# AMERICAN SOLENOCERID SHRIMPS OF THE GENERA HYMENOPENAEUS, HALIPOROIDES, PLEOTICUS, HADROPENAEUS NEW GENUS, AND MESOPENAEUS NEW GENUS

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# ABSTRACT

Twelve American species, one from Hawaii, are assigned to five genera: five to Hymenopenaeus, one to Haliporoides, two to Pleoticus, three to Hadropenaeus, and one to Mesopenaeus; the latter two genera are described herein. Each of the genera is defined and the relationships among them are discussed. The species are described in detail mostly on the bases of collections made in the western Atlantic and eastern Pacific during cruises of 29 exploratory vessels. For each species a diagnosis, illustrations, references, disposition of types, locality records, and geographic as well as bathymetric ranges are provided. The affinities of each species are indicated, and variations of several morphological and morphometric characters are analyzed. Keys for the identification of all taxa are given. Photophores were discovered in Hadropenaeus affinis, here recognized as a distinct species, and Mesopenaeus tropicalis. The spermatophores of three, Pleoticus robustus, P. muelleri, and M. tropicalis (those of the latter previously unknown), are described and their mode of attachment to the females is discussed. The range of Hymenopenaeus debilis was found to extend south of the Gulf of Mexico, through the Caribbean to Guyana, and that of H. aphoticus to include the Caribbean. Pleoticus muelleri is now known to occur north of the state of Rio de Janeiro, off Espírito Santo, and Hadropenaeus affinis is newly reported from the southeast Atlantic coast of the United States, where it ranges as far north as Cape Lookout, N.C.

This work is part of a continuing study of the systematics and distribution of the American members of the superfamily Penaeoidea. Extensive collections made during cruises of 26 exploratory vessels provided excellent series of specimens from the western Atlantic. In contrast, the material available from the tropical and subtropical eastern Pacific (including that obtained during cruises of three exploratory vessels) is rather meager and these waters still remain appallingly unexplored, particularly beyond the 100-m contour. Few benthic collections from the latter region have been deposited in American institutions since the expeditions of the Albatross in 1889 and 1891. The only major ones are those resulting from the explorations sponsored by the Allan Hancock Foundation and Scripps Institution of Oceanography among which no member of the genera investigated in the present project has been found.

The only species treated here from waters not adjacent to the American continent is one which ranges throughout the Indo-West Pacific, reaching Hawaii. This shrimp is included because it is the third member of a new genus, the other two being found off American shores. Inasmuch as the Hawaiian population of the species has not been adequately described and because numerous specimens from the area are available to me, a detailed account of its morphology is presented.

The five genera treated in this paper, together with Solenocera and Haliporus, constitute the family Solenoceridae, a group that has been previously considered one of the four subfamilies of Penaeidae. I am of the opinion that because of the basic differences among these four suprageneric groups they should be elevated to the category of families, i.e., Aristeidae, Solenoceridae, Penaeidae, and Sicyoniidae, as has been defended by Pérez Farfante (in press). The western Atlantic species of Solenocera (the other genus of Solenoceridae which is present in the region, in addition to four of those discussed here) were recently monographed by Pérez Farfante and Bullis (1973).

In the diagnoses of the genera and descriptions of the 12 species discussed here, many morphological characters have been studied in order to base relationships at generic and specific levels.

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For each taxon a synonymy, bibliographic references (selected for the genera, and complete for the species), location of type-specimens, descriptions, and distributional data are given, as are variations for some species. Detailed accounts of the spermatophores (both as attached to the females and as they appear when removed from the terminal ampullae of the males) of three species are also presented. These are the only species for which spermatophore-bearing females were secured.

Bate (1881) was the first to describe species of the generic complex treated here, assigning all except one-which was assigned to Solenocera Lucas (1849)—in a new genus, Haliporus. A year later, Smith (1882) proposed the genus Hymenopenaeus for another new species belonging to that complex. Subsequently, Bate (1888) expanded his preliminary descriptions of Haliporus and corresponding species, and pointed out that the one he had placed in Solenocera, together with two others, should be relegated to a new genus, *Philonicus*. After his manuscript was in press, he discovered that the latter name was preoccupied and changed it to *Pleoticus* in the Introduction. Bouvier (1906b) presented a revision of the genus Haliporus in which he recognized 19 species, most of which had been described after Bate's last contribution (1888). He separated them into three groups on the basis of the relative length of the posterior two pairs of percopods, the relative diameter of the proximal part of the respective carpi, and the consistency of the integument. He failed to recognize other important supraspecific differences which led him to group together species which are not closely related. Burkenroad (1936) disagreed with Bouvier's arrangement and, as a result of an extensive investigation, recognized two genera, Haliporus and Hymenopenaeus. Several other generic names have been proposed and later synonymized with Hymenopenaeus, a clear indication of the taxonomic difficulties presented by this complex.

The genus *Hymenopenaeus* was defined by Burkenroad (1936) as those "Solenocerinae without podobranchs behind VIII; with well-developed prosartema and only a single pair of lateral telson spines in adult stages, and with cylindrical filiform antennular flagella." Within it, he recognized four separate groups based on the presence or absence of branchiostegal or pterygostomian spines and the arrangement of the epigastric and rostral teeth.

An examination of Atlantic, eastern Pacific, and Hawaiian species, supplemented by material from the Indo-West Pacific region, convinces me that, in addition to the arrangement of the middorsal teeth on the carapace, the following characters are more reliable than the branchiostegal and pterygostomian spines in ascertaining interrelationships of the species previously included in *Hymenopenaeus:* shape of the antennular flagella and rostrum, proportions of the carapace, number and comparative size of the articles of the mandibular palp, presence or absence of certain carinae on the carapace, relative dimensions of the posterior two pairs of percopods, location of the distolateral spine (terminal or subterminal) of the lateral ramus of the uropod, structure of the petasma, and degree of development of the arthrobranchia on somite VII.

A comparative study based on the characters cited above indicates that the species under consideration should be assigned to five genera: *Hymenopenaeus*, *Pleoticus*, and *Haliporoides* which had been erected previously—and *Hadropenaeus* and *Mesopenaeus*—which are proposed here.

Diagnoses of the four groups established by Burkenroad (1936) within *Hymenopenaeus* together with the conclusions resulting from my revision of this species-complex follow.

Group I. This division contained the western Atlantic H. muelleri and H. tropicalis, and the Indo-West Pacific (Red Sea) H. steindachneri. As pointed out by Burkenroad, these species share the arrangement of the epigastric and rostral teeth, which are separated by regularly decreasing intervals anteriorly, and the absence of branchiostegal and pterygostomian spines; to these characters may be added the presence of orbital spines and the lack of distinct branchiocardiac carinae. Several different features occur in tropicalis which I consider to be of sufficient importance to justify a separate genus, for which I propose the name Mesopenaeus. Moreover, the western Atlantic robustus, which was placed in Group II by Burkenroad, shares basic characters with *muelleri* and *steindachneri*; consequently, the three are grouped herein under the available generic name Pleoticus Bate (1888).

Group II. The species assigned to this group were characterized by possessing branchiostegal but lacking pterygostomian spines and, like those of Group I, exhibit epigastric and rostral teeth separated by regularly decreasing intervals. Burkenroad subdivided the group into two sections: section 1, with orbital spines, to which only *H. robustus* was assigned, and section 2, without orbital spines, to which the western Atlantic *H. modestus* and the Indo-West Pacific *H. lucasii* were referred. As stated above, the former species is here transferred to the genus *Pleoticus*, and the latter two, together with the amphi-Atlantic *H. affinis* (which Burkenroad considered as "very doubtfully distinct" from *H. modestus*), are placed in the genus *Hadropenaeus*.

Group III. This group comprised the species with pterygostomian but lacking branchiostegal spines, and with the epigastric tooth separated from the rostral teeth by a long interval. The eastern Pacific H. diomedeae and the Indo-West Pacific H. sibogae and H. triarthrus were included, but these three species are referred here to the genus Haliporoides Stebbing 1914.

Group IV. This assemblage contained those species that are armed with branchiostegal spines, and have the epigastric and first rostral teeth separated from the remaining rostral teeth by a conspicuous interval. It was subdivided into two sections characterized by the presence or absence of pterygostomian spines. In section 1, Burkenroad cited Hymenopenaeus laevis, found on both sides of the Atlantic and in the Indo-West Pacific, and H. doris and H. nereus of the American Pacific; in section 2, he included the Atlantic H, aphoticus and H, debilis and the Indo-West Pacific H. aequalis, H. obliquirostris, H. neptunus, and H. propinguus. Since the publication of Burkenroad's work, one species, the Indo-West Pacific H. sewelli, has been added to section 1, and three have been added to section 2: one from the eastern Atlantic, H. chacei, and two from the Indo-West Pacific, H. fattahi, and H. halli. These species are included in Hymenopenaeus as restricted here, and their separation into two sections is recognized.

Burkenroad also discussed under Hymenopenaeus the two following Indo-West Pacific species: Haliporus villosus Alcock and Anderson 1894 (syntype illustrated in Alcock and Anderson 1896), and Haliporus taprobanensis Alcock and Anderson 1899 (holotype illustrated in Alcock 1899b). He indicated that the former perhaps would merit being placed in an independent group, and pointed out that although the latter shares several characters with members of Group III, it differs from them in other basic features. Our knowledge of H. villosus prior to Kensley's

(1968) study was limited to the brief description by Alcock and Anderson (1894) and their illustration published in 1896 (plate 26, figure 1). The lack of detail in the figure of the telson, exhibiting no movable spines, was probably responsible for Burkenroad's assigning this shrimp to the genus Hymenopenaeus. Kensley presented a detailed description and several illustrations which demonstrate that this species exhibits two basic features characteristic of the genus *Haliporus* (as restricted by Burkenroad 1936): in addition to the podobranchia on the second maxilliped, another, small one is present on the third maxilliped, and the telson is armed with movable spines situated anterior to the fixed pair. My examination of two specimens of H. taprobanensis has shown that the same characters are present in them; thus, in respect to these two features, both this species and H. villosus are more closely allied to the members of Haliporus than to those assigned to Hymenopenaeus. It should be pointed out, however, that H. villosus and H. taprobanensis differ from Haliporus curvirostris Bate 1881, the type-species, in several characters (e.g., shape of rostrum, number of podobranchiae posterior to the second maxilliped, carinae present on the carapace) which seem to me to be of supraspecific significance. Consequently, I believe that a study of adequate material might demonstrate that they should be relegated to separate monotypic genera.

Although the illustration of the entire animal of H. villosus by Alcock and Anderson (1896) and that by Kensley (1968) leave little doubt that both correspond to the same species, the specimens available to the former authors were densely covered by setae, as they explicitly stated, whereas that studied by Kensley as well as the specimens examined by me are glabrous. The material available to Alcock and Anderson was from the Laccadive Sea, off southwest India; Kensley's specimen was caught off southwest of South Africa, and the two at my disposal were collected off eastern Madagascar.

All five genera (together with *Haliporus* and *Solenocera*) are believed to have arisen from a common solenoceroid ancestor, some of the characters of which are presented in the accompanying dendrogram. In the latter only the newly acquired characters or those modified or lost in each lineage are indicated. As shown in the dendrogram, one of the lines arising from the solenoceroid ancestor led to *Haliporus*, apparently not only the most primitive solenocerid, but

#### CHARACTERISTICS INVOLVED IN THE EVOLUTION OF SOLENOCERIDAE (See text for explanation)



according to Burkenroad (1963b) "the Recent Peneid which seems in several respects the nearest of these to the stem-form of the relatively primitive suborder Dendrobranchiata." A second line gave rise to *Hymenopenaeus* and *Haliporoides*, and a third lineage is believed to have been ancestral to two stocks, one of which terminated in *Pleoticus* and from the other evolved *Hadro*- penaeus, Mesopenaeus, and Solenocera; the latter appears to be the most specialized of all seven genera.

The members of Solenoceridae, in general, occupy deep water beyond the continental and insular shelves; however, most of the species of *Solenocera* as well as *Pleoticus muelleri* are restricted to shallow water. *Mesopenaeus tropicalis*  is found both on the shelves, at a minimum depth of 30 m, and on the slopes to about 500 m.

#### Material

Abbreviations of the repositories of the specimens examined during this study follow:

AMNH	American Museum of Natural His-
	tory, New York, N.Y.
BMNH	British Museum (Natural History), London.
IOUSP	Instituto Oceanográfico, Universi- dad de São Paulo, São Paulo.
MCIP	Ministerio de Comercio e Industrias, Panama.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
MP	Muséum National d'Histoire Natu- relle, Paris.
RMNH	Rijksmuseum van Natuurlijke His- toire, Leiden, Netherlands.
TAMU	Texas A&M University, College Sta- tion, Tex.
UMML	Rosenstiel School of Marine and At- mospheric Sciences, University of Miami, Fla.
UNC-IMS	University of North Carolina - Insti- tute of Marine Sciences, Morehead City, N.C.

USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C. Peabody Museum of Natural History, Yale University, New Haven, Conn.

# Presentation of Data

YPM

The measurement of carapace length (cl) is the linear distance between the orbital margin and the midposterior margin of the carapace, and that of total length (tl) is the distance between the apex of the rostrum and the posterior end of the telson. The scales accompanying the illustrations are in millimeters. Figures 1 and 2 depict many characters used in the descriptions. For the terminology employed in the accounts of the spermatophores, see Pérez Farfante (1975).

# Key to Genera of Solenoceridae



FIGURE 1.—Diagrammatic lateral view of cephalothorax showing terms used in descriptions of solenocerid shrimps.

# Hymenopenaeus Smith 1882

- Haliporus Bate 1881:185 [part, excluding Haliporus curvirostris Bate 1881]. Bate 1888:284
  [part]. Faxon 1893:213 [part]; 1895:189 [part].
  Alcock 1901:22 [part]. Bouvier 1906b:1 [part]; 1908:78 [part]. A. Milne Edwards and Bouvier 1909:206 [part]. de Man 1911:31 [part]. Fowler 1912:542 [part].
- Hymenopenaeus Smith 1882:91 [type-species by monotypy, Hymenopenaeus debilis Smith 1882.
  Gender, masculine. Placed on the Official List of Generic Names in Zoology as Name No. 1816, International Commission on Zoological Nomenclature (1969), Opinion 864]. Smith 1885: 179 [part]. Burkenroad 1936:102 [part]. Kubo 1949:212 [part]. Holthuis 1962:108. International Commission on Zoological Nomenclature 1969:139. Roberts and Pequegnat 1970: 29 [part].

Diagnosis.-Body slender, carapace elongate, integument thin, flexible. Rostrum variable in



FIGURE 2.—Left half of petasma (dorsal view) of Hymenopenaeus debilis showing terms used in descriptions.

length, reaching between distal 0.25 of first antennular article and end of peduncle; ventral margin straight; usually armed only with dorsal teeth, occasionally also with ventral teeth; epigastric and first rostral teeth separated from remaining teeth by relatively long interval. Orbital spine absent; postorbital, antennal, hepatic, and branchiostegal spines present; pterygostomian spine present or absent. Cervical sulcus deep, long, extending to, but not across, middorsum of carapace; hepatic sulcus well marked; branchiocardiac carina sharp, accompanying sulcus deep; posthepatic and submarginal carinae present. Abdomen carinate dorsally at least along posterior three somites. Prosartema moderately long, flexible. Telson with pair of conspicuous fixed, lateral spines. Antennular flagella similar, filiform, and longer than carapace. Mandibular palp twojointed, articles relatively narrow, distal one much shorter than basal, and tapering to blunt apex. First maxilla with unsegmented palp (endite of basis), gently narrowing to rounded apex. Fourth and fifth percopods extremely long and flagelliform. First percopod with spine on

basis and usually on ischium. Exopods on all maxillipeds and pereopods. Lateral ramus of uropod armed with distolateral spine, reaching distal margin of lamella (terminal spine). In males, petasma with distal part of ventral costa fused to flexible flap of ventrolateral lobule; distal end of rib of dorsolateral lobule elevated above adjacent area and not projecting beyond distal margin; ventromedian lobule usually produced in conspicuous processes distally; endopod of second pleopod bearing appendices masculina and interna, and with basal sclerite produced distally into elongate, ventrolateral ("posterior") spur. Thelycum of open type, lacking enclosed seminal receptacle. Pleurobranchia present on somites IX to XIV; rudimentary arthrobranchia on somite VII, and anterior and posterior arthrobranchiae on somites VIII to XIII. Podobranchia present on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

List of species.-Following are the species listed in each of the two sections proposed by Burkenroad (1936), a division with which I am in full agreement.

Section 1. Pterygostomian spine present. Atlantic, Indo-West Pacific: Hymenopenaeus laevis (Bate 1881). Indo-West Pacific: Hymenopenaeus sewelli Ramadan 1938. Eastern Pacific: Hymenopenaeus doris (Faxon 1893); Hymenopenaeus nereus (Faxon 1893).

Section 2. Pterygostomian spine absent.
Atlantic: Hymenopenaeus aphoticus Burkenroad 1936; Hymenopenaeus debilis Smith 1882; Hymenopenaeus chacei Crosnier and Forest 1969. Indo-West Pacific: Hymenopenaeus aequalis (Bate 1881); Hymenopenaeus fattahi Ramadan 1938; Hymenopenaeus halli Bruce 1966; Hymenopenaeus neptunus (Bate 1888); Hymenopenaeus obliquirostris (Bate 1881); Hymenopenaeus propinquus (de Man 1907).

Affinities.—The members of the genus Hymenopenaeus differ from those of the closely related Haliporoides, Pleoticus, Hadropenaeus n. gen., and Mesopenaeus n. gen., in having a more slender body; a thin, flexible, almost membranous integument; the epigastric and first rostral teeth separated from the remaining teeth by an interval longer than the spaces between the more anterior teeth; and in possessing a posthepatic carina. They also differ from those of the other genera in having a slender mandibular palp in which the distal article is much shorter than the basal; extremely long and flagelliform fourth and fifth pairs of pereopods, and in certain features of the petasma: the terminal part of the ventrolateral lobule forms a flap to which the ventral costa is fused, the rib of the dorsolateral lobule is elevated distally from the surrounding area, and the ventromedian lobule is produced distally into conspicuous processes.

Remarks.-In the widely utilized work of Kubo (1949) several statements are made which should be discussed. Kubo based his description of the genus Hymenopenaeus primarily on two species found in Japanese waters [H. lucasii (Bate 1881) and H. aequalis (Bate 1888)], which led him to make erroneous generalizations. First, he considered the presence of two, instead of one, arthrobranchiae on somite VII as a character typical of Solenocera, and in his key to the genera of the subfamily Solenocerinae utilized this character to distinguish it from other genera in the subfamily. In at least one species (*Pleoticus robustus*, previously included in *Hymenopenaeus*), of a genus other than Solenocera, however, I find that there are two arthrobranchiae on somite VII. Secondly, Kubo noted that the petasma in "Hymenopenaeus" possessed spinules along the distal margin; actually, in some species they are absent. Finally, in the section "Arrangement of branchiae" Kubo indicated the restriction of podobranchia to somite VIII (on second maxilliped) in the members of the subfamily Solenocerinae, and in his table 6D he noted the presence of only one podobranchia in Hymenopenaeus and Parahaliporus (=Haliporoides). In the key to the genera of the subfamily, however, he utilized the occurrence of a rudimentary podobranchia on somites IX and X as the only feature to distinguish Hymenopenaeus from Haliporus and Parahaliporus. He used this feature in the key although in the following description of the genus Hymenopenaeus, he stated that in the specimens of H. lucasii and H. aequalis at his disposal, the epipods of none of the thoracic appendages behind the second maxilliped are furnished with podobranchia. It thus seems that in the key the line corresponding to Hymenopenaeus and the line corresponding to Parahaliporus and Haliporus were transposed; however, podobranchiae are present behind somite VIII in Haliporus

(at least on the third maxilliped and as far as the third percopod) but not in *Parahaliporus*.

# Key to Species of Hymenopenaeus in American Waters

- 1. Pterygostomian spine present (section 1) ...2 Pterygostomian spine absent (section 2) ...4
- 2. Scaphocerite, at most, barely overreaching antennular peduncle. Rostrum, in adult, falling short of distal end of first article of antennular peduncle. Females with pyramidal, median protuberance on sternite XIV projecting ventrally. Males with ventromedian lobule of petasma bearing two or three small triangular processes distomesially ....

Hymenopenaeus debilis Smith 1882

Figures 2, 3, 4B, 5-9

Hymenopenaeus debilis Smith 1882:91, pl. 15, fig. 6-11, pl. 16, fig. 1-3 [syntypes: 1 9, SE of Savan-

nah Beach, Ga., 31°57'00"N, 78°18'35"W, 333 fm (609 m), 12 July 1880, Blake stn 317. 1 9, MCZ 3270, SE of Cape Fear, N.C., 33°19'00"N. 76°12'30"W, 457 fm (836 m), 14 July 1880, Blake stn 323. 1 9, USNM 4920, E of Cape Fear, N.C., 33°42'15"N, 76°00'50"W, 464 fm (849 m), 14 July 1880, Blake stn 326]. Smith 1887:687, pl. 16, fig. 7. Burkenroad 1936:111, fig. 63-64. Yokoya 1941:52. Anderson and Lindner 1945: 289. Harvey 1952:352. Ramadan 1952:9, fig. 22-23. Springer and Bullis 1956:7. Holthuis 1962: 108. Boschi 1964:38. Bullis and Thompson 1965:5. Zariquiey Alvarez 1968:47, fig. 24b. Crosnier and Forest 1969:545. International Commission on Zoological Nomenclature 1969: 139. Roberts and Pequegnat 1970:31. Pequegnat and Roberts 1971:8. Crosnier and Forest 1973:269, fig. 85 c-d, 87b, 89a.

- Haliporus debilis. Faxon 1896:163. Bouvier 1905a:980; 1906a:253; 1906b:3; 1908:83, pl. 1, fig. 6, pl. 14, fig. 9-18. A. Milne Edwards and Bouvier 1909:206, pl. 2, fig. 8. de Man 1911:7. Fowler 1912:543. Boone 1927:78. Maurin 1961: 530; 1968:484. Vilela 1970:122.
- Haliporus debilis var. africanus Bouvier 1908:83 [syntypes: 4 & 3 \, MP, off Mazaghan, 33°46'N, 9°02'W, 1,319 m, 14 June 1883, Talisman stn 21].

#### Material

UNITED STATES-New Jersey: 1 9, USNM, Hudson Canyon, 550-600 m, 17 August 1972, Gosnold stn 123. 1 3, USNM, off Barnegat Inlet, 768 m, 3 August 1884, Albatross stn 2187. 1 J, USNM, N of Little Egg Inlet, 984 m, 19 August 1884, Albatross stn 2201. North Carolina: 6 3 6 9, UNC-IMS, E of Cape Fear, 495-490 m, 29 July 1970, Eastward 19 stn 14954. 1 9 syntype, USNM 4920, E of Cape Fear, 849 m, 14 July 1880, Blake stn 326. 1 9 syntype, MCZ 3270, SE of Cape Fear, 836 m, 14 July 1880, Blake stn 323. 5 & 4 9, USNM, SE of Cape Fear, 744 m, 6 May 1886, Albatross stn 2676. Georgia: 1 9, USNM, off St Catherines I, 814 m, 25 June 1961, Atlantis stn A-266-2. Florida: 4 9, USNM, NE of Cape Kennedy, 922 m, 3 May 1886, Albatross stn 2660. 6 J, USNM, NE of Cape Kennedy, 931 m, 3 May 1886, Albatross stn 2659. 3 9, USNM, SE of Key West, 558-514 m, 29 August 1967, Gerda stn 861. 1 9, USNM, off St Petersburg, 465 m, 29 September 1951, Oregon stn 489. 1 9, USNM, off Destin, 512 m, 14 March 1885, Albatross stn 2397. 1 & 1 9, TAMU, off Santa Rosa I, 565 m, 4 August 1968, Alaminos stn 68A7-10A. 1 9, TAMU, off Gulf Beach, 1,061 m, 7 August 1968, Alaminos stn 68A7-13A. Alabama: 2 9, USNM, off Orange Beach, 585 m, 13 August 1970, Oregon II stn 11146. 1 & 5 9, USNM, S of Mobile Bay, 366 m, 18 December 1962, Oregon stn 4151. Louisiana: 1 & 1 º, USNM, E of Mississippi Delta, 439-448 m, 17 July 1960, Oregon stn 2825. 1 9, USNM, E of Southeast Pass, Mississippi Delta, 626 m, 11 February 1885, Albatross stn 2376. 3 9, TAMU, off Garden I Bay, Mis-

sissippi Delta, 476 m, 15 October 1969, Alaminos stn 69A13-40. 1  $\circ$  7  $\circ$ , USNM, E of Mississippi Delta, 457 m, 10 June 1959, Silver Bay stn 1203. 1  $\circ$  1  $\circ$ , MCZ, SE of Mississippi Delta, 587 m, 1878, Blake stn 47. 28  $\circ$  121  $\circ$  110 juv and larvae, YPM, S of Grand Terre Is, 302 m, 26 March 1936, Atlantis stn 2381. 1  $\circ$ , YPM, S of Grand Isle, 356 m [in Atlantis log 300 fm, 549 m], 23 March 1937, Atlantis stn 2831. 6  $\circ$  11  $\circ$ , USNM, SW of Ship Shoal Lighthouse, 549 m, 23 February 1964, Oregon stn 4709. Texas: 1  $\circ$ , TAMU, off Port Aransas, 476 m, 19-20 November 1968, Alaminos stn 68A13-22. 2  $\circ$ , USNM, off Padre I, 585-658 m, 20 July-6 August 1969, Western Gulf stn 35. 1  $\circ$ , USNM, off Padre I, 501 m, 21 March 1969, Oregon II stn 10456.

MEXICO—Tamaulipas: 1 °, TAMU, SW of Matamoros, 713 m [according to label], 12 November 1968, *Alaminos* stn 68A13-3. 1 °, TAMU, SW of Matamoros, 878 m, 12 November 1968, *Alaminos* stn 68A13-1. Quintana Roo: 2 °, USNM, off Cabo Catoche, 585 m, 13 August 1970, *Oregon II* stn 11146.

BAHAMA ISLANDS—1 , RMNH, NW of Matanilla Reef, 662-702 m, 18 July 1965, Gerda stn 671. 2 5 , RMNH, NW of Great Stirrup Cay, 733-897 m, 4 July 1963, Gerda stn 190. 1 , USNM, off Dog Rocks, Cay Sal Bank, 618 m, 22 June 1967, Gerda stn 815.

GREATER ANTILLES-1 & 4 9, USNM, N of Puerto Rico, 732-658 m, 30 January 1933, Johnson-Smithsonian DeepSea Exp., stn 1. 1 <sup>Q</sup>, USNM, N of Puerto Rico, 476 m, 4 February 1933, Johnson-Smithsonian Deep-Sea Exp., stn 23. 1 <sup>J</sup>, USNM, N of Puerto Rico, 512 m, 4 February 1933, Johnson-Smithsonian Deep-Sea Exp., stn 24. 1 <sup>Q</sup>, RMNH, SW of Navassa I, Jamaica Channel, 1,034 m, 2 July 1970, *Pillsbury* stn 1187.

LESSER ANTILLES-13 5 9, USNM, SW of Sombrero I, 664-704 m, 23 July 1969, Pillsbury stn 989. 1 ♂ 2 ♀, USNM, off Dog I, 688 m, 6 December 1969, Oregon II stn 10834. 1 9, USNM, W of Dog I, 658 m, 10 December 1969, Oregon II stn 10847. 5 9, USNM, W of Saba Bank, 786 m, 3 December 1969, Oregon II stn 10833. 1 & 3 9, USNM, E of Standfast Pt, Antigua, 786-1,125 m, 18 July 1969, Pillsbury stn 954. 2 9, USNM, Guadeloupe Passage, 738-832 m, 17 July 1969, Pillsbury stn 946. 1 º, USNM, off Point du Nord, Marie Galante I, 704-732 m, 12 July 1969, Pillsbury stn 919, 3 & 14 9, USNM, E of Capesterre, Guadeloupe I, 549-686 m, 14 July 1969, Pillsbury stn 923. 8 9, USNM, off Dominica I, 808 m, 5 March 1966, Oregon stn 5930. 2 9, USNM, off Dominica I, 607 m, 4 March 1966, Oregon stn 5927. 2 & 3 9, USNM, off Vieux Fort, St Lucia. 417-589 m, 9 July 1969, Pillsbury stn 904, 2 J, USNM, NE of Soufrière, St Vincent, 576-842 m. 6 July 1969, Pillsbury stn 881.

BELIZE—2 & 4 9, YPM, N of Glover Reef, 885 m, 20 March 1925, Pawnee.

NICARAGUA-5 9, USNM, off Punta de Perlas, 613 m, 22 November 1968, Oregon II stn 10207.



PANAMA—1  $\Im$ , RMNH, Golfo de los Mosquitos, 664-681 m, 21 July 1966, *Pillsbury* stn 447.

COLOMBIA---1 <sup>Q</sup>, USNM, Golfo del Darién, 731 m, 28 May 1964, Oregon stn 4902.

VENEZUELA-1 ?, USNM, E of San Juan de los Cayos, 421 m, 9 October 1963, Oregon stn 4439.

GUYANA-1 9, USNM, N of Fort York, 1,373-1,446 m, 15 July 1968, *Pillsbury* stn 689.

AZORES ISLANDS-1 9, MP, between Pico and São Jorge, 1,257 m, 15 August 1883, *Talisman* stn 139.

MOROCCO-4  $\diamond$  3  $\heartsuit$  syntypes of Haliporus debilis var. africanus Bouvier, MP, off Mazaghan, 1,319 m, 14 June 1883, Talisman stn 21. 1  $\diamond$  9  $\heartsuit$ , MP, off Cap Cantin, 1,590 m, 17 June 1883, Talisman stn 33.

Description.-Body slender, integument thin, flexible and glabrous (Figure 3). Rostrum straight or slightly to strongly upturned, moderately long, reaching as far as distal end of second antennular article, its length not greater than 0.55 that of carapace, low and with dorsal and ventral margins straight. Rostral plus epigastric teeth  $\frac{8-11}{0-4}$ (usually  $\frac{9-10}{2}$ , only 3% lacking ventral teeth); epigastric tooth located at about 0.4 cl from orbital margin, first rostral tooth (largest of all) at about 0.3 cl, and third above orbital margin; ventral teeth variously arranged, either closely grouped together or rather broadly spaced. Advostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina strong to just caudal to cervical sulcus. weak posteriorly, and followed by minute dorsal tubercle very near margin of carapace. Lateral

spines on carapace slender and sharp: postorbital spine situated directly posterior to antennal and almost as long as branchiostegal; latter (largest of all) continuous with short, sharp basal carina; pterygostomian spine absent. Cervical carina sharp, cervical sulcus deep, extending to, but not crossing, postrostral carina, its dorsal extremity located at 0.55 cl from orbital margin, or slightly more posteriorly; hepatic sulcus with two ventral convexities, extending from below hepatic spine to anterior end of branchiocardiac sulcus; weak posthepatic carina extending posteriorly from junction of latter sulci. Branchiocardiac carina strong, accompanying sulcus moderately deep; submarginal carina slender, extending along entire length of branchiostegite.

Eye (Figure 4B) with basal article produced mesially into small scale. Cornea broad, its greatest diameter approximately twice that of base of ocular peduncle (1.6-2.1,  $\bar{x}$  1.95; N = 32), and proportion of diameter to carapace length varying between 15.5 and 23.0,  $\bar{x}$  19.7. Cornea subreniform, with proximal margin oblique, slanting posterolaterally; an imaginary line drawn parallel to base of short ocular peduncle at level of its mesial tubercle intersects cornea.

Antennular peduncle length equivalent to about 0.55 that of carapace; prosartema short, not quite reaching distomesial margin of cornea, falling short of distal margin of first antennular article, but its long distal setae overlapping base of second article; stylocerite rather short, its length about 0.6 of distance between its proximal extrem-



FIGURE 4.—Eyes. A, Hymenopenaeus laevis,  $\Im$  21 mm cl, off Martha's Vineyard, Mass. B, Hymenopenaeus debilis,  $\Im$  10.5 mm cl, northwest of Great Stirrup Cay, Bahama Islands. C, Hymenopenaeus aphoticus,  $\Im$  18 mm cl, northwest of Península de la Guajira, Colombia.



FIGURE 5.—Hymenopenaeus debilis, ? 19.5 mm cl, off Cape Kennedy, Fla. A, Mandible. B, First maxilla. C, Second maxilla. D, First maxilliped. E, Second maxilliped. f, Rudimentary arthrobranchia. f<sup>1</sup>, Enlargement of f (all from left side).

ity and mesial base of distolateral spine; latter long, slender, and sharp. Antennular flagella very long and considerably unequal in length, ventral 2.15 and dorsal 7.5 times carapace length in shrimp 7 mm cl, and 1.7 and 5.5 times, respectively, in shrimp 10 mm cl. Scaphocerite overreaching antennular peduncle by as much as 0.25 of its own length; lateral rib ending in slender spine, falling short to slightly surpassing distal margin of lamella. Antennal flagellum incomplete in all specimens examined; however, in one individual about 35 mm tl, antennal length 155 mm, thus not less than 4.4 times total length of shrimp.

Mandibular palp (Figure 5A) reaching to about level of distal 0.2 of carpocerite; proximal article

2.4 times as long as wide; distal article considerably shorter and narrower than proximal, and tapering to blunt tip. First and second maxillae, and first and second maxillipeds as illustrated (Figure 5*B*-*E*, virtually identical throughout genus); somite VII bearing rudimentary arthrobranchia at base of first maxilliped (Figure 5*D*f- $f^1$ ). Third maxilliped overreaching antennular peduncle by length of dactyl and propodus; length of dactyl about 0.7 that of propodus.

First percopod, stoutest of five, reaching distal end of carpocerite or surpassing it by as much as length of dactyl. Second percopod overreaching antennular peduncle by at least half length of dactyl or by entire propodus. Third percopod exceeding antennular peduncle by length of dactyl, propodus, and as much as 0.4 that of carpus. Fourth pereopod reaching beyond antennular peduncle by length of last three podomeres. Fifth percopod exceeding antennular peduncle by length of last three podomeres or by latter and as much as 0.1 length of merus. Pereopods increasing in length from first to fifth. First percopod with rather inconspicuous spine on basis, and either slender spine or no spine on ischium; second percopod with small spine on basis. In female, coxa of third percopod produced into large subtrapezoidal plate directed mesially, and bearing minute anteromesial spine in juveniles. In both sexes spine present on anteromesial corner of coxa of fifth percopod, considerably stronger in males than in females, spine minute in latter and borne on rounded coxal plate.

Abdomen with middorsal carina from fourth through sixth somites, posterodorsal margin of fourth and fifth with short median incision; sixth somite about 1.8 times as long as high, bearing small, sharp spine at posterior end of carina, and pair of minute spines posteroventrally. Telson with rather shallow median sulcus practically disappearing before reaching level of base of lateral spines; sulcus flanked by ridges, blunt anteriorly, sharp and slender posteriorly; terminal portion length 5-6 times basal width; lateral spines length 1.5-2.0 times basal width of terminal portion. Mesial ramus of uropod falling short of apex of telson or slightly overreaching it; lateral ramus overreaching mesial ramus by as much as 0.25 of its own length, and armed with slender, distolateral spine, reaching as far as contiguous margin of ramus.

Petasma (Figures 2, 6A, B) with row of cincinnuli (hooklike structures along mesial margin of median lobes of petasma that serve to interlock its two halves) occupying only proximal 0.3 of median line, and entire terminal margin armed with spines; ventromedian lobule deeply cleft distally forming two elongate processes: mesial one subspatulate and armed with rather conspicuous spines mesially and minute ones distolaterally; lateral process subelliptical, raised inwardly in elongate prominence, and produced proximally in small auricular process lacking spinules; distal flap of ventrolateral lobule extending only to basal portion of lateral process, and turned strongly outward; ventral costa forming low prominence at base of, and imperceptibly merging with, flap.

Appendix masculina (Figure 6C, D) elevated in sharp mesial ridge and with proximal part produced laterally into rounded, flattened lobe; distal part narrowing and bearing lateral row of setae terminating in apical tuft of longer ones. Appendix interna elongate ovate, extending almost as far as appendix masculina, and also armed with apical tuft of setae. Ventrolateral spur of basal sclerite long, its length 0.7-0.8 that of appendix masculina.



FIGURE 6.—Hymenopenaeus debilis, & 13 mm cl, off Cape Kennedy, Fla. A, Petasma, dorsolateral view of left half. B, Ventral view. C, Right appendices masculina and interna, dorsolateral view. D, Ventral view.



FIGURE 7.—Hymenopenaeus debilis, 9 15.5 mm cl, Dominica Island, Lesser Antilles. Thelycum, ventral view.

Thelycum (Figure 7) with median protuberance on sternite XIV pyriform, strongly produced anteriorly into acute, freely projecting apical portion overlapping, and closely appressed to, sternite XIII; latter bearing paired subtriangular elevations with bases raised in horizontal ridges flanking tip of protuberance on sternite XIV; anterior part of sternite XIII with setose transverse prominence; sternite XII bearing pair of large, setose, posterolateral horns reaching or slightly surpassing midlength of sternite XIII.

*Photophores.*-Six present on sternum: pair in elevated posterior margin of sternite XIII, just mesial to coxae of fourth pereopods; pair between second pleopods; single one between bases of fourth pereopods, and another between bases of fifth pleopods. Details of their structure given by Burkenroad (1936).

Color.-Bouvier (1908) on the basis of a water color illustration made at the moment of capture stated that the color is "d'un rouge-orange presque uniform." Burkenroad (1936) described fresh material as "transparent, speckled with minute scarlet chromatophores which were concentrated at the bases of the pleopods and uropods and at the tip of the telson. The ocular peduncle at the base of the cornea, the mouthparts, and the tip of the second maxillipede were scarlet. The stomach was red, the pleonic gut and nerve-cord orange; the gastric gland brownish, the ovary creamy (as seen through the overlying tissues). The eyes were reddish brown."

Maximum size.-Males, 55 mm tl; females, 78 mm tl (Bouvier 1908). Largest specimens examined by me: males 15.5 mm cl, 52 mm tl; females, 19.5 mm cl, 75 mm tl.

Geographic and bathymetric ranges.-Western Atlantic: from Hudson Canyon, New Jersey (39°55'N, 70°31'W) through the Gulf of Mexico and Caribbean Sea to Guyana (08°14'N, 57°38'W). Eastern Atlantic: Azores Islands and northwest Africa—from Cap Spartel, Morocco, to Cape Verde Islands, including Canary Islands (Figure 8). It has been found at depths (Figure 9) between 300 and 2,163 m (latter in Bouvier 1908).

Affinities.-Hymenopenaeus debilis closely resembles H. aphoticus, but differs from it in that the rostrum is usually armed with ventral teeth (only 3% of the specimens examined by me lack such teeth), and the sternum bears six photophores which are absent in H. aphoticus. The cornea is subreniform, and it is disposed such that its proximal margin is oblique to the basal margin of the ocular peduncle and an imaginary line extending from the medial tubercle parallel to the basal margin of the peduncle crosses its proximolateral extremity. The cornea (actually the entire eye) of H. debilis is also much larger than that of H. aphoticus: its maximum diameter about twice that of the basal margin of the peduncle, and the proportion of the diameter to the carapace length ranges from 15.5 to 22.0, averaging 19.7. Furthermore, in males of H. debilis the petasma exhibits larger distal processes than does that of H. aphoticus, but the lateral one is produced proximally in an auricle which is small and unarmed, and the proximomesial spinules on the free margin of the mesial process are only slightly longer than the remaining ones instead of considerably so as in H. aphoticus. Finally, the length of the ventrolateral spur borne by the sclerite at the base of the appendices masculina and interna is equivalent to 0.50-0.75 that of the appendix masculina. The thelyca of the two species are



FIGURE 8.—Ranges of Hymenopenaeus aphoticus and Hymenopenaeus debilis based on published records and specimens personally examined.



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similar but the median protuberance of sternite XIV tends to be broader in *H. debilis* than in *H. aphoticus*.

According to Burkenroad (1936), in this species the proportion of the maximum diameter of the eye to carapace length is even greater than that given above, ranging between 19.3 and 26.9,  $\bar{x}$  22.3. My measurements of specimens studied by Burkenroad resulted in proportions not exceeding 23.0. This could be due to a slight reduction of the cornea caused by the preservatives, or the cornea is now deformed in the specimens with larger corneae examined by me.

Very similar to *H. debilis* is *H. chacei* which is known only from off West Africa. According to Crosnier and Forest (1969, 1973), these two species differ in that in *H. chacei* the ventral border of the rostrum is unarmed (actually, as stated above, 3% of the individuals of *H. debilis* examined by me lack such teeth), and no photophores are present. The cornea of *H. chacei* is narrower than that of *H. debilis*, in the former the ratio of the greatest diameter to the carapace length ranges from 13.2 to 16.0 ( $\bar{x}$  15.0), and it is disposed such that its proximolateral extremity lies slightly distal to the level of the medial tubercle.

A careful study of the western Atlantic specimens in which the rostrum is ventrally unarmed has left no doubt in my mind that they are H. *debilis*. *Hymenopenaeus chacei*, which typically lacks teeth on the ventral margin of the rostrum, is not represented in the extensive collections from the western Atlantic examined by me.

I have found that in males of H. debilis the disposition of both the mesial and lateral processes of the petasma varies from slightly to rather

strongly inclined mesially, the former illustrated herein (Figure 6A, B), and the latter, illustrated by Crosnier and Forest (1973, plate 85, figure c-d, a male from Morocco). This variation is not associated with the size of the animal, and occurs throughout the entire range of the species in the western Atlantic. Males in which the processes are only slightly inclined mesially resemble those of H. chacei in which, according to Crosnier and Forest (1973), the roughly angular portion of the lateral process is typically directed forward. The males of the two species can still be distinguished by the size and armature of the auricular process of the petasma, which in *H. debilis* is very small and unarmed but relatively large in H. chacei and provided with marginal spinules (Crosnier and Forest 1969:546, figure 2).

*Remarks.*-The coordinates of the *Talisman* stations, cruise of 1883, where the material examined by me was collected, are given herein according to the data presented by Crosnier and Forest (1973).

The disposition of the third syntype, from southeast of Savannah Beach, Ga., caught at *Blake* stn 317 is unknown.

# Hymenopenaeus aphoticus Burkenroad 1936

#### Figures 4C, 8-12

Hymenopenaeus aphoticus Burkenroad 1936:112, fig. 62, 65, 66, 67 [holotype: ♀, YPM 4556; typelocality: Turks Is Passage, 1,646-1,728 m, 21°15′40″N, 71°17′06″W, Pawnee stn 54]. Yokoya 1941:52. Crosnier and Forest 1969:547.



FIGURE 10.—Hymenopenaeus aphoticus, 9 18 mm cl, northwest of Península de la Guajira, Colombia. Cephalothorax, lateral view.

Roberts and Pequegnat 1970:31, fig. 3-1D. Pequegnat and Roberts 1971:8. Crosnier and Forest 1973:253, fig. 85e-f, 87c, 88b, 89c.

#### Material

UNITED STATES—Florida:  $5 \delta 3 \circ$ , RMNH-UMML, SW of Marquesas Keys, 1,373-1,428 m, 1 December 1964, Gerda stn 449. 2  $\delta$ , USNM, SW of Marquesas Keys, 948-969 m, 29 August 1967, Gerda stn 858. 2  $\delta$ , TAMU, NW of Dry Tortugas, 3,256 m, 29-30 July 1968, Alaminos stn 68A7-4E. 1  $\delta$ , TAMU, SW of Cape San Blas, 1,097 m, 1 August 1968, Alaminos stn 68A7-7B. Alabama: 1  $\delta$ , USNM, off Mobile Bay, 2,160 m, 3 March 1885, Albatross stn 2383. Texas: 1  $\circ$ , TAMU, off Padre I, 1,399 m, 7 August 1969, Alaminos stn 69A11-7.

MEXICO—Tamaulipas: 1  $\Im$ , USNM, off Boca de San Rafael, 1,668 m, 24 January 1970, Oregon II stn 10881. Veracruz: 1  $\Im$   $\Im$ , TAMU, NE of Tuxpan, 1,326 m, 24 August 1969, Alaminos stn 69A11-83. 1  $\Im$ , TAMU, Bahia de Campeche, 2,122 m, 16 August 1969, Alaminos stn 69A11-44.

BAHAMA ISLANDS—1 & paratype, YPM 4557, Tongue of the Ocean, "Wire 7000 feet" [2,134 m], 2 March 1927, *Pawnee* stn 11. & holotype 1 ? paratype, YPM 4556, Turks I Passage, 1,646-1,728 m, 12 March 1927, *Pawnee* stn 54.

JAMAICA-1 9, USNM, W of South Negril Point, 1,591-1,829 m, 8 July 1970, *Pillsbury* stn 1238.

EASTERN CARIBBEAN—1  $\delta$  6  $\Re$ , USNM, S of I Aves, 1,249 m, 27 January 1884, Albatross stn 2117.

COLOMBIA—10 3 6 %, USNM, NW of Península de la Guajira, 1,500 m, 27 July 1966, *Pillsbury* stn 454. 3 %, USNM, off Península de la Guajira, 2,500 m, 27 July 1966, *Pillsbury* stn 455.

Description.-Rostrum (Figure 10) slightly to rather strongly upturned, reaching as far as distal margin of second antennular article, its length about 0.45 that of carapace, and with both margins almost straight. Rostral plus epigastric teeth 7-8, sharp: epigastric tooth located at about 0.4 cl from orbital margin, first tooth (largest of all) at about 0.25, and second with apex at level of orbital margin; ventral teeth absent. Adrostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina strong to just caudal to cervical sulcus, from there weak or indistinct porteriorly, and followed by minute tubercle located close to margin of carapace. Spines on lateral surface of carapace slender and sharp: postorbital spine situated directly posterior to antennal, and branchiostegal, largest of all, continuous with short, sharp carina; pterygostomian spine absent. Cervical sulcus deep, extending to, but not crossing, postrostral carina, its dorsal extremity placed at about 0.54 cl (or slightly farther anteriorly) from orbital margin; hepatic sulcus biconvex ventrally, running from base of hepatic spine to ventral end of branchiocardiac sulcus; weak posthepatic carina extending posteriorly from junction of latter sulci. Branchiocardiac sulcus long, accompanying carina strong. Submarginal carina slender.

Eye (Figure 4C) with basal article produced mesially into small scale. Cornea comparatively narrow, its greatest diameter approximately 1.5 times that of base of ocular peduncle (1.25-1.75,  $\bar{x}$  1.55; N = 20), and proportion of diameter to carapace length varying between 10.0 and 12.5,  $\bar{x}$  11.1. Cornea hemispherical, with proximal margin subperpendicular to longitudinal axis of elongate ocular peduncle; an imaginary line drawn parallel to base of ocular peduncle at level of its mesial tubercle intersects lateral border far proximal to cornea.

Antennular peduncle length equivalent to about 0.5 that of carapace; prosartema short, extending only as far as distomesial margin of cornea, falling short of distal margin of first antennular article, but with long distal setae reaching base of second antennular article; stylocerite moderately long, extending 0.60-0.65 of distance between its proximal extremity and mesial base of distolateral spine; latter rather long, slender, and sharp. Antennular flagella long and unequal in length, ventral one 2.25 times as long as carapace in shrimp 17.5 mm cl; dorsal flagellum longer than ventral, unfortunately incomplete in all specimens examined. Scaphocerite length approximately 3.65 times maximum width, overreaching antennular peduncle by as much as 0.3 of its own length; lateral rib ending in slender spine extending to, or slightly surpassing, distal margin of lamella. Antennal flagellum long, at least 6.8 times total length of shrimp: male with total length of 45 mm bearing incomplete flagellum 300 mm long. Mandibular palp, maxillae and first two maxillipeds similar to those in H. debilis (see Figure 5). Third maxilliped overreaching antennular peduncle by length of dactyl and propodus or by their lengths plus 0.1 that of carpus; length of dactyl about 0.7 that of propodus.

First perceoped, stoutest of five, reaching about distal end of carpocerite. Second perceoped overreaching antennular peduncle by, at least, tip of dactyl, or by as much as length of propodus. Third perceoped exceeding antennular peduncle by length of propodus and, at most, 0.4 that of carpus. Fourth perceoped overreaching antennular peduncle by length of distal three podomeres. Fifth perceoped exceeding antennular peduncle by length of distal three podomeres, or by length of



FIGURE 11.—Hymenopenaeus aphoticus, ♂ 14.5 mm cl, south of Isla Aves, eastern Caribbean. A, Petasma (extended), dorsolateral view. B, Ventral view. C, Right appendices masculina and interna, dorsolateral view. D, Ventromesial view.

those podomeres and as much as 0.15 length of merus. Pereopods increasing in length from first to fifth. First pereopod with rather inconspicuous spine on basis, and long slender spine on ischium; second pereopod with small spine on basis. In female, coxa of third pereopod produced into subtrapezoidal plate, latter broadest mesially, disposed almost at right angle to podomere, and bearing minute anteromesial tooth in juvenile. In both sexes, tooth present on anteromesial angle of coxa of fifth pereopod, considerably stronger in male than in female, in latter tooth minute and borne on rounded coxal plate.

Abdomen with middorsal carina from fourth through sixth somites, posterodorsal margin of fourth and fifth with short median incision; sixth somite about 1.8 times as long as high, bearing small, sharp spine at posterior end of carina and pair of minute spines posteroventrally. Telson with rather shallow median sulcus extending posteriorly to level of base of lateral spines, and flanked by well-developed ridges; terminal portion length 5-6 times its basal width; lateral spines length 1.4-1.7 times basal width of terminal portion. Mesial ramus of uropod falling short of, or slightly overreaching, apex of telson; lateral ramus overreaching mesial ramus by as much as 0.25 of its own length, and armed with small, slender distolateral spine, falling slightly short of, or barely overreaching, contiguous margin of ramus.

Petasma (Figure 11A, B) with row of cincinnuli occupying proximal 0.4 of median line, and entire terminal margin armed with spines; ventromedian lobule distally cleft forming two moderately long processes: mesial one subtrapezoidal and armed with conspicuous spines mesially and minute ones distolaterally, lateral process subelliptical, raised inwardly in strong prominence, and produced proximally in rather large auricular process armed with marginal spinules; distal flap of ventrolateral lobule free, extending as far distally as lateral process, and only slightly turned outward; ventral costa forming low prominence at, and imperceptibly merging with, base of flap.

Appendix masculina (Figure 11C, D) strongly elevated along mesial portion and with proximal part produced laterally into rounded, flattened lobe; distal part narrowing and bearing lateral row of setae continuous with apical tuft of long setae. Appendix interna elongate-ovate, extending slightly farther distally than appendix masculina, and armed with apical tuft of setae. Ventrolateral spur short, its length not greater than 0.5 that of appendix masculina.

Thelycum (Figure 12) similar to that of H. *debilis* (see above).



FIGURE 12.—Hymenopenaeus aphoticus, \$ 18.5 mm cl, south of Isla Aves, eastern Caribbean. Thelycum, ventral view.

Maximum size.-Males: 18 mm cl; females: 19.5 mm cl.

Geographic and bathymetric ranges.-Western Atlantic: southwest Florida (23°56'N, 82°13'W), throughout the Gulf of Mexico, and the Caribbean Sea (12°55'N, 72°04'W). Eastern Atlantic (according to Crosnier and Forest 1973): south of the Azores Islands and off Morocco (Figure 8). It occurs at depths between about 950 m and 3,256 m (Figure 9).

Affinities.-Hymenopenaeus aphoticus is closely allied to H. debilis, but may be readily distinguished from it by the lack of teeth on the ventral margin of the rostrum, the absence of photophores, and the shape and disposition of the cornea (see above). In males of H. aphoticus, the petasma exhibits smaller distal processes than does that of H. debilis, and the auricle of the distolateral process is larger and armed with marginal spinules; also the proximomesial spinules on the free margin of the mesial process are considerably longer than the remaining ones, instead of only slightly longer as in *H.debilis*. Furthermore, in H. aphoticus the length of the ventrolateral spur at the base of the appendices masculina and interna is equivalent to only 0.5 that of the appendix masculina. Although the petasmata of the two species are different, the thelyca are markedly similar: the only detectable distinction is that the median protuberance on sternite XIV tends to be narrower in *H. aphoticus* than in *H. debilis*.

*Remarks.*-In examining a lot of seven specimens of H. aphoticus obtained at Albatross stn 2117. Roberts and Pequegnat (1970) misread the number on the accompanying label. They stated that in the Smithsonian Institution there is a lot of H. aphoticus taken by the Albatross at "Stn 2217, 1889" in the western Atlantic. Actually, the number on the label is 2117 for which the coordinates are 15°24'40"N, 63°31'30"W (south of Isla Aves in the eastern Caribbean, visited by the Albatross in 1884) instead of 2217, an 1889 station situated at 39°47'20"N, 69°34'15"W, which is off New Jersey. Because the authors thought the lot had been obtained at the latter locality, they stated that the species ranges as far north as 39°47' (actually it has not been recorded from off the Atlantic coast of the United States). The misreading of the label also caused them to be unaware of the Caribbean record for H. aphoticus and to state that "It may eventually be found in the Caribbean also."

#### Hymenopenaeus laevis (Bate 1881)

Figures 4A, 9, 13-16

- Haliporus laevis Bate 1881:185 [syntypes: 2 φ, BMNH; type-locality: SW of Sierra Leone (W of Cameroon), 2°25'N, 20°01'W, 2,500 fm (4,573 m), Challenger stn 104]. Bate 1888:289, pl. 42, fig. 2. Bouvier 1906b:3; 1908:80. de Man 1911:7. Estampador 1937:494.
- Hymenopenaeus microps Smith 1884:413, pl. 10, fig. 1 [syntypes: 1 ♀, USNM 7148, E of Georges Bank, Mass., 41°13'00"N, 60°00'50"W, 906 fm (1,657 m), Albatross stn 2076; 1 ♀ oral appendages, YPM 4559, off New Jersey, 38°50'00"N, 69°23'30"W, 1,731 fm (3,166 m), Albatross stn 2037]. Smith 1886:189; 1887:688, pl. 16, fig. 8. Wood-Mason 1891:277. Wood-Mason and Alcock 1891:188.
- Haliporus microps. Alcock and Anderson 1894: 146. Alcock 1901:25. Bouvier 1906a:255; 1906b: 3; 1908:80. de Man 1911:7. Fowler 1912:543.
- Hymenopeneus microps. Alcock 1899a:30.
- Haliporus androgynus Bouvier 1906a:253 [syntypes: 1 ♀, MP, between "Dakar et la Praya," (off Mauritania), 16°38'N, 20°44'W, 3,200 m, *Talisman* stn 105. 1 ♀, MP, between "Dakar et

la Praya," (off Senegal), 15°48'N, 20°23'W, 3,655 m, *Talisman* stn 106]. Bouvier 1906b:3; 1908:80. de Man 1911:7.

Haliporus sp. Lenz and Strunck 1914:300, fig. 2.

Hymenopenaeus laevis. Burkenroad 1936:106; 1938:61. Anderson and Lindner 1945:289.Crosnier and Forest 1973:253, fig. 82a, 83b.

# Material

UNITED STATES—Massachusetts: 1  $\degree$  syntype of *H.* microps Smith, USNM 7148, E of Georges Bank, 1,657 m, 4 September 1883, Albatross stn 2076. 1  $\degree$ , USNM, SE of Martha's Vineyard, 2,844 m, 30 July 1883, Albatross stn 2042. New Jersey: 1  $\degree$ , USNM, off Atlantic City (Hudson Canyon), 1,977 m, 9 August 1885, Albatross stn 2550. 1  $\degree$  [oral appendages] syntype of *H. microps* Smith, YPM 4559, 3,166 m, 18 July 1883, Albatross stn 2037. Virginia: 4  $\degree$ , USNM, 1  $\degree$ , AMNH, E of Delmarva Peninsula, 4,792 m, 29 August 1885, Albatross stn 2566. North Carolina: 1  $\degree$  1  $\degree$ , USNM, NE of Kitty Hawk, 4,708 m, 8 September 1884, Albatross stn 2224.

BERMUDA ISLANDS-1 3, YPM, N of Bermuda Is, "10000 feet wire" [3,048 m], 20 April 1927, *Pawnee* stn 58. 1 9, YPM, N of Bermuda Is, "8000 feet wire" [2,438 m], 21 April 1927, *Pawnee* stn 59.

BAHAMA ISLANDS—1 & 2 9, YPM, Turks I Passage, "8000 feet wire" [2,438 m], 11 April 1927, *Pawnee* stn 52. 2 9, YPM, Turks I Passage, "6500 feet wire" [1,981 m], 13 April 1927, *Pawnee* stn 56.

MAURITANIA---1 9 syntype of *H. androgynus* Bouvier, MP, between "Dakar et la Praya" [off Mauritania], 3,200 m, 18 July 1883, *Talisman* stn 105.

SENEGAL—1  $\Im$  syntype of *H. androgynus* Bouvier, MP, between "Dakar et la Praya" [off Senegal], 3,655 m, 19 July 1883, *Talisman* stn 106.

CAMEROON-2 9 syntypes, BMNH, "south-west of Sierra Leone," 2°25'N, 20°1'W [W of Cameroon], 4,573 m, 23 August 1873, *Challenger* stn 104.

PHILIPPINE ISLANDS—1 2, BMNH, off Manila, 1,920 m, 13 November 1874, *Challenger* stn 205.

Description.-Rostrum (Figure 13) short, its length about 0.2 that of carapace, falling short of distal margin of first antennular article, horizontal or slightly upturned, tapering to very sharp tip, and with ventral margin slightly sinuous.

Rostral plus epigastric teeth 7-9, sharp; epigastric tooth situated at about 0.4 cl from orbital margin. first rostral tooth (largest of all) at approximately 0.3, and third opposite to, or slightly forward of, orbital margin. Adrostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina well defined to near posterior margin of carapace, followed by small tubercle. Pterygostomian spine small; postorbital (situated directly posterior to relatively small antennal spine), branchiostegal, and pterygostomian spines continuous with sharp basal carina. Cervical carina sharp, notched dorsal to hepatic spine; cervical sulcus deep, extending to, but not crossing postrostral carina, its dorsal extremity located at or slightly posterior to midlength of carapace; hepatic carina blunt, its accompanying sulcus deep; additional short carina lying dorsal and parallel to posterior part of hepatic sulcus; posthepatic carina long, running almost to posterior margin of carapace; branchiocardiac carina also long, virtually reaching posterior margin of carapace; short sulcus extending posterodorsally from near posterior end of branchiocardiac carina; submarginal carina well defined, extending along entire length of branchiostegite.

Eye (Figure 4A) with basal article produced mesially into barely distinct scale; ocular peduncle long; cornea comparatively narrow, its greatest diameter about 1.4 times that of base of ocular peduncle, its proximal margin only slightly slanting posterolaterally.

Antennular peduncle length equivalent to about 0.55 that of carapace; prosartema short, extending only as far as distomesial margin of cornea, falling considerably short of distal margin of first antennular article; stylocerite short, extending only 0.4-0.5 of distance between its prox-



FIGURE 13.—Hymenopenaeus laevis, 912.5 mm cl, Turks Island Passage, Bahama Islands. Cephalothorax, lateral view.

imal extremity and mesial base of distolateral spine; latter long, slender, and sharp. Antennular flagella incomplete in all specimens examined by me, according to Bate (1888) "about two-thirds the length of the animal." Scaphocerite reaching as far as antennular peduncle or barely overreaching it; lateral rib ending in slender spine falling slightly short of, or slightly overreaching, distal margin. Antennal flagellum broken in specimens examined by me, according to Bate (1888) "rather longer than the animal." Mandibular palp reaching to about distal 0.25 of carpocerite. Third maxilliped overreaching antennular peduncle by length of dactyl and propodus; length of dactyl about 0.75 that of propodus.

First perceoped extending to about distal end of carpocerite. Second perceoped reaching distal end of antennular peduncle, or exceeding it by as much as length of dactyl. Third perceoped surpassing antennular peduncle by length of dactyl, propodus, and at least 0.25 that of carpus. Fourth perceoped exceeding antennular peduncle by length of dactyl, propedus, and 0.4-0.5 that of carpus. Fifth perceoped overreaching antennular peduncle by length of dactyl, propedus, and 0.75-0.80 that of carpus. Perceopeds increasing in length from first to fifth. First perceoped with minute spine on basis, and small one on ischium; second perceoped with small spine on basis. Coxal plate of third percopod in females broadening mesially and produced posteriorly into setose, rounded lobe. Tooth present on anteromesial corner of coxa of fifth percopod in both sexes, strong and blunt in males, minute, and borne by rounded coxal plate in females.

Abdomen with middorsal carina from fourth through sixth somites, posterodorsal margin of fourth and fifth with short median incision, sometimes bearing minute spine at base; sixth somite about twice as long as high, armed with small, sharp spine at posterior end of carina and pair of posteroventral spines. Telson with median sulcus deep anteriorly, increasingly shallower posteriorly to level of base of lateral spines, flanked by paired ridges, blunt anteriorly, sharp posteriorly; length of terminal portion about 5 times its basal width; spines moderately long, 1.20-1.35 basal width of terminal portion. Mesial ramus of uropod falling short of apex of telson, or overreaching it by no more than 0.1 of its length; lateral ramus exceeding mesial ramus by as much as 0.2 of its own length, and armed with small, terminal, distolateral spine.

Petasma (Figure 14A, B) with row of cincinnuli occupying about proximal 0.5 of median line, its entire terminal margin lacking spines; ventromedian lobule bearing two, rarely three, small, triangular processes distomesially, and short,



FIGURE 14.—Hymenopenaeus laevis, & 15 mm cl, Turks Island Passage, Bahama Islands. A, Petasma, dorsolateral view of left half. B, Ventrolateral view. C, Right appendices masculina and interna, dorsolateral view. D, Ventromesial view.

rigid, transversely elliptical process distolaterally; distal part of ventrolateral lobule roughly elliptical and strongly trending toward ventromedian lobule; ventral costa broad proximally, considerably narrower distally and, in young, ending in minute marginal spine projecting from base of elliptical part of ventrolateral lobule.

Appendix masculina (Figure 14C, D) with proximal part produced laterally into rounded lobe bearing row of long setae on distal margin continuous with row extending along midventral line of narrow distal portion; latter armed with apical tuft of long setae; appendix interna abruptly narrowing from rounded base and bearing apical tuft of long setae; ventrolateral spur with distal part subovate, bearing longitudinal submarginal rib on dorsal surface.

Thelycum (Figure 15) with median protuberance on sternite XIV setose, pyramidal, and with triangular base, its apical portion produced into short ventrally directed projection; median lamella projecting vertically from posterior margin of sternite XIII, flat, its distal margin slightly to deeply emarginate (emargination angular or curved), lateral margins straight or slightly concave; posterior part of sternite XII bearing paired, setose horns overreaching midlength of sternite XIII.

Maximum size.-Males: 15 mm cl; females: 22 mm cl.

Geographic and bathymetric ranges.-Western Atlantic: from off Georges Bank, Mass.  $(41^{\circ}13'00''N, 60^{\circ}00'50''W)$ , to the Bahamas (21°20'15"N, 71°13'20"W), including the Bermudas (Figure 16). Eastern Atlantic: from west of Mauritania to off Equatorial Guinea (Bate 1888). Indo-West Pacific: in the Arabian Sea (Laccadive Sea, Wood-Mason and Alcock 1891), the Bay of Bengal (off Andaman Islands, Wood-Mason 1891; Alcock 1901), and the Philippines (Bate 1888). If the record of "Haliporus sp." by Lenz and Strunck (1914) is actually one for this species, its range off west Africa reaches farther south, at least to off Liberia (0°39'N, 18°57'W). This shrimp has been found at depths between 1.657 and 4,792 m (Figure 9). Its habitat together with its small size are most probably responsible for the few collections available.

Affinities .- Hymenopenaeus laevis is closely allied



FIGURE 15.—Hymenopenaeus laevis, 9 17 mm cl, Turks Island Passage, Bahama Islands. Thelycum, ventral view.

to the American Pacific H. doris and H. nereus, and to the Indo-West Pacific H. sewelli. These four species form the compact section 2 of Burkenroad's group IV. They are the only members of the genus which possess both branchiostegal and pterygostomian spines.

Females of H. laevis differ strikingly from those of H. nereus in the structure of the thelycum. In those of H. nereus, the median lamella of sternite XIII is directed anteriorly, and has arched or sinuous lateral margins converging basally. Furthermore, in H. nereus the median lamella is flanked by paired, caudally inclined processes, which are lacking in H. laevis, and sternite XIV is raised in a median longitudinal ridge, very different from the strong pyramidal prominence present in the latter. This shrimp, in turn, can be separated readily from H. doris by the median lamella of



FIGURE 16.—Ranges of Hymenopenaeus laevis and Hadropenaeus lucasii based on published records and specimens personally examined.

sternite XIII which in the latter is concave anteriorly, has a usually convex, never emarginate, distal margin. The median lamella also is flanked by paired ridges which are triangular in cross section and as high as the lamella. Furthermore, in *H. doris*, sternite XIV bears a median protuberance which is strongly produced in an elongate projection lying quite close to the lamella.

Males of *H. laevis* differ markedly from those of *H. nereus* in that the petasma of the latter bears a single, large, mesial process distally which, moreover, is subrectangular, directed perpendicular to the main axis of the petasma, and armed with long spines; in addition, the lateral process is directed distomesially instead of extending transversely, and is strongly curved outward. Finally, the distal part of the ventrolateral lobule of the petasma is acuminate instead of subelliptical, and is only slightly inclined toward the ventromedian lobule.

As previously indicated by Burkenroad (1936) and Crosnier and Forest (1973), females of this species exhibit considerable variation in the shape and size of the median lamella on sternite XIII. Extending ventrally, it may be short or long, reaching between midheight and slightly beyond the apex of the median protuberance on sternite XIV. In the young, the lamella is truncate, and in the adult it ranges from shallow to deeply emarginate distally, forming a fork with the projections varying from rather broadly triangular to spinelike.

In the young male, as stated above, the petasma bears a minute subdistal spine at the free margin of the costa, and the more mesial of the two distal projections of the ventromedian lobule is at best only slightly developed.

Remarks.-Burkenroad (1936) presented a detailed account of the external morphology and an enlightened analysis of the taxonomic status of this species; as a result, he placed two well-known scientific names, *H. microps* and *H. androgynus*,

in the synonymy of H. *laevis*. In this same contribution, Burkenroad mentioned a "minute denticle of variable size" posterior to the epigastric tooth, and suggested that it is "probably the remains of the larval anterior dorsal organ." In that location, however, I have observed nothing more than an extremely slight elevation of the postrostral carina, and that only in two specimens. Had this feature not been mentioned by Burkenroad, I should have overlooked it, and, after observing it, I believe it to be insignificant.

Bouvier (1906b) described Haliporus androgynus on the basis of two specimens which bear, in addition to a fully developed thelycum, both petasma and appendices masculinae. Burkenroad (1936) stated that the simultaneous presence of the female and male external genitalia in these specimens probably represents an abnormality. Recently, Crosnier and Forest (1973) indicated that this combination of secondary sexual characters could represent an expression of protandric hermaphroditism, as reported by Heegaard (1967) in Solenocera membranacea (Risso 1816). They added that in a rather large number of penaeids the maximum size of males corresponds to the minimum size of females. It should be noted, however, that Burkenroad (1936) cited a female of H. laevis, also examined by me, with a carapace length of 8 mm, which is about half the length of the largest known male, 15 mm cl.

In the two syntypes of H. androgynus, which have a carapace length of about 20 mm, the petasmata are shorter than in other males of equal size, and exhibit and armature with these juvenile features. In one of the specimens, the mesial projection is extremely small, whereas the lateral projection and the distolateral process are well developed; in the other, the mesial projection is distinct, the lateral one very small, the distolateral process is well developed, and a subdistal spine is present on the free margin of the ventral costa.

## Hymenopenaeus doris (Faxon 1893)

- Haliporus doris Faxon 1893:214 [syntypes: 4 φ, MCZ 4648, off Cabo Velas Costa Rica, 10°14'N, 96°28'W, 2,232 fm (4,082 m), 8 April 1891, Albatross stn 3414. 1 φ, USNM 21182, S of Punta Maldonado, Guerrero, Mexico, 14°46'N, 98°40'W, 1,879 fm (3,437 m), 10 April 1891, Albatross stn 3415]. Faxon 1895:191, pl. 49, fig. 1-1c. Bouvier 1906b:3; 1908:80. de Man 1911:7
- Hymenopenaeus doris. Burkenroad 1936:104; 1938:60. Crosnier and Forest 1973:256, fig. 83d. Aliporus doris. del Solar C. 1972:4.

#### Material

MEXICO—Territorio de Baja California: 1  $\circ$ , USNM, off Punta Chivato, Golfo de California, 1,567 m, 20 March 1889, *Albatross* stn 3009. 1  $\circ$ , AMNH, 54 km off Punta Arena, mouth of Golfo de California, 914 m, 29 April 1936, Templeton Crocker Expedition stn 159 T-3 [station data from Beebe 1937].

COSTA RICA-4 9 syntypes, MCZ 4648, off Cabo Velas, 4,082 m, 8 April 1891, *Albatross* stn 3414. 1 9, USNM, off Cabo Velas, 4,082 m, 8 April 1891, *Albatross* stn 3414.

Description.-Rostrum (Figure 17) relatively short, its length about 0.2 that of carapace, reaching between base and midlength of second antennular article, upturned, tapering to sharp tip, and with ventral margin straight. Rostral plus epigastric teeth 7-8, sharp; epigastric tooth situated about 0.4 cl from orbital margin, first rostral tooth (largest of all) at approximately 0.3, and base of



FIGURE 17.—Hymenopenaeus doris, syntype 9 32.5 mm cl, off Cabo Velas, Costa Rica. Cephalothorax, lateral view.

third in line with orbital margin. Adrostral carina low and sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting in narrow shelf. Postrostral carina strong to near posterior margin of carapace, followed by small tubercle. Pterygostomian spine slender and sharp like other lateral spines on carapace; postorbital (situated directly posterior to antennal), pterygostomian, and branchiostegal spines with sharp basal carina, that continuous with branchiostegal spine merging with hepatic carina. Cervical carina strong, extending to, but not crossing, postrostral carina, its dorsal extremity located immediately posterior to midlength of carapace: hepatic carina blunt, its accompanying sulcus deep; additional short carina lying dorsal and parallel to posterior part of hepatic sulcus; posthepatic carina long, running from posterior extremity of hepatic sulcus to posterior margin of carapace; branchiocardiac carina also long, reaching posterior margin of carapace; short sulcus extending posterodorsally from near posterior end of branchiocardiac carina; submarginal carina well defined, extending along entire length of branchiostegite.

Eye as illustrated (Figure 18A).

Antennular peduncle length equivalent to about 0.4 that of carapace; prosartema extending to distal margin of eye, but falling short of distal end of first antennular article; stylocerite short, extending 0.5 of distance between its proximal extremity and mesial base of distolateral spine; latter rather long, slender, and sharp. Antennular flagella incomplete in specimens examined.



FIGURE 18.—Eyes. A, Hymenopenaeus doris, syntype  $\Im$  32.5 mm cl, off Cabo Velas, Costa Rica. B, Hymenopenaeus nereus, syntype  $\Im$  21.5 mm cl, south of Cabo Blanco, Costa Rica.

Scaphocerite overreaching antennular peduncle by 0.25 of its own length; lateral rib ending in slender spine, extending to distal margin of lamella. Antennal flagellum broken in specimens studied. Mandibular palp reaching distal 0.2 of carpocerite; proximal article about 2.5 times as long as wide; distal article considerably shorter and narrower than proximal, and tapering to blunt tip. First maxilliped with single rudimentary arthrobranchia at base. Third maxilliped reaching beyond antennular peduncle by dactyl and almost entire length of propodus; length of dactyl about 0.65 that of propodus.

First percopod extending to distal end of carpocerite. Second pereopod overreaching antennular peduncle by length of propodus. Third percopod exceeding antennular peduncle by length of propodus and about 0.33 that of carpus. Fourth pereopod overreaching antennular peduncle by dactyl, propodus, and almost entire length of carpus. Fifth percopod reaching beyond antennular peduncle by length of distal three podomeres. Pereopods increasing in length from first to fifth. First pereopod with rather inconspicuous spine on basis, and slender spine on ischium; second pereopod with minute spine on basis. In female, coxa of third percopod produced into large, subtrapezoidal plate, broadest mesially, and disposed almost at right angle to podomere; coxa of fifth pereopod armed with minute anteromesial tooth.

Abdomen with middorsal keel from fourth through sixth somites, and strong longitudinal rib along lateral surface of fourth and fifth somites; posterodorsal margin of latter two somites with short median incision; sixth somite very elongate, 2.5 times as long as high, bearing small, sharp spine at posterior end of keel and pair of minute posteroventral spines. Telson with broad median sulcus deep anteriorly, quite shallow posteriorly, and flanked by low, sharp ridges; terminal portion length 5-6 times basal width: lateral spines short, their length about 1.5 times basal width of terminal portion. In only specimen with complete uropod, mesial ramus falling short of apex of telson; lateral ramus overreaching mesial ramus by 0.2 of its own length, and armed with small, terminal, distolateral spine.

Petasma unknown; males not recorded.

Thelycum (Figure 19A, B) with median protuberance on sternite XIV subpyramidal, with subtriangular base and apical portion strongly produced into elongate, acute projection directed ventrally or anteroventrally, and lying quite near



FIGURE 19.—Hymenopenaeus doris, syntype  $\Im$  32.5 mm cl, off Cabo Velas, Costa Rica. A, Thelycum, ventral view. B, syntype  $\Im$  32 mm cl, same locality, thelycum, ventrolateral view (setae omitted).

median lamella of sternite XIII; lamella, projecting vertically, heavily sclerotized, excavate anteriorly, with distal margin truncate or convex; pair of high ridges (triangular in cross section) flanking and posteriorly overlapping median lamella; posterior part of sternite XII bearing paired short, blunt horns covered by long setae.

Maximum size.-Females: 33.5 mm cl.

Geographic and bathymetric ranges.-Eastern Pacific: from off Punta Chivato  $(27^{\circ}09'N, 111^{\circ}42'W)$ , Gulf of California, to Isla del Coco, Costa Rica (Figure 20), at depths between 549 and 4,082 m (Figure 9). Burkenroad (1938) cited the depth, 300 fm (549 m), at which one juvenile specimen was taken from the *Arcturus* off Isla del Coco, but did not give the coordinates of the locality. Beebe (1926), however, indicated that the various hauls from the *Arcturus* in the area were made slightly south of Isla del Coco, and cited the following coordinates: 4°30'N, 87°00'W.

Affinities.-Hymenopenaeus doris is closely allied to H. nereus, the only other member of the genus known from the American Pacific. Females of the

two species can be distinguished readily by thelycal features: in H. doris a strong median protuberance is present on sternite XIV, and the lamella on the posterior margin of sternite XIII is disposed vertically, is deeply excavate anteriorly, and its distal margin is truncate or convex; in H. nereus only a median longitudinal rib is present on sternite XIV, and the lamella on XIII is inclined anteriorly, is flattened, and its distal margin is concave. Finally, in H. doris the lamella is flanked by high ridges whereas in H. nereus these are replaced by flattened, scalelike processes directed caudally.

Remarks.-Only nine specimens of H. doris are known. Seven, five of which are syntypes, were collected by the Albatross (1891); one of these (not designated by Faxon as part of the type-series) was taken with four syntypes at Albatross stn 3414, and the seventh was caught in the Gulf of California at Albatross stn 3009. Two additional specimens were cited by Burkenroad (1938), a juvenile female from the mouth of the Gulf of California, and another juvenile from off Isla del Coco (Costa Rica) taken by the Arcturus in 300 fm (549 m).



FIGURE 20.—Ranges of Hymenopenaeus doris, Hymenopenaeus nereus, and Haliporoides diomedeae based on published records and specimens personally examined.

#### Hymenopenaeus nereus (Faxon 1893)

#### Figures 9, 18B, 20-23

- Haliporus nereus Faxon 1893:213 [syntypes:  $1 \$ MCZ 4645, S of Cabo Blanco, Costa Rica, 5°30'N. 86°45'W, 1,067 fm (1,952 m), 27 February 1891. Albatross stn 3366. 1 9, USNM 21177, S of Morro de Puercos, Panama, 7°06'15"N, 80°34'00"W. 695 fm (1,271 m), 23 February 1891, Albatross stn 3353. 2 9, USNM 21178, off Pen de Azuero, Panama, 6°21'N, 80°41'W, 1,793 fm (3,279 m), 7 March 1891, Albatross stn 3382. 1 ♂ 2 ♀, USNM 21180, NW of Is Galápagos, Ecuador, 2°34'N, 92°06'W, 1,360 fm (2,487 m), 5 April 1891, Albatross stn 3413. 2 9, MCZ 4646, NW of Punta Galera, Ecuador, 1°07'N, 80°21'W, 1,573 fm (2,877 m), 23 March 1891, Albatross stn 3398. 1 J, MCZ 4647, NW of Punta Galera, Ecuador, 1°07'N, 81°04'W, 1,740 fm (3,182 m), 24 March 1891, Albatross stn 3399. 2 9, USNM 21179, E of Is Galápagos, Ecuador, 00°36'S. 86°46'W, 1,322 fm (2,418 m), 27 March 1891, Albatross stn 3400. 1 9, Is Galápagos, Ecuador, 00°04'00"S, 90°24'30"W, 885 fm (1,619 m), 3 April 1891, Albatross stn 3407]. Faxon 1895: 189, pl. 48, fig. 1-1d. Bouvier 1906b:3; 1908:80. de Man 1911:7.
- *Hymenopenaeus nereus.* Burkenroad 1936:104; 1938:60. Ramadan 1938:60. Crosnier and Forest 1973:256, fig. 83c.

Material.-Syntypes, which are the only material ever recorded;  $1 \ \bigcirc$  collected at Albatross stn 3407 has not been located.

Description.-Rostrum (Figure 21) relatively short, its length about 0.3 that of carapace, reaching about midlength of second antennular article, horizontal or slightly upturned, tapering to sharp tip, and with dorsal and ventral margins straight. Rostral plus epigastric teeth 8; epigastric tooth situated at about 0.4 cl from orbital margin, first rostral (largest of all) at approximately 0.3, and base of third opposite to orbital margin. Adrostral carina low, sharp, extending from orbital margin almost to apex of rostrum; orbital margin projecting anteroventrally in narrow shelf. Postrostral carina strong to near posterior margin of carapace, followed by small tubercle. Ptervgostomian spine slender and sharp, like other lateral spines on carapace; postorbital (located directly posterior to antennal), pterygostomian, and branchiostegal continuous with sharp basal carina, that continuous with branchiostegal merging with sharp hepatic carina. Cervical carina strong; sulcus extending to, but not crossing, postrostral carina, its dorsal extremity located immediately posterior to midlength of carapace; hepatic carina sharp, its accompanying sulcus deep; additional short carina lying dorsal and parallel to hepatic sulcus; posthepatic carina long, running almost to posterior margin of carapace; branchiocardiac carina also long, extending nearly to posterior margin of carapace: short sulcus extending posterodorsally from near posterior end of branchiocardiac; submarginal carina well defined, running along entire length of branchiostegite.

Eye as illustrated (Figure 18B).

Antennular peduncle length equivalent to about 0.4 that of carapace; prosartema broad, reaching distal margin of eye, but falling short of distal margin of first antennular article; stylocerite short, extending 0.45-0.50 of distance between its proximal extremity and mesial base of distolateral spine; latter rather long and sharp; second antennular article with transverse row of sharp spines near distal margin; antennular fla-



FIGURE 21.—Hymenopenaeus nereus, syntype ? 23.5 mm cl, northwest of Islas Galápagos. Cephalothorax, lateral view.

gella incomplete in specimens examined; however, in Faxon's (1895) illustration both subequal, about 1.25 times as long as carapace. Scaphocerite overreaching antennular peduncle by as much as 0.3 of its own length, with lateral rib ending in sharp, slender spine reaching, or overreaching, distal margin of lamella. Mandibular palp extending to distal 0.3 of carpocerite; proximal article about 2.6 times as long as wide. Third maxilliped reaching beyond antennular peduncle by length of dactyl and about 0.5 that of propodus; length of dactyl about 0.65 that of propodus.

First perceoped extending to distal end of carpocerite or overreaching it by 0.5 length of dactyl. Second perceoped exceeding antennular peduncle by length of propodus or by latter and 0.15 that of carpus. Third perceoped overreaching antennular peduncle by propodus and about 0.5 length of carpus. Fourth perceoped surpassing antennular peduncle by dactyl, propodus, and almost entire length of carpus. Fifth perceoped exceeding antennular peduncle by length of distal three podomeres. Perceopeds increasing in length from first to fifth. First perceoped with rather inconspicuous spine on basis, and long slender spine on ischium; second perceoped with minute spine on basis. In female, coxa of third pereopod produced into large plate disposed at right angle to podomere, its anteromesial margin bearing blunt, strong tooth. Coxa of fourth pereopod produced in short, prominent plate armed with numerous strong setae. In both sexes, tooth present on anteromesial angle of coxa of fifth pereopod, tooth considerably stronger in males than in females, in latter minute and borne on rounded coxal plate.

Abdomen with middorsal keel from fourth through sixth somites, and strong longitudinal rib along lateral surface of fourth and fifth somites; posterodorsal margin of latter somites with shallow median incision; sixth somite very elongate, 2.25 times as long as high, bearing small sharp spine at posterior end of keel and pair of minute posteroventral spines. Telson with broad median sulcus, deep anteriorly, quite shallow posteriorly, and flanked by low sharp ridges; terminal portion length about 5 times basal width; lateral spines short, their length 1.5-1.6 times basal width of terminal portion of telson; mesial ramus of uropod falling short, or slightly overreaching, apex of telson; lateral ramus exceeding mesial ramus by 0.15-0.20 of its own length, and armed with acute, terminal, distolateral spine.



FIGURE 22.—Hymenopenaeus nereus, syntype & 15.5 mm cl, northwest of Punta Galera, Ecuador. A, Petasma (partly bent laterally), dorsal view of right half. B, Ventrolateral view. C, Right appendices masculina and interna, dorsal view. D, Ventromesial view.

Petasma (Figure 22A, B) with row of cincinnuli occupying proximal 0.35 of median line; ventromedian lobule bearing two processes distally; mesial one (disposed almost at right angle to lobule) subrectangular, and armed with few long spines, distolateral one (directed at about 45 degrees to lobule) unarmed, and produced proximolaterally in small auricular process; distal flap of ventrolateral lobule acuminate, large, extending as far as lateral process, and almost straight rather than conspicuously inclined; ventral costa projecting in strong rounded prominence at base of flap.

Appendix masculina (Figure 22C, D) with proximal part produced into rounded lobe; distal part extremely narrow and bearing lateral row of short setae continuous with apical tuft of longer setae. Appendix interna abruptly narrowing, setting off distal part from rounded proximal part. Ventrolateral spur short, roughly semicircular in outline distally.

Thelycum (Figure 23) with median, longitudinal ridge on sternite XIV; lamella at posterior margin of sternite XIII rather flat, directed anteriorly, with distal (cephalic) margin slightly to deeply concave, and lateral margins convex basally, straight or concave distally; lamella flanked by pair of flattened, subtriangular to rounded processes directed caudally; posterior margin of sternite XII bearing paired, setose, long horns, reaching almost midlength of sternite XIII.

Maximum size.-Males: 18 mm cl; females: 27 mm cl.

Geographic and bathymetric ranges.-From south of Cabo Blanco (5°30'N, 86°45'W), Costa Rica, to northwest of Punta Galera and Islas Galápagos (00°36'S, 86°46'W), Ecuador (Figure 20). It has been found at depths between 1,271 and 3,279 m (Figure 9).

Affinities.-Hymenopenaeus nereus and H. doris are very similar in external morphology. However, the external genitalia allow a ready separation of these two species as well as both from the closely related H. laevis and H. sewelli. Females of H. nereus are unique among the four species in possessing a longitudinal ridge, instead of a large protuberance, on sternite XIV; furthermore, the median lamella of sternite XIII is directed anteriorly, its lateral margins tend to converge proximally (posteriorly), and the lamella is



FIGURE 23.—Hymenopenaeus nereus, syntype 9 21.5 mm cl, south of Cabo Blanco, Costa Rica. Thelycum, ventral view.

flanked by a pair of processes which are flattened and directed caudally. In the other species, these processes are lacking or, if present, are directed anteroventrally. Males of H. *nereus* differ from those of H. *laevis* in that the petasma of the latter bears two, occasionally three, small, triangular projections on the distomesial margin of the ventromedian lobule instead of a single, subrectangular process bearing spines distally. Moreover, the lateral process is small and extends transversely rather than being directed distomesially, and the distal part of the ventrolateral lobule is broadly semicircular and strongly inclined toward the ventromedian lobule.

# Haliporoides Stebbing 1914

Peneopsis. Faxon 1893:212; 1895:185.

- Faxonia Bouvier 1905a:981 [part, excluding typespecies, Penaeopsis ocularis Faxon 1895 = Pleoticus robustus (Smith 1885)].
- Haliporus. Bouvier 1906b:1 [part]; 1908:78 [part]. de Man 1911:31 [part]. Calman 1925:9.

Haliporoides Stebbing 1914:20 [type-species, by monotypy, Haliporoides triarthrus Stebbing 1914. Gender, masculine]. Calman 1925:9.
Hymenopenaeus. Burkenroad 1936:102 [part].

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Parahaliporus Kubo 1949:207.

Hymenopenaeus (Haliporoides). Barnard 1950: 619.

Diagnosis.-Body moderately robust, carapace elongate, integument firm. Rostrum relatively long, extending at least to, often beyond, second antennular article, ventral margin straight or concave; armed with dorsal and, frequently, with ventral teeth; epigastric tooth separated from rostral teeth by interval noticeably longer than spaces between latter. Orbital and branchiostegal spines absent; postorbital, antennal, pterygostomian, hepatic, and suprahepatic spines present. Cervical sulcus deep, long, extending to, but not across, middorsum of carapace; hepatic sulcus long, turning anteroventrally from almost horizontal posterior part and reaching base of pterygostomian spine; orbital-antennal and branchiocardiac carinae and sulci well marked; submarginal carina sharp. Abdomen carinate dorsally at least along three posterior somites. Telson with pair of fixed, lateral spines. Prosartema moderately long, broad, and flexible. Antennular flagella similar, subcylindrical and long, not less than 3 times carapace length. Mandibular palp three jointed (occasionally two jointed in H. triarthrus, Ivanov and Hassan 1976), proximal article short and narrow, intermediate one larger, scalene-triangular in shape, and distal article considerably shorter and narrower than preceding one and tapering to blunt apex. First maxilla with unsegmented palp, gently narrowing to rounded apex. Fourth and fifth percopods relatively stout proximally, fifth not much longer than fourth. First percopod with or without spine on basis. Exopods (quite small) on all maxillipeds and pereopods. Lateral ramus of uropod armed with subterminal, distolateral spine. In males, petasma with distal part of ventral costa fused to flexible flap of ventrolateral lobule; distal portion of rib of dorsolateral lobule not elevated above, but at level of adjacent area, and not projecting beyond distal margin; ventromedian lobule lacking paired processes distally; endopod of second pleopod bearing appendices masculina and interna, its basal sclerite produced into very short, toothlike, ventrolateral spur. Thelycum of open type. Pleurobranchia present on somites IX to

XIV; single, rather conspicuous arthrobranchia on somite VII, and anterior and posterior arthrobranchiae on somites VIII to XIII. Podobranchia present on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

List of species.-Eastern Pacific: Haliporoides diomedeae (Faxon 1893). Indo-West Pacific: Haliporoides sibogae (de Man 1907); Haliporoides triarthrus Stebbing 1914.

Affinities.—The members of Haliporoides can be distinguished readily from those belonging to other related genera by the following features: the epigastric tooth is separated from the series of rostral teeth by an interval conspicuously longer than the spaces between the latter; the presence of a suprahepatic spine and an orbitoantennal sulcus which, although shallow, is clearly distinct; the spine of the lateral ramus of the uropod which is subterminal. Also, the arthrobranchia on somite VII is well developed instead of being rudimentary and, in males, the basal sclerite of the second pleopod is produced into a very short, toothlike, rather than foliaceous, ventrolateral spur.

In addition to the characters cited above, Haliporoides, in contrast to Hymenopenaeus, possesses a thick, rigid integument, and lacks a branchiostegal spine and a posthepatic carina; it also possesses a petasma in which the ventromedian lobule is not produced distally into conspicuous processes, and the rib of the dorsolateral lobule is flush with the surrounding area. Finally, Haliporoides may be separated from Pleoticuswhich it resembles in its general mien and in the shape of the rostrum-not only by the characters cited, but also by possessing a sharp branchiocardiac carina and deep branchiocardiac sulcus as well as by the petasma, in which the ventral costa is fused to the terminal part of the ventrolateral lobule. The above clearly indicates that Hali*poroides* is the most distinct of the genera treated here, except perhaps for Mesopenaeus.

# Haliporoides diomedeae (Faxon 1893)

Figures 9, 20, 24-28

Peneopsis diomedeae Faxon 1893:212 [syntypes: 3 ♀, USNM 21175, off Golfo de Panamá, 7°31'30"N, 79°14'00"W, 458 fm (838 m), 8 March

1891, Albatross stn 3384. 1  $\circ$  1  $\circ$ , USNM 21176, SW of Golfo de Panamá, 7°30'36"N, 78°39'00"W, 730 fm (1,335 m), 11 March 1891, Albatross stn 3395. 2  $\circ$  1  $\circ$ , MCZ 4644, SE of Golfo de Panamá, 7°21'N, 79°35'W, 511 fm (935 m), 10 March 1891, Albatross stn 3394. 3  $\circ$ , off Punta Mala, Panama, 7°15'N, 79°36'W, 1,020 fm (1,866 m), 10 March 1891, Albatross stn 3393. 2  $\circ$ , off Punta Mariato, Panama, 7°06'15"N, 80°34'00"W, 695 fm (1,271 m), 23 February 1891, Albatross stn 3353. 1  $\circ$ , USNM 21174, S of Península de Azuero, 6°30'N, 81°44'W, 555 fm (1,015 m), 24 February 1891, Albatross stn 3358]. Faxon 1895:185, pl. G.

Faxonia diomedeae. Bouvier 1905a:981.

Haliporus diomedeus. Bouvier 1906b:4; 1908:80. Haliporus diomedeae. de Man 1911:7.

Hymenopenaeus diomedeae. Burkenroad 1936: 104. Hancock and Henríquez 1968:445. Idyll 1969:641. Chirichigno Fonseca 1970:13, fig. 18. del Solar C. et al. 1970:18. Arana Espina and Cristi V. 1971:25. Illanes B. and Zúñiga C. 1972: 3, pl. 1-2.

- Hymenopenaeus diomedaea. Bahamonde 1963:3 (unnumbered).
- Vernacular names; gamba roja (Peru); gamba, camarón de mar, camarón de profundidad (Chile).

#### Material

PANAMA—2  $\circ$ , MCIP, 32 km SE of Punta Mala, Península de Azuero, 823-1,006 m, 1973, Canopus. 3  $\circ$  syntypes, USNM 21175, off Golfo de Panamá, 458 fm (838 m), 8 March 1891, Albatross stn 3384. 1  $\circ$  1  $\circ$  syntypes, USNM 21176, SW of Golfo de Panamá, 730 fm (1,335 m), 11 March 1891, Albatross stn 3395. 2  $\circ$  1  $\circ$  syntypes, MCZ 4644, SE of Golfo de Panamá, 511 fm (935 m), 10 March 1891, Albatross stn 3394. 1  $\circ$  syntype, USNM 21174, S of Península de Azuero, 555 fm (1,015 m), 24 February 1891, Albatross stn 3358.

PERU—i ♀, USNM, off Casitas, Tumbes, 550 m, 16 December 1968, *Kaiyo Maru.* 58 ♂ 56 ♀, USNM, W of I Macabi, 607-735 m, 5 September 1966, *Anton Bruun* stn 754.

CHILE—4  $\Im$ , USNM, off Paposo, Antofagasta, 950 m, 16 August 1966, Anton Bruun stn 714. 8  $\Diamond$  13  $\heartsuit$ , USNM, off Bahía Pichidangui, Coquimbo, 960 m, 12 August 1966, Anton Bruun stn 703. 1  $\Diamond$  1  $\heartsuit$ , USNM, Valparaíso, 10 February 1956, John Manning. 14  $\Diamond$  17  $\heartsuit$ , USNM, off Punta Topocalma, Colchagua, 750-730 m, 5 August 1966, Anton Bruun stn 687.



FIGURE 24.—Haliporoides diomedeae, 9 37.5 mm cl, off Bahía Pichidangui, Coquimbo, Chile. Lateral view.

Description.-Body rather robust (Figure 24), integument firm and glabrous. Rostrum straight or gently sinuous with upturned tip, moderately long, at most slightly overreaching antennular peduncle, its length 0.45-0.60 that of carapace. Rostral plus epigastric teeth 3-6 (mode 5; N =100); epigastric tooth situated at about 0.3 length of carapace from orbital margin, first rostral at level of, or immediately posterior to, orbital margin. Adrostral carina strong, extending from orbital margin almost to apex of rostrum; postrostral carina very strong to near posterior margin of carapace, there merging with inconspicuous dorsal tubercle. Antennal. ptervgostomian. postorbital, and hepatic spines long, slender, and sharp; both antennal and postorbital spines (latter situated directly posterior to antennal) continuous with short, blunt, basal carina; basally broad suprahepatic spine (occasionally accompanied by smaller dorsal one) present, giving rise to deep notch dorsal to hepatic spine: orbitoantennal sulcus shallow, but clearly distinct; cervical carina sharp, cervical sulcus deep, extending to, but not crossing, postrostral carina, its dorsal extremity located almost 0.45 length of carapace from orbital margin; hepatic sulcus deep, hepatic carina sharp anteriorly and turning anteroventrally to base of pterygostomian spine; both hepatic carina and sulcus almost indistinct posteriorly, to anteroventral end of branchiocardiac sulcus. Branchiocardiac carina long, sinuous, and sharp, accompanying sulcus deep and broad; submarginal carina long, extending from base of pterygostomian spine to posterior margin of carapace.

Eye (Figure 25) with basal article produced distomesially into pubescent, relatively short scale; ocular peduncle short, bearing rather small mesial tubercle; cornea subreniform, greatest diameter about 2 times that of base of ocular peduncle, strongly slanting posterolaterally.

Antennular peduncle length equivalent to about 0.5 that of carapace; prosartema broad and short, extending only to distomesial extremity of ocular peduncle; stylocerite extending about 0.6 of distance between its proximal extremity and mesial base of distolateral spine; latter moderately long, slender, and sharp. Antennular flagella long, although incomplete in all specimens examined, in shrimp 32.5 mm cl, broken dorsal flagellum 118 mm long, thus 3.65 times as long as carapace. Scaphocerite overreaching antennular peduncle by about 0.2 of its own length;



FIGURE 25.—Haliporoides diomedeae, ♀ 44.5 mm cl, off Punta Topocalma, Colchagua, Chile. Eye.

lateral rib ending in rather slender spine, falling short of distal margin of lamella. Antennal flagellum broken in specimens examined, according to Illanes and Zúñiga (1972) "longer than total length of body."

Mandibular palp (Figure 26A) extending as far as basal 0.4 length of carpocerite; proximal article scalene-triangular, about 2.65 times as long as wide; distal article considerably shorter and narrower than proximal, and tapering to blunt tip. First and second maxillae as illustrated (Figure 26B, C); somite VII bearing single conspicuous arthrobranchia at base of first maxilliped (Figure 26De- $e^{1}$ ). Third maxilliped reaching beyond antennular peduncle by tip or by length of dactyl in males and by as much as dactyl and 0.5 length of propodus in females; dactyl with acute tip in females, clublike in males, its length 0.90-0.95 that of propodus.

First percopod reaching between base and distal end of carpocerite in males, and almost to distal end of carpocerite or overreaching it by as much as length of dactyl in females. Second pereopod extending, at most, to midlength of second antennular article in males, and as far as distal end of third article in females. Third percopod reaching distal end of third antennular article or overreaching it by not more than length of dactyl in males, and by entire propodus plus 0.15 length of carpus in large females. Fourth pereopod exceeding antennular peduncle by, at most, length of dactyl in males, and by dactyl or by entire propodus in females. Fifth percopod overreaching antennular peduncle by as much as length of dactyl and 0.8 that of propodus in males, and by distal two podomeres plus 0.15-0.25 length



FIGURE 26.—Haliporoides diomedeae, 9 45.5 mm cl, Valparaíso, Chile. A, Mandible. B, First maxilla. C, Second maxilla. D, First maxilliped. e, Arthrobranchia. e<sup>1</sup>, Enlargement of e (all from left side).

of carpus in females. Pereopods increasing in length from first to fifth; third and fourth extending distally for about same distance. First pereopod with spine on basis and ischium, and one movable distal spine and one or two fixed proximal ones on merus; basis of second pereopod lacking spine. In females, coxal plate of third pereopod directed and broadening mesially, strongly convex posteriorly. In both sexes, anteromesial spine present on coxae of third through fifth percopods; in females, spine on third long, slender, and situated anterodorsally to coxal plate, and spines on fourth and fifth small and sharp; in males, spines on third and fourth pereopods small and sharp, but spine on fifth large, flattened, curved laterally.

Abdomen with middorsal keel from fourth through sixth somites and strong, sharp spine at posterior end of keel on each; sixth somite short, about 1.25 times as long as high, bearing posteroventral spines. Telson with broad median sulcus deep anteriorly, shallower posteriorly, ending at level of base of lateral spines, and flanked by well-defined ridges; terminal portion length 4-5 times basal width, spines short, 1.0-1.65 times basal width of terminal portion. Mesial ramus of uropod reaching apex of telson or overreaching it by about 0.15 of its own length; lateral ramus, in turn, overreaching mesial by almost 0.2 of its own length, armed with rather strong, subterminal, distolateral spine. Third through fifth pleopods in males bearing strong dorsomesial ridge, that of third bearing distally strong subrectangular tooth with minute tooth at its base; ridge on fourth ending in also large, subtriangular tooth; last three pleopods in females with barely marked dorsomesial ridge.

Petasma (Figure 27A, B) with row of cincinnuli occupying only proximal 0.3 of median line; terminal part of ventromedian lobule abruptly broadening distally with terminal margin serrate laterally; rib of dorsolateral lobule broad proximally, its distal extremity reaching, but not overreaching, margin of adjacent membranous portion; distal part of ventrolateral lobule free, forming roughly subelliptical flap diverging from ventromedian lobule; ventral costa broad proximally, tapering along margin of flap.



FIGURE 27.—Haliporoides diomedeae, & 34.5 mm cl, off Bahía Pichidangui, Coquimbo, Chile. A, Petasma, dorsal view (partly bent laterally). B, Ventral view of left half. C, Right appendices masculina and interna, dorsal view. D, Ventromesial view.

Appendix masculina (Figure 27*C*, *D*) short, length about 1.5 times maximum width, produced laterally into broad semicircular lobe, ventrally excavated and bearing patch of long setae along entire distal margin. Appendix interna falling short of distal margin of appendix masculina, and armed with thickly set setae along entire distal margin; distolateral spur very short and obtuse.

Thelycum (Figure 28) with no ridge or protuberance on sternite XIV, latter smoothly convex or low subconical, often bearing minute central tubercle; posterior part of sternite XIII armed with strong median, acute to blunt subconical protuberance directed anteriorly and studded with numerous setae on anterior half; posterior margin of sternite XII lacking horns.

*Color.*-Overall pink with red and orange patches and bands, both longitudinal and transverse. For detailed account of coloration see Illanes B. and Zúñiga C. (1972).

Maximum size.-Males: 50 mm cl; females: 57 mm cl (in material examined by me).

Geographic and bathymetric ranges.-Off Península de Azuero, Panama (Figure 20) to Talcahuano, Chile (36°40'S), in depths between 240 (Illanes B. and Zúñiga C. 1972) and 1,866 m (Figure 9). Information on the geographic and bathymetric distributions of this species, as well as of its other two congeners in the American Pacific, is extremely meager.

Affinities.-Haliporoides diomedeae is the only member of the genus occurring in American waters and may thus be readily distinguished from the other solenocerids in the region by generic characters. Its two congeners, the Indo-West Pacific H. sibogae and H. triarthrus, differ from it in possessing an arcuate, ventrally toothed rostrum, and in lacking meral spines on the first pair of percopods, as well as in petasmal and thelycal features. In both of them, the ventromedian lobule of the petasma is neither expanded distally nor serrate along its terminal margin, and the thelycum exhibits a midridge on sternite XIII instead of a subconical, median protuberance.

*Remarks.*-Studies of this species are extremely few, and almost entirely restricted to its external morphology. The most recent contribution is one by Illanes B. and Zúñiga C. (1972), who presented many fine observations on numerous features. Previously, Arana Espina and Cristi V. (1971) had determined the relations between the following parameters: carapace length, total length,

whole weight, and abdominal weight (cl/tl, cl/ww, cl/aw, tl/ww, tl/aw). They found statistically significant differences between males and females in all relations with the exception of carapace length/total length.

Economic importance.-At present this species is not taken commercially. However, dense concentrations have been located in various areas within its range. Off the west coast of America three deepwater shrimps—Solenocera agassizii Faxon 1893; Solenocera florea Burkenroad 1938, and Heterocarpus reedi Bahamonde 1955—are utilized; consequently, it is to be expected that H. diomedeae, a species larger than those mentioned above, eventually will be exploited.

# Pleoticus Bate 1888

Philonicus Bate 1888:273 [part, excluding Philonicus lucasii (Bate 1881) = Hadropenaeus lucasii, and Philonicus pectinatus Bate 1888 = Solenocera pectinata]. [Type-species, by



FIGURE 28.—Haliporoides diomedeae, 9 44.5 mm cl, off Punta Topocalma, Colchagua, Chile. Thelycum, ventral view.

subsequent designation of Fowler 1912:543, *Philonicus mülleri* Bate 1888]. Preoccupied by *Philonicus* Loew 1849:144 (Diptera).

- Pleoticus Bate 1888:xii [part]. [Replacement name for Philonicus Bate. Type-species, Philonicus mülleri Bate 1888. Gender, masculine].
- Faxonia Bouvier 1905a:981 [part, excluding Faxonia diomedeae (Faxon 1893)]. [Typespecies, by subsequent designation of Fowler 1912:543, Penaeopsis ocularis Faxon 1895 = Pleoticus robustus (Smith 1885)].
- Parartemesia Bouvier 1905b:747 [part, excluding Parartemesia tropicalis Bouvier 1905b = Mesopenaeus tropicalis (Bouvier 1905b)]. [Typespecies, by subsequent designation of Fowler 1912:543, Parartemesia carinata Bouvier 1905b = Pleoticus muelleri (Bate 1888)].
- Haliporus. Bouvier 1906b:1 [part]; 1908:78 [part].
   A. Milne Edwards and Bouvier 1909:206 [part].
   de Man 1911:31 [part]. Fowler 1912:542 [part].
- Hymenopenaeus. Smith 1885:179 [part]. Burkenroad 1936:102 [part]. Kubo 1949:212 [part].Roberts and Pequegnat 1970:29 [part].

Diagnosis.-Body robust, carapace elongate, integument thick, firm. Rostrum moderately long, reaching midlength of second antennular article or slightly overreaching peduncle; ventral margin straight to concave; armed only with dorsal teeth; epigastric tooth and first rostral separated by interval equal to, or only slightly greater than. that between first and second rostral teeth. Orbital, postorbital, antennal, and hepatic spines present; pterygostomian spine absent; branchiostegal spine present or absent. Cervical sulcus deep, long, extending to, but not across, middorsum of carapace; hepatic sulcus well marked; posthepatic and branchiocardiac carina lacking; branchiocardiac sulcus usually absent; submarginal carina sharp; posthepatic carina absent. Abdomen carinate dorsally at least along posterior three somites. Telson with pair of conspicuous, fixed lateral spines. Prosartema long or moderately long, flexible. Antennular flagella similar, subcylindrical, and longer than carapace. Mandibular palp two jointed, articles broad, distal one as long, or almost as long, as basal, tapering to blunt apex. First maxilla with unsegmented palp, gently narrowing to rounded apex. Fourth and fifth percopods rather stout proximally, fifth moderately longer than fourth. First percopod with spine on basis and ischium. Exopods on all maxillipeds and percopods. Lateral ramus of uropod armed with terminal, distolateral spine. In males, petasma with ventral costa free from distally flexible terminal part of ventrolateral lobule; ventromedian lobule not expanded distally. Endopod of second pleopod bearing appendices masculina and interna, and with basal sclerite produced distally into elongate ventrolateral spur. Thelycum of open type, lacking enclosed seminal receptacle. Pleurobranchia present on somites IX to XIV; one or two rudimentary arthrobranchiae on somite VII; and anterior and posterior arthrobranchiae on somites VIII to XIII. Podobranchia present on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

List of species.-Western Atlantic: Pleoticus robustus (Smith 1885); Pleoticus muelleri (Bate 1888). Red Sea: Pleoticus steindachneri (Balss 1914).

Affinities.-The members of Pleoticus resemble those of Hymenopenaeus and Haliporoides in the character of the rostrum and general form of the carapace; however, in Pleoticus the epigastric tooth is separated from the first rostral by an interval which is equal to, or only slightly greater than, that between the first and second rostral teeth; an orbital spine is present as it only is in the more distantly related Mesopenaeus; the branchiocardiac carina is absent; and the branchiocardiac sulcus is usually absent. Furthermore, the mandibular palp is two jointed unlike the usually three jointed one of Haliporoides but like that of Hymenopenaeus; however, in contrast to the palp of the latter, that of *Pleoticus* is broad and its distal article is as long as, or longer than, the basal. Finally, in the petasma of *Pleoticus* the distal extremity of the ventral costa is free from the ventrolateral lobule instead of being fused to it.

*Pleoticus* agrees with *Hadropenaeus* in the arrangement of the epigastric and rostral series of teeth, the lack of branchiocardiac and posthepatic carinae, the absence of pterygostomian spines, as well as in having the distal extremity of the ventral costa of the petasma free from the adjacent part of the ventrolateral lobule. The considerably more elongate carapace, the low and longer rostrum, and the presence of strong submarginal carina, and orbital spine separate the former from the latter.

The similarities cited above indicate that *Pleoticus* occupies a position somewhat intermediate between the more primitive *Hymenopenaeus* and *Haliporoides*, on one hand, and *Hadropenaeus* on the other.

The genus *Pleoticus* is less homogeneous than the other genera treated here. In P. robustus and P. muelleri the branchiocardiac sulcus is abent or indistinct whereas in P. steindachneri it is distinctly marked; the branchiostegal spine, while present in P. robustus and P. muelleri, is lacking in P. steindachneri. Whereas in the petasma of P. robustus and P. steindachneri the row of cincinnuli occupies almost the entire median line, and the ventromedian lobule is distally membranous and entire, in that of P. muelleri the row of cincinnuli is limited to the proximal 0.4 of the median line, and the ventromedian lobule is heavily sclerotized distally and bears strong projections. In spite of these differences, it seems to me that the many features shared by these species justify their being grouped within a single genus. I have not examined specimens of P. steindachneri, but the descriptions and illustrations of Balss (1914. 1915) indicate that this shrimp is more closely related to P. robustus and P. muelleri than to members of other genera.

# Key to the Species of *Pleoticus* in the western Atlantic

- Body entirely pubescent. Prosartema not overreaching distal margin of first antennular article. Branchiostegal spine present. Females with paired, triangular projections near anterior margin of sternite XIV, and strong median ridge on sternite XIII. Males with petasma cincinnulate along entire median line, its ventromedian lobule entire distally ...... P. robustus
  - Body almost entirely polished. Prosartema considerably overreaching distal margin of first antennular article. Branchiostegal spine absent. Females lacking triangular projections on sternite XIV, bearing strong, median projection on sternite XIII. Males with petasma cincinnulate along proximal 0.4 of median line, its ventromedian lobule produced in two projections....

.....P. muelleri
#### Pleoticus robustus (Smith 1885)

#### Figures 9, 29-36

Hymenopenaeus robustus Smith 1885:180 [syntypes: 2  $\circ$  7  $\circ$ , USNM 6907; 2  $\circ$  5  $\circ$  (1  $\circ$  in original lot = Penaeopsis serrata Bate 1881), USNM 6908; type-locality: 11°43'00"N, 69°09'30"W, 208 fm (380 m), S of Curaçao, Albatross stn 2125]. Burkenroad 1936:118. Anderson and Lindner 1945:288. U.S. Fish and Wildlife Service 1948:2. Springer 1951a:80; 1951b: 6. Springer and Bullis 1952:11. Popovici and Angelescu 1954:509. Springer and Bullis 1954: 3. Voss 1955:9, fig. 6. Bullis 1956:1 [not Fig. 1 = Aristeus antillensis A. Milne Edwards and Bouvier 1909]. Springer and Bullis 1956:8. Clifford 1956:438. Guest 1956:7. Lindner 1957:87. Anderson 1958:1, fig. 6. U.S. Fish and Wildlife Service 1958:1, fig. I-6. Bullis and Thompson 1959a:35; 1959b:1. Hutton et al. 1959:7. Eldred and Hutton 1960:91, fig. 12. Cummins and Rivers 1962:19. Bullis and Cummins 1963:9. Davant 1963:21, fig. 19-20. Boschi 1964:38. Hutton 1964:439. Bullis and Thompson 1965:5. Holthuis and Rosa 1965:1. Pericchi López 1965: 24. Joyce and Eldred 1966:24. Kutkuhn 1966: 21. Christmas and Gunter 1967:1442. Thompson 1967:1454. Idyll 1969:638. Klima 1969:1.

Roe 1969:161, fig. 1. Anderson and Bullis 1970: 112. Pérez Farfante 1970:13, fig. 3F-H. Roberts and Pequegnat 1970:30, fig. 3-1B-C. Anderson and Lindner 1971:313, fig. 1-7. García Pinto 1971:5. Pequegnat and Roberts 1971:8. García del Barco 1972:172.

Peneopsis ocularis Faxon 1895:187.

- Faxonia ocularis. Bouvier 1905a:981.
- Haliporus robustus. Bouvier 1906b:4; 1908:8.
  A. Milne Edwards and Bouvier 1909:210, fig. 29-37, pl. 1, fig. 14-15, pl. 2, fig. 1-7. de Man 1911:7. Lenz and Strunck 1914:303. Burkenroad 1934:69.

Parapenaeus paradoxus Boone 1927:79 [part].

- Hymenopeneus robustus. Burkenroad 1963a:173.
- Royal red shrimp. Bates 1957:9, figures. Bullis and Rathjen 1959:1. Anonymous 1977:2.
- Vernacular names: royal red shrimp (United States), camarón rojo gigante (Mexico), camarón real rojo (Cuba), langostino rojo (Venezuela).

#### Material

UNITED STATES—Massachusetts:  $2 \delta 2 \varphi$ , USNM, S of Martha's Vineyard, 320 m, 28 January 1960, Delaware stn 39.  $1 \varphi$ , USNM, off Georges Bank, 20 July 1955, Delaware. North Carolina:  $1 \delta 1 \varphi$ , USNM, NE of Cape Lookout, 348-384 m, 13 November 1956, Combat stn 171.  $6 \varphi$ , USNM, off Cape Lookout, 366 m, 22 June 1957, Combat



FIGURE 29.—Pleoticus robustus, & 31 mm cl, east of Península Valiente, Panama. Lateral view.

stn 410. 5 & 5 9, USNM, SE of Cape Fear, 402 m, 29 January 1972, Oregon II stn 11746. South Carolina: 1 & 1 P, USNM, off Port Royal Sound, 366 m, 23 January 1972, Oregon II stn 11734. Florida: 3 3, USNM, off St Augustine, 384-393 m, 9 February 1965, Oregon stn 5231. 1 ♂ 3 ♀, USNM, off St Augustine, 344-338 m, 1 May 1956, Pelican stn 41. 3 9, USNM, off St Augustine, 316-329 m, 2 May 1956, Pelican stn 46. 1 & 22 9, USNM, off St Augustine, 324-333 m, 3 February 1962, Silver Bay stn 3725. 28 & 30 9, USNM, off Flagler Beach, 384 m, 16 November 1964, Oregon stn 5107. 1 ♂ 2 ♀, USNM, off Coronada Beach, 348 m, 10 February 1965, Oregon stn 5241. 9 & 6 9, USNM, off Oak Hill, 402-430 m, 11 February 1965, Oregon stn 5247. 4 9, USNM, off Cape Kennedy, 338 m, 27 January 1962, Silver Bay stn 3714. 5 ♂ 6 ♀, USNM, off Cocoa Beach, 329 m, 11 March 1956, Pelican stn 13. 11 ♂ 15 ♀, RMNH, E of Hutchinsons I, 324 m, 16 July 1965, Gerda stn 654. 11 & 13 9, UMML, off St Lucie Inlet, 366-375 m, 21 May 1968, Gerda stn 998. 15 & 14 º, USNM, SE of St Lucie Inlet, 287-262 m, 16 July 1965, Gerda stn 655. 2 3, USNM, E of Carysfort Reef, 549 m, 23 July 1957, Combat stn 444. 1 & 1 9, USNM, off Islamorada, 457-476 m, 18 July 1955, Oregon stn 1351. 3 & 2 9, USNM, off Double Headed Shot Cays, 558-514 m, 29 August 1967, Gerda stn 861. 1 9, UMML, S of Marquesas Keys, 512 m, 2 February 1968, Gerda stn 970. 9 9, USNM, SW of Marquesas Keys, 402-267 m, 2 February 1968, Gerda stn 969. 6 & 4 9, USNM, SW of Marguesas Keys, 437-320 m, 2 February 1968, Gerda stn 968. 1 9, UMML, S of Dry Tortugas, 622 m, 28 April 1969, Gerda stn 1099. 2 & 3 9, UMML, S of Dry Tortugas, 459-494 m, 28 April 1969, Gerda stn 1098. 26 ♂ 27 ♀, USNM, SW of Dry Tortugas, 348 m, 13 April 1954, Oregon stn 1005. 5 & 8 9, USNM, SW of Dry Tortugas, 402 m, 15 June 1956, Oregon stn 1539. 1 &, USNM, NW of Dry Tortugas, 311-366 m, 7 July 1955, Oregon stn 1321. 2 & 2 9, USNM, S of St George I, 366 m, 21 August 1970, Oregon II stn 11180. 2 & 2 P, USNM, S of Santa Rosa I, 439 m, 28 August 1970, Oregon II stn 11189. 1 9, USNM, S of Santa Rosa I, 527 m, 4 February 1970, Oregon II stn 10899. 9 ♂ 6 ♀, USNM, off Gulf Beach, 576-622 m, 28 April 1951, Oregon stn 319. Alabama (all from off Mobile Bay): 4 9, USNM, 549 m, 10 August 1970, Oregon II stn 11137. 1 9, USNM, 594 m, 10 August 1970, Oregon II stn 11139. 2 3 2 9, USNM, 433 m, 22 June 1969, Oregon II stn 10640. 1 & 4 9, USNM, 366 m, 18 December 1962, Oregon stn 4151. 8 9 juv, YPM, 219-238 m, 24 March 1935, Atlantis stn 2377. 3 9, USNM, 512 m, 10 July 1952, Oregon stn 597. Louisiana: 1 3, AMNH, E of Mississippi Delta, 384 m, 11 February 1885, Albatross stn 2377. 1 &, USNM, E of Mississippi Delta, 357 m, 1 September 1970, Oregon II stn 11202. 4 9, USNM, E of Mississippi Delta, 549 m, 23 October 1962, Oregon stn 4005. 14 ♂ 9 ♀, USNM, E of Mississippi Delta, 357 m, 23 September 1950, Oregon stn 126. 7 ♂ 10 ♀, USNM, E of Mississippi Delta, 402 m, 22 April 1951, Oregon stn 307. 3 ♂ 17 ♀, USNM, E of Mississippi Delta, 402 m, 25 August 1962, Oregon stn 3733. 1 9, YPM, E of Mississippi Delta, 302 m, 26 March 1935, Atlantis stn 2381. 3 d, USNM, off Atchafalaya Bay, 402 m, 11 November 1951, Oregon stn 501. Texas: 2 ♂ 3 9, USNM, SSE of Galveston, 366 m, 18 November 1951, Oregon stn 503. 3 ♂ 4 ♀ 2 juv, USNM, E of St Joseph I, 503 m, 6 May 1956, Oregon stn 1506. 1 8, USNM, off Corpus Christi, 640-732 m, 16 April 1952, Oregon stn 543. 1 ♂ 2 ♀, USNM, off Padre I, 549 m, 23 January 1964, Oregon stn 4637. 1 & juv, USNM, off Port Isabel, 640 m, 6 August 1969, Western Gulf stn 38. 1 9, USNM, off Brownsville, 457 m, 6 August 1969, Western Gulf stn 39.

MEXICO-Tamaulipas: 1 & 1 9, USNM, off Las Lava-

deros, 558 m, 2 June 1970, Oregon II stn 10953. 2  $\Im$ , USNM, off Las Lavaderos, 677 m, 2 June 1970, Oregon II stn 10954. Veracruz: 2  $\Im$  2  $\Im$ , USNM, N of Punta Roca Partida, 357 m, 5 June 1970, Oregon II stn 10959. 1  $\Im$  1  $\Im$ , USNM, NE of Punta Roca Partida, 613 m, 5 June 1970, Oregon II stn 10960. Tabasco: 1  $\Im$ , USNM, NW of Laguna del Carmen, 430 m, 6 June 1970, Oregon II stn 10963. 1  $\Im$ , USNM, N of Punta Frontera, 613 m, 9 June 1970, Oregon II stn 10984.

HAITI-14  $\circ$  7  $\circ$ , USNM, off Cape-Haitien, 640 m, 12 February 1963, Silver Bay stn 5142.

DOMINICAN REPUBLIC—1 & 1  $\Im$ , USNM, E of Puerto Plata, 732-640 m, 15 October 1963, Silver Bay stn 5168.

LESSER ANTILLES—4  $\Im$ , USNM, off Dog I, 628 m, 6 December 1969, Oregon II stn 10835. 2  $\Im$ , USNM, off Dog I, 688 m, 6 December 1969, Oregon II stn 10834. 7  $\Im$  6  $\Im$ , USNM, NE of Saba I, 649-668 m, 18 May 1967, Oregon stn 6696. 4  $\Im$  5  $\Im$ , USNM, E of Sint Eustatius, 642 m, 8 December 1969, Oregon II stn 10840. 2  $\Im$  6  $\Im$ , USNM, E of St Christopher, 644 m, 8 December 1969, Oregon II stn 10841. 34  $\Im$  31  $\Im$ , USNM, off St Christopher, 640-676 m, 20 May 1967, Oregon stn 6701. 2  $\Im$ , USNM, E of Capesterre, Guadeloupe, 466-640 m, 16 July 1969, Pillsbury stn 936. 2  $\Im$  7  $\Im$  syntypes, USNM 6907, S of Curaçao, 380 m, 18 February 1884, Albatross stn 2125. 2  $\Im$  5  $\Im$  syntypes, USNM 6908, S of Curaçao, 380 m, 18 February 1884, Albatross stn 2125. 1  $\Im$ , USNM, NW of Aruba, 622 m, 26 November 1970, Oregon II stn 11307.

WESTERN CARIBBEAN—2  $\delta$  1  $\circ$ , USNM, W of Rosalind Bank, 366 m, 7 June 1962, Oregon stn 3627. 2  $\delta$  1  $\circ$ , USNM, NE of Cayos Hobbies, 521 m, 25 October 1970, Oregon II stn 11220. 3  $\circ$ , USNM, W of Rosalind Bank, 457 m, 24 August 1957, Oregon stn 1889. 32  $\delta$  26  $\circ$ , UMML, W of Quita Sueño Bank, 450-576 m, 31 January 1971, Pillsbury stn 1355. 5  $\delta$  2  $\circ$ , USNM, W of Quita Sueño Bank, 439-457 m, 21 May 1962, Oregon stn 3565. 1  $\circ$ , USNM, SW of I de Providencia, 549 m, 13 September 1957, Oregon stn 1927. 1  $\delta$  2  $\circ$ , USNM, W of I de San Andrés, 549 m, 27 October 1970, Oregon II stn 11225. 1  $\circ$ , USNM, W of Cayos de Albuquerque, 585 m, 27 October 1970, Oregon II stn 11226. 1  $\circ$ , USNM, W of Cayos de Albuquerque, 192 m, 7 February 1967, Oregon stn 6444.

MEXICO—Quintana Roo: 1 & 5 %, USNM, off I de Cozumel, 412-457 m, 16 March 1968, *Pillsbury* stn 602.

BELIZE—8 ♂ 2 ♀, YPM, off Glover Reef, 669 m, 29 April 1925, *Pawnee*. 4 ♂ 6 ♀, USNM, off Stann Creek, 457-732 m, 10 June 1962, *Oregon* stn 3635. 2 ♂ 3 ♀, USNM, off Jonathan Point, 348 m, 9 June 1962, *Oregon* stn 3643.

NICARAGUA-2 3 2 9, USNM, NE of Islas del Maíz, 549-585 m, 23 May 1962, Oregon stn 3576.

PANAMA—8  $\diamond$  14  $\diamond$ , USNM, E of Península Valiente, 512 m, 25 May 1962, Oregon stn 3583. 6  $\diamond$  9  $\diamond$ , USNM, Golfo de los Mosquitos, 549 m, 31 May 1962, Oregon stn 3600. 1  $\diamond$  3  $\diamond$ , USNM, Golfo de los Mosquitos, 732 m, 31 May 1962, Oregon stn 3601. 2  $\diamond$ , USNM, NE of Belén, 439 m, 30 May 1962, Oregon stn 3592. 1 juv, USNM, off Punta Manzanillo, 421 m, 19 October 1965, Oregon stn 5740. 1  $\diamond$ , USNM, 5 July 1972, Canopus.

COLOMBIA—1  $\Im$ , USNM, off Punta Broquelles, 732 m, 28 May 1964, Oregon stn 4902. 3  $\Im$  3  $\Im$ , USNM, N of Islas de San Bernardo, 549 m, 6 November 1970, Oregon II stn 11244. 7  $\Im$  8  $\heartsuit$ , USNM, off Puerto Colombia, 366 m, 2 December 1968, Oregon II stn 10260. 4  $\heartsuit$ , USNM, W of Santa Marta, 631 m, 9 November 1970, Oregon II stn 11250. 1  $\Im$  1  $\heartsuit$ , USNM, W of Riohacha, 567-531 m, 30 July 1968, Pillsbury stn 781. 6  $\Im$  3  $\heartsuit$ , UMML, W of Cabo de la Vela, 408-576 m, 29 July 1968, Pillsbury stn 776. 3  $\Im$  7  $\heartsuit$ , USNM, W of Cabo de la Vela, 366 m, 2 June 1964, Oregon stn 4922. 21  $\diamond$  15  $\heartsuit$ , USNM, W of Cabo de la Vela, 439-448 m, 2 June 1964, Oregon stn 4923. 3  $\diamond$  2  $\heartsuit$ , USNM, off Cabo de la Vela, 485 m, 9 October 1965, Oregon stn 5689.

VENEZUELA—8  $\circ$ , USNM, E of Península de Paraguaná, 421 m, 27 September 1963, *Oregon* stn 4406. 4  $\circ$ , USNM, off Península de Paraguaná, 457 m, 4 October 1963, *Oregon* stn 4419. 4  $\circ$ , USNM, NE of San Juan de los Cayos, 384-607 m, 26 July 1968, *Pillsbury* stn 753. 3  $\circ$  9  $\circ$ , USNM, off Península de Araya, 402 m, 20 October 1963, *Oregon* stn 4477. 2  $\circ$  9  $\circ$ , USNM, NE of Islas Los Testigos, 366-439 m, 24 September 1964, *Oregon* stn 5037. 10  $\circ$  11  $\circ$ , USNM, NE of Islas Los Testigos, 388-457 m, 23 September 1958, *Oregon* stn 2353. 5  $\circ$  6  $\circ$ , USNM, NE of Punta Araguapiche, 366 m, 3 November 1957, *Oregon* stn 1981. 3  $\circ$  3  $\circ$ , USNM, NE of Punta Araguapiche, 457 m. 3 November 1957, *Oregon* stn 1982.

GUYANA—1 &, USNM, off Waini Beach, 137 m, 4 November 1957, Oregon stn 1993.

Description.-Body robust, integument thick. and entirely covered by densely set, short setae (Figure 29). Rostrum almost reaching or slightly overreaching distal end of antennular peduncle, nearly horizontal and straight in large adults, somewhat shorter, elevated, and broadly convex dorsally almost to tip in young; tip saber or spear shaped, 0.2-0.3 rostrum length, longest in adult. Rostral plus epigastric teeth 10-12 (mode 11: N = 200; teeth regularly closer from epigastric to ultimate; epigastric tooth located almost at level of dorsal extremity of cervical sulcus and fourth rostral tooth near level of orbital margin. Adrostral carina slender, extending from orbital margin almost to apex of rostrum; postrostral carina strong, long, almost reaching posterior margin of carapace; small tubercle present behind postrostral carina; antennal carina short but prominent. Orbital spine short, broad basally; postorbital spine slender, rather short, located posterodorsal to base of antennal spine; latter longest of lateral spines on carapace; branchiostegal spine moderately long; hepatic spine relatively short; pterygostomian spine lacking. Cervical sulcus sinuous, deep, ending lateral to postrostral carina at about midlength of carapace; cervical carina sharp. Hepatic sulcus almost horizontal posteriorly, merging with depressed area ventral to hepatic spine, from there inclining anteroventrally, and ending in pit below branchiostegal spine; hepatic carina accompanying anterior portion of sulcus sharp and prominent; branchiocardiac carina indistinct or barely perceptible; submarginal carina well marked, subparallel to free ventral margin of carapace.

Eye (Figure 30E) with basal article produced distomesially into pubescent, broad scale, bearing

spinelike distal projection; ocular peduncle short, cornea broad, greatest diameter slightly more than twice that of base of ocular peduncle, its proximal margin strongly slanting posterolaterally.

Antennular peduncle length equivalent to about 0.6 that of carapace: prosartema ending slightly proximal to distal margin of first article; stylocerite extending only to about 0.45 of distance between its proximal extremity and mesial base of distolateral spine, produced distally into short, rather blunt spine; distolateral spine slender and moderately long, sensibly overreaching distal margin of article. Antennular flagella (Figure 30A) rather broad proximally, subfiliform distally, markedly unequal in length, but both long, and increasing proportionately in length with age: dorsal flagellum about 1.4 times carapace length and ventral about 1.2 times carapace length, in shrimp 8.5 mm cl, and 3.5 and 2 times carapace length, respectively, in shrimp 32 mm cl (flagella incomplete in all larger animals examined). Dorsal flagellum with distal half of proximal portion bearing longitudinal row of combs of long setae on slightly concave ventral surface (Figure 30D) and stiff short setae on remaining surfaces: stiff setae increasingly sparse toward tip of flagellum. Ventral flagellum exhibiting strong sexual dimorphism: in mature male, proximal portion resembling bottle brush, with mesial surface flattened and bearing longitudinal band of stiff, dense setae with apices directed proximally (Figure 30B); lateral surface armed with numerous, simple setae directed distally (Figure 30C); dorsal and ventral surfaces bearing flexible, plumose setae, most thickly set in comblike clusters. In females, ventral flagellum with proximal portion covered by long flexible setae.

Scaphocerite exceeding antennular peduncle by as much as 0.2 of its own length; lateral rib ending in slender spine, falling short of distal margin of lamella. Antennal flagellum long, as much as 5 times total length of shrimp. Mandibular palp (Figure 31A) relatively short, extending to about distal extremity of ischiocerite, proximal article 1.25 times as long as wide; distal article only slightly longer and narrower than proximal one, tapering to blunt tip. Maxillae and first and second maxillipeds as figured (Figure 31*B-E*). Two rudimentary arthrobranchiae on somite VII, near base of coxa of first maxilliped (Figure  $31Dg-g^1$ ), both anterior and posterior arthrobranchiae on somite VIII, and podobranchia on



FIGURE 30.—Pleoticus robustus,  $\delta$  28 mm cl, south of Dry Tortugas, Fla. A, Antennular flagella. B, Mesial view of proximal part of ventral flagellum. C, Lateral view of same. D, Ventrolateral view of proximal portion (distal half) of dorsal flagellum. E, Eye,  $\Im$  34 mm cl, same locality.

corresponding second maxilliped; pleurobranchia, and anterior and posterior arthrobranchiae on somite IX (Figure 31E, F), pleurobranchiae present through somite XIV, and both arthrobranchiae through XIII. Third maxilliped exceeding antennular peduncle by at least 0.5 length of dactyl, or by dactyl and about 0.2 length of propodus.

First percopod reaching between base and distal end of carpocerite. Second percopod overreaching carpocerite by at least 0.5 length of dactyl, but by as much as entire propodus and 0.1 length of carpus. Third percopod surpassing antennular peduncle by length of dactyl or by length of propodus and 0.2 that of carpus. Fourth percopod extending to distal end of carpocerite or overreaching it by length of dactyl and 0.5 that of propodus. Fifth percopod exceeding antennular peduncle by at least 0.5 length of dactyl or by length of dactyl and 0.4 that of propodus. Order of percopods in terms of their maximal anterior extensions: first, second, fourth, third, and fifth. First percopod with moderately long, sharp spine at distomesial extremity of basis and ischium, and midlength of merus. In female, coxa of third percopod expanded into thick, roughly trapezoidal plate,



FIGURE 31.—Pleoticus robustus,  $\Im$  56 mm cl, off Dog Island, Lesser Antilles. A, Mandible. B, First maxilla. C, Second maxilla. c, Endite of basipodite.  $c^1$ , Enlargement of c, ventral view.  $c^2$ , Dorsal view. D, First maxilliped. g, Rudimentary arthrobranchiae.  $g^1$ , Enlargement of g. E, Second maxilliped and proximal portion of third. F, Somites VIII and IX with proximal portions of second and third maxillipeds, showing attachments of gills.

raised in strong, densely setose prominence on ventral surface. Coxa of fifth pereopod in male bearing blunt spine on anteromesial margin; in female, coxa produced into setose, short plate.

Abdomen with middorsal carina from third

through sixth somites, carina rounded on third, sharp and high from fourth posteriorly; sixth somite with small spine at posterior end of carina and paired, posteroventral spines. Telson with median sulcus rather shallow, short, occupying about 0.35 length of telson, flanked by low carinae, latter becoming sharp posteriorly, reaching base of lateral spines; length of spine 1.1 to 1.5 times width of terminal portion at base; terminal portion length 3 to 4 times basal width. Mesial ramus of uropod overreaching apex of telson by about 0.2 of its length; lateral ramus, in turn, overreaching mesial by as much as 0.25 of its own length, and bearing minute, terminal, distolateral spine.

Petasma (Figure 32A, B) cincinnulate along entire median line, with distal margin spinulous; midrib of dorsolateral lobule broadest proximally, and ending distally in narrow, sometimes sinuous tip; ventrolateral lobule almost entirely sclerotized, but produced distally into rather flexible, elongate flap, strongly inclined toward median lobe; ventral costa with free terminal part curved dorsally and armed with minute spines on distal margin.

Appendix masculina (Figure 32C, D) elongate, deeply excavate ventromesially for reception of appendix interna, broad proximal part raised in longitudinal, lateral rib extending to base of narrower distal part; strong dorsal thickness along distal part curving around terminal margin, there bearing tuft of rigid setae. Appendix interna considerably shorter than appendix masculina and consisting of short bulbous basal portion and elongate, narrow but thick distal portion. Ventrolateral spur abruptly narrowing slightly distal to midlength, becoming fingerlike.

Thelycum (Figure 33A) microscopically setosepunctate (Figure 33B), with paired subtriangular projections on anteriormost part of sternite XIV, usually inclined anteriorly, overlapping posterior margin of sternite XIII; posterior part of sternite XIV strongly bulging, often bearing midlongitudinal groove. Median plate of sternite XIII delimited anteriorly by paired deep depressions, and armed with strong anteromedian rib; sternite XII with central elevation, and paired, transverse marginal ridges overlapping sternite XIII.

Color.-Both coloration, as previously indicated by various authors, and color pattern are very variable. Burkenroad (1936) described fresh, though dead, juveniles, caught in the waters off Alabama, as follows: "Eyes deep reddish-brown with greenish reflections; gastric gland grayishbrown with light yellow-green flecks, stomach red; body pale orange-red, with a band of deeper salmon on the posterior part of each pleonic tergum; an iridescent blue-green area on the dorsum of each pleonic segment and of the telson." Springer (1951b) indicated that shrimp taken in the northern Gulf of Mexico were "brick red as they come from the water." Anderson and Bullis



FIGURE 32.—Pleoticus robustus, 3 32 mm cl, east of Península Valiente, Panama. A, Petasma, dorsolateral view of left half. B, Ventrolateral view (extended). C, Right appendices masculina and interna, lateral view. D, Mesial view.



FIGURE 33.—Pleoticus robustus, syntype  $\Im$  49 mm cl, south of Curaçao. A, Thelycum, ventral view. B,  $\Im$  61 mm cl, west of Riohacha, Colombia. Portion of sternite XIV showing setabearing depressions.

(1970) found that in animals observed from a submarine the "Color varied from grayish pink to red—similar to color observed on trawl-caught specimens." A diel color change was pointed out by Bullis (1956), who stated "nighttime catches are typically bright red, while catches landed during daylight hours are a light pink." Recently, García del Barco (1972) has confirmed this circadian variation.

My examination of large quantities of freshly collected animals during a 1969 cruise of the Oregon II in the Caribbean (Puerto Rico to Antigua) corroborated earlier observations of the great variation in this character, and disclosed the existence of many color patterns. The overall body color ranges from off white through pink and salmon to deep red, and the color pattern may consist of a few bright lines—mostly on various carinae—or even an abundance of strong markings. Opaque white and, particularly, reddish with white markings individuals were very common, whereas salmon ones, apparently similar in color to those shrimps from the northern Gulf of Mexico described by Burkenroad, were infrequent.

Descriptions of three color phases observed follow:

Pink-red phase: Body pink, marked with red and white. Gastric region intense pink; rostrum brilliant red with tip paler; anterior rostral teeth with bases red and apices light, but teeth posterior to orbital margin with brilliant deep red apices; small white patch in area between orbital, postorbital, and antennal spines; cardiac region light red; anteroventral border as well as antennal and cervical carinae and contiguous spines deep red: longitudinal opaque white stripe tapering from anteroventral margin (dorsal to branchiostegal spine) to depressed area below hepatic spine, from there broadening abruptly along entire cervical sulcus, then tapering again to about level of third percopod, there forming narrow, short stripe, continuing along posterior margin of carapace then recurving anteriorly, parallel to ventral margin, to level of base of second maxilliped, ending there in elongate white patch; deep red stripe inserted between arms of pink one. Abdomen light pink anteriorly, increasingly deep pink posteriorly, turning red on sixth somite; first five somites with posterior margin of tergum bordered by transverse red band, and posterior margin of pleuron with white band continuing anteriorly onto ventral margin; middorsal carina as well as posterior and ventrolateral margins of sixth somite brilliant red. Telson light red, with carinae, lateral margins, and transverse band proximal to terminal portion deep red. Basal podomere of uropod pink with lateral margin red; lateral ramus intense pink except for deep red tip; mesial ramus with pink proximal portion followed by white transverse band and latter, in turn, by red marking covering distal portion except for white mesial patch. Antennular peduncle light red, but apex of stylocerite and distolateral spine brilliant red, and prosartema pink; flagella red proximally fading to pink distally. Antenna pink. Third maxilliped and pereopods with coxa and basis white, remaining podomeres reddish. Pleopods with basis white but bearing pink semicircular, lateral patch; exopods white proximally, with red and pink transverse bands on midportion, and white distal patch; endopods white with pink band at midlength. Eye with peduncle white, and separated from cornea by two lines, proximal pink and distal red; basal article pink.

Salmon phase: Carapace anterior to cervical sulcus deep salmon, cardiac region, and ground color of abdomen pale salmon; rostrum (except for white tip) and branchiostegite bright reddish orange, that on branchiostegite sharply delimited dorsally along hepatic sulcus and branchiocardiac carina: apices of rostral teeth and spines, as well as postrostral and cervical carinae deep orangered; bases of teeth and spines, and cervical sulcus opaque white. Tergum of first through fifth abdominal somites with posterior, transverse band of reddish orange, band broad on middorsal portion, tapering ventrally to base of pleuron, from there extending along posterior margin and onto ventral margin; middorsal carina as well as posterior and ventrolateral margins of sixth somite deep reddish orange. Telson with ground color deep salmon, except for yellowish white basal portion; lateral portion of margins and paired carinae bright orange-red, giving rise on each side to angle with vertex on spine. Pereopods with coxa and basis white, and remaining podomeres salmon with longitudinal orange-red strip. Pleopods yellowish, but basis with roughly semicircular lateral white patch subtended by bright reddish orange stripe on lateral margin. Uropod mostly salmon; lateral ramus with distalmost portion bright red and mesial ramus with tip white.

Opaque white phase: Ground color opaque white with very pale salmon suffusion, more intense on rostrum; however, tip of rostrum, teeth and adrostral carina corneous; cardiac region grayish white, and entire branchiostegite milky white; branchiostegal and hepatic spines as well as cervical and postrostral carinae orange-red; longitudinal streak of orange-red extending posteriorly from dorsal end of cervical carina well beyond midlength of carapace. Pleura of first five abdominal somites with milky white Ushaped band following contour of margin; middorsal carina and posterior and ventrolateral margins of sixth somite orange-red. Telson almost white with median sulcus orange-red. Lateral ramus of uropod with oblique, milky white stripe at base of distal fourth, and subtended distally by intense salmon colored band and this, in turn, by white tip; mesial ramus with large, proximomesial, suboval, milky white patch bounded laterally by salmon band, and with distalmost portion milky white. Antennular peduncle deep salmon proximally, becoming pink distally; prosartema, antennular flagella, and antenna pink. Third maxilliped and percopods with coxa and basis white, and remaining podomeres white with very light pink suffusion. Pleopods pinkish white bearing milky white, semicircular, lateral patch. Ocular peduncle white, and bearing orange-red stripe along border with cornea.

Maximum size.—The largest male examined by me has a carapace length of 42 mm, about 173 mm tl, and the largest female, 61.5 mm cl, about 219 mm tl; however, Klima (1969), in his work on lengthweight relation, recorded larger specimens of both sexes, a male within the range of 180-184 mm tl and a female within 225-229 mm tl.

The sizes at which maturation occurs were determined by Anderson and Lindner (1971) to be at about 125 mm tl in males and about 155 mm tl in females.

Geographic and bathymetric ranges.-Pleoticus robustus ranges (Figure 34) from immediately south of Martha's Vineyard, Mass. (40°00'15"N. 70°54'00"W), through the Gulf of Mexico, and the Caribbean to French Guiana (07°05'N, 52°47'W). occurring on the upper continental slope at depths between about 180 and 730 m (Figure 9). It has been found only occasionally north of Cape Hatteras, and seems to be scarce off the Guianas. Inasmuch as this species has not been reported from Brazilian waters, French Guiana is cited here as the southernmost limit of the species on the basis of samples taken during the Oregon cruises off northeastern South America. The southern range of the species given by Bullis and Cummins (1963) was based on the same collections; consequently their statement that the royal red reaches Brazil should be understood to mean that it extends to about the border between French Guiana and Brazil.

The highest concentrations of P. robustus—off the northeast coast of Florida and in the north-



FIGURE 34.—Ranges of *Pleoticus muelleri*, *Pleoticus robustus*, and *Mesopenaeus tropicalis* based on published records and specimens personally examined.

eastern part of the Gulf of Mexico-occur at depths between 250 and 475 m. The species is scarce in less than 256 m, and not abundant at depths greater than 500 m. If the data are correct, the male found in 137 m off Guyana at Oregon stn 1993 represents an extremely rare occurrence of the shrimp in waters shallower than 180 m, as does the presence of the species at 70 m (at Oregon stn 2669, 18°31'N, 66°47.5'W, north of Puerto Rico), reported by Bullis and Thompson (1965). Although Roberts and Pequegnat (1970) stated that this shrimp has been found at depths as great as 500 fm (915 m), there is no precise record of its presence below 400 fm (732 m). Their statement seems to have been based on a catch from the Alaminos, in 289-472 fm (529-863 m); however, their remaining records, as well as those of all others, suggest that the specimens obtained in that haul were caught in the shallower part of

Throughout the Caribbean and northeastern South America, the royal red shrimp seems to be rather sparsely distributed; various explorations by the *Oregon* and *Oregon II* in the region have indicated a dense concentration only off Cabo de la Vela, Colombia.

the depth range cited.

Affinities.-Pleoticus robustus can be separated from *P. muelleri*, the only other western Atlantic representative of the genus, by the following characteristics: the densely pubescent body, the relatively short prosartema, which does not overreach the distal margin of the first antennular article, the presence of a branchiostegal spine, the lack of an orbital spine, and the disposition of the submarginal carina which is subparallel to the free border of the carapace along its entire length. The external genitalia of the two species are also quite different: whereas in the petasma of P. robustus the row of cincinnuli occupies the entire median line, the ventromedian lobule is flexible and entire distally, and the ventral costa is plain, in P. muelleri the row of cincinnuli extends only along the proximal 0.4 of the median line, the ventromedian lobule is produced distally in cornified oval and hooklike projections, and the distal part of the ventral costa bears a flange along the inner border. Also, the thelycum of P. robustus exhibits a pair of anterior triangular projections on the flexible anterior part of sternite XIV, and a median ridge on sternite XIII, whereas that of P. muelleri bears nothing more than a pair of minute tubercles on the heavily

sclerotized anterior part of sternite XIV, and a strong median projection on sternite XIII.

Spermatophore.-Compound spermatophore (as attached to female) consisting of broad, dorsoventrally depressed geminate body, with conspicuous transverse fold at about midlength, and bearing anterolateral wings; also provided with sculptured lateral flaps, and produced posterolaterally in short flanges (Figure 35).

Ventral and lateral walls of each spermatophore (Figure 36A) thick, opaque, fusing imperceptibly, their anterior margins broad and perpendicular to medial line. Spermatophore lacking anterior lobe, deeply concave at base of wing, there bearing conspicuous constriction; transverse angular fold present at about midlength, followed by depressed caudal half. Dorsomesial wall (Figure 36C) largely translucent, with globular anterior evagination (Figure 36B) markedly expanding lumen of sperm sac; posterior part of latter attenuated caudally by close proximity of opposing walls. Flap broad anteriorly and merg-



FIGURE 35.—Pleoticus robustus, compound spermatophore attached to female,  $\Im$  44 mm cl, west of Quita Sueño Bank, western Caribbean (setae omitted).

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FIGURE 36.—Pleoticus robustus,  $\delta$  37 mm cl, east of St Lucie Inlet, Fla. A, Left spermatophore dissected from terminal ampulla, ventrolateral view. B, Lateral view. C, Dorsal view. D,  $\delta$  38 mm cl, off St Augustine, Fla. Distal portion of left spermatophore (wing extended).

ing insensibly with lateral base of flange. Wing (Figure 36D) heavy, opaque, with broad base forming rounded lobe continuous with lateral wall, and tapering to short, blunt tip. Flange short, broadly subelliptical. Dorsal plate nearly triangular, anteriorly fitting snugly into deep groove of dorsomesial wall.

Compound spermatophore applied to female with anterior margin lying approximately at posterior margin of gonophores, and sperm masses—protruding through dorsomesial walls (apparently torn by forced release of those masses during mating)—lodged in paired concavities of sternite XIII. Bases of the wings attached to sternite XIII, their distal parts resting on same sternite, and on ventral articular membranes of fourth percopods. Lateral flaps affixed to sternite XIV, and just posterior to transverse folds of sacs, geminate body sloping caudodorsally over bulge of sternite XIV; adjoining flanges resting on posterior thoracic ridge. Wings and lateral flaps lie under (dorsal) setose coxae of fourth and fifth pereopods, respectively, which also aid in securing compound spermatophore on female. Dorsal plates, subjacent (dorsally) to caudal part of sacs, directly anchored to sternite XIV, thus helping to hold spermatophore in place.

The exceedingly large spermatophores of this shrimp appear to become attached to the female more firmly than those of many other penaeids with open type thelyca. This statement is based on the observation that females with attached spermatophores are frequently found in collections, whereas in other species with open type thelycum such females are rarely encountered. Most of the compound spermatophores that I have detached from impregnated females are practically empty. This suggests that the sperm are released with the entire spermatophore present, i.e., that the spermatophore is not torn or split leaving the sperm masses with the paired wings flanking them on the female while the geminate body and adjoining flanges fall away, as seems to occur in some members of the subgenus *Litopenaeus*, genus *Penaeus*.

Reproduction.-Anderson and Lindner (1971) reported that on the St. Augustine Grounds, *P. robustus* probably spawns throughout the year, with a peak between January and May. Recruitment begins when the shrimp are approaching 1 yr of age and are less than 100 mm tl; maturity is reached in about 3 yr. Most shrimp on the grounds are mature, and the life span appears to be no less than 5 yr.

The larvae of *P. robustus* are unknown. Burkenroad (1936) identified as "juveniles" the only postlarvae of the species ever recorded, specimens that I have examined. Curiously, Anderson and Lindner (1971) found neither larval nor postlarval stages in a large number of plankton samples collected over an extensive area seaward of the St. Augustine Grounds. They stated that only a single larva was considered as possibly belonging to "Hymenopenaeus."

Ecological notes.-In the northestern Gulf of Mexico and off the southeastern coast of the United States, this shrimp has been found within a temperature range of 5°-15°C, and is commercially abundant betwen 9° and 12°C (Bullis 1956; Bullis and Cummins 1963). The preference of P. robustus for this range of temperature was revealed by the observations of Bullis and Cummins, who stated that within 1 or 2 days after two incursions of cold bottom water off the northeast coast of Florida, shrimp moved inshore to waters 75 m shallower than those where they had been observed previously. Later, Roe (1969) reported that the maximum densities of this shrimp is in water temperatures of 9° to 10°C.

Commercial concentrations of royal red have been reported (Bullis 1956; Bullis and Rathjen 1959; Roe 1969) to occur on the following types of bottoms: blue-black terrigenous silt and silty sand off the Mississippi River Delta; whitish, gritty, calcareous mud off Tortugas; and basically similar sand or silty sand (called "green mud" by the fishermen) off the northeast coast of Florida.

Anderson and Bullis (1970) presented direct observations of this shrimp made from the submarine Aluminaut off Davtona Beach, Fla., at a depth of 459 m. They stated that "The bottom was remarkably free from obstructions and consisted of a gravish, loosely constituted sediment that readily clouded the water at the least disturbance. It was formed into a myriad of shallow depressions and mounds, pitted with holes.... Bottom photographs had previously indicated that royal-red shrimp stayed on the sea-floor surface, but we saw numerous shallow furrows (1 to 3 feet long) in the bottom in which royal-red shrimp were partly buried. They apparently do not burrow as deeply or completely as do brown and pink shrimp. We believe the shrimp plow into the bottom in search of food rather than protection, and that this feeding activity produces the grooves or furrows."

Remarks.-Smith (1885) cited 14 males and 4 females in USNM lots 6907 and 6908. My examination of this material has shown that the first lot consists of 2 males and 7 females, but the second lot includes 2 males and 5 females of "Hymenopenaeus" robustus and 1 female of Penaeopsis serrata (Bate 1881). Consequently Smith's statement is in error since there are only 4 males and. furthermore, the total number of females (including that of the latter species) must have been either 13 or 12 if one of them is missing from the lots. In the original description of the species, Smith stated that the proximal portion of the ventral antennular flagellum "is densely hairy in the male"; however, the marked difference that occurs between the pubescence of the flagellum in the male and the female has not been cited in subsequent morphological studies of the shrimp. Here, for the first time, detailed accounts of the setation of the ventral flagellum in both sexes are presented.

The petasma of P. robustus has been described previously by various investigators. Smith (1885) gave the first brief account. Later, A. Milne Edwards and Bouvier (1909) described and illustrated it in more detail; however, the two figures presented by them include several inaccuracies which were pointed out by Burkenroad (1936). In the same publication, the latter gave an accurate description of this structure. More recently, Roberts and Pequegnat (1970) presented observations as well as a sketch of the petasma, and Anderson and Lindner (1971) have provided the most complete illustration available. The account of the petasma herein, utilizing Kubo's (1949) terminology, is given in order that comparisons of this species with others treated in this work may readily be made.

*Economic importance.*-*Pleoticus robustus* is the only deep-water penaeoid in the western Atlantic that is now commercially exploited.

This large wide ranging shrimp has been found in commercial quantities only in three areas off the coast of the United States:

- 1. off northeast Florida on the St. Augustine Grounds
- 2. south to southwest of Dry Tortugas Islands
- southeast of the Mississippi River Delta to off Tampa Bay.

The commercial potential of the species was reported by Springer (1951b) and Springer and Bullis (1952) on the basis of its abundance off the Mississippi Delta. Subsequent explorations in the northern and northeastern Gulf of Mexico confirmed previous findings, and disclosed the concentration off the Dry Tortugas (Springer and Bullis 1954; Bullis 1956). Later, Bullis and Rathjen (1959) investigated the density of the populations off the southeast Atlantic coast of the United States and indicated the high potential of the St. Augustine Grounds, the exploitation of which began in 1962 (Cummins and Rivers 1962). The grounds in the northeastern Gulf of Mexico remained unexploited until this decade, when fishing was initiated. Total landings of royal red shrimp in 1976 (Anonymous 1977) amounted to 167,000 pounds (75,751 kg), heads-off, caught almost entirely off northwest Florida.

## Pleoticus muelleri (Bate 1888)

Figures 9, 34, 37-42

- Philonicus mülleri Bate 1888:275, pl. 39, fig. 1-2
  [syntypes: 5 ♂ 25 ♀, BMNH, off Montevideo, Uruguay, 35°02'S, 55°15'W, 13 fm (24 m), 25 February 1876, Challenger stn 321]. Fowler 1912:543.
- Pleoticus mülleri. Bate 1888:939. Berg 1898:38.
   Fesquet 1933:6, fig. 1-4, pl. 1-8; 1936:61. Barattini and Ureta 1960:49.
- Parartemesia carinata Bouvier 1905b:748 [syntypes: 1 ♂ 3 ♀, MP 59, off mouth Río de la Plata,

35°42'S, 56°20'W, 44 fm (80 m), Hassler. 1  $\circ$ , Río de la Plata, Montevideo, 7 fm (13 m), Hassler].

- Haliporus carinatus. Bouvier 1906b:4.
- Haliporus mülleri. Bouvier 1908:80. A. Milne Edwards and Bouvier 1909:214, fig. 38-44, pl. 2, fig. 9-10. Pesta 1915:102.
- Hymenopenaeus mülleri. Burkenroad 1936:103.
  Fesquet 1941:64. Rioja 1941:200, fig. 13, 17; 1942:659, fig. 20, 21, 30, 31. Anderson and Lindner 1945:288. López 1954:46. Popovici and Angelescu 1954:505. Lindner 1957:4. Angelescu and Boschi 1960:1, fig. 4, 10-16, pl. 1, 2, 5, 6. Eldred and Hutton 1960:91. Boschi and Angelescu 1962:1, fig. 1-17, pl. 1, 2. Boschi 1963:5, fig. 4. Mistakidis and Neiva 1964:471. da Silva 1965:4. Tremel and Mistakidis 1965:2. Mistakidis 1965:1. Neiva and Mistakidis 1966:4, fig. 4a, b. Mistakidis and Neiva 1966:434. Idyll 1969:642. Pérez Farfante 1970:13, fig. 3I-K. Iwai 1973:44.
- Hymenopendeus mülleri. Carcelles 1947:4, pl. 1, fig. 2.
- Hymenopenaeus muelleri. Boschi 1964:38. Holthuis and Rosa 1965:1. Boschi 1966:452. Boschi and Mistakidis 1966:1. Boschi and Scelzo 1969a:3; 1969b:152, pl. 1. Boschi 1970:65; 1974:3. Scelzo and Boschi 1975:193. Boschi and Scelzo 1976:1. Boschi 1976:63.
- Camarão barbado. Tremel et al. 1964:8.
- Vernacular names: langostino, langostín (Uruguay, Argentina), camarão de Santana, lagostinho da Argentina, camarão vermelho, camarão barbado, camarão ferro (Brazil).

### Material

BRAZIL-Espírito Santo: 2 9, USNM, off Praia de Santana, June 1962, G. de Souza Neiva. Rio de Janeiro: 2 9, USNM, off Macaé, 23 m. Superintendência do Desenvolvimento da Pesca, Seçao de Pesquisas. 9 9, USNM, Ilha dos Franceses, Cabo Frio, 50 m, 17 October 1975, Staff Instituto de Pesquisas da Marinha, Estaçao de Biologia Marinha. 4 9, YPM, off Rio de Janeiro, May 1934, M. W. Feingold. 1 9, USNM, off Ilha Grande, 23 m, 8 December 1961, Calypso stn 115. 3 9, USNM, off Baía da Ilha Grande, 36 m, 9 December 1961, Calypso stn 122. São Paulo: 3 3, USNM, Ubatuba, 15 m, 10 April 1972, J. de Abreu. 1 3 5 9, MP, S of Ilha de São Sebastiaõ, 25 m, 11 December 1961, Calypso stn 135. 15 3 9 9, USNM, Baía de Santos, 6 September 1964, G. Vazzoler. 4 & 3 9, USNM, Baia de Santos, 29 September 1964, G. Vazzoler. 3 & 3 9, USNM, Baía de Santos, 1 October 1962, G. de Souza Neiva. 3 & 5 9, USNM, Farol de Moela, Santos, 9 September 1964, G. Vazzoler. Paraná: 1 º, USNM, off Paranaguá, Ex. H. Jakobi. Santa Catarina: 37 & 47 9. MP. off Ensenada de Tijucas, 18 m, 16 December 1961, Calypso stn 149. 5 9, USNM, Armação de Piedade, 19 November 1965,

E. Tremel. Rio Grande do Sul: 16  $\diamond$  14  $\heartsuit$ , MP-USNM, off Barra Casino, 21 m, 18 December 1961, *Calypso* stn 153. 1  $\diamond$  1  $\heartsuit$ , USNM, Xuí, 19 m, 8 January 1962, *Calypso* stn 183.

URUGUAY—8  $\delta$  9  $\Im$ , MP-USNM, off Punta del Palmar, Rocha, 20-22 m, 21 December 1961, *Calypso* stn 156. 26  $\delta$  35  $\Im$ , MP, off Punta del Este, 57 m, 21 December 1961, *Calypso* stn 157. 1  $\delta$ , MP, N of La Paloma, 33 m, 21 December 1961, *Calypso* stn 157. 1  $\delta$ , MP, N of La Paloma, 33 m, 21 December 1961, *Calypso* stn 158. 34  $\delta$  63  $\Im$ , MP-USNM, N of Cabo Santa María, 25 m, 8 January 1962, *Calypso* stn 182. 26  $\delta$  48  $\Im$ , MP-USNM, off Laguna Rocha, 30 m, 22 December 1961, *Calypso* stn 161. 7  $\delta$  7  $\Im$ , MP, off Punta Negra, 18 m, 27 December 1961, *Calypso* stn 167. 1  $\delta$  3  $\Im$ , MP, off Maldonado, 115 m, 21 December 1961, *Calypso* stn 160. 1  $\delta$  5  $\Im$ , ANSP, Bahía Maldonado, W. H. Rush. 8  $\delta$  15  $\Im$  syntypes of *Philonicus mülleri*, BMNH, off Montevideo, 13 fm (24 m), 25 February 1876, *Challenger* stn 321.

ARGENTINA—1  $\circ$  3  $\circ$  syntypes of *Parartemesia carinata* Bouvier, MP 49, mouth of Río de la Plata, 44 fm (80 m), Hassler. 13  $\circ$  11  $\circ$ , YPM, "Buenos Aires," 15 June 1936. 2  $\circ$ , USNM, Mar del Plata, 15 December 1922, H. M. Smith. 2  $\circ$  2  $\circ$ , UMML, Mar del Plata, January 1959 Ex. E. Boschi. 2  $\circ$ , Quequén, 7 January 1924, G. Haedo. 1  $\circ$ , USNM, Puerto Madryn, Chubut, Ex. Museo Argentino de Ciencias Naturales. 1  $\circ$  2  $\circ$ , Rawson, Chubut, November 1963, E. Boschi.

Description.-Body robust, integument thick, polished except for dorsally pubescent rostrum, narrow bands of setae flanking middorsal carina of sixth abdominal somite, and similar bands along borders of median and lateral sulci of telson: also broad bands of longer setae flanking paired longitudinal ridges of mesial ramus of uropod. Rostrum horizontal (Figure 37), straight, rather short, not reaching beyond distal 0.3 length of second antennular article, with dorsal margin slightly convex, and ventral margin almost straight, occasionally with apical concavity. Rostral plus epigastric teeth 7-13 (mode 9; N = 200), epigastric tooth separated from first rostral by interval similar to that between first and second, epigastric tooth located at level of dorsal extremity of cervical sulcus and usually fourth tooth at level of orbital margin. Adrostral carina

slender, extending from orbital margin to base of ultimate tooth; postrostral carina strong, long, almost reaching posterior margin of carapace, where flanked by paired depressions. Orbital spine short; broad postorbital, antennal, and hepatic spines moderately long and sharp; ptervgostomian and branchiostegal spines lacking. Cervical sulcus only slightly sinuous, deep, with dorsal extremity situated relatively far from postrostral carina; cervical carina sharp. Hepatic sulcus nearly horizontal from posterior end to depression below hepatic spine, there turning anteroventrally and reaching to pterygostomian region; hepatic carina accompanying anterior part of sulcus sharp; branchiocardiac carina lacking; submarginal carina well marked, horizontal posteriorly, turning anteroventrally at about midlength of carapace and then continuing close to free ventral margin of carapace almost to pterygostomian region.

Eye (Figure 38) with basal article produced distomesially into pubescent, broad scale; ocular peduncle short; cornea broad, greatest diameter slightly less than 2 times that of base of ocular peduncle, its proximal margin moderately slanting posterolaterally.

Antennular peduncle length equivalent to about 0.6 that of carapace; prosartema long, reaching distal 0.4 of second antennular article; stylocerite spiculiform distally, moderately long, its length about 0.65 of distance between its proximal extremity and mesial base of distolateral spine; latter sharp and long. Dorsal flagellum filiform, ventral flagellum broad proximally, tapering distally, and bearing marginal (lateral and mesial) patches of long setae proximally, latter continuous with single row distally; in shrimp 24 mm cl, ratio of length of



FIGURE 37.—Pleoticus muelleri, 9 27.5 mm cl, off Laguna Rocha, Uruguay. Cephalothorax, lateral view.



FIGURE 38.—*Pleoticus muelleri*, 9 33 mm cl, north of Cabo Santa María, Uruguay. Eye.

dorsal and ventral flagella to that of carapace 2.90 and 2.25 respectively and in shrimp 30 mm cl, 2.5 and 2.0. Scaphocerite exceeding antennular peduncle by 0.2 to 0.3 its own length; lateral rib ending in long spine falling short of distal margin of lamella; antennal flagellum almost 3 times total length of shrimp. Third maxilliped reaching almost to distal margin of third antennular article or surpassing it by as much as 0.5 length of dactyl.

First percopod reaching between proximal 0.3 and distal margin of carpocerite. Second pereopod overreaching antennular peduncle by almost length of dactyl or by entire propodus. Third pereopod surpassing antennular peduncle by at least length of dactyl and, at most, by propodus and 0.15 length of carpus. Fourth pereopod exceeding carpocerite by as much as entire length of dactyl. Fifth percopod, longest of all appendages, exceeding antennular peduncle by length of dactyl and 0.15 or 0.20 length of propodus. Order of pereopods in terms of their maximal anterior extensions: first, fourth, second, third, and fifth. First pereopod with spine at midlength of mesial border of basis very long and sharp, and spine on ischium sharp, but smaller than that on basis; second pereopod with setose, squamiform tubercle on distoventral border of coxa, and with long sharp spine on basis. In females, coxa of fifth pereopod produced as rounded, posteromesially directed plate, terminating in tooth anteriorly, plate hinging on horn of posterior plate of sternite XIV; coxa of fourth pereopod narrow, thick, with two rounded mesial projections, base of posterior one hinging on anterior horn of median plate of sternite XIII; coxa of third pereopod produced mesially in subtrapezoidal plate provided with long mesial setae overlapping those of opposite plate, coxa bearing gonopore on dorsomesial surface. In males, coxa of fifth pereopod with large tooth on anterior margin.

Abdomen with middorsal carina along entire length, carina low and rounded from first to third somites (imperceptible in young), and keellike posteriorly; posterodorsal margins of third through fifth somites with median incision; sixth bearing small, sharp spine at posterior end of carina, and small posteroventral spines. Telson with median sulcus moderately deep anteriorly, posteriorly bearing median elevation merging into convex terminal portion; lateral spines moderately long; length of terminal portion about 4 times width at base. Mesial ramus of uropod surpassing apex of telson by 0.15-0.25 of its own length; lateral ramus slightly overreaching mesial ramus and bearing small, terminal distolateral spine.

Petasma (Figure 39A, B) cincinnulate along proximal 0.4 of median line; distal part of ventromedian lobule cornified, forming plate bearing terminal suboval projection and lateral spurlike projection; much of lateral lobe heavily sclerotized, overlapping ventral costa, and with shallow lateral emargination marking base of distal portion; latter flexible, subelliptical, directed toward, and partly covered (dorsally) by, ventromedian lobule; ventral costa bearing membranous flap, broadening distally and terminating in paired unequal convexities; free terminal part of costa forming dorsally directed, strongly curved, sharp projection.

Appendix masculina (Figure 39C, D) elongate, with heavily sclerotized dorsolateral portion and flexible, subelliptical mesial portion. Appendix interna spatulate, embracing ventromesial margin of appendix masculina proximally, and bearing distolateral tuft of rigid, long setae. Basal sclerite with deep distolateral groove along base of sharp dorsal ridge; ventrolateral spur relatively short.

Thelycum (Figure 40) microscopically setosepunctate, with posterior plate on sternite XIV often divided by median longitudinal groove, and bearing lateral elevations terminating anteriorly in small knob; short anterior part of sternite XIV heavily sclerotized, forming slightly convex,



FIGURE 39.—Pleoticus muelleri, & 20 mm cl, off Laguna Rocha, Uruguay. A, Petasma, dorsal view. B, Ventrolateral view of left half. C, Right appendices masculina and interna, lateral view. D, Mesial view.



FIGURE 40.—*Pleoticus muelleri*, 9 43 mm cl, off Praia de Santana, Espírito Santo, Brazil. Thelycum, ventral view.

paired plates, each bearing pair of minute tubercles. Median plate of sternite XIII elevated laterally in ribs ending anteriorly in blunt horns, and armed with strong, blunt, setose median projection; latter flanked anteriorly by setose protuberances borne on articular membranes of fourth pereopods; sternite XII markedly convex, its strong transverse marginal ridge with deep median depression and blunt, lateral, posteriorly directed horns.

Color.-Pale yellow or yellowish red to tomato red (Boschi and Angelescu 1962); reddish orange of various shades in different areas of the body (Boschi 1963); wine-red in young from 50 mm tl through adulthood (Iwai 1973).

Maximum size.-Males: 37.5 mm cl; females: 58 mm cl.

Geographic and bathymetric ranges.-From off Praia de Santana, about 20°S, 40°W, Espírito Santo (data on label accompanying two specimens collected by Getulio de Souza Neiva), south to the northwestern portion of the Golfo de San Jorge, Comodoro Rivadavia (Figure 34). It occurs most

abundantly in littoral waters at depths between 2 and 20-30 m (Figure 9), and rarely as deep as 80-100 m (Angelescu and Boschi 1960; Boschi and Scelzo 1969a), and from near the shoreline to 0.5 km offshore, occasionally as far as 56 km (Angelescu and Boschi 1960). This species was reported by Iwai (1973) to range north to 21°36'S, the first record north of Ilha Santana, 22°25'S, Rio de Janeiro, where da Silva (1965) had reported a fishery for this shrimp. The specimens taken at Praia de Santana, Espírito Santo, about 178 km north of the locality where Iwai recorded the species, have confirmed the presence of H. muelleri beyond the state of Rio de Janeiro. The southernmost limit of the species given above is based on Boschi and Scelzo (1969a), who identified a number of large specimens caught in the Golfo de San Jorge at a depth of 80 m.

Affinities.-Pleoticus muelleri has its closest affinities with its Atlantic congener P. robustus, but it may be readily separated from it by its almost entirely glabrous body, long prosartema, which may overreach the midlength of the second antennular article, the absence of branchiostegal spines and the presence of orbital spines. Also it may be distinguished by the disposition of the submarginal carina, the posterior part of which is horizontal and situated far from the free ventral border of the carapace, instead of extending subparallel to that border as it does in all other species of this generic complex. The external genitalia of the two are also markedly different, as pointed out under P. robustus. In the petasma of P. muelleri the ventromedian lobule is cornified distally, terminates in a rounded to ovate platelike projection which bears at its base a spurlike projection, and the ventral costa is produced into a dorsally directed hook. The thelycum, in turn, exhibits paired short plates on the anterior part of sternite XIV, each bearing a pair of minute knobs, and also an exceedingly strong projection on the median plate of sternite XIII.

Spermatophore.-Compound spermatophore (Figure 41) consisting of broad geminate body with angular hump at about midlength, and bearing small pair of wings anterolaterally; also provided with large, highly sculptured midlateral flaps, and pair of broad, posterolateral flanges. Thick, opaque ventral wall of each spermatophore (Figure 42A) truncate, lacking anterior lobe, broadened and swollen at about midlength forming hump; area posterior to hump dorsally depressed, and strengthened by longitudinal ridge. Lateral wall mostly thick, concave, and insensibly continuous with wing anteriorly, merging with broad, subrectangular flap, and posteriorly bearing prominent longitudinal ridge parallel to that of ventral wall. Dorsomesial wall largely translucent, but heavily sclerotized and opaque mesially forming axial part of complex armature (Figure 42C). Latter bearing three transverse ribs: 1) anterior, forming arc, with one arm (ventral) strengthening ventral hump and another running across dorsomesial wall, then ending in foliaceous process; 2) intermediate, close to former, very strong, tonguelike, and deeply excavated; 3) posterior, forming shelf projecting inside lumen of sperm sac from dorsomesial wall. Wing short, broad, and flexible except for posterior thickening running along its entire length. Anterior part of flap broad, subrectangular, elevated in marginal



FIGURE 41.—Pleoticus muelleri. Compound spermatophore attached to female,  $\Im$  37 mm cl, Rawson, Chubut, Argentina (setae omitted).



FIGURE 42.—Pleoticus muelleri,  $\delta$  37 mm cl, off Buenos Aires Province, Argentina. A, Right spermatophore dissected from terminal ampulla, ventrolateral view. B, Dorsomesial view. C, Left spermatophore dislodged from female,  $\Im$  59 mm cl, Puerto Madryn, Chubut, Argentina.

ridge continuous with hump; posterior part narrow, extending as flexible band joining flange. Flange short, with broad mesial base and sinuous lateral margin. Dorsal plate (Figure 42B) large, extending almost from anterior extremity of spermatophore to base of flange, and irregular in contour.

Compound spermatophore applied to thelycum much as it is in *P. robustus*. Anterior extremity of geminate body lying opposite female gonopores, with wings attached to ventral articular membranes of third percopods. Ventral walls fused mesially while lateral walls diverge dorsally becoming affixed to sternite XIII, their lateral margins embracing mesial prominences of dorsal articular membranes of fourth pereopods. Strong humplike prominences projecting ventrally from sternite XIV, latter serving as place of attachment for broad anterior parts of flaps as well as for intimately fused dorsal plates. From humplike prominences, compound spermatophore sloping posterodorsally, and held in position by paired flanges affixed to ventral articular membranes of fifth pereopods.

The sperm is freed from each sac through an anterior rupture of dorsomesial wall, close to corresponding gonopores. The gelatinous substance which accompanies the sperm within the sperm sac may be observed covering the gonopores in Figure 41. Spermatophore-bearing females are not infrequent in collections; it seems that the spermatophores in this species as in *P. robustus*, which are also exceedingly large, become firmly anchored to the thelycum. According to Angelescu and Boschi (1960), the spermatophores in recently caught impregnated females are light green.

Postembryonic stages.-Boschi and Scelzo (1969a) prepared illustrated keys for the identification of larvae of the three more common Penaeidea in the waters off Argentina. These keys include diagnoses of protozoeae, mysis, and postlarvae of *P. muelleri* based both on specimens caught in plankton samples and others reared in the laboratory. Later, Scelzo and Boschi (1975) presented the results of their successful rearing of this shrimp from eggs spawned in the laboratory to

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juveniles of an average total length of 21.3 mm. They stated that spawning generally took place the night following the capture of mature females, and eggs hatched between 12 and 24 h (according to the temperature) after being released. The young passed through 6 nauplii, 3 protozoeae, 3 mysis, and an undetermined number of postlarvae before becoming juveniles. The larval development was completed in 19-23 days at 19.0°-23.5°C and juveniles reached 21.3 mm (average) in 81 days after hatching. In more recent experiments, Boschi and Scelzo (1976) found that, at 24°C, P. muelleri attained an average of 61 mm tl and 2.7 g in 180 days after hatching. The studies mentioned above are the only ones that have been made on the development of any of the 12 species treated here.

Remarks.-Much of our knowledge of the morphology of this species is due to the study of Angelescu and Boschi (1960) and their subsequent contribution (Boschi and Angelescu 1962). These authors presented detailed accounts of the external and internal anatomy, and included outlines and a brief description of the "green" spermatophores on the female. In addition, they calculated the rate of growth of the species in Argentinian waters, studied the development of the testis and ovaries, and determined that the spawning season there extends from December to February (i.e., through the summer months). Furthermore, they found that it feeds on organic detritus as well as on small animals, such as sergestids and polvchaetes, and plants.

*Ecological notes.-Pleoticus muelleri* is the only species of the genus which frequents shallow littoral waters; it even invades seawater channels and rías like those in the vicinity of Bahía Blanca, Buenos Aires, where, according to Boschi (1963), the "langostino" is trapped in weirs by the fishermen. Furthermore, this shrimp not only inhabits such shallow waters, but occurs in sufficient abundance to support commercial exploitation in many areas.

This species completes its entire life cycle in the sea but, as stated above, may frequent inshore waters of high salinity. It occupies tropical and subtropical waters off Brazil, where surface temperatures are as high as 25°-27°C during the warm months of the year, and 16°-17°C during the cold ones; farther south, off Argentina, it occurs in temperate waters where surface temperatures range between  $10^{\circ}$  and  $23^{\circ}$ C during the summer, and  $5^{\circ}$  and  $10^{\circ}$ C during the winter (Boschi 1964).

This shrimp lives on mud and sand bottoms.

Economic importance.-Pleoticus muelleri is taken commercially from Ilha Santana, Rio de Janeiro, to Punta Clara, Chubut. Significant catches, however, are made only from Santa Catarina to Punta Clara, and the largest fisheries are in Argentinian waters (Boschi 1964), between Punta Rasa (province of Buenos Aires) and Punta Clara, i.e., between 41° and 44°S. This species constitutes the largest percentage of the shrimp landings (which also include Artemesia longinaris Bate 1888) in Argentina.

### Hadropenaeus New Genus

- Hymenopenaeus. Smith 1885:179 [part]. Burkenroad 1936:102 [part]. Kubo 1949:212 [part].
- Philonicus Bate 1888:273 [part].

Pleoticus Bate 1888:xii [part].

Haliporus. Bouvier 1906b:1 [part]; 1908:78 [part]. A. Milne Edwards and Bouvier 1909:206 [part]. de Man 1911:31 [part].

Diagnosis.-Body stout, carapace proportionately short, integument moderately thick, firm, Rostrum short, not overreaching distal margin of first antennular article, deep, ventral margin pronouncedly convex; armed only with dorsal teeth; epigastric tooth and first rostral separated by interval equal to, or only slightly greater than, that between first and second rostral teeth. Orbital and pterygostomian spines absent; postorbital, antennal, hepatic, and branchiostegal spines present. Cervical sulcus long, almost reaching middorsum of carapace; hepatic sulcus deep; branchiocardiac sulcus and carina absent, posthepatic and submarginal carinae absent. Abdomen carinate dorsally from third through sixth somites. Telson with pair of conspicuous. fixed, lateral spines. Prosartema long, flexible. Antennular flagella longer than carapace, usually subcylindrical, ventral flagellum occasionally depressed. Mandibular palp two jointed, articles moderately broad, distal one as long as or slightly shorter than basal, and tapering to blunt apex. First maxilla with unsegmented palp (endite of basis) gently narrowing to rounded apex. Fifth percopod subflagelliform and considerably longer than fourth. First percopod with spine on basis,

ischium, and merus. Exopods on all maxillipeds and pereopods. Lateral ramus of uropod armed with distolateral spine reaching distal margin of lamella (terminal spine). In males, petasma with ventral costa free from heavily sclerotized, platelike terminal part of ventrolateral lobule; ventromedian lobule broadly expanded distally. Endopod of second pereopod bearing appendices masculina and interna, and with basal sclerite produced distally into elongate ventrolateral spur. Thelycum of open type, not enclosing seminal receptacle. Pleurobranchia on somites IX to XIV; single rudimentary arthrobranchia on VII, and anterior and posterior arthrobranchiae on somites VIII to XIII; podobranchia on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

*Hadropenaeus* is an extremely homogeneous genus, the three known species being quite similar.

- Type-species.-Hymenopenaeus modestus Smith 1885.
- *Etymology.*—From the Greek *hadros*, stout, in combination with the generic name *Penaeus*, alluding to the comparatively short and thick carapace.

Gender.-Masculine.

List of species.-Amphi-Atlantic: Hadropenaeus affinis (Bouvier 1906b). Western Atlantic: Hadropenaeus modestus (Smith 1885). Indo-West Pacific: Hadropenaeus lucasii (Bate 1881).

Affinities.-The members of Hadropenaeus resemble those of *Pleoticus* (as here defined) in having the epigastric tooth separated from the first rostral by an interval equal to, or only slightly greater than, that between the first and second rostral teeth, in lacking both branchiocardiac and posthepatic carinae, and in possessing a petasma in which the ventral costa is free from the platelike, terminal part of the ventrolateral lobule. However, Hadropenaeus differs from Pleoticus (as well as from the other closely related genera except Mesopenaeus) in the proportionately higher carapace, in the shape of the rostrum which is short, deep, and possesses a strongly convex ventral margin, and in lacking submarginal carinae.

The members of this genus are closely allied to those of *Mesopenaeus*. They share a stout appearance, short, deep rostrum in which the ventral margin is convex, similar arrangement of the epigastric and rostral teeth, and they lack branchiocardiac sulci and carinae. Furthermore, the ventral flagellum, which is typically flattened in Mesopenaeus, is occasionally depressed in one species of Hadropenaeus; the depressed flagellum seemingly represents the first step in a process of specialization which progressed through the flattened ventral flagellum in Mesopenaeus, and culminated in the two lamellate flagella (both ventral and dorsal) in Solenocera. Hadropenaeus. in contrast to Mesopenaeus, lacks submarginal carinae and orbital spines; it possesses branchiostegal spines and, most significantly, exhibits a petasma in which the ventral costa is free from the terminal part of the ventrolateral lobule.

## Key to Species of Hadropenaeus

- - Rostrum with conspicuous carina dorsal to adrostral one. Thelycum with median protuberance on sternite XIV low, not projecting ventrally as far as posterior convexities of sternite XIII; latter with median, keellike ridge lacking tooth anteriorly. Petasma with ventromedian lobule not produced into distolateral projection ....

2. Scaphocerite reaching distal end of antennular peduncle or overreaching it by not more than 0.1 of its own length. Prosartema extending only to distomesial extremity of first antennular article. Thelycum with median protuberance on sternite XIV projecting ventrally, and tooth of median keel of sternite XIII directed anteriorly. Petasma with distomesial projection of PEREZ FARFANTE: AMERICAN SOLENOCERID SHRIMPS

ventromedian lobule directed mesially

H. affinis Scaphocerite overreaching antennular peduncle by about 0.25 of its own length. Prosartema conspicuously overreaching distomesial margin of first antennular article. Thelycum with median protuberance on sternite XIV projecting anteriorly, and tooth of median keel of sternite XIII directed ventrally or posteriorly. Petasma with distomesial projection of ventromedian lobule directed distally.....

.....H. modestus

Hadropenaeus affinis (Bouvier 1906)

Figures 9, 43, 44A, 45-49

- Haliporus modestus Bouvier 1905a:980. [Not Hymenopenaeus modestus Smith 1885.]
- Haliporus affinis Bouvier 1906b:4 [syntypes: 1 & 2 & 4 & 4 & 4 & 2 & 2 & 2 & MP; type-locality: off Cape Verde Is, 16°53'N, 25°10'W, 410-460 m, 29 July 1883, Talisman stn 116. Unrecorded number of syntypes from off Cape Verde Is, "100 m" from uncited Talisman station. 1 & 3, MCZ 7196, off Barbados, 188 m, 5 March 1879, Blake stn 273, 13°03'05"N, 59°36'18"W]. Bouvier 1908:80. A. Milne Edwards and Bouvier 1909:209. de Man 1911:7.

Hymenopenaeus affinis. Burkenroad 1936:104. Crosnier and Forest 1973:258, fig. 82b, 84, 94d.

Hymenopenaeus modestus. Bullis and Thompson 1965:5 [part]. [Not Hymenopenaeus modestus Smith 1885.]

#### Material

UNITED STATES—North Carolina: 2  $\circ$ , UNC-IMS, SE of Cape Lookout, 229 m, 8 June 1949, Albatross III stn 21-4. 3  $\circ$  14  $\circ$ , USNM, E of Port Fisher, 366 m, 15 November 1956, Combat stn 177. 2  $\circ$  1  $\circ$ , UNC-IMS, about 111 km SE of Cape Fear, 412-369 m, 23 June 1956, Pelican stn 75. South Carolina: 2  $\circ$ , USNM, E of Cape I, 366 m, 20 April 1957, Combat stn 288. Florida: 1  $\circ$ , USNM, off Hobe Sound, 302-285 m, 21 May 1968, Gerda stn 997. 1  $\circ$ , USNM, off Boca Raton, 366 m, 29 March 1956, Pelican stn 17. 1  $\circ$ , USNM, SE of Key Largo, 185 m, 22 January 1965, Gerda stn 452. 1  $\circ$ , USNM, Sof Pine Is, 293-302 m, 25 February 1969, Gerda stn 1029. 2  $\circ$ , USNM, NW of Double Headed Shot Cays, 223 m, 29 August 1967, Gerda stn 864. 1  $\circ$ , USNM, NW of Charlotte Harbor, 366 m, 21 August 1970, Oregon II stn 11180.

BAHAMA ISLANDS—1 &, RMNH, NW of Matanilla Reef, 549-567 m, 1 July 1963, Gerda stn 179. 1 &, USNM, NW of Matanilla Reef, 466-417 m, 30 September 1967, Gerda stn 935. 1  $\circ$ , USNM, NW of Matanilla Reef, 421 m, 3 February 1957, Combat stn 238. 1  $\circ$ , USNM, N of Matanilla Reef, 393 m, 3 February 1957, Combat stn 237. 2  $\circ$ , RMNH, W of Bimini Is, 452-474 m, 30 January 1964, Gerda stn 234. 3  $\circ$ , USNM, SW of Bimini Is, 403-421 m, 30 January 1964, Gerda stn 233. 5  $\circ$ , RMNH, off Gun Cay, 439-421 m, 29/30 January 1964, Gerda stn 232. 1  $\circ$ , USNM, SW of Gun Cay, 312-348 m, 30 March 1964, Gerda stn 274. 1  $\circ$  1  $\circ$ , USNM, Santaren Channel, 384-366 m, 6 November 1960, Silver Bay stn 2468. 1  $\circ$ , USNM, Santaren Channel, 412-220 m, 22 June 1967, Gerda stn 820. 1  $\circ$ , USNM, S of Great Inagua, 311 m, 13 December 1969, Oregon II stn 10849.

PUERTO RICO-3 9, USNM, Mona Passage, 366 m, 17 October 1963, Silver Bay stn 5190.

HAITI—1  $\Im$  juv, USNM, W of Anse d'Hainault, [?] 77 m, 2 July 1970, *Pillsbury* stn 1186.

LESSER ANTILLES—1 &, USNM, E of Rivière Pilote, Martinique I, 170-214 m, 9 July 1969, *Pillsbury* stn 907. 1 &, USNM, SE of Georgetown, St Vincent I, 165-201 m, 6 July 1969, *Pillsbury* stn 874. 1 & syntype + 1 &, MCZ 7196, off South Point, Barbados, 188 m, 5 March 1879, *Blake* stn 273.

WESTERN CARIBBEAN—2  $\delta$  4  $\circ$ , USNM, Arrowsmith Bank, 311-146 m, 28 January 1968, Gerda stn 954. 1  $\circ$ , USNM, Arrowsmith Bank, 307-192 m, 28 January 1968, Gerda stn 951. 1  $\delta$ , UMML, Arrowsmith Bank, 252-293 m, 14 March 1968, Pillsbury stn 591. 2  $\delta$  2  $\circ$ , USNM, Arrowsmith Bank, 155-205 m, 15 March 1968, Pillsbury stn 598. 1  $\delta$ , USNM, W of I de Providencia, 289-274 m, 4 February 1967, Oregon stn 6423.

MEXICO—Quintana Roo: 1  $\eth$  juv, UMML, SE of Isla Mujeres, 241-320 m, 10 September 1967, Gerda stn 893. 1  $\heartsuit$ , UMML, SE of Isla Mujeres, 210-366 m, 23 August 1970, Gerda stn 1286. 3  $\heartsuit$ , USNM, off Puerto de Morelos, 165-168 m, 10 September 1967, Gerda stn 899.

PANAMA—1 9, USNM, off Caribbean coast of Panama, 274 m, 5 July 1972, *Canopus*.

PORTUGAL—Cape Verde Is: 1 3 2 9, 4 3 4 9, 2 3 2 9 syntypes, MP, 410-460 m, 29 July 1963, *Talisman* stn 116.

Description.-Body stout (Figure 43), integument moderately thick, firm. Carapace with restricted pubescent areas, setae dense and long at base of rostrum, on pterygostomian region, and in patch extending from orbital margin to epigastric tooth; minute, sparsely set setae on dorsum and hepatic region. Abdomen polished, almost entirely naked except for setae on posterior part of dorsal keel; telson and mesial ramus of uropod rather densely pubescent. Rostrum short, its length 0.20-0.25 that of carapace, falling short of distal margin of first antennular article, almost horizontal, with dorsal margin straight and ventral margin strongly convex, with subapical concavity giving rise to saber-shaped tip; latter almost 0.4 length of rostrum. Rostral plus epigastric teeth 5-7 (mode 6; N = 60), base of third rostral tooth at level of orbital margin. Adrostral carina extending from orbital margin to ultimate tooth; more dorsal barely perceptible carina extending from second to ultimate rostral tooth; postrostral



FIGURE 43.-Hadropenaeus affinis, 9 21.5 mm cl, Mona Passage, off Puerto Rico. Lateral view (third pereopod slightly raised).

carina ending immediately posterior to cervical sulcus. Orbital margin produced anteriorly into ventrally inclined, short shelf. Postorbital spine, longest of four lateral spines on carapace, located dorsal to base of small antennal spine; branchiostegal and hepatic spines sharp. Cervical sulcus deep, ending dorsally just posterior to midlength of carapace, and close to postrostral carina; cervical carina sharp; hepatic sulcus subhorizontal posteriorly, inclined anteroventrally from depressed area below hepatic spine to pit below branchiostegal spine.

Eye (Figure 44A) with basal article produced distomesially into pubescent, elongate scale; ocular peduncle moderately long, bearing minute tubercle; cornea broad, greatest diameter 1.5-1.9 times that of base of ocular peduncle, strongly slanting posterolaterally.

Antennular peduncle length equivalent to 0.65 that of carapace; prosartema falling short, or barely reaching, distomesial margin of first article; stylocerite length about 0.65 of distance between lateral base of first article and base of distolateral spine, terminating in sharp spine; distolateral spine very slender and long, conspicuously surpassing proximal margin of second article. Antennular flagella long, length of dorsal flagellum 2.2 and 1.9 times carapace length in shrimp 8 and 23 mm cl, respectively; ventral shorter and broader than dorsal, gently tapering distally, and armed with marginal rows of long plumose setae. Scaphocerite extending to distal margin of antennular peduncle or exceeding it by less than 0.1 of its own length; lateral rib ending in slender spine, reaching to or very slightly beyond distal margin of lamella. Antennal flagellum long, although incomplete in all specimens examined, longest observed by me 3 times total length of shrimp. Mandibular palp (Figure 45A) moderately broad, distal article slightly shorter than basal. First maxilliped as illustrated (Figure 45B); rudimentary arthrobranchia of corresponding somite VII situated near its base (Figure  $45c-c^{1}$ ). Third maxilliped exceeding antennular peduncle by length of dactyl and half or as much as entire length of propodus.



FIGURE 44.—Eyes. A, Hadropenaeus affinis, 21 mm cl, southeast of Cape Lookout, N.C. B, Hadropenaeus modestus,  $\delta$ 11 mm cl, southwest of Dry Tortugas, Fla. C, Hadropenaeus lucasii, 18 mm cl, Pailolo Channel, Hawaiian Islands.

First percopod, stoutest of all, reaching at least basal 0.65 length of carpocerite, and, at most, exceeding it by tip of dactyl. Second percopod moderately stout, extending to distal end of carpocerite or exceeding it by as much as entire propodus. Third pereopod surpassing antennular peduncle by length of dactyl or by entire propodus. Fourth percopod exceeding antennular peduncle by dactyl and 0.2-0.6 length of propodus; length of dactyl about 0.4 that of propodus; length of carpus about 1.25 times that of merus. Fifth percopod slender and long, overreaching antennular peduncle at least by length of dactyl and propodus. or by as much as their length and almost 0.3 length of carpus. Order of pereopods in terms of their maximal anterior extensions: first, second, fourth, third (occasionally third, fourth), and fifth. First percopod with very long, slender spine on basis, small spine on distomesial margin of ischium, and small one near midlength of mesial margin of merus. Second pereopod with long spine on basis. Coxa of fourth and fifth percopods in males armed with anterior spine. Coxa of fifth pereopod in females produced mesially into short plate bearing sharp spine anteromesially.

Abdomen with middorsal keel from fourth through sixth somites; low rounded carina sometimes present on third; posterodorsal margin of third, fourth, and fifth somites with median incision; sixth somite bearing sharp spine at pos-



FIGURE 45.—Hadropenaeus affinis,  $\Im$  21.5 mm cl, southeast of Cape Lookout, N.C. A, Mandible. B, First maxilliped. c, Arthrobranchia.  $c^1$ , Enlargement of c (all from left side).

terior end of keel, and minute spine at posteroventral angles. Telson (Figure 46A) pubescent except for median sulcus and terminal portion; sulcus deep anteriorly, increasingly shallow posteriorly, ending before reaching lateral spines; spines long, their length 1.6-1.9 basal width of terminal portion; latter long, length 3.5-4.5 times basal width; mesial ramus of uropod barely overreaching apex of telson, or exceeding it by about 0.15 of its own length; lateral ramus distinctly surpassing mesial, and armed with small, distolateral spine, projecting beyond contiguous distal margin of ramus.

Petasma (Figure 47A, B) cincinnulate along proximal 0.65 of median line; broad distal part of ventromedian lobule strongly produced into elongate, distally directed distomesial projection, and short distolateral projection; entire terminal margin of lobule spinulous; distal part of ventrolateral lobule heavily sclerotized, forming plate, with border adjacent to ventral costa bearing



FIGURE 46.—Telsons. A, Hadropenaeus affinis,  $\Im$  20 mm cl, southwest of Bimini Islands, Great Bahama Bank. B, Hadropenaeus modestus,  $\Im$  19 mm cl, west of Isla de Providencia, western Caribbean.

emargination delimiting basal part from subovate terminal part; latter strongly inclined toward, and partially covered by, ventromedian lobule, and armed with minute spinules along ventral margin; ventral costa with distal part free from contiguous plate, bent outward and bearing spinules on distalmost margin.

Appendix masculina (Figure 47C, D) with proximal part broad, strongly produced mesially into thickened lobe, and bearing long setae along lateral margin; distal part narrow, strongly turned laterally, with apical portion armed with tuft of long setae; appendix interna shorter than appendix masculina, narrow, sinuous, and bearing apical tuft of long setae. Ventrolateral spur large, subelliptical to paddlelike.

Thelycum (Figure 48A, B) with median protuberance on sternite XIV subconical, its apical portion directed anteriorly or ventrally and produced into spinelike projection; protuberance situated distinctly posterior to prominent, setose, paired convexities of posteriormost part of sternite XIII; longitudinal median keel on sternite XIII produced anteriorly into anteriorly directed blunt tooth, its cephalic margin concave, its posterior margin convex.

*Photophores.*-Paired photophores situated on posterolateral margins of sternites X through XIII just mesial to coxae of first four pairs of pereopods.

Color.-Color notes made by Lipke B. Holthuis (pers. commun.) on a male caught southeast of Georgetown, St. Vincent Island, at *Pillsbury* stn 874, state that the shrimp was "uniformly red, with darker bands parallel to the posterior margins of the abdominal terga."

The following description is based upon a freshly caught specimen observed by me during a 1969 cruise of *Oregon II*, south of Great Inagua Island, Bahamas. Body translucent pinkish orange, with gnathal appendages, and pereopods reddish orange. Carapace with milky white subtriangular patch lying immediately dorsal to hepatic spine, its broad base abutting cervical sulcus; small, middorsal, diamond shaped marking (formed by white lines) just posterior to midlength of carapace; anterolateral sides of marking continuing posterolaterally in dorsalmost arm of transverse, strongly sinuous, opaque white, narrow band; ventral arm of U-shaped dorsal portion of band extending anteriorly to cervical sulcus, PEREZ FARFANTE: AMERICAN SOLENOCERID SHRIMPS



FIGURE 47.—Hadropenaeus affinis, & 16 mm cl, about 11 km southeast of Cape Fear, N.C. A, Petasma (partly bent laterally), dorsal view of right half. B, Ventral view. C, Right appendices masculina and interna, dorsal view. D, Ventromesial view.

there turning caudad reaching posterior end of hepatic sulcus; middorsal patch of white specks extending from posterior sides of diamond to posterior margin of carapace. First five abdominal somites with reddish orange band along posterior margin of tergum, band broader dorsally, tapering posteroventrally to level of articular knob, then extending anteroventrally to about mid-



length of ventral margin of pleuron and from there anteriorly to ventral angle of latter.

Maximum size.-Males: 15 mm cl, about 66 mm tl; females: 23 mm cl, about 82 mm tl.

Geographic and bathymetric ranges.-In the western Atlantic: from off Cape Lookout, N.C. (34°15'N, 75°58'W), southward to the Straits of Florida, in the northeastern part of the Gulf of Mexico (northwest of Charlotte Harbor, Fla.), and throughout the Caribbean. In the eastern Atlantic: off Cape Verde Islands (Figure 49). This species has been found at depths between 165 and 570 m (Figure 9), with one dubious record from Haiti at 77 m.

Affinities.-Hadropenaeus affinis, which is amphi-Atlantic, and H. modestus, found only in the western Atlantic, are closely allied, but can be distinguished by the characters presented in Table 1.

Burkenroad (1936), for unexplained reasons,

expressed doubt that H. affinis is different from H. modestus, an opinion apparently shared by Bullis and Thompson (1965) who recognized only H. modestus in their western Atlantic collections. I have examined part of their material and found that it also includes H. affinis. On the basis of the original description of H. modestus (Smith 1885), Bouvier (1906b) distinguished H. affinis from the former species by six features. I have found that two of them are diagnostic: the relative length of the scaphocerite, and the ratio length of dactyl/length of propodus of the fourth pereopod (see Table 1). The number of rostral teeth is not 7 in H. modestus as Smith indicated, but 6 in all specimens I have examined, the number usually possessed by H. affinis. The relative length of the antennular flagella, which Bouvier indicated was greater in H. affinis, varies within a given length of carapace, and may be the same in animals of the two species, e.g., 1.9 times carapace length in shrimp 23 mm cl. The carpus of the fourth percopod is longer than the merus in both species, and not shorter in H. modestus, as Bou-



FIGURE 49.—Ranges of Hadropenaeus affinis and Hadropenaeus modestus based on published records and specimens personally examined.

Feature	H. affinis	H. modestus
Scaphocerite	Reaching distal end of antennular peduncle or surpassing it by less than 0.10 of its own length	Surpassing antennular peduncle by as much as 0.25 of its own length
Prosartema	Extending only to distomesial extremity of first antennular article	Conspicuously overreaching distomesial extremity of first antennular article
Fourth pereopod	Extending farther anteriorly than third pereopod; surpassing antennular peduncle by as much as length of dactyl and that of propodus; length of dactyl less than 0.5 that of propodus	Not extending so far anteriorly as third pereopod, reaching at most distal end of first antennular article; length of dactyl greater than 0.5 that of propodus
Coxa of fifth pereopod in females	Bearing strong anteromesial spine	Lacking anteromesial spine in adult, occasionally with in- conspicuous one in juvenile
Terminal portion of telson	Long, length 3.5-4.5 its basal width	Short, length 2.5-3.3 its basal width
Telsonic spines	Long, length more than 1.5 basal width of terminal portion of telson	Short, length not more than basal width of terminal portion of telson
Telsonic pubescence	Extensive, lacking on terminal portion	Limited to paired rows flanking median sulcus and lateral margins
Petasma	Ventromedian lobule with distomesial projection directed mesially; distal part of dorsolateral lobule subelliptical	Ventromedian lobule with distomesial projection directed distally, distal portion of dorsolateral lobule subrectangular
Thelycum	Protuberance of sternite XIV mammiform, with apical part directed ventrally; median keel of sternite XIII produced into anteriorly directed blunt tooth	Protuberance of sternite XIV subovate, with apical part di- rected anteriorly; median keel of sternite XIII produced into ventrally or posteriorly directed blunt tooth

TABLE 1.—Characteristics distinguishing Hadropenaeus affinis from H. modestus.

vier calculated from Smith's erroneous data. Finally, the lateral ramus of the uropod is similar in shape in the two species, its distal part truncate and turning gently proximomesially. The descriptions of both the petasma and the thelycum of H. affinis presented by A. Milne Edwards and Bouvier (1909), together with the two diagnostic characters mentioned above, adequately diagnose the species.

Specimens from various localities in the western Atlantic exhibit differences in the shape of coxal spine of the fifth percopod which varies from nearly blunt to sharply acute. Also in the sculpture of the thelycum, the apical portion of the protuberance on sternite XIV may be directed anteriorly or ventrally. The observed variations, however, intergrade and, furthermore, in some specimens the shape of the spine and the direction of the protuberance are identical to those exhibited by the syntypic material.

*Remarks*.-The numerous records cited above are the first from the western Atlantic since Bouvier (1906b) cited a syntypic male from off Barbados (*Blake* stn 273) in the original description of the species, and A. Milne Edwards and Bouvier (1909) recorded an additional juvenile male, which had been taken with the syntype.

The presence of photophores on the thoracic sternites of this species is revealed here for the first time. The photophores were observed in a recently caught specimen obtained from the Oregon II, south of Great Inagua, Bahamas; they are similar to those described by Burkenroad (1936) in Hymenopenaeus debilis. Hadropenaeus modestus (Smith 1885)

#### Figures 9, 44B, 46B, 49-52

- Hymenopenaeus modestus Smith 1885:183 [holotype: <sup>Q</sup> USNM 7267; type-locality: off Bethany Beach, Del., 38°31'N, 73°21'W, 156 fm (285 m), Fish Hawk stn 1047]. Burkenroad 1936:104. Bullis and Thompson 1965:5 [part]. Crosnier and Forest 1973:259.
- Haliporus modestus. Bouvier 1905a:980; 1906b:4; 1908:80. A. Milne Edwards and Bouvier 1909: 209. de Man 1911:7. Fowler 1912:543.

#### Material

UNITED STATES-Delaware: 9 holotype, USNM 7267. off Bethany Beach, 285 m, 10 October 1881, Fish Hawk stn 1047. North Carolina: 1 J, USNM, SE of Cape Lookout. 348-384 m, 13 November 1956, Combat stn 171. 1 S. USNM. SE of Cape Lookout, 329 m, 1 February 1972, Oregon II stn 11762. 1 & 2 9, USNM, SE of Cape Fear, 187-190 m, 29 February 1960, Silver Bay stn 1693. Georgia: 1 9, USNM, off Ossabaw, 238 m, 21 January 1972, Oregon II stn 11720. Florida: 1 &, USNM, off Melbourne Beach, 329 m, 31 January 1957, Combat stn 226. 1 9, USNM, off Hobe Sound, 302-285 m. 21 May 1968, Gerda stn 997. 1 9, AMNH, 21 km E of Boynton, 320-266 m, 17 May 1948, Burey. 1 9, RMNH, off Miami, 418 m, 27/28 August 1962, Gerda stn 53. 1 9, RMNH, E of Old Rhodes Key, 146 m, 25 September 1964, Gerda stn 427. 2 9, USNM, off Elliott Key, 194-187 m, 25 August 1967, Gerda stn 857, 1 9, UMML, NE of Key Largo, 265-275 m, 24 January 1964, Gerda stn 229. 3 8 3 9, USNM, SE of Key Largo, 185 m, 22 January 1965, Gerda stn 452. 1 ♀, RMNH, SW of Marquesas Keys, 188-199 m, 28 November 1964, Gerda stn 432. 1 d, USNM, SW of Marquesas Keys, 177-229 m, 26 April 1969, Gerda stn 1087. 1 Å, UMML, S of Dry Tortugas Is, [?] 68 m, 12 April 1965, Gerda stn 564. 1 9, USNM, SW of Dry Tortugas. 348 m, 13 April 1954, Oregon stn 1005. 1 part of carapace.

USNM, NW of Charlotte Harbor, 274 m, 22 August 1970, Oregon II stn 11181.

BAHAMAS—2  $\Im$ , RMNH, W of Gun Cay I, 458-531 m, 30 January 1964, Gerda stn 242. 1  $\Im$ , RMNH, N of Double

Headed Shot Cays, 443 m, 27 January 1965, Gerda stn 483.

LESSER ANTILLES.—3 & 1 \, USNM, E of The Grenadines, 357-658 m, 4 July 1969, *Pillsbury* stn 861.

WESTERN CARIBBEAN-1 <sup>Q</sup>, USNM, W of Old Providence I, 549 m, 12 September 1957, *Oregon* stn 1918.

PANAMA-1 9, USNM, Golfo de los Mosquitos, 274-293 m, 31 May 1962, Oregon stn 3597.

VENEZUELA—1 ♀, USNM, E of Península de Paraguaná, 366 m, 4 October 1963, Oregon stn 4421. 1 ♂, USNM, off San Juan de los Cayos, 384 m, 9 October 1963, Oregon stn 4440.

TRINIDAD - TOBAGO-2 3, USNM, NW of Tobago, 146 m, 2 July 1969, Pillsbury stn 848.

BRAZIL—Alagoas: 1 3, BMNH, off Barra Grande, 10 September 1873, Challenger stn 122-122C.

Description.-Carapace (Figure 50) finely pubescent; setae dense and long on base of rostrum, gastric, and epigastric regions; small setae on cardiac region, and minute ones sparsely set on hepatic and branchial regions; abdomen polished, and almost entirely naked except for setae on posterodorsal keel; pubescence of telson as in Figure 46B. Rostrum short, its length 0.25-0.30 that of carapace, reaching little beyond midlength of first antennular article, almost horizontal, with dorsal margin straight and ventral margin strongly convex but with subapical concavity giving rise to saber shaped tip; latter 0.3-0.4 length of rostrum. Rostral plus epigastric teeth 6, apex of third rostral tooth or fourth tooth at level of orbital margin. Advostral carina extending from orbital margin to ultimate tooth; postrostral carina ending immediately behind cervical sulcus. Orbital margin produced anteriorly in ventrally inclined short shelf. Postorbital spine, longest of four lateral spines on carapace, situated dorsal to base of small antennal spine; branchiostegal and hepatic spines sharp. Cervical sulcus deep, ending dorsally just posterior to midlength of carapace at base of postrostral carina; cervical carina sharp; hepatic sulcus almost horizontal posteriorly, inclined anteroventrally from depressed area below hepatic spine to pit below branchiostegal spine.

Eye as illustrated (Figure 44B).

Antennular peduncle length equivalent to about 0.65 that of carapace; prosartema long, conspicuously overreaching distomesial margin of first article; stylocerite length about 0.65 of distance between lateral base of first article and base of distolateral spine; latter slender and long; flagella long, length of dorsal flagellum 1.9 cl in shrimp 23 mm cl, proximal portion of flagellum slightly broader than subfiliform distal portion; ventral flagellum slightly shorter and broader than dorsal, gently tapering distally, and bearing long, marginal plumose setae. Scaphocerite overreaching antennular peduncle by as much as 0.2of its own length, gently tapering from base to narrow distal portion; lateral rib ending in long, slender spine, barely or conspicuously overreaching distal margin of lamella. Antennal flagellum long, at least 3 times total length of shrimp. Mandibular palp with distal article slightly shorter than basal and almost reaching or barely overreaching distal margin of carpocerite. Third maxilliped surpassing antennular peduncle by length of dactyl and 0.2-0.5 length of propodus.

First percopod stout, reaching between midlength and distal end of carpocerite. Second percopod moderately stout, extending almost to distal end of carpocerite or overreaching it by not more



FIGURE 50.-Hadropenaeus modestus, 19 mm cl, west of Isla de Providencia, western Caribbean. Cephalothorax, lateral view.

than 0.5 length of dactyl. Third pereopod rather slender, exceeding antennular peduncle by tip or by entire length of dactyl. Fourth pereopod very slender, shorter than third, surpassing carpocerite by tip or by entire length of dactyl; length of dactyl 0.65-0.75 that of propodus; length of carpus about 1.1 times that of merus. Fifth pereopod very slender and long, overreaching antennular peduncle at least by length of dactyl and propodus, and at most by their length and 0.2 length of carpus. Order of pereopods in terms of their maximal anterior extensions; first, second, fourth, third, and fifth. First pereopod with very long, slender spine on basis, small spine on distomesial margin of ischium, and rather minute one near midlength of mesial margin of merus. Second percopod with long spine on basis. Coxa of fourth and fifth pereopods in males armed with anterior spine. Coxa of fifth percopod in females mesially produced into short plate, lacking spine on anteromesial margin; minute spine present in young.

Abdomen with high, sharp, median keel from fourth through sixth somites, low, rounded carina sometimes present on third; posterodorsal margin of third, fourth, and fifth somites with median incision; sixth somite bearing sharp spine at posterior end of keel, and minute spine on posteroventral angles. Telson (Figure 46B) with median sulcus deep anteriorly, disappearing well anterior to terminal portion; fixed lateral spines relatively short, their length 0.7-0.8 basal width of terminal portion; latter broad, length 2.5-3.3 times basal width; mesial ramus of uropod overreaching apex of telson by as much as 0.2 of its own length; lateral ramus conspicuously surpassing mesial, and armed with small distolateral spine, slightly projecting beyond contiguous distal margin of ramus.

Petasma (Figure 51A, B) cincinnulate along proximal 0.6 of median line; broad distal part of ventromedian lobule strongly produced into elongate, distally directed distomesial projection, and short distolateral projection, and with terminal margin spinulous; distal part of ventrolateral lobule heavily sclerotized, forming plate with border undulate adjacent to ventral costa, its terminal portion subrectangular, strongly inclined toward, and partially covered by, ventro-



FIGURE 51.—Hadropenaeus modestus, & 16.5 mm cl, southeast of Cape Fear, N.C. A, Petasma (partly bent laterally), dorsal view of right half. B, Ventral view. C, Right appendices masculina and interna, dorsal view. D, Ventromesial view.



FIGURE 52.—Hadropenaeus modestus, holotype  $\Im$  8 mm cl, off Bethany Beach, Del. A, Thelycum, ventral view. B, Ventrolateral view.

median lobule; ventral costa with distal part free from contiguous plate, bent outward and bearing minute spinules on distalmost margin.

Appendix masculina and appendix interna together with ventrolateral spur (Figure 51C, D) similar to those of H. affinis (see above).

Thelycum (Figure 52A, B) with median protuberance on sternite XIV pyriform or subovate, its apical portion directed anteriorly, and lying between prominent, setose, paired convexities of posteriormost part of sternite XIII; longitudinal, high, median keel on sternite XIII produced anteriorly into ventrally or posteroventrally directed blunt tooth, with anterior margin straight or convex and posterior margin concave.

Maximum size.-Females: 19.5 mm cl; males: 17.5 mm cl.

Geographic and bathymetric ranges.-Off Delaware Bay  $(38^{\circ}31'N, 73^{\circ}21'W)$ , to the Straits of Florida, and in the Gulf of Mexico, northwest of Charlotte Harbor, Fla.; also from the Bahamas, throughout the Caribbean to off Barra Grande (about 9°10'S, 34°52'W), Brazil (Figure 49). This species has been recorded at a depth range of about 150-550 m (Figure 9).

Affinities.-Hadropenaeus modestus may be readily distinguished from its close relative *H. affinis* by the characters included in Table 1.

Remarks.-I have examined the holotype of H. modestus and found that, contrary to the data presented by Smith (1885), it possesses 6 rostral teeth (including epigastric), not 7, and that the merus of the fourth percopod is only 6.5 mm long, not 7.5 mm. Therefore the carpus, which is 7.2 mm long, is not shorter than the merus, but about 1.1 times the length of the latter. These incorrect statements led Bouvier (1906b) to point out differences in the rostral armature and relative length of the carpus between H. modestus and H. affinis which do not exist.

Hadropenaeus modestus is newly reported here in the Caribbean and the Atlantic off northeast South America. The locality record from off Barra Grande, Brazil, is based on a single male taken during the voyage of the *Challenger* (1873-76). On the label accompanying this specimen is "Barra Grande, Brazil, *Challenger*." Although there are several towns in Brazil bearing the name Barra Grande, the locality referred to above must be that in the State of Alagoas, because according to Tizard et al. (1885), the white cliffs of Barra Grande could be seen from *Chal*- *lenger* stn 122, 122A, 122B, and 122C, which are between 9°5' and 9°10'S. This specimen has not been recorded in the literature previously probably because it is a juvenile, not readily identifiable.

## Hadropenaeus lucasii (Bate 1881)

Figures 9, 16, 44C, 53-55

- Solenocera lucasii Bate 1881:185 [holotype: φ, BMNH, off Kai Is, south of New Guinea, 5°49'15"S, 132°14'15"E, 140 fm (256 m), 26 September 1874, Challenger stn 192]. [Not Solenocera lucasii. Miers 1884:15. Rathbun 1906:904, pl. 20, fig. 9.]
- Philonicus lucasii. Bate 1888:277, pl. 42, fig. 4. ? Thomson 1904:254.
- Pleoticus lucasii. Bate 1888:939.
- Haliporus modestus. Rathbun 1906:905, pl. 20, fig. 4. [Not Hymenopenaeus [Hadropenaeus] modestus Smith 1885.]
- Haliporus lucasi. Bouvier 1908:80.
- ?Haliporus malhaensis Borradaile 1910:258, fig. 2 [type not extant; type-locality: off Saya de Malha, Indian Ocean, 145 fm (265 m)]. de Man 1911:7.

Haliporus lucasii. de Man 1911:7.

*Hymenopenaeus lucasii*. Burkenroad 1936:104. Anderson and Lindner 1945:289. Kubo 1949: 213, fig. 8 B<sup>1</sup>, 20 Q, 27 K-N, 66 O, P, 72 C, I, 80 H, 91, 92 A, C.

?Hymenopenaeus lucassi. Ramadan 1938:57.

Hymenopenaeus lucasi. Crosnier and Forest 1973: 256, fig. 83a.

## Material

HAWAII-6 & 5 9, USNM, Pailolo Channel, 271-223 m, 23 July 1902, Albatross stn 4101. 1 & 1 P, USNM, Pailolo Channel, 223-241 m, 23 July 1902, Albatross stn 4102. 1 9, USNM, Pailolo Channel, 241-258 m, 23 July 1902, Albatross stn 4103. 1 9, USNM, N coast of Maui I, 369-402 m, 21 July 1902. Albatross stn 4081. 3 3 10 9, USNM, NW coast of Maui I, 214 m, 16 November 1968, Townsend Cromwell stn 40-43. 4 9, USNM, NW coast of Maui I, 218 m, 17 November 1968, Townsend Cromwell stn 40-48. 4 & 12 9, USNM, NW coast of Maui I, 218 m, 17 November 1968, Townsend Cromwell stn 40-49. 1 & 12 9, USNM, NW coast of Maui I, 216-232 m, 28 April 1968, Townsend Cromwell stn 36-11. 1 & 16 º, USNM, Kaiwi Channel, 177-183 m, 5 May 1968, Townsend Cromwell stn 36-26. 3 9, USNM, S coast of Oahu I, 538-470 m, 6 May 1902, Albatross stn 3920. 2 9, USNM, N coast of Oahu I, 176-201 m, 12 July 1972, Townsend Cromwell stn 59-3. 2 S, USNM, NW coast of Oahu I, 395-459 m, 25 July 1902, Albatross stn 4121. 1 & 1 9, USNM, vicinity of Laysan I, 271-298 m, 16 May 1902, Albatross stn 3938. 1 &, USNM, vicinity of Laysan I, 364-177 m, 19 May 1902, Albatross stn 3947.

NEW GUINEA-1 9 holotype, BMNH, off Kai Is, 256 m, 26 September 1874, *Challenger* stn 192.

REPUBLIC OF MALDIVES—1 ?, BMNH, off Maldive Is, 256-293 m, 4 April 1934, The John Murray Expedition stn 153. MADAGASCAR—1 3, USNM, NW of Baie du Currier, 350-360 m, 15 September 1972, A. Crosnier.

Description.-Carapace (Figure 53) with restricted pubescent areas: setae dense and long at base of rostrum, on pterygostomian region, and in patch extending from orbital margin to epigastric tooth. Abdomen polished and naked; telson with rows of minute setae flanking median sulcus and lateral margins; mesial ramus of uropod sparsely pubescent. Rostrum short, its length 0.30-0.35 that of carapace, reaching to, or almost to, distal margin of first antennular article, horizontal, with dorsal margin straight and ventral margin strongly



FIGURE 53.-Hadropenaeus lucasii, 9 18.5 mm cl, northwest coast of Maui, Hawaiian Islands. Cephalothorax, lateral view.

convex; tip about 0.2 length of rostrum. Rostral plus epigastric teeth 6-8 (mode 7: percentage distribution: 6-13.3, 7-83.3, 8-3.3; N = 60; third rostral tooth usually situated at level of orbital margin. Advostral carina extending from orbital margin to base of ultimate tooth, and shorter, more dorsal, conspicuous carina extending from second rostral tooth to penultimate; postrostral carina ending immediately behind cervical sulcus. Orbital margin produced anteriorly into ventrally inclined, short shelf. Postorbital spine, longest of four lateral spines on carapace, usually more slender than middorsal teeth on carapace. and located dorsal to base of small antennal spine; branchiostegal and hepatic spines sharp. Cervical sulcus deep, ending dorsally just anterior to midlength of carapace, near postrostral carina; cervical carina sharp; hepatic sulcus subhorizontal posteriorly, originating almost at level of dorsal extremity of cervical sulcus, shallow and inclined anteroventrally from depressed area below hepatic spine to pit below branchiostegal spine.

Eye as illustrated (Figure 44C).

Antennular peduncle length equivalent to 0.65 that of carapace; prosartema long, conspicuously overreaching distomesial margin of first article; stylocerite length about 0.65 of distance between

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its proximal extremity and mesial base of distolateral spine; latter very slender and long, considerably surpassing proximal margin of second article. Antennular flagella long and considerably unequal in length, dorsal 1.85 times carapace length and ventral 1.30 in shrimp 12.5 mm cl. and 1.35 and 0.90, respectively, in shrimp 27 mm cl: dorsal flagellum subcylindrical, ventral subcylindrical to depressed. Scaphocerite reaching to distal margin of antennular peduncle or overreaching it by as much as 0.15 of its own length; lateral rib ending in spine reaching to, or slightly beyond, distal margin of lamella. Antennal flagellum long, although incomplete in all specimens, longest observed 3 times total length of shrimp. Mandibular palp with article as long as or slightly shorter than basal, reaching between midlength and distal 0.35 of carpocerite. Third maxilliped reaching to midlength of third antennular article or overreaching it by as much as 0.5 length of propodus; length of dactyl 0.75 that of propodus.

First percopod, stoutest of five, reaching between midlength and distal 0.15 of carpocerite. Second percopod extending to distal end of carpocerite or overreaching it by as much as entire length of dactyl. Third percopod overreaching antennular peduncle by 0.5 length of dactyl or by



FIGURE 54.—Hadropenaeus lucasii, 3 13 mm cl, Pailolo Channel, Hawaiian Islands. A, Petasma (partly bent laterally), dorsal view of right half. B, Ventral view. C, Right appendices masculina and interna, dorsolateral view. D, Ventromesial view.

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as much as entire propodus. Fourth percopod exceeding carpocerite by almost length of dactyl and sometimes by as much as length of dactyl and 0.15 that of propodus. Fifth pereopod reaching beyond antennular peduncle by length of dactyl and 0.6 to entire length of propodus. Order of percopods in terms of their maximal anterior extensions: first, second, fourth, third, and fifth. First percopod bearing very long spine on distomesial extremity of basis, long one on that of ischium, and relatively small spine almost at midlength of merus. Second pereopod with long spine on basis. In female, coxa of third percopod produced mesially into rather short densely setose plate; coxa of fourth pereopod bearing narrow plate. In both sexes, coxa of fourth and fifth pereopods bearing conspicuous anterior spine.

Abdomen with strong middorsal carina from third through sixth somites, carina rounded on third, forming keel from fourth posteriorly; posterodorsal margin of third, fourth, and fifth with long median incision; sixth somite length about 1.3 times maximum height, bearing sharp spine at posterior end of keel and minute spines at posteroventral angles. Telson with median sulcus deep anteriorly, progressively shallower posteriorly, disappearing just before reaching base of lateral spines; terminal portion length 3.3-4.0 times basal width; lateral spines short. 1-1.4 times basal width of terminal portion. Mesial ramus of uropod reaching to, or slightly surpassing, apex of telson; lateral ramus overreaching mesial by as much as 0.2 of its own length, and armed with minute distolateral spine, reaching distal margin of ramus.

Petasma (Figure 54A, B) cincinnulate along proximal 0.70 of median line; broad distal part of ventromedian lobule produced into blunt, distomesial projection, its lateral part turned strongly inward; entire terminal margin of lobule spinulous; distal part of ventrolateral lobule heavily sclerotized, forming plate, border adjacent to ventral costa bearing emargination delimiting basal part from short, broadly subelliptical terminal part; latter inclined toward, and partially covered by, ventromedian lobule, and armed with spinules along entire distal margin; ventral costa with distal part free from, and falling short of, contiguous plate, its distal margin bearing very minute spinules.

Appendix masculina (Figure 54C, D) with proximal part broad, produced mesially into thickened lobe, and bearing long setae along lateral margin; distal part narrow, directed strongly laterally, and bearing apical tuft of long setae. Appendix interna shorter than appendix masculina, narrow, and lacking setae. Ventrolateral spur large, paddlelike.

Thelycum (Figure 55) with median protuberance on sternite XIV roughly elliptical, low, markedly less elevated than prominent setose, paired convexities of sternite XIII; median ridge of latter long, lacking tooth, sometimes ending in small knob at one or both extremities.

Maximum size.-Female (holotype), 25.5 mm cl, 100 mm tl; male, 18.5 mm cl, 72.5 mm tl (Kubo 1949). Largest male examined by me, 14 mm cl, about 64 mm tl.

Geographic and bathymetric ranges.-Madagascar (off northwest coast) through the Indo-West Pacific to Hawaii (Figure 16), in depths between 180 and 500 m (Figure 9). The few records available are from scattered localities.



FIGURE 55.—Hadropenaeus lucasii, 9 19.5 mm cl, Pailolo Channel, Hawaiian Islands. Thelycum, ventral view.

Affinities.-Hadropenaeus lucasii is closely allied to its two Atlantic congeners, H. affinis and H. *modestus*, but it may be distinguished from them by the possession of a conspicuous carina on the rostrum dorsal to the adrostral carina, and by certain petasmal and thelycal features. In H. *lucasii* the ventromedian lobule of the petasma is not produced into a distolateral projection; instead, its lateral portion is turned strongly inward; the distal plate of the ventrolateral lobule bears spinules along the entire terminal margin and is produced in a blunt, ventral projection; in addition, the ventral costa falls conspicuously short of the distalmost part of the adjacent plate. The thelycum, in turn, is characterized by a median protuberance on sternite XIV, which does not project ventrally so far as the posterior convexities of sternite XIII, and the latter bears a low median ridge which is not produced anteriorly in a large tooth. Furthermore, in females of H. *lucasii*, the coxae of the fourth pair of percopods bear a conspicuous anteromesial spine which is lacking in the other two species.

Hadropenaeus lucasii exhibits some morphological variations which are undoubtedly taxonomically insignificant because extremes of variations occur in animals from the same region and even from the same locality. Among them are the relative extension of the scaphocerite, gnathal and thoracic appendages, the total number of rostral teeth as well as the number situated on the carapace. The evidence at hand, however, indicates that the ventral antennular flagellum and some features of the petasma differ regionally. The ventral antennular flagellum is somewhat depressed in the holotype from New Guinea, in Japanese specimens (Kubo 1949) and in two specimens from Madagascar examined by me, and subcylindrical in individuals from Indonesia (de Man 1911) as well as in all those available from Hawaii. In addition, the distomesial projections of the ventromedian lobules of the petasma are larger in specimens from Japan than in males from Madagascar and Hawaii. Whereas the shape of the flagellum exhibits definite variations which seem to be regionally restricted, the differences in the petasma are limited to degree of development and are perhaps insignificant. Except for the collection from Hawaii, available material is extremely meager; consequently, the variations that I have noted are pointed out, with the conviction that definite conclusions as to their taxonomic value must await examination of adequate collections from various areas throughout the Indo-West Pacific.

I have examined the female from the Maldive Islands, Indian Ocean, that Ramadan (1938) identified as H. lucasii. This specimen differs from other specimens of the latter species in the following features: the rostral and epigastric teeth are slenderer-not much stronger than the postorbital spine-and inclined more anteriorly; the anteromesial spine on the coxa of the fifth pereopod is longer and more slender; and the median protuberance on sternite XIV is smaller and surrounded by a shallow depression. Crosnier and Forest (1973), who presented an illustration of the thelycum of the specimen (plate 85, figure a), suggested that the slight differences between the thelycum of the latter and that of the type of H. lucasii could be due to the difference in size of the animals, the type being 90 mm long (23.5 mm cl) and Ramadan's specimen 70 mm. As these authors indicated, Ramadan's specimen exhibits 6 middorsal teeth (rostral plus epigastric), 3 of which are located on the carapace; this number and arrangement of teeth occurs infrequently in members of H. lucasii, but has been observed in several specimens by both Rathbun (1906) and me. Crosnier and Forest suggested further that because of the number and arrangement of the middorsal teeth and the relative size of those behind the rostrum (which are not much stronger than the postorbital spine), Ramadan's specimen might be referable to Borradaile's (1910) Haliporus malhaensis. This species was described from Saya de Malha, Indian Ocean, and its identity is still uncertain, primarily because the holotype, the only specimen on which the description was based, is no longer extant (Ramadan 1938). The features pointed out above suggest that the shrimp from the Maldive Islands might belong to a species other than H. lucasii, but an understanding of its systematic position must await more material from the Indian Ocean.

Both Burkenroad (1936) and Ramadan (1938) were inclined to think that H. malhaensis was identical with H. lucasii, and placed the former name in the synonymy of the latter preceded by a question mark. Previously, de Man (1911) had indicated that he would have identified them as one species, except for Borradaile's statement that in H. malhaensis neither the fourth nor the fifth pereopod is "particularly slender." De Man also called attention to the fact that in Borradaile's illustration the propodi of the fourth and fifth percopods are missing. Kubo (1949) considered that H. malhaensis and H. lucasii are distinct species: he stated that his specimens of *H. lucasii* cannot be referred to H. malhaensis because in the latter there are 3 teeth on the carapace, the scaphocerite does not overreach the antennular peduncle, and the dorsal antennular flagellum is not longer than the ventral which also lacks "rather long setae" on the dorsal and ventral borders. Actually, the first two features are not typical of H. malhaensis but occur in H. lucasii, in which, as stated above, 3 teeth may be present on the carapace, and the scaphocerite, which usually overreaches the antennular peduncle, extends only to the distal end of the peduncle in some individuals. Features of the antennular flagella of H. malhaensis cited by Kubo could be due to the fact that the dorsal flagellum was incomplete in the type, as it often is in preserved specimens, or to omissions of the artist. The two species discussed seem to me to be quite similar, and if there is doubt in my mind as to the status of H. malhaensis, it is mainly because of Borradaile's statement that the fourth and fifth percopods are not "particularly slender." The species exhibits most of the features of *Hadropenaeus*: stout body, thick carapace, short rostrum with ventral margin convex, middorsal teeth on the carapace separated by regularly decreasing intervals, lack of branchiocardiac carina and sulcus, and relative length of the last two percopods having "fourth leg rather longer and fifth considerably longer than the third." These features of Hadropenaeus combined with a fifth percopod that is not very slender, however, are unique. Perhaps the question of the identity of Borradaile's species will be resolved when large collections of solenocerids from the Indian Ocean are studied. Meanwhile, I am inclined, tentatively, to assign H. malhaensis to the synonymy of H. lucasii.

## Mesopenaeus New Genus

- Parartemesia Bouvier 1905b:747 [part, excluding Parartemesia carinata Bouvier 1905b = Pleoticus muelleri (Bate 1888)].
- Haliporus. Bouvier 1906b:1 [part]; 1908:78[part]. A. Milne Edwards and Bouvier 1909:206 [part].
- Hymenopenaeus. Burkenroad 1936:102 [part]. Roberts and Pequegnat 1970:29 [part].

*Diagnosis.*-Body stout, carapace proportionately short; integument thick, firm. Rostrum short,

reaching approximately to base of second antennular article; deep, with ventral margin pronouncedly convex, and armed only with dorsal teeth; epigastric tooth and first rostral separated by interval similar to that between first and second rostral teeth. Orbital, postorbital, antennal, and hepatic spines present; pterygostomian and branchiostegal spines absent. Cervical sulcus long, almost reaching middorsum of carapace; hepatic sulcus deep; branchiocardiac carina and sulcus, posthepatic, and submarginal carinae lacking. Abdomen carinate dorsally from third through sixth somites. Telson with pair of conspicuous, fixed lateral spines. Prosartema long, flexible. Antennular flagella not much longer than carapace and dissimilar: dorsal flagellum subcylindrical and slender, ventral one conspicuously depressed. Mandibular palp two jointed, articles broad, distal one almost as long as basal and tapering to blunt apex. First maxilla with unsegmented palp (endite of basis) gently narrowing to rounded apex. Fourth and fifth percopods rather stout proximally, fifth moderately longer than fourth. First percopod with spine on basis and ischium. Exopods on all maxillipeds and pereopods. Lateral ramus of uropod armed with distolateral spine reaching distal margin of lamella (terminal). In males, petasma with ventral costa not projecting free distally, there bearing flexible flap: distal portion of rib of dorsolateral lobule projecting beyond margin of adjacent area; endopod of second pleopod bearing appendices masculina and interna, and with basal sclerite produced distally into long ventrolateral spur. Thelycum of open type, lacking enclosed seminal receptacle. Pleurobranchia on somites IX to XIV; single, rudimentary arthrobranchia on VII, and anterior and posterior arthrobranchiae on somites VIII to XIII: podobranchia on second maxilliped, and epipod on second maxilliped (and on first if proximal exite of coxa considered an epipod) through fourth pereopod.

# Type-species.-Parartemesia tropicalis Bouvier 1905b.

*Etymology.*—The generic name is derived from the Greek mesos, something in between, in combination with the generic name *Penaeus*, alluding to the fact that the dorsal antennular flagellum is subcylindrical and filiform, as in *Pleoticus*, *Haliporoides* and *Hymenopenaeus*, and the ventral one flattened, much as in *Solenocera*.

Gender.-Masculine.

List of species.-This genus includes only one species: the western Atlantic Mesopenaeus tropicalis (Bouvier 1905b).

Affinities.-Mesopenaeus resembles Solenocera in possessing a flattened ventral flagellum, but in the former this appendage is neither so flattened and broad nor is it channeled as it is in the latter. It shares with its more closely allied genera-Hymenopenaeus, Haliporoides, Pleoticus, and Hadropenaeus—a subcylindrical dorsal flagellum, and a similar armature of the lateral ramus of the uropod, the lateral rib of which ends in a welldefined spine. The stout body, deep rostrum with the ventral margin pronouncedly convex, arrangement of the epigastric and rostral teeth, and absence of both branchiocardiac sulcus and carina place Mesopenaeus closer to Hadropenaeus than to the other genera. Mesopenaeus differs from Hadropenaeus, however, in that the ventral flagellum is invariably depressed, whereas in the latter it is almost always subcylindrical (in occasional individuals of H. lucasii the ventral flagellum is depressed). In Mesopenaeus orbital and branchiostegal spines are present, and the thelycum exhibits paired anterior protuberances on sternite XIV which are present elsewhere among the solenocerids only in the members of the nominal genus. Finally, in Mesopenaeus the ventral costa of the petasma is fused to the flexible terminal part of the ventrolateral lobule, whereas in Hadropenaeus the ventral costa is distally free from the sclerotized terminal part of the lobule.

# Mesopenaeus tropicalis (Bouvier 1905)

# Figures 9, 34, 56-63

- Parartemesia tropicalis Bouvier 1905b:748 "mer des Antilles" in 80-175 fm (146-329 m). [No type designated.]
- Haliporus tropicalis. Bouvier 1906b:4; 1908:80. A. Milne Edwards and Bouvier 1909:217, fig. 45-54, pl. 3, fig. 1-19 [lectotype  $\Im$ , MCZ 7199; type-locality: "Blake: Florida Bank, lat. N. 26° 31', long. 0. 85° 03', 119 brasses." Paralectotype  $\Im$ , MP, off Barbados, 13°04'12"N, 59°36'45"W, 76 fm (139 m), 5 March 1879, Blake stn 272]. de Man 1911:7.
- Hymenopenaeus tropicalis. Burkenroad 1936:103. Springer and Bullis 1956:8. Boschi 1964:38.

Bullis and Thompson 1965:5. Williams 1965:15, fig. 5-7. Cerame-Vivas and Gray 1966:263. Mistakidis and Neiva 1966:434. Roberts and Pequegnat 1970:29. Pequegnat and Roberts 1971:8. Iwai 1973:44, fig. 13.

Solenocera weymouthi Lindner and Anderson 1941:181, fig. 1a-e [holotype ♀, USNM 79357; type-locality: off Orange Beach, Ala., 29°28'N, 87°30'W, 46 fm (84 m), Pelican stn 137-2, 1 March 1939; allotype ♂, USNM 79359, 23 km S of Dry Tortugas, 110 m, 5 August 1932, Anton Dohrn stn 74-32; paratype ♂, USNM 79358, locality as in holotype; 71 ♂ 78 ♀, USNM 23420, between Cape Hatteras and Cape Lookout, N.C., 34°35'30"N, 75°45'30"W, 32 fm (59 m), 18 October 1885, Albatross stn 2605]. Anderson and Lindner 1945:286.

Hypenepenaeus tropicalis. Mistakidis 1965:9.

# Material

UNITED STATES-North Carolina: 2 & 1 9, UNC-IMS, NE of Cape Lookout, 90-110 m, 27 April 1965, Eastward stn 1087. 71 & 78 ♀ (paratypes Solenocera weymouthi), USNM 23420, NE of Cape Lookout, 59 m, 18 October 1885, Albatross stn 2605. 1 9, USNM, SE of Cape Lookout, 82 m, 21 June 1957, Combat stn 406. 1 & 1 9, UNC-IMS, SE of Cape Lookout, 229 m, 8 June 1949, Albatross III stn 21-4. 8 & 8 9, USNM, SE of Cape Lookout, 154 m, 8 June 1949, Albatross III. 2 & 4 9, UNC-IMS, E of Cape Fear, 100 m, 27 April 1965, Eastward stn 1089. 1 d, UNC-IMS, SE of Cape Fear, 140-145 m, 27 April 1965, Eastward stn 1086. 2 3 2 9, USNM, SE of Cape Fear, 183 m, 29 January 1972, Oregon II stn 11747. 3 & 5 9, USNM, off Cape Fear, 190-187 m, 29 February 1960, Silver Bay stn 1694. 1 & 8 9, USNM, SE of Cape Fear, 187-190 m, 29 February 1960, Silver Bay stn 1693. South Carolina: 1 9, USNM, off Cape I, 183 m, 28 January 1972, Oregon II stn 11743. 1 9, USNM, E of Bull Bay, 181 m, 5 January 1885, Albatross stn 2313. 2 9, USNM, E of Bull Bay, 155 m, 5 December 1960, Silver Bay stn 2535. 1 º, USNM, off Santa Helena Sound, 83 m, 28 April 1966, Oregon stn 6073. Georgia: 4 9, USNM, off Savannah, 68-91 m, 14 December 1961, Silver Bay stn 3658. 7 & 2 9, USNM, off Savannah, 73 m, 12 March 1956, Bowers stn 54. 1 9, USNM, off Savannah Beach, 73 m, 26 April 1966, Oregon stn 6062. 1 3, USNM, off Catherines Sound, 37 m. 13 March 1940, Pelican stn 195-10. Florida: 1 9, USNM, off Fernandina, 179 m, 18 January 1972, Oregon II stn 11699. 1 ♂ 9 ♀, USNM, off St Augustine, 75 m, 24 April 1966, Oregon stn 6044. 1 & 3 ♀, USNM, off St Augustine, 40 m, 5 September 1962, Silver Bay stn 4340. 1 9, USNM, off Matanzas Inlet, 183 m, 18 November 1965, Oregon stn 5741. 1 9, USNM, off Matanzas Inlet, 64-87 m, 7 October 1962, Silver Bay stn 4451. 1 º, USNM, off Ponce de Leon Inlet, 73-97 m, 5 October 1962, Silver Bay stn 4420. 1 & 1 9, USNM, off Edgewater, 51-37 m, 24 August 1965, Oregon stn 5603. 1 9, USNM, off Cape Kennedy, 70 m, 16 January 1966, Oregon stn 5860. 1 º, USNM, off Melbourne Beach, 73 m, 14 July 1961, Silver Bay stn 3279. 1 °, UMML, NE of St Lucie Inlet, 38-42 m, 21 May 1968, Gerda stn 1002. 1 3, UMML, SE of St Lucie Inlet, 60-62 m, 21 May 1968, Gerda stn 1001. 1 ♀, RMNH, E of Miami, 119 m,
16 April 1965, Gerda stn 622. 3 9, RMNH, off Elliott Key, 82-77 m, 15 April 1965, Gerda stn 610. 2 9, USNM, off Old Rhodes Key, 91 m, 10 November 1961, Silver Bay stn 3524. 2 & 3 9, USNM, off Key Largo, 86-79 m, 10 July 1967, Gerda stn 834. 1 & 2 9, RMNH, off Key Largo, 86-95 m, 14 September 1965, Gerda stn 752. 1 & 2 9, RMNH, off Key Largo, 92-97 m, 14 September 1965, Gerda stn 751, 1 9, UMML, off Key Largo, 108-88 m. 26 January 1966, Gerda stn 767. 2 9, RMNH, off Key Largo, 146 m, 26 January 1966, Gerda stn 770. 1 9, USNM + 4 & 2 9, RMNH, off Key Largo, 99-91 m, 10 July 1967, Gerda stn 833. 4 & 2 9, RMNH, SE of Key Largo, 95 m, 15 April 1965, Gerda stn 602. 1 & 1 9, USNM, off Key Largo, 102 m, 9 April 1886, Albatross stn 2639. 1 9, USNM, Hawk Channel, 110 m, 27 October 1960, Silver Bay stn 2391. 1 & 9 9, USNM, Hawk Channel, 128 m, 27 October 1960, Silver Bay st<br/>n 2392. 1 $\eth$ 1 $\heartsuit$ USNM, SE of Key West, 93-106 m, 25 February 1969, Gerda stn 1024. 2 & 2 9, USNM, SE of Key West, 135-146 m, 25 February 1969, Gerda stn 1028. 2 &, USNM, off Key West. 179 m, 14 February 1902, Fish Hawk stn 7279. 1 3, USNM, SW of Marquesas Keys, 196-210 m, 26 April 1969, Gerda stn 1084. 1 &, USNM, SW of Marquesas Keys, 201-210 m, 26 April 1969, Gerda stn 1085. 2 9, USNM, SW of Marquesas Keys. (depth not given), 12 December 1962, Oregon stn 4142.  $2 \circ 2 \circ$ , USNM, S of Dry Tortugas, 366 m, 10 July 1965, Oregon stn 1330. 1 d, USNM, S of Dry Tortugas, 229-274 m, 28 April 1969, Gerda stn 1095. & (allotype S. weymouthi), USNM 79359, 23 km S of Dry Tortugas, 110 m, 5 August 1932, Anton Dohrn stn 74-32. 1 d, USNM, SW of Dry Tortugas, 348 m, 13 April 1954, Oregon stn 1005. 1 9, USNM, SW of Dry Tortugas, 183 m, 6 August 1963, Oregon stn 4370. 1 & 21 9, USNM, NW of Dry Tortugas, 298 m, 19 April 1954, Oregon stn 1026. <sup>9</sup> lectotype, MCZ 7199, Florida Bank, 218 m, Blake. 4 & 1 9, USNM. off St Petersburg, 106 m, 18 March 1954, Oregon stn 938. 2 9, USNM, W of Clearwater, 146 m, 11 March 1956, Oregon stn 920. 6 & 12 9, USNM, off Apalachicola Bay, 88 m, 10 March 1954. Oregon stn 917. 2 & 7 9, USNM, S of St Vincent I, 64 m, 7 March 1954, Oregon stn 896. 1 &, USNM, off Panama City, 101-130 m, 26 July 1957, Silver Bay stn 100. 4 & 3 9, USNM, off Choctawhatchee Bay, 91 m, 21 March 1954, Oregon stn 944. 2 9, USNM, off Gulf Beach, 165 m, 1 March 1955, Oregon stn 1254. Alabama: 9 (holotype S. weymouthi), USNM 79357, off Orange Beach, 84 m, 1 March 1939, Pelican stn 137-2. 1 & (paratype S. weymouthi), USNM 79358, same locality as holotype.

MEXICO—Quintana Roo: 2 & 18 \, USNM, NE of Cape Catoche, 183 m, 22 January 1967, Oregon stn 6399.

BAHAMA ISLANDS—1  $\delta$  3  $\circ$ , USNM, NE of Little Bahama Bank, 183 m, 25 October 1961, Silver Bay stn 3466. 1  $\circ$ , RMNH, Northwest Providence Channel, 278-329 m, 3 March 1965, Gerda stn 526. 1  $\delta$  4  $\circ$ , RMNH, off Great Isaac I, 311-329 m, 2 March 1965, Gerda stn 509. 1  $\delta$ , USNM, off Dog Rocks, Cay Sal Bank, 618 m, 22 June 1967, Gerda stn 815. 1  $\circ$ , USNM, off Great Inagua, 183-137 m, 5 November 1961, Silver Bay stn 3502. 1  $\delta$  1  $\circ$ , USNM, S of Great Inagua, 311 m, 13 December 1969, Oregon II stn 10849. 1  $\delta$  4  $\circ$ , USNM, S of Great Inagua, 311 m, 13 December 1969, Oregon II stn 10850.

CUBA-2 3, USNM, N of Las Villas, 461 m, 15 December 1969, Oregon II stn 10860.

DOMINICAN REPUBLIC—1 & 1 \, USNM, off Cabo Engaño, 201 m, 17 October 1963, Silver Bay stn 5188.

PUERTO RICO-2 & 2 9, USNM, Mona Passage, 366 m, 17 October 1963, Silver Bay stn 5190.

LESSER ANTILLES—2 9, USNM, Dominica Passage, 640 m, 1 December 1969, Oregon II stn 10825. 1 9, USNM, off Barbados, 91-366 m, J. B. Lewis. 1 9 paralectotype, MP, off Barbados, 139 m, 5 March 1878, Blake stn 272.

WESTERN CARIBBEAN-18 & 12 9, USNM, Arrowsmith Bank, 311-146 m, 28 January 1968, Gerda stn 954. 1 & 5 9, USNM, Arrowsmith Bank, 252-293 m, 14 March 1968, Pillsbury stn 591. 1 & 2 9, USNM, Arrowsmith Bank, (depth not given), 15 November 1968, Pillsbury stn 598, 1 d. UMML. Arrowsmith Bank, 115-190 m, 23 August 1970, Gerda stn 1286. 1 & 1 9, USNM, Arrowsmith Bank, 307-192 m, 28 January 1968, Gerda stn 951. 1 S. USNM, Arrowsmith Bank, 225-437 m. 21 August 1970, Gerda stn 1275. 1 9, USNM, NE of Banco Gorda, 265-274 m, 6 June 1962, Oregon stn 3622. 2 9, UMML, NW of Quita Sueno Bank, 296-375 m, 31 January 1971, Pillsbury stn 1356. 1 & 1 º, USNM, W of Quita Sueño Bank, 201-207 m, 12 February 1967, Oregon stn 6460. 22 & 24 9, USNM, W of Isla de Providencia, 289-274 m, 4 February 1967, Oregon stn 6423. 1 & 5 9, USNM, SW of Isla de San Andrés. 201-219 m, 4 February 1967, Oregon stn 6424. 18 & 20 9, USNM, W of Isla de San Andrés, 139 m, 6 February 1967, Oregon stn 6434. 6  ${}^\circ$  10  ${}^\circ$ , USNM, W of Cayos de Albuquerque, 192 m, 7 February 1967, Oregon stn 6444.

BELIZE---1  $\diamond$  3  $\circ$ , USNM, W of Lighthouse Reef, 329-274 m, 24 January 1966, *Oregon* stn 6404. 1  $\circ$ , USNM, W of Lighthouse Reef, 262 m, 23 January 1967, *Oregon* stn 6403. 6  $\diamond$  7  $\circ$ , USNM, W of Lighthouse Reef, 183 m, 24 January 1967, *Oregon* stn 6405.

NICARAGUA---1  $\Im$ , USNM, NE of Puerto Cabezas, 183-219 m, 21 May 1962, Oregon stn 3568. 1  $\Im$ , USNM, NE of Puerto Cabezas, 274-293 m, 21 May 1962, Oregon stn 3566. 11  $\Diamond$  23  $\Im$ , USNM, 190 m, off La Barra de Río Grande, 5 February 1967, Oregon stn 6426. 7  $\Diamond$  3  $\Im$ , USNM, off La Barra de Río Grande, 176-110 m, 5 February 1967, Oregon stn 6427. 18  $\Diamond$  10  $\Im$ , USNM, NE of Islas del Maíz, 119 m, 5 February 1967, Oregon stn 6432. 23  $\Diamond$  18  $\Im$ , USNM, NE of Islas del Maíz, 192-198 m, 7 February 1967, Oregon stn 6448. 5  $\Im$ , USNM, NE of Islas del Maíz, 198-201 m, 7 February 1967, Oregon stn 6447.

PANAMA-1 3, USNM, off Coclé del Norte, 137 m, 29 May 1962, Oregon stn 3587.

VENEZUELA—2  $\delta$  1  $\circ$ , USNM, off Golfo de Venezuela, 201 m, 26 September 1963, Oregon stn 4398. 1  $\circ$ , USNM, off Puerto Cumarebo, 161-187 m, 27 July 1968, Pillsbury stn 757. 2  $\delta$  3  $\circ$ , USNM, E of Pen de Paraguaná, 915 m, 4 October 1963, Oregon stn 4416. 1  $\delta$ , USNM, off La Guaira, 97 m, 13 October 1963, Oregon stn 4459. 1  $\delta$  1  $\circ$ , USNM, off La Guaira, 97 m, 13 October 1963, Oregon stn 4461. 2  $\delta$ , UMML, W of I La Tortuga, 68-60 m, 22 July 1968, Pillsbury stn 734. 26  $\delta$  11  $\circ$ , USNM, off Cabo Cordera, 60-73 m, 22 July 1968, Pillsbury stn 737. 6  $\delta$  3  $\circ$ , USNM, NE of Islas Los Testigos, 585-439 m, 24 September 1964, Oregon stn 5039. 2  $\circ$ , USNM, NE of Islas Los Testigos, 128-119 m, 24 September 1964, Oregon stn 5040.

BRAZIL—Amapá:  $1 \diamond 1 \diamond 1 \diamond 1$ , USNM, mouths of the Amazon River, 229 m, 17 November 1957, Oregon stn 2080. Maranhão:  $1 \diamond 1$ , USNM, off São Luis, 183 m, 9 March 1963, Oregon stn 4225. São Paulo:  $1 \diamond 1 \diamond 1 \diamond 1$ , IOUSP, SSE of I de São Sebastião, 156-152 m, 3 July 1971, Prof. W. Besnard stn 1471.  $4 \diamond 2 \diamond 1$ , USNM-MP, SE of Quemado Grande I, 97-100 m, 11 December 1961, Calypso stn 138.

*Description.*-Body robust (Figure 56), integument firm, mostly glabrous, but carapace with rather long densely set setae on rostrum above adrostral carina; patch of minute setae extending from orbital margin to base of epigastric tooth; and elongate patch of sparsely set setae below hepatic sulcus.



FIGURE 56.—Mesopenaeus tropicalis, 9 23.5 mm cl, east of Cayos de Albuquerque, western Caribbean. Lateral view.

Rostrum rather short, its length not exceeding 0.4 that of carapace, reaching, at most, base of second antennular article, straight or slightly tilted upward, moderately high, its ventral margin strongly convex, often with subapical concavity giving rise to saber shaped tip. Rostral plus epigastric teeth 7-10, mode 8 (percentage distribution in North America: 7-2, 8-60, 9-36, 10-2, N = 100; percentage distribution in South America: 7-4, 8-80, 9-15, 10-1, N = 100; teeth long and sharp; usually third rostral tooth, sometimes second, at level of orbital margin. Adrostral carina sharp, extending from orbital margin to ultimate tooth; postrostral carina low, short, extending only to level of cervical sulcus. Orbital spine with broad base, short but sharp; postorbital spine longest of lateral spines on carapace; antennal spine moderately long, and hepatic spine about same length. Cervical sulcus deep, gently sinuous, extending almost to, but not crossing, postrostral carina, ending at about 0.55 cl; hepatic sulcus almost horizontal posteriorly, turning anteroventrally in broad arc below hepatic spine,

and nearly reaching anterior margin of carapace.

Eye (Figure 57) with basal article produced distomesially into densely pubescent, elongate, narrow scale; ocular peduncle short; cornea rather broad, greatest diameter about 1.8 times that of base of ocular peduncle, its proximal margin strongly slanting posterolaterally.

Mandibular palp (Figure 58A) broad, distal article almost as long as proximal, and armed with unique distomesial series of hooks. First maxilliped as illustrated (Figure 58B); rudimentary arthrobranchia on articular membrane (Figure  $58Bc-c^1$ ). Antennular peduncle length about 0.6 cl; prosartema long, reaching as far as midlength of second antennular article; stylocerite long, spiculiform distally, its length about 0.7 of distance between its base and that of distolateral spine; latter rather long, very slender, and sharp. Ventral antennular flagellum typically depressed, slightly shorter than subcylindrical dorsal flagellum. Flagella longer in North American than in West Indian, Central American, and South American populations (Figure 59). Ratio of

length of dorsal flagellum to length of carapace in North American shrimp ranging from about 1.15 in 10-mm cl individuals to about 0.95 in 23-mm cl shrimp. In Bahamian and southern populations. ratio decreasing from about 0.95 in shrimp 10 mm cl to about 0.6 in shrimp 24 mm cl. Scaphocerite not reaching distal margin of antennular peduncle or exceeding it by as much as 0.1 of its own length; lateral rib ending distally in long spine, usually extending to level of distal margin of lamella; antennal flagellum at least 3.5 times total length of shrimp: 110-mm tl female with flagellum 385 mm long (measurements taken by me of specimen caught south of Great Inagua, Bahama Islands, in 311 m, at Oregon II stn 10849). Third maxilliped usually exceeding antennular peduncle by length of dactyl, occasionally surpassing it by length of dactyl and as much as 0.2 that of propodus; length of dactyl about 0.75 that of propodus.

First perceoped, stoutest of five, reaching at most distal end of carpocerite. Second perceoped surpassing carpocerite by length of dactyl or by entire length of propodus. Third perceoped exceeding antennular peduncle by 0.6 to entire length of propodus. Fourth perceoped overreaching carpocerite by 0.5 or more length of dactyl. Fifth perceoped, longest of five, exceeding antennular peduncle by length of dactyl or by latter and as much as 0.2 length of propodus. Order of perceopeds in terms of their maximal anterior extensions: first and fourth, second, third and fifth. First perceoped with long, strongly pointed spines on basis and ischium; second perceoped with long sharp spine



FIGURE 57.—Mesopenaeus tropicalis, 9 25 mm cl, off Key Largo, Fla. Eye.



FIGURE 58.—Mesopenaeus tropicalis,  $\Im$  20 mm cl, west of Light House Reef, Belize. A, Mandible. B, First maxilliped. c, Arthrobranchia. c<sup>1</sup>, Enlargement of c (all from left side).

on basis. In female, coxa of third percopod produced into plate extending mesially, then uniquely folded ventrolaterally; coxa of fourth percopod produced in strong plate resembling head of bird, "beak" consisting of long, sharp spiniform projection directed posteriorly, entire plate curving around lateral horn on plate of sternite XIII; coxa of fifth percopod bearing short plate produced anteromesially in blunt projection. In male, coxa of fourth percopod with short plate bearing small anterior tooth; fifth percopod with large subtriangular tooth on anterior margin.

Abdomen with sharp, high, middorsal carina from third to sixth somites; low, rounded, sometimes barely perceptible carina on second somite in larger specimens; posterodorsal margin of third through fifth somites with median incision; sixth somite with small, sharp spine at posterior end of carina, and pair of small spines posteroventrally. Telson with median sulcus deep anteriorly and penetrated posteriorly by longitud-



FIGURE 59.-Mesopenaeus tropicalis. Relationship between length of dorsal antennular flagellum and carapace length.

inal elevation merging with convex terminal portion; latter moderately long, its length 4-5 times basal width; lateral spines short, 0.9-1.4 times basal width of terminal portion; mesial ramus of uropod reaching tip of telson or overreaching it by no more than 0.1 of its own length; lateral ramus surpassing mesial ramus by 0.1-0.2 of its own length, and bearing small, terminal, distolateral spine.

Petasma (Figure 60A, B) cincinnulate along proximal 0.7 of median line and with terminal margin lacking spinules, often minutely rugose across ventromedian lobule; distal portion of ventromedian lobule thick, flexible, folded, its mesial portion strongly excavate ventrally, and overlying its shorter lateral portion; latter produced laterally into process resembling bird head in silhouette, dorsolateral lobule with heavy rib curved in hooklike terminal portion lying against ventral surface of process; inner surface of dorsolateral lobule studded with minute setae mesially and bearing proximolateral row of long setae; corresponding, but shorter, row of long setae on outer surface. Ventral costa reaching distally as far as, or slightly overreaching, row of cincinnuli, trending dorsally, and bearing flexible subrectangular, marginal flap, extending horizontally almost perpendicular to costa.

Appendix masculina (Figure 60C, D) very elongate, convex dorsally, deeply channeled ventrally, its proximal part produced laterally into rounded, ventrally turned lobe; distal part tapering, its tip twisted mesiad, mesial surface deeply concave, and armed with densely set, relatively long setae on proximolateral border, short setae on borders of concavity, and tuft of long setae apically. Appendix interna almost as long as appendix masculina, broad, subelliptical, bearing lateral rib, abutting corresponding border of appendix masculina, and armed with tuft of long setae on distolateral border, and very short setae on mesial border. Basal sclerite obliquely crossed by heavy ridge separating deep proximal concavity from anterior depressed area, and with its ventrolateral spur proximally rounded and strongly attenuate distally.

Thelycum (Figure 61) with paired short, blunt, cushionlike protuberances on flexible anterior part of sternite XIV, contiguous to ventrally raised, heavily sclerotized posterior shield; free border of shield sharp or thickened, and varying from slightly concave to produced into anteromedian, minute spine. Median plate of sternite XIII divided by median longitudinal incision into paired rounded to subrectangular lobes overhanging sternite XIV, each bearing blunt horn anterolaterally. Sternite XII with paired blunt, distally flattened projections overhanging sternite XIII.

Photophores.-Observations by me on freshly collected specimens demonstrated that this species, like H. affinis and H. debilis, bears photophores, which are arranged as follows: one adjacent to the base of the podobranchia of both the third maxilliped and fourth pereopod, and a pair on the anterior part of the sternum from the second through the sixth abdominal somites, immediately posterior to the transverse ridge of the preceding segment. The seven pairs of photophores consist of a yellow conical portion and a red lens.

Color.-Body translucent salmon with obliquely vertical, deep yellow stripes, and milky white patches of various sizes on carapace. Rostrum vellow from second rostral tooth to apex, epigastric and first rostral teeth salmon. Carapace with three anterior stripes resembling chevron: anteriormost short, arched, extending from near base of orbital spine posterodorsally to below first rostral tooth; second extending almost from base of postorbital spine to posterior base of epigastric tooth; third posteriorly flanking cervical sulcus, and broadening on middorsum, forming diamondshaped mark. Additional posterior stripe on carapace narrow on middorsum, broadening rapidly anteroventrally, and then narrowing again, forming band along dorsal part of branchiostegite. White patches on carapace very conspicuous: anterior one subcircular, situated on depression below hepatic spine; second oblong, lying ventral to hepatic sulcus; posteriormost ovate and large, almost covering entire branchiostegite. First abdominal somite with yellow spot immediately anterior to posterolateral hinge, remaining five somites with broad, uniformly wide yellow stripe extending from anterior half of middorsum posteroventrally to lateral hinge, except stripe on sixth reaching posteroventral extremity of pleuron; sixth somite also with short posterodorsal vellow stripe extending from dorsum to lateral base of telson; midventral part of pleura of anterior five somites with deep salmon spot, sixth somite with deep salmon patch on anteroventral part of pleuron. Telson salmon, with median sulcus yellow; uropodal rami bearing broad transverse band across midlength. Antennulae and antennae deep salmon, darker on basicerite of antenna and on adjacent anteroventral portion of carapace. Thoracic sternites, first and second maxillipeds, and proximal podomeres (including merus) of third maxilliped and percopods pale salmon; distal podomeres deep salmon except for narrow milky white longitudinal band. Basis of pleopods deep salmon preaxially with lateral part milky white; endopods and exopods whitish with orange line along midlength; ventral surface of



FIGURE 60.—Mesopenaeus tropicalis, \$ 17.5 mm cl, east of Cayos de Albuquerque, western Caribbean. A, Petasma, dorsal view. B, Ventral view. C, Right appendices masculina and interna, dorsal view. D, Ventromesial view.



FIGURE 61.—Mesopenaeus tropicalis,  $\Im$  25.5 mm cl, east of Cayos de Albuquerque, western Caribbean. Thelycum, ventral view.

abdomen with orange transverse rib at posterior margin of sternites, interrupting overall translucent salmon.

Although the color pattern described is altered with the expansion and contraction of the chromatophores, this basic arrangement of colors was usually recognizable in all specimens examined by me. However, according to Iwai (1973), this species exhibits an overall red in Brazilian waters.

Maximum size.-Males: 20.5 mm cl; females: 28 mm cl.

Geographic and bathymetric ranges.-Northeast of Cape Lookout, N.C. (34°43'N, 76°40'W), to the Straits of Florida, and into the Gulf of Mexico to Alabama. Also off the Bahamas, through the Caribbean, and along the Atlantic coast of South America as far as Rio Grande do Sul (Figure 34). The record from Rio Grande do Sul (34°00'S) is from Iwai (1973). This species occurs at depths between 30 and 915 m (Figure 9), thus from relatively shallow waters (where it is infrequent) on the continental shelf to the upper zone of the continental slope. This bathymetric range is not peculiar to M. tropicalis, but is also exhibited by various other penaeoids. The single record of the shrimp from northeast of Cape Catoche, and its apparent absence in the Gulf of Mexico from Mississippi to northern Yucatán, suggest inadequate sampling in the region. Its presence on the continental slope, even if only in the shallower zone, where no barriers prevent its dispersion, also favors this conclusion.

According to the limited data at my disposal, in the warm temperate waters of North America this species tends to remain on the continental shelf, where 85% of the samples examined by me were caught; in contrast, off the Bahamas and to the south, it seems to be more abundant off the shelf edge, where 76% of the samples were taken. In neither region do the animals appear to exhibit a seasonal migration, moving from warmer waters of the shelf to greater depth in late fall and returning in the spring.

Affinities.-Mesopenaeus tropicalis, the sole member of the genus, differs strikingly from the other solenocerids occurring in the western Atlantic in possessing antennular flagella which are dissimilar in shape, the dorsal one subcylindrical and the ventral depressed.

Variations in the relative length of the antennular flagella were pointed out by Lindner and Anderson (1941). I have confirmed their observations and, in addition, have found that the range of variations in North American populations is different from that in populations occurring from the Bahamas to Brazil, the former having longer flagella than the latter. Noteworthy is the parallelism that exists in the relative length of the antennular flagella between Mesopenaeus tropicalis and two closely related allopatric species of the genus Solenocera. Like the northern population of M. tropicalis, S. vioscai, a North American species, possesses longer flagella than does S. acuminata, which occurs from the Bahamas to Brazil (Pérez Farfante and Bullis 1973). A similar tendency was observed by Pérez Farfante and Bullis in S. atlantidis, the northern populations of which tend to have longer flagella than do those from the Bahamas southward. The thelvcum of M. tropicalis also exhibits considerable variation, even within a single population, the shield of sternite XIV varying from flat with the anterior

margin bladelike, to deeply excavated on the median portion, and with the anterior margin elevated in a strong ridge; in addition, this margin ranges from bearing a minute anteromedian spine to being concave. Furthermore, the anterolateral protuberances of sternite XIII may be low or rather strongly raised.

Spermatophore.-Compound spermatophore consisting of slender, laterally compressed geminate body continuous with broad anterior lobes, bearing lateral wings, and produced posterolaterally in relatively narrow flanges (Figure 62).

Thick opaque ventral wall and lateral wall of each spermatophore (Figure 63A) extending anteriorly forming ventral portion of anterior lobe; lateral wall, opaque anteriorly, translucent posteriorly, bearing fleshy wing; dorsomesial wall (Figure 63B) mostly translucent but thickened mesially, continuous with dorsomesial portion of anterior lobe, and extending posteromesially beyond fundus of sac, there joining flange, and giving rise to pocketlike caudal projection. Anterior lobe forming obliquely truncate collar opening laterally and through posterior slit, with ventrolateral surface subrectangular, and dorsomesial surface elongate trapezoidal, broadest laterally. Wing flexible (lacking heavily sclerotized supporting structures), bearing rounded lobe anteriorly. Flange extending from about midlength of sac around posterolateral margin, bearing anteriorly cornified, reniform projection, and produced laterally in roughly semicircular flap. Spermatophore supported by strong C-shaped armature, its mesial part fused to dorsomesial wall and its anterior arm extending across and supporting ventral wall, with lateral extremity forked: anterior branch forming foliaceous process, directed dorsally, facing posterior slit of anterior lobe; posterior branch spirally twisted and located just cephalic to reniform projection of flange. Dorsal plate elongate ovate, extending from base of wing to posterior margin of flange.

Compound spermatophore attached to female with anterior lobes on sternite XII, their elongate lateral openings lying close to gonopores; angles formed by anterior lobes and wings embracing posterior corners of coxal plates of third pereopods; wings extending laterally, attached to sternite XIII, pressing against marginal ridge of XII. Posterior part of geminate body affixed by dorsal plates to shieldlike posterior plate of sternite XIV, elevated (ventrally) well above level of anterior



FIGURE 62.—Mesopenaeus tropicalis. Compound spermatophore attached to female,  $\Im$  19.5 mm cl, off Gulf Beach, Fla. (setae omitted).

lobes, thus geminate body directed anterodorsally. Posterior parts of flanges sloping posterodorsally, lateral parts attached to sternite XIV, and reniform projections lying near coxae of fourth pereopods. Finally, foliaceous processes meeting on middorsal line, whereas spirally turned branches of C-shaped armature (diverging from bases of foliaceous processes) projecting laterally.

I have observed sperm masses protruding from the sperm sacs into the cavity of the respective anterior lobe, from which the sperm must be dispersed into the surrounding water adjacent to the female gonopores. A complete compound spermatophore detached by me from an impregnated female was found to lack sperm masses, suggesting that the sperm had been freed while the intact spermatophore was still anchored to the animal; furthermore, there was no trace of such masses on



FIGURE 63.—Mesopenaeus tropicalis,  $\delta$  19 mm cl, south of Great Inagua, Bahama Islands. A, Left spermatophore dissected from terminal ampulla (wing slightly displaced), ventrolateral view. B, Dorsomesial view (dorsal plate removed).

the thelycum. Unlike the release of the sperm masses in certain members of the subgenus *Litopenaeus* (genus *Penaeus*) the sperm appears to be liberated in *M. tropicalis* without a rupture of the spermatophore.

Three females with spermatophores attached were examined by me. The smallest of these specimens, 12 mm cl, was caught off Savannah, Ga., at *Silver Bay* stn 3658. The other two were 19.5 mm cl, and one was taken south of St Vincent Island at *Oregon* stn 896 and the other off Gulf Beach at *Oregon* stn 1254, both localities off northwestern Florida.

Remarks.-In his original brief diagnosis of Parartemesia tropicalis, Bouvier (1905b) stated that the species is from the "mer des Antilles," where it had been collected between 80 and 175 fm (146 and 320 m), during a cruise of the Blake; he cited neither the number of specimens he had examined nor the locality where they had been found. Later, he (1906b) mentioned the same shrimp (including it among the species of the genus Haliporus found in the tropical subtropical Atlantic) as occurring in the "Antilles." However, A. Milne Edwards and Bouvier (1909)—in a rather detailed account of various morphological features of the female of the species, including the thelycum—

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referred to the same specimen (17.5 mm cl, about 74 mm tl), as the "type," and added the following information: "Habitat, . . .--Blake: Florida Bank, lat. N. 26° 31', long. O. 85° 03', 119 brasses.-Le type femelle décrit plus haut." Furthermore, on plate 3, eight figures are explicitly identified as parts of the "type." A. Milne Edwards and Bouvier also recorded and illustrated a smaller female, "25 à 30 mm de longeur" (5.5 mm cl, about 27 mm tl), from Barbados taken in 76 fm (139 m) which, according to a label dated 1907, in Bouvier's handwriting, is a "cotype juvenile," evidently thus designated during the course of the investigations published 2 yr later. The minimum depth of the bathymetric range (80-175 fm) originally given for the species is only slightly greater than that at which the small female was collected, but the maximum depth is considerably deeper than that reported for the larger female, suggesting that the authors had examined additional specimens. Of the material first studied by Bouvier, these two females are the only specimens of this species known to have been taken during cruises of the Blake and, furthermore, the small one was identified by Bouvier on a piece of paper accompanying the specimen in the bottle as Parartemesia tropicalis, i.e., within the genus proposed in 1905. Consequently, I am convinced that these two specimens are part of the syntypic series. Inasmuch as the larger female was treated as the type by A. Milne Edwards and Bouvier, I am furthering the latter authors' intent by designating it the lectotype of *Parartemesia tropicalis* [=*Mesopenaeus tropicalis*], and the small female is, therefore, a paralectotype.

The type-locality of *H. tropicalis* is uncertain. A. Milne Edwards and Bouvier (1909) copied the coordinates of Blake stn 50 from the label enclosed in the jar with the specimen; I have examined this label and confirmed their data. However, the locality corresponding to those coordinates is beyond the 1,500-fm (2,744-m) contour, and thus considerably deeper than the greatest depths otherwise recorded for this shrimp, a species that penetrates only the shallower portion of the upper slope. Prior to the publication of A. Milne Edwards and Bouvier, the coordinates and depth of Blake stn 50 were recorded, in a serial list of Blake stations (Anonymous 1879), as follows: 26°31'N, 85°53'W, 119 fm (218 m). Later, S. Smith (1889) quoted the latter data, noting that "The position or depth must be wrong as there are 1700 fm (3109 m) there, perhaps 28°31'." S. Smith's suggestion concerning the latitude was perhaps based on that of the three previous Blake stations, which were 28°42'00"N, 28°47'30"N, and 28°51'30"N; however, these are at longitudes greater than 88°W, situated off the Delta of the Mississippi River, and thus far from Florida. The confusion regarding the location of station 50 is even greater, because the name "Florida Bank" is not found on American hydrographic charts, although it can be deduced that A. Milne Edwards and Bouvier referred to West Florida Shelf, the edge of which lies just east of where, according to the label, the specimen was obtained. It seems to me that the type-locality of this species will remain indeterminable.

Under the name Solenocera weymouthi, Lindner and Anderson (1941) presented an excellent description of *M. tropicalis*. Two of their statements seem to be in need of modification: only the ventral antennular flagellum is flattened (but not canaliculate), the dorsal one being subflagelliform. The locality given for the allotype is in error. W. L. Schmitt kindly allowed me to examine his logbook of the collections made off the Dry Tortugas in 1932, the time at which the specimen was collected. His records show that "boat sta 74," the locality in question, corresponds to the Anton Dohrn trawl haul made 14 miles (22.5 km) south of the Dry Tortugas in 60 fm (110 m) on 5 August 1932. The data given by Lindner and Anderson are those for *Anton Dohrn* station 71, made the same day but, as they quoted, 19.5 miles (31.4 km) south of the Dry Tortugas at 190-280 fm (347.5-512 m).

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