparent with faint red flecks.

Habitat.—Littoral oceanic and estuarine waters to 23 fathoms.

Type locality.—Typical form, mouth of Pará (=Tocantins) River, [State of Pará], Brazil. Northern form, off Beaufort Inlet, N.C.

Known range.—Cape Lookout, N.C., to mouth of Pará River, Brazil.

Remarks.—Burkenroad (1934b) found larval stages of this *Acetes* 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.

Subfamily *Luciferinae*

Carapace extremely compressed. Antennules without inferior flagella in both sexes. Third pair of legs only terminated by a pincer. Gills absent. Sixth abdominal segment of male with two ventral processes, second far behind first. Telson of male with a strong protuberance on internal face. Petasma sessile, proximal part fixed like a large disc on peduncle of first pleopod; each peduncle,

near disc, possessing a protuberance with distal spines (after Hansen, 1922; Burkenroad, 1934b).

Genus *Lucifer* Thompson, 1829

Hansen, 1919, p. 48.

Lucifer fazoni Borradaile

Figure 32

Lucifer fazoni Borradaile, 1915, p. 227.—Hay and Shore, 1918, p. 381, text-fig. 4, pl. 26, fig. 10.—Holthuis, 1959, p. 52 (rev.).

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 mouth parts and legs. Rostrum small, a 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 one-fourth to one-third 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 two 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 two segments, posterolateral angles spiniform near

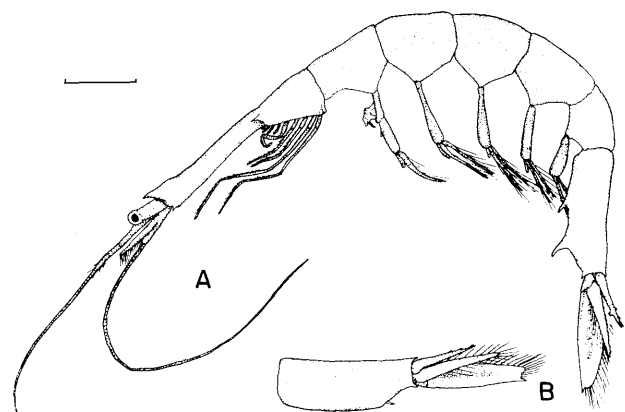


FIGURE 32.—*Lucifer fazoni* Borradaile. A, male in lateral view; B, sixth abdominal segment and tail fan of female in lateral view; 1 mm. indicated.

base of uropods; a small median spine above base of telson; male with two strong ventral spines, posterior spine curved and about twice length of anterior spine. Telson slender, about half length of uropods; truncate distally with a strong spine at each corner; two pairs of intermediate spines on distal border, and two pairs of lateral spines about equidistant; males with a prominent ventral projection on distal half. Outer ramus of uropod longer and broader than inner.

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

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

Color.—Almost perfectly transparent in life.

Habitat.—Oceanic and estuarine waters from surface to 50 fathoms.

Type locality.—Off Chesapeake Bay.

Known range.—Off Nova Scotia along coast of United States to Louisiana; through West Indies and along coast of South America to off Rio de Janeiro, Brazil; Bermuda and mid-Atlantic (lat. 42°50'26" N. long. 41°48' W., lat. 41°39'34" N. long. 39°21' W., and lat. 4°30' N. long. 28°20' W.); Rea Sea; Malay Archipelago; Marshall Islands; Hawaiian Islands; Fanning Island (Holthuis, 1959).

Remarks.—This interesting little shrimp is abundant near Beaufort Inlet, N.C., throughout most of the year (collected from February through October), and often occurs in swarms outside the harbor.

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 found larvae as late as September. Since then, egg-bearing females have been found through the summer into October in Bogue Sound near Morehead City, N.C. Brooks illustrated the egg, a number of larval stages (two nauplius, three protozoa, one zoea, one schizopod, one mastigopus, and one lucifer), and a final adult stage in males.

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 the ocean.

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.

Section *Caridea*

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

Family *Pasiphaeidae*

Rostrum small or obsolete. Mandibular palp absent, one or two jointed. Legs with exopods; first two pairs of legs chelate, chelae slender, cutting edges pectinate; third, fourth, and fifth legs smaller than chelipeds, fourth generally smallest (Rathbun, 1901; Holthuis, 1955).

Genus *Leptochela* Stimpson, 1860

Stimpson, 1860, p. 111.—Hemming, 1958b, p. 157.

Leptochela serratorbita Bate

Figures 33–34

Leptochela serratorbita Bate, 1888, p. 859, pl. 139, fig. 1.—Rathbun, 1901, p. 127.—Schmitt, 1935a, p. 134.

Recognition characters.—Carapace smooth, anterior half with low carina. Rostrum nearly horizontal, unarmed, about as long as eyestalks. Upper portion of orbits finely serrated or spinulose.

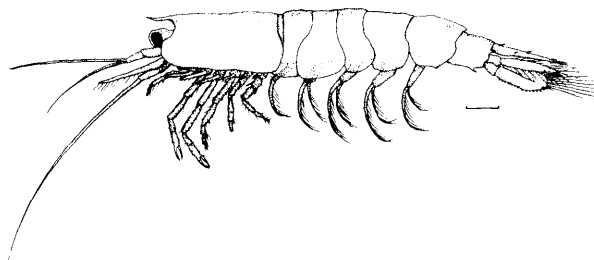


FIGURE 33.—*Leptochela serratorbita* Bate. Animal in lateral view, 1 mm. indicated.

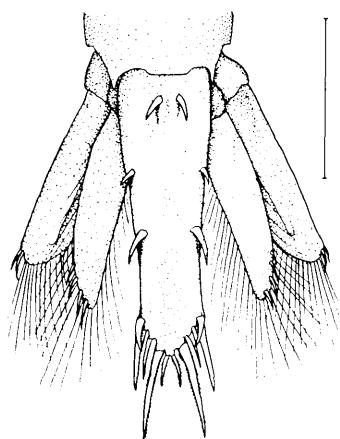


FIGURE 34.—*Leptochela serratorbita* Bate. Uropods and telson in dorsal view, 1 mm. indicated.

Antennal spine small or absent. Antennular peduncle reaching beyond middle of antennal scale.

First two pairs of legs chelate; fingers a little longer than palm, cutting edges pectinate.

Abdomen with fourth and fifth segments broadly carinate; sixth segment with an anterior middorsal tubercle, a posterior spine either side of middle and a prominent spine preceding each posterolateral angle. Telson with an anterior submedian pair of spines and three pairs of lateral marginal spines, anterior lateral spines at anterior fourth, second at middle, third near posterior extremity; tip with three pairs of unequal spines and two pairs of strong setae, all more or less fimbriated. Exopod of uropod with a row of spines along ventrolateral border, a long curved spine at tip; endopods spiny near tip.

Measurements.—Length of body: 21 mm.

Habitat.—Known only from coastal and occasionally estuarine waters, from surface to 23 fathoms (perhaps to 33 fathoms).

Type locality.—St. Thomas, shallow water.

Known range.—Near Beaufort Inlet, N.C.; Charleston Harbor, S.C.; Key West, Fla.; Puerto Rico, and Virgin Islands.

Remarks.—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. The specimen taken in May was ovigerous. Lunz (1939) collected a specimen in July in South Carolina.

Family Palaemonidae

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

KEY TO SUBFAMILIES IN THE CAROLINAS

- a. Posterior margin of telson with three pairs of spines
Pontoniinae (p. 42).
- aa. Posterior margin of telson with two pairs of spines
and two or more setae.....Palaemoninae (p. 50).

Subfamily Pontoniinae

Upper antennular flagellum with both rami fused in basal part. Appendix masculina generally present on second pleopod of male; appendix interna on second pleopod of female. Pleurobranch absent from third maxilliped. Posterior margin of telson with three pairs of spines (Holthuis, 1951a).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

(Holthuis, 1951a, modified)

- a. All maxillipeds with well-developed exopods.
 - b. Hepatic spine present.....*Periclimenes* (p. 42).
 - c. Antennal spine absent; dactyls of last three legs bifurcate.....*P. longicaudatus* (p. 42).
 - cc. Antennal spine present; dactyls of last three legs simple.....*P. americanus* (p. 43).
 - bb. Hepatic spine absent.
 - c. Rostrum compressed, with distinct teeth
Periclimenaeus (p. 45).
 - d. Antennal scale with no terminal tooth
P. schmitti (p. 45).
 - dd. Antennal scale with terminal tooth
P. wilsoni (p. 46).
 - cc. Rostrum depressed, with at most two small teeth near tip.....*Pontonia* (p. 47).
 - d. Dorsal spines of telson small and rather inconspicuous.....*P. domestica* (p. 47).
 - dd. Dorsal spines of telson well developed
P. margarita (p. 48).
- aa. Second and third maxillipeds without exopods
Neopontonides beaufortensis (p. 49).

Genus *Periclimenes* Costa, 1844

Subgenus *Periclimenes* Costa, 1844

Holthuis, 1951a, p. 23, 26.—Hemming, 1958b, p. 159.

Periclimenes (Periclimenes) longicaudatus (Stimpson)

Figure 35

Urocaris longicaudata Stimpson, 1860, p. 39.—Hay and Shore, 1918, p. 394, pl. 27, fig. 7.

Periclimenes (Periclimenes) longicaudatus: Holthuis, 1951a, p. 26, pl. 6, figs. a-m; pl. 8, fig. m (rev.).

Recognition characters.—Rostrum straight, short, reaching to end of second or third article

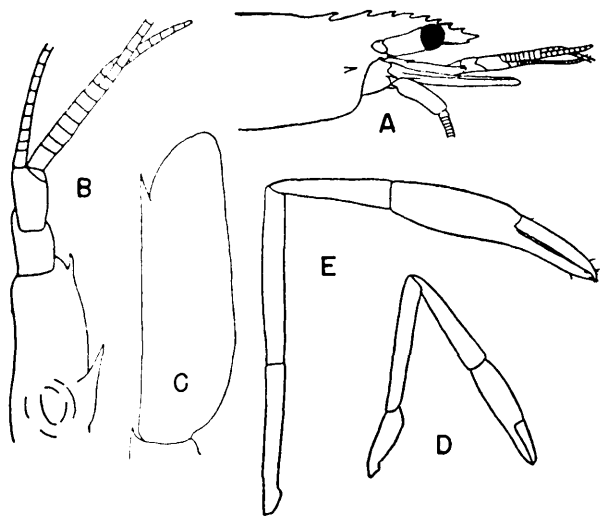


FIGURE 35.—*Periclimenes (Periclimenes) longicaudatus* (Stimpson). A, anterior part of body in lateral view, $\times 5$; B, antennule, $\times 11.5$; C, antennal scale, $\times 11.5$; D, first leg, $\times 13.0$; E, second leg, $\times 13.0$ (after Holthuis, 1951a).

of antennular peduncle; upper margin raised into a high arcuate crest with seven to nine teeth, first two teeth behind orbit more widely spaced than distal teeth; lower margin with one or two small spines near tip. Carapace with lower angle of orbit produced into a lobe constricted at base; supraorbital and antennal spines absent; anterolateral angle rounded. Eyes well developed and elongate. Stylocerite well developed but not reaching to middle of basal antennular article; basal antennular article convex and ending in a strong spine; upper antennular flagellum with two rami fused for four to eight joints. Antennal scale with outer margin slightly concave, ending in a strong tooth exceeded distally by lamella; antennal peduncle reaching almost to middle of scale, with distinct outer spine near base of scale. All maxillipeds with well-developed exopods.

First legs slender, reaching almost to end of antennal scale; second legs equal in size and shape, stronger and longer than first legs.

Abdomen smooth; all pleura rounded. Third abdominal segment somewhat produced in middle of posterior margin. Sixth abdominal segment twice length of fifth and longer than telson. Telson with two pairs of dorsal spines both lying behind middle; posterior margin with three pairs of spinules.

Measurements.—Length of body: male, 17 mm.; ovigerous females, 15 to 22 mm.

Color.—Body transparent in life.

Habitat.—This species is found in abundance on submerged vegetation along with *Hippolyte* and *Tozeuma*, on *Leptogorgia*, algae and *Sargassum*, or from sponges (Schmitt, 1924b); however, it is hard to detect because of its almost perfect transparency. Surface to 6 fathoms, rarely to 15 fathoms.

Type locality.—Coast of Carolina.

Known range.—Hatteras, N.C., to southwestern Florida; West Indies to State of Paraíba, Brazil. There are doubtful records from the Indian Ocean and deeper waters of the Gulf of Mexico (Holthuis, 1951a).

Remarks.—This species is abundant in the Beaufort, N.C., area, and has been collected there throughout the year. Ovigerous females have been found from May through October. They occur in Cuba in January and March (Schmitt, 1924b) and in Texas in May. Pearse and Williams (1951) found the form on reefs off the North Carolina coast along with an unidentified *Periclimenes*. Last larval, postlarval, and early juvenile stages doubtfully assigned to this species have been described by Gurney and Lebour (1941) from Bermuda.

Subgenus *Harpilius* Dana, 1852

Holthuis, 1951a, p. 23.

Periclimenes (Harpilius) americanus (Kingsley)

Figure 36

Anchistia americana Kingsley, 1878b, p. 96.

Periclimenes (Harpilius) americanus: Holthuis, 1951a, p. 60, pl. 18, figs. a–j; pl. 19, figs. a–e (rev.).

Recognition characters.—Rostrum rather high and straight; tip directed upward, reaching about to end of antennular peduncle; upper margin nearly straight, with 7–10 teeth, first two behind orbit and considerably separated; lower margin with 2, sometimes 3 teeth but with an unarmed stretch before tip. Carapace with only antennal and hepatic spines; lower orbital angle acute; postorbital ridge paralleling orbit; anterolateral angle broadly rounded. Eyes well developed; cornea globular, two dark-colored bands visible on cornea in fresh material; an ocellus present. Stylocerite rather strong, sharply pointed, almost reaching middle of basal antennular article; outer

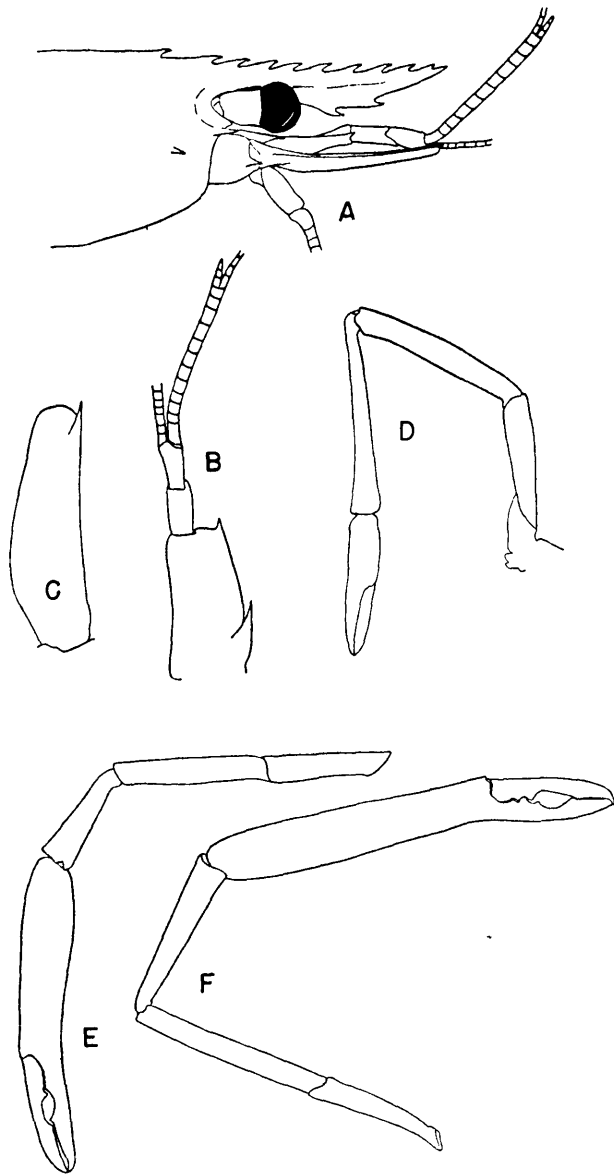


FIGURE 36.—*Periclimenes (Harpilius) americanus* (Kingsley). A, anterior part of body in lateral view, $\times 8.5$; B, antennule, $\times 11$; C, antennal scale, $\times 11$; D, first leg, $\times 11$; E, F, second leg (different specimens), $\times 7.5$ (after Holthuis, 1951a).

margin of basal antennular article convex, ending in well-developed anterolateral tooth; second and third articles elongate, second slightly shorter than third; upper antennular flagellum with 2 rami fused for 8–12 joints (often 6 in younger specimens), free portion of shorter ramus with 3 or 4 joints, length less than one-fourth that of fused part. Antennal scale slightly exceeding

antennular peduncle, outer margin straight or slightly concave and ending in a strong tooth slightly exceeding distally narrowed lamella; scale with a distinct spine near base; antennal peduncle not reaching to middle of scale. All maxillipeds with well-developed exopods.

First legs slender; chela and sometimes a small portion of carpus extending beyond antennal scale; fingers smooth, as long as palm. Second legs equal in size and shape, very strong and longer than first; adult males with fingers less than half as long as palm, three or four teeth on cutting edges leaving gape at midlength when closed; second legs shorter and fingers not agape in juveniles and adult females.

Abdomen with pleura of first four segments rounded, of fifth ending in a small tooth; median posterior margin of third only slightly produced posteriorly. Sixth segment about 1.5 times as long as fifth and about three-fourths length of telson. Telson with two dorsal pairs of spines at one-third and two-thirds length; posterior margin with three pairs of spines, intermediate pair less than twice length of inner spines.

Measurements.—Length of body: male 22 mm.; ovigerous females, 13 to 20 mm.

Variations.—The carpus of the second pair of legs varies in length as do the dactyls of the last three pairs of legs.

Color.—Ground color translucent grayish white; carapace with three oblique orange-brown lateral lines and a pair of dorsal lines running back from base of rostrum; each abdominal segment crossed by a narrow brown band and a row of small dark spots on posterior margin; tail fan with two larger lateral and median spots and an orange-brown tip (Verrill, 1922).

Habitat.—This species lives in coastal waters, preferring sandy or rocky bottom, often between algae or coral. Verrill (1922) found large schools near the surface in Bermuda, and Gurney (1943a) found it to swim singly or in small numbers at the surface at night in certain periods of the lunar cycle (see Holthuis, 1951a). Shallow water to 40 fathoms.

Type locality.—Key West, Fla.

Known range.—Beaufort, N.C.; Jupiter Inlet, Fla., to west coast of Florida off Hernando County; off Cape Catoche, Yucatan, Mexico; through West Indies to Aruba; Bermuda.

Remarks.—Gurney (1943a) listed this species as one of the commonest decapod crustaceans in the littoral region of Bermuda. Females outnumbered males two to one; however, ovigerous females were never collected there. From plankton, Gurney (1936c, 1943a) described the first and fifth larval, and the first postlarval stages, and gave remarks on allometric growth of the second legs. These legs are stronger and longer in males than in females, with fingers agape in old males. The center of greatest growth is in the palm.

Ovigerous females have been found from January to May and from September to November in Florida, the West Indies, and South America.

Holthuis (1951a) listed *P. americanus* as common in North Carolina, but it has been taken only once (August 5, 1958) in surface plankton tows in Bogue Sound that have produced hundreds of *P. longicaudatus*.

Genus *Periclimenaeus* Borradaile, 1915

Holthuis, 1951a, p. 76.—Hemming, 1958b, p. 159.

Periclimenaeus schmitti Holthuis

Figure 37

Periclimenaeus schmitti Holthuis, 1951a, p. 90, pl. 27, figs. a–m.

Recognition characters.—Rostrum short, straight, or somewhat decurved, not reaching to end of basal article of antennular peduncle; upper margin bearing one or two teeth, exclusive of upturned tip; lower margin convex, unarmed. Carapace smooth; postorbital ridge paralleling orbit, extending from strong antennal spine dorsally and becoming gradually obsolete; anterolateral angle broadly rounded, produced forward. Eyes well developed, cornea globular, shorter and narrower than eyestalk. Basal article of antennular peduncle with short, broad, blunt tipped stylocerite reaching about to middle of article; outer margin with blunt angle at level of stylocerite tip, concave beyond angle, anterolateral angle of article with rather large tooth; second and third articles short; upper antennular flagellum with three fused joints, free part of short ramus with one short joint. Antennal scale broadly ovate; outer margin nearly straight, with no terminal tooth.

First leg with carpus and chela extending beyond antennal scale; chela slender, fingers two-thirds length of palm, unarmed, carpus about as

long as chela, slightly shorter than merus. Second legs unequal, both reaching with chela and part of carpus beyond antennal scale. Larger second leg heavy, fingers slightly less than half as long as palm, inwardly curved; upper margin of dactyl broadly rounded, cutting edge finely denticulate distally, with large rectangular-shaped tooth fitting into pit on immovable finger when closed; fixed finger with strong, narrow tooth at inner margin of pit; palm swollen, covered with a number of small scalelike tubercles; carpus conical, about one-fourth length of palm; merus about one-third length of palm, sometimes with small tubercles at lower edge. Smaller second leg with fingers straight, slightly shorter than one-third length of palm; cutting edge of dactyl denticulate throughout, that of fixed finger straight; tubercles on palm fewer than on opposite member. Third leg with propodus and part of

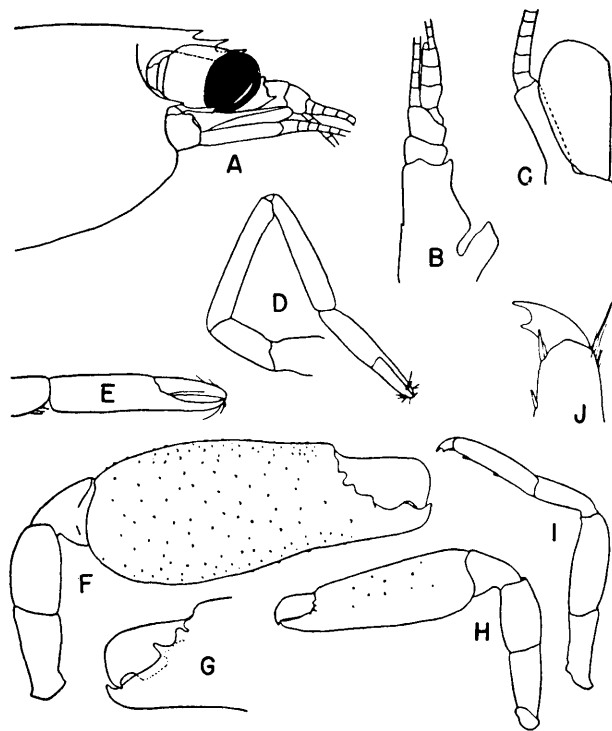


FIGURE 37.—*Periclimenaeus schmitti* Holthuis. A, anterior part of body in lateral view, $\times 17$; B, antennule, $\times 22.5$; C, antenna, $\times 22.5$; D, first leg, $\times 22.5$; E, chela of first leg, $\times 33.5$; F, larger second leg, outside, $\times 15$; G, fingers of larger second leg, inside, $\times 15$; H, smaller second leg, $\times 15$; I, third leg, $\times 15$; J, dactyl of third leg, $\times 56.5$ (after Holthuis, 1951a).

carpus reaching beyond antennal scale, dactyl short, distinctly bifurcate.

Abdomen smooth; pleura of first five segments rounded; sixth segment about as long as fifth and about two-thirds length of telson. Telson with two pairs of small dorsal spines somewhat removed from lateral margin, placed at one-third and two-thirds length; six spines on posterior margin placed in one row, intermediate spines longest. Uropods broadly ovate, exopod with outer margin ending in a tooth flanked medially by a movable spine.

Measurements.—Length of body: ovigerous female, 20 mm.

Variations.—Specimens with a single rostral tooth are young.

Habitat.—Shallow water.

Type locality.—Tortugas, Fla.

Known range.—Bogue Sound, N.C.; Tortugas, Fla.

Remarks.—Two specimens from North Carolina were taken August 16, 1957, in a nighttime surface plankton tow on flood tide near Beaufort Inlet. Though these have intermediate spines on the telson longer than the other terminal pairs, they agree well with specimens of *P. schmitti* from Tortugas.

***Periclimenaeus wilsoni* (Hay)**

Figure 38

Coralliocaris wilsoni Hay, 1917, p. 71.—Hay and Shore, 1918, p. 394, text-fig. 13; pl. 27, fig. 8.

Periclimenaeus wilsoni: Holthuis, 1951a, p. 103, pl. 31, figs. a-m; pl. 32, figs. b-c (rev.).

Recognition characters.—Rostrum nearly straight or somewhat decurved, almost reaching end of antennular peduncle; upper margin somewhat convex, bearing 10 to 12 regularly spaced teeth, first tooth directly over or immediately behind orbital margin; lower margin straight or concave, unarmed. Carapace smooth with only an antennal spine placed close to acute lower orbital angle; postorbital ridge paralleling orbit indistinct; anterolateral angle somewhat anteriorly produced, broadly rounded. Eyes well developed. Stylocerite of antennular peduncle broad, short, and pointed, almost reaching middle of basal article; outer margin of basal article with a blunt angle near tip of stylocerite, concave beyond angle, ending in a strong tooth; second

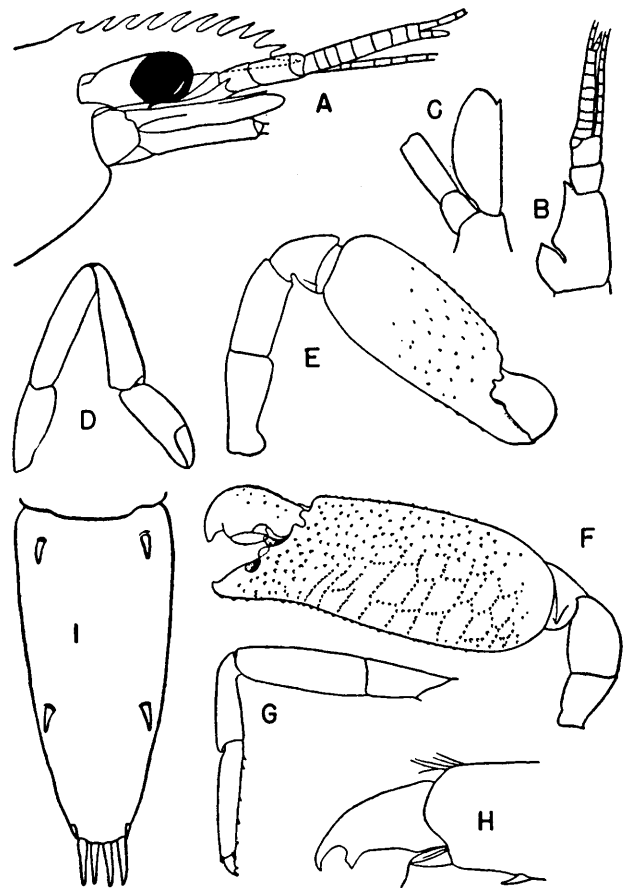


FIGURE 38.—*Periclimenaeus wilsoni* (Hay). A, anterior part of body in lateral view, $\times 11.5$; B, antennule, $\times 9.5$; C, antenna, $\times 9.5$; D, first leg, $\times 9.5$; E, smaller second leg, $\times 9.5$; F, larger second leg, $\times 4.5$; G, third leg, $\times 9.5$; H, dactyl of third leg, $\times 56$; I, telson in dorsal view, $\times 17$ (after Holthuis, 1951a).

and third antennular articles about same size; upper antennular flagellum with six to nine fused joints; free part of short ramus with two joints. Antennal scale a little longer than antennal peduncle; outer margin straight, ending in a small spine; lamella broadest proximally.

First legs with carpus and chela extending beyond tip of antennal scale; chela rather thickset; fingers shorter than palm, unarmed; carpus about as long as merus. Second legs strong, unequal, with part of carpus and chela extending beyond tip of antennal scale. Larger second legs with chela almost equal to bulk of body; fingers inwardly curved, somewhat less than half length of palm; dactyl with upper margin convex, cut-

Genus *Pontonia* Latreille, 1829

Holthuis, 1951a, p. 115.—Hemming, 1958b, p. 124.

Pontonia domestica Gibbes

Figure 39

Pontonia domestica Gibbes, 1850, p. 196.—Holthuis, 1951a, p. 122, pl. 38, figs. a-j (rev.).

Recognition characters.—Rostrum depressed, rather narrowly triangular, decurved; reaching to second article of antennular peduncle; tip acute

ting edge with large rectangular tooth fitting into pit on immovable finger when closed; immovable finger with distinct tooth at inner margin of pit; palm swollen, tuberculate at base and on base of fingers, tubercles on proximal lower part of palm arranged in rows or honeycomb pattern; carpus smooth, short, cup-shaped; merus about one-third length of palm. Smaller second leg much as larger one in general shape; palm somewhat swollen, with scattered tubercles anteriorly. Third leg with greater part of propodus reaching beyond tip of antennal scale; dactyl short, broad, bifurcate.

Abdomen smooth; pleura of first five segments broadly rounded; sixth segment half length of telson. Telson with two pairs of dorsal spines somewhat removed from lateral margin, anterior pair close to anterior margin, posterior pair slightly behind midlength; posterior margin with three pairs of spines, outer pair short and located in advance of larger intermediate and inner pairs. Uropods broadly ovate, outer margin of exopod ending in a tooth flanked medially by a movable spine.

Measurements.—Length of body: male, 20 mm.; ovigerous females, 16 to 20 mm.

Variations.—Juveniles may have a shorter rostrum with fewer dorsal teeth, and in some specimens the second chelae may be smooth.

Color.—Clear, milky white; integument so transparent that color of internal organs is plainly visible; egg masses light bluish green.

Habitat.—This species is known to live in sponges in coastal waters in company with *Synalpheus longicarpus* and *S. townsendi*; 10–40 fathoms.

Type locality.—Fishing grounds, 20 miles off Beaufort Inlet, N.C.

Known range.—Off Beaufort, N.C.; off Loggerhead Key, near Tortugas, and Franklin County, Fla.

Remarks.—Ovigerous females have been reported from Florida in July and North Carolina in August. Gurney and Lebour (1941) described the last larval stage of a shrimp doubtfully referred to *P. wilsoni*.

When disturbed, the animals are able to make a snapping sound with the large chela quite as loud as that made by one of the true snapping shrimps.

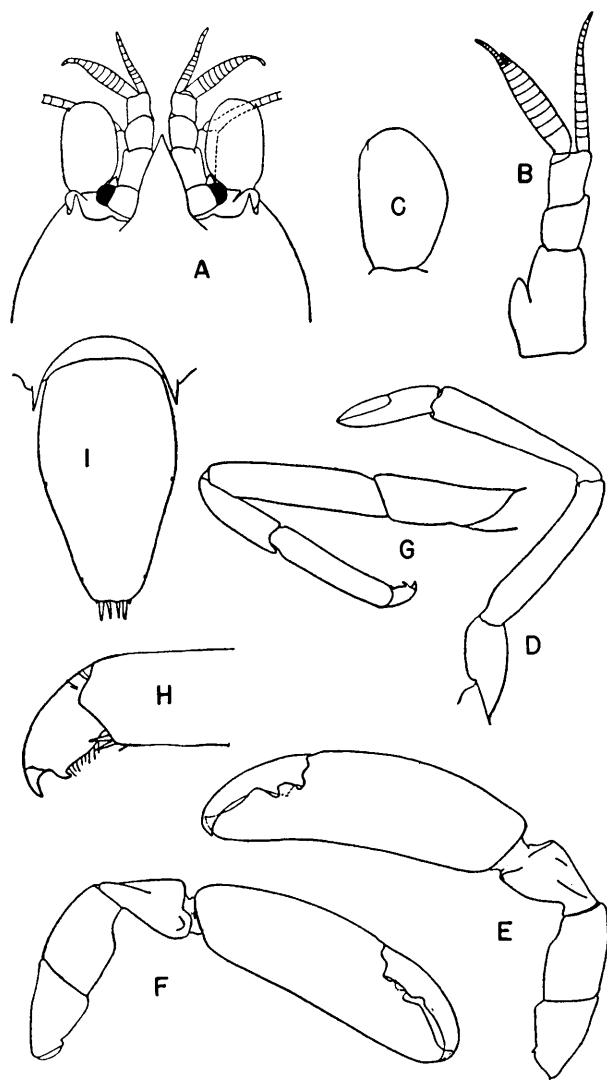


FIGURE 39.—*Pontonia domestica* Gibbes. A, anterior part of body in dorsal view, $\times 5.5$; B, antennule, $\times 7.5$; C, antennal scale, $\times 7.5$; D, first leg, $\times 5.5$; E, larger second leg, $\times 2.5$; F, smaller second leg, $\times 2.5$; G, third leg, $\times 5.5$; H, dactyl of third leg, $\times 20$; I, telson in dorsal view, $\times 9.1$ (after Holthuis, 1951a).

in dorsal and lateral view, flat dorsally; an inconspicuous longitudinal carina ventrally; an inconspicuous dorsal and ventral tooth near tip with tuft of long hairs between upper tooth and apex. Carapace with lower orbital angle bluntly triangular, a strong antennal spine below angle; anterolateral angle broadly rounded and anteriorly produced. Eyes well developed, not reaching laterally to antennal spine. Antennular peduncle with stylocerite broad, bluntly pointed; anterolateral angle of basal article produced forward, rounded; third article longer than second; upper antennular flagellum with 7-10 fused joints; short ramus with 2 or 3 joints. Antennal scale broadly oval, outer margin a little convex, terminal tooth small, exceeded by lamella; antennal peduncle reaching beyond middle of scale.

First leg with carpus and chela reaching beyond antennal scale; fingers of chela somewhat longer than palm; carpus as long as merus. Second legs strong, unequal in size and shape; carpus and chela reaching beyond antennal scale. On one leg, fingers about half length of palm; immovable finger somewhat higher than dactyl and bearing two large teeth on cutting edge, anterior tooth triangular, at middle of edge, posterior tooth truncate with crenulate margin; dactyl with one tooth; palm with upper and lower margin somewhat compressed, surface appearing minutely roughened under magnification; carpus short, conical, with a depression above and a knob below; merus a little longer than carpus. Other second leg much as above but with relatively longer fingers; immovable finger higher in comparison to dactyl; teeth smaller and carpus more slender. Remaining legs with bifurcate dactyls.

Abdomen with first five pleura broadly rounded. Sixth segment with pleura and posterolateral angle ending in slender, sharp spines; slightly longer than fifth segment. Telson half again as long as fifth segment; two dorsal pairs of spines on lateral margin of telson small, almost invisible; anterior pair about in middle, posterior pair closer to posterior border than to anterior pair; posterior border with three pairs of spines in a row; inner two pairs equal in length, outer pair smaller; uropods broadly ovate, outer margin of exopod ending in blunt angle with small movable spine at tip.

Measurements.—Length of body: male 32 mm.

Color.—Translucent white.

Habitat.—The species lives commensally in lamellibranch mollusks in coastal waters and has been recorded from *Atrina seminuda*, *A. serrata*, and *Pecten* sp. (Holthuis, 1951a); shallow water to 23 fathoms.

Type locality.—South Carolina.

Known range.—Atlantic Beach near Beaufort Inlet, N.C., to Chandeleur Islands, La.; Bahamas; Madeira.

Remarks.—Brooks and Herrick (1892) illustrated a section through the segmenting egg of *Pontonia domestica* on plate 28.

Pontonia margarita Smith

Figure 40

Pontonia margarita Smith, 1869c, p. 245.—Holthuis, 1951a, p. 137, pl. 43, figs. a-1; pl. 44, figs. a-h (rev.).

Recognition characters.—Rostrum depressed and decurved, dorsally flat and triangular; tip reaching to end of basal article of antennular peduncle or slightly beyond; an inconspicuous dorsal and ventral tooth near tip with small tuft of hairs between upper tooth and apex; a longitudinal median carina ventrally. Carapace smooth; with strong antennal spine located well below narrowly rounded lower orbital angle; anterolateral angle broadly rounded and anteriorly produced. Eyes somewhat larger than in *P. domestica*, reaching laterally beyond antennal spine. Basal article of antennular peduncle with blunt-pointed stylocerite more or less pressed against outer border; anterolateral angle of article produced forward, rounded; upper antennular flagellum short, thick, curved backward; fused part with six or seven joints; short ramus with two joints. Antennal scale with convex outer margin ending in small inwardly curved distal tooth, lamella far exceeding tooth.

First leg with half or more than half of carpus reaching beyond antennal scale; fingers longer than palm, unarmed; carpus longer than merus. Second legs unequal in size but similar in shape. Larger leg with fingers a little over half length of palm; palm twice as long as deep, somewhat inflated; dactyl narrower than immovable finger and bearing one large tooth slightly behind middle; cutting edge of immovable finger with two large teeth fitting on each side of opposed dactylar

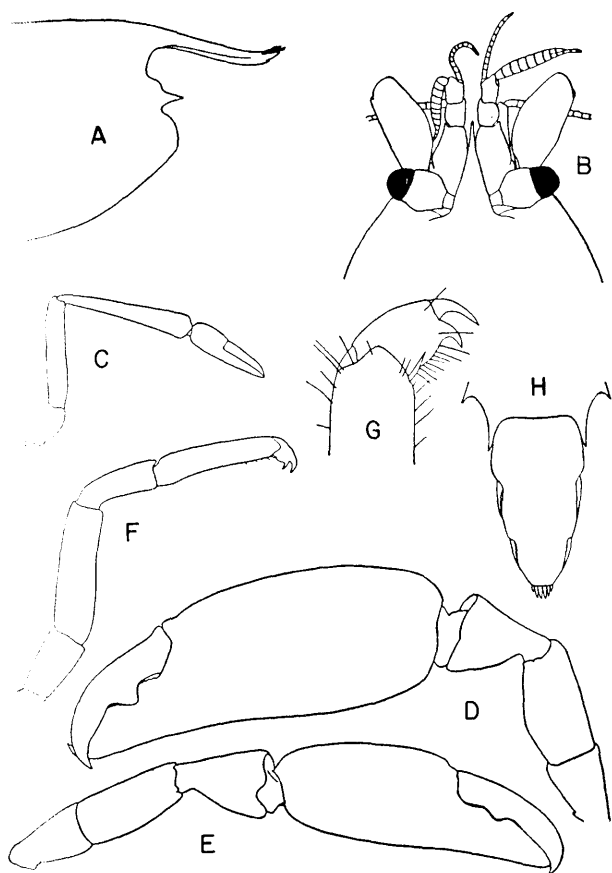


FIGURE 40.—*Pontonia margarita* Smith. A, anterior part of carapace in lateral view, $\times 11.5$; B, anterior part of body in dorsal view, $\times 11.5$; C, first leg, $\times 5.9$; D, larger second leg, $\times 6$; E, smaller second leg, $\times 6$; F, third leg, $\times 9.5$; G, dactyl of third leg, $\times 35$; H, telson in dorsal view, $\times 11.5$ (after Holthuis, 1951a).

tooth and separated by a hole on inner side of edge, posterior tooth with denticles at apex; carpus shorter than merus, conical. Smaller second leg resembling larger except for relatively longer fingers. Dactyls of last three walking legs bifurcate.

Abdomen with pleura of first five segments broadly rounded, of sixth ending in a strong spine overlapping base of uropods. Sixth segment a little more than half length of telson. Telson with two pairs of large dorsal spines placed laterally, and at one-third and two-thirds of length; posterior border with three pairs of spines in a row, inner two pairs equal, outer pair smaller. Uropods broadly ovate, exopods ending in a minute movable spine on outer margin.

Measurements.—Length of body: male, 19 mm.; ovigerous females, 17 to 27 mm.

Color.—Glassy, translucent; internal organs clearly visible; ovigerous females with two colors of eggs, one with light, muddy green eggs and ovarian ova of same color, another with pale orange eggs (from specimens taken in *Aequipecten gibbus* off Drum Inlet, N.C., in 20-fathom water, April 14, 1960).

Habitat.—The species lives commensally in lamellibranch mollusks in coastal waters. It has been found in *Aequipecten gibbus* and *Pteria colymbus* in North Carolina, and in the pearl oyster *Pinctada fimbriata* on the west American coast; tidal flats to 33 fathoms.

Type locality.—Bay of Panama.

Known range.—Atlantic coast: Drum Inlet to Beaufort Inlet, N.C.; east and west Florida. Pacific coast: Gulf of California to Colombia; Galapagos Islands.

Remarks.—Ovigerous females have been taken in North Carolina in January and April.

Genus *Neopontonides* Holthuis, 1951

Holthuis, 1951a, p. 189.

Neopontonides beaufortensis (Borradaile)

Figure 41

Periclimenes beaufortensis Borradaile, 1920, p. 132.

Neopontonides beaufortensis: Holthuis, 1951a, p. 190, pl. 59, figs. g-k; pl. 60, figs. a-k (rev.).

Recognition characters.—Rostrum slender, straight; a little shorter than antennular peduncle; laterally compressed but broadened at base, covering eyestalks, lateral margin of widened base not merging with orbital margin; upper margin with none to five teeth, most proximal teeth, when present, in front of posterior margin of orbit on a crest, crest remaining visible in absence of teeth; lower margin unarmed. Carapace smooth or somewhat areolated; anterior margin of carapace with lower angle of orbit produced in a rounded lobe; antennal spine strong, located considerably below orbit; a rounded lobe slightly below antennal spine followed by an emargination ending in a produced anterolateral angle; hepatic and supraorbital spines absent. Eyes large, reaching almost to end of rostrum. Basal article of antennular peduncle with sty-

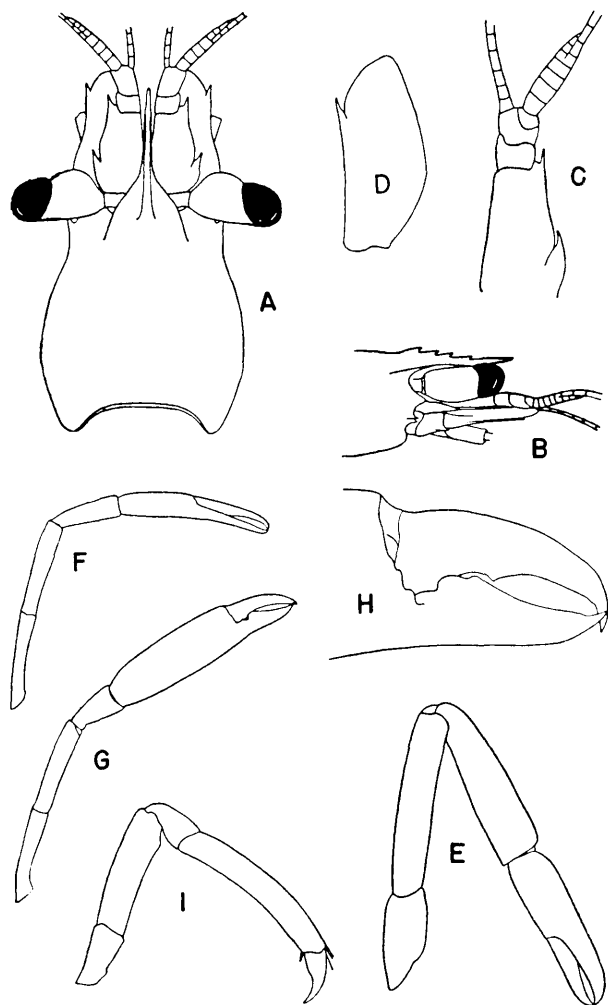


FIGURE 41.—*Neopontonides beaufortensis* (Borradaile). A, anterior part of body in dorsal view, $\times 19.5$; B, anterior part of body in lateral view, $\times 13$; C, antennule, $\times 26$; D, antennal scale, $\times 26$; E, first leg, $\times 39$; F, smaller second leg, $\times 26$; G, larger second leg, $\times 26$; H, fingers of larger second leg, $\times 65$; I, third leg, $\times 26$ (after Holthuis, 1951a).

locerite rather broad, ending in slender point reaching almost to middle of article; outer margin of article slightly concave ending in strong anterolateral spine reaching end of second article; upper antennular flagellum with rami fused for two to four joints; short ramus with two to four free joints. Antennal scale reaching beyond antennular peduncle; concave outer margin ending in strong tooth; lamella exceeding tooth; a small lateral tooth at base; antennal peduncle reaching about to middle of scale.

First leg reaching beyond end of antennal scale; fingers slightly shorter than palm, unarmed, slightly agape; carpus about as long as merus. Second legs unequal. Part of palm of larger leg exceeding antennal scale; fingers half or less length of palm, dactyl with two, immovable finger with one tooth on cutting edge; palm slightly swollen; carpus short, conical; merus about twice length of carpus. Smaller second leg with fingers as long as palm, slender, unarmed; carpus nearly as long as palm. Third leg with heavy, simple dactyl.

Abdomen smooth, all pleura broadly rounded. Sixth segment as long as telson. Telson with two pairs of dorsolateral spines; posterior pair midway between anterior pair and tip; three pairs of spines on posterior border, intermediate pair less than twice length of inner pair. Uropods elongate; outer margin of exopod ending in a tooth flanked medially by a movable spine.

Measurements.—Length of body: male, 9 mm.; ovigerous females, 7 to 9 mm.

Variations.—In young specimens, the legs are relatively shorter than in adults, and the larger second leg resembles the smaller second leg of adults.

Color.—Nearly transparent, but with faint coloration of *Leptogorgia* from which individuals are taken (yellow or orange).

Habitat.—This species is found in coastal waters where it lives in association with *Leptogorgia*; surface to a few fathoms.

Type locality.—Beaufort, N.C.

Known range.—Beaufort, N.C., to Grand Isle, La. (Dawson, 1963); Caledonia Bay, Panama; Antigua.

Remarks.—Ovigerous females have been taken in Bogue Sound near Beaufort Inlet, N.C., in August and November, in Panama in April, and in Antigua in May.

Subfamily Palaemoninae

Upper antennular flagellum with both rami fused in basal part. Appendix masculina generally present on second pleopod of male, appendix interna on second pleopod of female. Pleurobranch present on third maxilliped. Posterior margin of telson with two pairs of spines and one or more pairs of setae (Holthuis, 1952).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

(Holthuis, 1952, modified)

- a. Hepatic spine present, branchiostegal spine absent; chelate second legs enlarged and greatly elongated.
 - b. Dactyls of last three legs bifurcate; marine
Brachycarpus biunguiculatus (p. 51).
 - bb. Dactyls of last three legs simple; fresh or brackish water-----*Macrobrachium* (p. 52).
 - c. Fingers of chelae on second legs thickly pubescent throughout length; rostrum with teeth extending up to tip-----*M. acanthurus* (p. 52).
 - cc. Fingers of chelae on second legs with scattered hairs, except thicker on fingers along cutting edges; rostrum with toothless daggerlike tip
M. ohione (p. 54).
- aa. Hepatic spine absent, branchiostegal spine present; chelate second legs not greatly enlarged.
 - b. Mandible with a palp---*Lcander tenuicornis* (p. 55).
 - bb. Mandible without a palp---*Palaeomonetes* (p. 56).
 - c. Carpus of second leg in adult female shorter than palm, in males slightly longer or shorter (1.1 times) than palm; dactyl of second leg with two, immovable finger with one tooth on cutting edge; rostrum with first two teeth of dorsal margin behind orbit, dorsal rostral teeth reaching to apex, lower margin with three to five teeth
P. vulgaris (p. 56).
 - cc. Carpus of second leg in adult female much longer than palm (1.3 to 1.5 times), in males almost as long as whole chela; dactyl of second leg with a single tooth or without teeth, immovable finger without teeth on cutting edge; rostrum with only one dorsal tooth behind orbit.
 - d. Dorsal teeth of rostrum reaching up to apex, apex often bifurcate; lower margin of rostrum with four or five, seldom three teeth; dactyl of second leg with one distinct tooth on cutting edge -----*P. intermedius* (p. 58).
 - dd. Dorsal and ventral margins of rostrum with an unarmed stretch before dagger-shaped tip; lower margin of rostrum with two to four, generally three, teeth; fingers of second leg without teeth on cutting edges-----*P. pugio* (p. 59).

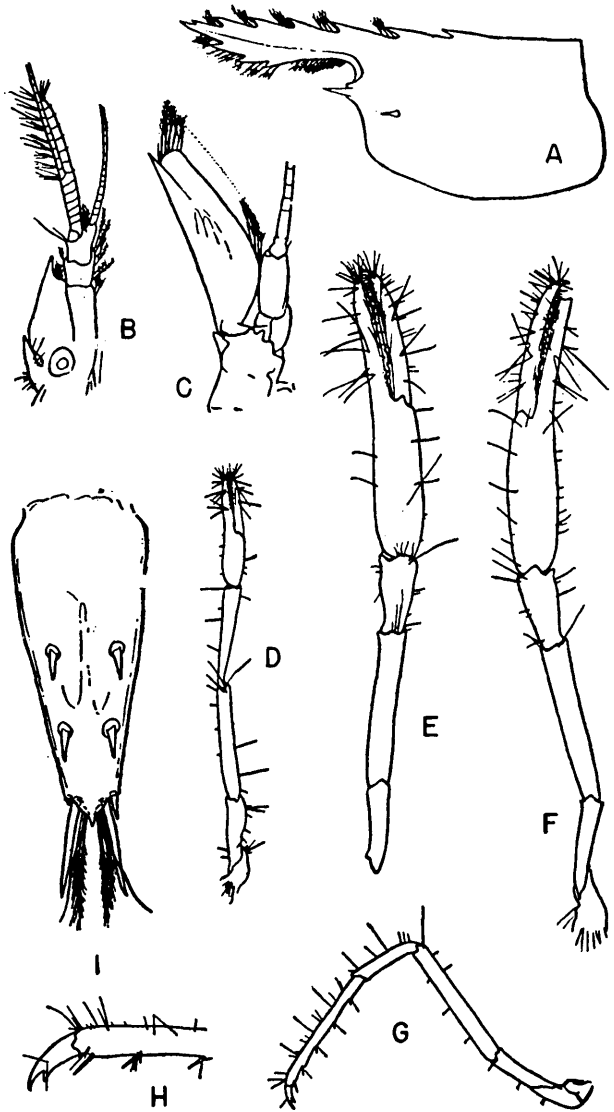


FIGURE 42.—*Brachycarpus biunguiculatus* (Lucas). A, carapace in lateral view, $\times 6$; B, antennule, $\times 7$; C, antenna, $\times 7$; D, first leg, $\times 6$; E, left second leg, $\times 6$; F, right second leg, $\times 6$; G, third leg, $\times 6$; H, dactyl of third leg, $\times 16$; I, telson, $\times 15$ (after Schmitt, 1939).

Genus *Brachycarpus* Bate, 1888

Holthuis, 1952, p. 2.—Hemming, 1958b, p. 154.

Brachycarpus biunguiculatus (Lucas)

Figure 42

Palaeomon biunguiculatus Lucas, 1849, p. 45, pl. 4, fig. 4.

Brachycarpus biunguiculatus: Holthuis, 1952, p. 3, pl. 1, figs. a-q (rev.).

Recognition characters.—Rostrum well developed, rather high, directed straight forward, reaching about to end of antennal scale; upper margin with seven (seldom eight) teeth, first two teeth placed behind orbit with first tooth at about

midlength of carapace; lower margin with three (seldom two or four) teeth. Carapace smooth; antennal and hepatic spines present; a strong postorbital ridge paralleling orbit. Eyes well developed. Basal article of antennular peduncle with anterolateral spine strong, reaching beyond second article of peduncle; stylocerite small, acute, closely appressed to article; rami of inner antennular flagellum fused for 8 to 23 joints; free part

of shorter ramus about as long as fused portion. Antennal scale about three times longer than broad, outer margin concave, terminal spine overreaching lamella.

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

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

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

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

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

Habitat.—Found near shore among corals or rocks, and on sea buoys; surface to 4 fathoms.

Type locality.—Oran and Bône, Algeria.

Known range.—Virtually pantropical; East and West American coasts, Mediterranean; West Africa; and Indo-Pacific region. Western Atlantic distribution: Cape Fear, N.C., through West Indies to Curaçao and Old Providence Island; Bermuda.

Remarks.—Gurney and Lebour (1941) described a complete series of 11 larval stages and

a postlarval stage of this species from Bermuda. They pointed out that the larval life of this form may be indefinite in length and number of developmental stages; and that this feature of development may account for the wide distribution of the species. Gurney (1943a) noted proportional changes in growth of the segments of the second legs in the last larval stage, first postlarval stage, and adult female.

Genus *Macrobrachium* Bate, 1888

Holthuis, 1952, p. 10.

Macrobrachium acanthurus (Wiegmann)

Figures 43-44

Palaemon acanthrus Wiegmann, 1836, p. 150.

Macrobrachium acanthurus: Holthuis, 1952, p. 45, pl. 9, figs. a-b (rev.).

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

First legs with chela and sometimes part of carpus reaching beyond scale; fingers as long as palm; carpus one-third longer than merus. Second legs equal, with carpus and sometimes part of merus reaching beyond scale; fingers slender, thickly pubescent throughout length, slightly shorter than palm, cutting edges with a tooth on each finger in proximal quarter (that of dactyl more advanced) preceded by row of about four denticles; palm elongate, cylindrical, with several longitudinal rows of spinules largest and widest apart on inner and lower regions; carpus and merus spinulose like palm. Articles of last three walking legs with numerous densely placed small spinules.

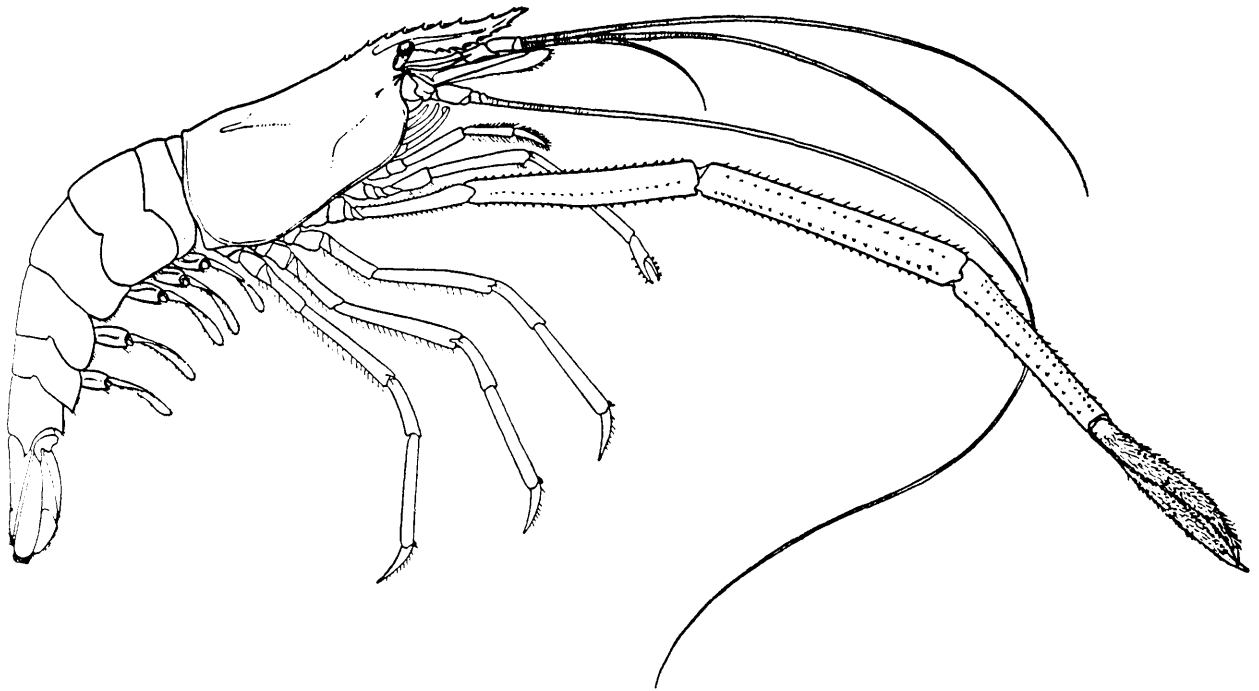


FIGURE 43.—*Macrobrachium acanthurus* (Wiegmann). Animal in lateral view (after Hedgpeth, 1949).

Abdomen smooth; pleura of fifth segment ending in an acute point. Telson 1.5 times length of sixth segment, with pairs of dorsal spines at middle and three-fourths of length; posterior margin ending in sharp median point flanked by two pairs of spinules, inner pair overreaching median point.

Measurements.—Length of body: male, 166 mm.; ovigerous females, 36 to 110 mm.

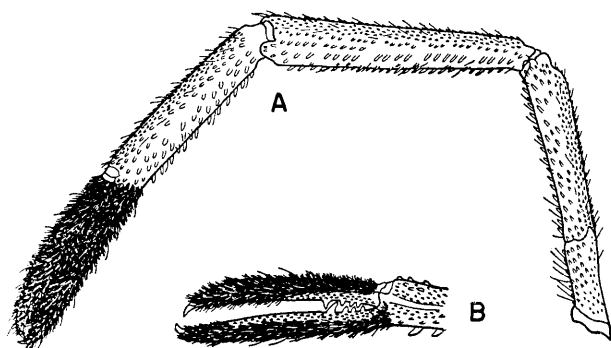


FIGURE 44.—*Macrobrachium acanthurus* (Wiegmann). A, second leg of adult male; B, fingers of second leg of adult male (part of hairs removed); A, B, $\times 0.75$ (after Holthuis, 1952).

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

Color.—Green or pale yellow with red speckles; carapace with middorsal stripe of red or brownish orange and occasionally with irregular red bands laterally; chelipeds greenish becoming blue distally, articulations orange; abdomen with mid-dorsal stripe similar to carapace, pleura green with blue edges and striped with red; eggs green (Hedgpeth, 1949; Schmitt in Holthuis, 1952).

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

Type locality.—Brazilian coast.

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

Remarks.—This species probably has a later breeding season than *Macrobrachium ohione* (Hedgpeth, 1949). The recent discovery of *M. acanthurus* in the Neuse River estuary of North Carolina may indicate an active northward extension of range similar to the case of *M. ohione*.

Macrobrachium ohione (Smith)

Figure 45

Palaemon Ohionis Smith, 1874, p. 640.

Macrobrachium ohione: Holthuis, 1952, p. 62, pl. 14, fig. b (rev.).

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

First legs with chelae reaching beyond scale; chelae slender; fingers about as long as palm; carpus twice length of chela. Second legs in adult female stronger than in male, with carpus and chela reaching beyond scale; fingers somewhat shorter than palm, cutting edges pubescent and

with four to eight small denticles of equal size on proximal half, remainder of surface with scattered hairs; palm elongate, cylindrical, entirely pubescent, most conspicuous pubescence along lower surface; carpus, merus, and palm of equal length, these articles and fingers with longitudinal rows of small spinules; carpus most pubescent anteroventrally; merus somewhat pubescent anteroventrally.

Abdomen smooth; pleura of fifth segment ending in acute point. Telson about 1.5 times length of sixth segment; pairs of dorsal spines at middle and three-fourths of length; posterior margin ending in an acute tip overreached by inner pair of posterior spines.

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

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

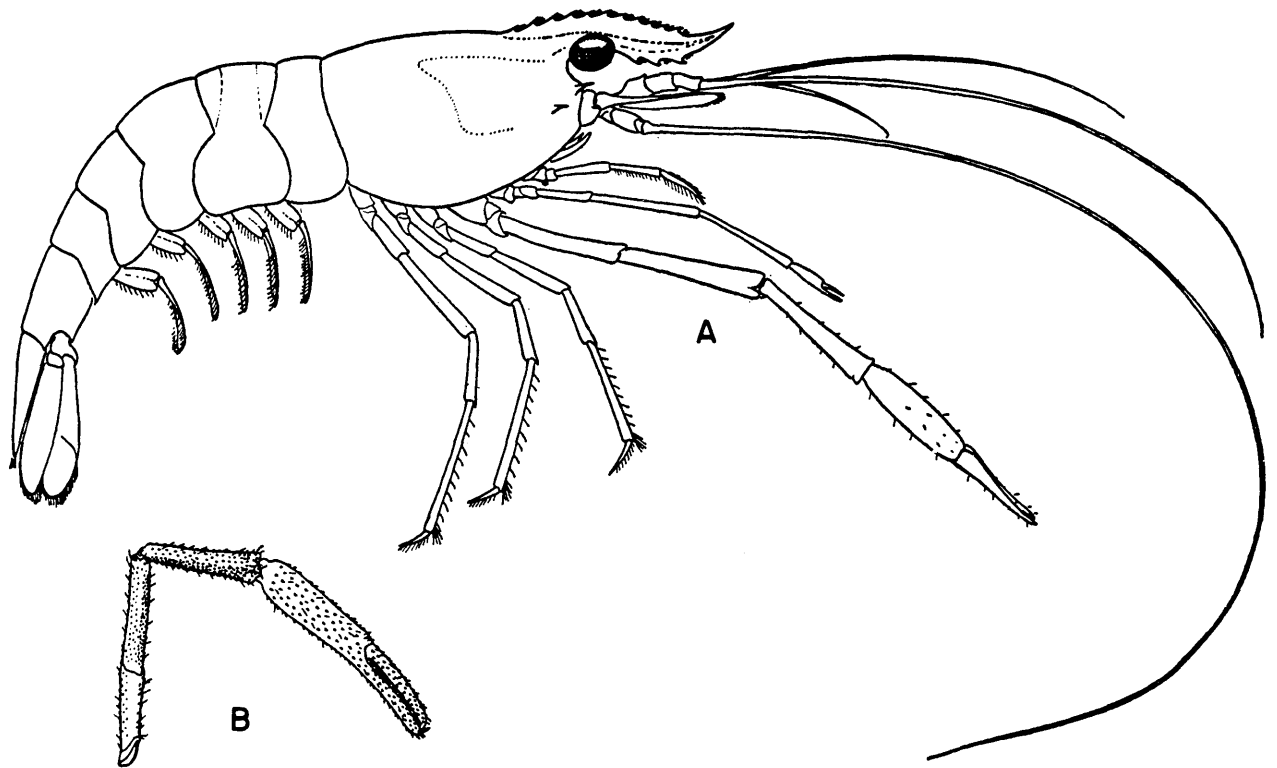


FIGURE 45.—*Macrobrachium ohione* (Smith). A, animal in lateral view (after Hedgpeth, 1949); B, second leg of adult male (after Holthuis, 1952).

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

Habitat.—This species lives in rivers and estuaries.

Type locality.—Ohio River at Cannelton, Ind.

Known range.—A narrow zone along Atlantic seaboard from James River, Hopewell, Va. (Hobbs and Massmann, 1952), to southern Georgia; widespread from coastal Alabama to Aransas Bay, Tex.; Mississippi River and tributaries upstream to McCurtain County, Okla.; Fort Smith, Ark.; St. Louis, Mo.; Washington County, Ohio.

Remarks.—This species is distributed chiefly in brackish and fresh water, ranging far inland in the Mississippi River drainage. It is abundant enough, especially in Louisiana, to provide a fishery of some importance though the exact magnitude is not known. Gunter (1937) described the Louisiana fishery and gave information on ecology of the species. Commercially, the shrimp are taken in traps made of wooden slats, similar to lobster traps, baited with meat scraps or cottonseed cake. The shrimp are sometimes captured by lifting submerged willow branches from the water and catching the animals as they drop off. Such catches are best made at night. Commercial shrimping is done in the warmer months, as the animals are scarce in winter. The shrimp will attack fish kept in live boxes in the river, and, though the feeding habits of the species are not known completely, the animals are thought to be primarily carnivorous.

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

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

Gunter found ovigerous females in bay water with salinities ranging from 1.38 to 14.24 ‰. He noted that when the river was on a rise, with turbidity high, few shrimp were taken in water over 20 feet deep, and these were sometimes dead. He conjectured that because these shrimp were not buried in mud, high turbidity in deep water during flood may have an adverse effect on respiration. Hedgpeth (1949) suggested that silt causing interference with respiration may drive the shrimp from rivers to estuaries during such seasons, but he also suggested that in regions such as the Atlantic seaboard, where the species is apparently a comparatively recent immigrant, it may still depend on bay waters to complete its breeding cycle. In any case, it is thought that these shrimp and other species of the genus move from river to river through the salty estuaries at the river mouths (Gunter, 1937).

Especially interesting is the fact that this species and *M. acanthurus* are forms which may be advanced in the process of moving from the sea to fresh water. Few such examples exist.

Genus *Leander* Desmarest, 1849

Holthuis, 1952, p. 167.

Leander tenuicornis (Say)

Figure 46

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

Leander tenuicornis: Holthuis, 1952, p. 155, pl. 41, figs. a–g; pl. 42, figs. a–f (rev.).

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

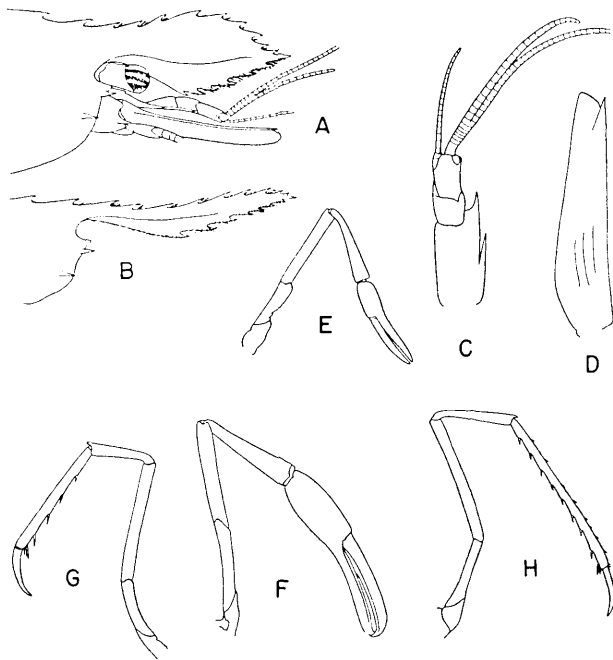


FIGURE 46.—*Leander tenuicornis* (Say). A, anterior part of body of female in lateral view; B, anterior part of carapace of male in lateral view; C, antennule; D, antennal scale; E, first leg; F, second leg; G, third leg; H, fifth leg (after Holthuis, 1952).

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

First pair of legs slender; reaching about to end of scale; fingers longer than palm. Second legs more robust than first, equal in size and shape; chelae reaching beyond scale; fingers longer than slightly swollen palm, cutting edges of fingers entire except for small basal tooth in males; carpus shorter than chela and about as

long as merus. Last three legs slender, dactyls simple, slender; propodi armed with posterior spinules; fifth leg more slender than third.

Abdomen smooth; first three pleura broadly rounded; pleura of fourth and fifth segments narrower, ending in a minute, acute tooth. Sixth segment slightly longer than fifth and about two-thirds length of telson. Telson with two pairs of dorsal spines, first pair at midlength, second at three-fourths length; inner of two pairs of posterior spines overreaching acute tip of telson, a pair of strong feathered setae between inner pair of spines.

Measurements.—Length of body: 47 mm.; males generally smaller than females; ovigerous females 26 mm. long have been reported (Holthuis, 1952).

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

Color.—Green or olive, with opaque spots (Schmitt in Holthuis, 1952, for specimens from Tortugas).

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

Type locality.—Newfoundland Banks.

Known range.—Tropical and subtropical waters all over world except for west coast of Americas; Newfoundland Banks to Falkland Islands in western Atlantic (Holthuis, 1952).

Remarks.—Ovigerous females have been observed from July to October in the Carolinas, in June in the middle and western Atlantic (Sivertsen and Holthuis, 1956), and in August at Old Providence Island (Schmitt, 1939). Gurney (1939) described the fifth(?) larval and first postlarval stages and compared them to related forms, with remarks on the statocyst in adults.

Genus *Palaemonetes* Heller, 1869

Holthuis, 1952, p. 199. Hemming, 1958b, p. 158.

Subgenus *Palaemonetes* Heller

Holthuis, 1952, p. 207.

Palaemonetes (Palaemonetes) vulgaris (Say)

Figure 47

Palaemon vulgaris Say, 1818, p. 248.

Palaemonetes carolinus: Hay and Shore, 1918, p. 393, pl. 27, fig. 4.

Palaemonetes (Palaemonetes) vulgaris: Holthuis, 1952, p. 231, pl. 54, figs. f-1 (rev.).

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

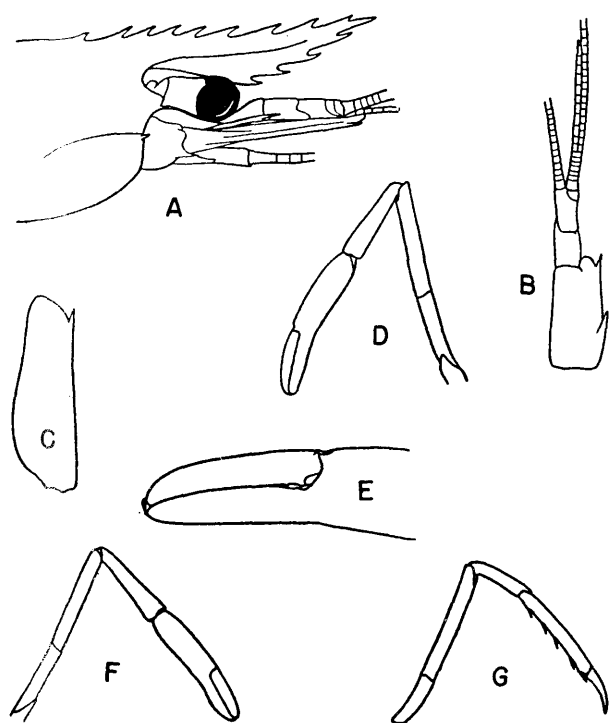


FIGURE 47.—*Palaemonetes* (*Palaemonetes*) *vulgaris* (Say). A, anterior part of body in lateral view; B, antennule; C, antennal scale; D, second leg of female; E, fingers of second leg of female; F, second leg of male; G, third leg; A-G $\times 5$ (after Holthuis, 1952).

First leg usually not reaching to end of antennal scale; fingers about as long as palm; carpus 1.3 to 1.7 times as long as chela and a little longer than merus. Second legs longer and stronger than first, stronger in adult females than in males with fingers and sometimes entire palm reaching beyond scale; fingers a little over half length of palm, cutting edge of dactyl with two small teeth proximally, immovable finger with one similar tooth fitting between those of dactyl; carpus shorter than palm and about three-fourths length of merus. Second legs of male not so large as in female; teeth on fingers indistinct. Third leg with propodus less than twice length of carpus. Fifth leg with propodus about three times length of dactyl, twice as long as carpus.

Abdomen smooth; fifth segment with tip of pleura rectangular or slightly acute. Sixth segment 1.5 times length of fifth, shorter than telson. Telson with two pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by two pairs of spines, inner pair longest and between them two feathered setae. Outer margin of uropodal exopod with a strong terminal tooth flanked by a slender movable spine medially.

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

Color.—Transparent in life.

Habitat.—Estuarine waters, especially in beds of submerged vegetation; water's edge to (rarely) 8 fathoms. Salinity of 3‰ is apparently lethal (Nagabhushanam, 1961).

Type locality.—Atlantic coast of United States.

Known range.—Barnstable County, Mass., to Cameron County, Tex. (from specimens examined by Holthuis, 1952). Literature records: Gaspé, Quebec, Canada, to Rio Champoton and near Progreso, Yucatan, Mexico (Holthuis, 1952).

Remarks.—Correct identification of the species of *Palaemonetes* occurring on the east coast of the United States was not possible until Holthuis (1949) introduced his key. As Holthuis (1952) pointed out, two names, *vulgaris* and *carolinus*, were applied indiscriminately to three species but the description of *carolinus* was actually based on a specimen of *vulgaris*; hence, this name is a synonym of *vulgaris*. With the status of *vulgaris* stabilized, Holthuis went on to show that two

other closely related and newly described species, *intermedius* and *pugio*, occupy much the same habitat and geographic range as *vulgaris*. An unfortunate but natural result of such confusion is that the voluminous literature on "*vulgaris*" undoubtedly concerns all three species in unknown ways, and all such literature must now be viewed with reserve.

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

The breeding season for the species in Virginia and the Carolinas extends from April to mid-October. Larval stages of *P. vulgaris* have been described by Broad (1957a) and are summarized below under the account for *P. pugio*.

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

Eggs are released simultaneously from both oviducts in a continuous stream. Fertilization is external and, because sperm cells of decapod crustaceans in general are nonmotile, it was suggested that entry of the sperm cell precedes development of the egg membranes in all decapods.

All parts of the eggshell are produced by the ovum or the embryo. The first membrane is developed upon contact with water. The second is developed about half an hour after spawning, and the third about 12 hours after spawning in fertile eggs only. The fourth and last membrane is an embryonic molt skin.

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

Since the early 1930's much experimental work has been done on the endocrine system in relation to color control in *Palaemonetes* assumed to be *vulgaris*. The shrimp has been found to have four kinds of pigment under independent hormonal control—red, yellow, white, and blue. These pigments are mediated through the eyes by the background on which the animal is found. The source of the hormones is principally the sinus gland in the eyestalk and the central nervous organs (Brown, 1933, 1935a, 1935b, 1948; Brown, Finger-man, and Hines, 1952; Brown, Hines, and Finger-man, 1952; Brown, Webb, and Sandeen, 1952). Persons interested are referred to the source material, for the conclusions are too detailed for adequate summary here.

Palaemonetes (Palaemonetes) intermedius Holthuis

Figure 48

Palaemonetes (Palaemonetes) intermedius Holthuis, 1949, p. 94, fig. 2, j-1.—Holthuis, 1952, p. 241, pl. 55, figs. a-f (rev.).

Recognition characters.—Rostrum reaching to or somewhat beyond end of antennal scale, tip directed upward making upper margin more or less concave; upper margin with 7 to 10 (usually 8 or 9) teeth, first tooth placed behind orbital margin, second tooth before or just over posterior orbital margin; teeth rather evenly divided over

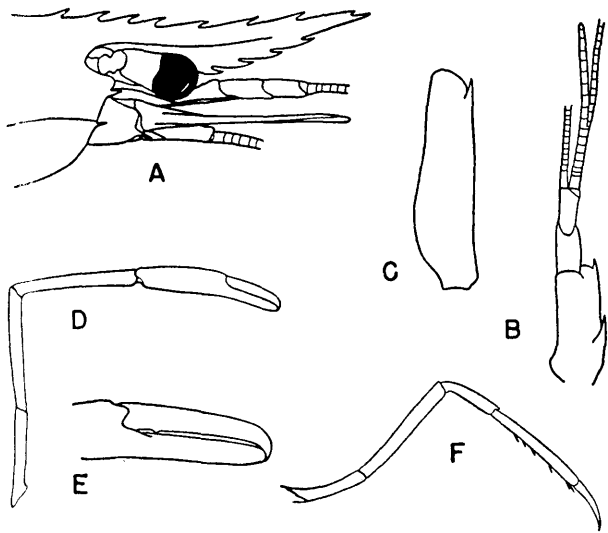


FIGURE 48.—*Palaemonetes (Palaemonetes) intermedius* Holthuis. A, anterior part of body in lateral view; B, antennule; C, antennal scale; D, second leg of female; E, fingers of second leg of female; F, third leg; A–F $\times 4.75$ (after Holthuis, 1952).

dorsal margin up to often bifurcate tip, distal teeth more widely spaced than proximals; lower margin with 4 or 5 (occasionally 3) teeth. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle as in *vulgaris*, basal article with slender stylocerite reaching about to middle of article, anterolateral spine of article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 7 to 10 joints; free part of shorter ramus with 7 to 12 joints, longer than fused portion. Antennal scale slender, 3 to nearly 4 times as long as broad in females, even more slender in males; outer margin straight or slightly concave; terminal tooth reaching about to end of lamella.

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

as long as merus. Third leg with propodus less than twice as long as carpus. Fifth leg with propodus about three times as long as dactyl, twice as long as carpus.

Abdomen smooth; pleura of fifth segment with tip rectangular or slightly acute; sixth segment 1.5 times length of fifth, somewhat shorter than telson. Telson with two pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by two pairs of spines, inner pair longest and between these, two feathered setae. Outer margin of uropodal exopod with a strong terminal tooth flanked by a slender movable spine medially.

Measurements.—Length of body: male, 30 mm.; ovigerous females, 20 to 42 mm.

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

Color.—Transparent in life.

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

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

Known range.—Long Island, N.Y., to Port Aransas, Tex. (from specimens examined by Holthuis, 1952). Literature records: Vineyard Sound to Aransas National Wildlife Refuge, Tex. (Holthuis, 1952).

Remarks.—The confused taxonomic status of this species in literature is discussed in the account for *P. vulgaris* and dealt with in more detail by Holthuis (1952). Ovigerous females have been found from February to April in Texas (Hedgpeth, 1950), and from May to September in Virginia and the Carolinas.

Palaemonetes (Palaemonetes) pugio Holthuis

Figure 49

Palaemonetes vulgaris: Hay and Shore, 1918, p. 393, pl. 27, fig. 5.

Palaemonetes (Palaemonetes) pugio Holthuis, 1949, p. 95, figs. 2, m–o.—Holthuis, 1952, p. 244, pl. 55, figs. g–l (rev.).

Recognition characters.—Rostrum reaching to or slightly beyond end of antennal scale; straight, sometimes slightly upturned at tip; dorsal margin with 7 to 10 (usually 8 or 9) teeth, distal teeth more widely spaced than proximal teeth, first

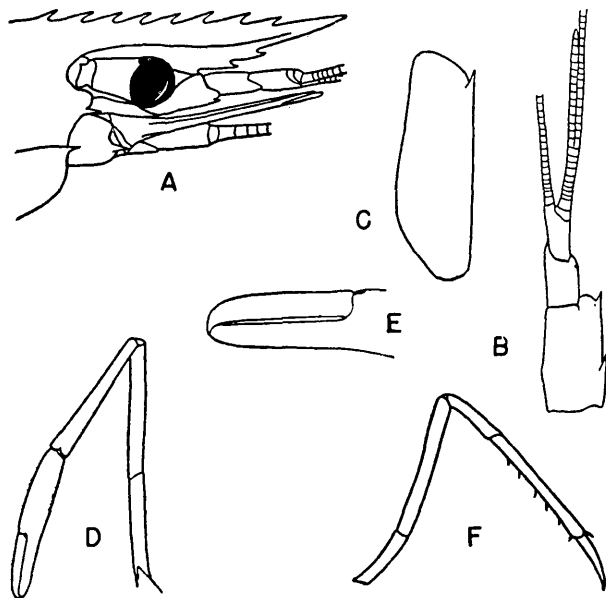


FIGURE 49.—*Palacmonetes (Palacmonetes) pugio* Holthuis.
A, anterior part of body in lateral view; B, antennule;
C, antennal scale; D, second leg of female; E, fingers
of second leg of female; F, third leg; A-F $\times 4.75$ (after
Holthuis, 1952).

tooth placed behind orbital margin, distal tooth placed at a distance from tip leaving space before tip unarmed; lower margin with 2 to 4 (usually 3) teeth, distal tooth also placed at distance from tip, tip dagger shaped. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle as in *vulgaris*; basal article with slender stylocerite reaching slightly beyond middle of article, anterolateral spine of article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 10 to 14 joints; free part of shorter ramus with 12 to 18 joints, longer than fused portion. Antennal scale 2.5 to 3 times longer than broad (length 3 times breadth in males); outer margin convex; terminal tooth strong, almost reaching end of lamella.

First legs not quite reaching tip of antennal scale; fingers as long as palm; carpus nearly twice length of chela and slightly longer than merus. Second legs stronger than first; in adult female, fingers reaching beyond scale, fingers more than half length of palm, cutting edges of both fingers

with no teeth, often gaping proximally; carpus 1.3–1.5 times length of palm but shorter than entire chela; merus as long as carpus. Male with second legs more slender and shorter than in female; fingers shorter than palm; carpus nearly as long as whole chela and as long as merus. Third legs with propodus twice length of carpus. Fifth leg with propodus about 2 times length of dactyl, 2.5 times as long as carpus.

Abdomen smooth; fifth abdominal segment with pleura ending in an acute tooth, sometimes extremely small; sixth segment half again as long as fifth, somewhat shorter than telson. Telson with two pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by two pairs of spines, inner pair longest, and between them two feathered setae. Outer margin of uropodal exopod with a strong terminal tooth flanked by a slender movable spine medially.

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

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

Color.—Transparent in life.

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

Type locality.—Lagoon near Cove Point Light, Chesapeake Bay.

Known range.—Essex County, Mass., to Port Aransas, Tex. (from specimens examined by Holthuis, 1952). Literature records: Cold Spring Harbor, Long Island, N.Y., to Corpus Christi, Tex.

Remarks.—The confused taxonomic status of this species in literature is discussed in the account for *P. vulgaris* and dealt with in more detail by Holthuis (1952).

Broad (1957a) worked out the larval development of *P. pugio* and *P. vulgaris*. He found mature individuals of both species were abundant in the Beaufort, N.C., area from April until mid-

October. Larval development of the 2 species is similar, and 10 zoeal stages and a postlarval stage were described for both. The chief difference between larvae of the two species is in the presence of a pair of chromatophores found on the second abdominal sternite of *P. pugio* but lacking in *P. vulgaris*. The number of larval stages and length of the developmental period may vary, and such variation is apparently due to availability of suitable food. In rearing *Palaeomonetes* with artificial diets, Broad (1957b) found that algae alone were not sufficient to promote survival; mixtures of plant and animal food were better, but best survival was obtained by feeding living *Artemia* nauplii. Frequency of molting and rate of development were directly correlated with amount of suitable food available.

Responses of the white chromatophores of *P. pugio* to light and temperature have been investigated by Fingerman and Tinkle (1956). The tendency of white pigment to disperse in bright light, especially on a white background, is normally antagonized by a tendency of the pigment to concentrate with increased temperature. This mechanism is interpreted as maintaining a steady state of white chromatophores in nature.

Pearse (1952b) reported *Probopyrus pandicola* (Parkard) from the gill chamber of this species in Texas.

Family Gnathophyllidae

Caridea with first two pairs of legs chelate, first pair smaller than second; carpus of second pair not subdivided. Rostrum short and toothed. Third article of third maxillipeds very broad. Mandibles simple. Second maxillipeds with short seventh article. The family contains but a single genus (Hay and Shore, 1918).

Genus *Gnathophyllum* Latreille, 1819

Armstrong, 1940, p. 6 (rev.).—Hemming, 1958b, p. 156.

Gnathophyllum modestum Hay

Figure 50

Gnathophyllum modestum Hay, 1917, p. 72.—Hay and Shore, 1918, p. 395, pl. 28, fig. 1.—Manning, 1963, p. 48, figs. 1-2.

Recognition characters.—Body short and thick; carapace with a moderate carina continuous in front with rostrum and extending about two-thirds of distance to posterior margin. Rostrum

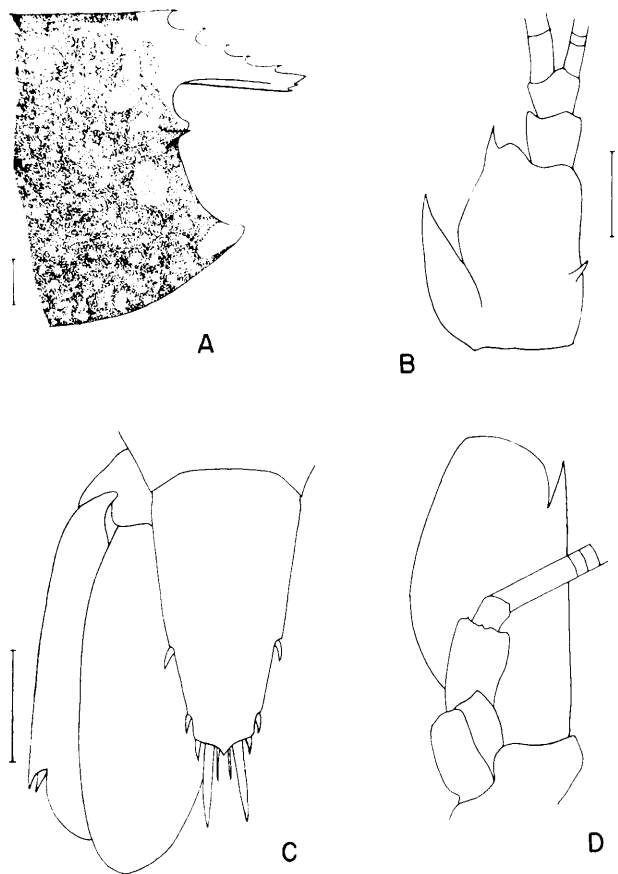


FIGURE 50.—*Gnathophyllum modestum* Hay. A, anterior portion of carapace, lateral view; B, antennular peduncle, ventral view; C, telson and left uropod; D, antennal scale; 1 mm. indicated. B and D to same scale (after Manning, 1963).

obliquely truncate dorsally and armed with five or six dorsal teeth; one or two small ventral teeth near tip; tip reaching to distal end of basal article of antennule. Suborbital angle prominent; antennal spine present; anterolateral angle strongly produced. Eyes rather large and with a prominent, conical, black protuberance on cornea. Antennular peduncles with basal article large, stylocerite reaching beyond middle of article, a spine at anterolateral corner of article; second article with a similar but smaller and blunter anterolateral spine; second and third articles of about equal length; outer antennular flagellum bifurcate, upper ramus longer and thinner than lower ramus. Antennal scale reaching beyond antennular peduncles, lateral margin almost

straight, terminating in a spine, lamella of scale rounded distally, slightly exceeding spine.

Third maxillipeds with merus and carpus broad, closing whole front of buccal region; two terminal articles flattened, much more slender, and extended straight forward. Second pair of legs much stronger than first, exceeding rostrum by length of chela; fingers more than half length of palm. Last three pairs of legs with dactyls bifurcate.

Abdomen with last three segments abruptly smaller than preceding segments and strongly flexed. Telson with a pair of marginal spines at about distal third and a minute pair near tip, tip with median point and with three pairs of spines, intermediate pair longest.

Measurements.—Length of ovigerous holotypic female, 21 mm.

Color.—Body deep brown with many scattered small yellow and a few larger orange spots; antennal scale, distal portions of rostrum and tail fan clear; orbital margins and eyestalks white; legs grading from brown proximally through purple to white distally but barred with purple on distal portion of some elements; markings of yellow below and on some articles of appendages (Manning, 1963).

Habitat.—Found around clumps of coral and sponges in shallow water; to 15 fathoms.

Type locality.—Beaufort, N.C.

Known range.—Beaufort, N.C.; Biscayne Bay, Fla.

Remarks.—This species, long known only from Hay's type specimen, has recently been reported from Florida (Manning, 1963). Manning reviewed the east American species of *Gnathophyllum*, pointing out the close similarity of *G. modestum* to the eastern Atlantic species *G. elegans*, and giving detail on the importance of color patterns in living material as diagnostic characters in the genus. Excellent figures accompany Manning's discussion.

Ovigerous females are known from Florida in June. The date of collection for Hay's specimen is unknown.

Family Alpheidae

Carapace smooth, with cardiac grooves; rostrum reduced; antennal and branchiostegal spines always absent; carapace almost always projecting

over eyes (*Automate* excepted). Antennular base cylindrical, basal article not longer than sum of other two articles. Antennal scale rarely longer than antennal peduncle. Mandible bipartite with palp of two points. Chela of first leg predominant, always large (usually asymmetrical); carpus short. Second legs weakly developed; carpus multiarticulate. Third to fifth legs with spinous propodi and simple or bifurcate dactyls; propodus of fifth leg with more or less well-developed brush of bristles in transverse to oblique rows. Abdomen usually with gradual curve, no pronounced bend at third segment; sixth segment short, broad, sexually dimorphic. (Adapted from Banner, 1953).

The biology of snapping shrimp occurring on the east coast of the United States has been reviewed by Knowlton (1960) and the reader is referred to this unpublished but useful work for more complete information than is included here.

KEY TO GENERA IN THE CAROLINAS

- a. Eyestalks completely exposed
Automate kingsleyi (p. 62).
- aa. Eyestalks covered by carapace.
 - b. Epipods present on at least first two pairs of legs
Alpheus (p. 63).
 - bb. Legs without epipods.....*Synalpheus* (p. 69).

Genus *Automate* de Man, 1887

Man, J. G. de, 1887, p. 529.

Automate kingsleyi Hay

Figure 51

Automate kingsleyi Hay, 1917, p. 72.—Hay and Shore, 1918, p. 387, text-fig. 10; pl. 26, fig. 7.

Recognition characters.—Carapace about half length of abdomen; subcylindrical; deeply emarginate dorsally behind eyestalks with rostrum a small median projection; anterior margin entire, produced farthest forward at base of antennular and antennal peduncles. Eyestalks contiguous, broad at base; cornea well developed with a minute point on anterior surface in lateral view. Antennular and antennal peduncles long; stylocerite scalelike, reaching to end of basal antennular article; second antennular article nearly equal in length to first; third very short. Antennal scale extending to middle of terminal article of antennal peduncle; lateral border ending in a small spine; lamella broadly rounded distally, equaling spine. Third maxilliped exceeding an-

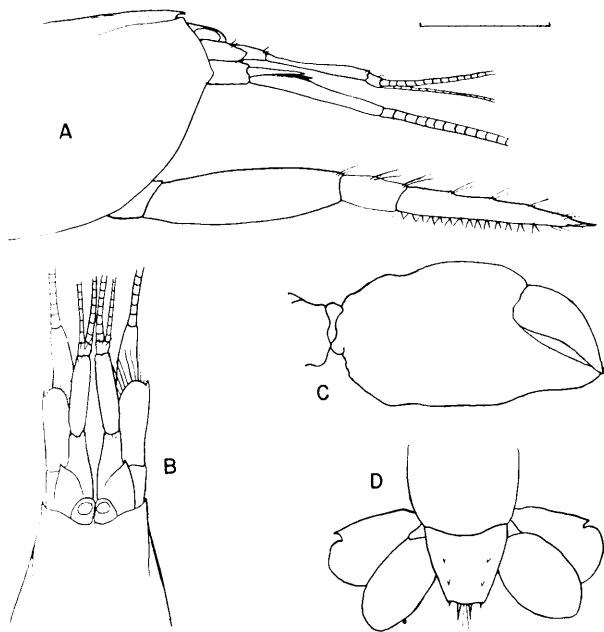


FIGURE 51.—*Automate kingsleyi* Hay. A, anterior part of ovigerous female in lateral view; B, anterior part of body in dorsal view; C, large chela; D, uropods and telson in dorsal view; 1 mm. indicated (C after Hay and Shore, 1918).

tennal peduncle by less than length of terminal article.

First pair of legs chelate, prismatic, unequal; larger one appearing somewhat rougher and stouter than smaller one; fingers slightly gaping, immovable finger in line with hand and broad at base; dactyl narrower and moderately curved; carpus short; merus nearly as long as dactyl. Second pair of legs nearly as long as first but slender, weakly chelate, and with carpus divided into five joints with proportions of 1 : 1.25 : 0.80 : 0.66 : 0.80. Third to fifth legs with dactyls simple.

Abdomen well developed; compressed; with strong pleopods. Telson tapering; truncate terminally, ending in two short lateral spines flanked medially by two longer spines and a median pair of feathered setae; dorsally armed with two pairs of spines, first pair at midlength, second at three-fourths length. Uropods with oval blades; lateral border of exopod deeply notched distally, border ending in a small tooth flanked medially by a strong movable spine.

Measurements.—Length of body: ovigerous females, 7 to 16 mm.

Color.—Almost transparent except for a small amount of red pigment on appendages and telson.

Habitat.—Unknown.

Type locality.—Shark Shoal breakwater, near Beaufort Inlet, N.C.

Known range.—Known only from and near type locality, and from Pelican Island, English Harbor, Barbados (Schmitt, 1924a).

Remarks.—Aside from the Barbados specimen, only three specimens from the Beaufort, N.C., area are known. The ovigerous type was taken July 9, 1916, and another ovigerous female on September 7, 1960. The third specimen is immature. Hay and Shore (1918) reported that the type remained alive in the laboratory for over a month, during which time the eggs dropped off and the specimen molted twice without appreciably increasing in size.

Genus *Alpheus* Fabricius, 1798

Banner, 1953, p. 46.—Hemming, 1958b, p. 108.

The status of the name *Alpheus* (and its confusion in usage with the name *Crangon*, at least among American workers during the first half of this century) was in doubt until nomenclatural stability was effected by the International Commission on Zoological Nomenclature (Opinion 334). The Official List of Generic Names in Zoology (Hemming, 1958b) now lists *Alpheus* Fabricius, 1798, as the correct generic name for the species here considered, and the Official Index of Rejected and Invalid Generic Names in Zoology (Hemming, 1958a) lists the suppressed generic names *Alpheus* Weber, 1795, and *Crangon* Weber, 1795, formerly applied to the species here considered.

KEY TO SPECIES IN THE CAROLINAS

- a. Orbital hoods of carapace with a small spine in front
formosus (p. 64).
- aa. Orbital hoods of carapace without a distinct spine.
 - b. Orbital hoods forming an anterior toothlike projection; large hand with a groove above and below along outer margin and between these grooves a thick tooth
normanni (p. 65).
 - bb. Orbital hoods rounded anteriorly; large hand broad and notched on both margins.
 - c. Base of rostrum passing gradually into lateral dorsal surface.....*heterochaelis* (p. 66).
 - cc. Base of rostrum with borders sharply defined
armillatus (p. 67).

Alpheus formosus Gibbes. Striped snapping shrimp

Figure 52

Alpheus formosus Gibbes, 1850, p. 196.—Verrill, 1922, p. 84, text-figs. 5d, 6a; pl. 20, fig. 3; pl. 23, figs. 5 a, b; pl. 29, figs. 4, a-u; pl. 25, figs. 6-6a.

Crangon formosus: Hay and Shore, 1918, p. 384, pl. 26, fig. 5.—Schmitt, 1935a, p. 144.

Recognition characters.—Rostrum beginning at posterior line of eyes and reaching about to second article of antennular peduncle; flat above; margins concave at base but regularly convergent anteriorly and with scattered stiff hairs; tip rounded, often bearing two or three minute spines. Carapace half length of abdomen, compressed, not grooved; orbital hoods each with an acute, anteriorly directed spine much shorter than rostrum; anterior margin emarginate below orbital hoods. Eyes completely covered by carapace. Antennular peduncles with scalelike stylocerite, slender tip reaching slightly beyond basal article; second article twice length of third; inner flagellum filiform, outer flagellum thick proximally, filiform distally. Antenna longer than body;

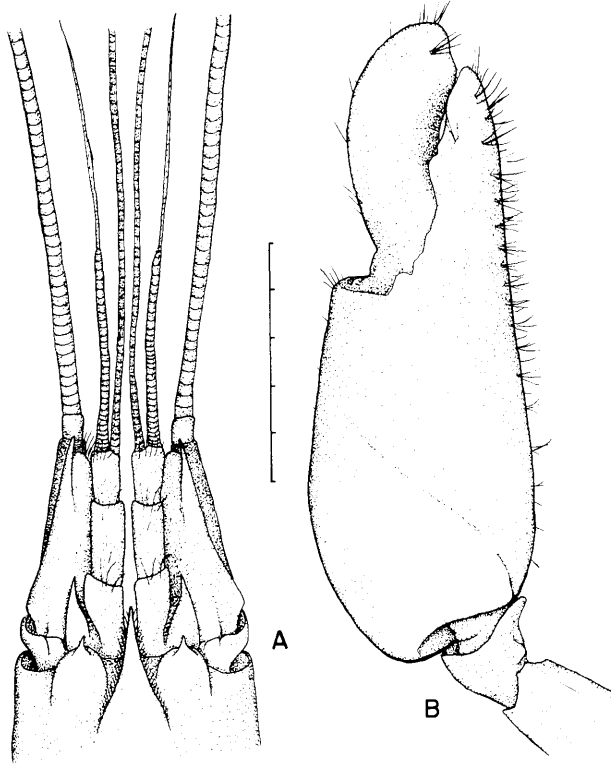


FIGURE 52.—*Alpheus formosus* Gibbes. A, anterior part of body in dorsal view; B, outer surface of large chela; 5 mm. indicated.

antennal scale with strong apical spine reaching to or beyond tip of antennular peduncle, spine separated from and exceeding lamella; a weak spine (basicerite) below near base of scale. Third maxillipeds with terminal joint hairy; slightly exceeding antennal peduncle.

First legs strongly chelate, very unequal. Larger leg compressed, smooth above and unnotched along margins; immovable finger acute, incurved at tip, shorter than stout and gradually arched, blunt dactyl; carpus short, convex above, with a distal tooth; merus with an acute distal spine. Smaller chela much more slender, long, and smooth, inner surface with a stout spine overhanging base of dactyl; immovable finger nearly straight, slender, somewhat turned up near tip; dactyl about half length of hand, nearly straight to about middle, then gently arched to tip, hairs arising from a nearly straight groove below ridge on both sides; inner surfaces of fingers with a slender groove and carina; fingers shutting closely. Second pair of legs slender; weakly chelate; carpus subdivided, with joints diminishing in length as follows (numbered from proximal end): 1, 5, 2, 3-4. Third to fifth legs with simple dactyls.

Telson with two pairs of dorsal spines at about one-third and two-thirds length; posterolateral corners with a pair of spines, medial spine much longer than lateral, distal margin with long hairs. Uropodal exopods with lateral margin ending in a black movable spine between two fixed spines; black spine remaining amber colored after long preservation.

Measurements.—Length of body: ovigerous females, 17 to 35 mm.

Color.—Color pattern conspicuous and characteristic; ground color yellowish or greenish brown finely speckled with orange; a narrow light stripe along middorsal line extending from distal end of antennular peduncle to base of telson, line light orange anteriorly merging into yellowish green and finally gray posteriorly, a brown stripe on each side dorsolaterally and below this another stripe of white, or colors similar to dorsal stripe, along each side followed by a stripe of light reddish brown and still another stripe of blue bordering abdomen; chelae greenish brown with orange red fingers; antennules, antennae, and walking

legs blue; telson and uropods white at base blotched and bordered with yellow.

Habitat.—Lives in holes and crevices in shell bars, stones, and dead corals; water's edge to 23 fathoms.

Type locality.—Key West, Fla.

Known range.—Near Beaufort, N.C., through West Indies to Santos, São Paulo, Brazil; Bermuda.

Remarks.—Ovigerous females have been taken off Venezuela in April, Beaufort, N.C., in July, Bimini in October, and Santos, Brazil, in June. Manner (1934) found metacercariae of *Heliocotyle nimia* encysted in muscles of *A. formosus* at Tortugas.

Alpheus normanni Kingsley. Green snapping shrimp

Figure 53

Alpheus affinis Kingsley, 1878a, p. 195.

Alpheus normanni Kingsley, 1878b, p. 93.

Alpheus packardii Kingsley, 1880, p. 417.—Verrill, 1922, p. 80, pl. 20, figs. 2-5; pl. 21, fig. 5; pl. 22, fig. 7; pl. 23, figs. 6, c-d; pl. 25, figs. 4, a, b; pl. 31, figs. 1, b-1, 2, b-u, 3, u, t (rev.).

Alpheus packardii: Hay and Shore, 1918, p. 385, pl. 26, fig. 4. Schmitt, 1935a, p. 144.

Recognition characters.—Rostrum with carina extending as far back as base of eyestalks, spiniform tip not reaching to base of second article of antennule. Carapace about two-thirds length of abdomen, somewhat compressed; cervical groove hardly evident; front with ocular hoods produced into an obtuse angle above each eye; anterior margin emarginate below ocular hoods. Eyes well developed but completely covered by carapace. Stylocerite scalelike with spiniform tip reaching about to end of basal article of antennule; third article much shorter than second; inner antennular flagellum slender, outer one shorter with proximal four-fifths enlarged. Antennae a little longer than body, slender; antennal scale reaching a little beyond end of antennular peduncle, lateral margin slightly sinuous with strong terminal spine separated from and exceeding lamella; a strong ventral spine (basicerite) near base of scale. Third maxillipeds slender, not reaching tip of antennal scale; terminal article with long hairs.

First legs strongly developed with chelae unequal. Larger leg broad and flattened; slightly sinuate along inner margin; outer margin with a longitudinal groove above and below, a ridge

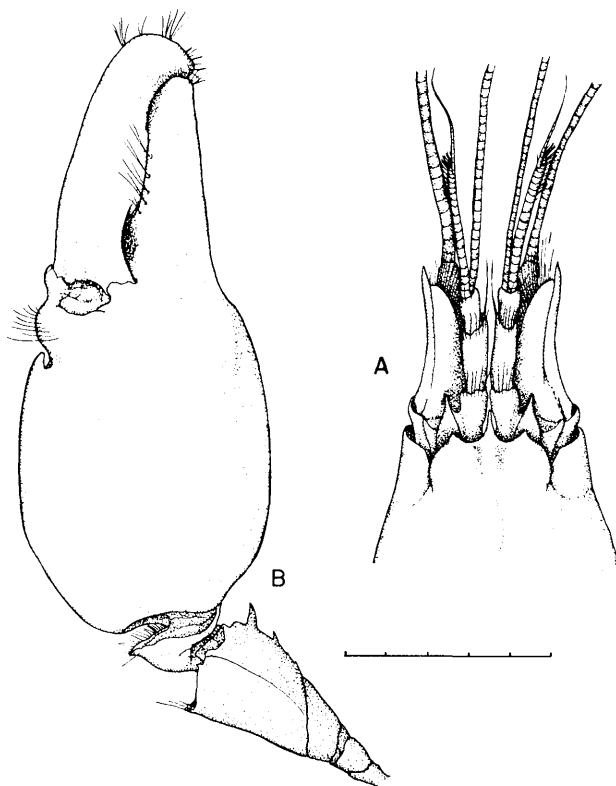


FIGURE 53.—*Alpheus normanni* Kingsley. A, anterior portion of body in dorsal view; B, large chela in ventro-lateral view; 5 mm. indicated.

between grooves ending in a strong tooth behind base of dactyl; dactyl heavy, curved, toothed at base. Smaller chela about half as wide and three-fourths as long as larger one; similarly formed but with a sharp spine above (and a small one below in males) at base of dactyl; no basal tooth on dactyl; sexually dimorphic fingers in males broad externally but with keeled, closely fitting opposed edges fringed by dense hairs; females with hand a bit hairy but fingers unornamented; carpus of both legs short, broad, irregularly cup shaped, merus with a spiniform tooth near distal end and one or two spines below, distal end cupped to receive carpus with leg extended. Second legs very slender, weakly chelate; with carpus subdivided, joints diminishing in length as follows (numbered from proximal end): 2, 1, 5, 3-4. Third to fifth legs with dactyls simple.

Abdomen somewhat compressed. Telson with sides slightly convergent distally; two pairs of dorsal spines, first pair at one-third, second at

two-thirds length; tip broadly rounded, a pair of spines at each posterolateral corner, distal margin heavily setose; a pair of anal tubercles beneath with accompanying cups on uropods forming locking devices. Uropods oval; exopod with lateral margin ending in a small spine flanked medially by a strong movable tooth.

Measurements.—Length of body: male, 26 mm.; ovigerous female, 16 mm.

Color.—Gray or dull green, sometimes with a median and lateral stripe of whitish often clouded or mottled with dark green or brown, a paler spot behind each eye; large chela dark green usually banded with yellowish brown or yellow on inner surface; smaller chela and other legs paler, often banded with dull gray or reddish; occasionally body banded with red and pale yellow, large chela with two pale bands, immovable finger blackish, dactyl reddish (various authors).

Habitat.—Shelly or rocky bottoms, in burrows in sand or on pilings in shallow water; common in saltier portions of estuaries; water's edge to 40 fathoms.

Type locality.—Key West, Fla.

Known range.—North Carolina through West Indies to Barbados, Curaçao, and Aruba; Alligator Harbor, Fla., to Sabine, Tex.; Bermuda; Sonora, Mexico (?).

Remarks.—This is one of the commonest snapping shrimps in the Beaufort, N.C., region. As Hay and Shore (1918) pointed out, this was probably the species called *Alpheus minor* in early lists for the area. The latter species is correctly referred to *Synalpheus minus* (Say) and is found only in offshore waters, a different habitat from that frequented by *Alpheus normanni*. Brooks and Herrick (1892) followed the older lists in calling this species *Alpheus minor* (*minus*) and illustrated the adult in color on plate 1 and larval stages on plates 16 and 17. They illustrated the first three larval stages, as well as stages in segmentation of the embryo, but their specific identifications are somewhat unreliable.

Ovigerous females have been taken through much of the annual cycle in various localities: January and March, Cuba; June, Louisiana; August, Bermuda, Louisiana, Mississippi; April to September in the Carolinas; November and December, Puerto Rico.

Alpheus heterochaelis Say. Big-clawed snapping shrimp

Figure 54

Alpheus heterochaelis Say, 1818, p. 243.—Verrill, 1922, p. 76, pl. 22, figs. 1, 2, 4, a-c; pl. 24, figs. 7, 7a; pl. 30, figs. 1-1a, 1t, 2a-2e; pl. 33, figs. 1, 2 (rev.).

Crangon heterochaelis: Hay and Shore, 1918, p. 386, text-fig. 8, pl. 26, fig. 6.—Schmitt, 1935a, p. 144.

Recognition characters.—Rostrum carinate, extending back about as far as base of eyestalks; tip not reaching to base of second article of antennular peduncle. Carapace more than half length of abdomen, somewhat compressed; without grooves; front produced into a rounded ocular hood over each eye; rostro-orbital depressions passing gradually into dorsal surface; emarginate below eye on anterior border. Eyes relatively small, covered by carapace. Antennular peduncles with scalelike stylocerite, minute spine at tip not reaching end of basal article; second article twice length of third; inner flagellum filiform, about half length of antenna; outer flagellum with proximal two-thirds thickened. Antennae a little longer than body; antennal scale with strong apical spine reaching slightly beyond antennular

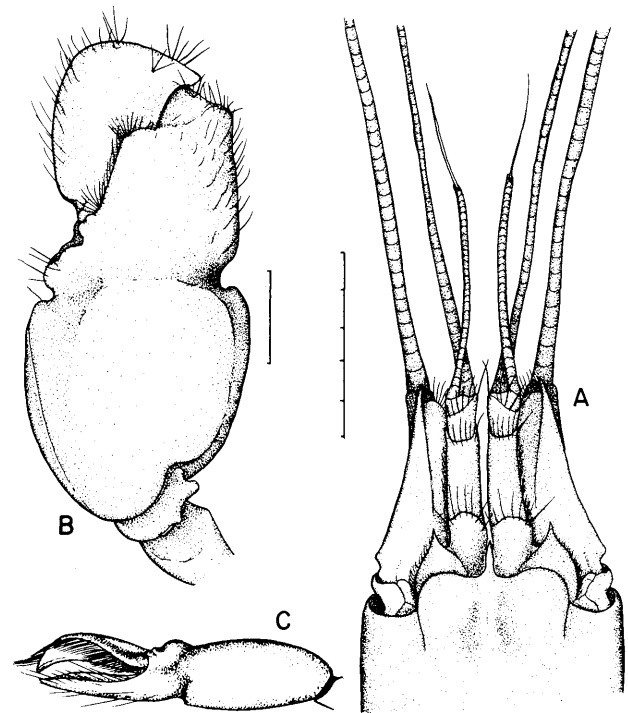


FIGURE 54.—*Alpheus heterochaelis* Say. A, anterior portion of body in dorsal view, 5 mm. indicated; B, large chela in dorsal view, 5 mm. indicated; C, small chela of male (after Verrill, 1922).

peduncle, spine separated from and slightly exceeding lamella; a weak spine (basicerite) below near base of scale. Third maxillipeds with terminal article hairy; slightly exceeding antennal peduncle.

First legs strongly chelate, very unequal. Larger chela thick; outer and inner margins deeply notched near base of fingers; upper and lower surfaces with irregular shallow grooves; dactyl broad, heavy, strongly curved, with large basal tooth. Small chela sexually dimorphic; in male broad, elongate; proximal dorsal area of palm bounded by an impressed line, upper margin notched distally; dactyl flattened and expanded on outer surface; opposed edges of fingers keeled, closely fitting, fringed by dense hairs. Fingers of small chela in both sexes weaker, less curved, and more hairy than in large chela; carpus short; merus smooth. Second legs slender, weakly chelate; carpus subdivided with joints diminishing in length as follows (numbered from proximal end): 1, 2, 5, 4, 3. Third to fifth legs with simple dactyls.

Abdomen compressed, smooth, tapering. Telson with subparallel sides and rounded tip; dorsal surface with two pairs of movable spines, first pair at about midlength, second at a little less than three-fourths length; a pair of spines at each posterolateral corner, medial spine longest; distal margin heavily setose, a pair of anal tubercles beneath with accompanying cups on uropods forming locking devices. Uropodal exopods with lateral border ending in a fixed spine flanked medially by a longer movable spine.

Measurements.—Length of body: male, 40 mm.; female, 50 mm.

Color.—Dark translucent green, slightly flushed with purple on sides of carapace; white markings on chelipeds; walking legs pale red; tips of uropods blue with narrow border of orange on distal margin, outer blade with patch of red just above blue, and a narrow white border; articular surfaces and joints of abdominal segments, and a small streak along cervical groove, white.

Habitat.—Lives among broken shells and stones or in burrows in mud among shells; water's edge to 16 fathoms.

Type locality.—Amelia Island, Nassau County, Fla. (Holthuis, 1959, restr.).

Known range.—Near Hatteras, N.C., to Aransas County, Tex.; Colon, Panama; through West Indies to Iguape, São Paulo, Brazil; Bermuda (Holthuis, 1956).

Remarks.—Brooks and Herrick (1892) gave a good colored figure of this species (plate 2), as well as a series of figures of segmenting eggs and developing larval stages. Because the material they studied originated from both North Carolina and the Bahamas, there is some doubt as to its identity, but a total of four larval stages were illustrated.

This is the largest snapping shrimp found in the Carolinas. It is nearly as abundant as *A. normanni*.

Ovigerous females have been taken through much of the annual cycle in various localities: February and April in Surinam (Holthuis, 1959); March in Panama and Texas; April and May in Louisiana and Florida; July in North Carolina; August and September on the Gulf Coast; October to January in Cuba, Puerto Rico, and Bonaire.

Alpheus armillatus Milne Edwards. Banded snapping shrimp

Figure 55

Alpheus armillatus H. Milne Edwards, 1837, p. 354.—Verrill, 1922, p. 73, text-figs. 5a, 6b; pl. 20, fig. 4b; pl. 21, figs. 4, 4a; pl. 26, figs. 1-1d; pl. 23, fig. 4; pl. 27, figs. 1-1s (rev.).

Crangon armillatus: Hay and Shore, 1918, p. 386, text-fig. 9; pl. 27, fig. 1. Schmitt 1935a, p. 142.

Recognition characters.—Rostrum in form of a narrow raised crest from base to tip, projecting beyond orbital hoods, widening abruptly just behind eyes into a triangular area with borders slightly concave and distinctly limiting rostrorobital depressions, slightly overhanging depressions in adult specimens. Carapace compressed; orbital hoods prominent in front with a slight obtuse anterior lobe, but without spine or denticle, and with a strong emargination below eyes. Eyes entirely covered by carapace. Antennules with stylocerite large, scalelike, not very acute, and not reaching to end of basal antennular article; second article longer than third; inner flagellum filiform; outer flagellum thickened in about proximal half. Antennal scale with a strong terminal spine equal to or extending beyond antennal peduncle, scale distinctly curved outward in distal two-thirds; a small spine (basicerite) near base of scale. Third

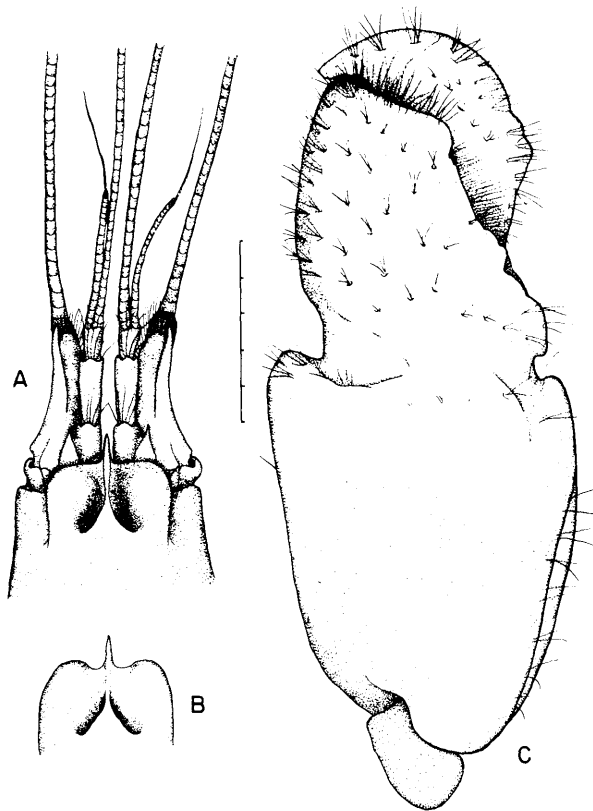


FIGURE 55.—*Alpheus armillatus* Milne Edwards. A, anterior portion of body in dorsal view; B, rostral region in dorsal view with light showing from posterior; C, large chela in dorsal view; A–C, 5 mm. indicated.

maxilliped covered with long hairs distally, reaching about to end of antennal peduncle.

First legs strongly chelate, hairy, unequal. Larger chela thick; outer and inner margin deeply notched near base of fingers; upper and lower surfaces with irregular shallow grooves; dactyl broad, heavy, curved, with large basal tooth. Small chela slender; cutting edges of fingers closely fitting, dactyl with a small tooth at base, dactyl in males lacking setose crests and expanded external surface characteristic of *A. heterochaelis*. Second legs long, slender, weakly chelate, with part of merus reaching beyond rostrum; carpus subdivided with joints diminishing in length as follows (numbered from proximal end): 1, 2, 5, 3–4. Third to fifth legs with simple dactyls.

Abdomen smooth, compressed. Telson with two pairs of dorsal spines, first pair at one-third, second at two-thirds length; sides somewhat

convergent distally, tip rounded, with a pair of spines at each posterolateral corner, medial spine twice length of outer spine. Uropodal exopod with outer margin ending in a small spine flanked medially by a larger spine.

Measurements.—Length of body: ovigerous females, 31 to 38 mm.

Color.—Body with dark gray or brown ground color, crossed by nine conspicuous lunate or elliptical spots or bands of translucent white equal in width to intervening dark bands; carapace with three white bands, third one at posterior margin; abdomen with six bands, first blending with last on carapace; abdominal bands usually whiter or more clearly defined than bands on carapace; abdomen often dark green with spots bordered by line of orange; uropods and telson usually with a broad crossband and sometimes tipped with orange; chelae thickly speckled with dark gray, whitish bands above, tipped with pale pink or white; antennal peduncles grayish, flagella and walking legs orange yellow banded with white (Verrill, 1922).

Habitat.—Under rocks and shells or in holes in rocks; shallow water.

Type locality.—West Indies.

Known range.—North Carolina, through West Indies to Cananéia, São Paulo, Brazil; Bermuda (Holthuis, 1956).

Remarks.—This species closely resembles *A. heterochaelis*, its similar sized and (in the Carolinas) much more abundant congener. *Alpheus armillatus* is named for its conspicuously banded body, but in preserved material it can be distinguished from similar species by the distinctive form of the rostrum and from *A. heterochaelis* males by the lack of the specialized dactyl on the small first chela.

The species is rarely taken in the Beaufort region of North Carolina. Hay and Shore (1918) found males and females living in pairs under rocks at Fort Macon. Ovigerous females are known from only the first half of the annual cycle: March, Panama; April, Venezuela; May, Barbados; June, Florida and Brazil; August, Bermuda.

Pearse (1932b) reported encysted larvae of *Rhyncobothrius* in viscera of *A. armillatus*.

Coonfield (1940) observed the chromatophore system of this shrimp in one of the early studies

of this kind, showing that it reacts to different backgrounds under varying light conditions.

Hess (1940, 1941) demonstrated that *A. armillatus* is sensitive to light in many regions of the body, regardless of the amount of time elapsed since the preceding molt. At Tortugas, he found that diurnal molting in this shrimp is apparently controlled by daily temperature changes, molting occurring when the temperature rises to or above 29° C. Animals in constant temperature failed to exhibit diurnal molting as did ovigerous females.

Darby (1934) studied regeneration of chelae in *A. armillatus* and *Synalpheus longicarpus* together with determination of right or left handedness. He found that in development of chelae a stage was reached that permitted determination of which side would have a large chela. Equal chelae were produced experimentally and were of three varieties: (1) both small (pinch claws); (2) both large (snap claws); and (3) both intermediate.

Darby offered an hypothesis, involving two substances and a metabolic condition, which could explain the regenerative phenomena in these and allied crustaceans. In such animals, a substance A is produced which controls production of pinch claws; but at certain stages in the intermolt cycle a substance B is produced, for a limited time, and is concentrated in whichever claw is regenerating or already modified as a snap claw. This circumstance will produce or reinforce production of a snap claw. Chance alone is responsible for whether a snap claw will be on one side or the other, or whether the animal will be symmetrical. Also, time at which regeneration occurs depends on chance.

Genus *Synalpheus* Bate, 1888

Banner, 1953, p. 26.—Hemming, 1958b, p. 161.

KEY TO SPECIES IN THE CAROLINAS

- a. Dactyls of third, fourth, and fifth legs with two very unequal hooks, ventral strongest (broadest); an inconspicuous, obtuse supernumerary process proximal to ventral hook.....*fritzmuelleri* subsp. (p. 69).
- aa. Dactyls of third to fifth legs with two hooks approximately equal in width at base.
 - b. Dactyls long and slender, hooks continuing general direction of axis of dactyl; stylocerite longer than basal article of antennular peduncle; lamella of antennal scale present.

c. Frontal teeth more or less equilaterally triangular, at times with concave margins, but never with an inferior vertical prolongation to rostrum; basicerite strongly spinous above

.....*minus* (p. 70).

cc. Frontal teeth always longer than wide, spinous; rostrum armed with a ventral prolongation which embraces ocellary beak; basicerite unarmed above.....*townsendi* (p. 72).

bb. Dactyls short, hooks strongly curved, ventral one usually bent at considerable angle to axis of dactyl; stylocerite not exceeding first article of antennular peduncle; antennal scale lacking lamella in male, small in female.....*longicarpus* (p. 73).

Synalpheus fritzmuelleri Coutiere

Figure 56

Synalpheus fritzmuelleri Coutiere, 1909, p. 35, fig. 18.—Verrill, 1922, p. 97. Schmitt, 1935a, p. 148.

Recognition characters.—Rostrum slender, compressed, acute from dorsal view, a little longer than orbital spines, reaching to midlength of visible portion of basal antennular article. Orbital spines wide at base, acuminate; margins incurved. Eyes completely covered by carapace. Antennular peduncle with stylocerite of basal article reaching

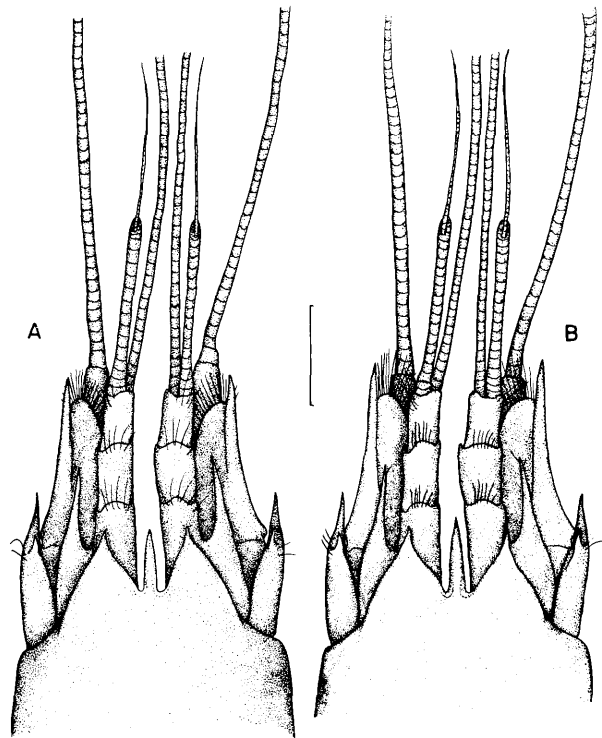


FIGURE 56.—A, *Synalpheus fritzmuelleri* Coutiere, anterior portion of animal in dorsal view; B, *Synalpheus fritzmuelleri elongatus* Coutiere, anterior portion of animal in dorsal view; 1 mm. indicated.

to middle of second article; third article slightly shorter than second; inner flagellum filiform outer bifurcate beyond about eighth joint, thickened proximally. Spine of antennal scale equaling terminal article of antennal peduncle, both reaching a little beyond antennular peduncle, spine separated from and exceeding narrow lamella distally; basicerite with a short, sharp lateral spine nearly as long as stylocerite; above it a smaller, acute, secondary spine.

First pair of legs chelate, unequal. Large chela ellipsoidal, only a little swollen in middle; a small obtuse tubercle on distal dorsal margin; width of palm about one-third total length of chela; dactyl heavy, strongly arched above; immovable finger narrow at tip; carpus short and wide, prolonged downward and inward; merus stout, superior margin ending distally in a sharp angular point. Smaller chela similar in form; fingers pointed; carpus short, cup shaped; merus like that of larger chela. Second legs slender, weakly chelate; carpus subdivided, first joint about equal to remaining four. Third to fifth legs with bifurcate dactyls, hooks unequal; outer one thinner and a little longer, regularly curved, sharp; inner one wider at base, strongly divergent, curved inward; proximal to inner hook a slight obtuse protuberance or rudimentary spur.

Telson broad, tapering, obtusely rounded distally; each posterior angle with a pair of unequal spines; two pairs of small dorsal spines, first pair at midlength, second at three-fourths length. Uropodal exopods with lateral margin ending in a notch with a fixed spine on each side, a longer movable spine between them.

Measurements.—Length of body: ovigerous female, 22 mm.

Variations.—In the subspecies *S. f. elongatus* Coutiere (1909, p. 37, fig. 19) the lateral spine of the antennal scale greatly exceeds the terminal article of the antennal peduncle, and the rostrum is decidedly longer than the ocular spines. In the subspecies *S. f. carolinensis* Verrill (1922, p. 99, pl. 22, fig. 6; pl. 39, figs. 1-1d) and *S. f. caribaea* Verrill (1922, p. 98, text-fig. 8; pl. 39, figs. 3a-3c) the basicerite is shorter than in typical specimens.

Color.—*Synalpheus fritzmuelleri*: chela varying shades of green, darker toward extremities of fingers; body more or less colorless, specked with

quite numerous tiny red chromatophores. *Synalpheus fritzmuelleri elongatus*: similar to preceding; chelipeds and second legs blue, except anterior part of chela light green (Schmitt, 1930).

Habitat.—Often found living in sponges; low tide mark to 28 fathoms.

Type locality.—*Synalpheus fritzmuelleri*, Marco, Fla.; *S. f. elongatus*, Mouth of Bull Creek, S.C.

Known range.—Typical *fritzmuelleri*: Nege, Greenland (Stephensen, 1950); off Beaufort, N.C., to Port Aransas, Tex.; West Indies to Curaçao; Old Providence Island; Tres Marias Archipelago, Mexico; Bermuda. Subspecies *elongatus*: off Beaufort, N.C., to Florianopolis, Santa Catarina, Brazil, including Jamaica and Barbados; Tres Marias Archipelago, Mexico. Subspecies *carolinensis*: Fort Macon, N.C. Subspecies *caribaea*: Dominica.

Remarks.—Distribution of the named subspecies and varieties of *Synalpheus fritzmuelleri* shows that modern revisionary work in the Western Atlantic is needed. Until thorough study is made, the various names must be retained, but it is likely that the present designations do not adequately explain local populations which parallel each other at widely separated locations. As Banner (1953) pointed out, earlier workers, with only a few specimens from these widely separated localities, naturally tended to name the variants, the range of variation being then unknown. Varietal names, therefore, must be regarded as conditional. Verrill (1922, p. 89) may have concurred for he quoted Stebbing's dim view of naming infinite variations but proceeded to name varieties anyway.

In the Carolinas, this species lives on offshore reefs (Pearse and Williams, 1951) in large sponges. Specimens may be found in beach drift after severe storms. Ovigerous females of typical *fritzmuelleri* are known from the Carolinas in February, and June to October, indicating a long breeding season. Ovigerous females of *S. f. elongatus* are known from Barbados in May, and North Carolina in June and July.

Synalpheus minus (Say)

Figure 57

Alpheus minus Say, 1818, p. 245.

Synalpheus minus: Hay and Shore, 1918, p. 382, text-fig. 5; pl. 26, fig. 3 (rev.).—Verrill, 1922, p. 102, pl. 21, fig. 1; pl. 23, fig. 3; pl. 25, fig. 3; pl. 31, fig. 4; pl. 33, figs. 4, 4a; pl. 36, figs. 1-1d, 2; pl. 47, figs. 1-1c, 2; pl. 48, figs. 3-3c (rev.).—Schmitt, 1935a, p. 149.

Recognition characters.—Front of carapace with three teeth each in form of equilateral triangle; rostrum usually a little wider at base, compressed and sometimes slightly longer than orbital teeth. Eyes completely covered by large orbital hoods. Basal article of antennular peduncle with stylocerite reaching to distal third of second article; third article half length of second; second of intermediate length; inner flagellum filiform, outer flagellum thickened proximally. Antennal scale narrow, inner edge regularly curved; lateral spine a little longer than antennular peduncle, separated from and exceed-

ing lamella; basicerite reaching to distal end of basal antennular article, above it a prominent secondary spine.

First legs chelate, unequal, thicker in male than in female. Large chela ovoid; palm about 2.5 times length of fingers, anterior dorsal margin with a strong, sharp tooth at inner side and a blunter tooth on lateral and ventral side near base of dactyl; dactyl broad, larger than immovable finger, tip obtuse, cutting edge a little sinuous, a large tooth at base, dorsal edge curved distally; immovable finger with tip nearly straight, inner edge a little sinuous. Smaller chela elongate, slender, about one-third length of larger; fingers a little shorter than palm, with tufts of hair, acute at tips and curved a little downward; palm narrowly elliptical, surface plain. Second legs slender, weakly chelate; carpus subdivided with joints diminishing as follows (numbered from proximal end): 1, 5, 2-3-4.

Telson with sides slightly sinuous, tip broadly rounded; two pairs of dorsal spines, first pair at about midlength, second pair at about three-fourths length; distal margin with a pair of spines at each posterolateral corner. Uropodal exopods with lateral margin ending in notch armed with two spines separated by a longer movable spine.

Measurements.—Length of body: female, 35 mm.

Color.—Body translucent, yellowish white; large chela white or translucent gray, fingers orange, tips red; banded near base of fingers with white in female, white tipped with green in male.

Habitat.—Lives in dead corals and commensally in sponges; shallow water to 37 fathoms.

Type locality.—Southern [United] States.

Known range.—Near Cape Hatteras, N.C., through West Indies to Alagoas, Brazil; Bermuda.

Remarks.—A number of authors, among them Hay and Shore (1918) and Verrill (1922), have pointed out that Brooks and Herrick (1892) erroneously called *Alpheus normanni* (= *packardii*) by the name *A. minus* in their profusely illustrated monograph. The true *Synalpheus minus* was not treated by them, however, and, at least in the Beaufort, N.C., area, was not available to them in the harbor area studied.

A long breeding season is indicated for this species. Ovigerous females have been taken from

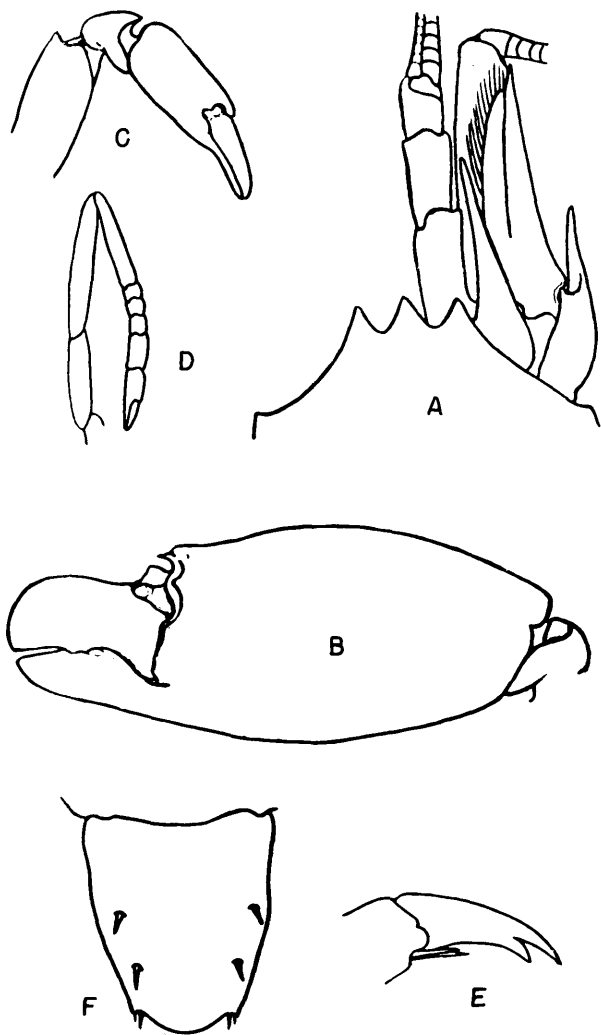


FIGURE 57.—*Synalpheus minus* (Say). A, anterior part of body in dorsal view, with appendages of right side; B, large chela; C, small first cheliped; D, second leg showing subdivided carpus; E, dactyl of third leg; F, telson in dorsal view (after Coutiere, 1909).

February to November in various localities from North Carolina to the Gulf coast; in April in Bermuda; and September in Venezuela. Adults usually occur in pairs (Wass, 1955).

Synalpheus townsendi Coutiere. Small snapping shrimp

Figure 58

Synalpheus townsendi Coutiere, 1909, p. 32, figs. 14-17; Hay and Shore, 1918, p. 384, pl. 26, fig. 1 (rev.).—Verrill, 1922, p. 100 (rev.).

Recognition characters.—Rostrum slender, 1.5 times as long as lateral teeth and reaching usually to end of proximal third of second article of antennular peduncle, armed with a ventral prolongation embracing ocellary beak. Teeth on orbital hoods slender; eyes completely covered by hoods. Basal antennular article with stylocerite reaching about as far as rostrum; third article about half length of second; inner flagellum filiform, outer flagellum thickened proximally, bifurcate beyond fourth joint. Antennal scale with strong, slender lateral spine separated from and exceeding lamella distally, spine reaching about to or beyond end of antennal peduncle; basicerite well developed, angled above but lacking dorsal spine, extremity reaching to distal third of basal antennular article.

First pair of legs chelate, very unequal. Large chela with a small, acute dorsal spine at distal margin of palm; upper margin of dactyl elevated into a thick crest; carpus small, irregularly shortened; merus with dorsolateral margin convex, ending in a hooked spine. Small chela one-third length of large one; no brush of hairs on dactyl. Second pair of legs slender, weakly chelate; carpus subdivided, first joint longer than others combined. Third to fifth legs with bifurcate dactyls, both hooks nearly parallel, ventral one narrower and much shorter than dorsal.

Abdomen compressed. Telson with sides somewhat convergent; posterior angles sharp and each provided with a pair of spines, inner spine longer than outer; two pairs of strong dorsal spines, first pair at one-third, second at two-thirds length. Uropods ovate, exopod with lateral margin ending in a notch with a strong fixed spine at its outer and inner angles, between these spines a longer movable spine.

Measurements.—Length of body: ovigerous females, 13 mm.

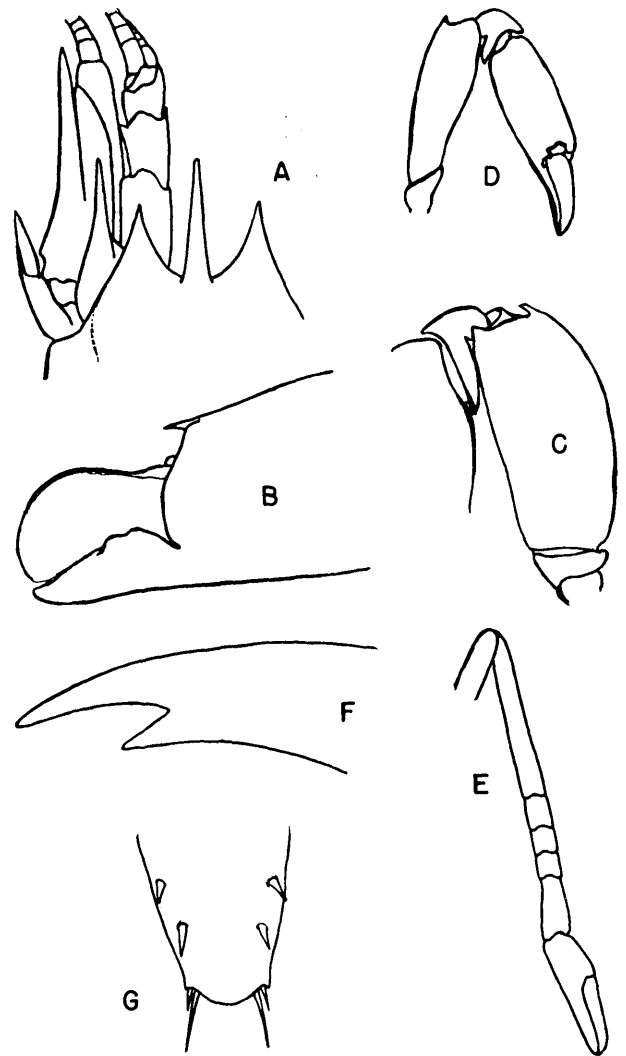


FIGURE 58.—*Synalpheus townsendi* Coutiere. A, anterior part of body in dorsal view, with appendages of left side; B, tip of large chela; C, large cheliped, merus, carpus and proximal end of propodus; D, small first cheliped; E, second leg showing subdivided carpus; F, dactyl of third leg; G, telson in dorsal view (after Coutiere, 1909).

Variations.—The rostrum is variable in length, often shorter than as described above.

Color.—Body and legs translucent pinkish red; large chela pink, changing to green on fingers.

Habitat.—Often found in large sponges; low tide mark to 56 fathoms.

Type locality.—Gulf of Mexico, Albatross station 2373.

Known range.—Off Beaufort, N.C., to Yucatan; through West Indies to Bahia, Brazil; Bermuda.

Remarks.—This species has been taken from offshore reefs in North Carolina at depths of 7 to 8 fathoms (Pearse and Williams, 1951), and from sponges at depths of 16 to 20 fathoms. Wass (1955) remarked that the species seems less dependent on sponges than other members of the genus taken in the Alligator Harbor area of Florida.

Ovigerous females have been taken from the Carolinas in February and August; Obregon, Mexico, in July and August; and Venezuela in September.

Synalpheus longicarpus (Herrick)

Figure 59

Alpheus saulcyi var. *longicarpus* Herrick [in part], 1892, p. 383.

Synalpheus longicarpus: Hay and Shore, 1918, p. 383, text-fig. 6; pl. 26, fig. 2 (rev.).—Verrill, 1922, p. 113, pl. 25, figs. 1a–1h; pl. 34, figs. 3, 3c; pl. 36, figs. 5, 5a (rev.).

Recognition characters.—Rostrum carinate, slender, and slightly longer than triangular, obtuse orbital hoods, reaching about to middle of basal antennular article; space between rostrum and hoods U-shaped, broadest in females. Eyes small, completely covered. Basal article of antennular peduncle with short stylocerite reaching to distal third of article; second article one-third longer than third article; inner flagellum filiform, outer branching at seventh joint, thickened proximally. Terminal article of antennular peduncle exceeding antennular peduncle; antennal scale with strong terminal spine separated from and exceeding rudimentary lamella distally; spine variable in length, often exceeding antennular peduncle by half length of distal article; lamella of scale rudimentary in males, small and variable in females; basicerite slender, acute, with an angle but no accessory spine above, tip reaching to end of second article of antennular peduncle.

First legs chelate, very unequal. Large chela elongate, somewhat ovate, about 2.75 times longer than broad; margins somewhat convex; posterior end swelled and produced backward beyond articulation with small, short carpus inserted below central axis of palm; anterior dorsal margin of palm with small, acute spine near base of dactyl; dactyl somewhat oblique at end, toothed at base,

about one-fourth to one-fifth length of chela. Small chela elongate, about one-third length of larger; dactyl elongate, gently arched dorsally, a dense tuft of erect hairs on dorsal surface along most of length, cutting edge nearly straight with two apical teeth; immovable finger with three teeth, apical one stronger. Second pair of legs slender, weakly chelate; stronger in male than in female; carpus subdivided, first joint shorter than

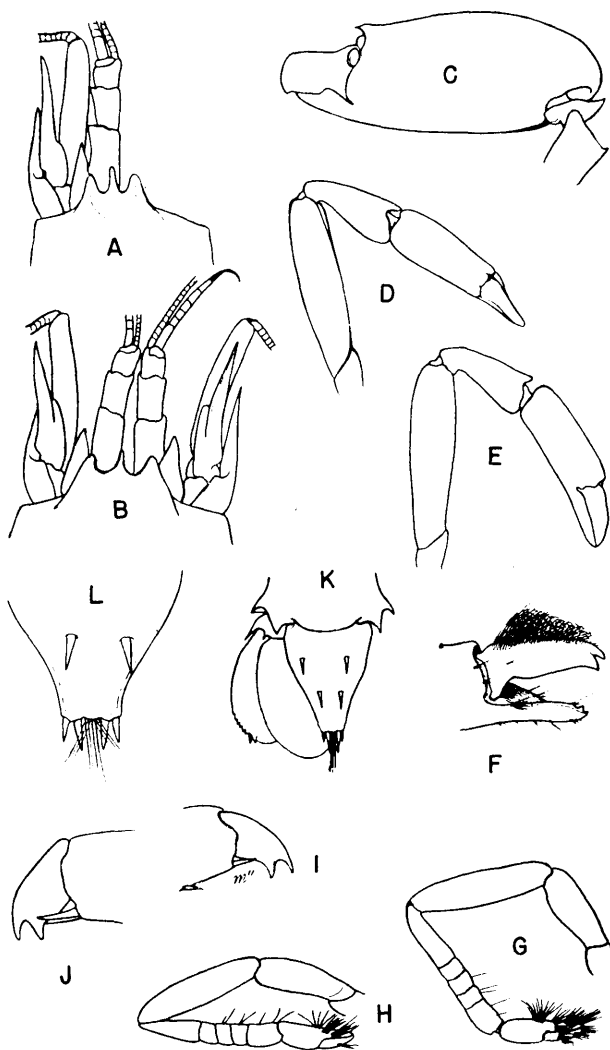


FIGURE 59.—*Synalpheus longicarpus* (Herrick). Anterior part of body in dorsal view, A, male, B, female; C, large chela; D, small first cheliped, male; E, same, female; F, fingers of small first cheliped; G, second leg of male showing subdivided carpus; H, same, female; I, dactyl of third leg; J, same in large adult; K, telson and left uropods in dorsal view, female; L, tip of telson (after Coutiere, 1909).

sum of remaining four. Third to fifth legs with dactyls bifurcate.

Sixth abdominal segment with a strong triangular tooth on each posterior angle. Telson with sinuous sides tapering to subtruncate tip; dorsal spines strong, first pair at one-third, second at two-thirds length; tip with two pairs of strong spines, inner pair slightly longer. Uropodal exopod broadly oval; lateral border spined with seven or eight denticles, a movable spine at distal end of series.

Measurements.—Length of body: ovigerous females, 16 to 22 mm.

Variations.—Length of the carpus of the small claw varies with age. The rostrum and projections on the orbital hoods may be entirely lacking or their relative lengths may vary (Wass, 1955).

Color.—Translucent white; fingers brown.

Habitat.—Lives at depths of 15 to 28 fathoms in interior of sponges; especially abundant in *Spheciospongia* (= *Spirastrella*) (Wells, Wells, and Gray, 1960). Sometimes found in sponges cast on beach during storms at Beaufort, N.C.

Type locality.—Specimens upon which Herrick's description is based were taken in the Bahamas, probably at Nassau, New Providence Island.

Known range.—Beaufort, N.C., to Yucatan, Mexico; through West Indies to Curaçao.

Remarks.—This species is common in the Carolinas and often occurs in enormous numbers in the canals of large sponges. Infestation by parasitic isopods is common, *Phryxus subcaudalis* Hay occurring on the surface of the abdomen and *Synsynnella deformans* Hay in the branchial chambers.

Ovigerous females have been taken off North Carolina in August and December. The species hatches in essentially the adult form (Herrick, 1892). Coutiere (1909) and Wass (1955) remarked on the fact that few ovigerous females occur among crowded populations in sponges.

Family Ogyrididae

Caridea with first two pairs of legs chelate, nearly equal in size and not much if any larger than other legs. Carpus of second legs subdivided. Rostrum small or wanting. Eyestalks long, slender, fully exposed but with corneal surface reduced. Telson thick, obtusely pointed. Blades

of uropods curved outward. Thelycum present in females (Hay and Shore, 1918).

Genus *Ogyrides* Stebbing, 1914

Stebbing, 1914, p. 31; Hemming, 1958b, p. 158.

KEY TO SPECIES IN THE CAROLINAS

- a. Postrostral crest with 8 to 14 small, fixed spines
limicola (p. 74).
- aa. A single movable spine behind rostrum on middorsal line-----*alphacrostris* (p. 75).

Ogyrides limicola Williams

Figure 60

Ogyrides limicola Williams, 1955c, p. 57, fig. 1.

Recognition characters.—Rostrum short, depressed, equilaterally triangular. Postrostral carina with 8 to 14 teeth, flanked on each side by row of setae extending to tip of rostrum. Pterygostomian area broadly obtuse. Eyestalks long, lightly setiferous dorsally and dorso-medially, narrowest in middle, exceeding antennular peduncles by approximately 2.5 times corneal length. Antennal and antennular peduncles nearly equal in length; second antennular article 3 times as long as third article; stylocerite of basal article terminating in two strong acuminate spines of nearly equal length. Antennal scale and second article of antennular peduncle reaching nearly same level distally; scale evenly

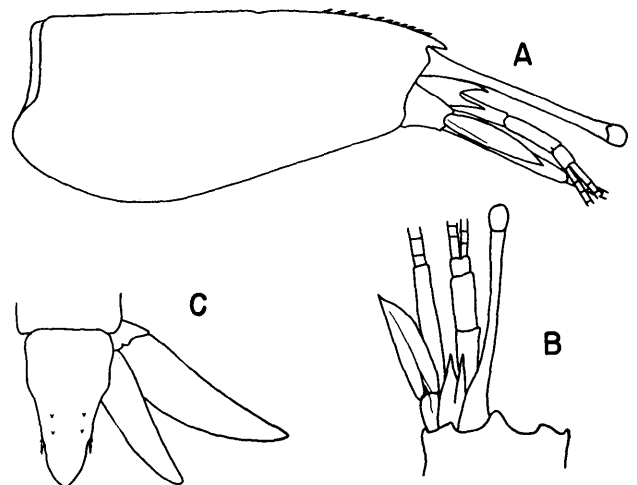


FIGURE 60.—*Ogyrides limicola* Williams. A, carapace and anterior appendages in lateral view; B, anterior appendages and portion of carapace in dorsal view; C, telson and uropods of right side in dorsal view; A-C approximately $\times 10$ (after Williams, 1955c).

rounded medially, 3 times longer than greatest width, greatest width in basal half. Third maxilliped, when extended, exceeding eyestalks.

First legs exceeding midlength of antennal peduncle by full length of chelae; fingers of chelae pointed, agape when closed.

Telson with anterior pair of spines placed well behind lateral prominences. Uropods with exopods slightly falciform, lateral borders nearly straight. Telson with three horny ridges at proximolateral corners ventrally, and uropods with an interlocking horny eminence on basal article dorsally.

Measurements.—Length of body: ovigerous holotypic female, 16 mm.

Variations.—Individual variations are shown in the number of spines on the postrostral crest and in the lengths of the spines of the stylocerite.

Color.—Female with general body structure colorless, clear; internal organs visible; gut dark; hepatopancreas light brown; eyestalks, antennal and antennular peduncles, and distal portions of anterior appendages with red and yellow spots; uropods and sixth segment of abdomen with scattered red spots. Ovigerous females with yellow green (chartreuse) colored eggs on swimmerets (Williams, 1955c).

Habitat.—On (or in) the bottom of muddy estuaries, or in plankton; surface to 2.5 fathoms. Collections have been made in an observed bottom salinity range of 9 to 31‰, but salinities in sounds near inlets often range higher than this.

Type locality.—Mouth of Far Creek at Engelhard, Hyde County, N.C.

Known range.—Eastern shore of Accomac County, and lower James River, Va., to Lake Pontchartrain, La.

Remarks.—The systematic confusion surrounding the two species *O. alphaerostris* and *O. limicola* was discussed by Williams (1955c). The two species are quite distinct morphologically and differ in total size, *O. limicola* being the smaller. The latter occurs most frequently in collections from estuaries. Young specimens have frequently been taken in plankton tows made at night in Bogue Sound, N.C., but adults are seldom taken by this method of collection. Occurrence of adults in samples taken with a beam trawl suggests burrowing habits similar to those described for *O. alphaerostris*, but in muddier situations and

often in low salinities. The type locality and a number of other productive collecting spots in North Carolina are shallow, mud-bottomed, non-tidal estuarine streams.

In North Carolina, collections of *O. limicola* have been made in all seasons of the year, and ovigerous females have been taken from May to September.

Ogyrides alphaerostris (Kingsley)

Figure 61

Ogyris alphaerostris Kingsley, 1880, p. 420, pl. 14, fig. 7.

Ogyrides alphaerostris: Stebbing, 1914, p. 31.—Hay and Shore, 1918, p. 388, fig. 11, pl. 26, fig. 9.

Recognition characters.—Rostrum depressed, equilaterally triangular, tipped with setae. A single, postrostral, movable spine. Pterygostomian area obtuse. Eyestalks long, setiferous medially, narrowest in middle, exceeding antennular peduncle by approximately twice corneal length. Antennal and antennular peduncle nearly equal in length; second article of antennular peduncle slightly over twice as long as third article;

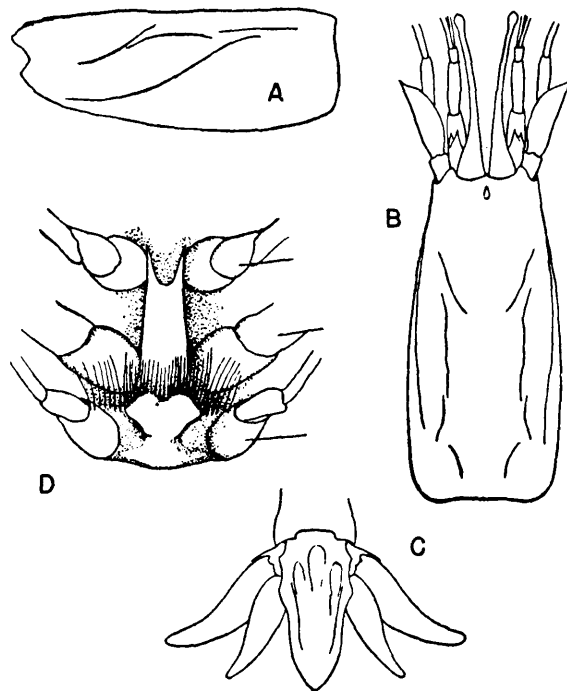


FIGURE 61.—*Ogyrides alphaerostris* (Kingsley). A carapace in lateral view; B, carapace and anterior appendages in dorsal view; C, uropods and telson in dorsal view; D, sterna of last three thoracic segments showing thelycum of female; A-C female $\times 5$, D $\times 7.8$ (after Hay and Shore, 1918).

stylocerite terminating in two acuminate spines; lateral spine longer. Antennal scale and second article of antennular peduncle reaching same level distally; scale evenly rounded medially, approximately three times longer than greatest width, greatest width near base. Third maxilliped, when extended, exceeding eyestalks.

First legs scarcely extending to tip of antennal scale. Second legs exceeding antennal scale by full length of chelae; fingers of chelae pointed, agape when closed.

Telson with anterior pair of spines placed approximately at level of lateral prominences. Uropods with exopods somewhat falciform, curvature greatest distally. Telson with three horny ridges at proximolateral corners ventrally, and uropods with an interlocking horny eminence on basal article dorsally.

Measurements.—Length of body: ovigerous female, 27 mm.

Color.—Body nearly transparent; red and green spots or flecks on eyestalks, antennules, and antennae; green only on distal joints of third maxillipeds; red only on basal articles of legs, on first pleopods, at bases of all pleopods, and on abdominal pleura and sterna; a conspicuous red area on sixth abdominal segment distoventrally and another around mouth.

Habitat.—Often found on firm bars of sand just offshore along open ocean in water 1 m. deep (Pearse, Humm, and Wharton, 1942); surface to 5 fathoms.

Type locality.—Eastern shore of Northampton County, Va.

Known range.—Northampton County, Va., to St. Simons Island, Ga.; Alligator Harbor, Fla., to Horn Island, Miss.

Remarks.—*Ogyrides alphaerostris* apparently is more restricted to high-salinity waters than *O. limicola*, for it has seldom been collected in the sounds of North Carolina and then only near inlets. Pearse, Humm, and Wharton (1942) described burrowing habits of the species on sandy bars and commented that members of the genus are unusual in that they have long eyestalks like *Uca*, yet are burrowers. *Ogyrides alphaerostris* burrows forward (head first), using the third maxillipeds and legs for digging and propulsion. Sand is pushed upward and over the head, the abdomen often being left above sand for a time,

especially in ovigerous females. The fifth leg is held high on the sides and stroked dorsally and posteriorly, legs one to four are stroked laterally and posteriorly, and the third maxillipeds moved anteriorly and dorsally. The animals scrape food from the antennae with setose mouth parts.

Ovigerous females have been taken in July in North Carolina, and in July and August in Florida and Mississippi. The above authors imply that the breeding season is extended through the summer months.

Family Hippolytidae

Caridea with first two pairs of legs chelate, first pair not much stronger than rest; carpus of second pair of legs subdivided. Eyes well developed and not covered by carapace. Mandibles usually deeply cleft. Second maxillipeds with a very short dactyl.

KEY TO GENERA AND SOME SPECIES IN THE CAROLINAS

- a. Carpus of second legs with three to five joints.
 - b. Carpus of second legs with five joints
Thor floridanus (p. 76).
 - bb. Carpus of second legs with three joints.
 - c. Series of small spines (five to nine) along anterior margin of carapace below eye
Latreutes (p. 78).
 - cc. Without series of small spines on anterior margin below eye.
 - d. Rostrum shorter than carapace proper, with spines above and below-----*Hippolyte* (p. 80).
 - dd. Rostrum nearly twice length of carapace proper. smooth above, serrate below
Toxuma carolinense (p. 83).
- aa. Carpus of second legs with more than six joints (multiarticulate) -----*Hippolysmata* (p. 84).

Genus *Thor* Kingsley, 1878

Kingsley, 1878b, p. 94.—Hemming, 1958b, p. 161.

Thor floridanus Kingsley

Figure 62

Thor floridanus Kingsley, 1878b, p. 95.—Verrill, 1922, p. 136, pl. 35, figs. 2-2f; pl. 41, fig. 1; pl. 46, figs. 2-2e; pl. 47, figs. 4, 4a.—Holthuis, 1947, p. 47, 49 (rev.).

Recognition characters.—Rostrum shorter than eyes; dorsal margin with four or five teeth, first tooth a little behind margin of orbit, distal tooth near tip making tip appear bifid; ventral margin unarmed. Carapace smooth, with prominent antennal spine below orbit. Eyes well developed. Antennules with basal article large; stylocerite long, acute, reaching beyond tip of basal article

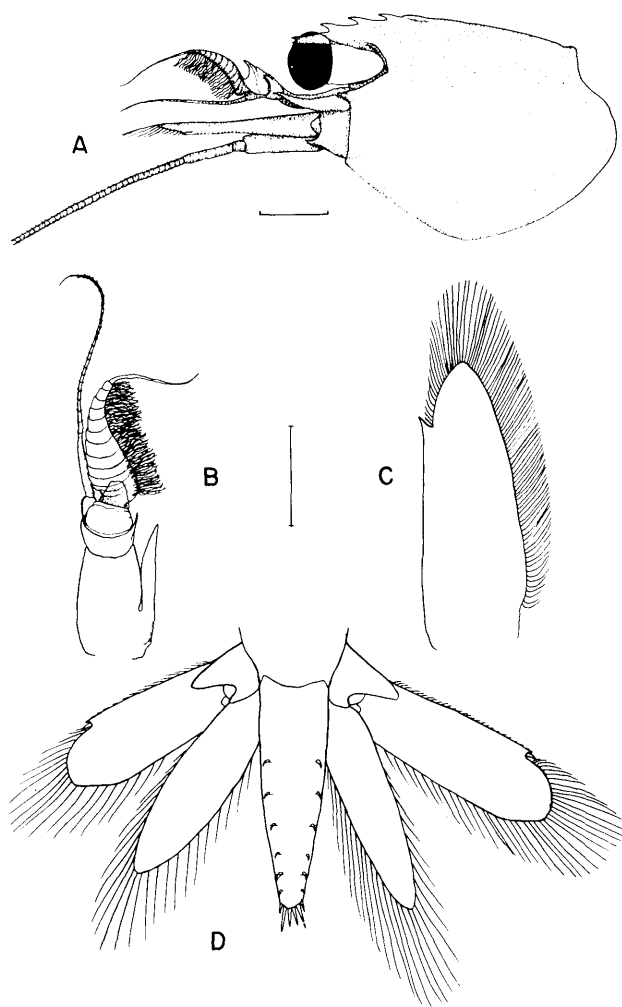


FIGURE 62.—*Thor floridanus* Kingsley. A, carapace and anterior appendages in lateral view, 1 mm. indicated; B, antennule; C, antennal scale; D, uropods and telson; B-D, 1 mm. indicated.

to level of tip of spine on second article; a tiny, erect spinule at base of stylocerite; second and third articles short; second with slender, acute spine on lateral surface; third with a thin, flat, blunt projection on upper side; inner flagellum slender, slightly longer than peduncle; outer flagellum stout basally, tapering abruptly to thin terminal portion, densely hairy on outer margin, about as long as peduncle. Antennal scale with outer margin nearly straight, terminating in a stout spine, lamella exceeding spine, an outer spine near base of scale. Third maxilliped reaching a little beyond tip of antennal scale; last article terminating in slender spines.

First legs with merus and carpus subequal; carpus with minute spinules on inner margin; chelae subcylindrical, dactyl two-fifths total length of hand. Second legs with carpus subdivided into six joints of varying lengths; chela as long as fifth and sixth carpal joints. Dactyls and propodi of third to fifth legs spinulose beneath; dactyls bifurcate but with accessory spines proximally.

Abdomen smooth; pleura of fourth, fifth, and sixth segments with posterolateral angles acute. Telson elongate, triangular, with five prominent pairs of dorsal spines a little remote from edges and spaced equidistantly in posterior three-fourths of length; tip somewhat rounded and armed with three pairs of subequal spines, outer pair shortest. Uropodal exopods with outer edge ending in a small spine flanked medially by a strong movable spine.

Measurements.—Length of body: ovigerous females, 11 to 13 mm. (Wass, 1955).

Habitat.—Among sponges, ascidians, algae, and soft corals; shallow water to 32 fathoms.

Type locality.—Key West, Fla.

Known range.—Beaufort, N.C., to Alabama; through West Indies to Curaçao and Yucatan; Bermuda.

Remarks.—This species has often been referred to *Thor paschalis* (Heller), an Indo-west Pacific form. Holthuis (1947) considered the West Indian species distinctive, and, in fact, it is the type species of the genus. As far as known, *T. floridanus* is not common in the Carolinas.

Ovigerous females have been reported (Broad, 1957c; Lunz, 1939; Verrill, 1922; Wass, 1955) or are known from collections from April to August in southeastern United States, Bermuda, and the West Indies. In addition, they are known from Cuba in November and January.

Broad (1957c) worked out the larval stages of this form, using various species of algae as food for the developing larvae. Though survival varied with species of algae fed, he considered at least certain species of algae to be an adequate diet for survival, molting, and metamorphosis. Broad described eight zoeal stages and a postlarval stage. Comparison of these stages with earlier descriptions by Lebour (1940) led Broad to question the conspecificity of *Thor* from Bermuda and the Carolinas.

Genus *Latreutes* Stimpson, 1860

Stimpson, 1860, p. 27.—Hemming, 1958b, p. 157.

KEY TO SPECIES IN THE CAROLINAS

- a. Carapace and rostrum unarmed dorsally except for a single, small, median spine on gastric region; rostrum an elongate blade nearly as long as carapace
fucorum (p. 78).
- aa. Carapace strongly humped and armed dorsally with five or six spiniform teeth; rostrum a deep ovoid blade, shorter than carapace-----*parvulus* (p. 79).

Latreutes fucorum (Fabricius)

Figure 63

Palaemon fucorum Fabricius, 1798, p. 404.

Latreutes ensiferus: Hay and Shore, 1918, p. 390, pl. 26, fig. 13.

Latreutes fucorum: Verrill, 1922, p. 131, pl. 16, figs. 5-5b; pl. 42, figs. 2-2t; pl. 44, figs. 1-1m, 2a-2n, 3 (rev.).

Recognition characters.—Rostrum thin, nearly as long as carapace, smooth edged, broadest at base and deepest near base, slightly concave dorsally and upturned at tip, convex ventrally; tip subtruncate and armed with about five to seven small, acute spinules. Carapace smooth; a small middorsal spine on gastric region; anterior margin produced into an acute lobe below eye followed ventrally by a wide, nearly rectangular emargination and a series of four to nine small denticles at anterolateral angle; a spine removed from margin near suborbital lobe. Eyes well developed, with a tuberculate swelling antero-medially near cornea. Antennular peduncle with basal article excavate laterally; stylocerite broad, thin, cupped dorsally; distal spine on lateral border of basal article reaching about to base of third article; second and third articles short; distal border of third obscurely denticulate, outer flagellum thick at base. Antennal peduncle stout; antennal scale wide at base, tapering to acute terminal spine, scale about as long as rostrum. Third maxilliped elongated, leglike; distal article long, with eight or nine acute marginal spines.

First legs incurved, short, relatively stout, unequal; larger chela thick, proximally broad, ovate, tapering distally; dactyl wide, longer than immovable finger, with broad lateral lobe and about three denticles at tip; immovable finger bent slightly inward and arched, tip subacute or slightly bidentate; fingers hairy; carpus large, cup-shaped, broader than long; merus and carpus excavate beneath. Second legs slender; chelae slender, somewhat unequal; fingers about as long as palm,

hairy at tip; carpus with three unequal joints, middle one longest. Third to fifth legs long, slender, subequal; propodi and dactyls with row of spines on lower edge.

Abdomen smooth. Telson long, narrow, tapering to narrow tip with spiniform median process flanked by two pairs of unequal spines, inner pair longer than median process; two pairs of dorsal spines, at half and three-fourths of length. Uropodal exopods with outer edge terminating in a small spine flanked medially by a movable spine.

Measurements.—Length of body: adults, 12 to 20 mm.; males smaller than females.

Variations.—The rostrum varies greatly in length, depth, and number of spines (Wass, 1955).

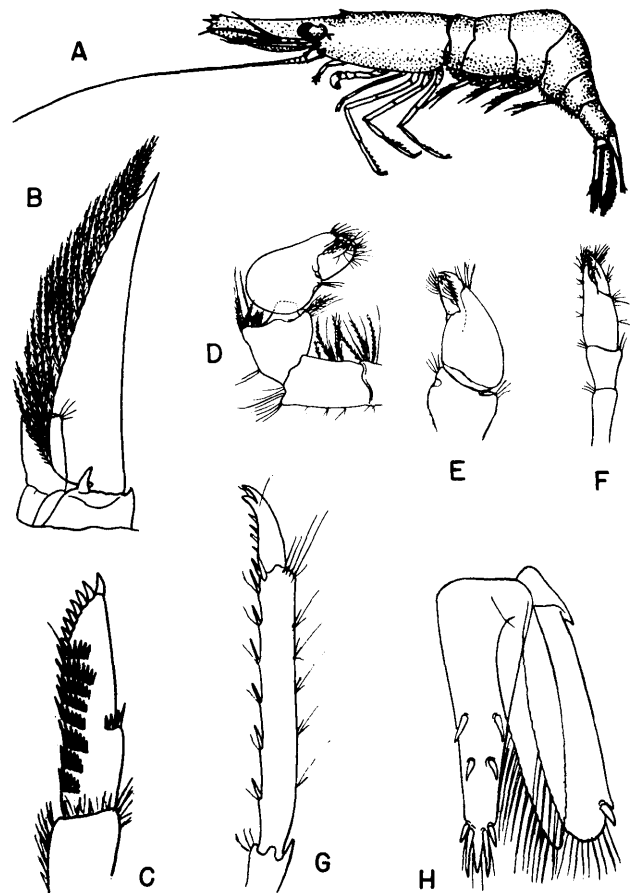


FIGURE 63.—*Latreutes fucorum* (Fabricius). A, animal in lateral view, $\times 17$ (after Bate, 1888); B, antennal scale, $\times 17$; C, distal article of third maxilliped, $\times 42$; D, right first cheliped, $\times 17$; E, left first cheliped, $\times 25$; F, second cheliped, $\times 17$; G, distal articles of third leg, $\times 17$; H, telson and uropods, $\times 17$ (after Verrill, 1922).

Color.—Often nearly colorless and transparent; sometimes with body pale yellow, yellowish green, greenish brown, brown, red, black, black with white spots and bars; bright blue patches on dorsal and lateral surfaces; often mottled, striped, or barred, and corresponding in pattern to irregularly colored bits of weed (various authors).

Habitat.—Common in floating masses of *Sargassum*; surface waters.

Type locality.—Floating gulfweed.

Known range.—Newfoundland to Puerto Rico, through Gulf of Mexico to Texas; Bermuda; near the Azores and Cape Verde Islands; Cape of Good Hope (?) (Holthuis, 1951b; Sivertsen and Holthuis, 1956).

Remarks.—Ovigerous females have been observed in inshore waters of the Carolinas and adjacent western Atlantic region from July to October. They have been observed in the Gulf of Mexico from April to June. In the middle and western Atlantic they have been observed in June (Sivertsen and Holthuis, 1956). Gurney (1936a) described the first stage larva.

Pearse (1952b) reported the parasitic *Protophyrus latreuticola* (Gissler) in the gill cavity of this shrimp near Port Aransas, Texas.

Brown (1939) found four kinds of pigment in this shrimp (white, red, yellow, and blue) similar to pigments found in *Hippolyte*, *Leander*, and *Palaemonetes* species. The red and yellow pigments respond to white background by concentration into the chromatophore centers and to black background by dispersion into the chromatophore branches. *Latreutes* has a great abundance of white pigment which may vary in color from yellowish white to clear white. Darkness produces concentration, and darkness or black background with low intensity of incident light calls forth concentration of the reflecting white chromatophores. Direct sunlight of a bright sky produces dispersion of white pigment in spite of black background. Blue patches on the animals apparently consist of blue pigment accumulated in particular white chromatophores. Brown concluded that the different color patterns in this species are not solely results of responses to particular situations, but are at least partly genetic patterns repressed or encouraged by light intensity in color of the background. The re-

sponse is similar to responses in crustaceans having far less ability to change color.

Latreutes parvulus (Stimpson)

Figure 64

Rhynchoicyclus parvulus Stimpson, 1866, p. 48.—1871b, p. 124.
Concordia gibberosus: Hay and Shore, 1918, p. 391, pl. 26, fig. 11.

Latreutes parvulus: Holthuis, 1947, p. 59.—1951b, p. 131, fig. 28 (rev.).

Recognition characters.—Rostrum laterally compressed, almost circular in outline in female, more elongate in male; upper margin with six to eight teeth in female, two to four in male; a few small teeth on tip; lower margin unarmed or with up to five shallow teeth; ventral part of rostrum produced somewhat backward. Carapace

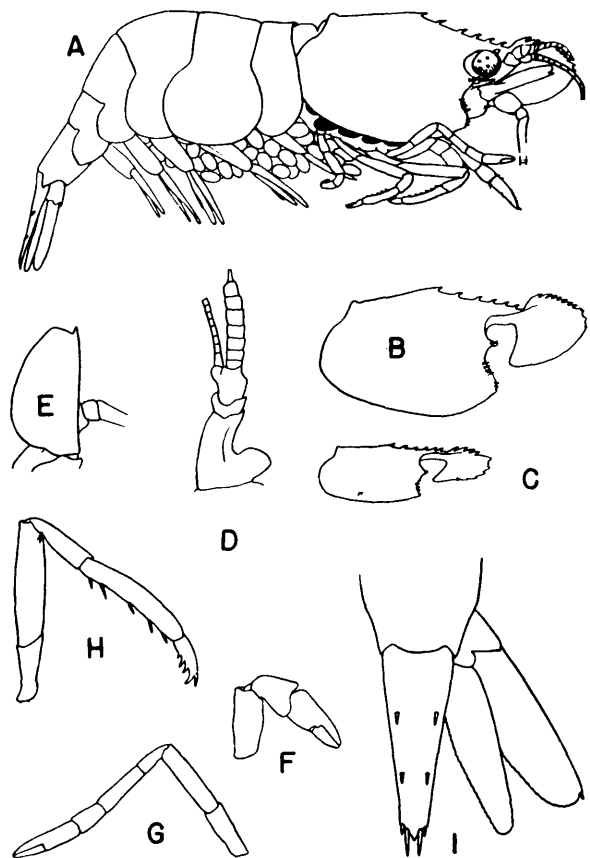


FIGURE 64.—*Latreutes parvulus* (Stimpson). A, ovigerous female in lateral view, $\times 6$; B, carapace of ovigerous female in lateral view, $\times 6$; C, carapace of male in lateral view, $\times 6$; D, antennule, $\times 13$; E, antennal scale, $\times 13$; F, first leg, $\times 17$; G, second leg, $\times 17$; H, third leg, $\times 17$; I, telson and right uropod in dorsal view, $\times 17$ (after Holthuis, 1951b).

with middorsal row of five to seven small, erect teeth, row starting somewhat anterior to middle of carapace, extending to base of rostrum; carapace somewhat swollen in female, making an angle at base of middorsal row of teeth; upper margin nearly straight in males; anterior margin with a narrow, anteriorly directed lobe forming lower angle of orbit, a slender spine on lobe; anterolateral angle serrate with two to four teeth; between anterolateral angle and lower margin of orbit a row of three or four slender spines a bit removed from and parallel to margin. Eyes well developed; cornea globular; eyestalk with a truncated process at upper inner margin overlapping line separating cornea from stalk. Antennular peduncle with stylocerite broad and rounded, hollowed above and together with basal article of peduncle forming concavity for reception of eye; second article of peduncle much shorter than third; upper flagellum shorter than lower, with seven or eight broad and one or two narrow joints. Antennal scale about twice as long as broad, overreaching antennular and antennal peduncles, but not reaching end of rostrum; outer margin nearly straight, ending in a small tooth reaching about as far as lamella; a small spine on outer surface of peduncle near base of scale.

First legs equal, short, thickset, slightly overreaching base of antennal scale; fingers somewhat shorter and narrower than palm, tips of fingers ending in dark-colored nails; palm broadened posteriorly; carpus somewhat conical, about as long as palm. Second legs more slender, reaching about to end of antennal peduncle; chelae with fingers shorter than palm; carpus almost twice length of chela, three-jointed, median joint longest; merus two-thirds as long as carpus. Third to fifth legs with dactyls ending in a sharp tooth, posterior margin with four comblike teeth progressively smaller proximally.

Abdomen smooth. Telson triangular; with two pairs of dorsal spines at half and three-fourths length; tapering to a narrow tip with spiniform median process flanked by two pairs of spines, inner pair longest; terminal portion with feathered setae. Uropodal exopods with outer margin ending in a small spine flanked medially by a movable spine.

Measurements.—Length of body: 7 to 12 mm.; males smaller than females.

Variations.—Shape of the rostrum, as well as its spination, is subject to some variation.

Habitat.—Littoral waters from (in?) sponges, and among shells and hydroids; surface to 24 fathoms.

Type locality.—St. Joseph Island, Tex.

Known range.—Beaufort, N.C., to Texas; Cuba; Puerto Rico; French Guiana; Rio de Janeiro, Brazil; Sierra Leone, West Africa.

Remarks.—For many years this species has been known as *Concordia gibberosus* Kingsley or *Latreutes gibberosus* (Kingsley). Holthuis (1947) showed that these names fall into the synonymy of Stimpson's species.

Latreutes parvulus is not known to be common anywhere in its range. It has been taken throughout the year in the Carolinas. Oviparous females have been taken throughout the year in various parts of the range north of the equator and in February in Brazil.

Genus *Hippolyte* [Leach, 1814]

Verrill, 1922, p. 124.—Holthuis, 1947, p. 53.—Hemming, 1958b, p. 157.

KEY TO SPECIES IN THE CAROLINAS

- a. Basal article of antennular peduncles without distal spines dorsally.....*pleuracantha* (p. 80).
- aa. Basal article of antennular peduncles with distal spines dorsally.....*zostericola* (p. 82).

Hippolyte pleuracantha (Stimpson)

Figure 65

Virbius pleuracanthus Stimpson, 1871b, p. 127.

Hippolyte pleuracantha: Hay and Shore, 1918, p. 390, pl. 26, fig. 8.—Holthuis, 1947, p. 15 (rev.).

Recognition characters.—Body smooth, with tufts of plumose hairs on dorsal surface of carapace and abdomen, tips of abdominal pleura, and distal portion of eyestalks. Rostrum rather stout at base, thin distally, slightly decurved, armed dorsally with one to three teeth and ventrally with one to three teeth near tip; tip reaching about to end of antennular peduncle; a strong spine on each side at base of rostrum. Anterior margin of carapace produced into a lobe below eye followed ventrally by an antennal spine, an emargination at base of antenna followed by a slightly produced, broadly rounded anterolateral angle; hepatic spine strong. Eyes well developed. Antennular peduncle with basal article long and broad, stylocerite slender, lanceolate, reaching

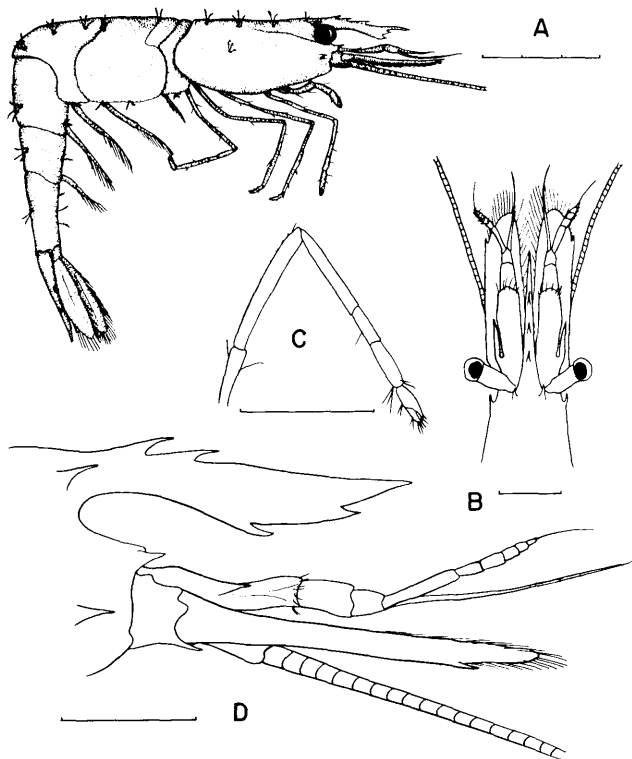


FIGURE 65.—*Hippolyte pleuracantha* (Stimpson). A, animal in lateral view, 3 mm. indicated; B, anterior portion of body in dorsal view; C, second leg; D, anterior portion of body in lateral view; B-D, 1 mm. indicated.

about to middle of article and separated from lateral border of article by about width of stylocerite, article ending in a short, broad, elevated, bladelike projection, a short spine at anterolateral corner under blade; second and third articles much shorter than first; antennular flagella of about equal length; outer ramus stout, broadest in middle, tapering to slender distal portion, hairy on ventral border. Antennal scale large, exceeding rostrum and reaching nearly to end of antennular flagella, length a little over three times width; outer margin slightly concave, terminating in a small spine, spine exceeded by lamella; a spine near base of scale.

First legs short, nearly equal, reaching a little beyond base of distal article of antennal peduncle; chelae setose, palm inflated, fingers about half length of palm, cutting edges finely serrate; carpus irregularly conical in shape, about three-fourths length of chela, lower outer border with spiniform setae. Second legs slender, reaching to

tip of antennular peduncle; carpus longer than merus, divided into three joints; fingers two-fifths length of chelae, tips of cutting edges with spines; chelae hairy. Third to fifth legs long; third reaching to tip of antennal scale; dactyls with series of spines in comblike arrangement on inner border; propodi spined on inner border.

Abdomen strongly bent at third segment; posterior portion of third segment raised with hoodlike projection overhanging fourth segment. Telson with two pairs of dorsal spines on lateral border, one about at half, another at three-fourths length; tip truncate, bearing three pairs of spines, inner two pairs nearly equal, outer pair much shorter. Uropodal exopods with lateral border ending in a small spine flanked medially by a movable spine.

Measurements.—Length of body: ovigerous females, 12 to 18 mm.; males somewhat smaller.

Variations.—The rostrum in this species varies conspicuously in number of teeth, in shape from lateral view, and in length. Dorsal and ventral rostral teeth occur in all combinations from 1/1 to 3/3. Males are more slender than females.

Color.—Usually mottled brown or red, often a bright green.

Habitat.—Extremely abundant in beds of vegetation (*Zostera* and *Diplanthera*) in sounds and bays. Also found among rocks of jetties.

Type locality.—Norfolk Harbor, Va., and Somers Point, Great Egg Harbor, N.J.

Known range. New Jersey to Galveston, Tex.; Bermuda.

Remarks.—The two species, *Hippolyte pleuracantha* and *H. zostericola*, have been much confused over the years, and it is not at all certain that differences pointed out here adequately distinguish them. No attempt has been made here to give complete synonymies. This task must be approached by a thorough revisionary work in which all existing collections are studied.

In general, it can be stated that *H. pleuracantha* has no prominent distal spines on the basal article of the antennular peduncle; it has a relatively shorter rostrum, and appears to be somewhat larger than *H. zostericola*. *Hippolyte zostericola* has a prominent, distal, dorsal pair of spines on the basal article of the antennular peduncle. I am much indebted to L. B. Holthuis for pointing out

the latter character to fellow workers on the American coast.

Because identifications in the literature are probably confused, the geographic limits of the species given here must be regarded with reserve.

Ovigerous females of *H. pleuracantha* occur in North Carolina at least from April to October in the Beaufort area. Gurney (1936b) pointed out some differences between adults of *H. pleuracantha* and *H. zostericola* (as well as other species of *Hippolyte*) and described four larval and two postlarval stages of what he considered to be a Bermudian subspecies, *H. pleuracantha bermudensis*.

Hippolyte zostericola (Smith)

Figure 66

Virbius zostericola Smith, 1873c, p. 550, pl. 3, fig. 11.
Hippolyte zostericola: Holthuis, 1947, p. 16.

Recognition characters.—Body smooth. Rostrum rather stout at base, thin distally, slightly decurved, armed dorsally with three or four teeth and ventrally with two to five teeth distally; tip reaching beyond antennular peduncle and often nearly to tip of antennal scale; a strong spine on each side at base of rostrum. Anterior margin of carapace produced into a prominent narrow lobe below eye followed ventrally by an antennal spine; a shallow emargination at base of antenna and a broadly rounded anterolateral angle; hepatic spine well developed. Antennular peduncle with basal article long and broad, stylocerite slender, divergent at tip and well separated from article, basal article terminating in a pair of well-developed spines on anterolateral corner; second and third articles much shorter than first; antennular flagella of about equal length, outer ramus stout basally, tapering to slender distal portion, hairy on ventral border. Antennal scale large, slightly exceeding rostrum and reaching nearly to end of antennular flagella, length a little over three times width; outer margin slightly concave, terminating in a small spine, spine exceeded by lamella; a spine near base of scale.

First legs short, nearly equal, reaching base of distal article of antennal peduncle; chelae lightly setose, palm inflated, fingers about half length of palm, cutting edges finely serrate;

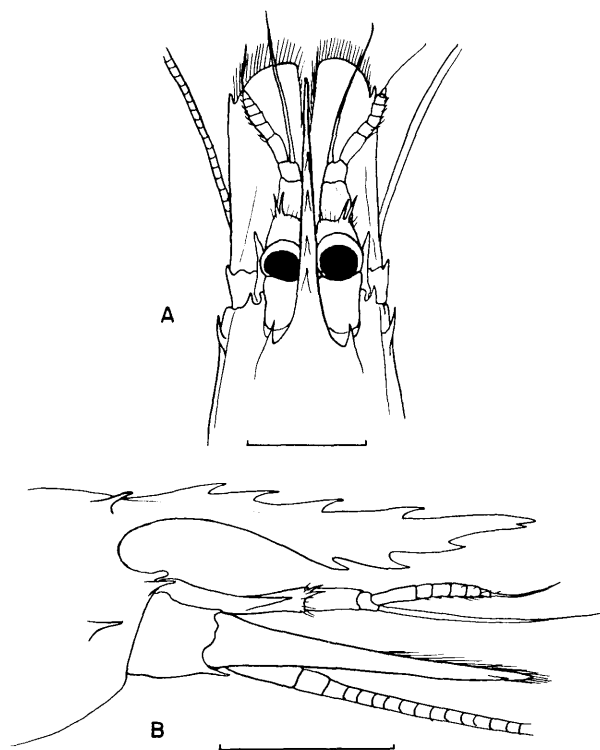


FIGURE 66.—*Hippolyte zostericola* (Smith). A, anterior portion of body in dorsal view; B, anterior portion of body in lateral view; 1 mm. indicated.

carpus irregularly conical in shape, about three-fourths length of chela, lower outer border with spiniform setae. Second legs slender, reaching to distal end of basal article of antennular peduncle; carpus longer than merus, divided into three joints; fingers about two-fifths length of chelae, tips of cutting edges with spines; chelae hairy. Third to fifth legs long; third reaching to tip of antennal scale; dactyls with series of spines in comblike arrangement on inner border; propodi spined on inner border.

Abdomen strongly bent at third segment; posterior portion of third segment raised with hoodlike projection overhanging fourth segment. Telson with two pairs of dorsal spines on lateral border, one at half, another at three-fourths length; tip truncate, bearing three pairs of spines, inner two pairs about equal, outer pair much shorter. Uropodal exopods with lateral border ending in a small spine flanked medially by a movable spine.

Measurements.—Length of body: ovigerous females, 10 to 12 mm.; males somewhat smaller.

Variations.—The rostrum in this species varies considerably in number of teeth, shape from lateral view, and relative length. Dorsal and ventral teeth have been observed in the combinations 3/3, 3/4, 3/5, 4/2, 4/4, and the range of variation may be greater than this because only a few specimens from the Beaufort, N.C., area have been studied. Males are more slender than females.

Color.—Bright green, pale or translucent tinged with green; sometimes specked with reddish brown and with a broad median band of dark brown extending whole length of body (Smith, 1873c).

Habitat.—Beds of vegetation such as eelgrass.

Type locality.—Vineyard Sound, Mass.

Known range.—Southern Massachusetts, through Gulf of Mexico and West Indies to Curaçao (Holthuis, 1947).

Remarks.—Differences between this species and *H. pleuracantha* are discussed in the account for *H. pleuracantha*. Ovigerous females have been found in North Carolina in September.

Genus *Tozeuma* Stimpson, 1860

Stimpson, 1860, p. 26.—Holthuis, 1955, p. 112 (rev.).

Tozeuma carolinense Kingley. Arrow shrimp

Figure 67

Tozeuma carolinensis Kingsley, 1878b, p. 90.—1880, p. 413.—Schmitt, 1935a, p. 155.

Tozeuma carolinense: Rathbun, 1901, p. 114.—Hay and Shore, 1918, p. 391, pl. 27, fig. 2.

Angasia carolinensis: Holthuis, 1947, pp. 17, 61.

Recognition characters.—Body elongate, compressed. Rostrum slender, almost twice as long as remainder of carapace, inclined slightly upward distally, rounded and unarmed dorsally, base somewhat flattened and horizontal, deepest anterior to orbit and decreasingly lamellate distally; ventral border with many appressed teeth. Carapace smooth, polished; a strong spine at either side of base of rostrum; anterior margin produced into a triangular tooth below eye; anterolateral angle with a spine. Eyes well developed. Antennular peduncle rather slender; first article longest, with slender stylocerite slightly exceeding distal border; second and third articles progressively shorter; outer flagellum thick and much shorter than inner, neither quite reaching tip of antennal scale. Antennae longer than rostrum; antennal

scale lanceolate, less than half length of rostrum; basal antennal article with a strong ventrolateral spine on anterior border.

Legs relatively short; first pair very short, stout, hand inflated, fingers curved, closing completely, spines on fingers dark colored; second pair slender, longer, carpus with three joints, proximal joint nearly as long as merus; legs three to five with comblike spines on curved dactyls.

Abdomen smooth; strongly bent between third and fourth segments; third segment of male bearing a low dorsal hump; fifth segment with a spine at each side of posterior border; sixth with a spine at posterolateral angle and a broad spine at base of telson. Elements of tail fan long and narrow. Telson with one pair of dorsal spines at midlength, another at three-fourths length; tip with a strong pair of median spines flanked by a weak lateral pair. Uropodal exopods with outer border terminating in a small spine flanked medially by a movable spine.

Measurements.—Length of body: ovigerous females, 28 to 50 mm.

Variations.—The humped third abdominal segment is pronounced in young individuals of both sexes.

Color.—Apparently varying to some degree depending on background; shades of green from light yellowish green to rich deep green, or occasionally brownish or red in beds of *Diplanthera wrightii* and *Zostera marina* (Bryce, 1961); purple on alcyonarian corals *Antillologorgia* and *Pterogorgia* (Voss, 1956); nearly colorless (Verrill, 1922).

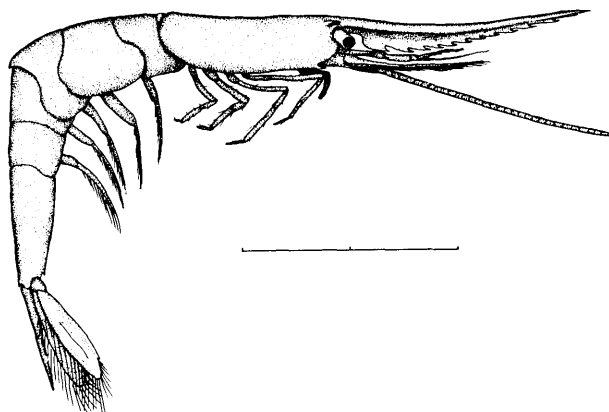


FIGURE 67.—*Tozeuma carolinense* Kingsley. Female in lateral view, 10 mm. indicated.

Habitat.—Common in beds of vegetation or similar habitats in shallow water, this species often swims in a vertical position and rests in a clinging position on blades of grass. It blends well with the background because of shape and color and is aptly named “arrow shrimp”. Surface to 41 fathoms (Holthuis, 1947).

Type locality.—Fort Macon, N.C.

Known range.—Vineyard Sound, Mass., to Colon, Panama; through West Indies to Curaçao.

Remarks.—Bryce (1961) gave general ecological observations on *T. carolinense* along with a detailed study of larval development. The adults apparently feed by grazing on faunal and floral growths on marine grasses.

In North Carolina, ovigerous females are present from May to October, with one doubtful record in February. Elsewhere they have been taken in February from Bimini, March to November in Florida and Louisiana, and in December from Puerto Rico.

Bryce found that larvae hatched from ovigerous females and reared in culture dishes usually passed through eight or nine larval stages before metamorphosing into postlarvae. However, the larvae did not always transform at these stages, and, in one group reared in early fall, continued molting for an indefinite number of stages. One individual passed through 25 larval stages before the experiment was terminated. Variations in larval stages and examples of asymmetry were discussed, as were the effects of diet and temperature.

Genus *Hippolysmata* Stimpson, 1860

Stimpson, 1860, p. 26.—Holthuis, 1955, p. 115.—Hemming, 1958b, p. 156.

KEY TO SPECIES IN THE CAROLINAS

- a. Rostrum not exceeding antennular peduncles
wurdemanni (p. 84).
- aa. Rostrum greatly exceeding antennular peduncles
optophoroides (p. 85).

Hippolysmata (Hippolysmata) wurdemanni (Gibbes)

Figure 68

Hippolyte wurdemanni Gibbes, 1850, p. 197.

Hippolysmata wurdemanni: Hay and Shore, 1918, p. 392, pl. 26, fig. 12.

Recognition characters.—Rostrum reaching distal end of second article of antennular peduncle,

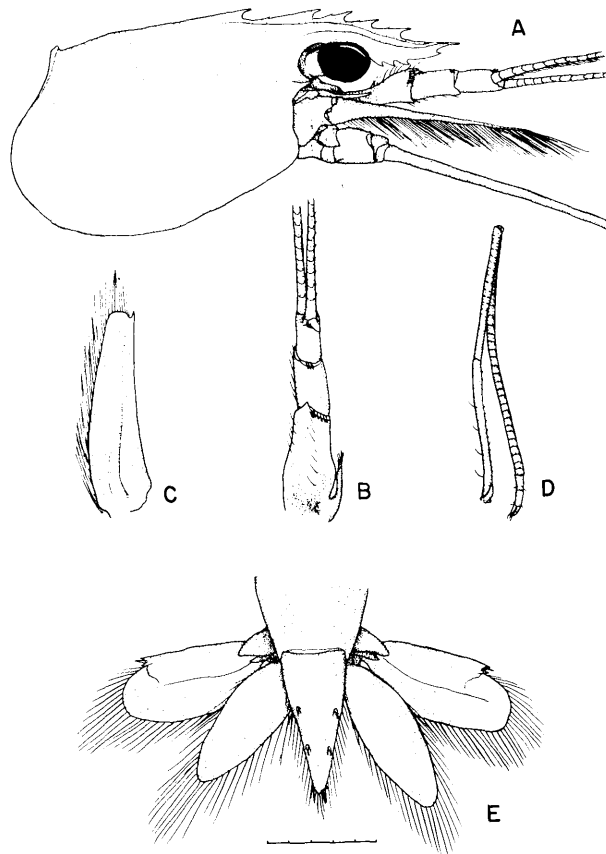


FIGURE 68.—*Hippolysmata (Hippolysmata) wurdemanni* (Gibbes). A, anterior portion of body in lateral view; B, antennule; C, antennular scale; D, second leg; E, uropods and telson in dorsal view; A–E, 5 mm. indicated.

slightly decurved, armed dorsally with four or five teeth and ventrally with three to five teeth. Carapace smooth; carinate dorsally on anterior half with a spine near base of rostrum about midway between rostral tip and posterior border; anterior margin with a strong antennal spine; anterolateral corner rounded. Eyes well developed. Basal article of antennular peduncle large, stylocerite slender, flattened, pointed, reaching a little beyond middle of article; second and third articles progressively shorter; inner flagellum slender; outer flagellum with about 20 to 30 thickened basal joints. Antennular scale long, narrow; outer margin about straight, terminating in a strong spine; lamella of scale truncate distally, about equal to spine.

Epipods on first four pairs of legs. First legs stout, about equal, reaching to end of antennal

scale; fingers about one-third length of palm, spines at tips of fingers darkened; carpus and hand of nearly equal length. Second legs much longer, slender; chela small; carpus divided into about 30 joints, last joint longest. Third to fifth legs not so slender as second; dactyls with a few coarse spines on inner border.

Abdomen smooth; posterolateral angle of fifth and sixth segments acute. Telson tapering to nearly truncate tip with a minute median projection flanked by two long, slender spines and outside these a short spine on each side; armed dorsally with two pairs of dorsal spines, anterior pair at one-third length, posterior pair at two-thirds length. Uropodal exopods with outer margin ending in two distinct teeth, between these a slender movable spine.

Measurements.—Length of body: males, 28 to 54 mm.; ovigerous females, 38 to 55 mm. (Wass, 1955, in part).

Variations.—Individuals from the northern extreme of the range differ in some respects from those in South America (Holthuis, 1959). The rostrum in South American specimens has four to seven dorsal teeth, and in specimens from the United States, four or five. Some southern specimens have stylocerites nearly as long as the basal antennular articles. In southern specimens, the tip of the lamella on the antennal scale is more truncate than in northern specimens. The second leg in Guiana material is more slender than in northern material, and the number of articulations in the carpus is higher, 33–37 as opposed to 27–31.

Color.—Translucent white with beautiful longitudinal and transverse markings of red.

Habitat.—Commonly found on stone jetties or among hydroids growing on piles or buoys; surface to 16 fathoms.

Type locality.—Key West, Fla.

Known range.—Lower Chesapeake Bay to Port Aransas, Tex.; Surinam; French Guiana; Mamanguape, São Paulo, Brazil.

Remarks.—Ovigerous females have been reported in January from Florida and in May from the Guianas (Holthuis, 1959; Wass, 1955). They have been collected in April and August from North Carolina, and in August from Louisiana.

Subgenus *Exhippolysmata* Stebbing, 1915

Stebbing, 1915, p. 94.

Hippolysmata (Exhippolysmata) oplophoroides Holthuis

Figure 69

Hippolysmata (Exhippolysmata) oplophoroides Holthuis, 1948, p. 1106.—1959, p. 112, fig. 17.

Recognition characters.—Rostrum long, slender, directed somewhat upward, reaching beyond antennal scale by nearly half of length; basal portion elevated into a crest bearing 9 to 10 closely placed teeth, one tooth some distance behind crest, remainder of upper margin with 1 to 6 widely separated teeth; ventral margin with 10 to 14 teeth. Carapace coarsely pitted; anterior margin produced into a slight lobe below eye closely followed ventrally by an antennal spine; a pterygostomial spine at anterolateral angle. Eyes well developed. Basal article of antennular peduncle with stylocerite rather broad and pointed, reaching beyond middle of article; second article somewhat longer than third; upper flagellum simple with about 20 to 25 basal joints thickened, hairy below. Antennal scale almost

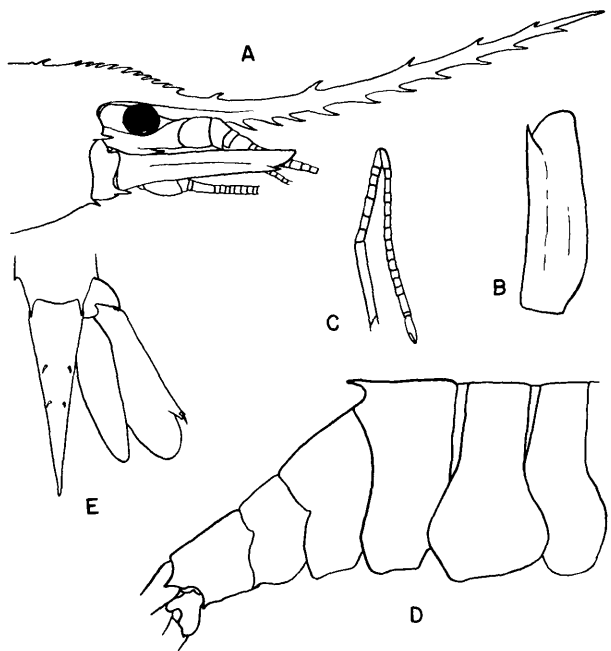


FIGURE 69.—*Hippolysmata (Exhippolysmata) oplophoroides* Holthuis. A, anterior portion of body in lateral view, $\times 3.5$; B, antennal scale, $\times 4$; C, second leg, $\times 4$; D, abdomen in lateral view, $\times 3.5$; E, telson and right uropod in dorsal view, $\times 3.5$ (after Holthuis, 1948).

three times as long as broad; outer margin slightly concave, ending in a strong tooth; lamella of scale exceeding spine; outer spine near base of scale directed ventrally.

Epipods on first four pairs of legs small but distinct. First legs equal, reaching somewhat beyond end of antennal peduncle; fingers short and blunt, immovable finger ending in a dark colored, sharp point fitting between two dark points on end of dactyl, outer surface of fingers convex, inner surface concave, fingers about five-eighths length of palm; carpus slightly shorter than chela and three-fourths length of merus. Second legs slender; slightly unequal in size, reaching almost to end of third maxilliped; chela small and slender; carpus five times length of chela and divided into 13 to 15 joints, first and last joints longest. Third to fifth legs slender; dactyls simple.

Abdomen coarsely and shallowly pitted; third segment with a dorsal carina ending in a strong, posteriorly directed spine; pleura of second to fourth segments produced posteroventrally in a narrowly rounded tip, pleura of fifth and sixth ending in a distinct sharp tooth; posterolateral angle of sixth spiniform. Telson tapering gradually to a slender point; dorsal surface with two pairs of spines, anterior pair at one-third length, second pair closer to first pair than to tip. Uropods elongate; outer margin of exopod ending in two distinct teeth, between these a slender movable spine.

Measurements.—Length of body: ovigerous females, 47 to 79 mm.

Variations.—In the case of a rostrum with one distal tooth dorsally, there were suggestions of three other small, malformed teeth.

Color.—General color pink; rostrum and anterior part of carapace pink, posterior part of carapace white and yellowish; abdomen white with pink most pronounced along posterior margins of first to fourth segments, spine on third segment almost red, fifth and sixth segments entirely pink; tail fan red, pink at base; antennular and antennal flagella pink; legs red, sometimes purplish distally; pleopods red; eggs yellow or greenish (Holthuis, 1959).

Habitat.—The species has been taken near shore, often in estuaries (15.89 ‰ over mud bottom) (Holthuis, 1959); 4 to 15 fathoms.

Type locality.—Mouth of Suriname River near Resolutie, Surinam.

Known range.—Off Cape Fear River, N.C., to Port Aransas, Tex.; British Guiana to Santos Harbor, São Paulo, Brazil.

Remarks.—Most information on this recently described species is summarized in Holthuis' (1959) account. Ovigerous females have been reported from December to July in South America and from August to October in the Carolinas. The species is more abundant than *Xiphopeneus* in British Guiana but apparently less abundant to the eastward in the other Guianas. Records from the United States are sporadic.

Family Processidae

Rostrum horizontal with dorsal surface of carapace. First pair of legs asymmetrically chelate; first leg of one side ending in a simple clawlike dactyl. Second pair of legs minutely chelate; slender; with segmented carpus.

Genus *Processa* Leach, [1815]

Holthuis, 1955, p. 116 (rev.).—Hemming, 1958b, p. 143.

Processa bermudensis (Rankin)

Figure 70

Nika bermudensis Rankin, 1900, p. 536.

Processa canaliculata: Verrill, 1922, p. 138.—Schmitt, 1935a, p. 169 (part).

Processa bermudensis: Gurney, 1936c, p. 624, figs. 44–52 (rev.).—Lebour, 1941, p. 410, figs. 28–33.—Holthuis, 1959, p. 120.

Recognition characters.—Rostrum slender, nearly straight, extending about two-thirds length of eye, bifid at end with upper process shorter than lower, a few hairs between tips. Carapace lacking antennal spine; anterior border rounded, somewhat sinuous. Eyes large, shorter than basal antennular article. Antennular peduncle with basal article excavate dorsally, longer than succeeding two articles combined, stylocerite short, somewhat truncate; second article about half again as long as third; inner flagellum filiform; outer flagellum thick, fusiform at base, slender distally, hairy, about as long as peduncle. Antennal scale about six times as long as wide; sides nearly parallel, truncate terminally; lateral spine small, slightly exceeding lamella; antenna a little longer than body. Third maxilliped with ter-

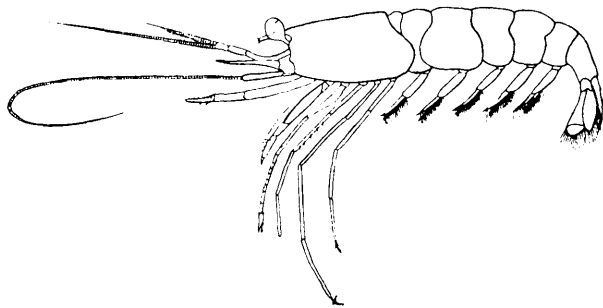


FIGURE 70.—*Processa bermudensis* (Rankin). Animal in lateral view (after Rankin, 1900).

minal article and a portion of adjacent article extending beyond antennular peduncle.

First pair of legs strong; chelate on right side; carpus a little over one-third length of merus, length about 1.5 times width; palm 1.5 times length of dactyl; left leg not chelate, carpus three times as long as wide and about two-thirds length of propodus. Second legs long, slender, unequal, chelate; carpus and merus subdivided; right leg with 18 carpal, 12 meral joints; left leg with 17 carpal, 6 meral joints; merocarpal bend of right leg reaching to or beyond end of antennal scale. Remaining legs long, slender; third shortest; fourth slightly longer than fifth; dactyls simple; propodus of fifth leg with groups of long setae, a single small spine at end and one to five additional spines along article.

Abdomen with pleura rounded. Telson three times as long as basal width; two pairs of large dorsolateral spines, first pair close to anterior end; tip subacute, armed with two pairs of stout spines, and a strong median pair of feathered setae, outer spines short, intermediate spines long. Uropods elongate; outer border of exopod ending in an acute spine flanked medially by a strong movable spine.

Measurements.—Length of body: males 14 to 16 mm.; females, 50 mm.

Variations.—The first pair of legs is usually chelate on only the right side but this asymmetry may be reversed. Relative length of the carpus of the first legs changes with age.

Color.—Larvae pale brown with glistening white chromatophores; whole body pale (Lebour, 1941).

Habitat.—Oceanic water; surface to possibly 180 fathoms.

Type locality.—Harrington Sound, Bermuda.

Known range.—Bermuda; North Carolina (restricted to recently identified material).

Remarks.—Gurney (1936c), Lebour (1941), and Holthuis (1959) have all pointed out the confusion which exists concerning identity of the species of *Processa* in the Western Atlantic. Formerly, the species found in the Western Atlantic were lumped under the name *P. canaliculata*, a name now restricted to a species in European waters (Lebour, 1936), but Lebour (1941) showed that three or perhaps four species occur at Bermuda. It is likely that more than one species occurs in the Carolinas as well.

From descriptions given by the above authors, it appears that one species occurring in the Carolinas is *P. bermudensis*, a species lacking antennal spines, although the stylocerite in North Carolina material is not shaped exactly as that shown in Gurney's illustrations. In addition, there is apparently a second species (represented by a few immature specimens in the Institute of Fisheries Research collection, all taken in night plankton tows in Bogue Sound) which has an antennal spine present, shorter legs than *P. bermudensis*, fewer joints in the carpi of the second legs than the above, and exhibits considerable variation in spination of the third and fourth legs. These specimens appear to be close to Lebour's *P. wheeleri*, but because they are so few in number and immature it is best to reserve determination until more material is available for study.

Lebour (1941) showed that *P. bermudensis* larvae are common in the plankton almost throughout the year in Bermuda, and adults were commonly found in the dredge at night, with ovigerous females occurring at least from June to October. Gurney (1936c) described eight larval stages.

Pearse (1934) too *P. "canaliculata"* from loggerhead sponges at Tortugas, Florida.

Family Pandalidae

Rostrum long and slender, laterally compressed, armed with teeth or spines. Eyes well developed. Mandibles with incisor process and a two or three-jointed palp. First pair of legs simple or microscopically chelate; second pair long, slender, chelate, carpus subdivided.

Genus *Pantomus* Milne Edwards, 1883

Rathbun, 1901, p. 117.—Hemming, 1958b, p. 159.

Pantomus parvulus Milne Edwards

Figure 71

Pantomus parvulus Milne Edwards, 1883, pl. 26, fig. 1. 1a.—Rathbun, 1901, p. 118.—Schmitt, 1935a, p. 138.

Recognition characters.—Rostrum longer than carapace, articulated with anterior margin of carapace; basal portion with three dorsal spines; lower margin with numerous slender overlapping spines; terminal half directed upward; tip bifid, lower prong longest. Carapace carinated on anterior half and armed with three spines, posterior two near together and movable, anterior spine adjoining articulation of rostrum; antennal and pterygostomial spines present. Eyes large. Antennular peduncle with basal article excavate above and longer than nearly equal second and third articles combined; stylocerite wide, broadly pointed, inner margin sinuous, tip reaching to midlength of cornea; upper flagellum about twice diameter of lower flagellum at base. Antennal scale, slender, reaching two-thirds length of rostrum, broadest near base; lateral spine exceeded by lamella.

Third maxilliped and first pair of legs reaching to tip of antennal scale. Second pair of legs longer than first; carpus subdivided; one leg with 15 to 17 carpal joints, other leg shorter, with 10 to 12 carpal joints. Third to fifth legs progressively longer than second pair.

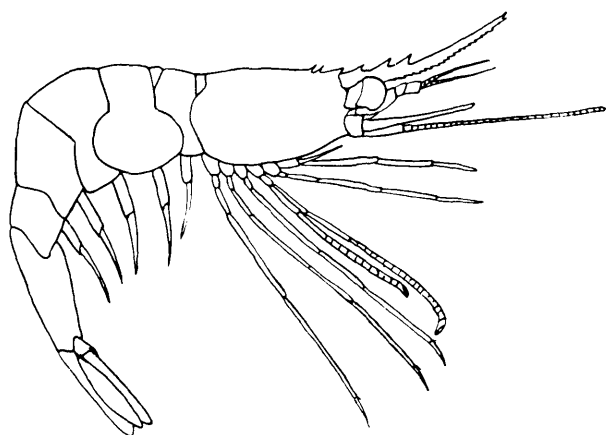


FIGURE 71.—*Pantomus parvulus* Milne Edwards. Animal in lateral view (after Milne Edwards, 1883).

Abdomen with third segment broadly carinated on posterior half; sixth segment elongate, 2.5 times length of fifth. Telson nearly as long as sixth segment, slender; sides concave, tapering to tip ending in a small, median, bulblike enlargement; two pairs of spines at tip, outer pair longest and sinuous at base, inner spines shorter, arising on terminal bulb; a row of seven or eight small dorsolateral spines on each side in distal two-thirds of length. Uropods long, narrow; exopod with lateral border ending in a slender movable spine.

Measurements.—Length of body: ovigerous female, approximately 30 mm.

Variations.—Among four of the cotypes, the rostrum varies somewhat in length and the number of carpal segments in the second legs is subject to variation.

Habitat.—Seventy-five to 248 fathoms.

Type locality.—Northern part of Yucatan Bank, lat. 23°13' N. long. 89°16' W., 84 fathoms.

Known range.—Cape Lookout, N.C., to Yucatan, Mexico; Puerto Rico; St. Croix, V.I.

Remarks.—The Catalogue of the Books, Manuscripts, Maps and Drawings in the British Museum (Natural History), vol. VI, Supplement, 1922, lists Milne Edwards' 1883 paper as follows: "The title-page (wanting to this copy), the 'Liste des Planches,' and many of the plates themselves are lithographed. Only fifty copies were issued and sent mostly to fellow workers, but a few were sold, (See letter by the Author in 'Ann. and Mag. Nat. Hist.' Vol. vi, 1890, p. 471)."

Family Crangonidae

First pair of legs subchelate, stouter than second. Second pair of legs slender, equal; carpus not subdivided; minutely chelate or simple. Rostrum small, usually dorsally flattened, not toothed.

Genus *Crangon* Fabricius, 1798

Holthuis, 1955, p. 134.—Hemming, 1958b, p. 108.

The name *Crangon* confused with the name *Alpheus* during the first half of this century, had doubtful status until nomenclatural stability was effected by the International Commission on Zoological Nomenclature (Opinion 334). The Official List of Generic Names in Zoology (Hemming,

1958b) now lists *Crangon* Fabricius, 1798, as the correct generic name for the species here considered, and the Official Index of Rejected and Invalid Generic Names in Zoology (Hemming, 1958a) lists the suppressed generic name *Crangon* Weber, 1795, and the invalid name *Crago* Lamarck, 1801, formerly applied to the species here considered.

Crangon septemspinosus Say

Figure 72

Crangon septemspinosus Say, 1818, p. 246.

Crago septemspinosus: Hay and Shore, 1918, p. 396, pl. 27, fig. 9.—Rathbun, 1929, p. 20.

Recognition characters.—Rostrum shorter than eyestalks, unarmed, tip obtuse. Carapace somewhat depressed, subcylindrical; dorsal surface with a small appressed spine back of rostrum; anterior margin with suborbital spine obtuse; antennal spine strongly produced, equaling or slightly exceeding eyes and with a minute spine below; hepatic spine well developed; anterior portion of carapace with two impressed lines, one originating in fissure in superior margin of orbit, another originating lateral to suborbital spine, both uniting above hepatic spine and disappearing posteriorly; a broad groove below and anterior to hepatic spine. Eyes moderately developed. Antennular peduncle with basal article hollowed out above, stylocerite broad, cupped longitudinally forming portion of socket for reception of eye, tip reaching nearly to end of article; second article of peduncle slightly shorter than third; inner flagellum hairy below, a little longer than antennal scale; outer flagellum shorter, smooth. Antennal scale broadest in posterior half, lamella tapering

to narrow rounded tip; lateral border slightly convex; well-developed lateral spine exceeding lamella and as long as distal width of blade. Third maxilliped reaching nearly to tip of antennule; hairy.

First pair of legs strong, subchelate; hand less than 3.5 times as long as wide, palm with a strong spine at distal end of finger; merus with a small spine on lower margin. Second pair of legs almost filiform; minutely chelate, hand hairy. Third legs stronger; fourth and fifth normal.

Abdomen, viewed dorsally, tapering from broad first and second segments to narrow sixth segment. Telson slender, tapering; with four small spines above on lateral border, first pair at two-thirds length, second midway between these and acute tip; tip flanked by three pairs of movable spines, median pair longest and stoutest. Uropodal exopods with lateral border ending in a spine flanked medially by a longer movable spine.

Measurements.—Length of body: ovigerous females from North Carolina, 25 to 60 mm. Specimens from Delaware: males, to 47 mm.; females, to 70 mm. (Price, 1962).

Color.—Ash-gray with numerous irregular, stellate, blackish-brown spots or speckled with gray, imitating the color of sand; color subject to considerable variation in shade, tail often darker (various authors).

Habitat.—Usually near bottom over sand: low-water mark to 50 fathoms, rarely to 246 fathoms.

Type locality.—"Bay shores and inlets of the sea" [east coast of United States].

Known range.—Baffin Bay to east Florida; Arctic Alaska southward to Shumagin Islands, Alaska, and Ranshima, Hokkaido, Japan.

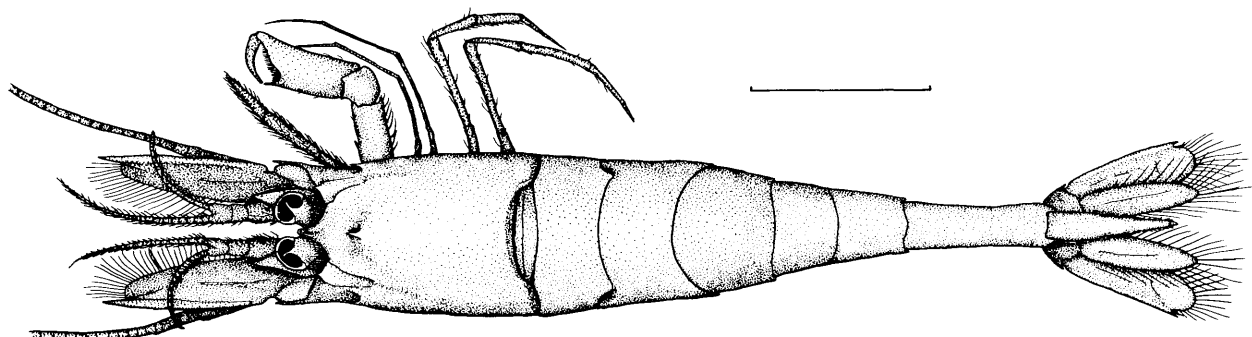


FIGURE 72.—*Crangon septemspinosus* Say. Ovigerous female in dorsal view, legs of left side not shown, 10 mm. indicated.

Remarks.—At the time of Hay and Shore's account, it was apparent that *C. septemspinosa*, with northern rather than southern affinities, fluctuates in abundance seasonally in estuaries near Beaufort, N.C. Ovigerous females have been found in North Carolina from December through May and in August and late fall (Hay and Shore, 1918, in part). Individuals taken in winter are larger than those found in spring. Juveniles have been found in this region from December to July, but from midsummer to late fall juveniles and adults disappear from estuaries.

Bigelow and Sears (1939) reported much the same pattern of occurrence in waters of the Continental Shelf from Cape Cod to Chesapeake Bay, with greatest occurrence in February dwindling to rare occurrence in July, but never abundant anywhere. They found the species limited, probably by depth and not by distance from shore, at about the 27-fathom curve, and remarked on probable importance of the species in the diet of predatory fishes. The role of the species in diets of fishes has long been recognized (Whitley, 1948).

On Georges Bank, where Whitley (1948) made all collections inside the 100-fathom curve, *C. septemspinosa* was most common in September and January, rarest in June, and usually occurred near the bottom. He reported maximum numbers in July at Woods Hole, and in August in the Bay of Fundy. Ovigerous females were found in spring and early summer. The species was judged to produce one brood a year and to have a life span of 1 year.

Price (1962), studying the biology of *C. septemspinosa* in Delaware Bay, made collections in a salinity range of 4.4 to 31.4‰ at temperature extremes of 0.0° to 26.0° C. Growth rate was estimated to be 1.6 mm. per month, with no observed seasonal variation in rate. The major breeding season was judged to be March to October, but ovigerous females were found throughout the year in salinities of 17.7 to 29.3‰, and temperatures of 0.0° to 25.0° C. First egg bearers of the year were found to be large females, with smaller ovigerous females more numerous in July. Females outnumbered the males, especially during the most active spawning season. At 21° C., eggs hatched after 6 or 7 days in the laboratory.

Contrary to the appraisal of other authors, Price judged that 3 year classes of females and 2 year classes of males occur in the shoal waters of Delaware Bay in spring. Food studies indicated a diet of planktonic crustacea and scavenged material. Sanders, Goudsmit, Mills, and Hampson (1962) found a diet of small bottom plants and animals.

Fish (1925) found the larvae appearing from February to May and as late as December at Woods Hole. Needler (1941) recorded hatching times from late spring to early summer (July) around Prince Edward Island, Canada. She described five larval stages and a postlarval stage. All these stages were obtained in July from plankton tows made about a meter below the surface along the shores of estuaries. Larvae were hatched in the laboratory, but the series of stages was worked out from plankton.

These data indicate an extended breeding season in high latitudes. Variations in seasonal abundance in different localities north of Chesapeake Bay are possibly the result in part of varied sampling methods in different years by different investigators.

Work on color control of *Crangon* and related species, too involved for appropriate summary here, has been reviewed by Kleinholz (1961).

Suborder **Reptantia**

Usually lobsterlike or crablike in form. Cephalothorax usually depressed. Rostrum usually small or absent, depressed if present. Antennules without stylocerite. Legs strong, first pair usually, but others never, stronger than remainder. Abdomen, whether well developed or greatly reduced, more or less depressed with first segment distinctly smaller than rest; pleopods often reduced or absent.

Section **Macrura**

Abdomen straight, symmetrical; usually well armored, with well-developed pleura and a strong tail fan (Schmitt, 1921).

Superfamily **Scyllaridea**

First article of antennule fused with epistome. Antennal scale absent. All legs nearly equal in length and none chelate except subchelate last pair in females. First abdominal segment without

pleopods; tail fan divided into a soft membranous and striated hinder part and a harder anterior portion.

Family Palinuridae

Carapace subcylindrical. Eyes not enclosed in separate orbits formed by edge of carapace. Antennae not flattened but furnished with large, long, rather rigid, multiarticulate, usually spinose flagellum.

The fossil record for the family Palinuridae extends back to the Cretaceous in North America (Rathbun, 1926, 1935).

Genus *Panulirus* White, 1847

White, 1847b, p. 69.—Hemming, 1958b, p. 174.

Panulirus argus (Latreille). Spiny lobster, crawfish

Figure 73

Panulirus argus Latreille, 1804, p. 393.

Panulirus argus: White, 1847b, p. 69.—Hay and Shore, 1918, p. 398, pl. 28, fig. 3 (rev.).—Crawford and deSmidt, 1922, p. 291, figs. 265–271.—Schmitt, 1935a, p. 172, fig. 36 (rev.).

Recognition characters.—Carapace covered with strong spines arranged more or less in regular longitudinal rows; spines above orbits very large, compressed, and curved upward and forward.

Eyes large and prominent. Antennules nearly two-thirds length of body; peduncles slightly exceeding antennal peduncle; outer flagellum shorter and thicker than inner, and strongly ciliated distally. Antennal segment with a pair of spines in front, a weaker pair about halfway to eye, a strong median spine and weaker lateral spines below insertion of antennules. Antennae very large, heavy, exceeding body by more than length of carapace; peduncles with numerous strong spines; flagellum stout, stiff, a line of cilia along inner margin and ringed with spines at intervals.

Legs rather weak, tips acute and bristly; female possessing a small subchela on fifth legs with concave opposed surfaces formed between distal portion of propodus and proximal portion of dactyl.

Abdomen smooth, each segment crossed by a furrow more or less distinctly interrupted at middle; pleural angles each produced into a strong, sharp, backwardly directed tooth deeply notched and serrated on posterior margin. Pleopods absent from first segment of abdomen; exopod of pleopods broad, laminate; endopods missing in males, females with endopods of second pleopods laminate, last three endopods bifurcated. Proxi-

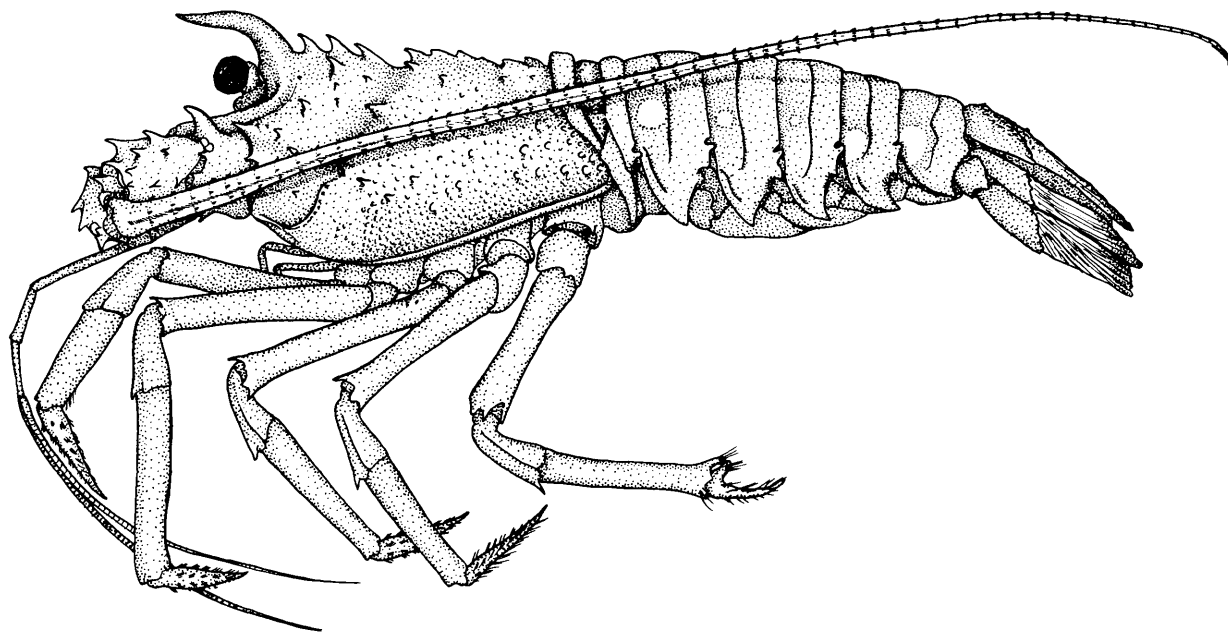


FIGURE 73.—*Panulirus argus* (Latreille). Female in lateral view, approximately $\times 0.5$.

mal division of telson with rather strong spines; distal division with weak spines and cilia in longitudinal lines. Uropods hard proximally, membranous distally; basal article bispinose, a row of denticles along margin of hard part, and lines of minute spines and setae on upper surface of membranous part.

Measurements.—Length of body from orbit to tip of telson: to approximately 450 mm. (18 inches), occasionally larger.

Variations.—Aside from individual variations which will not be discussed here, the species exhibits marked allometric variations with age as well as sexual dimorphism. These features were discussed in detail by Crawford and deSmidt (1922) and are summarized here. Antennae of the young are longer in proportion to the body than in adults. Setae present on the young disappear in the adult and the sharpness of spines on the body tends to diminish with age, except for those on anterior portions of the carapace.

As pointed out in the description, only the females have chelate fifth legs. In adult males, the second pair of legs is extraordinarily developed. They are long, rarely used in walking, and the dactyl is long, curved, and provided with a brush of setae. The length of the dactyl, its curvature and setation increase with age. Sexual differences in the pleopods are given in the description.

Males have a relatively more inflated and longer carapace than females. Conversely, in females the abdomen represents a greater proportion of total length of the body than in males. Maximum lengths of the two sexes, however, are about the same (Creaser, 1952). The posterior margin of the sternum in males is narrower than the comparable structure in females and the sternum is longer.

Color.—Coloration largely separable into two groups, (1) lightly colored individuals ranging from light gray and tan to shades of green and light brown, and (2) darkly colored individuals varying from shades of red to deep brown and blue. Abdomen spotted with yellowish ocelli; posterior margin of each segment edged with yellow or orange, lower angles of segments marked with bluish or greenish tints and sometimes additional colors. Tail fan crossed by bands of orange, yellow, and black, fringed with white. Pleopods usually orange, about half of surface covered by

a black blotch. Legs striped longitudinally with blue. Ventral surfaces of body light yellow; thoracic sternum marked with irregular radiating stripes.

Young with coloration of carapace arranged in transverse bands, usually three, middle one dark; antennae frequently ringed with alternate light and dark bands; legs ringed with blue (Crawford and deSmidt, 1922).

Habitat.—On reefs or among rocks, among growths of sponges or other objects which afford protection or places of concealment; low-tide mark to depths of about 50 fathoms. Experimentally, lobsters at Bermuda have withstood depths of 250 fathoms (Creaser and Travis, 1950).

Type locality.—Erroneously given as East Indies ("des Grandes-Indies").

Known range.—North Carolina through Gulf of Mexico and West Indies to Rio de Janeiro, Brazil; Bermuda.

Remarks.—A number of papers have been published concerning the general ecology of *Panulirus argus*. Only a summary of this work can be given here. The most comprehensive single, general treatment is that of Crawford and deSmidt (1922) for the species in Florida, but substantial additions to this work have been given by Dawson (1949, 1954), Dawson and Idyll (1951), Lewis (1951), Lewis, Moore, and Babis (1952), Marshall (1948), and Smith (1951). Mattox (1952) gave biological notes on the species in Puerto Rico, and Creaser (1950, 1952), Creaser and Travis (1950), and Sutcliffe (1952, 1953, 1957) discussed the species in Bermuda.

North Carolina must be regarded as the extreme northern edge of the range of this species, and, indeed, concentrations of the species large enough to be exploited commercially occur only in southern Florida, the West Indies southeast to Puerto Rico, and at Bermuda. A large population may exist in deep water in the northern Gulf of Mexico (Moore, 1962). Differences in growth rate and breeding habits may exist among these areas.

Panulirus argus grows to a large size. In its first year of life it reaches a length of about 2 inches (measurements of this species usually given in inches in U.S.A.) and, though growth in the young individuals is more rapid than in older animals, increments in length after that time are

about an inch a year. Adults of 16-inch length are approximately 16 years of age, the males attaining somewhat greater lengths than females.

After juvenile stages are past, molts average about $2\frac{1}{2}$ times per year, occurring most frequently from March to July and from December to February, at least in the Florida area. Among captive animals, molts without growth can occur. About 12 days elapse from the first sign of molting until the new exoskeleton is hard enough to resist denting, though hardening of the new shell is not complete until the 28th day. Travis (1954, 1955a, 1955b, 1957) gave an exhaustive study of the molting process among spiny lobsters near the age of sexual maturity. This work is beyond the scope of the present summary, but her findings show that molting among captive adolescent animals is largely confined to the warmer months at Bermuda and is more frequent than among Florida specimens. Other evidence shows that growth of the young is more rapid in Bermuda than in Florida, and that sexual maturity is reached sooner.

The mating season in Florida is principally from March through July. Sexual maturity is reached in females as small as 6 inches long, but ovigerous females under 8 inches in length are rare. Mating pairs are judged to be about the same age, and mating usually occurs in the hard-shelled stage. At the time of mating the male places a waxy spermatophore on the thoracic sternum of the female. Prior to spawning, the female scratches the surface of this packet with the chelate fifth legs. The actual egg laying is accomplished in about one-half hour, during which the female lies partially on her back forming a trough of the underside of her abdomen with the aid of the exopods of the pleopods. Eggs extruded from the oviducts pass backward from the bases of the third legs over the spermatophore and become attached to the endopods of the last three pairs of pleopods. After spawning, the spermatophore appears eroded as if enzymatic action had partially destroyed it. The eggs hatch in about 1 month. A second mating and egg laying may occur about a week after the hatch of the first batch and at this time the ovary is spent and the spermatophore almost completely eroded away. Molting of females during this season occurs only after spawning.

The spawning season in Florida is principally from March through June, and mostly in April. However, a few ovigerous females occur as late as October (December in the Bahamas). In Puerto Rico, the spawning season may be more extended than in Florida, for 22 percent of females in the commercial catch in Puerto Rico are ovigerous in September and 18 percent in October.

Direct evidence from the studies in Bermuda shows that females may lay eggs twice in a season. The number of eggs laid depends on the size of the individual, and the second brood is smaller than the first. Estimates show that a 9-inch female can lay 500,000 eggs, a 12-inch female 1,118,656, a 15-inch female 2,566,916. A second laying by a 13-inch female consisted of 1,008,788 eggs. Thus, it is estimated that a 15-inch female might lay 4 million eggs a season.

In Bermuda and elsewhere, there is apparently a movement of females from shallow to intermediate depths and from deeper water to these depths for spawning. Aside from these movements, there is evidence in Bermuda that the lobsters exhibit considerable homing tendencies, often moving as much as 5 miles against strong tides to return to the place of original capture. Adults tagged in Florida, on the other hand, have moved as much as 100 miles in 100 days (Smith, 1954), but such movement is probably exceptional.

The larva of the spiny lobster is a flattened, leaf-shaped, planktonic organism which, before its identity was known, was given the name phyllosoma. Development of the phyllosoma larvae of *P. argus* has been studied off Florida and at other points in the Atlantic Ocean from the West Indies to the southeastern coast of the United States and north of Bermuda. Bigelow and Sears (1939) found phyllosoma larvae (*P. argus?*) off Chincoteague Bay in July, 1929. Eleven stages have been described from plankton. In Florida, the bulk of freshly hatched larvae appear between June and August, the last stages being taken in December and January. The first postlarval, or puerulus, stages appear in inshore waters from January to March. Thus, larval development is judged to require 6 months, and during that time the larvae may be swept hundreds of miles from the spawning place. (Feliciano (1956) described a prenaup-

pliosoma stage which may at times be freed in the water but this has yet to be confirmed.) The puerulus is shaped like a miniature adult, but is about 17 mm. long, colorless, and has a soft exoskeleton. It is nonplanktonic and settles in shallow water. Ten postlarval stages have been distinguished. Stages one through three avoid light, but later stages show no such reactions. At the end of the first year, at the eleventh postlarval stage, the young are approximately 2 inches long.

Aside from reactions of the very young postlarvae to light, Hess (1940) showed that freshly molted adults are sensitive to light in many regions of their bodies, but as soon as the body is again sclerotized no such reactions are apparent. Sutcliffe (1956) demonstrated that in clear, shallow water lobsters sought cover in bright moonlight. He concluded that movements attributed to tidal responses were actually responses to light.

Stridulation by spiny lobsters (Palinuridae) has been described by a number of workers (Moulton, 1957) and in *P. argus* it is produced primarily by a toothed ridge medial to the bases of the antennae and extending anteriorly from beneath each eye. A corrugated membrane at the base of each antenna is played against this ridge, producing sound when the membrane is moved proximally. Two types of sound are produced, a slow rattle normally produced by animals in small groups, and a rasp which accompanies defensive behavior. A squeaking sound is also produced in an unknown manner, by vibration of the body, when a specimen is held in the hand of an observer. The effect of these sounds on other lobsters or marine life is unknown.

Pearse (1932a) determined the freezing point of *P. argus* blood at Tortugas (range -1.86° to -2.39° C.).

Family *Scyllaridae*. Spanish lobsters

Carapace depressed; exoskeleton thick, hard, sculptured or tuberculate; orbits excavated in margins of dorsal surface. Antennae short and broad with flat scalelike, stiff articles. Mandibles with a one-jointed palp. Legs simple except minutely chelate fifth pair in female.

The fossil record for the family *Scyllaridae* extends back to the lower Eocene of the Gulf Coast in North America (Rathbun, 1935).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

(Adapted in part from manuscript key by
F. A. Chace, Jr.)

- a. Exognath of outer maxillipeds without a flagellum; terminal article of antennae with edge cut into deep lobes distally.....*Scyllarus* (p. 94).
- b. Prominences on carapace blunt; second article of antennular peduncles dorsally flattened; distal articles of antennae meeting, or nearly meeting, in midline; first four abdominal tergites obscurely notched posteriorly in midline; pleura of fourth abdominal segment rounded laterally.
 - c. Pregastric tooth of carapace broadly rounded; two, seldom three, distinct parallel grooves between posterior marginal groove and posterior margin of carapace; first to fourth abdominal segments with notch in posterior margin very shallow; fourth abdominal segment not elevated in midline
chacei (p. 95).
 - cc. Pregastric tooth almost always bilobed, incised; almost always a single distinct groove between posterior marginal groove and posterior margin of carapace; first to fourth abdominal segments showing a deep, narrow, median notch in posterior margin; fourth abdominal segment elevated, more or less ridgelike in midline.....*americanus* (p. 96).
- bb. One gastric and all lateral prominences on carapace sharp; second article of antennular peduncles cylindrical; distal articles of antennae not nearly meeting in midline; first four abdominal tergites deeply and acutely notched posteriorly in midline; pleura of fourth abdominal segment sharply rectangular or acute laterally.....*nearcticus* (p. 97).
- aa. Exognath of outer maxillipeds with a flagellum; terminal article of antennae with edge nearly smooth or crenulate distally.....*Scyllarides nodifer* (p. 98).

Genus *Scyllarus* Fabricius, 1775

Fabricius, 1775, p. 413.

Recognition characters.—Carapace flattened, width at anterolateral corners equal to or slightly greater than length in midline; middorsal ridge and an oblique ridge on each side prominent. Antennules with first articles broad, flattened, and immovable, second article much narrower and elongate; third and fourth articles slender; flagella short; abdomen, including telson, much longer (nearly twice) than carapace; pleura of first segment incised in center of lower edge, second broad and pointed distally. Anterior pleopods of male with both rami slender, flattened, hairy on outer border; remainder with exopods small and lamellate, endopods rudimentary. Anterior pleopods of female with both rami broad and flattened; exopods of remainder lamellate,