REVISION OF THE PENAEID SHRIMP GENUS PENAEOPSIS (CRUSTACEA: DECAPODA)

ISABEL PEREZ FARFANTE¹

ABSTRACT

The genus *Penaeopsis*, comprising six species, is defined and its relationships discussed. Five of the species occur in the Indo-West Pacific, *P. balssi*, *P. eduardoi*, *P. challengeri*, *P. jerryi*, and *P. rectacuta*, and one, *P. serrata*, on both sides of the Atlantic. A key for their identification is provided. References, disposition of types, locality records, diagnoses, descriptions, and illustrations for each species are presented. The descriptions, except that of *P. balssi*, are based on material that includes type-specimens. The male of *P. challengeri*, which was not previously known, is described in detail. Intraspecific variation is noted, and distinguishing morphological features as well as affinities are discussed. In addition, geographic and bathymetric ranges are presented, and a graph of depth-temperature relationships of *P. serata* in four areas within its range is included.

A study of the types of the three species of Penaeopsis described by Bate (1881) made obvious not only the need for redescriptions of these specimens, as was pointed out first by Burkenroad (1934a) and most recently by Ivanov and Hassan (1976), but also confirmed the necessity for a revision of the genus. As stated by Pérez Farfante (1977b), misidentifications, incomplete descriptions, and lack of detail in some of the illustrations presented by Bate (1881, 1888) have been responsible for much of the persistent confusion in the recognition of the species of *Penaeopsis*. The examination of Bate's types and the study of collections made during the cruises of 26 research vessels have enabled me to: clarify the problems associated with his work; describe two previously unnamed species (Pérez Farfante 1977b, 1979), as well as the male of another that had not been known before; prepare detailed accounts of the remaining members of the genus; and determine intraspecific variation. I have also discussed their affinities and delimited their respective geographic and bathymetric distribution. The distributional studies resulted in the restriction of the range of P. rectacuta and the considerable extension of that of P. serrata, the latter reported by Pérez Farfante and Ivanov (1979).

The species of the genus are benthic and, except in the eastern Pacific where none has been recorded, occur in the upper part of the continental and insular slopes of tropical, subtropical, and certain temperate regions of the world. All species have been found in the Indo-West Pacific, except P. serrata, which is restricted to the Atlantic, where it is present on both the eastern and western slopes. These shrimps are frequent and often abundant components of the catches made between 250 and 600 m, and two of the species are commercially exploited.

PRESENTATION OF DATA

In the account of the species, most of the terminology used for features of the petasma, thelycum, and appendix masculina follows that proposed by Pérez Farfante (1969, 1971). The measurement of rostrum length is the linear distance from apex to orbital margin, that of carapace length (cl) is the distance between orbital margin and the midposterior margin of the carapace, and, finally, that of total length (tl) is the distance from the apex of the rostrum to posterior end of the telson. All measurements are made to the nearest 0.5 mm. The petasmata have been described and depicted unfolded, and the illustrations made from stained specimens.

MATERIAL

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

BMNH British Museum (Natural History), London.

¹Systematics Laboratory, National Marine Fisheries Service, NOAA, National Museum of Natural History, Washington, DC 20560

FISHERY	BUL	LETIN:	VOL.	77,	NO.	4
---------	-----	--------	------	-----	-----	---

- FIU Department of Biological Sciences, Florida International University, Miami, Fla.
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
- MP Muséum National d'Histoire Naturelle, Paris.
- ORI Oceanographic Research Institute, Durban.
- RMNH Rijksmuseum van Natuurlijke Historie, Leiden.
- SAM South African Museum, Cape Town.
- UMML Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Fla.
- USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C.
- VNIRO All Union Research Institute of Marine Fisheries and Oceanography, Moscow.
- YPM Peabody Museum of Natural History, Yale University, New Haven, Conn.
- ZSI Zoological Survey of India, Calcutta.

Penaeopsis Bate 1881

- Penaeus. Bate 1881:173 [part]. Alcock and Anderson 1899:278. [Not Penaeus Fabricius 1798].
- Penaeopsis Bate 1881:182 [type-species, Penaeopsis serratus Bate 1881, designated by Bouvier 1905a:981]; 1888:273. Bouvier 1905b:747; 1908:3. A. Milne Edwards and Bouvier 1909:220 [part]. De Man 1911:53 [part]. Balss 1925:228. Schmitt 1926:319 [part]. Burkenroad 1934a:48 [part, subgenus Penaeopsis]. Kubo 1949:320. Balss 1957:1519 [part]. Burkenroad 1959:285 [Neither Peneopsis Faxon 1895, or Penaeopsis Yokoya 1941, Barnard 1950]. Gender: feminine. Placed on the Official List of Generic Names in Zoology as Name 1821, International Commission on Zoological Nomenclature 1969, Opinion 864:139.
- Parapenaeus Smith 1885:172 [part]. Alcock 1905:519 [part]; 1906:30 [part]. De Man 1911:77 [part]. Balss 1925:228.

Metapenaeus Wood-Mason 1891:271 [part].

Diagnosis.—Body slender, integument glabrous. Rostrum armed only with dorsal teeth; epigastric

tooth separated from first rostral tooth by approximately 0.35 length of carapace; two low and sharp adrostral carinae, dorsal one running along bases of teeth. Carapace without longitudinal or transverse sutures; orbital and branchiostegal spines lacking; antennal and hepatic spines moderately long; pterygostomian spine well developed; cervical sulcus well defined, its posterior extremity placed slightly anterior to midlength of carapace, and relatively far ventral to dorsal midline; hepatic sulcus, reaching pterygostomian spine, well marked anteriorly, shallow posterior to hepatic spine; anterior part accompanied by sharp carina; branchiocardiac carina present. Abdomen carinate dorsally from fourth through sixth somites (carina rounded on fourth, keellike on posterior somites, continuous posterolaterally with paired short spines on fourth and fifth somites, and with sharp spine posteriorly); sixth somite bearing interrupted cicatrix on lateral surface, and pair of minute spines posteroventrally. Telson with median sulcus flanked by sharp carinae, and pair of moderately long, fixed lateral spines preceded by two or three pairs of small, movable spines. First article of antennular peduncle bearing long subdistal "parapenaeid spine" on ventromedian margin; antennular flagella with length about 0.75 to almost twice that of carapace; ventral flagellum sexually dimorphic, in male shorter than dorsal and strongly modified, with proximal part forming rigid, flattened, semicircular loop, bearing basal scale and ending distally in usually conspicuous, blunt knob; distal part straight and somewhat compressed. In female, ventral flagellum also bearing basal scale, but straight and longer than dorsal. Mandibular palp two jointed, proximal article short, subtriangular (oriented with base distally), distal article considerably longer than proximal, broadly oval. First maxilla with broad unjointed palp not produced distally. Flagellum of first maxilliped slender, overreaching distal exite of coxa. Third maxilliped lacking basial spine. Basial and ischial spines on first percopod, always lacking on third. Exopods (small but not vestigial) on all maxillipeds and pereopods. Petasma symmetrical, lacking channeled, hornlike distolateral projections; dorsomedian lobule bearing distal and proximal plates; rib of dorsolateral lobule produced into conspicuous, flattened, proximal process. Appendix masculina small but well developed and relatively heavily sclerotized. Thelycum with well-developed median plate on

sternite XIII, plate on sternite XIV elongate and bearing paired seminal receptacles disposed longitudinally rather than transversely. Pleurobranchia on somites IX-XIII; rudimentary, filamentose arthrobranchia on somite VII, anterior and posterior arthrobranchiae on somites VIII-XII, and only posterior arthrobranchia on somite XIII. Epipod on first maxilliped (if proximal exite of coxa is considered an epipod) and second maxilliped and on first to third pereopods.

In this genus the petasma is structurally very simple, consisting of a plain trough that is neither produced as distal or distolateral hornlike or broad projections, nor bears distal elements associated with the four lobules. The pestasmal lobules are reinforced by plates and ribs: a distal plate and a proximal plate on the dorsomedian lobule, and two longitudinal ribs. One of the longitudinal ribs extends along the dorsolateral lobule and is typically produced proximally as a process the shape of which varies with the species, the other rib forms the ventral costa and occupies the free margin of the ventrolateral lobule. This petasma is similar to that of the genus Penaeus, but, in other respects, Penaeopsis does not resemble the latter; instead, it is closely related to *Metapenaeopsis* which, surprisingly, exhibits an asymmetrical petasma that is also the most complex among the Penaeoidea.

Small juvenile *Penaeopsis* are armed with an anteriorly directed, sharp spine on sternites XIII and XIV. Both spines disappear in larger males, whereas in females that on sternite XIII is either lost or persists, although considerably reduced, at the apex of the median plate, which, in itself, represents an expansion of the basal portion of the spine. The spine on sternite XIV disappears entirely or becomes incorporated in the median ridge or protuberance of that sternite. As Burkenroad (1934a) has stated, the occurrence of these sternal spines is a larval character present on the postmysis stages of many Penaeidae.

Despite the homogeneity of the few species (six, of which only four were known prior to 1976) currently assigned to the genus *Penaeopsis*, the first three described were assigned to two genera

(Bate 1881). Subsequently, various authors have referred Bate's species to four different genera. Schmitt (1926) contributed to our knowledge of the genus when he recognized common superspecific characters in the "small '*Pengeopsis* serratus' group." Unfortunately, the characters he chose led him to include within this assemblage two species that are currently recognized as members of the genus Metapenaeopsis: M. coniger (Wood-Mason 1891) and M. andamanensis (Wood-Mason 1891). Schmitt cited the absence of anterior arthrobranchia on somite XIII as one of the characters of the "group," a valid Penaeopsis character common to all of the species except those two mentioned above, which he assigned to *Penaeopsis* although he was aware that they possessed such arthrobranchia.

A few years later Burkenroad (1934a) presented an enlightened discussion of two of the four Series—Parapenaeus and Trachypenaeus -into which he (1934b) divided the Penaeinae [= Penaeidael. His excellent choice of characters for the definition of the genera resulted in very few changes in his classification during the 45 yr that have elapsed since the publication of the two contributions. Among the few alterations that have been made in the taxa recognized by him was the reelevation of Metapenaeopsis to generic rank; he had considered *Penaeopsis* and *Metapenaeopsis* to be subgenera of the genus *Penaeopsis*. The members of these two species-groups are closely allied, because both species-groups possess a carapace lacking longitudinal and transverse sutures but bearing pterygostomian spines, two or more well-developed movable spines on the lateral margins of the telson anterior to the fixed pair, and exopods on all maxillipeds and percopods. However, the two taxa exhibit characters that are now considered to be of generic value, i.e., branchial formula, thelycal features, and basic structure of both the petasma and appendix masculina (for a detailed account of Metapenaeopsis see Pérez Farfante 1971). These characters were employed by Kubo (1949) in diagnosing the two groups as distinct genera, a revision that is now generally accepted.

Key to Species of Penaeopsis

1.	Telson bearing three pairs of movable spines	2
	Telson bearing two pairs of movable spines	3

Hepatic spine situated distinctly ventral to level of antennal spine; branchiocardiac carina short, its anterior extremity relatively far from hepatic sulcus. Thelycum with plate of sternite XIV angular anterolaterally; median plate of sternite XIII cordiformP. rectacuta

Penaeopsis balssi Ivanov and Hassan 1976

Figures 1-6

- Penaeopsis challengeri?. Balss 925:228, fig. 4 [not Penaeopsis challengeri De Man 1911].
- Penaeopsis serratus. Ramadan 1938:68, fig. 13a-d [not Penaeus serratus Bate 1881, or Penaeopsis serratus Bate 1881].
- ?Penaeopsis rectacuta. Kensley 1969:154 [not Penaeus rectacutus Bate 1881].
- Penaeopsis rectacuta. Kensley 1972:20, fig. 8G-I [not Penaeus rectacutus Bate 1881].
- Penaeopsis serrata. Starobogatov 1972:390, fig. 40. Crosnier and Jouannic 1973:11, pl. 2, fig. 3 [not

Penaeus serratus Bate 1881, or Penaeopsis serratus Bate 1881].

Penaeopsis balssi Ivanov and Hassan 1976:1, fig.
1-2 [holotype, ⁹, Zool. Mus. Acad. Sci. U.S.S.R. Leningrad, 1/62552; type-locality, off southern Mozambique, 25°26' S (not 23°26' S as stated in original description, Boris G. Ivanov²), 33°31' E, 410 m, Van Gogh stn 264]. Pérez Farfante 1977b:173.

Material.

KENYA-29, BMNH, off mouth of Tana

²Boris G. Ivanov, All Union Research Institute of Marine Fisheries and Oceanography (VNIRO), Moscow, pers. commun. 1979.

River, Kipini, staff Institute of Oceanographic Sciences. 3° , BMNH, off Formosa Bay, 290 m, 15 February 1975, staff Institute of Oceanographic Sciences. 1° 1° , USNM, off Ras Ngomeni, 300-310 m, 12 December 1975, *Professor Mesyatsev.* 4° , BMNH, off Kenya, 15 February 1975, staff Institute of Oceanographic Sciences.

TANZANIA—3 \circ , BMNH, Pemba Channel, 329 m [in Sewell 1935], 14 January 1934, John Murray Expedition stn 110. 1 \circ , BMNH, Pemba Channel, 439 m, 12 January 1934, John Murray Expedition stn 107. 11 \circ 17 \circ , BMNH NW of Zanzibar I, 280 m, 11 January 1934, John Murray Expedition stn 105A. 2 \circ 2 \circ , RMNH, off Kunduchi, 20 km N of Dar es Salaam, 370-400 m, July 1974, C. Sankarankutty.

MOZAMBIQUE—4 \heartsuit , USNM, Monte Belo, 270 m, 28 October 1975, E. Sorensen.

SOUTH AFRICA—4 δ , USNM, 1 \circ , ORI, off Zululand, Natal, 280 m, A. J. de Freitas. 3δ $11\circ$, SAM-USNM, off Natal, 454-280 m, 25 May 1975, *Meiring Naude* stn SM15.

Diagnosis.—Rostrum arched (usually strongly so) and short, reaching at most midlength of second antennular article. Anteroventral angle of carapace obtuse. Telson with two pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing strong mesial crest; proximal process of rib of dorsolateral lobule suboval and directed mesially; ventral costa ending distally in roughly semicircular process. Thelycal plate of sternite XIV with anterior border usually concave on each side of posteromedian projection of sternite XIII and distinctly slanting posterolaterally; median ridge broadest and highest posteriorly, usually gently tapering anteriorly (sometimes reduced to posterior protuberance), and flanked by deep, broad depressions; median plate of sternite XIII subtriangular to orbicular.

Description.-Rostrum (Figure 1) usually markedly arcuate (always strongly so in young), deep basally, and short, in adult reaching at most midlength of second antennular article, its length ranging from about 0.35 to 0.45 that of carapace. Rostral plus epigastric teeth 9-13; rostral teeth evenly spaced and close together along entire margin, second rostral tooth, occasionally third, located in line with orbital margin. Postrostral carina extending posteriorly for short distance beyond epigastric tooth, ending at level of dorsal extremity of cervical sulcus; small dorsal tubercle (occasionally indistinct) located near posterior margin of carapace. Antennal spine slender, sharp, and followed by short but well-defined carina; hepatic spine about as long as, and positioned ventral to but close to level of, antennal spine. Anteroventral angle of carapace (ventral membrane excluded) moderately to broadly obtuse (Figure 2A). Cervical carina sharp, accompanying sulcus well marked; hepatic carina descending obliquely in arc anteroventrally from below hepatic spine, then continuing in almost straight line to apex of pterygostomian spine; hepatic sulcus barely distinct posteriorly; branchiocardiac carina strong to almost indistinct, extending posterodorsally in arc, occasionally in sigmoidal curve, from behind hepatic sulcus to rather near posterior margin of carapace.

Mandible, first maxilla, and first maxilliped as illustrated (Figure 3 A-C).

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in male than in female, about 1.65 as long as second in former and 1.45 in latter; prosartema falling conspicuously short of distal margin of eye, but its long setae reaching that far; stylocerite ending in small spine, length about 0.4 that of first article; distolateral spine long, slender, and sharp, reaching base of distal



FIGURE 1.—Penaeopsis balssi, 9 21.5 mm cl, Formosa Bay, Kenya. Cephalothorax, lateral view. Scale = 5 mm.



FIGURE 2.—*Penaeopsis balssi*, \Im 21.5 mm cl. Formosa Bay, Kenya. A, Anteroventral part of carapace. B, \Im 25 mm cl, off Kunduchi, 20 km N of Dar es Salaam, Tanzania. Telson and right uropod, lateral view. C, Same specimen, tip of telson, dorsal view. Scales: A, C = 2 mm; B = 5 mm.

0.3 of second article. Flagella in both male and female similar to those of *P. rectacuta* (see p. 743).

Scaphocerite falling short of, or slightly overreaching, distal end of antennular peduncle; lateral rib ending in sharp spine not quite reaching terminal margin of lamella. Antennal flagellum incomplete in specimens studied.

Third maxilliped extending at least to base of second antennular article and at most to distal 0.4 length of third; ratio of dactyl/propodus 0.75-0.80.

First perceoped extending to distal end of carpocerite or exceeding it by length of dactyl. Second perceoped surpassing carpocerite at least by dactyl and at most by propodus and 0.2 length of carpus (also reaching between distal 0.3 of first antennular article and about midlength of second). Third perceoped reaching at least to midlength of second article and at most to near end of peduncle. Fourth perceoped overreaching carpocerite by 0.8 length of dactyl or by as much as length of dactyl and propodus. Fifth pereopod extending to distal 0.2 of first article or as far as distal 0.3 of second. Order of pereopods in terms of their maximum anterior extensions: first (shortest), fourth, second, fifth, and third. Third maxilliped falling slightly short of third pereopod.

Abdomen with sixth somite elongate, about 1.7 times maximum height, bearing almost indistinct, interrupted cicatrix on lateral surface. Telson (Figure 2B) armed with two pairs of small, movable spines; pair of fixed spines long, extending about midlength of terminal portion (Figure 2C); terminal portion hastate, convex dorsally, its length about 7 times basal width. Mesial ramus of uropod overreaching apex of telson by as much as 0.15 its own length; lateral ramus exceeding mesial one by as much as 0.3 its own length.

Petasma (Figure 4A, B) with dorsomedian lobule produced in relatively broad distomedian projection, bearing elongate distal plate and subtriangular proximal plate raised mesially in strong crest; rib of dorsolateral lobule terminat-



FIGURE 3.—Penaeopsis balssi, \Im 38.5 mm cl, off Natal, South Africa. A, Mandible. B, First maxilla. C, First maxilliped (all from left side). Scale = 5 mm.

PEREZ FARFANTE: REVISION OF PENAEID SHRIMP GENUS PENAEOPSIS



FIGURE 4.—Penaeopsis balssi, & 25 mm cl, off Kunduchi, 20 km N of Dar es Salaam. A, Petasma, dorsal view. B, Ventral view. C, Right appendix masculina, dorsal view. Scales = 1 mm.

ing proximally in flattened, mesially directed suboval process. Ventrolateral lobule with distolateral portion broadly rounded, its rather flexible marginal part broad (extending beyond level of tip of ventral costa) and slightly reflexed inwardly; distal part of ventral costa curving dorsomesially and ending in conspicuous, subsemicircular process (free from, though closely appressed to, margin of dorsolateral lobule) reaching about level of cincinnuli.

Appendix masculina (Figure 4C) transversely oval, about twice as broad as long, dorsally convex but for lateral depression, and bearing mesial patch of long setae continuing as increasingly narrower band of shorter setae along distal margin.

Thelycum (Figure 5) with anterior border of plate of sternite XIV posterolaterally inclined, plate produced into paired rather elongate, small lobules flanking posteromedian projection of sternite XIII, almost flat to distinctly convex ventrolaterally, and abruptly slanting dorsomesially toward deep, usually broad, submedian depressions flanking median ridge; latter broad and most prominent basally, tapering and becoming low anteriorly, sometimes reduced to short basal protuberance; lateral portions of sternite XIV densely studded with long setae, row of similar ones extending along anterior border of thoracic ridge, and others forming patch at base of median



FIGURE 5.—Penaeopsis balssi, ♀ 21 mm cl, off Formosa Bay, Kenya, Thelycum ventral view. Scale = 1 mm.

ridge. Median plate of sternite XIII subtriangular to orbicular, densely studded with long setae radiating from naked central depression; posteromedian projection broad, subrectangular, with posterior margin straight or emarginate. Sternite XII armed with posteromedian subconical tooth (apex slightly displaced anteriorly and sometimes produced in slender spine) and bearing narrow median carina; oblique pair of ridges extending posterolaterally from base of tooth.

Spermatophore similar to that of P. rectacuta (see p. 746).

Maximum lengths.—Males 30 mm cl, 128 mm tl; females 37 mm cl, 150 mm tl.

Geographic and bathymetric ranges.—Indian Ocean, off the coast of Africa (Figure 6), from Somalia to Natal, South Africa, and also off Madagascar, at depths between 280 and 977 m (northernmost record and maximum depth from Balss 1925). The records of this species, as well as those of *P. jerryi*, from Madagascar are not included in Figure 6, because Crosnier and Jouannic (1973) reported the occurrence of these shrimps and their bathymetric ranges in the surrounding waters, but did not cite the localities at which they have been found.

Affinities.-Penaeopsis balssi can be distinguished readily from other members of the genus by the usually strongly arcuate and short rostrum, which in adults does not surpass midlength of the second antennular article; in the other species it is straight, slightly sinuous or only somewhat arched, and overreaches the second article or often even the peduncle. The structure of the genitalia in P. balssi is closer to that of P. rectacuta than to those of its other congeners. In the petasma of P. balssi, however, the rather flexible, distolateral part of the ventrolateral lobule is broad, and the ventral costa terminates apically in a broad, nearly rounded process, whereas in that of P. rectacuta the distolateral part is relatively narrow, and the ventral costa terminates in a much narrower process. Furthermore, the proximal process of the dorsolateral lobule is suboval and directed mesially in P. balssi; whereas in P. rectacuta it is nearly circular and extends proximally. The thelycum in P. balssi has the plate of sternite XIV flat to strongly convex laterally instead of slanting directly from the border as it does in *P. rectacuta*, and its median ridge is more prominent caudally than in the latter species. These two shrimps differ also by the anteroventral angle of the carapace, about 90° in the latter and obtuse in P. balssi.

Variation.-In this species the rostrum is usually strongly arched, but in occasional specimens it is only sightly so; the number of rostral teeth ranges from 8 to 12, and although in most specimens the second tooth is situated opposite the orbital margin, in some, the third tooth occupies this position so that two teeth, instead of one, are on the carapace. As in P. rectacuta, the scaphocerite falls short of, reaches, or overreaches the end of the antennular peduncle. In males the distomedian projections of the petasma may be asymmetrical (Ivanov and Hassan 1976), and in some their free margin is scalloped; also the rounded distolateral portion of the ventrolateral lobule occasionally is conspicuously expanded distally. In females, the thelycal plate of sternite XIV varies from nearly flat to strongly convex laterally, and the median ridge may extend to, or end before reaching, the posteromedian projection of the median plate of sternite XIII; the latter plate may be subtriangular, cordiform, or orbicular, and its projection has the caudal margin either straight or shallowly emarginate; also, the posteromedian tooth of sternite XII, often low conical, may be produced into a rather long apical spine directed anteriorly.

Remarks.—According to Boris G. Ivanov (see footnote 2) the coordinates provided by Ivanov and Hassan (1976) for Van Gogh stn 34, where two female and two male paratypes were obtained, were incorrect, that the latitude should have been cited as $25^{\circ}23'$ S instead of $23^{\circ}23'$ S.

Ramadan (1938) illustrated the thelyca of an adult and two juveniles in different stages of development. In the juveniles, the submesial depressions are represented by paired pits, and the median plate of sternite XIII is well defined and produced into a sharp, slender, apical spine. This latter feature is not included in Ramadan's illustrations but was observed by me during the examination of the juveniles available to Ramadan, which range in size from 8 to 12 mm cl.

Penaeopsis challengeri De Man 1911

Figures 6-10

Penaeus serratus Bate 1881:182 [lectotype, by present action, ⁹, BMNH 1978.323; type-locality, off Matuku, Fiji Is., 19°09'35" S. 179°41'50" E, 315 fathoms (576 m), Challenger stn 173]; 1888:268 [part], pl. 37,



FIGURE 6.-Ranges of Penaeopsis balssi, P. challengeri, P. eduardoi, P. jerryi, and P. rectacuta based on published records and specimens personally examined.

fig. 1, 1a-b, 1", 1z, 1br. Alcock and Anderson 1899:278. A Milne Edwards and Bouvier 1909:225.

Penaeus (Metapenaeus) serratus. Alcock and Anderson 1894:145.

Parapeneus serratus. Alcock 1905:520; 1906:52.

Penaeopsis challengeri De Man 1911:76 [part, replacement name only; not female from Siboga Expedition stn 253, which belongs to P. eduardoi]. Schmitt 1926:325. Ivanov and Hassan 1976:4. Pérez Farfante 1977b:173; 1979:208.

Penaeopsis (Penaeopsis) serratus. Burkenroad 1934a:8. Anderson and Lindner 1945:309.

Penaeopsis serratus. Kubo 1949:322.

Penaeopsis serrata. Burukovsky 1974:31.

Not Penaeopsis serratus Bate 1881.

Material.

Bate's syntypic series—Lectotype. Paralectotypes:

Fiji Islands—13 39, BMNH 1978.324, from type-locality (13 from syntypic series assigned to P. eduardoi by Pérez Farfante 1977b).

Diagnosis.—Rostrum slightly arched. Anteroventral angle of carapace obtuse. Telson with two pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa bearing flexible distolateral projection and ending distally in moderately long spine, not reaching level of cincinnuli. Thelycal plate of sternite XIV with anterior border strongly arched on each side of posteromedian projection of sternite XIII, raised in submesial elevations, and bearing posteromedian subrectangular protuberance (sometimes continuous with depressed ridge) armed with median tooth anteriorly.

Description.-Rostrum (Figure 7) slightly arched in adult, considerably so in young, and deep basally. Rostral plus epigastric teeth 12 (12 or 13 according to Bate 1888) in single specimen available (male) with rostrum unbroken, second rostral tooth situated in line with orbital margin. rostral teeth close together except for more anterior ones. Postrostral carina extending posteriorly for short distance beyond epigastric tooth. ending at about level of dorsal extremity of cervical sulcus; minute dorsal tubercle located near posterior margin of carapace. Antennal spine relatively small; hepatic spine larger than, and positioned distinctly ventral to, antennal spine. Anteroventral angle of carapace broadly obtuse (Figure 8A). Antennal carina short; cervical carina sharp, accompanying sulcus well marked; hepatic carina sharp, slanting sinuously from below hepatic spine to pterygostomian spine; branchiocardiac carina very conspicuous, sinuous, and long, extending from short distance behind posterior end of hepatic sulcus posterodorsally almost to margin of carapace.

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in male than in female, about 1.5 times as long as second in former and 1.3 times in latter; prosartema extending to distal margin of first article; distolateral spine slender and sharp, reaching as far as proximal 0.4 of second article; stylocerite ending in small spine, length about 0.4 that of first article. Antennular flagella similar to those of *P. rectacuta*. Scaphocerite almost reaching or slightly sur-



FIGURE 7.—Penaeopsis challengeri, lectotype 9 24.5 mm cl, off Matuku, Fiji Islands. Cephalothorax, lateral view. Scale = 5 mm.



FIGURE 8.—*Penaeopsis challengeri*, lectotype. A, Anteroventral part of carapace. B, Telson and right uropod, lateral view. C, Tip of telson, dorsal view. Scales: A, C = 2 mm; B = 5 mm.

passing distal end of antennular peduncle; lateral rib ending in sharp spine falling short of distal margin of lamella. Antennal flagellum incomplete in available specimens. Third maxilliped reaching between distal 0.4 of second article and proximal 0.3 of third; ratio of dactyl/propodus about 0.65 in males and 0.75 in females.

First percopod surpassing carpocerite by half to entire length of dactyl, armed with distomesial spine on basis and ischium. Second percopod overreaching carpocerite by length of propodus and 0.2 that of carpus (also reaching distal end of first antennular article), with basis and ischium unarmed. Fourth percopod overreaching carpocerite by length of dactyl and 0.2 that of propodus. Remaining percopods broken in specimens studied.

Abdomen with sixth somite elongate, about 1.7 times as long as maximum height, bearing barely distinct cicatrix on lateral surface. Telson (Figure 8B) with lateral margins armed with two pairs of small movable spines; pair of fixed spines (Figure 8C) long, extending as far as base of distal third of terminal portion; terminal portion hastate, distinctly convex dorsally, its length about 5 times basal width. Mesial ramus of uropod slightly overreaching apex of telson (Bate 1888) or overreaching it by as much as 0.2 of its own length, and lateral ramus, in turn, surpassing mesial by as much as 0.3 of its own length.

Petasma (Figure 9A, B) with dorsomedian lobule produced into well-defined distomedian projection, and bearing small distal plate and



FIGURE 9.—Penaeopsis challengeri, & 19 mm cl, off Matuku, Fiji Islands. A, Petasma, dorsal view. B, Ventral view of same. C, Right appendix masculina, dorsal view. Scale = 1 mm.

much larger proximal one, latter raised mesially in conspicuous crest; rib of dorsolateral lobule terminating proximally in subcircular process. Ventrolateral lobule bearing flexible, roughly triangular, subterminal projection distolaterally; ventral costa continuing beyond projection, curving gently dorsomesially, and forming moderately long blunt spine (free from, although closely appressed to, margin of dorsolateral lobule), not reaching level of row of cincinnuli.

Appendix masculina (Figure 9C) transversely oval (considerably broader than long), strongly convex dorsally, and with about two-thirds of dorsal surface covered with short setae.

Thelycum (Figure 10A, B) with anterior border of plate of sternite XIV strongly arched (delimiting broad lobes) on each side of posteromedian projection of sternite XIII, and bearing long setae, latter also present along lateral borders; plate raised in paired submesial elevations separated anteriorly by deep depression, sometimes interrupted by low median ridge, and bearing posteromedian, strong, subrectangular protuberance armed with anterior, compressed tooth. Median plate of sternite XIII roughly pentagonal, setose, bearing central depression continous with median groove reaching, or almost reaching, apex; posteromedian projection short, with posterior margin entire, Sternite XII armed with small subconical, posteromedian tooth and oblique paired ridges across posterior border.

Maximum lengths.—Only male available, a juvenile 14 mm cl, 65 mm tl; lectotypic female, 24 mm cl, 114 mm tl.

Geographic and bathymetric ranges.—Known only from the type-locality, off Matuku, Fiji Islands, (lat. 19°09'35" S, long. 179°41'50" E), 576 m, Challenger stn 173 (Figure 6).

Affinities.—The affinities of *P. challengeri* and *P. balssi* are evident in the rostrum, which in both is arched (although considerably more so in the latter) and deep basally, and in the telsonic armature, which consists of two pairs of movable spines in addition to the fixed pair. *Penaeopsis challengeri*, however, differs strikingly from *P. balssi*, as well as from its other congeners, in the unique structure of the external genitalia. In males of *P. challengeri* the ventrolateral lobule of the petasma bears a flexible, roughly triangular process which does not extend beyond the level of



FIGURE 10.—*Penaeopsis challengeri. A*, \Im 22 mm cl, off Matuku, Fiji Islands. Thelycum, ventral view. *B*, Lectotype. Thelycum, ventrolateral view (*t* airs not shown). Scales = 1 mm.

the tip of the ventral costa, and the latter ends distally in a spine similar to, but shorter than, that of P. eduardoi. The proximal process of the rib of the dorsolateral lobule is subcircular in P. challengeri like that in P. eduardoi and P. rectacuta, but different from the transversely oval one in P. balssi. In females of P. challengeri the plate of sternite XIV is produced in paired, broad anterior lobes, is raised ventrally in a pair of longitudinal, submesial elevations, and bears a subrectangular posteromedian protuberance sometimes continuing anteriorly as a weak, depressed ridge. In the other species the plate, if produced, forms only small anterior lobes, is flat or (in P. balssi) raised in lateral, rather than submesial, elevations, and the posteromedian protuberance is caudally pedunculate in *P. eduardoi* (in the other species a strong median ridge instead of a protuberance is usually present). Finally, in *P. challengeri* the median plate of sternite XIII is subpentagonal instead of semicircular or cordiform and exhibits a central depression which continues anteriorly as a median groove.

Remarks.-As Pérez Farfante (1977b) pointed out, Bate (1888) illustrated the petasma of a male of his Penaeus serratus [7 Penaeopsis challengeri] that actually belongs to a different species, Penaeopsis eduardoi. This male together with nine females and at least one other male were taken of Matuku, Fiji Islands, at Challenger stn 173. Five of these females were identified by Bate as Penaeus rectacutus [they are actually, at least the three that are now in the BMNH, Penaeopsis eduardoi], the other four females are syntypes of his *Penaeus serratus*, and the male must be assumed to be a member of the syntypic series. It is beyond question that the male depicted by Bate as P. serratus is a specimen of Penaeopsis eduardoi: the dorsomedian projections of the petasma are obsolete and each ventral costa is produced in a long spine extending considerably farther distodorsally than that in Penaeus serratus. The probability that Bate also examined the syntypic second male (which is P. serratus, 65 mm tl) is indicated by his statement "Length ... of the largest male 76 mm"; this clearly indicates that he had at least one other male in addition to the "largest" one. The smaller male was in the jar with the three females of "Penaeus rectacutus" [= Penaeopsis eduardoi], but Bate mentioned no male of this species whereas he referred to males of Penaeus serratus; consequently, it seems most likely that the small male P. serratus was mistakingly placed with the three females of the former species. In regard to the number of male specimens recognized by Bate as "Penaeus serratus," it should be mentioned that Alcock and Anderson (1899) stated that "there are two Challenger specimens [of P. serratus] from Fiji in the Indian Museum" and it is possible that one of them is a male that was examined by Bate.

Inasmuch as the type-material of P. servatus Bate included a second species, *Penaeopsis eduardoi*, and a holotype was not designated, it is desirable to select one specimen as the lectotype to associate the name with the species to which it is applied. Although Bate (1888:269) mentioned the "type" of *Penaeus serratus*, there is no indication as to which specimen he was referring; however, he stated that some specimens taken off the Fiji Islands "were placed under *Penaeus rectacutus* because the thelycum corresponds with that species rather than with the type of this [*Penaeus serratus*]." His statement leaves no doubt that it was a female to which he was referring. Because the first specimen specifically cited by him (p. 268) was the "largest female, 114 mm" [24 mm cl], I have selected it as the lectotype of *Penaeus serratus* Bate 1881. This specimen has been assigned BMNH 1978.323.

The very young specimen (a female) taken in the Torres Strait, at *Challenger* stn 184, which Bate (1888) recorded as "*Penaeus serratus*," is actually a member of the genus *Metapenaeopsis*, *M. sinuosa* Dall 1957, or a closely related species.

In the last 45 yr various authors (Burkenroad 1934a; Kubo 1949; Ivanov and Hassan 1976) have pointed out the difficulty in defining the specific characters of "*Penaeus serratus*." The uncertainty was due to Bate's (1881) imprecise original diagnosis and the inadequate, although rather elaborate, description, accompanied by figures lacking detail (e.g., a sketchy one of the thelycum and incomplete representations of the telson which is depicted as lacking movable spines), that was subsequently presented by him (1888). I have studied part of the type-series and offer a new description and illustrations of those specimens, including the only available description of the petasma.

Penaeopsis challengeri, like all of its congeners except P. rectacuta and P. jerryi, possesses only two pairs of movable spines on the telson. This character was noted by Bate (1888); however, in discussing the relationships of P. eduardoi with other members of Penaeopsis, I (1977b) erroneously stated that P. challengeri exhibits three pairs of movable telsonic spines. The specimens examined by me at the time were the four female syntypes in only one of which the telson is entire, but it had been bent and torn in such a way that its sharp edge projected laterally in what appeared to be a pair of minute movable spines. My confirmation of Bate's observation on the spination of the telson has been based on a reexamination of the just mentioned female, and a study of the male which, although caught together with the four female syntypes of "Penaeus serratus," was not explicitly cited by him.

Alcock and Anderson (1899) concluded that "P.

serratus" [= P. challengeri] lacks an epipod on somite XII (third pereopod), whereas P. rectacuta has one. This observation is in error; not only both of these species possess such an epipod, but also its presence is typical of all members of the genus.

Penaeopsis eduardoi Pérez Farfante 1977

Figures 6, 11-14

- Penaeus rectacutus. Bate 1888:266 [part], pl. 36, fig. 2z. ? Villaluz and Arriola 1938:38, pl. 3, fig. 3.
- Penaeus serratus. Bate 1888:268 [part], pl. 37, fig. 1", 1q.
- Parapenaeus rectacutus. De Man 1911:82; 1913, pl. 8, fig. 26a-c. Yokoya 1933:9.
- Penaeopsis rectactus. Kubo 1949:322, fig. 1H; 8J; 19C; 23A-B; 36K-L; 47J; 58P; 76A, F; 78K; 118 A-E, [?F], G; 119.
- Penaeopsis challengeri. De Man 1911:76 [part, \Im from Siboga-Expedition stn 253]. Ivanov and Hassan 1976:4.
- Penaeopsis rectacutus. Burukovsky 1974:31, fig. 37a-c.
- Penaeopsis eduardoi Pérez Farfante 1977b:172, fig. 1-4 [holotype, [♀], USNM 168298; typelocality, Balayan Bay, Luzon I., Philippines, 13°41'00" N, 120°47'05" E, 366 m, Albatross stn 5116]. Pérez Farfante 1979:208.
- Not Penaeus rectacutus Bate 1881, or Penaeus serratus Bate 1881, or Penaeopsis challengeri De Man 1911.

Material.—For list of records see Pérez Farfante 1977b. Additional records are:

PHILIPPINES-13, USNM, Wof Cabo Engaño, N Luzon, 410 m, 12 November 1908, *Albatross* stn 5325. 3, USNM, W of San Fernando Pt, Luzon, 315 m, 10 May 1909, *Albatross* stn 5440. 9δ 8 \circ , USNM, Balayan Bay, Luzon, 366 m, 20 January 1908, *Albatross* stn 5116. $1\circ$, VNIRO, Burias Pass, Sibuyan Sea, 400 m, 1 June 1973, *Lira* haul 71. 1δ , USNM, off Calapan, Mindoro I, 198 m, 2 February 1908, *Albatross* stn 5121. 2δ 1 \circ , USNM, Macajalar Bay, Mindanao, 479 m, 5 August 1909, *Albatross* stn 5506.

INDONESIA—1 $^{\circ}$, USNM, off Tanakeke I, Flores Sea, 386 m, 21 December 1909, *Albatross* stn 5662. 1 $^{\circ}$, VNIRO, S of Roti I, Timor Sea, 400 m, 1 June 1973, *Lira*, Ó. A. Petrov. 1 $^{\circ}$ 2 $^{\circ}$, VNIRO, S of Timor I, Timor Sea, 320-355 m, 5 May 1973, *Lira*, O. A. Petrov.

Diagnosis.-Rostrum straight or sinuous, and long, reaching or overreaching third antennular article. Anteroventral angle of carapace broadly obtuse. Telson with two pairs of movable spines. Petasma with proximal plate of dorsomedian lobule lacking mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa lacking distolateral projection and ending distally in long spine extending beyond level of row of cincinnuli. Thelycal plate of sternite XIV with anterior border weakly to distinctly arched on each side of posteromedian projection of sternite XIII and strongly sloping posterolaterally; lateral borders turning mesially behind midlength, then posteriorly; short posteromedian protuberance caudally pedunculate.

Description.—Rostrum (Figure 11) horizontal or somewhat upturned, straight or slightly sinuous (strongly arched in young), and long, reaching at least midlength of third antennular article and often overreaching peduncle, its length ranging from about 0.7 to 0.9 that of carapace. Rostral



 $\label{eq:FIGURE 11.-Penaeopsis eduardoi, holotype \ \ \ 27\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5\ mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral$

plus epigastric teeth 8-15, basal rostral teeth close together, ultimate 3 or 4 usually relatively widely spaced; first rostral tooth situated in line with orbital margin. Postrostral carina low, although well defined, behind epigastric tooth, ending at about posterior 0.4 length of carapace, beyond level of dorsal extremity of cervical sulcus; small dorsal tubercle located near posterior margin of carapace. Antennal and hepatic spines subequal in size, latter situated distinctly ventral to antennal spine. Anteroventral angle of carapace broadly obtuse (Figure 12A). Antennal carina short; cervical carina sharp, accompanying sulcus well marked; hepatic carina sigmoid anteriorly (from below hepatic spine to apex of ptergostomian spine), hepatic sulcus well marked along carina, very shallow posteriorly. Branchiocardiac carina, extending well behind hepatic sulcus posterodorsally to near margin of carapace, indistinct in many large individuals.

Antennular peduncle with length equivalent to about 0.65 that of carapace, third article stouter and longer in male than in female, about 1.50 as long as second in former and 1.25 in latter; prosartema not quite reaching distal margin of first article; distolateral spine long, slender, and sharp, reaching between basal 0.65 and distal margin of second article; stylocerite ending in small spine, length about 0.4 that of first article. Flagella similar to those of *P. rectacuta*, but ventral flagellum in male with less conspicuous knob at junction between semicircular proximal part and straight distal part.

Scaphocerite extending to, or barely surpassing, antennular peduncle; lateral rib ending in sharp spine ending slightly short of distal margin of lamella. Antennal flagellum broken in specimens examined, but not <2.5 as long as body.

Third maxilliped of male extending as far as distal 0.35 of third antennular article, that of female to distal margin; ratio of dactyl/propodus about 0.70 in male and 0.75 in female.

First perceoped extending to about distal end of carpocerite. Second perceoped overreaching carpocerite by length of dactyl or by almost entire propodus (i.e., reaching at least distal 0.4, at most 0.1, of first antennular article). Third perceoped of male reaching between proximal 0.35 and distal end of second article, that of female, between midlength and distal end of third article. Fourth perceoped extending to distal end of carpocerite or surpassing it by length of dactyl. Fifth perceoped reaching at least midlength of second article or



FIGURE 12.—Penaeopsis eduardoi, holotype. A, Anteroventral part of carapace. B, Telson and right uropod, dorsal view. Scales = 5 mm.

slightly overreaching third. Order of percopods in terms of their maximum anterior extensions: first, fourth, second, third, and fifth (or fifth, and third). Third maxilliped reaching about as far as fifth percopod.

Abdomen with sixth somite elongate, about 1.7 times maximum height, bearing rather strong, usually interrupted cicatrix on lateral surface. Telson (Figure 12B) with lateral margins armed with two pairs of small, movable spines; pair of fixed spines very long, in young reaching level of apex of telson; terminal portion hastate, its length 6-7 times basal width. Mesial ramus of uropod reaching, or slightly overreaching, apex of telson; lateral ramus surpassing mesial one by almost 0.2 of its own length.

Petasma (Figure 13A, B) with distomedian projection virtually obsolete, distal plate relatively broad, and proximal plate flush with surrounding membranous portion, lacking mesial crest. Rib of dorsolateral lobule terminating proximally in subcircular process. Ventral costa with distolateral portion situated marginally (where bent inward), curving rather gently at about 120° and continuing in long spine distodorsally beyond row of cincinnuli.

Appendix masculina (Figure 13C) transversely oval, broader than long, width 1.35-1.60 length, strongly convex dorsally, and bearing short setae around entire margin.

Thelycum (Figure 14) with anterior border of



FIGURE 13.—*Penaeopsis eduardoi*, δ 16.5 mm cl, off Matuku, Fiji Islands. *A*, Petasma, lateral view of left half. *B*, Ventral view. *C*, Right appendix masculina, dorsal view. Scales = 1 mm.



FIGURE 14.—*Penaeopsis eduardoi*, holotype. Thelycum, ventral view. Scale = 1 mm.

plate of sternite XIV faintly to distinctly convex on each side of posteromedian projection of sternite XIII, and conspicuously sloping posterolaterally; lateral borders sharply turning mesially behind midlength then posteriorly before joining posterior thoracic ridge; plate densely setose anteriorly, strongly slanting dorsomesially toward deep anteromedian portion, and armed with short, caudally pedunculate posteromedian protuberance. Median plate of sternite XIII semicircular to subcordiform (with blunt apex), flat, covered with setae; posteromedian projection caudally bifurcate. Sternite XII bearing posteromedian, semiconical, broad (rather than compressed) tooth; oblique pair of strong, sharp ridges extending posterolaterally from base of tooth.

Maximum lengths.—Males 26 mm cl, about 114 mm tl; females 34 mm cl, about 130 mm tl.

Geographic and bathymetric ranges.—Penaeopsis eduardoi has been found off the Fiji Islands and from Japan through the Philippines and Indonesia to the Timor Sea (Figure 6), in depths between 289 and 570 m.

Previously, Pérez Farfante (1977b) noted that the range of this species extends to the "southwestern part of the Bay of Bengal." In their treatment of "Metapenaeus rectacutus" [= P. jerryi], Alcock and Anderson (1894) stated (in the account of the deep sea Crustacea collected in the Bay of Bengal and Laccadive Sea by the Investigator during the seasons 1891-92 and 1893-94) that they had little hesitation in identifying the females with Bate's "Penaeus rectacutus," but that the males "appear to agree in every detail ... with Spence Bate's figures and descriptions of Penaeus serratus." Because the male "Penaeus serratus" figured by Bate is a member of Penaeopsis eduardoi, I assumed that the males available to them belonged to the latter species. On the basis of their statement that "M. rectacutus" was common in the Bay of Bengal between 100 and 280 fm (183 and 357 m) and my noting the fact that the stations established by the Investigator during the years and within the depth limits cited above were all located in the southwestern part of the Bay of Bengal, I was led to the conclusion that P. eduardoi had been found in the latter area. Further studies, together with the fact that no specimen of *P. eduardoi* has been reported west of the Strait of Malacca, have inclined me to believe that Alcock and Anderson probably misidentified the males of "Metapenaeus rectacutus" [= Penaeopsis jerryi] as "Penaeus serratus" [= Penaeopsis eduardoi]. It should be added that the specimens of "M. rectacutus" examined by the later authors are no longer extant (G. Ramakrishna³).

Affinities.-Penaeopsis eduardoi differs from P. rectacuta and P. jerryi in possessing two pairs of movable spines on the telson, a character it shares with two other Indo-West Pacific species, P. challengeri and P. balssi, as well as with the amphi-Atlantic P. serrata. Penaeopsis eduardoi, however, can be distinguished from all its congeners by features of the petasma and thelycum. It is the only species in which the distomedian projections of the petasma are obsolete, the proximal plate lacks mesial crest, and the ventral costa is produced in a long, distal spine extending beyond the row of cincinnuli. The thelycum, in turn, is unique in that the plate of sternite XIV exhibits a caudally pedunculate posteromedian protuberance, whereas in all the other species the latter is represented by a ridge or protuberance which is broad caudally or lacks a peduncle. Furthermore, sternite XII is armed with an elongate, broad basally, semiconical, anteriorly directed tooth, which in the other members of *Penaeopsis* is indistinct or either laterally compressed, or short, subconical and directed ventrally or anteroventrally.

Variation.-Discussed by Pérez Farfante 1977b.

Penaeopsis jerryi Pérez Farfante 1979

Figures 6, 15-19

- Metapenaeus rectacutus. Wood-Mason 1891:274. Alcock 1901b:50. Alcock and Anderson 1894:145.
- Peneus rectacutus. Alcock 1898:73.
- Penaeus rectacutus. Alcock and Anderson 1899:278.
- Peneus (Parapeneus) rectacutus. Alcock 1901a:17 Alcock and McArdle 1901, pl. 49, fig. 5.
- Parapeneus rectacutus. Alcock 1902:268, fig. 62;
 1905:520 [part]; 1906:33, pl. 6, fig. 19, 19a-b.
 Kemp and Sewell 1912:16. ?Balss 1925:228.
- Parapenaeus rectacutus. Schmitt 1926:319.
- Penaeopsis rectacutus. Schmitt 1926:321. Ramadan 1938:67, fig. 12a-b. Sewell 1955:202. Kurian 1964:216.
- Penaeopsis rectacuta. Holthuis and Rosa 1965:3
 [part]. George 1966:342. Jones 1967:1337;
 1969:747. George 1969:27. Longhurst 1971:224. Starobogatov 1972:390 [key, but not figures]. Crosnier and Jouannic 1973:12, pl. 3, fig. 3. Ivanov and Hassan 1976:5, fig. 3.
- Penaeopsis jerryi Pérez Farfante 1979:208, fig. 1-4 [holotype, ^Q, BNMH 1978:325; type-locality: off Berbera, Somalia, Gulf of Aden, 10°29'48" N, 45°01'48" E, John Murray Expedition stn 16].
 Not Penaeus rectacutus Bate 1881.

Material.

Holotype. Paratypes:

YEMEN—23 29, USNM 171430, off Saihut (15°10' N, 50°58' E), 240-239 m, 16 May 1971, A. D. Druzhinin.

SOMALIA—203 499, BMNH 1978.326, collected with holotype.

INDIA—23 29, USNM 171431, off Cochin, summer 1978, Staff of the Department of Marine Science, University of Cochin. 19, USNM 42755, off False Divi Pt (15°56'50"N, 81°30'30"E), 439-505 m, 24 December 1890, *Investigator* stn

³G. Ramakrishna, Superintending Zoologist, Zoological Survey of India, pers. commun. 20 March 1978.

120. 23 19, ZSI 2589-95/10, N of North Andaman I (14°13' N, 93°40' E), 677-766 m, 8 April 1898, Investigator stn 235.

Diagnosis.-Rostrum straight or sinuous (occasionally convex basally, straight anteriorly), and long, reaching or overreaching third antennular article. Anteroventral extremity of carapace forming angle of about 90°; hepatic spine located at about same level as that of antennal spine; branchiocardiac carina with anterior end very close to hepatic sulcus. Telson with three pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa ending distally in short, relatively narrow process. Thelycal plate of sternite XIV with anterior border broadly arched on each side of posteromedian protuberance of sternite XIII and strongly inclined posterolaterally; anterolateral and posterolateral corners of plate arched; median ridge broadest and most salient posteriorly, often gradually tapering anteriorly, sometimes reduced to posterior tubercle; median plate of sternite XIII subsemicircular to trilobed.

Description.—Rostrum (Figures 15, 16) almost horizontal, straight or slightly sinuous (occasion-

ally convex basally, straight anteriorly), falling short of to overreaching distal margin of antennular peduncle, its length 0.8-0.9 that of carapace. Rostral plus epigastric teeth 12-16 (usually 12-14), second (occasionally first) rostral tooth situated in line with orbital margin, basal teeth close together, those toward apex more widely spaced, and extending almost to tip of rostrum, but sometimes only to base of anterior 0.2. Postrostral carina extending posteriorly to about level of dorsal extremity of cervical sulcus; minute dorsal tubercle located near posterior margin of carapace. Antennal spine moderately long; antennal carina short but prominent. Hepatic spine slightly larger than, and situated at about same level as (rather than ventral to), antennal spine. Anteroventral extremity of carapace forming angle of about 90° (Figure 17A). Cervical carina sharp, accompanying sulcus well marked; hepatic carina slanting sinuously from below hepatic spine to pterygostomian spine; branchiocardiac carina strong, with anterior extremity almost reaching posterior end of hepatic sulcus and extending posteriorly to near margin of carapace.

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in mature male than in



FIGURE 15.—Penaeopsis jerryi, 9 17.5 mm cl, off Berbera, Gulf of Aden, Somalia. Lateral view. Scale = 5 mm.



FIGURE 16.—Penaeopsis jerryi, holotype ♀ 20.5 mm cl, off Berbera, Gulf of Aden, Somalia. Cephalothorax, lateral view. Scale = 5 mm.



FIGURE 17.—*Penaeopsis jerryi*, holotype. A, Anteroventral part of carapace. B, Telson and left uropod, dorsal view. Scales: A = 2 mm, B = 5 mm.

female, about 1.6 times as long as second in former and 1.4 in latter; prosartema almost attaining distal margin of first article; distolateral spine slender, sharp, and reaching about midlength of second article. Flagella similar to those of P. rectacuta.

Scaphocerite falling short of to overreaching distal end of antennular peduncle; lateral rib ending in slender spine, falling slightly short of margin of lamella. Antennal flagellum more than twice the length of the animal (Kurian 1964).

Third maxilliped and percopods in most specimens too poorly preserved to allow observations on their maximum anterior extensions.

Abdomen with sixth somite elongate, about 1.7 times height, bearing long, strong, interrupted cicatrix on lateral surface; cicatrix also on fifth and fourth somites. Telson (Figure 17B) with lateral margins bearing three pairs of small, movable spines (occasionally only one or two pairs, rarely with different numbers of spines on margins); fixed spines variable in length, reaching at most base of distal third of terminal portion; terminal portion with length about 6-7 times basal width, narrowly hastate or with lateral margins basally rounded, and dorsal surface moderately convex. Mesial ramus of uropod falling short of to overreaching apex of telson by as much as 0.2 of its own length; lateral ramus overreaching mesial ramus by about 0.2 of its own length.

Petasma (Figure 18A, B) with dorsomedian lobule produced into rather broad distomedian projection, and bearing elongate distal plate and broader, subtriangular proximal plate raised mesially in blunt crest; rib of dorsolateral lobule with distal part straight or turning laterally, and terminating proximally in semicircular or subcircular process. Ventrolateral lobule bearing distally rather flexible and translucent marginal region, reflexed inwardly; distal part of ventral costa curving abruptly dorsomesially and ending in short, relatively narrow process reaching approximately to level of cincinnuli.

Appendix masculina (Figure 18C) considerably broader than long (width about 1.7 length), roughly oval; band of setae extending around free margin, broadening and forming patch mesially.

Thelycum (Figure 19) with plate of sternite XIV roughly subelliptical in outline, its anterior border strongly arcuate and inclined posterolaterally, and anterolateral and posterolateral corners arched, plate sloping toward submedian depressions of variable length, and bearing long marginal setae; median ridge broadest and most prominent posteriorly, tapering anteriorly, sometimes reduced to posterior tubercle. Posterior thoracic ridge narrow and projecting anteroventrally at base of median ridge, fringed anteriorly with closely set setae. Median plate of sternite XIII subsemicircular to roughly trilobed, sometimes with minute anteromedian spine, and covered with setae except for central depression; posteromedian projection broad, with posterior margin entire or very shallowly emarginate. Sternite XII bearing posteromedian, subconical tooth with apex directed anteroventrally; oblique pairs of sharp ridges extending posterolaterally from base of tooth.



FIGURE 19.—Penaeopsis jerryi, holotype. Thelycum ventral view. Scale = 1 mm.

Spermatophore bearing mesial element which in impregnated females lies exposed on the thelycum.

Color.—Red (Wood-Mason 1891), or dark brown with reddish tint (Kurian 1964).



FIGURE 18.—*Penaeopsis jerryi*, δ 19 mm cl, of Berbera, Gulf of Aden, Somalia. A, Petasma, dorsal view. B, Ventral view. C, Paratype δ 21 mm cl, off Cochin, India, right appendix masculina, dorsal view. Scales = 1 mm.

Maximum lengths.—160 mm tl (Crosnier and Jouannic 1973). Largest specimens examined by me: males 23 mm cl, about 107 mm tl; females 33 mm cl, about 138 mm tl.

Geographic and bathymetric ranges.—Indian Ocean (Figure 6), from the Bay of Bengal (Andaman Sea; off Madras) through the Arabian Sea (off Cochin) to the Gulf Aden (off Berbera) and south to off Mozambique and Madagascar. It has been found at depths between 183 and 677 m.

Affinities.—Penaeopsis jerryi differs from the closely related P. rectacuta, from the South China Sea, Philippines, and Indonesia, mainly by the position of the hepatic spine, the length of the branchiocardiac carina, and features of the thelycum.

In *P. rectacuta* the hepatic spine is located at a level distinctly ventral to, instead of about the same level as, that of the antennal spine, and the branchiocardiac carina ends farther from the hepatic sulcus than it does in *P. jerryi*.

The petasmata of the two species, although similar, differ in that the rib of the dorsolateral lobule in P. rectacuta is straight distally and terminates proximally in a subcircular process, whereas in P. jerryi the rib sometimes turns laterally and often ends in a semicircular process.

In P. rectacuta the thelycal plate of sternite XIV is usually roughly trapezoidal, with the anterior border almost straight on each side of the posteromedian projection of sternite XIII, and the anterolateral corners forming angles, whereas in P. jerryi this plate is roughly elliptical with the anterior border arcuate and the anterolateral and posterolateral corners arched. Finally, in P. jerryi the median plate of sternite XIII is subsemicircular [e.g., in females illustrated by Alcock (1906, pl. 6: fig. 19a) and by Ivanov and Hassan (1976, fig. 3) as well as in most of those examined by me], or occasionally weakly trilobed as in the specimen figured by Ramadan (1938, fig. 12b). In a few females I have studied, the plate, although almost semicircular, is produced into a minute anteromedian spine, its general shape thus being quite different from the cordiform median plate of P. rectacuta.

In occasional specimens of P. *jerryi*, the basis of the second pair of percopods is armed with a distomesial spine (Alcock 1901a), a feature that has not been observed in the other species. Also, as pointed out by Ramadan (1938) and confirmed by my observation, some individuals bear less than the tree typical pairs of movable spines on the telson (one or two pairs) and I found one with the spination asymmetrical.

Remarks.—On the basis of the scant information provided by Balss (1925) it has not been possible for me to determine the identity of the two females he recorded as "Parapenaeus rectacutus" from the Nicobar Islands, Bay of Bengal. According to him, the telson bears two pairs of movable spines, a characteristic of three of the five Indo-West Pacific members of the genus-Penaeopsis balssi, P. challengeri, and P. eduardoi. In the same work, however, he identified specimens belonging to P. balssi, which were taken off east Africa, as "?Penaeopsis challengeri"; consequently, it seems very unlikely that the two females belong to P. balssi. It also seems improbable that they are members of *P*. challengeri or *P*. eduardoi because these species are not known to occur in the Indian Ocean. Balss added that in his specimens the second pair of percopods is armed with spines; such have been observed only in occasional individuals of P. jerryi; but three, not two pairs of movable telsonic spines are characteristic of this shrimp typically. Balss' specimens, however, may prove to be atypical P. jerryi because this shrimp is the only species of the genus that has been recorded from the area.

Commercial importance.—Survey fishing off the west coast of India at depths between 175 and 375 m (George 1966, 1969; Jones 1967; Longhurst 1971) demonstrated the presence of P. *jerryi* in sufficient numbers for possible commercial exploitation of this shrimp. Crosnier and Jouannic (1973) noted that this species eventually will become commercially fished off Madagascar.

Penaeopsis rectacuta (Bate 1881)

Figures 6, 20-27

- Penaeus rectacutus Bate 1881:180 [\bigcirc holotype, BNMH; type-locality, between Bohol and Cebu, Philippines, 10°14' N, 123°54' E, 95 fathoms (174 m), Challenger stn 209]; 1888:266 [part], pl. 36, fig. 2, 2", 2 p [fig. 2z = P. eduardoi]. Estampador 1937:493. Domantay 1956:363. Pérez Farfante 1977b:172.
- Parapeneus rectacutus. Alcock 1905:520 [part, references only].

Penaeopsis (Penaeopsis) rectacutus. Burkenroad 1934a:5 Anderson and Lindner 1945:309.

- Penaeopsis rectacuta. Hall 1962:18, fig. 89, 89a, 89b. Holthuis and Rosa 1965:3 [part]. Starobogatov 1972, pl. 5, fig. 39a-b (figures, but not key). Pérez Farfante 1977b:180; 1979:208.
- Common names: needle shrimp; camarón aguja; crevette aiguille.

Material.

PHILIPPINES—Luzon: 5δ 10 %, USNM, SW of Nasugbu, 247 m, 15 January 1908, *Albatross* stn 5110. 1 %, USNM, Balayan Bay, 324 m, 17 January 1908, *Albatross* stn 5112. 1 δ , USNM, Balayan Bay, 366 m, 20 January 1908, *Albatross* stn 5116. 1 %, USNM, off Malabrigo Pt., 198 m, 2 February 1908, *Albatross* stn 5121. 2δ 1 %, USNM, Tabayas Bay, 274 m, 24 February 1909, *Albatross* stn 5372. 3 %, USNM, Tabayas Bay, 348 m, 2 March 1909, *Albatross* stn 5374. 2%, USNM, Albay Gulf, 368 m, 8 June 1909 *Albatross* stn 5459.

Leyte: 2, USNM, off Palompon, 344 m, 16 March 1909, *Albatross* stn 5402. 10 $\stackrel{\circ}{\circ}$ 13 $\stackrel{\circ}{\circ}$, USNM, off Palompon, 333 m, 16 March 1909, *Albatross* stn 5403.

Camotes Is: 2δ 1°, USNM, Off Pacijan, 291 m, 18 March 1909, *Albatross* stn 5408. 1°, USNM, off Pacijan, 346 m, 18 March 1909 *Albatross* stn 5409.

Between Bohol and Cebu (Bohol Strait): Holotype. 13, USNM, 274 m, 15 March 1909, *Albatross* stn 5416. 43 39, USNM, 265 m, 23 March 1909, *Albatross* stn 5411. 33 99, USNM, 296 m, 23 March 1909, *Albatross* stn 5412. 29, USNM, 291 m, 25 March 1909, *Albatross* stn 5418. 39, USNM, 320 m, 25 March 1909, *Albatross* stn 5419. 13 159, USNM, 318 m, 9 April 1908, *Albatross* stn 5197.

Mindanao: $1 \circ 1 \circ$, USNM, off Tagolo Pt, 401 m, 20 August 1909, Albatross tn 5541. $3 \circ 8 \circ$, USNM, off Tagolo Pt, 366 m, 9 August 1909, Albatross stn 5518. $1 \circ 1 \circ$, USNM, off Tagolo Pt, 320 m, 9 August 1909, Albatross stn 5516. $4 \circ 5 \circ$, USNM, NE Tagolo Pt, 320 m, 9 August 1909, Albatross stn 5517. $1 \circ 2 \circ$, USNM, E of Illana Bay, 289 m, 22 May 1908, Albatross stn 5256. $5 \circ$, USNM, Gulf of Davao, 247 m, 18 May 1908, Albatross stn 5247.

INDONESIA-23 82, BMNH, off Sarawak, Borneo, 198 m, 8 December 1955, Manihini stn C5-19. 23 (19 tentatively assigned), VNIRO. SE Timor I, Timor Sea, 320-355 m, 5 May 1963, Lira, O. A. Petrov.

Diagnosis.-Rostrum usually straight, sometimes slightly arched or sinuous, and long, reaching or overreaching third antennular article. Anteroventral extremity of carapace forming angle of about 90°; hepatic spine located ventral to level of antennal spine: branchiocardiac carina with anterior end relatively far from hepatic sulcus. Telson with three pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa ending distally in short, relatively narrow process. Thelycal plate of sternite XIV with anterior border transverse or slightly inclined posterolaterally, straight or somewhat sinuous and with anterolateral corners almost forming right angles; median ridge broadest and most salient posteriorly, usually flasklike or gently tapering anteriorly; median plate of sternite XIII cordiform, with acute apex.

Description.-Rostrum (Figure 20) almost horizontal, usually straight, sometimes slightly arched or sinuous in adult (straight or barely arcuate in young), falling short of or overreaching distal margin of antennular peduncle, its length ranging from about 0.7 to 0.8 that of carapace. Rostral plus epigastric teeth 11-18 (usually 11-14), second rostral tooth (occasionally third) located in line with orbital margin, basal teeth close together, those toward apex variously spaced, and extending almost to end of rostrum but occasionally only to base of distal 0.25. Postrostral carina low, although well defined, behind epigastric tooth, ending just behind dorsal extremity of cervical sulcus; minute dorsal tubercle located near posterior margin of carapace. Antennal spine relatively small; hepatic spine slightly larger than, and situated ventral to level of, antennal spine. Anteroventral extremity of carapace forming angle of about 90° (Figure 21B). Antennal carina almost indistinct; cervical carina sharp, accompanying sulcus well marked; hepatic carina broadly sigmoid, descending obliquely anteroventrally from below hepatic spine, then turning almost anteriorly in slightly concave line to apex of pterygostomian spine; branchiocardiac carina well marked, with anterior extremity not nearly reaching posterior end of hepatic sulcus and ex-



FIGURE 20.—Penaeopsis rectacuta, 9 27 mm cl, Albay Gulf, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5 mm.



FIGURE 21.—Penaeopsis rectacuta. A, 325 mm cl, Balayan Bay, Luzon, Philippines, right flagella (mesial view). B, 227 mm cl, Albay Gulf, Luzon, Philippines, anteroventral part of carapace. C, 228.5 mm cl, Gulf of Davao, Mindanao, telson and left uropod, lateral view. D, Same specimen, tip of telson, dorsal view. Scales: A, B, D = 2 mm; C = 5 mm.

tending posterodorsally to rather near margin of carapace.

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in male than in female, about 1.65 times as long as second in former and 1.40 times in latter; prosartema almost attaining distal margin of first article; distolateral spine slender, sharp, and reaching between proximal 0.3 and, at least, midlength of second article; stylocerite ending in small spine, length about 0.4 that of first article. In both sexes dorsal flagellum not evenly tapering, its stout proximal part suddenly narrowing into filiform distal part; but in male, dorsal flagellum longer than ventral, its length about 1.7 that of carapace, whereas in female, dorsal flagellum shorter than ventral, about as long as carapace. Ventral flagellum in male (Figure 21A) with strong knob at junction between semicircular proximal part and straight distal part; in female, ventral flagellum straight, tapering to filiform distal part. (Shape of both flagella in male and female characteristic of all species of genus.)

Scaphocerite falling short of to surpassing distal end of antennular peduncle, reaching at most as far as base of distal fourth of thickening of dorsal flagellum; lateral rib ending in slender spine, not quite reaching distal margin of lamella. Antennal flagellum broken in shrimp examined.

Third maxilliped extending at least to basal 0.2 of second antennular article and at most to midlength of third; ratio of dactyl/propodus about 0.65 in males and 0.70 in females.

First percopod exceeding carpocerite by tip of dactyl or by as much as length of propodus. Second percopod surpassing carpocerite at least by length of propodus and at most by propodus and 0.3 length of carpus (i.e., reaching between base of second article and proximal 0.2 of third). Third pereopod of male overreaching antennular peduncle by as much as length of dactyl, that of female, by propodus. Fourth pereopod surpassing carpocerite by length of dactyl or by a maximum of dactyl and propodus. Fifth pereopod exceeding antennular peduncle by dactyl or by latter plus 0.4 length of propodus. Order of pereopods in terms of their maximum extensions: first, fourth, second, fifth, and third; fourth pereopod extending almost as far as second, and fifth almost as far as (occasionally farther than) third.

Abdomen with sixth somite elongate, about 1.7 times maximum height, bearing rather prominent interrupted cicatrix on lateral surface. Telson (Figure 21C) with lateral margins bearing three pairs of short movable spines; fixed spines moderately long, extending at most as far as base of distal third of terminal portion; terminal portion (Figure 21D) with length 6-8 times basal width, flasklike in shape, its lateral margins convex or forming widely obtuse angles anteriorly, converging posteriorly, and with dorsal surface subplane. Mesial ramus of uropod reaching apex of telson or overreaching it by as much as 0.20 of its own length; lateral ramus overreaching mesial by about 0.25 of its own length.

Petasma (Figure 22A, B) with dorsomedian lobule produced into rather broad distomedian projection, and bearing elongate distal plate and broader, subtriangular proximal plate raised mesially in low, sometimes sharp crest; rib of dorsolateral lobule terminating proximally in subcircular process. Ventrolateral lobule with distolateral portion broadly rounded, bearing distally rather flexible and translucent marginal region, strongly reflexed inwardly; distal part of ventral costa curving abruptly dorsomesially at about right angle, and ending in short, relatively narrow process (free from, though closely appressed to, margin of dorsolateral lobule) reaching approximately to level of cincinnuli.

Appendix masculina (Figure 22C) considerably broader than long (width 1.7-2.0 length), roughly kidney-shaped; band of relatively long setae extending around free margin, broadening and forming patch mesially, or setae covering more than half of dorsal surface.

Thelycum (Figures 23; 24A, B) with anterior border of plate of sternite XIV transverse or slightly inclined posterolaterally, almost straight or somewhat sinuous on each side of posteromedian projection of sternite XIII, and forming almost right angle with lateral borders. Plate (produced anteriorly in paired small submesial lobules), densely setose laterally, strongly slanting dorsomesially toward deep, usually narrow, submedian depressions; median ridge of variable length, broadening and much higher posteriorly, usually appearing flask-shaped, its bulbous portion cov-



FIGURE 22.—*Penaeopsis rectacuta*, & 17.5 mm cl, Singapore. A, Petasma, dorsal view. B, Ventral view. C, Right appendix masculina, dorsal view. Scale = 1 mm.



FIGURE 23.—Penaeopsis rectacuta, holotype \Im 24 mm cl, Bohol Strait, Philippines. Thelycum, ventral view. Scale = 1 mm.

ered with setae. Posterior thoracic ridge fringed anteriorly with closely set setae. Median plate of sternite XIII cordiform (with acute apex), covered with setae except for central depression (occasionally prolonged across entire width of plate); posteromedian projection subrectangular or subelliptical, with posterior margin entire or, occasionally, shallowly emarginate. Sternite XII bearing posteromedian, often laterally compressed tooth of variable size, sometimes produced in apical spine; oblique pair of sharp ridges extending posterolaterally from base of tooth.

Thelycum in young females (9-11 mm cl) with median plate of sternite XIII produced anteriorly in long, slender spine, and posteromedian projection consisting of only minute knob; plate of sternite XIV bearing short median ridge also produced anteriorly in long, slender spine, latter indistinct in females 13 mm cl.

The female holotype, 26 mm cl, is in poor condition, with many parts missing; however, except for the rostrum, which is almost entirely lost, the carapace is well preserved as are the antennular peduncle, most of the abdomen, and the thelycum. The following characters of the carapace may be readily observed: the second rostral tooth is situated opposite the orbital margin, while the



FIGURE 24.—Penaeopsis rectacuta. A, 9 25.5 mm cl, off Tagolo Point, Mindanao, Philippines. B, 9 24 mm cl, Tabayas Bay vicinity of Marinduque Island, Philippines. Thelyca, ventral view (setae omitted on the legs). Scale = 2 mm.

epigastric tooth is found at the anterior 0.35 of the carapace, and the hepatic spine lies conspicuously ventral to the antennal spine; the postrostral carina extends along anterior 0.55 of the carapace, ending just posterior to the cervical sulcus; and the anteroventral corner forms an angle of about 90°. The antennular peduncle is 0.75 as long as the carapace, the third article is 1.35 times the length of the second, and the stylocerite is 0.4 that of the first article. The scaphocerite falls slightly short of the end of the antennular peduncle, and the terminal spine of the lateral rib does not reach the distal margin of the lamella. The low, sharp middorsal keel of the abdomen extends from the fourth to the sixth somites, and the length of the latter is 1.7 times its maximum height. The thelycum is depicted in Figure 23.

In this species each spermatophore bears a conspicuous, somewhat rigid element which in impregnated females lies over the plate of sternite XIV (Figure 25). The paired elements, which project from the mesial extremity of the sperm sacs enclosed in the seminal receptacles, are joined along their mesial margins and form a roughly circular scale covering a large part of the plate. A similar spermatophore is also found in *P. balssi*, *P. eduardoi*, and *P. jerryi*, the other three Indo-West Pacific species in which I have observed impregnated females.

Maximum lengths.—Males 25 mm cl, about 110 mm tl; females 31 mm cl, about 135 mm tl.

Geographic and bathymetric ranges.—Indo-West Pacific (Figure 6) from the Philippines (Bate 1881) and Timor Sea to the south China Sea (north of Borneo, Hall 1962). It has been found at depths between 174 and 401 m.

Affinities.—Two features of the carapace distinguish P. rectacuta from the closely allied, western Indo-West Pacific P. jerryi: 1) the position of the hepatic spine, which in the former is situated distinctly ventral to the antennal spine whereas it occurs at about the same level in P. jerryi, and 2) the length of the branchiocardiac carina which is relatively short in P. rectacuta (its anterior extremity situated well behind the posterior end of the hepatic sulcus) and is long in P. jerryi (its anterior extremity located quite near the posterior end of the sulcus). In addition, the thelycum of P. rectacuta has the anterior border of the plate of sternite XIV almost straight or slightly sinuous



FIGURE 25.—Penaeopsis rectacuta, \Im 25.5 mm cl, vicinity of western Bohol, Philippines. Compound spermatophore attached to female. Scale = 1 mm.

and forms an angle with the lateral border, whereas in P. *jerryi* it is strongly convex and continuous through a broad arc with the lateral border. Furthermore, the median plate of sternite XIII is cordiform and rather elongate in P. *rectacuta* and subsemicircular, or occasionally trilobed in P. *jerryi*.

Variation.—This shrimp exhibits a rather large number of morphological variations. In the adult the rostrum may be straight, slightly convex or sinuous, and the number of rostral teeth ranges from 10 to 17. The scaphocerite falls short of, reaches as far as or extends beyond, the antennular peduncle. In the females, the anterior border of the plate of sternite XIV (Figure 24A, B) varies from transverse to slightly inclined posterolaterally, the median ridge may be short or extend to the posteromedian projection of sternite XIII, and the submedian depressions that flank the ridge, although most often narrow, may be broad. Furthermore, the setation of the plate, usually extending over the lateral portions, sometimes is absent anteriorly and lacking posteriorly or vice versa. The median plate of sternite XIII usually bears a central depression, but occasionally the latter extends across the entire width of the plate, and the caudal margin of the posteromedian projection, which is straight in most specimens, sometimes exhibits a shallow emargination. Finally, the tooth on sternite XII may vary considerably in size and shape; although usually compressed, it may be subconical or infrequently strongly produced in an apical spine. Sometimes the entire range of variation of certain characters is represented within a single lot. Among the 16 specimens collected at Albatross stn 5197, off western Bohol, Philippines, the number of rostral teeth ranges from 11 to 17 and in several lots females, in which the posteromedian projection of sternite XIII is straight caudally were found together with others bearing a slightly emarginate one. These variations, thus, are intraspecific, not even associated with local populations.

A discussion of the features that separate this species from *P. eduardoi* was presented by Pérez Farfante (1977b). As noted by Hall (1962), typical *P. rectacuta* possesses longer percopods than do specimens reported by De Man (1911) as "Parapenaeus rectacutus," which actually are Penaeopsis eduardoi. In *P. rectacuta*, however, the third maxilliped is slightly shorter than that of *P. eduardoi*.

Remarks.—The specimens from off Borneo recorded by Hall (1962) as P. rectacuta were in my opinion, correctly identified. The suggestion by Ivanov and Hassan (1976) that they might belong to P. balssi—under the synonymy of which the authors, "with some hesitation," included the record preceded by a question mark-is not justified. I have found that the petasmata of these specimens are typical and the thelyca vary but slightly from that of the holotype. The only obvious difference is that in the females, the median ridge of the plate of sternite XIV, although broadest posteriorly, is not flasklike. Also, this plate is rather densely setose laterally, as indicated by Ivanov and Hassan, and the transverse thoracic ridge bears a row of setae across the anterior border which is lacking in the holotype; it is probable that in the latter the setae have been lost, as have almost the entire rostrum, telson, and at least part of the appendages during or after capture.

Pérez Farfante (1978) described three specimens found in the waters of the Philippines having gonopores on the coxae of the fifth pair of pereopods and both male and female genitalia. The petasma, appendix masculina, and thelycum of the three exhibit unique features, but in most respects these shrimp are markedly similar to members of *P. rectacuta*. It was concluded that they are probably anomalus intersexes of this species. Recently, Boris G. Ivanov of VNIRO, kindly made available to me three specimens (two males and one female; Figures 26A-C; 27)



FIGURE 26.—Penaeopsis rectacuta, δ 21 mm cl, S of Timor Island, Timor Sea. A, Petasma, dorsal view. B, Ventral view. C, Right appendix masculina, dorsal view. Scales: A, B = 2 mm; C = 1 mm.



FIGURE 27.—?Penaeopsis rectacuta, \Im 31 mm cl, S of Timor Island, Timor Sea. Thelycum, ventral view. Scale = 2 mm.

collected in the Timor Sea by O. A. Petrov during a cruise of the RV Lira. There is little doubt in my mind that the males are members of P. rectacuta. The female, except for the thelycum, also possesses features typical of P. rectacuta. In the thelycum the anterior border of the plate of sternite XIV is considerably more inclined posterolaterally than in typical females. The anterior part of the median ridge is uniquely divided by a groove, and the bulbous posterior part is larger and overlaps the thoracic ridge. Finally, the posteromedian projection of sternite XIII is considerably larger than in any specimen of *P. rectacuta* examined by me. A bopyrid isopod was found in the branchial chamber of this specimen; it might have been responsible for these peculiar features of the female genitalia.

Commercial importance.—Although no estimates of the economic importance of this species have been recorded, it has been cited among the commercially exploited shrimps of the Philippines by Domantay (1956), and as of economic value throughout its range by Holthuis and Rosa (1965).

Penaeopsis serrata Bate 1881

Figures 28-38

- Penaeopsis serratus Bate 1881:183 [syntypes by implication, 1δ 1, MCZ 7200, 1, MP; typelocality, off Barbados, "Gulf of Mexico," Blake stn 275, 218 fathoms (399 m)]. Bouvier 1905a:981; 1908:5. A. Milne Edwards and Bouvier 1909:221, pl. 4, fig. 1-4. De Man 1911:53. Balss 1925:229. Schmitt 1926:320. Boone 1927:80 [part]. Maurin 1952:91; 1961:530; 1962:210; 1963:1. Burkenroad 1963:172. Maurin 1965:116; 1968a:33; 1968b:479, fig. 3 P. s. Lagardère 1971:33, fig. 39-42. [Placed on the Official List of Specific Names in Zoology as Name No. 2276, International Commission on Zoological Nomenclature 1969, Opinion 864:141].
- Parapenaeus megalops Smith 1885:172 [syntypes, 2° , USNM 7262, S of Curaçao, 11°43' N, $69^{\circ}09'30''$ W, 208 fathoms (380 m), Albatross stn 2125. 5δ 1°, USNM 7263, Golfo de Urabá, $9^{\circ}30'45''$ N, 76°25'30'' W, 155 fathoms (283 m), Albatross stn 2143]. Rathbun 1901:102. Bouvier 1908:7. A. Milne Edwards and Bouvier 1909:225. Hay and Shore 1918:379, pl. 25, fig. 8. Schmitt 1926:319.
- Parapeneus megalops. Faxon 1896:163. Alcock 1905:520; 1906:52.
- Artemesia talismani Bouvier 1905a:982 [syntypes, 23 29, MP 304, off Guerguerat, Western Sahara, 25°41′ N, 15°56′ W (of Greenwich; 18°16′ W of Paris on label accompanying specimens), 410 m, 9 July 1883, Talisman stn 72; type-locality, "côtes du Maroc et du Sahara"]; 1908:7. A. Milne Edwards and Bouvier 1909:225.
- Penaeopsis serratus var. antillensis A. Milne Edwards and Bouvier 1909:226, pl. 3, fig. 10, pl. 4, fig. 5 [holotype, ♂, MCZ 7201; type-locality, off St. Kitts, 208 fathoms (380 m) 1978-79, Blake stn 148]. De Man 1911:53.
- Penaeopsis megalops. De Man 1911:53. Schmitt 1926:320. Burkenroad 1936:139. Kubo 1949:321. Voss 1955:8, fig. 19. Burkenroad 1963:172. Bullis and Thompson 1965:5. Joyce and Eldred 1966:26. Anderson and Bullis 1970:116. Roberts and Pequegnat 1970:49. Pequegnat and Roberts 1971:8. Longhurst 1971:237. Pérez Farfante 1971:4. Crosnier and Forest 1973:305. Burukovsky 1974:31.

Parapeneus paradoxus. Boone 1927:79 [part; not Neopenaeopsis paradoxus Bouvier 1905b = Peneus longirostris Lucas 1846].

- Penaeopsis (Penaeopsis) megalops. Burkenroad 1934a:12, fig. 1. Anderson and Lindner 1945:309. Springer and Bullis 1956:9.
- Peneopsis megalops. Bullis 1956:10. Bullis and Rathjen 1959:18.
- Penaeopsis serrata. Holthuis and Rosa 1965:4.
 Longhurst 1971:220. Ivanov and Hassan 1976:4. Pérez Farfante 1977a:297; 1977b:180. Pérez Farfante and Ivanov 1979:204. Pérez Farfante 1979:208. Wenner and Boesch 1979:110.
- Common names: megalops shrimp; camarón megalops; crevette megalops.

Material.

UNITED STATES—New Jersey: 19, USNM, E of Barnegat, 275-290 m, 12 August 1972, Gosnold cruise 197, stn 111.

North Carolina: $3 \circ$, USNM, off Back Bay, 331m, 23 July 1969, *Oregon II* stn 10659. $113 \otimes 9$, USNM, SE of Cape Lookout, 366 m, 10 June 1962, *Silver Bay* stn 4160. 113×79 , USNM, off Carolina Beach, 412 m, 16 November 1956, *Combat* stn 178. 273×379 , USNM, SE of Cape Fear, 459 m, 16 November 1956, *Combat* stn 179.

South Carolina: 2389, USNM, off Charleston, 366 m, 28 May 1949, *Albatross III* stn 19-22. 1319, USNM, off Port Royal Sound, 366 m, 23 January 1972, *Oregon II* stn 11734.

Georgia: 1° , USNM, off Ossawa, 183 m, 21 January 1972, Oregon II stn 11719. 1° , 1° , USNM, off Ossawa, 238 m, 21 January 1972, Oregon II stn 11720.

Florida: 23 69, USNM, off St Augustine, 329 m, 20 January 1972, Silver Bay stn 3677. 2, USNM, off Flagler Beach, 338 m, 3 February 1962, Silver Bay stn 3728. 23 29, UMML, off Delray Beach, 549 m, 13 September 1966, Gerda stn 806. 13 39, FIU, NW of Cayo Sal Bank, 366 m, 14 May 1978, Bellow stn 5 #3. 10 3 89, USNM, SW of Marguesas Keys 402-269 m, 2 February 1968, Gerda stn 969. 6♂ 7♀, USNM, S of Dry Tortugas, 366 m, 10 July 1955, Oregon stn 1330. 15 3 21 9, UMML, S of Dry Tortugas, 329-**366 m, 28 April 1969**, Gerda stn 1096. 30328, USNM, S of Dry Tortugas, 348 m, 13 April 1954, Oregon stn 1005. 73 389, USNM, 31 July 1930, stn 37-38; 3 3 20 9, USNM, 402-433 m, 31 July 1930, stn 38-30; 8 3 13 9, USNM, 366-430 m, 8 July 1931, stn 21-31; 28 δ 113 \Im , USNM, 256-329 m, 31 July 1931, stn 37-30; 2 δ , USNM, 256-360 m, 30 July 1932, stn 67-32; all from the Tortugas area, W. L. Schmitt. 9δ 15 \Im , USNM, NW of Dry Tortugas, 366 m, 10 June 1959, *Silver Bay* stn 1201. 7δ 2 \Im , USNM, S of St George I, 366 m, 21 August 1970, *Oregon II* stn 11180. 15 \Im , USNM, S of Gulf Beach, 274 m, 16 June 1964, *Oregon* stn 4946.

Alabama: 93 219, USNM, off Mobile Bay, 320 m, 27 April 1951, Oregon stn 314.

Louisana (all from Mississippi Delta area): 14 \Diamond 55 \heartsuit , USNM, 274 m, 23 October 1962, Oregon stn 4002. 9 \Diamond 15 \heartsuit , USNM, 732 m, 3 June 1959, Silver Bay stn 1181. 1 \Diamond 3 \heartsuit , USNM, 366 m, 31 January 1955, Oregon stn 1238.

Texas: 10° , USNM, off Galveston, 476 m, 13 March 1969, *Oregon II* stn 10616. 3° 16° , USNM, off Galveston, 457-549 m, 16 April 1952, *Oregon* stn 542. 32° 38° , USNM, off Padre I, 366 m, 28 November 1950, *Oregon* stn 162. 3° 8° , USNM, off Padre I, 430 m, 28 November 1950, *Oregon* stn 163. 1° , USNM, off Port Isabel, 457-476 m, 5 August 1969, *Western Gulf* stn 37.

MEXICO (GULF OF MEXICO)—Tamaulipas: 1 \circ 1 \circ , USNM, off Los Lavaderos, 558 m, 2 June 1970, Oregon II stn 10953. 3 \circ 2 \circ , USNM, SW of Soto la Marina, 329 m, 1 June 1970, Oregon II stn 10951.

Veracruz: $2 \heartsuit$, USNM, off Tecolutla, 375 m, 4 June 1970, Oregon II stn 10958. $2 \heartsuit$, USNM, NE of Punta Roca Partida, 613 m, 5 June 1970, Oregon II stn 10960.

Tabasco: 19, USNM, W of Laguna del Carmen, 430 m, 6 June 1970, Oregon II stn 10963.

Campeche: 1, USNM, off Punta Frontera, 366 m, 15 May 1954, *Oregon* stn 1054.

Yucatan; 463 78%, USNM, Yucatan Channel, 377 m, 19 June 1952, *Oregon* stn 590.

BAHAMA ISLANDS— $1\degree$, USNM, NW of Matanilla Reef, 567 m, 17 July 1965, Gerda stn 664. $2\eth 6\degree$, USNM, W of Grand Bahama I, 494-531 m, 13 June 1969, Gerda stn 1125. $9\eth 3\degree$, USNM, Santaren Channel, 508 m, 22 June 1967, Gerda stn 817.

CUBA-30 \eth 36 \heartsuit , USNM, NE of Las Villas 516 m, 27 June 1970, *Pillsbury* stn 1171. 67 \circlearrowright 24 \heartsuit , USNM, off Las Villas, 512 m, 16 July 1955, *Oregon* stn 1342. 34 \circlearrowright 37 \heartsuit , USNM, off Archipiélago de Sabana, 466 m, 16 December 1969, *Oregon II* stn 10863. 2 \circlearrowright 7 \heartsuit , MCZ, Bahía de Cochinos, 274-311 m, 25 February 1938, *Atlantis* stn 2963B. 3 \circlearrowright 2 \heartsuit , MCZ, Bahía de Cochinos, 402503 m, 25 February 1938, Atlantis stn 2963D.

JAMAICA—63 49, USNM, off Great Pedro Bluff, 530 m, 16 May 1962, Oregon stn 3552. 13 39, USNM, off Great Pedro Bluff, 311 m, 16 May 1962, Oregon stn 3549.

DOMINICAN REPUBLIC—1035, USNM, off Puerto Plata, 421-549 m, 15 October 1963, Silver Bay stn 5166. 29, USNM, off El Macao, 549 m, 17 October 1963, Silver Bay stn 5181.

VIRGIN ISLANDS—23 29, USNM, N of Virgin Is, 165-915 m, 4 March 1933, Johnson-Smithsonian Deep Sea Expedition stn 102. 19, USNM, off Charlotte Amalie, 402 m, 26 September 1959, *Oregon* stn 2606.

PUERTO RICO-19, USNM, N of Culebra I, 366-732 m, 26 February 1933, Johnson-Smithsonian Deep Sea Expedition stn 81. 23 69, USNM, off San Juan, 256-293 m, 25 September 1959, Oregon stn 2603. 43, USNM, NE of Puerto Rico, 183-549 m, 4 March 1933, Johnson-Smithsonian Deep Sea Expedition stn 100. 23 29, USNM, off Añasco, 549 m, 6 October 1959, Oregon stn 2652.

LESSER ANTILLES-79, USNM, NW of Dog I, 628 m, 6 December 1969, Oregon II stn 10835. 19, USNM, W of Anguilla, 658 m, 7 December 1969, Oregon II stn 10837. 29δ 14 , USNM, E of Saba, 549-585 m, 18 May 1967, Oregon stn 6695. 13 δ 179, USNM, E of St Christopher, 578 m, 8 December 1969, Oregon II stn 10842. 13 δ 99, UMML, E of Capesterre, Guadeloupe, 466-640 m, 16 July 1969, Pillsbury stn 936. 253 17♀, USNM, off Dominica, 503 m, 4 March 1966, Oregon stn 5926. 13 3 14 ♀, USNM, E of Dominica, 649 m, 5 March 1966, Oregon stn 5929. 2δ 49, UMML, SE of Pointe du Cap, St Lucia, 274-567 m, 7 July 1969, Pillsbury stn 891. 33 29, USNM, E of Georgetown, St Vincent, 348-466 m, 6 July 1969, Pillsbury stn 877. 13 19, MCZ 7200, + 19, MP, syntypes of Penaeopsis serratus Bate, off Barbados, 399 m, 5 March 1879, Blake stn 275. 11359, USNM, S of Bonaire, 393 m, 27 September 1963, Oregon stn 4405. 19, USNM, S of Curaçao, 380 m, 18 February 1884, Albatross stn 2125. 2, syntypes of Parapenaeus megalops Smith, USNM 7262, S of Curaçao, 380 m, 18 February 1884, Albatross stn 2125.

WESTERN CARIBBEAN—203 16°, USNM, Arrowsmith Bank, 225-250 m, 14 March 1958, *Pillsbury* stn 587. 183 5°, USNM, NW of Rosalind Bank, 274 m, 7 June 1962, Oregon stn 3628. 23°, USNM, NW of Rosalind Bank, 366 m, 23 August 1957, Oregon stn 1883. 8 \circ 83 \circ , USNM, W of Quita Sueño Bank, 450-576 m, 31 January 1971, *Pillsbury* stn 1355. 1 \circ 5 \circ , USNM, W of I de Providencia, 457 m, 21 November 1968, Oregon II stn 10200. 7 \circ 4 \circ , USNM, W of I de San Andrés, 457 m, 23 May 1962, Oregon stn 3572.

MEXICO (CARIBBEAN SEA)—Quintana Roo: 1 \degree , RMNH, SE of I Mujeres, 567-570 m, 23 May 1967, *Pillsbury* stn 585. 1 \degree , USNM, W of I de Cozumel, 439-463 m, 16 March 1968, *Pillsbury* stn 600. 26 \degree 34 \degree , USNM, W of I de Cozumel, 412-457 m, 16 March 1968, *Pillsbury* stn 602.

BRITISH HONDURAS—92 $\,^\circ$, USNM, NE of Stann Creek, 219-311 m, 10 June 1962, Oregon stn 3637. 25 $_{\circ}$ 11 $_{\circ}$, YPM, N of Glover Reef, 669 m, 20 April 1925, Pawnee stn 35. 9 $_{\circ}$ 32 $_{\circ}$, YPM, N of Glover Reef, 885 m, 20 April 1925, Pawnee stn 36.

NICARAGUA-2 \Im , USNM, NE of Is del Maíz, 549-585, 23 May 1962, Oregon stn 3576.

PANAMA-19, USNM, off Bocas del Toro, 512 m, 25 May 1962, Oregon stn 3583. 13 29, USNM, Golfo de los Mosquitos, 457 m, 31 May 1962, Oregon stn 3599. 39, USNM, NE of Belén, 439 m, 30 May 1962, Oregon stn 3592.

COLOMBIA— $5 \circ 1 \circ$, syntypes of Parapenaeus megalops Smith 1885, USNM 7263, Golfo de Urabá, 283 m, 23 March 1884, Albatross stn 2143. $1 \circ$, UMML, SW of I de Barú, 135-130 m, 14 July 1966, Pillsbury stn 375. $19 \circ$, USNM, off I de Barú, 366 m, 25 May 1964, Oregon stn 4882. $12 \circ$, USNM, W of Cartagena, 170-150 m, 1 August 1968, Pillsbury stn 797. $1 \circ$, USNM, off Cabo de la Aguja, 176-165 m, 31 July 1968, Pillsbury stn 785. $3 \circ 2 \circ$, USNM, W of Cabo de la Vela, 357 m, 20 November 1970, Oregon II stn 11289.

VENEZUELA—7 δ 7 \Im , UMML, NE of San Juan de los Cayos, 384-607 m, 26 July 1968, *Pillsbury* stn 753. 23 δ 6 \Im , USNM, off Is Los Testigos, 366-439 m, 24 September 1964, Oregon stn 5037. 5 δ 2 \Im , USNM, NE of Punta Araguapiche, 366 m, 3 November 1957, Oregon stn 1981.

TRINIDAD-TOBAGO— 1° , USNM, NE of Charlotteville, 165-183 m, 21 September 1964, Oregon stn 5021.

GUYANA-33 39, USNM, NE of Berbice R, 366 m, 6 November 1957, Oregon stn 2004.

FRENCH GUIANA—1 δ 14 \circ , USNM, N of Roche Brigandin, 457 m, 10 November 1957, *Ore*gon stn 2028.

PEREZ FARFANTE: REVISION OF PENAEID SHRIMP GENUS PENAEOPSIS

BRASIL—20 29, USNM, SE of Rio Grande do Sul, 345-260 m, 19 January 1967, Akademic Knipovich.

MOROCCO—2, RMNH, off Rabat, 300-600 m, 12 May 1971, Cadiz trawlers, RMNH Expedition. 2, RMNH, Casablanca, 28 June 1951, C. Maurin.

WESTERN SAHARA—133, VNIRO-USNM, N of Boca Grande, 640-600 m, 11 May 1965, R. N. Burukovsky. 1339, VNIRO-USNM, off Villa Bens, 420-380 m, 11 May 1965, R. N. Burukovsky. 2329, MP 304, syntypes of Artemesia talismani Bouvier 1905, off Guerguerat, 410 m, 9 July 1883, Talisman stn 72.

Diagnosis.—Rostrum straight, basally arcuate or sinuous, and long, reaching or overreaching third antennular article. Anteroventral angle of carapace broadly obtuse. Telson with two (rarely three) pairs of movable spines. Petasma with proximal plate of dorsomedian lobule thickened mesially but lacking mesial crest; proximal process of rib of dorsolateral lobule subrectangular; ventral costa ending distally in relatively broad, inwardly excavate process. Thelycal plate of sternite XIV with anterior border broadly arched on each side of posteromedian projection of sternite XIII, and anterolateral extremities uniquely produced into lobules of variable lengths; median ridge usually ovoid or tear-shaped; median plate of sternite XIII subsemicircular to roughly pentagonal with depression extending across entire width.

Description.—Rostrum (Figures 28, 29) almost horizontal or somewhat upturned, variable in shape, straight, or basally arcuate or sinuous (strongly arched in young, Figure 30), and long, reaching between midlength of third article of antennular peduncle and proximal fourth of thickened portion of dorsal flagellum, its length rang-



FIGURE 28.—Penaeopsis serrata, 9 27 mm cl, W of Puerto Rico. Lateral view. Scale = 10 mm.



FIGURE 29.—Penaeopsis serrata, 9 27 mm cl, Golfo de los Mosquitos, Panama. Cephalothorax, lateral view. Scale = 5 mm.



ing from about 0.65 to 0.85 that of carapace. Rostral plus epigastric teeth 10-19 (rarely <13 or >16), basal rostral teeth close together, those toward apex variously spaced; second or first (latter usually in young) rostral tooth situated in line with orbital margin. Postrostral carina low, although well defined, behind epigastric tooth ending at about level of dorsal extremity of cervical sulcus; small dorsal tubercle located near posterior margin of carapace. Antennal and hepatic spines subequal in size, latter situated distinctly ventral to antennal spine. Anteroventral angle of carapace broadly obtuse (Figure 31A). Antennal carina short; cervical carina sharp, accompanying sulcus well marked; hepatic carina sigmoid anteriorly (from below hepatic spine to apex of pterygostomian spine), hepatic sulcus well marked along carina, shallow posteriorly. Branchiocardiac carina very weak, extending posterodorsally to near margin of carapace.

Antennular peduncle with length equivalent to about 0.70 that of carapace, third article sexually dimorphic, slightly longer and considerably stouter in males than in females, about 1.4 times as long as second in former and 1.2 times in latter; prosartema reaching, or almost reaching, distomesial margin of eye; distolateral spine long, slender, and sharp, reaching between midlength and distal fourth of second article; stylocerite ending in small spine, about 0.4 as long as first article. In male, ventral flagellum shorter (even when forcibly straightened) than dorsal, with inconspicuous knob at junction between proximal and distal parts; dorsal flagellum 1.5-1.8 times as long as carapace. In female, ventral flagellum (tapering to filiform distal part) longer than dorsal, 1.5-1.7 times as long as carapace; dorsal flagellum 0.8-1.0 times as long.

Scaphocerite falling slightly short of to somewhat overreaching antennular peduncle; lateral rib ending in slender spine, falling short of distal margin of lamella. Antennal flagellum long, about 3 times tl of shrimp (based on measurements made by me on freshly collected specimens during a Caribbean Sea cruise of *Oregon II* in 1969).

Third maxilliped extending at least to basal 0.4 of second antennular article and at most to distal end of third; ratio of dactyl/propodus about 0.75 in males and 0.85 in females.

First percopod reaching distal end of carpocerite or overreaching it by as much as 0.8 length of propodus. Second percopod surpassing carpocerite by at least length of propodus and by as much as that of propodus and half length of carpus (i.e., reaching between base of second antennular article and midlength of third). Third percopod



FIGURE 31.—Penaeopsis serrata, \Im 29.5 mm cl, Dry Tortugas Islands, Fla. A, Anteroventral part of carapace. B, Telson and left uropod. C, Tip of telson. Scales: A, C = 2 mm; B = 5 mm.

attaining distal end of antennular peduncle or overreaching it by as much as length of propodus. Fourth pereopod surpassing carpocerite by tip of dactyl or by maximum of dactyl plus about onehalf length of propodus. Fifth pereopod extending at least to midlength of second antennular article and at most to distal end of third. Order of pereopods in terms of their maximum anterior extensions: first, fourth, second, fifth, and third; fourth pereopod extending almost as far as second. Third maxilliped reaching about as far as fifth pereopod.

Abdomen with sixth somite elongate, about 1.8 times maximum height, bearing faint, interrupted cicatrix on lateral surface. Telson (Figure 31B) with lateral margins armed with two (rarely three) pairs of short, slender movable spines; fixed spines moderately long, extending at most as far as base of distal third of terminal portion; terminal portion (Figure 31C) with length 6-9 times basal width, spear shaped and with dorsal surface convex. Mesial ramus of uropod almost reaching or surpassing apex of telson by as much as 0.15 of its own length; lateral ramus overreaching mesial ramus by 0.25-0.30 of its own length.

Petasma (Figure 32A, B) with dorsomedian lobule produced in well-defined distomedian projection, bearing narrow distal plate and broader proximal plate thickened mesially, but not form-



FIGURE 32.—Penaeopsis serrata, & 22 mm cl, Golfo de los Mosquitos, Panama. A, Petasma, dorsal view. B, Ventral view. C, Right appendix masculina, dorsal view. D, Mesial view. Scales = 1 mm.

ing crest; rib of dorsolateral lobule terminating proximally in flattened subrectangular process. Ventrolateral lobule with distolateral portion broadly rounded, its rather flexible marginal part narrow and turned inwardly; ventral costa curving abruptly dorsomesially and ending in relatively broad process (with interior surface excavate) reaching approximately to level of cincinnuli; costa bearing ventral (inner) row of setae along attached margin.

Appendix masculina (Figure 32C, D) considerably broader than long (width 1.7 to almost twice length), subelliptical, convex mesially, flat laterally, and bearing mesial patch of setae.

Petasmal endopods becoming joined in male 12 mm cl. Armature of sternites XIII and XIV in very small juvenile male (discussed on p. 723) illustrated in Figure 33.

Thelycum (Figure 34) with anterior border of plate of sternite XIV slightly to strongly inclined posterolaterally, broadly arched on each side of posteromedian projection of sternite XIII; plate of sternite XIV with anterolateral extremities produced laterally into lobules of variable lengths, and lateral portions setose and raised (ventrally), slanting dorsomesially toward corresponding, narrow, submedian depression; median ridge usually ovoid or tear-shaped, sometimes subtriangu-



FIGURE 33.—*Penaeopsis serrata*, ♂ 10 mm cl, NE of Puerto Rico. Somites XII-XIV, ventral view. Scale = 1 mm.



FIGURE 34.—Penaeopsis serrata, \Im 29.5 mm cl, Dry Tortugas Islands, Florida. Thelycum, ventral view. Scale = 1 mm.

lar, greatly raised except for short, low, anterior part abutting projection of sternite XIII, and naked posteriorly; posterior thoracic ridge also lacking setae. Median plate of sternite XIII broad, subsemicircular, cordiform or roughly pentagonal, with transverse depression across its entire width, bearing or lacking minute anteromedian spine, and covered with densely set setae anteriorly; posteromedian projection strongly developed, broad, with posterior margin slightly emarginate to deeply bifid and studded with numerous posteriorly pointed setae. Sternite XII bearing posteromedian subconical tooth, its apex pointed ventrally or anteroventrally; oblique pair of ridges extending posterolaterally from base of tooth.

Seminal receptacles (Figure 35A, B) consisting of paired bilobed membranous sacs, derived from invaginations of sternite XIV. Submedian sac large, extending posteriorly to rather near caudal margin of sternite XIV, other smaller one extending laterally; both diverging from broad anPEREZ FARFANTE: REVISION OF PENAEID SHRIMP GENUS PENAEOPSIS



FIGURE 35.—Penaeopsis serrata, 230 mm cl, N of Thunder Knoll, off Honduras. Sperm receptacles. A, Ventral view. B, Dorsal view (specimen stained). Scale = 2 mm.

teromedian sinus. Receptacles opening through long, paired slits located between sternites XIII and XIV, and separated by narrow, shallow, anteromedian portion of sternite XIV.

Stages in development of thelycum: in female 8 mm cl (Figure 36A), plate of sternite XIV bearing median ridge produced anteriorly in long, sharp spine not quite reaching sternite XIII; anterolateral portions ventrally convex, covering invaginations (seminal receptacles) from slitlike openings along anterior margin of plate. Sternite XIII with small triangular median plate produced in long, sharp anteromedian spine reaching margin of sternite XII. Sternite XII bearing minute, sharp posteromedian tooth and pair of ridges extending posterolaterally from base of tooth (tooth and ridges changing little except increasing in size to facies in adult).

In female 9.5 mm cl (Figure 36B), plate of sternite XIV with spine proportionately smaller than that in few preceding instars, farther removed from sternite XIII; anterolateral portions with openings of seminal receptacles enlarged and still exposed. Sternite XIII with spine on median plate distinctly overreaching sternite XII.

In female 10.5 mm cl (Figure 36C), plate of sternite XIV with median ridge virtually reaching sternite XIII and bearing no more than rudiment of spine; anterolateral portions overlapping sternite XIII mesially, obscuring openings of sperm receptacles, and frequently produced laterally in short lobules, continuous with well-defined, exposed hoods. Median plate of sternite XIII with spine still slightly overreaching sternite XII.

In female 12.5 mm cl (Figure 36D), plate of sternite XIV with elongate trapezoidal (usually becoming tear-shaped with increasing size) median ridge, reaching sternite XIII; basal part of ridge with strong median elevation; anterolateral portions broadly overlapping sternite XIII and bearing prominent lobules partly obscuring hoods. Median plate of sternite XIII considerably broadened, its anteromedian spine minute and far removed from sternite XII; plate produced in



FIGURE 36.—*Penaeopsis serrata*. Stages of development of thelycum in juvenile females. A, 8 mm cl; B, 9.5 mm cl; C, 10.5 mm cl; D, 12.5 mm cl. All from W of Cartagena, Columbia. Scale = 1 mm.

broad posteromedian projection markedly overlapping sternite XIV.

In *P. serrata* the spermatophore does not bear the mesially attached element which in impregnated females of *P. balssi*, *P. eduardoi*, *P. jerryi*, and *P. rectacuta* (i.e., all the Indo-West Pacific species except P. challengeri of which I have not examined females carrying spermatophores) lies exposed on the thelycum. Because of the absence of this element, impregnated females of the former species are not readily recognized. The presence of a certain accessory structure in the spermatophore of one species of a genus and its absence in others is not unique in *Penaeopsis*; for in the family Penaeidae a similar phenomenon occurs even within the species of a subgenus. In the genus *Penaeus*, for instance, of the eight species of the American subgenus *Farfantepenaeus* Burukovsky 1972, only one, *Penaeus (F.) brevirostris* Kingsley 1878, exhibits a large, fleshy structure attached to the sperm sac which in impregnated females entirely covers the plate of sternite XIV, much like the comparable accessory element of the spermatophores of *P. rectacuta* and *P. eduardoi*. The spermatophores of the remaining seven species of *Farfantepenaeus* lack such a membranous structure.

Color.—This is one of the most beautifully colored shrimp I have seen. The following description is based on observations of a large number of freshly collected specimens obtained during the 1969 cruise of the *Oregon II* in the Caribbean (from Puerto Rico to Antigua).

Body varying from translucent light pink (sometimes with salmon hue) to deep reddish pink, interrupted by an iridescent violet to purple subelliptical patch on gastric region and various other white, deep red, violet or purple markings (lines, bands, patches, dots) on other areas. In many individuals, rostrum with numerous red chromatophores and red tip. Carapace bearing small patch of red chromatophores at base of antennal spine; anterior cardiac region with narrow, deep violet arc or transverse band running ventrally and followed by median, reddish purple subrectangular area. Some coloration continuing laterally in short posterior band, then broadening abruptly on branchiostegites, extending ventrally to margin of carapace and anteriorly to hepatic sulcus; subrectangular area flanked by white band running anteriorly to hepatic region; posterior portion of carapace white. In other individuals entire branchiostegites of highly iridescent, deep reddish pink or reddish purple. Abdominal somites with transverse reddish to purple band along posterior margin of terga; band often divided by narrow white stripe extending along dorsal midline; anterodorsal extremities of pleura bearing brilliant red or purple spot forming striking paired rows; pleura of first five somites marked by reddish to purple marginal line; bearing larger median spot and, occasionally, narrow angular stripe extending from anterodorsal spot on pleuron to median spot of same color as line; sixth somite bordered

only posteriorly by line of same color as that on margin of pleura of preceding somites. Telson with paired ribs and lateral margins reddish to purple. sometimes also fixed spines and line joining their bases similarly colored. Ocular peduncle white with red stripe along margin of cornea; basal article bearing large, brilliant red or deep purple circle. Antennular peduncle highly iridescent pink proximally becoming increasingly reddish distally; distal and sometimes lateral margins of articles red or purple; flagella pink or reddish, fading distally; frequently ventral flagellum white and dorsal reddish. Antennal flagella pink. Pereopods of lighter shade than body, but lateral surfaces usually darker and strongly iridescent. Bases of pleopods white, light pink, or violet with posterolateral surfaces iridescent with deep pink or violet hues; endopods and exopods translucent, and bearing reddish or purplish spot proximally. Uropods with lateral portion of protopod of darker shade than mesial; rami usually of same or lighter color than body but deeper proximally.

Maximum lengths.—Males 120 mm tl; female 150 mm tl (Maurin 1952). Largest specimens examined by me: males 24 mm cl, 112 mm tl; females 34.5 mm cl, 135 mm tl.

Geographic and bathymetric ranges (Figure 37).—Western Atlantic: from east of Barnegat, N.J., south of Martha's Vineyard, Mass. (lat. 40°00' N, long. 70°47' W, coordinates from Haedrich et al. 1975, Gosnold cruise 197, stn 111), through the Gulf of Mexico and the Caribbean south to French Guiana (lat. 7°11' N, long. 52°58' W). Also found at a disjunct locality, off Rio Grande do Sul (lat. 32°45'24"S, long. 50°24'00" W). The record from off Barnegat, which represents the most northerly point at which this shrimp has been found, and that off Rio Grande do Sul, marking the southernmost record of the occurrence of the species, were both reported by Pérez Farfante and Ivanov (1979).

Eastern Atlantic: from south of Cabo San Vicente, Portugal, to off Cadiz, Spain (Maurin 1961, 1965) and off the northwest coast of Africa to Tamzak ("Tamxat") (lat. 17°26' N, long. 16°03' W), Mauritania (Maurin 1968b).

In the western Atlantic, *Penaeopsis serrata* frequents depths between 183 and about 750 m (records of its presence in shallower water are almost certainly erroneous), with maximum concentrations occurring from 300 to 450 m. In the eastern





Atlantic it has been reported between 120 (Lagardère 1971) and 700 m (Maurin 1961).

The temperature-depth relationship for *P. ser*rata is presented in Figure 38. In three areas, two in the Gulf of Mexico and one in the southern part of the Caribbean (off Venezuela), this shrimp shows similar ranges of temperature and depth. In the northeast Gulf, however, the range is apparently more extensive, the animals having penetrated shallower and warmer as well as deeper and colder waters. According to the available data, the population off the southeast coast of the United States occurs within the shallower range depths occupied by other populations, but at lower temperatures. Actually, in that area the shrimp is not restricted to the depths presented in the graph,



FIGURE 38.—Depth-temperature relationships for *Penaeopsis serrata* in four western Atlantic areas (data obtained from *Oregon* and *Oregon II* Station Lists).

because in at least one locality (for which temperature data are lacking) it has been found at about 550 m (see "Material" herein), i.e., only 150 m above the maximum depth at which it has been taken in the northeast Gulf. Because the temperature-depth distribution of the population off the southeast coast of the United States is based on only 12 records, one may only point out the unusual conditions existing in this segment of the range of P. serrata. According to my observations. the specimens of that population exhibit no morphological differences from those of other localities throughout the broad range of the species, but Harvey R. Bullis Jr.⁴ stated that the specimens, observed by him immediately after capture, had a different coloration from those caught elsewhere. Furthermore, Bullis and Rathjen (1959) found that off the southeast coast of the United States P. serrata was most abundant at slightly greater depths than Pleoticus robustus (Smith 1885), whereas in all other areas megalops was not abundant where it occurs with, or at shallower depths than, P. robustus.

Variation.—This species, like most members of the genus, exhibits a large number of characters that are highly variable. Among them, the rostrum, strongly arched in the young, may be straight, arcuate only basally or sinuous in the adult, and horizontal or upturned; the number of rostral teeth ranges from 10 to 19. The scaphocerite may fall short of or surpass the distal end of the antennular peduncle, and the mesial ramus of the uropod may not reach the apex of telson or may extend beyond it by as much as 0.15 of its own length. The thelycal features, especially, show a wide range of variation: the anterior border of the plate of sternite XIV, usually strongly arched on each side of the posteromedian projection of sternite XIII, sometimes is moderately or only slightly so; and the anterolateral lobules of that plate although generally strongly developed are sometimes quite short. The median plate of sternite XIII varies in shape (from subsemicircular to roughly pentagonal), while the posteromedian projection, although always broad, may range from slightly emarginate to deeply bifid. The entire range of variations in some of the characters cited have been observed in animals from the same locality.

ż

At least in the western Atlantic populations, there are also differences in the relative extension of the third maxilliped and pereopods. I have noticed that in the populations of the Caribbean and Atlantic coast of South America they extend distally slightly farther than they do in northern populations. In the former populations the range extension of these appendages falls within the upper half of the limits cited herein and in the northern ones within the lower half. Because most of the few specimens available to me from the eastern Atlantic are poorly preserved, I have been unable to arrive at definite conclusions as to the relative length of the appendages in the populations occurring in that region.

Affinities.—Penaeopsis serrata, the only Atlantic member of the genus, differs from its congeners in that the branchiocardiac carina and interrupted cicatrix on the sixth abdominal somite are very weak, and the knob at the distal end of the semicircular part of the ventral antennular flagellum in the male is rather inconspicuous. More strikingly, it differs from its allies in a number of features of the external genitalia, as pointed out below. It appears to be closer to P. rectacuta than to any of the other species. They share long rostra which tend to possess a large number of teeth (up to 18 in P. serrata and 17 in P. rectacuta), and the second tooth is located at the level of the orbital margin. In both, the hepatic spine is situated ventral to the level of the antennal spine, and the branchiocardiac carina does not approach closely the hepatic sulcus. The petasmata are also rather similar and the telson of P. serrata is sometimes, although rarely, armed with three pairs of movable spines as is typical of that of *P. rectacuta*.

The thelyca exhibit the most obvious differences between the two species. In P. serrata the plate of sternite XIV is uniquely produced into laterally directed lobules, bears an entirely naked and much stronger median ridge (usually subovoid instead of flasklike as it is generally in P. rectacuta), and the posterior thoracic ridge lacks setae across its anterior border. Furthermore, in P. serrata the median plate of sternite XIII, although variable in shape, is generally semicircular or roughly pentagonal, whereas in P. rectacuta it is cordiform. The posteromedian projection of sternite XIII is also broader and emarginate (often deeply) rather than entire as it usually is in P. rectacuta. The males of these species can also be distinguished by the proximal plate of the dorsomedian lobule of the

⁴Harvey R. Bullis, Jr., formerly Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun. December 1978.

petasma which in P. serrata, although thickened mesially, does not form a sharp crest as it does in P. rectacuta; by the proximal plate of the dorsolateral lobule subrectangular in the former and nearly circular in the latter; and by the apical process of the ventral costa which is conspicuously broader in P. serrata than in P. rectacuta.

Remarks.—With reference to the types of this species, both Bate (1881) and A. Milne Edwards considered the account of *P. serratus* included in the A. Milne Edwards' manuscript—later published jointly by A. Milne Edwards and Bouvier (1909)—to constitute the original description; therefore, it seems reasonable to me that the syntypes of this species, from Barbados, designated by A. Milne Edwards and Bouvier are, by implication, also those of Bate. Furthermore, Bate (1881:180) stated that "I have not had an opportunity of examining the branchial apparatus to feel quite certain that the genus [*Penaeopsis*] is a good determination," thereby indicating that he had not examined any specimens of *P. serrata*.

Commercial importance.—Extensive explorations in the Gulf of Mexico, the Caribbean, and along the northern coast of South America by the U.S. Government vessels Oregon and Oregon II demonstrated the occurrence of megalops in many areas on the upper slope of the continental and insular shelves. It is common in many localities, and, on the basis of collections made by the RV Alaminos, Roberts and Pequegnat (1970) stated that this shrimp "is the most abundant penaeid caught by the Alaminos in the Gulf, and it appears to be most abundant in the De Soto Canyon around 200 fathoms [366 m] and, secondarily, off the Rio Grande in 150 fathoms [274 m]." Even though it is frequently taken while trawling for the royal red shrimp, Pleoticus robustus (Smith 1885), Harvey R. Bullis, Jr. (see footnote 4) has informed me that no serious effort was made during the cruises of the Oregon and Oregon II to assess the commercial potential of P. serrata. The reason for lack of interest in investigating possibilities for commercial exploitations was the small size of this shrimpaccording to Bullis, the average count of megalops tails would have been in the range of 60-100/lb (132-220/kg). In the eastern Atlantic this species constitutes a part of the commercial catches: Maurin (1952) cited it as one of the shrimps commercially fished off Morocco at depths >200 m; I

have examined two females sorted by L. B. Holthuis from commercial catches made by a Cadiz trawler off Rabat, Morocco; and Holthuis and Rosa (1965) listed it among the shrimps of economic value in the "Southeast Atlantic Area."

ACKNOWLEDGMENTS

This study has been made possible through the generous cooperation of many colleagues on four continents who made available to me invaluable collections. In addition, some of them provided facilities for me to work at their respective institutions. I am deeply indebted to Anthony A. Fincham and Raymond W. Ingle (BMNH), Jacques Forest (MP), and Lipke B. Holthuis (RMNH) for placing at my disposal critical specimens and providing working space and encouragement. I am also grateful to the following individuals for making additional material available to me: Alan Crosnier, Office de la Recherche Scientifique et Technique Outre Mer, Paris; Antonio J. de Freitas (ORI); Richard L. Haedrich, Woods Hole Oceanographic Institution, Woods Hole, Mass.: Willard D. Hartman (YPM); Boris G. Ivanov (VNIRO): Brian Kensley (formerly SAM); Herbert W. Levi (MCZ); Patsy A. McLaughlin (FIU); G. Ramakrishna (ZSI); P. Subramanian, Center of Advanced Study in Marine Biology, Parangipettai; Krishna Kant Tiwari (ZSI); and Gilbert L. Voss (UMML).

Thanks are due Harvey R. Bullis, Jr., formerly of the Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, Fla., for the graph of the depth-temperature relationship and for his cooperation through the many years during which he, in charge of the Oregon and Oregon II, preserved and made available to me extensive collections of penaeoids from catches of those U.S. Government vessels.

I am also indebted to my colleagues Horton H. Hobbs, Jr. of the Smithsonian Institution for his invaluable advice and critical comments during the preparation of this work, and Fenner A. Chace, Jr. and Raymond B. Manning, both of the Smithsonian Institution, for the review of the manuscript and helpful suggestions.

An important contribution to this study was the cooperation of María M. Diéguez, who rendered the detailed illustrations and assisted me in the preparation of the lists of material. Finally, I am grateful to Arleen S. McClain and Virginia R. Thomas for typing the manuscript.

LITERATURE CITED

ALCOCK, A. W.

- 1898. A summary of the deep-sea zoological work of the Royal Indian Marine Survey ship *Investigator* from 1884 to 1897. Sci. Mem. Med. Off. Army India 11:45-93.
- 1901a. A descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala, in the Indian Museum. Being a revised account of the deep-sea species collected by the Royal Indian Marine Survey ship Investigator. Indian Mus., Calcutta, 286 p.
- 1901b. Zoological gleanings from the Royal Indian Marine Survey ship *Investigator*. Sci. Mem. Off. Army India 12:35-76.
- 1902. A naturalist in Indian Seas or, four years with the Royal Indian Marine Survey ship 'Investigator'. John Murray, Lond., 328 p.
- 1905. A revision of the "genus" *Peneus*, with diagnoses of some new species and varieties. Ann. Mag. Nat. Hist., Ser. 7, 16:508-532.
- 1906. Fasciculus I. The prawns of the *Peneus* group. Catalogue of the Indian decapod Crustacea in the collection of the Indian Museum. Part III. Macrura. Indian Mus., Calcutta, 55 p.

ALCOCK, A. W., AND A. R. ANDERSON.

- 1894. Natural history notes from H. M. Indian Marine Survey steamer *Investigator*, Commander, C. F. Oldham, 'R.N., commanding. Series II, No. 14. An account of a recent collection of deep sea Crustacea from the Bay of Bengal and Laccadive Sea. J. Asiat. Soc. Bengal 63(Part II, 3):141-185.
- 1899. Natural history notes from H. M. Royal Indian Marine Survey ship *Investigator*, Commander T. H. Heming, R.N., commanding. Series III, No. 2. An account of the deep-sea Crustacea dredged during the surveying-season of 1897-98. Ann. Mag. Nat. Hist., Ser. 7, 3:1-27, 278-292.

ALCOCK, A. W., AND A. F. MCARDLE.

1901. Illustrations of the zoology of the Royal Indian Marine Survey ship *Investigator*, under the command of Commander T. H. Heming, R.N., Crustacea. Part IX, plates 49-55. Off. Supt. Gov. Print. India, Calcutta.

ANDERSON, W. W., AND H. R. BULLIS, JR.,

1970. Searching the shrimp beds by sub. Sea Front. 16:112-119.

ANDERSON, W. W., AND M. J. LINDNER.

- 1945. A provisional key to the shrimps of the family Penaeidae with especial reference to American forms. Trans. Am. Fish. Soc. 73:284-319.
- BALSS, H.
 - 1925. Macrura der Deutschen Tiefsee-Expedition, 2. Natantia, A. Wiss. Ergeb. Dtsch. Tiefsee-Exped. Valdivia 20:217-315.
 - 1957. Decapoda. VIII. Systematik. In H. G. Bronn, Klassen and Ordnungen des Tierreichs. 5, sect. 1, book 7:1505-1672.
- BARNARD, K. H.

1950. Descriptive catalogue of South African decapod Crustacea. Ann. S. Afr. Mus. 38:1-837.

BATE, C. S.

- 1881. On the Penaeidea. Ann. Mag. Nat. Hist., Ser. 5, 8:169-196.
- 1888. Report on the Crustacea Macrura collected by H.M.S. Challenger during the years 1873-76. Rep. Sci. Res. Voy. H.M.S. Challenger 1873-76, Zool. 24, 942 p.

BOONE, L.

1927. Scientific results of the first oceanographic expedition of the "Pawnee" 1925. Crustacea from tropical east American seas. Bull. Bingham Oceanogr. Collect., Yale Univ. 1(2), 147 p.

BOUVIER, E. L.

- 1905a. Sur les Pénéides et les Sténopides recueillis par les expéditions françaises et monégasques dans l'Atlantique oriental. C. R. Acad. Sci., Paris 140:980-983.
- 1905b. Sur les macroures nageurs (abstraction faite des Carides), recueillis par les expéditions américaines du *Hassler* et du *Blake*. C. R. Acad. Sci., Paris 141:746-749.
 1908. Quelques observations systématiques sur la sousfamille des Penaeinae Alcock. Bull. Inst. Océanogr.

(Monaco) 119, 10 p. BULLIS, H. R., JR.

> 1956. Preliminary results of deep-water exploration for shrimp in the Gulf of Mexico by the M/V Oregon (1950-1956). Commer. Fish. Rev. 18(12):1-12.

BULLIS, H. R., JR., AND W. F. RATHJEN.

1959. Shrimp explorations off southeastern coast of the United States (1956-1958). Commer. Fish. Rev. 21(6):1-20.

BULLIS, H. R., JR., AND J. R. THOMPSON.

- 1965. Collections by the exploratory fishing vessels Oregon, Silver Bay, Combat, and Pelican made during 1956-1960 in the southwestern North Atlantic. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 510, 130 p.
- BURKENROAD, M. D.
 - 1934a. Littoral Penaeidea chiefly from the Bingham Oceanographic Collection, with a revision of *Penaeopsis* and descriptions of two new genera and eleven new American species. Bull. Bingham Oceanogr. Collect., Yale Univ. 4(7), 109 p.
 - 1934b. The Penaeidea of Louisiana with a discussion of their world relationships. Bull. Am. Mus. Nat. Hist. 68:61-143.
 - 1936. The Aristeinae, Solenocerinae and pelagic Penaeinae of the Bingham Oceanographic Collection. Bull. Bingham Oceanogr. Collect., Yale Univ. 5(2), 151 p.
 - 1959. Addenda et Corrigenda au Memoire XXV. Penaeidae par Martin D. Burkenroad (pages 67-92). In Mission Robert Ph. Dollfus en Egypte (décembre 1927 mars 1929), S. S. "Al Sayad." Résultats scientifiques, 3^e Partie [contributions] (XXIII-XXXIV), p. 285. Centre National de la Recherche Scientifique, Paris.
 - 1963. Comments on the petition concerning peneid names (Crustacea Decapoda) (Z. N. (S.) 962). Bull. Zool. Nomencl. 20:169-174.

- 1972. Some problems of the systematics and distribution of the shrimps of the genus *Penaeus*. [In Russ.] Fisheries Research in the Atlantic Ocean. Tr. Atl. Nauch.-Issled. Inst. Rybn. Khoz. Okeanogr. 42:3-21. (Translated by Israel Program Sci. Transl., TT72-50101.)
- 1974. Keys to the shrimps, spiny lobsters and homarids. [In Russ.] Moscow: Pishchevaia promyshlennost, "Food Industry," 126 p.

CROSNIER, A., AND J. FOREST.

- 1973. Les crevettes profondes de l'Atlantique oriental tropical. Faune Tropicale Tome XIX. O.R.S.T.O.M. (Off. Rech. Sci. Tech. Outre-Mer), Paris, 409 p.
- CROSNIER, A., AND C. JOUANNIC.

1973. Note d'information sur les prospections de la pente

BURUKOVSKY, R. N.

continentale malgache effectuées par le N. O. Vauban -Bathymétrie - Sédimentologie - Pêche au chalut. O.R.S.T.O.M. Centre Nosy-Bé Doc. Sci. 42, 18 p.

DOMANTAY, J. S.

1956. Prawn fisheries of the Philippines. Indo-Pac. Fish. Counc. Proc. 6:362-366.

ESTAMPADOR, E. P.

1937. A check list of Philippine crustacean decapods. Philipp. J. Sci. 62:465-559.

FABRICIUS, J. C.

1798. Supplementum entomologiae systematicae. Haf- `niae, 572 p.

FAXON, W.

1895. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross", during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding. XV. The stalk-eyed Crustacea. Mem. Mus. Comp. Zool. Harv. Coll. 18, 292 p.

1896. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and the Caribbean Sea, and on the east coast of the United States, 1877 to 1880, by the U.S. Coast Survey steamer "Blake," Lieut. Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. XXXVII. Supplementary notes on the Crustacea. Bull. Mus. Comp. Zool. Harv. Coll. 30:153-166.

GEORGE, M. J.

- 1966. On a collection of penaeid prawns from the offshore waters of the south-west coast of India. *In* Symposium on Crustacea, p. 337-346. Mar. Biol. Assoc. India, Symp. Ser. 2.
- 1969. Prawn fisheries of India. II Systematics-taxonomic considerations and general distribution. Cent. Mar. Fish. Res. Inst., Bull. 14:5-48.
- HAEDRICH, R. L., G. T. ROWE, AND P. T. POLLONI.

1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. J. Mar. Res. 33:191-212.

1962. Observations on the taxonomy and biology of some Indo-West-Pacific Penaeidae (Crustacea, Decapoda). Colon. Off., Lond. Fish. Publ. 17, 229 p.

HAY, W. P., AND C. A. SHORE.

1918. The decapod crustaceans of Beaufort, N.C., and the surrounding region. Bull. [U.S.] Bur. Fish. 35:369-475.

1965. List of species of shrimps and prawns of economic value. FAO Fish. Tech. Pap. 52, 21 p.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLA-TURE.

1969. Penaeid generic names (Crustacea, Decapoda): addition of twenty-eight to the Official List. Opinion 864. Bull. Zool. Nomencl. 25:138-147.

IVANOV, B. G., AND A. M. HASSAN.

1976. Penaeid shrimps (Decapoda, Penaeidae) collected off east Africa by the fishing vessel "Van Gogh", 2. Deepwater shrimps of the genera *Penaeopsis* and *Parapenaeus* with description of *Penaeopsis* balssi sp. nov. Crustaceana 31:1-10.

1967. The crustacean fishery resources of India. In Sym-

posium on Crustacea, p. 1328-1340. Mar. Biol. Assoc. India, Symp. Ser. 2.

1969. The prawn fishery resources of India. FAO Fish. Rep. 57:735-747.

JOYCE, E. A., JR., AND B. ELDRED.

1966. The Florida shrimping industry. Fla. State Board Conserv., Educ. Ser. 15, 47 p.

KEMP, S., AND R. B. S. SEWELL.

1912. II. Notes on Decapoda in the Indian Museum. III. The species obtained by R.I.M.S.S. 'Investigator' during the survey season 1910-11. Rec. Indian Mus. 7:15-32.

KENSLEY, B. F.

- 1969. Decapod Crustacea from the south-west Indian Ocean. Ann. S. Afr. Mus. 52:149-181.
- 1972. Shrimps and prawns of southern Africa. South Afr. Mus., Cape Town, 65 p.

KINGSLEY, J. S.

1878. Notes on the North American Caridea in the museum of Peabody Academy of Science at Salem, Mass. Proc. Acad. Nat. Sci. Phila. 30:89-98.

KUBO, I.

1949. Studies on penaeids of Japanese and its adjacent waters. J. Tokyo Coll. Fish. 36(1), 467 p.

KURIAN, C. V.

- 1964. On the occurrence of the deep-water prawn *Penaeopsis rectacutus* (Spence Bate) off the Kerla coast. Curr. Sci. (Bangalore) 33:216-217.
- LAGARDERRE, J. P.
 - 1971. Les crevettes des côtes du Maroc. Trav. Inst. Sci. Cherifien Fac. Sci., Ser. Zool. 36:1-140.
- LONGHURST, A. R.
 - 1971. Crustacean resources. In J. A. Gulland (editor), The fish resources of the ocean, p. 206-255. FAO, Rome.

1846. Crustacés, Arachnides, Myriapodes et Hexapodes. Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. Sciences physiques. Zoologie I. Hist. Nat. Anim. Articulés Part 1:1-403.

MAN, J. G. DE.

- 1911. The Decapoda of the Siboga Expedition. Part 1. Family Penaeidae. Siboga-Exped. Monogr. 39a, 131 p.
- 1913. The Decapoda of the Siboga Expedition. Part 1. Family Penaeidae. Siboga-Exped. Monogr. 39a, Part 1 (Suppl.), 10 pl.

MAURIN, C.

- 1952. Crustacés. Note préliminaire sur les crevettes des côtes du Maroc. Cons. Perm. Int. Explor. Mer, Ann. Biol. 8:91-92.
- 1961. Répartition des crevettes profondes sur les côtes sud du bassin occidental de la Méditerranée et dans la région atlantique ibéro-marocaine. Comm. Int. Explor. Sci. Mer Médit. Rapp. P.-V. Reun. 16:529-532.
- 1962. Etude des fonds chalutables de la Méditerranée occidentale (écologie et pêche). Résultats des campagnes de navires océanographiques "Président-Théodore-Tissier" 1957 à 1960 et "Thalassa" 1960 et 1961. Rev. Trav. Inst. Pêches Marit. 26:163-218.
- 1963. Les crevettes capturées par la "Thalassa" au large des côtes du Rio de Oro et de Mauritanie. Ecologie et pêche. Cons. Int. Explor. Mer, Comm. Mollusques Crustacés No. 48, 2 (unnumbered) + 3 p.
- 1965. Les crevettes profondes de la région atlantique ibéro-marocaine: répartition bathymétrique et géo-

HALL, D. N. F.

HOLTHUIS, L. B., AND H. ROSA, JR.

JONES, S.

LUCAS, H.

PEREZ FARFANTE: REVISION OF PENAEID SHRIMP GENUS PENAEOPSIS

graphique, importance économique. Comm. Int. Explor. Sci. Mer Médit. Rapp. P.-V. Reun. 156:116-119.

- 1968a. Ecologie ichthylogique des fonds chalutables atlantiques (de la baie ibéro-marocaine à la Mauritanie) et de la Mediterranée occidentale. Rev. Trav. Inst. Pêches Marit. 32:1-147.
- 1968b. Les Crustacés capturés par la "Thalassa" au large des côtes nord-ouest africaines. Rev. Roum. Biol., Ser. Zool. 13:479-493.

MILNE EDWARDS, A., AND E. L. BOUVIER.

1909. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78), in the Caribbean Sea (1878-79), and along the Atlantic coast of the United States (1880), by the U.S. Coast Survey steamer "Blake," Lieut. Com. C. D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. XLIV. Les Pénéides et Sténopides. Mem. Mus. Comp. Zool. Harv. Coll. 27:177-274.

PEQUEGNAT, W. E., AND T. W. ROBERTS.

1971. Decapod shrimps of the family Penaeidae. In W. E. Pequegnat, L. H. Pequegnat, R. W. Firth, Jr., B. M. James, and T. W. Roberts (editors), Gulf of Mexico deep-sea fauna Decapoda and Euphausiacea, p. 8-9. Ser. Atlas Mar. Environ., Am. Geogr. Soc. Folio 20.

PÉREZ FARFANTE, I.

- 1969. Western Atlantic shrimps of the genus Penaeus. U.S. Fish Wildl. Serv., Fish. Bull. 67:461-591.
- 1971. Western Atlantic shrimps of the genus Metapenaeopsis (Crustacea, Decapoda, Penaeidae), with descriptions of three new species. Smithson. Contrib. Zool. 79, 37 p.
- 1977a. American solenocerid shrimps of the genera Hymenopenaeus, Haliporoides, Pleoticus, Hadropenaeus new genus, and Mesopenaeus new genus. Fish. Bull., U.S. 75:261-346.
- 1977b. Penaeopsis eduardoi, a new species of shrimp (Crustacea: Penaeidae) from the Indo-West Pacific. Proc. Biol. Soc. Wash. 90:172-182.
- 1978. Intersex anomalies in shrimp of the genus Penaeopsis (Crustacea: Penaeidae). Fish. Bull., U.S. 76:687-691.
- 1979. Penaeopsis jerryi, new species from the Indian Ocean (Crustacea: Penaeoidea). Proc. Biol. Soc. Wash. 92:208-215.

1979. Range extension of *Penaeopsis serrata* (Crustacea: Penaeoidea) to off New Jersey and Rio Grande do Sul. Proc. Biol. Soc. Wash. 92:204-207.

RAMADAN, M. M.

1938. Crustacea: Penaeidae. John Murray Exped. 1933-34. Sci. Rep. 5:35-76.

RATHBUN, M. J.

1901. The Brachyura and Macrura of Porto Rico. [Preprint] U.S. Fish Comm. Bull. 1900 [1902], 20(2):1-127, [Preprint index] 129-137, 2 pl.

ROBERTS, T. W., AND W. E. PEQUEGNAT.

1970. Deep-water decapod shrimps of the family Penaeidae. In W. E. Pequegnat and F. A. Chace, Jr. (editors), Contributions on the biology of the Gulf of Mexico, p. 21-57. Tex. A & M Univ. Oceanogr. Stud. 1. SCHMITT, W. L.

1926. Report on the Crustacea Macrura (families Peneidae, Campylonotidae and Pandalidae) obtained by the F.I.S. "Endeavour" in Australian seas. With notes on the species of "*Penaeus*" described by Haswell and contained, in part, in the collections of the Macleay Museum, at the University of Sidney. Biological results of the Fishing Experiments carried on by the F.I.S. "Endeavour" 1909-14. Commonw. Aust. Dep. Trade Customs 5, Part 6:311-381.

1935. Introduction and list of stations. Br. Mus. Nat. Hist., John Murray Exped., 1933-34. Sci. Rep. 1(1):1-41.
1955. A study of the sea coast of southern Arabia. Proc. Linn. Soc. Lond. 165:188-210.

SMITH, S. I.

1885. On some genera and species of Penaeidae, mostly from recent dredgings of the United States Fish Commission. Proc. U.S. Natl. Mus. 8:170-190.

SPRINGER, S., AND H. R. BULLIS, JR.

- 1956. Collections by the Oregon in the Gulf Mexico. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 196, 134 p.
- STAROBOGATOV, Y. I.
 - 1972. Penaeidae (Crustacea Decapoda) of the Tonking Gulf. [In Russ.] Akad. Nauk. SSSR, Zool. Inst. Issled. Fauny Moreï 10(18):359-415.
- VILLALUZ, D. K., AND F. J. ARRIOLA.
 - 1938. Five other known species of *Penaeus* in the Philippines. Philipp. J. Sci. 66:35-41.

Voss, G. L.

1955. A key to the commercial and potentially commercial shrimp of the family Penaeidae of the western North Atlantic and the Gulf of Mexico. Fla. State Board Conserv., Tech. Ser. 14, 22 p.

WENNER, E. L, AND D. F. BOESCH.

1979. Distribution patterns of epibenthic decapod Crustacea along the shelf-slope coenocline, middle Atlantic bight, U.S.A. Bull. Biol. Soc. Wash. 3:106-133.

WOOD-MASON, J.

1891. Phylum Appendiculata. Branch Arthropoda. Class Crustacea. In J. Wood-Mason and A. Alcock (editors), Natural history notes from H. M. Indian Marine Survey steamer 'Investigator,' Commander R. F. Hoskyn, R. N., commanding. - Series II, No. 1. On the results of deep-sea dredging during the season 1890-91. Ann. Mag. Nat. Hist., Ser. 6, 8:269-286.

ΥΟΚΟΥΑ, Υ.

- 1933. On the distribution of decapod crustaceans inhabiting the continental shelf around Japan, chiefly based upon the materials collected by S. S. Sôyô-Maru, during the year 1923-30. J. Coll. Agric., Tokyo Imp. Univ. 12:1-226.
- 1941. On the classification of penaeid shrimps by the structural features of the appendix masculina. J. Coll, Agric., Tokyo Imp. Univ. 15:45-68.

PÉREZ FARFANTE, I., AND B. G. IVANOV.

SEWELL, R. B. S.