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# WESTERN ATLANTIC SHRIMPS OF THE GENUS *PENAEUS*

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## ABSTRACT

**Four subgenera of the genus *Penaeus* are described (*Litopenaeus, Penaeus* s.s., *Fenneropenaeus,* and *Melicertus*). Eight species and subspecies (*P. setiferus, P. schmitti, P. duorarum duorarum, P. duorarum notialis, P. aztecus aztecus, P. aztecus subtilis, P. paulensis,* and *P. brasiliensis*) are recognized as occurring in the western Atlantic. Synonymies are given. Lectotypes have been designated for two species, and the disposition of all types is shown. Diagnoses, detailed descriptions, and illustrations are presented for each species and subspecies. Geographic and bathymetric distributions are given. Affinities are discussed, and conclusions concerning ranges of variation and their spatial distribution are based on morphometric studies and other characters. The development of the external genitalia through the juvenile stage and the size range at which each taxon reaches the subadult stage are presented. Many details of ecology and life history are critically summarized and reviewed. A brief appraisal of the commercial importance of each form is also given.**

The economic importance of the shrimp industry in eastern America becomes abundantly clear when one realizes that in 1965 the United States produced over 100 million kg. of *Penaeus* shrimp, and Latin America together with the Guianas harvested no less than 57 million kg. The fact that these animals are of such value has undoubtedly been largely responsible for the extensive research that has been devoted to the many aspects of the biology of the members of the genus *Penaeus*. Even so, there has been a long-felt need for a comprehensive treatment of the systematics of the group. This need has been emphasized by the fact that, although much valuable information exists for the group as a whole, misidentifications of individuals and of populations have led to confusing and sometimes conflicting conclusions.

The extensive collections of *Penaeus* available for this study have enabled me to evaluate the interrelationships of the western Atlantic members of the genus and, in turn, their affinities with those occurring elsewhere. To express the supraspecific relationships that have been recognized, I propose four subgenera and provide a key to facilitate their recognition. This key, as well as that which follows, is arranged solely for convenience and no phylogenetic inferences should be drawn from it.

Because species descriptions are widely scattered in literature that is not readily available and because most of these descriptions do not take into account many of the characters that have been found to be of considerable taxonomic importance, each taxon occurring in eastern American waters has been redescribed and figured.

As nearly as possible, a complete synonymy and list of references (including misidentifications) are indicated for each species and subspecies, and the page citations are included. All references listed were consulted in the original. Every attempt has been made to correlate earlier findings with the taxa recognized here, but, as might be expected, I was not always successful. In listing the types and their dispositions, some modifications of the original designations have been made. A list of the material examined precedes a brief diagnosis and a detailed description of morphological characters.

In addition, for each species and subspecies, the range of variation of these characters is included

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and, insofar as possible, they are correlated with the geographical distribution of each animal. In the study of variation, I considered 40 characters other than those of the external genitalia. Those characters found to be of value are treated in the text and in figures and graphs. Data on color, size, and sex differences in size are presented. A survey of work on the biology and systematics of each taxon is also included. Until 1936–39 only five species were known to occur in the region. In 1967, I described one new species and two new subspecies from the western Atlantic.

Particular attention has been accorded the development of the systematic characters of the juveniles of each taxon. A description is given of the progressive changes in the development of the external genitalia which will aid in the identification of juveniles. The size range at which each taxon reaches the subadult stage, or at which the external genitalia attain adult form, has been determined.

Geographic and bathymetric ranges are derived from published data as well as material I examined. The commercial importance of each kind of shrimp is summarized. Comments on the systematics, interrelationships of the various taxa, items of special interest, and discussion of specific problems conclude the presentation.

The morphological nomenclature I adopted is, for the most part, that of Kubo (1949). A few slight modifications were made for the sake of brevity and clarity. For example, the lobules of the petasma are given single names—dorsomedian ventromedian, dorsolateral, and ventrolateral—to avoid such unnecessarily long wording, as, for instance, "ventral lobule of lateral lobe"; the "thickened ventral margin of the petasma" is called the ventral costa; and the two parts of the median protuberance of the thelycum are called the anterior and posterior processes. Whereas most previous investigators recognize "proximal" and "distal" pieces of the appendix masculina, it seems to me that the so-called proximal piece is only a modification of the endopod of the second pleopod; therefore, the "distal piece" appears to be equivalent to what in other decapods is called the appendix masculina. For this reason "appendix masculina" as used herein is the "distal piece" of other authors. A definitive terminology for the external genitalia, however, must await further study of their development and a demonstration of their homologies.

The measurement of total length is the distance from the tip of the rostrum to the posterior end of the telson, and that of the carapace is the distance from the dorsal portion of the postorbital margin to the midposterodorsal margin of the carapace. The latter dimension is accurate to 0.5 mm. In the text total length, carapace length, and rostrum length are often abbreviated t.l., c.l., and r.l., respectively. The citations to figures in the references listed for each taxon have been restricted to those illustrating morphological characters; other figures appear in the pages cited.

## GENUS *PENAEUS* FABRICIUS

*Penaeus* Fabricius, 1798: 408 (type species, by subsequent designation of Latreille, 1810, *Penaeus monodon* Fabricius; neotype for *Penaeus monodon*, designated by Holthuis, 1949, ♂, Leiden Museum); Latreille, 1802: 246–250; Latreille, 1806: 53, 54; Latreille, 1810: 102, 422; Heller, 1863: 292, 293; Smith, 1882: 92–95; Smith, 1885 (not 1886 as is commonly stated): 170, 171; Bate, 1888: xii, 229–230 [part]; de Man, 1911: 95–97; Balss, 1914: 13; Burkenroad, 1934: 73–77; Anderson and Lindner, 1945: 302; Kubo, 1949: 268–270; Dall, 1957: 140–142; Gunter, 1957: 98.

*Peneus* Weber, 1795: 94 (nomen nudum, Opinion 104, International Commission on Zoological Nomenclature); Philippi, 1840: 190; Smith, 1869a: 27; Smith, 1869b: 390; Alcock, 1901: 12–14; Alcock, 1905: 510–515.

*Melicertus* Rafinesque, 1814: 22.

*Penecus* H. Milne Edwards, 1837: 414.

*Penoeus* Lucas, 1840: 195, 196.

*Paneus* Collins and Smith, 1892: 102.

*Panaeus* Thallwitz, 1892: 3.

### DIAGNOSIS

Rostrum usually with ventral teeth. Carapace without longitudinal or transverse sutures; cervical and orbito-antennal sulci and antennal carinae always present. Hepatic and antennal spines pronounced, pterigostomial angle rounded. Longitudinal ridge of side of sixth abdominal somite interrupted. Telson with deep median sulcus, without fixed subapical spines, with or without lateral movable spines. First antennular segment without spine on ventral distomedian border. Antennular flagella usually shorter than carapace. Palp of first maxilla with two or three segments, usually three.

Basial spines on first and second pereopods, exopods on first four pereopods and usually on fifth. Petasma symmetrical, podlike, with or without distomedian projections, and with lateral lobes usually armed with long ventral costae. Appendix masculina subtriangular to ovoid, bearing spines. Thelycum often with median protuberance at posterior margin of sternite XIII, open or usually with two lateral plates covering or almost covering sternite XIV. Zygocardiac ossicle consisting of principal tooth followed by longitudinal row of smaller teeth often ending in cluster of minute teeth. Pleurobranchiae on somites IX to XIV; rudimentary arthrobranch on VII, and posterior arthrobranch on XIII somites; mastigobranchiae on VII to XII somites. Body glabrous (after Dall, 1957, modified). Figures 1 to 3 illustrate characters used in *Penaeus* taxonomy.

Two divisions of the genus *Penaeus* were recognized by Burkenroad (1934): in Division 1 he placed the species with a short adrostral carina (not approaching the posterior margin of the carapace) and lacking a gastrofrontal carina, and in Division 2 the species with a long adrostral carina (almost reaching the posterior margin of the carapace) and possessing a gastrofrontal carina. Kubo (1949) recognized Burkenroad's Division 2, although he used the adrostral sulcus instead of the

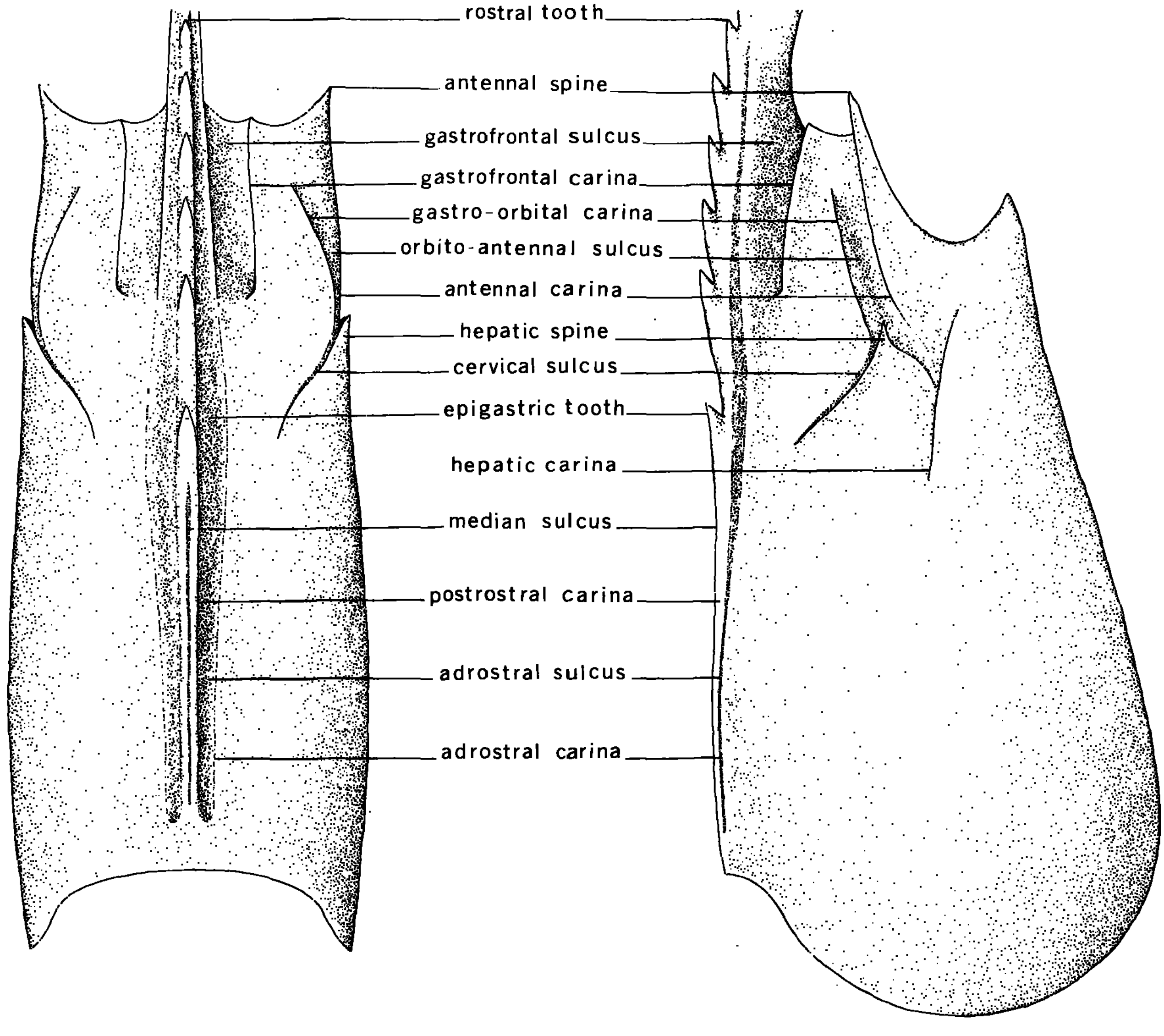

**Figure 1.**—Dorsal and lateral views of carapace showing features used in *Penaeus* taxonomy.

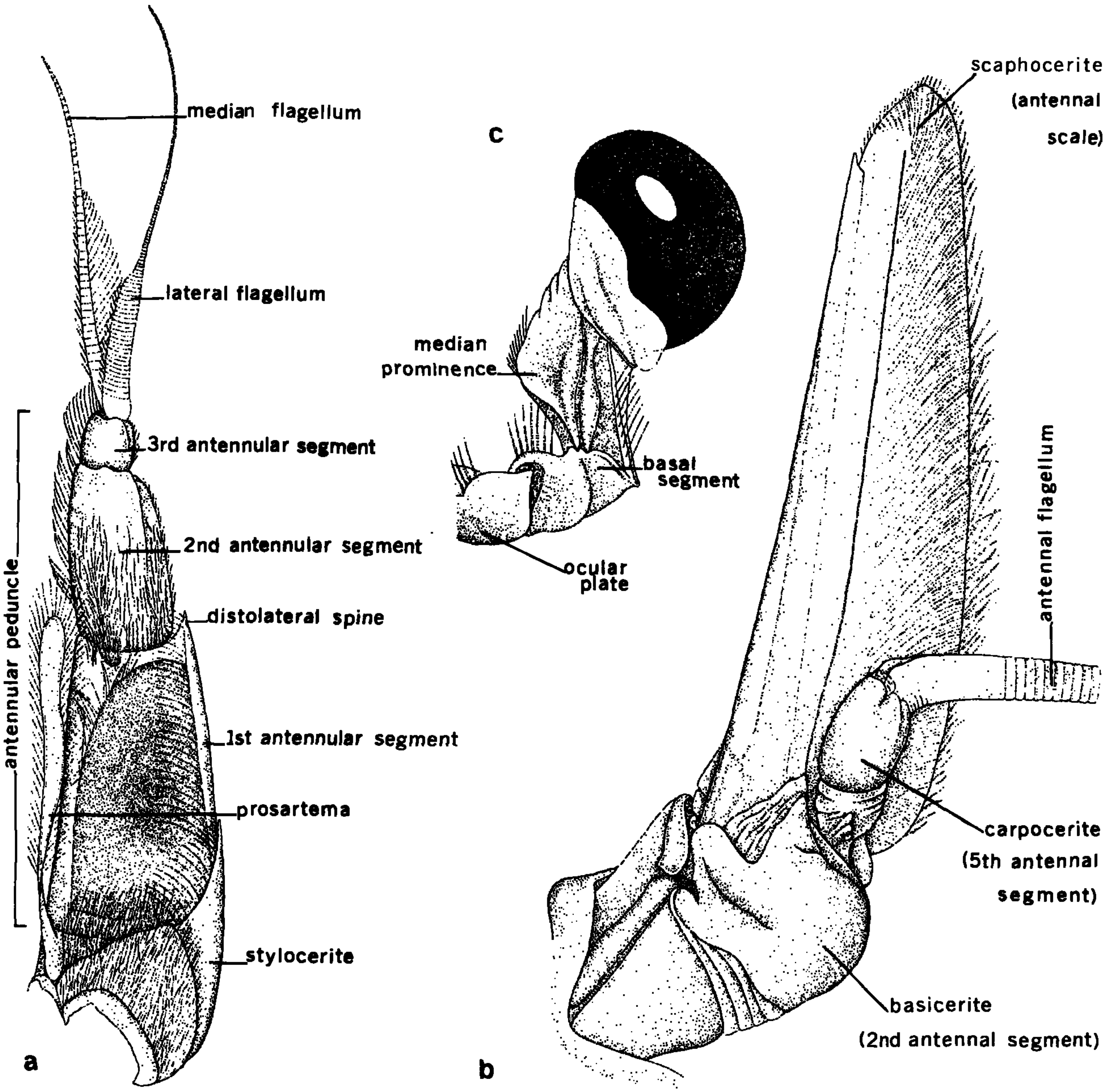

FIGURE 2.—Cephalic appendages and eye of a member of the genus *Penaeus*. a. Dorsal view of right antennule. b. Ventrolateral view of right antenna. c. Dorsal view of right eye.

adjacent adrostral carina. He also called attention to another character, a well-defined hepatic carina. Kubo grouped the nongrooved *Penaeus*, Division 1, into two subdivisions, characterized by the presence or absence of a hepatic carina, the depth of the adrostral sulcus, and the development of the adrostral carina.

I consider that within the genus *Penaeus* are four different groups which are here designated as subgenera.

## KEY TO THE SUBGENERA OF THE GENUS *PENAEUS*

1. Adrostral sulcus and carina short, not reaching posteriorly beyond midlength of carapace; gastrofrontal carina absent-------- 2

   Adrostral sulcus and carina long, reaching posteriorly much beyond midlength, usually almost to posterior margin of carapace; gastrofrontal carina present---------- *Melicertus*

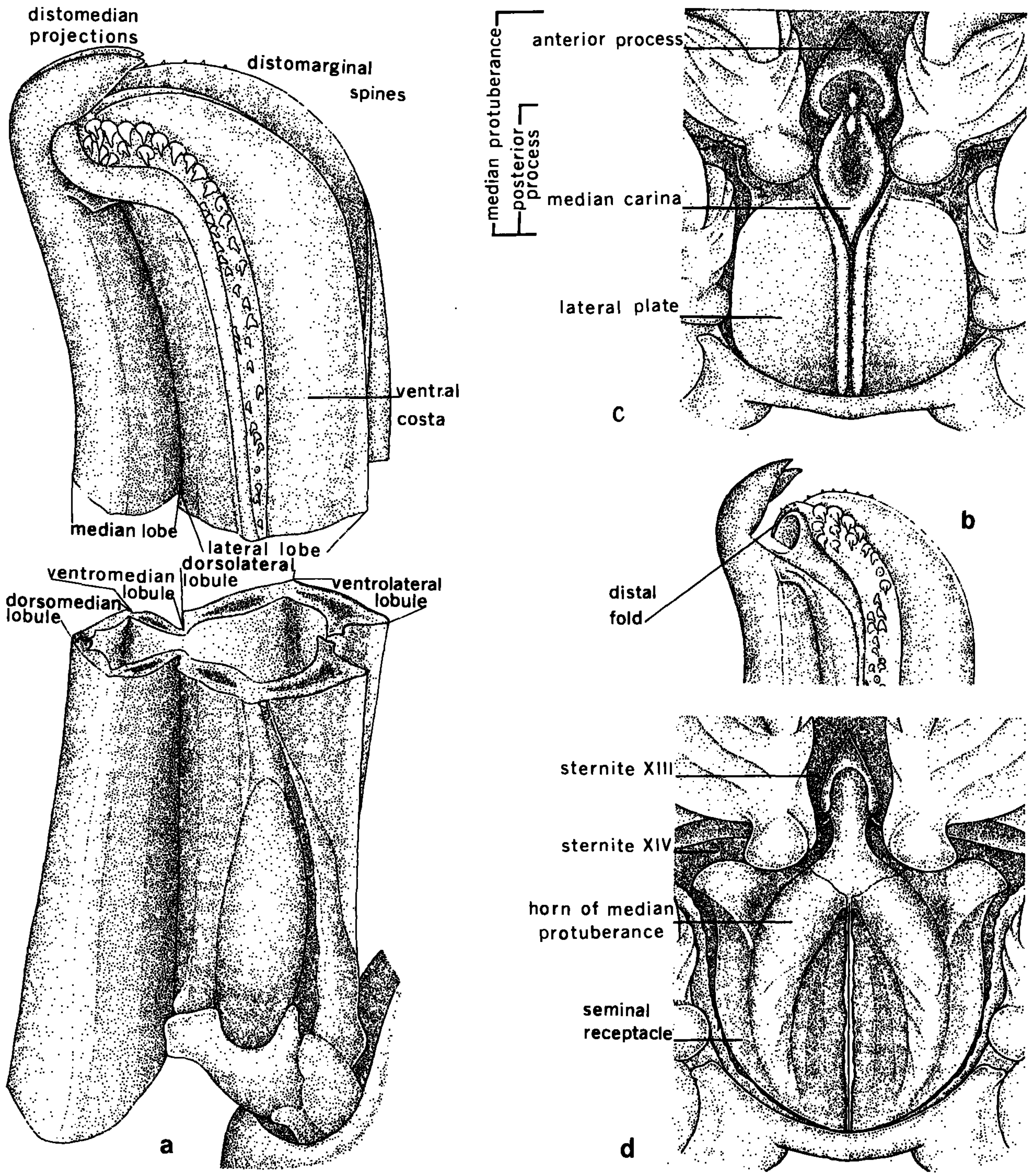

FIGURE 3.—Features of the external genitalia used in *Penaeus* taxonomy. Petasma: a. Cross section with arrangement of lobes. b. Distal portion. c. Thelycum. d. Thelycum with lateral plates removed showing seminal receptacle and position of horns of median protuberance.

2. Hepatic carina prominent................ 3
Hepatic carina absent or ill defined........................................*Fenneropenaeus*
3. Thelycum open type. Petasma with ventral costa short, not reaching distal margin of lateral lobe.................. *Litopenaeus*
Thelycum closed type. Petasma with ventral costa long, reaching distal margin of lateral lobe..........................*Penaeus* s.s.

### SUBGENUS *Litopenaeus* NEW SUBGENUS

Type species, *Penaeus* (*Litopenaeus*) *vannamei* Boone, here designated.

#### Diagnosis

Thelycum of open type, lacking sperm receptacle. Petasma formed by relatively simple petasmal endopods, with short ventral costae; median lobes of petasma not extended distally, not or just barely reaching distal margin of lateral lobes. Carapace with adrostral carina and sulcus short, extending to, or only slightly posterior to, epigastric tooth; gastrofrontal carina absent; hepatic carina well developed; gastro-orbital carina short, extending anteriorly not more than three-quarters, usually two-thirds, of the distance from hepatic spine to postorbital margin.

#### Etymology

*Litopenaeus*, from the Greek litos, meaning plain.

#### List of Species

*P.* (*L.*) *vannamei* Boone, *P.* (*L.*) *stylirostris* Stimpson, and *P.* (*L.*) *occidentalis* Streets in the eastern Pacific; *P.* (*L.*) *setiferus* (L.), and *P.* (*L.*) *schmitti* Burkenroad in the western Atlantic.

### SUBGENUS *Penaeus* s.s.

Type species, *Penaeus* (*Penaeus*) *monodon* Fabricius.

#### Diagnosis

Thelycum of closed type. Petasma with ventral costae long, strongly curved distally, and with median lobes only slightly prolonged distally. Carapace with adrostral carina and adrostral sulcus short, extending about to level of epigastric tooth; gastrofrontal carina absent; hepatic carina well defined and gastro-orbital carina short, extending anteriorly not more than two-thirds of the distance from hepatic spine to postorbital margin.

#### List of Species

*P.* (*P.*) *monodon* Fabricius and *P.* (*P.*) *esculentus* Haswell in the Indo-Pacific; and *P.* (*P.*) *semisulcatus* de Haan in the Indo-Pacific and eastern Mediterranean Sea.

### SUBGENUS *Fenneropenaeus* NEW SUBGENUS

Type species, *Penaeus* (*Fenneropenaeus*) *indicus* H. Milne Edwards, here designated.

#### Diagnosis

Thelycum of closed type. Petasma with ventral costae long, strongly curved distally, and with median lobes only slightly projected distally. Adrostral sulcus and carina short, extending about to level of epigastric tooth, sulcus shallow and carina attenuated posteriorly; gastrofrontal carina absent; hepatic carina absent or ill defined; gastro-orbital carina short or absent, if present extending anteriorly not more than two-thirds, or occupying middle one-third of the distance from hepatic spine to postorbital margin.

#### Etymology

*Fenneropenaeus* for Fenner A. Chace, Jr., whose advice through the years has been very helpful to me in my studies.

#### List of Species

*P.* (*F.*) *indicus* H. Milne Edwards, *P.* (*F.*) *merguiensis* de Man, *P.* (*F.*) *penicillatus* Alcock, and *P.* (*F.*) *orientalis* Kishinouye. The four species are Indo-Pacific.

### SUBGENUS *Melicertus*

Type species, by monotypy, *Melicertus tigrinus* Rafinesque, 1814: 22 (=*Cancer kerathurus* Forskål, 1775).
*Salambria* "Burkenroad" Balss, 1957: 1518 (nomen nudum).

#### Diagnosis

Thelycum of closed type. Petasma with ventral costae long, strongly curved or almost straight distally, and with distomedian projections usually prominent. Carapace with adrostral carina and sulcus long, extending posteriorly considerably beyond epigastric tooth, usually almost reaching posterior margin of carapace; gastrofrontal carina present; hepatic carina prominent; gastro-orbital carina long, extending anteriorly at least, usually more than three-quarters of the distance from hepatic spine to postorbital margin.

## List of Species

*P.* (*M.*) *brevirostris* Kingsley and *P.* (*M.*) *californiensis* Holmes from the eastern Pacific; *P.* (*M.*) *aztecus aztecus* Ives, *P.* (*M.*) *aztecus subtilis* Pérez Farfante, *P.* (*M.*) *paulensis* Pérez Farfante, *P.* (*M.*) *brasiliensis* Lat., *P.* (*M.*) *duorarum duorarum* Burkenroad, and *P.* (*M.*) *duorarum notialis* Pérez Farfante from the western Atlantic—the last-named subspecies from the eastern Atlantic (West Africa) also; *P.* (*M.*) *kerathurus* (Forskål) from the Mediterranean Sea and eastern Atlantic; *P.* (*M.*) *latisulcatus* Kishinouye, *P.* (*M.*) *longistylus* Kubo, *P.* (*M.*) *marginatus* Randall, *P.* (*M.*) *plebejus* Hess, and *P.* (*M.*) *teraoi* Kubo from the Indo-Pacific; and *P.* (*M.*) *japonicus* Bate (?=*P.* (*M.*) *canaliculatus* Olivier) from the Indo-Pacific and eastern Mediterranean Sea.

The list of Indo-Pacific species follows the conclusions of Hall (1962) and Racek and Dall (1965), as well as previous opinions by Kubo (1949), Holthuis (1949), and Dall (1957).

## REMARKS ON SUBGENERA

The five species of the subgenus *Litopenaeus* are restricted to American waters and differ markedly from other members of the genus in characters of the external genitalia which neither Burkenroad (1934) nor Kubo (1949) took into account when they recognized species groups of the genus *Penaeus*. In respect to both the thelycum and the petasma, these species are more primitive than the species of the other subgenera. The open thelycum, which is obviously less specialized than the closed type, has only ridges and protuberances for the fastening of the spermatophores, which are left exposed. In *Litopenaeus* the spermatophores have strong structures for attachment to the thelycum, whereas in the remaining species these structures seem to be represented—as suggested by Burkenroad (1934)—by vestigial processes. Only one species with a closed thelycum (*P. japonicus*) has spermatophores with large processes (Tirmizi, 1958), but the processes differ from those in the species with an open thelycum. The lack of a gastrofrontal carina and the possession of a hepatic carina seem to be primitive.

Since the species of the genus *Litopenaeus* appear to be more primitive and are restricted to American waters, I agree with Burkenroad (1934) that the genus could well have originated in the Western Hemisphere.

The remaining species of *Penaeus* have a closed thelycum, which possesses two flaps that occur as "lateral plates" on the ventral surface of sternite XIV; the lateral plates are separated by a median slit that opens into a seminal receptacle dorsal to and continuous with the lateral plates. *P. japonicus* provides an exception in having a pouchlike thelycum with an anterior opening on sternite XIV.

*Penaeus* s.s. is apparently the more primitive of the groups of species with a thelycum of the closed type, sharing with *Litopenaeus* the sculpture of the carapace, including a well-developed hepatic carina. Kubo placed the species of *Litopenaeus* and *Penaeus* s.s. together in his subdivision 2.

*Fenneropenaeus* differs from *Penaeus* s.s. in lacking a hepatic carina or, in one species (*P. penicillatus*), having only a barely noticeable one; the character seems to have been secondarily lost. The absence of this carina in most species of *Penaeus* s.s., and the shallow adrostral sulcus and posteriorly attenuated adrostral carina indicate a tendency for the carapace to become smoother.

There is little doubt that *Melicertus* includes the most advanced group of species; the long adrostral sulcus and carina appear late in development, at the beginning of the juvenile stage.

## KEY TO THE WESTERN ATLANTIC SPECIES OF *Penaeus*

1. Adrostral sulcus short, extending to epigastric tooth; gastrofrontal carina absent ("nongrooved shrimps") ______________________ 2

   Adrostral sulcus long, extending posteriorly beyond epigastric tooth; gastrofrontal carina present ("grooved shrimps") _____________ 3

2. Petasma with distal portion of lateral lobe bearing diagonal ridge on inner surface, and distal ventromedial corner rounded. Thelycum with anterolateral ridges turned mesially and pair of fleshy protuberances on sternite XIV ____ ____________ *P.* (*L.*) *setiferus* (L.) (p. 468)

   Petasma with distal portion of lateral lobe lacking diagonal ridge on inner surface, and distal ventromedial corner produced in subrectangular projection. Thelycum with subparallel anterolateral ridges, never turned mesially, and pair of rounded and rigid protuberances on sternite XIV ______________ _____ *P.* (*L.*) *schmitti* Burkenroad (p. 487)

3. Petasma with distomedian projection long; distal fold intruding considerably inside petasma

forming large auricle; ventral costa with apex free. Lateral plates of thelycum with anteromedial corners extended anteriorly forming two projections which cover posterior process ----------*P.* (*M.*) *brasiliensis* Lat. (p. 562)

Petasma with distomedian projection relatively short, distal fold not forming auricle; ventral costa with apex attached to adjacent membranous portion. Lateral plates of thelycum with anteromedial corners not extended; posterior process exposed----------------4

4. Petasma with distal portion of ventral costa armed along free border with minute spines, broadening and turning proximally rather abruptly. Lateral plates of thelycum with anteromedial corners slightly divergent; posterior process with undivided median carina ----------------------------------5

Petasma with distal portion of ventral costa unarmed along free border, almost straight or arc-shaped, gradually broadening and gradually turning proximally. Lateral plates of thelycum with anteromedian corners widely divergent; posterior process with median carina bifurcate anteriorly----------------6

5. Dorsolateral sulcus narrow, ratio between keel height and sulcus width (measured at about one-third of somite length from posterior margin) usually more than three, sulcus often almost closed---------------------*P.* (*M.*) *duorarum duorarum* Burkenroad (p. 499)

Dorsolateral sulcus broad, ratio between keel height and sulcus width usually less than three-----------------------------*P.* (*M.*) *duorarum notialis* Pérez Farfante (p. 520)

6. Adrostral sulcus long, almost reaching posterior margin of carapace, deep and broad posteriorly, ⅘ to 2 times width of postrostral carina (measured at posterior one-eighth of distance from posterior end of adrostral sulcus to epigastric tooth)---------------------------7

Adrostral sulcus relatively short, never approaching posterior margin of carapace, shallow and narrow posteriorly, ⅕ to ¾ times width of postrostral carina--------------*P.* (*M.*) *aztecus subtilis* Pérez Farfante (p. 546)

7. Median sulcus long and deep along entire length. Dorsolateral sulcus broad, ratio between height of keel and sulcus width usually less than three. Petasma with distal portion of ventral costa tapering to point, arc shaped, and armed with elongated group of closely set teeth on attached border. Thelycum with anterior and posterior processes broad--------------*P.* (*M.*) *aztecus aztecus* Ives (p. 527)

Median sulcus short, shallow and often interrupted. Dorsolateral sulcus narrow, ratio between height of keel and sulcus width usually more than three, sulcus often almost closed. Petasma with distal portion of ventral costa blunt, almost straight, and armed with irregularly arranged teeth. Thelycum with anterior and posterior processes narrow--------------------------------------*P.* (*M.*) *paulensis* Pérez Farfante (p. 555)

## ***Penaeus* (*Litopenaeus*) *setiferus***
## **(LINNAEUS)**

Figures 4 to 13

United States: white shrimp, grey shrimp, lake shrimp, green shrimp, green-tailed shrimp, blue-tailed shrimp, rainbow shrimp, Daytona shrimp, common shrimp, and southern shrimp. Mexico: camarón blanco.

*Astacus fluviatilis, Americanus* Seba, 1759: 41, pl. 17, fig. 2; [fide] Holthuis, 1962: 115, 116; [fide] Holthuis, 1964a: 227, 228; [fide] Holthuis, 1964b: 233.

*Cancer setiferus* Linnaeus, 1767: 1054, 1055 (neotype, designated by Burkenroad, 1939, ♂, YPM 4385—BOC 237[2]—off Matanzas Inlet, Fla., 8 to 10 fm., April 2, 1934, M.B. Bishop); Houttuyn, 1769: 434, 435; Müller, 1775: 1133; [fide] Holthuis, 1962: 115, 116; [fide] Holthuis, 1964a: 227–229; [fide] Holthuis, 1964b: 232–234; International Commission on Zoological Nomenclature, 1967: 151, 152.

?*Cancer* (*Gammarellus*) *setiferus:* Herbst, 1793: 106, 107, pl. 34, fig. 3.

?*Penaeus orbignyanus* Latreille, 1817: 155.

*Penaeus fluviatilis* Say, 1818: 236, 238; Gunter, 1962a: 109–112; Gunter, 1962b: 121; Gunter, 1962c: 216–224, 226; Gunter, 1963: 103–108; Gunter and Hall, 1963: 295, 297, 304; Gunter, 1964: 229; Gunter, Christmas, and Killebrew, 1964: 181–185; [fide] Holthuis, 1964a: 227; [fide] Holthuis, 1964b: 233, 234; Ingle, 1964:

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[2] The references made to specimens in the literature under the Bingham Oceanographic Collection catalog numbers are mentioned here with the initials BOC. This collection is in the Peabody Museum of Natural History, Yale University.

232; Hutton, 1964: 439; Joyce, 1965: 14–16, 24–26, 34–36, 44–46, 53–55, 62–64, 70–72, 79, 80, 88, 89, 93, 94, 99, 100, 103–112, 114–116, 121, 123, 128, 132, 136–146, 154, 171–173, 175, 178–180, 183, 184, 186–192, 220, 221; Loesch, 1965: 41, 42, 48, 49, 52, 54–56; Christmas, Gunter, and Musgrave, 1966: 196, 197, 199, 203, 205, 208–212, fig. 4; Joyce and Eldred, 1966: 9, 10, 11, 13, 16, 22, 23, 31, 32, 34–36.

*Penaeus setiferus:* H. Milne Edwards, 1837: 414, 415 [part]; De Kay, 1844: 30; Gibbes, 1850: 199; de Saussure, 1858: 471 [part]; Stimpson, 1871: 133; Kingsley, 1882: 107 [part]; Rathbun, 1884: 821–823, pl. 273; Smith, 1885: 170; Herrick, 1887: 46, 47, 55, pl. 5, fig. 6; Ives, 1891: 196; Evermann, 1892: 90; Rathbun, 1893: 821–823, pl. 273; Sharp, 1893: 110 [part]; Spaulding, 1908: 3–21, pls. 1–4; Andrews, 1911: 420–423, figs. 1, 2; de Man, 1911: 95; Fowler, 1913: 314, 316–318, 542, pl. 92; Tulian, 1920a: 104, 105; Tulian, 1920b: 106–114; Viosca, 1920: 121–124, 1 fig.; Viosca, 1924: 90–93; Weymouth, 1931: 11–13, 1 fig.; Weymouth, Lindner, and Anderson, 1932: 108–110; Lindner, 1933: 51–53; Weymouth, Lindner, and Anderson, 1933: 1–24, figs. 3a, 4a; Burkenroad, 1934: 61, 74, 77–91, 112, 134, 138, figs. 5–7; Johnson and Lindner, 1934: 4, 56, 57; Myers and Gowanloch, 1934: 9–12, 14–21; Pearson, 1935: 172; Burkenroad, 1936: 315–318, fig. 1b; Lindner, 1936: 155–158, 160–167, figs. 1, 2 (top); Viosca, 1938: 52; Burkenroad, 1939: 5, 17–25, 27, 48, 51, 52; Collier, 1939: 32, 33; Pearson, 1939: 2, 3, 5–30, 33, 35–43, 45–51, 53–56, 59, 61–63, 65–68, 70–72, figs. 1–20, 22–30, 36–39; Rioja, 1939: 316, 318, figs. 6–9; Rioja, 1940a: 261, 262, 266; Rioja, 1940b: 267, 268, 273; Viosca, 1940: 33, 34, 36; Gunter, 1941: 203, 204; Rioja, 1941a: 200, 206, 207, 213–215, figs. 10–12, 22; Rioja, 1941b: 225, 226; Anderson and Lindner, 1945: 303; Gunter, 1945: 25, 69, 77, 87, 90, 94, 100, 101, 105, 106, 113, 115, 119, 178, 179; Viosca, 1945: 276; Anderson, 1948: 1–4, 1 fig.; King, 1948: 244–262, pls. A–G; U.S. Fish and Wildlife Service, 1948: 1–5; Anderson, King, and Lindner, 1949: 168–171; Anderson, Lindner, and King, 1949: 16; Burkenroad, 1949: 688–689; Broad, 1950: 1–4, 4 figs.; Gunter, 1950: 13–24, 26, 40–49; Hedgpeth, 1950: 106, 107, 113; Idyll, 1950: 7, 9–15, 17, 19, 23, 25, fig. 1; Rioja, 1950: 149–150, pl. 1, figs. 2–5; Sprague, 1950: 4; Whitten, Rosene, and Hedgpeth, 1950: 78; Broad, 1951: 27, 30, 31, 33, 34, fig. 2; Sánchez Roig and Gómez de la Maza, 1951: 113–118; Gômez de la Maza, 1952: 167, 168, 171, fig. 2 b, c; Leone and Pryor, 1952: 27–31; Springer and Bullis, 1952: 7–12; Carlson, 1953: 32; Heegaard, 1953: 75–105, 12 pls.; Hedgpeth, 1953: 159–161, 210; Hildebrand and Gunter, 1953: 151–155; Lindner, 1953: 65–69; Pérez Farfante, 1953: 229, 232–235, 241; Williams, 1953: 156, 158–160, figs. 1, 2; Anderson, 1954: 98, 99; De Sylva, 1954: 10, 18, 19, 21, 23, 26, 33, 34, fig. 4; Gunter and Hildebrand, 1954: 95–102; Hildebrand, 1954: 233, 238–241, 243, 246, 261–263, 265, 324–326, 349, 350, 360, 362; Sprague, 1954: 248, 251; Springer and Bullis, 1954: 4, 5, 13–16; Hildebrand, 1955: 171–173, 176, 177, 190, 191, 220, 226, 227; Parker, 1955: 204, 205, 210; Voss, 1955: 5, 8, 10, figs. 9, 9 a, b; Williams, 1955a: 116–118, 127, 129–135, 140, 141, 143–145; Williams, 1955b: 200, 203, 204, 206; Anderson, 1956: 1, 2, 4, 5, 8, 11–13; Guest, 1956: 6, 10, 13, 14, 18, figs. 2, 3; Gunter, 1956: 99–105; Johnson and Fielding, 1956: 175–189; Lindner and Anderson, 1956: 555–645, figs. 1–46; Springer and Bullis, 1956: 9; Anderson, 1957: 399–403; Carranza, 1957: 147; Dall, 1957: 142; Dawson, 1957: 1068, fig. 1; Ingle, 1957: 10–12, 16, 17; Lindner, 1957: 69, 72, 83, 84, 129; Pearse and Gunter, 1957: 139, 147, 151; Simmons, 1957: 178, 191, 199; Viosca, 1957: 12, 13, 20, 2 figs.; Woodburn, Eldred, Clark, Hutton, and Ingle, 1957: 6–12, fig. 2; Anderson, 1958a: 1, 2, fig. 1; Anderson, 1958b: 1–7, 1 fig.; Anderson and Lindner, 1958: 1–13; Darnell, 1958: 385, 400, 405, 407, 408; Eldred, 1958: 6, 9, 11, 12, 20–24; Gunter and Shell, 1958: 16, 17, 19, 22, 23, 32; Hildebrand, 1958: 158, 159, 170; U.S. Fish and Wildlife Service, 1958b: 1, 6, 8, 12, 13, 16, 18, 22, 24–28, 30, 32, fig. I–5a; Williams, 1958: 283–286, 288–290; Collier, Gunter, Ingle, and Viosca, 1959: 1–5; Costello, 1959: 1; Eldred, 1959a: 75; Holthuis, 1959: 62; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959: 6, 7, 9, 10, 12, 16, 19–22, 24; Iversen and Manning, 1959: 130, 131; Kruse, 1959: 123, 126, 128, 130, 132, 134, 136, 137, 141, 142; Williams, 1959: 281, 282, 285, 289; Young, 1959: 1–168, 89 figs.; Chin, 1960: 135–141, figs. 1–5; Eldred and Hutton, 1960: 91, 97, 99, 101, 103, 108, fig. 10 a–d; Hoese, 1960a: 592, 593; Hoese, 1960b: 330, 331; Iversen and Idyll, 1960: 4, 6; Williams, 1960: 560; Bearden, 1961: 3–8; Dobkin, 1961: 321, 325, 327, 345–348; Eldred, Ingle, Woodburn, Hutton, and

Jones, 1961: 80, 86, 88, 89, 97, 98, 109; Gunter, 1961a: 599; Gunter, 1961b: 183, 184; Iversen and Jones, 1961: 16; Renfro, 1961: 10, 12; Anderson, 1962: 1, 2, fig. 1; George, 1962: 160, 162; Holthuis, 1962: 115, 118; Hutton, Ball, and Eldred, 1962: 327, 330, 331; Kutkuhn, 1962: 343, 355, 361, 369–388, 397, 401; Boschi, 1963: 5, 6, 19, 20; Kutkuhn, 1963: 66–77; McFarland and Lee, 1963: 391, 393–397, 399, 400, 402–415; Renfro and Brusher, 1963: 13–17; Zein-Eldin, 1963a: 188–196; Holthuis, 1964a: 227–229; Hutton, 1964: 439, 440, 444, 445; Klima, 1964: 60, 63, 64, fig. 3; Aldrich, 1965: 370–375; Anderson and Lunz, 1965: 1–5; Broad, 1965: 86–90; Bullis and Thompson, 1965: 6; Copeland, 1965: 19; Ewald, 1965c: 103, 107, 109, 113, 114, 2 figs.; Holthuis and Rosa, 1965: 6; Temple and Fischer, 1965a: 59, 61; Temple and Fischer, 1965b: 16; Williams, 1965: 18–21, 23, 24, 26, 27, figs. 8, 9; Van Engel, 1965: 38; Zein-Eldin and Aldrich, 1965: 210–213; Anderson, 1966: 1, 3–7, figs. 3–9; Copeland and Truitt, 1966: 68, 69, 72, 73; Kutkuhn, 1966a: 19, 20, 27, 28, fig. 2; St. Amant, Broom, and Ford, 1966: 4; Sykes and Finucane, 1966: 374; Aldrich, Wood, and Baxter, 1967: 80; Baxter and Renfro, 1967: 149, 151–158; fig. 3; Lyles, 1967: 315–317, 371–376; McCoy and Brown, 1967: 1–3, 8–10, 13, 14, 17, 20, 21, 24–27; Temple and Fischer, 1967: 323–325, 328, 331–333; Zamora and Trent, 1968: 17–19.

*Peneus setiferus:* Gibbes, 1848: xiv; Kingsley, 1878: 69; de Saussure, 1858: 421; Kingsley, 1879: 330; Hay and Shore, 1918: 378, pl. 25, fig. 5; Boone, 1930: 15, 105, 106, pl. 31.

*Penaeus setifer:* Agassiz, 1849: 63, fig. 17c; Doflein, 1900: 126, 127 [part], fig. 1.

*Paneus setiferus:* Collins and Smith, 1892: 102.

*Panaeus gracilirostris* Thallwitz, 1892: 3, fig. 5. (According to Burkenroad, 1939).

*Penaeus gracilirostris:* de Man, 1911: 100, 101.

*Penaeus setifera:* Cowles, 1930: 355, 356, 358.

*Palaemonetes setiferus:* Lunz, 1956: 93.

*Penaeus sertiferus:* Aldrich, Wood, and Baxter, 1967: 80.

White shrimp: Lunz, 1956: 93; Loesch, 1957: 39, 41; Lunz, 1958: 47; Baxter and Furr, 1964: 29; Renfro and Brusher, 1964: 13–15; Zein-Eldin, 1964: 65–67; Klima and Benigno, 1965: 38, 39; Renfro and Brusher, 1965: 10; Zein-Eldin and Griffith, 1965: 77, 78; Zein-Eldin, 1966: 41–43, fig. 39.

?Shrimp: Flint, 1956: 11, 12.

## Taxonomic Remarks

The International Commission on Zoological Nomenclature has used its plenary powers (Opinion 817, 1967) to validate the selection of Burkenroad's neotype of *Cancer setiferus* Linnaeus, and, thus, the white shrimp from the Atlantic Coast of the United States and the Gulf of Mexico is *Penaeus setiferus* (L.). Consequently, the white shrimp from the Caribbean Sea and the Atlantic Coast of South America are referable to *P. schmitti* Burkenroad. Both names—*Cancer setiferus* Linnaeus and *Penaeus schmitti* Burkenroad—have been placed on the Official List of Specific Names.

Holthuis (1962) selected as lectotype of *Astacus fluviatilis, Americanus* Seba, 1759, the figure No. 2 of plate 17, given by Seba to illustrate his description.

Gunter's (1962a) suggestion that *Penaeus orbignyanus* Lat. should be considered a nomen dubium seems logical. Latreille (1817) stated that the type specimen was sent to him by "Dr. d'Orbigny" from the Département de la Vendée in western France. Burkenroad (1939) failed in his attempt to locate the type, which, according to H. Milne Edwards (1837), could not be differentiated from *P. setiferus*. The specimen could have been a stray from the western Atlantic actually collected in that improbable locality, or it could have been collected in America and given to Dr. d'Orbigny. In either case, it does not seem probable that it will ever be determined if the name corresponds to *P. setiferus* or *P. schmitti.*

## Study Material

### UNITED STATES

**New Jersey:** 1 ♂, USNM, off Long Branch, August 1887, T. Steelman and G. H. Bean. 1 ♂, USNM, off New England Creek, 1 fm., October 19, 1929, H. G. Richards. 1 ♀, PANS, Atlantic City, Ch. Buvinger. 1 ♂ PANS, Ocean City, July 6, 1913, D. McCadden. 1 ♂, PANS, Ventnor, summer 1949, C. B. Atkinson. 1 ♀, YPM, Dennis Cove, August 27, 1932.

**Maryland:** 1 ♂, USNM, Saint Jeromes, September 17, 1889, USFC.

**Virginia:** 1 ♂, USNM, off Plantation Light, Chesapeake Bay, July 8, 1920, 25 fm., *Fish Hawk* Sta. 8826. 1 ♂, USNM, Chesapeake Bay, R. E. Earll and E. McDonald, 1880. 1 ♂, USNM, Rappahannock River, 12 to 15 fm., October 19, 1921, W. C. Schroeder. 13 ♂ 14 ♀, USNM, Pagan Creek, James River, October 31, 1930, J. C. Pearson. 1 ♂, CBL, Silver Beach, Chesapeake Bay, October 28, 1953. 2 ♂, USNM, Willoughby Point, May 1880, R. E. Earll and E. McDonald. 1 ♂, USNM, off mouth Chesapeake Bay, 18 fm., November 16, 1880, *Fish Hawk* Sta. 901.

**North Carolina:** 3 ♂ 3 ♀, USNM, off Beaufort Inlet, 40 to 50 fm., October 6, 1949, A. B. Williams. 3 ♂ 1 ♀, USNM, Beaufort, H. L. Osborn. 1 ♂, YPM, Fort Macon, H. C. Yarrow. 1 ♂, YPM, Fort Macon, J. E. Coues. 6 ♂ 8 ♀, AMNH, Morehead City.

**South Carolina:** 5 ♀, USNM, Stono Inlet, June 5, 1935, J. C. Pearson. 1 ♂ 6 ♀, USNM, Folly Beach, H. T. Ebner. 1 ♂ 2 ♀, USNM, off Hilton Head, October 11, 1941, *Madelena*.

**Georgia:** 1 ♀, USNM, Savannah, October 9, 1930, I. R. Tomkins. 1♂ 1♀, USNM, Savannah, 1930, I. R. Tomkins. 76 ♂ 75 ♀, YPM, mouth of Wilmington River, 6 to 8 fm., April 5, 1934. 89 ♂ 67 ♀, YPM, St. Simons Sound, April 4, 1934. 13 ♂ 10 ♀, USNM off Brunswick, 3 to 4 fm., August 26, 1965, W. W. Anderson. 5 ♂ 12 ♀, USNM, Jekyll Creek, March 25, 1940, 8 fm., *Pelican* Sta. 199–201.

**Florida:** 1 ♂, USNM, off Jacksonville, 6 to 8 fm., October 2, 1957, *Combat* Sta. 504. 28 ♂ 24 ♀, YPM, off Matanzas Inlet, 8 to 10 fm., April 2, 1934. 1 ♂ 1 ♀, USNM, off Matanzas Inlet, 8 fm., November 19, 1963, *Silver Bay* Sta. 5381. 3 ♂ 3 ♀, USNM, S. of Saint Augustine, 11 fm., April 16, 1940, *Pelican* Sta. 212–213. 8 ♂ 9 ♀, USNM, off Cape Kennedy, 9½ fm., January 26, 1962, *Silver Bay* Sta. 3710. 6 ♂ 3 ♀, USNM, off Cape Kennedy, 7½ fm., October 9, 1934, W. W. Anderson. 15 ♂ 25 ♀, USNM, off Cocoa Beach, 10 to 11 fm., January 13, 1965, *Oregon* Sta. 5181. 22 ♂ 20 ♀, USNM, off Melbourne Beach, 11 fm., January 13, 1965, *Oregon* Sta. 5182. 1 ♂ 1 ♀, USNM, off Melbourne Beach, 20 to 22 fm., January 13, 1965, *Oregon* Sta. 5183. 2 ♂ 3 ♀, USNM, N. of Fort Pierce, 8 fm., January 28, 1962, *Silver Bay* Sta. 3715. 3 ♂ 10 ♀, USNM, Pilot Cove, Apalachicola Bay, November 12, 1958, R. M. Ingle. 6 ♂ 5 ♀, SW. of Apalachicola Bay, 6 fm., October 31, 1953, *Oregon* Sta. 863. 15 ♂ 12 ♀, USNM, Apalachicola Bay, July 17, 1961, SPML.

**Alabama:** 1 ♀, YPM, off Mobile Bay, March 20, 1937, 12 fm., *Atlantis* Sta. 2812. 1 ♂ 1 ♀, USNM, off Mobile Bay, 7 fm., December 14, 1950, *Oregon* Sta. 185. 3 ♂ 5 ♀, USNM, off Mobile Bay, 7 fm., January 28, 1962, *Oregon* Sta. 3475. 2 ♀, USNM, off Alabama, 19 fm., December 14, 1950, *Oregon* Sta. 188.

**Mississippi:** 23 ♂ 25 ♀, GCRL, Mississippi Sound, September 5, 1963, J. Y. Christmas. 11 ♂ 10 ♀, GCRL, Mississippi Sound, September 25, 1963, J. Y. Christmas. 16 ♂ 14 ♀, GCRL, Mississippi Sound, October 30, 1963, J. Y. Christmas. 2 ♂ 5 ♀, USNM, Biloxi Bay, June 18, 1965, GCRL. 7 ♀, USNM, Biloxi Bay, March 1965, GCRL.

**Louisiana:** 2 ♂ 3 ♀, USNM, New Orleans, Louisiana Conserv. Comm. 1 ♂, YPM, New Orleans, R. W. Shuffeldt. 12 ♂ 7 ♀, USNM, Lake Pontchartrain, 2⅓ fm., November 25, 1953, R. M. Darnell. 24 ♂, AMNH, off Bayou Scofield, January 3, 1931, M. D. Burkenroad. 1 ♀, USNM, Breton Island, S. Springer. 1 ♂ 2 ♀, YPM, Grande Isle, 6 fm., July 21, 1930. 2 ♂ 1 ♀, USNM, Grande Isle, July 14, 1928, E. H. Behre. 25 ♂ 25 ♀, USNM, Puffer Point, Barataria Bay, July 22, 1932, J. C. Pearson.

**Texas:** 4 ♂ 1 ♀, USNM, off mouth of Sabine River, 10 fm., May 19, 1965, BCFBLG. 7 ♂ 4 ♀, USNM, off mouth of Sabine River, 10 fm., May 19, 1965, BCFBLG. 3 ♂, USNM, Swan Lake, Galveston, August 19, 1965, BCFBLG. 2 ♂ 1 ♀, USNM, Swan Lake, Galveston, June 24, 1965, BCFBLG. 3 ♂ 3 ♀, USNM, S. of Galveston Island, 5 fm., August 10, 1960, *Oregon* Sta. 2884. 9 ♂ 4 ♀, USNM, off Galveston, April 1965, BCFBLG. 2 ♂, USNM, off Port Aransas, 9 fm., November 26, 1950, *Oregon* Sta. 149. 2 ♂ 1 ♀, USNM, Corpus Christi, H. B. Parks. 2 ♂ 3 ♀, USNM, off Padre Island, 7½ fm., January 27, 1964, *Oregon* Sta. 4641.

MEXICO

**Tamaulipas:** 5 ♂ 2 ♀, INIBP–USNM, Tampico, May 14, 1963, S. García.

**Veracruz:** 1 ♀, USNM, Bocaina, Laguna de Tamiahua, June 9, 1964, R. Márquez and C. Tovar. 1 ♂ 1 ♀, INIBP, Villa Cuauhtémoc, April 8, 1962, S. García. 1 ♂ 1 ♀, USNM, Laguna de Pueblo Viejo, Villa Cuauhtémoc, June 20, 1963, S. García. 1 ♂ 1 ♀, INIBP, Laguna de Pueblo Viejo, Villa Cuauhtémoc, October 17, 1964, S. García. 1 ♂ 2 ♀, USNM, La Bocana, Tuxpan, March 7, 1964, A. Mendoza and R. Márquez. 14 ♂ 2 ♀, INIBP–USNM, Tuxpan, August 29, 1963, S. Basulto. 2 ♂ 3 ♀, INIBP–USNM, Estero Tabasco, Tuxpan, March 3, 1964, A. Mendoza. 6 ♂ 9 ♀, INIBP–USNM, Estero Jacome, Tuxpan, December 18, 1963, S. García. 3 ♀, USNM, Río Pantepec, Tuxpan. 5 ♀, INIBP–

USNM, Río Pantepec, Tuxpan, April 10, 1963, S. Basulto and M. C. Rodríguez de la Cruz. 2 ♀, USNM, Río Pantepec, Tuxpan, February 11, 1964, members Sociedad Cooperativa Río Pantepec. 3 ♂ 5 ♀, INIBP–USNM, mouth of Río Pantepec, Tuxpan, June 7, 1964, C. Tovar and R. Márquez. 6 ♂ 4 ♀, INIBP–USNM, Laguna La Tapada, November 28, 1963, A. Macías and U. Barron. 1 ♂, INIBP, Laguna de Buen País, 12 km. W. of Alvarado, F. Lachica and F. Carmona, April 1965.

**Tabasco:** 5 ♂ 5 ♀, INIBP–USNM, Laguna Pajonal, July 4, 1963, D. Fuentes.

**Campeche:** 2 ♀, INIBP–USNM, Golfo de Campeche, 26 fm., April 30, 1959, R. Ramírez and M. Flores. 5 ♂ 3 ♀, INIBP–USNM, Boca Nueva, Los Pinos, April 28, 1959, R. Ramírez and M. Flores. 3 ♂ 1 ♀, INIBP–USNM, N. of Isla del Carmen, 3 fm., May 5, 1959, R. Ramírez and M. Flores.

## Diagnosis

Adrostral carina and sulcus short, ending at epigastric tooth. Petasma with inner surface of distal portion of lateral lobe with diagonal ridge and prominent fold near rounded distoventral corner; emargination median to inner lappet shallow. Thelycum with pair of anterolateral, sharp ridges, posterior portions of which bend mesially, and pair of posterior, fleshy, closely set lobes on sternite XIV; posterior margin of sternite XII bearing pair of relatively small scalloplike projections.

## Description

### ROSTRUM (fig. 4)

Teeth $\frac{4\text{–}10}{0\text{–}3}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—70, 9/2—12, 7/2—13, 8/3—1.50, 9/3—1.25, 8/1—0.75, 10/2—0.50, 6/2—0.50, 7/0—0.25, 4/1—0.25; N=400) +epigastric; ventral teeth relatively far apart, first tooth usually opposite or anterior to last dorsal tooth; rostrum slender and long, in juveniles extending to base of distal one-fifth of thickened portion of lateral antennular flagellum; maximum length in relation to c.l. (carapace length) obtained at 10 to 16 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ (rostrum length) as high as 1.10); decreasing progressively with increasing length of shrimp, reaching midlength of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.55); rostrum straight, slightly concave posteroventrally; highest portion of blade usually at level of second, occasionally of third dorsal tooth, and at level of first tooth in some young; third dorsal tooth level with anterior margin of carapace; tip slender and long, almost one-half of length of rostrum. Postrostral carina narrow and relatively short, ending ⅕ to $\frac{1}{13}$ c.l. from posterior margin of carapace, shorter in larger individuals. Median sulcus shallow, interrupted and variable in shape: consisting of anterior elongated concavity in wider portion of postrostral carina, either blunt or continuing as line toward epigastric tooth, and leading posteriorly by a groove to a narrower concavity; sometimes both concavities separated by constriction, and often median sulcus consisting of a single blunt anterior concavity; median sulcus represented posteriorly by few minute pits. In small specimens median sulcus consisting of three or four pits. Adrostral carina rounded and short, ending at level of epigastric tooth. Adrostral sulcus shallow and short, same length as adrostral carina.

### CARAPACE (fig. 5)

Length in proportion to total length smaller in juveniles; according to my data increasing suddenly at subadult stage. Gastrofrontal sulcus absent; gastrofrontal carina absent except for a short, almost imperceptible rib present sometimes at level of first two dorsal teeth. Orbito-antennal sulcus wide anteriorly, narrowing posteriorly to below apex of hepatic spine, there widening into base of spine. Gastro-orbital carina pronounced, sharp, and relatively short, occupying posterior ⅗ to ⅔ distance between postorbital margin and hepatic spine. Cervical sulcus short and shallow extending dorsally to two-fifths c.l. from postorbital margin of carapace; in small individuals extending farther posteriorly as line. Hepatic carina ⅙ to ⅕ c.l., sharp, sloping anteroventrally to end $\frac{1}{18}$ to $\frac{1}{13}$ c.l. from anterior margin of carapace; hepatic sulcus shallow. Antennal spine acute and relatively short; hepatic spine prominent.

### ANTENNULES

Lateral flagellum long, seven-tenths to almost same length as antennular peduncle, slightly longer and with articles shorter than median flagellum. Median flagellum exhibiting sexual dimorphism: in adult males markedly flattened dorsoventrally, with two closely set rows of stout processes of unequal sizes along midportion of

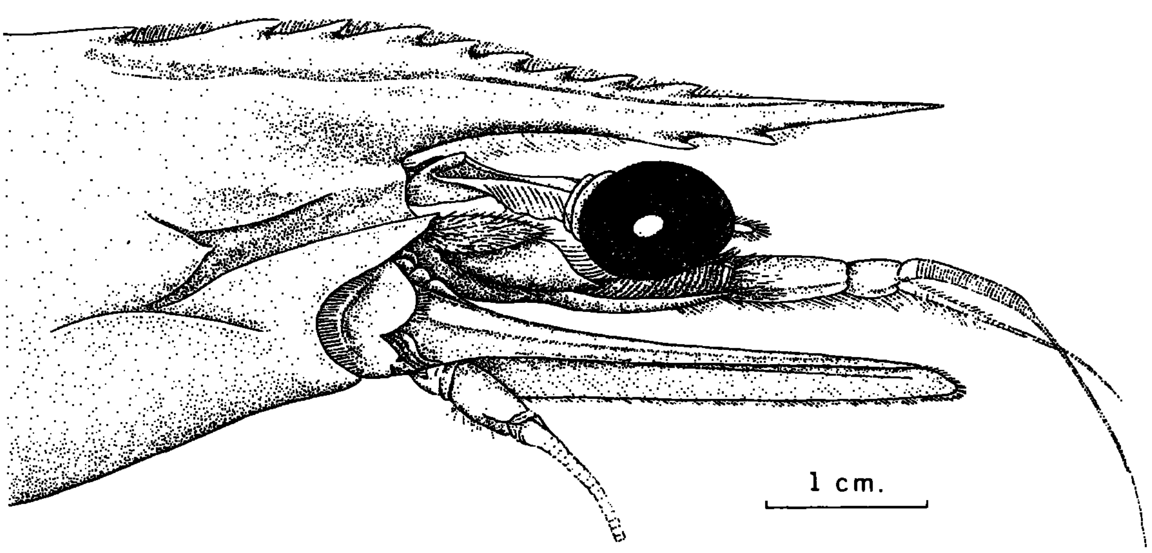

FIGURE 4.—*Penaeus* (*L.*) *setiferus* (*L*). Rostrum, ♀ 36 mm. c.l., off Cocoa Beach, Fla.

internal margin, and with long setae along proximal one-fourth of external margin; in females processes lacking but long setae present along proximal two-fifths of external margin. Those processes were described by Rioja (1939) and Young (1959); the latter worker stated that "Since the antennular flagella are olfactory, the sexually dimorphic medial flagellum of the male *Penaeus setiferus* probably functions to enable the male to find the sexually mature female during the time of mating." Anterolateral spine small, sharp. Stylocerite reaching slightly beyond midlength of first antennular segment. Prosartema extending to proximal fourth of second antennular segment.

### ANTENNAE

Scaphocerite length 2½ times maximum width; spine reaching or slightly surpassing distal end of third antennular segment. Carpocerite about 1¼ times longer than wide, its distal end reaching base of eye. Antennal flagellum very long, 2½ to 3 times body length (fig. 6).

### THORACIC APPENDAGES

Third maxilliped reaching at least distal end of first, and at most distal end of proximal ⅔ of second antennular segment; length of dactyl ⅔ to ¾ of propodus. First pereopod extending to distal end of carpocerite or surpassing it by as much as four-fifths length of dactyl. Second pereopod reaching distal end of first and, at most, distal end of proximal three-quarters of second antennular segment. Third pereopod extending to distal end of antennular peduncle or surpassing it by length of entire propodus. Fourth pereopod exceeding carpocerite by ⅓ to ¾ length of propodus. Fifth pereopod surpassing fourth by one-half to entire length of dactyl. Exopods on all pereopods; long ischial and basial spines on first pereopod, and rather long basial spine on second pereopod.

### ABDOMEN

Carinate dorsally from one-quarter of third or from fourth somite posteriorly, carina gradually increasing in height posteriorly forming keel on sixth somite, and ending in sharp spine on posterior margin of somite. Dorsolateral sulcus (fig. 7) very shallow and narrow, without lips; in young individuals running almost entire length of somite, in adults extending only from slightly anterior of midlength of somite to near posterior margin. Sixth abdominal somite with three cicatrices on each side, anterior one longest; fifth somite with one cicatrix and diagonal series of minute pits anterior to sinus on posterior margin of somite situated on rib in large specimens; fourth somite with similar series of pits dorsal to sinus on posterior margin of somite. Ventral margin of pleuron of first somite slightly to moderately indented. Telson (fig. 8) with deep median sulcus and acuminate tip. Dorsoventral axis of larger males much shorter than that of females of corresponding lengths.

### PETASMA (fig. 9 a–c)

Lateral lobe with distal portion of inner surface bearing conspicuous rounded fold and diagonal ridge, which undulates proximally to near mid-

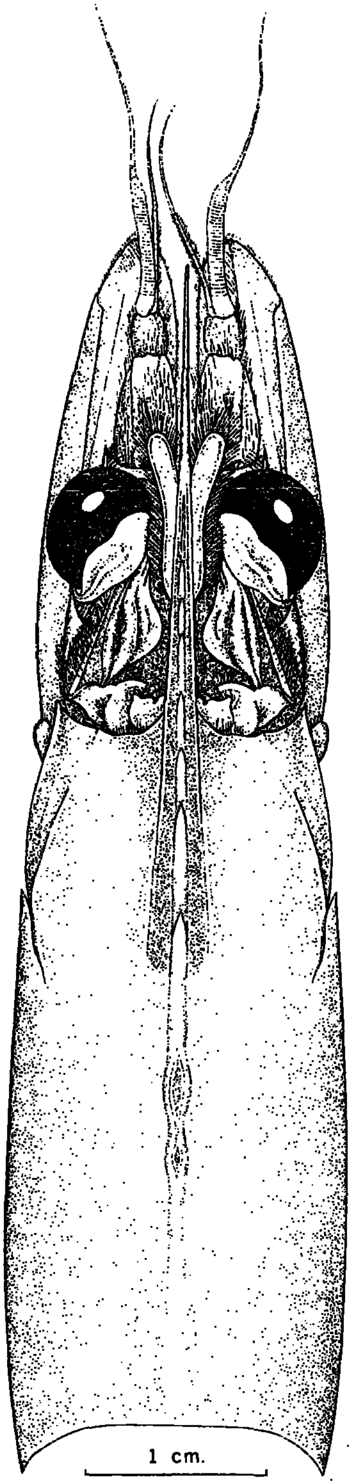

FIGURE 5.—*Penaeus* (*L.*) *setiferus* (L.). Cephalothorax, ♀ 41.5 mm. c.l., off Cocoa Beach, Fla.

length of petasma. Distoventral corner of lateral lobe rounded and with nearly symmetrical S-shaped ridge on free border; anterior half of ventral border with two narrow ribs joined at both ends. Emargination median to inner lappet shallow. Outer surface of lateral lobe with relatively narrow band of spines, three to four, rarely five, rows abreast distally and decreasing to one or two proximally. Pair of crests flanking band of spines distally, crest close to median lobe more prominent and sharp than crest near free ventral margin; latter crest plain, not bifurcated. Lateral lobe at almost same level as median lobe, extended only slightly anteriorly.

### APPENDIX MASCULINA (fig. 9 d, e)

Subtriangular, its length almost twice width at base, and armed with short spines along distal portion of median margin and with long spines on distal portion; distal spines slightly less than half length of appendix. Anterior surface subplane, posterior surface strongly concave, concavity bordered by strong arch-shaped ridge.

### SPERMATOPHORE

Elongate, podlike, actually consisting of two spermatophores; in mature males each lying completely formed in paired terminal ampullae and joined when discharged. Anterior end, when attached to female, bearing pair of winglike lateral processes, each armed with short triangular projection at posterior edge. Posterodorsal portion extended into horizontal plate.

### THELYCUM (figs. 10 and 11)

Open type. Sternite XIV with two anterolateral, prominent and sharp ridges; posterior portions of ridges converging mesially but not meeting near middle of sternite; occasional sharp, short rib present between converging ridges. Posterior portion of sternite XIV with pair of conspicuous, closely set, anteriorly produced, fleshy, usually light-colored lobes, separated in large individuals by low median rib. Sternite XIII with strong median plate extending posteriorly as fleshy, emarginated, shelflike projection overhanging sternite XIV; ridge on posterior margin of plate moderately strong; on anterior portion of sternite XIII, fleshy tonguelike lamella bordered by minute setae forming floor of cavity roofed by strong transverse ridge on posterior margin of

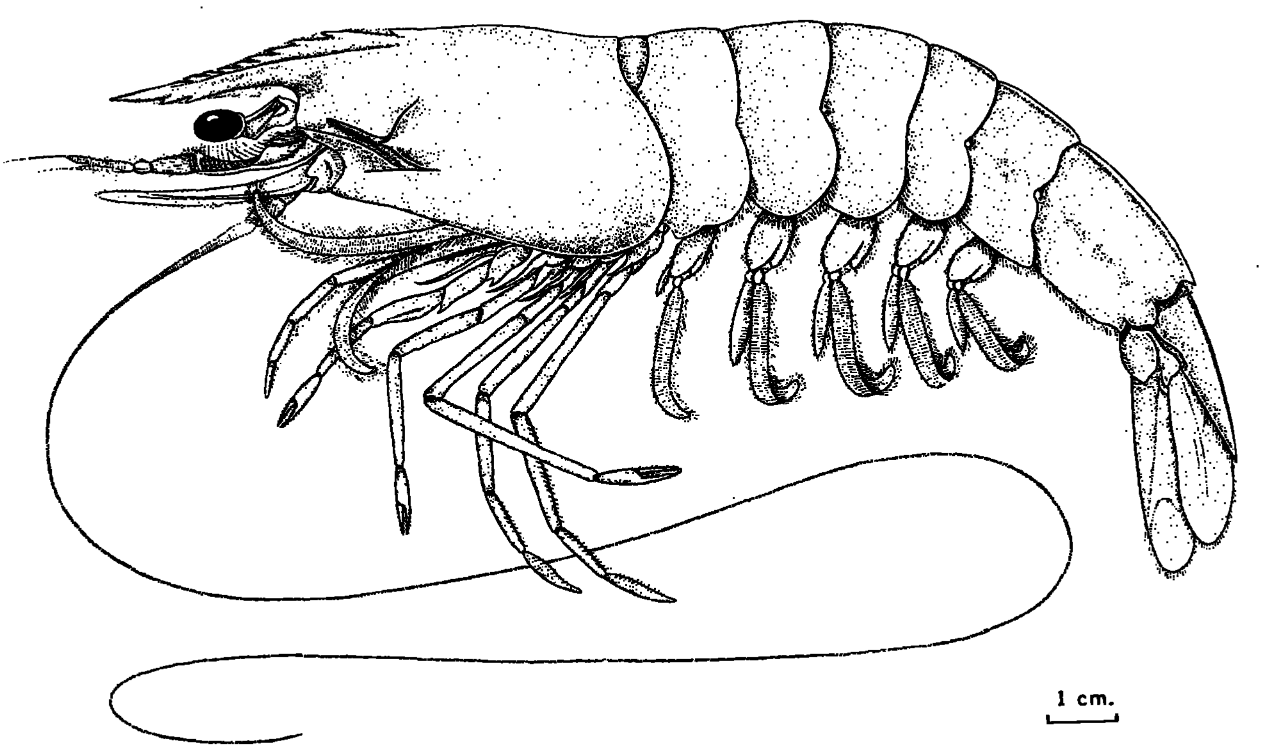

FIGURE 6.—*Penaeus* (*L.*) *setiferus* (L.). Lateral view, ♀ 49 mm. c.l., off Cape Kennedy, Fla.

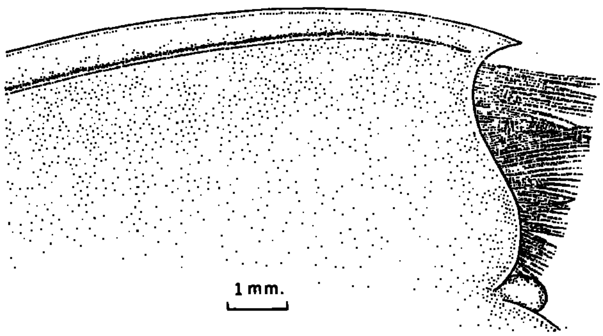

FIGURE 7.—*Penaeus* (*L.*) *setiferus* (L.). Sixth abdominal somite, posterodorsal portion, ♀ 38 mm. c.l., Biloxi, Miss.

sternite XII; ridge of sternite XII (hidden by structures surrounding gonopores and coxae of third pair of pereopods) with pair of relatively small, lateral scalloplike projections.

## COLOR

*Penaeus setiferus* has a translucent white, almost glasslike appearance and, thus, it is most commonly known as the "white shrimp." It is also often termed the "gray shrimp," and in some localities, because it is greenish, it is given the name

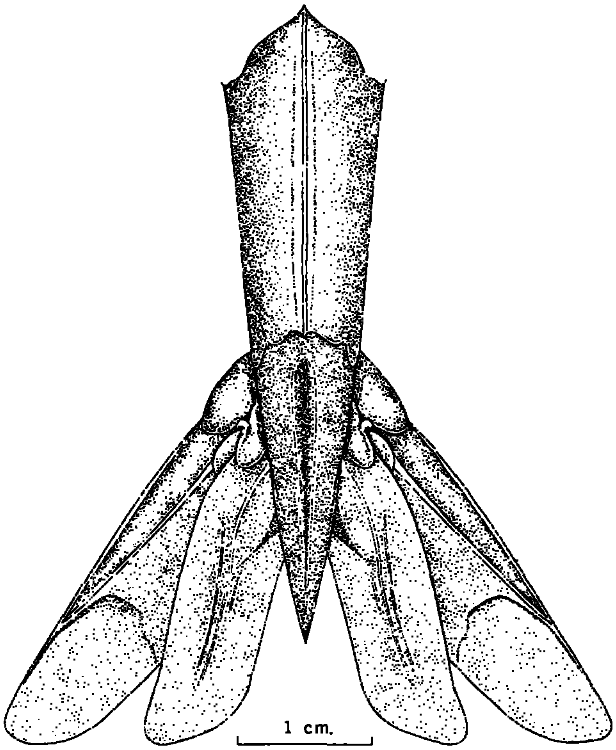

FIGURE 8.—*Penaeus* (*L.*) *setiferus* (L.). Dorsal view of sixth abdominal somite, telson and uropods. ♀ 36.5 mm. c.l., off Cocoa Beach, Fla.

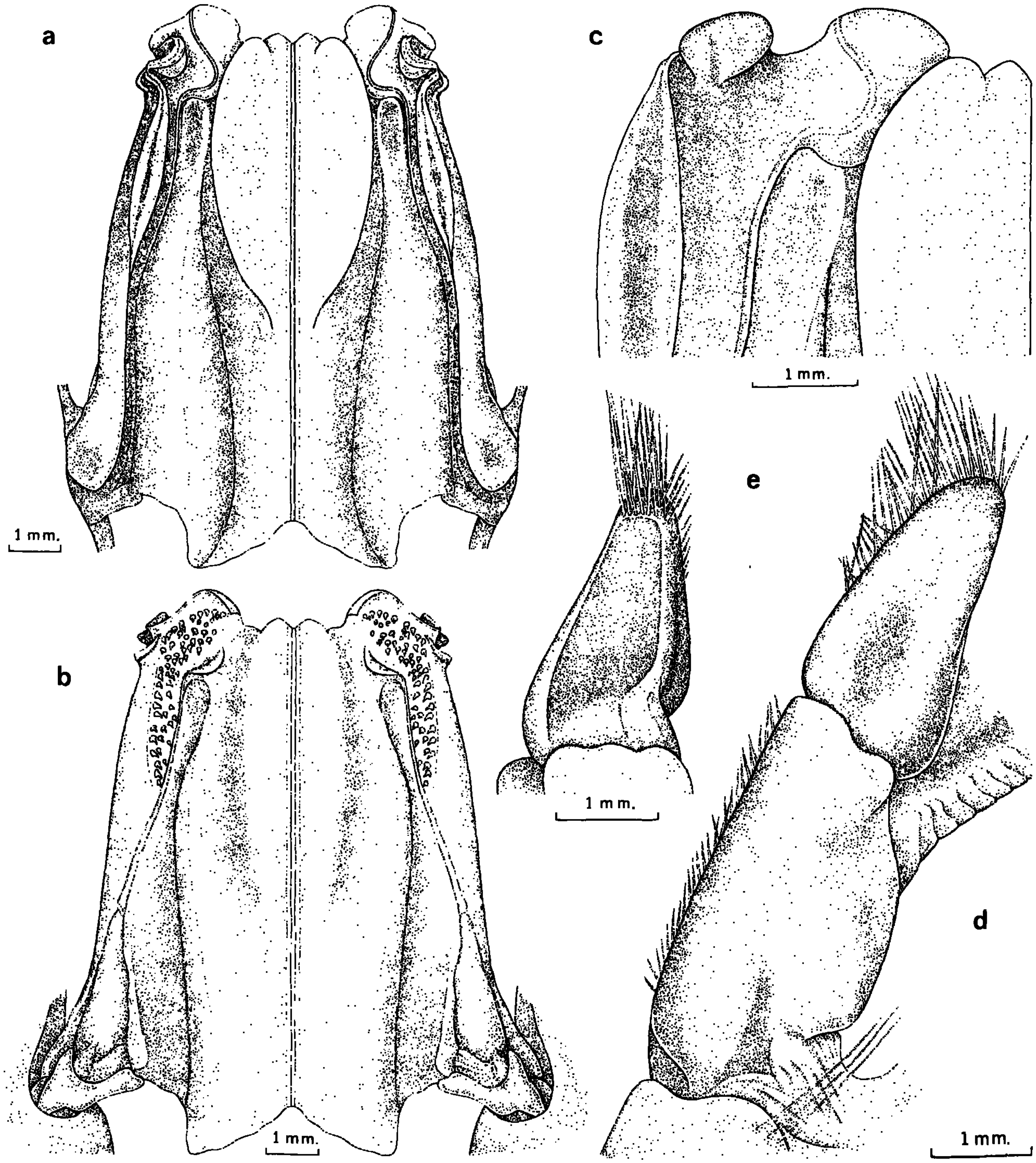

FIGURE 9.—*Penaeus (L.) setiferus* (L.). a. Petasma, interior surface. ♂ 39.5 mm. c.l., off Melbourne Beach, Fla. b. Petasma, exterior surface, ♂ 39.5 mm. c.l., off Melbourne Beach, Fla. c. Petasma, interior surface of distal portion of left half, ♂ 35 mm. c.l., Biloxi Bay, Miss. d. Appendix masculina, right. ♂ 35 mm. c.l., Biloxi Bay, Miss. e. Appendix masculina, posterior surface, ♂ 35 mm. c.l., Biloxi Bay, Miss.

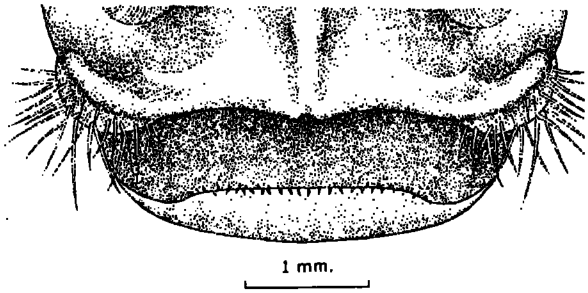

FIGURE 10.—*Penaeus* (*L.*) *setiferus* (L.). Posterior portion of sternite XII and tonguelike lamella of sternite XIII, ♀ 45 mm. c.l., off Cocoa Beach, Fla.

"green shrimp." The entire body of this species often has a bluish hue that is due to a predominance of blue chromatophores which are concentrated near the margins of the telson and uropods. Intermingled with the blue are red chromatophores in the distal portion of uropods that form a brownish-purple blotch; the uropods also bear a narrow yellowish marginal band. A dark band of black specks occurs close and parallel to the posterior margins of the carapace and the abdominal somites. The sides of the body are often pinkish and the pleopods as well as the tips of the pereopods are dark red.

## Distribution and Morphological Variations

*Penaeus setiferus* ranges along the Atlantic Coast of the United States from Fire Island, N.Y. (Burkenroad, 1934), to Saint Lucie Inlet in east Florida (Gunter and Hall, 1963); its center of abundance is in Georgia and northeast Florida (Anderson and Lunz, 1965). Its range along the coast of Florida is discontinuous; the species is absent around the southernmost portion of the peninsula and along the Gulf Coast to the mouth of the Ochlockonee River in the west portion of Apalachee Bay. The white shrimp appears again in the mouth of the Ochlockonee River (Eldred, *In* Joyce, 1965) and its range extends along the north coast of the Gulf and the northeastern Mexican Coast—with a center of abundance in Louisiana—and continues uninterrupted southward around the Golfo de Campeche to the vicinity of Ciudad Campeche—with another center of abundance in northeast Tabasco and the adjacent waters of Campeche.

Bullis and Thompson (1965) took this species at lat. 20° 17′ N., long. 91° 35′ W., which is the northernmost record on the Continental Shelf of Yucatán and is probably very close to the northern limit of its range along this Coast (fig. 12).

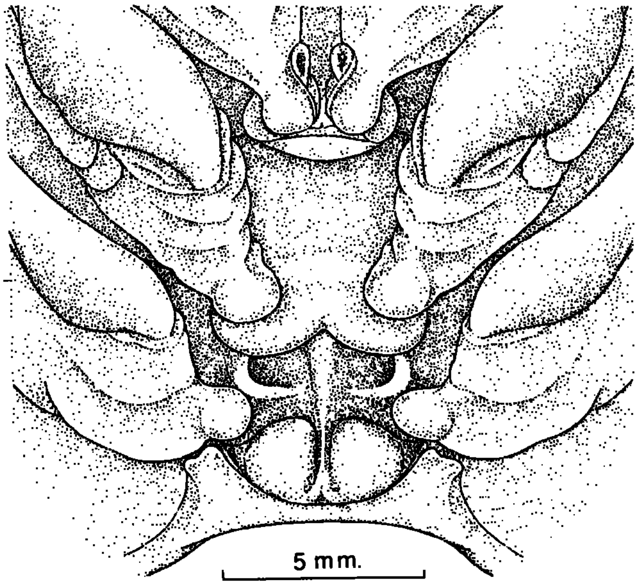

FIGURE 11.—*Penaeus* (*L.*) *setiferus* (L.). Thelycum, ♀ 44 mm., c.l., off Sabine River, Tex.

The white shrimp also has been recorded three times from near the Tortugas Islands. Springer and Bullis (1952) found a single specimen north of those islands in 25 fm. Boone (1930) described and illustrated a male which she stated had been taken in the Marquesas Keys in 30 fm. Thanks to the cooperation of Woodhull B. Young, I had the opportunity to examine *Penaeus* in the Vanderbilt Museum, where the specimen recorded by Boone was supposed to have been deposited, but I failed to locate it. Finally, Kutkuhn (1962) reported white shrimp from the Sanibel-Tortugas area on the basis of a processing plant's report. Because this species has not been found in the enormous amount of material examined in the many investigations carried out in southwestern Florida, the records of Boone and Kutkuhn may have been erroneous.

Formerly, white shrimp were believed to be absent from south of Cabo Rojo, along the coast of Veracruz to Tupilco, Tabasco. Recently, however, I examined a number of specimens from Tuxpan, and a single male from Laguna de Buen País, near Alvarado, Veracruz, so the species is present along that coast even though it may be scarce.

*P. setiferus* has a more localized distribution within its range than do the sympatric species of *Penaeus*. Its range not only has a wide gap but also has interruptions within restricted areas. A number of factors—salinity, temperature, substrate,

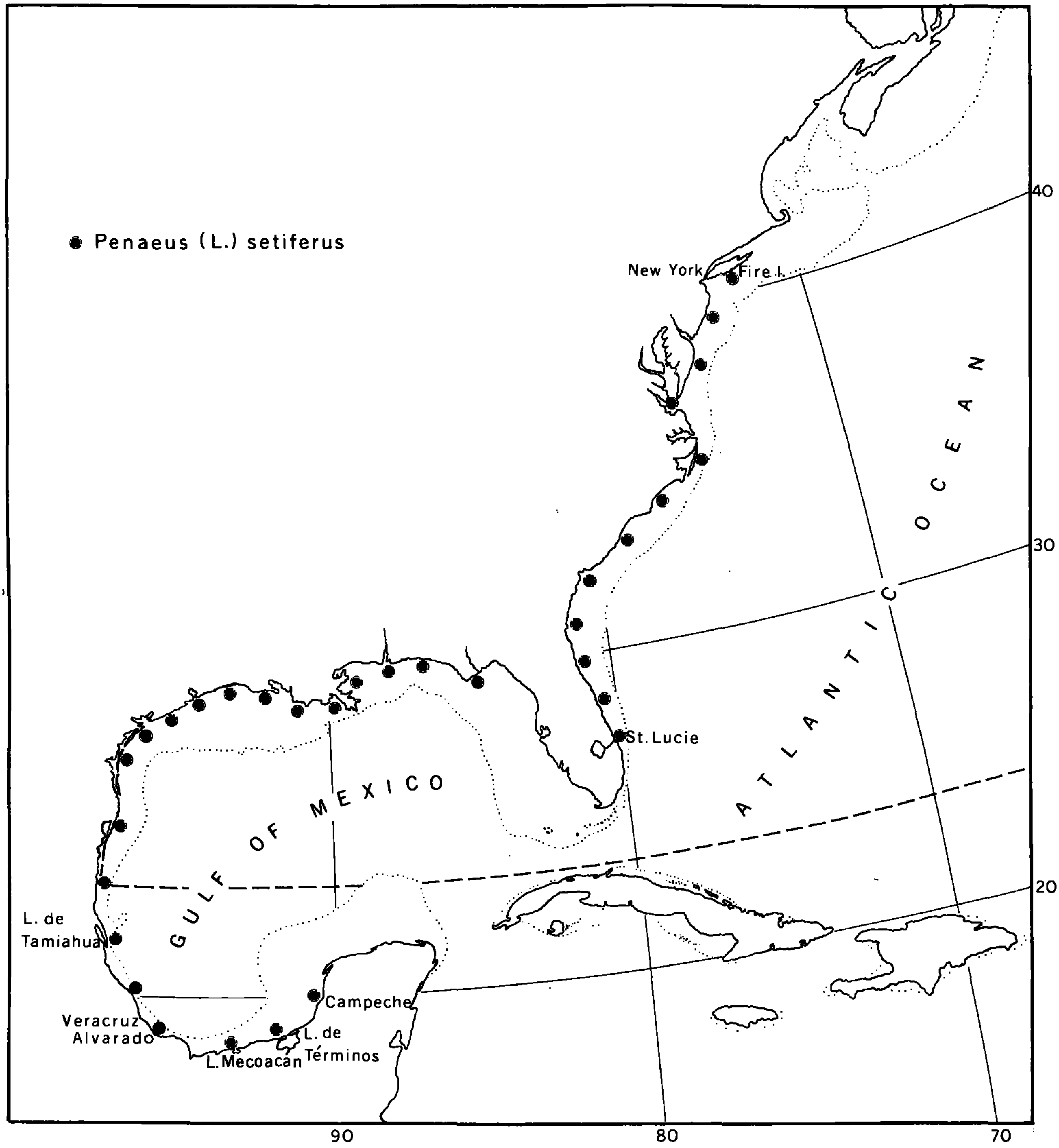

FIGURE 12.—Distribution of *Penaeus* (*L.*) *setiferus* (L.).

food, and cover—have been mentioned as responsible for these discontinuities, but no adequate explanation has been advanced.

The reported occurrence of *P. setiferus* in the waters of Cuba and Jamaica by Burkenroad (1936, 1939) was probably an error. In the many years of field work in Cuba, during which I have identified thousands of specimens, not a single *P. setiferus* was found, nor have specimens been encountered in the extensive collections from the Antilles that I have studied more recently. I have stated (Pérez Farfante, 1953) that it seems very unlikely this species could ever have reached Cuban waters, much less farther south, since it does not seem to live off the southernmost end of Florida.

Large concentrations of white shrimp are found in less than 20 fm.; it is rare at greater depths where brown shrimp (*P. a. aztecus*) and, in some areas, pink shrimp (*P. d. duorarum*) occur in quantities sufficient to sustain profitable fishing. Nevertheless, white shrimp do invade water deeper than 20 fm. Springer and Bullis (1952) reported them at 43 fm. off Alabama and Louisiana, and later Bullis and Thompson (1965) caught *P. setiferus* in 45 fm. off Louisiana. This latter depth is considered very close to the lower bathymetric limit of the species.

Extensive biometric studies that took into account 45 different characters have failed to show any significant morphological differences between the white shrimp from the Atlantic and those from the Gulf of Mexico.

Some time during the past, the range of *P. setiferus* became discontinuous—probably toward the close of the Pleistocene with the consolidation of the Florida Peninsula. The Pleistocene range of the white shrimp probably extended from the Carolina Coast southward across the Suwannee straits into the Gulf, and with the elevation of the peninsula and the closing of the straits, the population was divided. The northern segment has succeeded in moving south to middle Florida, as far as the Saint Lucie estuary. For some reason, perhaps ecological, however, the Gulf population has not become established beyond the eastern portion of Apalachee Bay along the west coast of the peninsula.

Although recent genetic interchange between the Atlantic population and the Gulf population seems unlikely, the two, as stated above, cannot be distinguished. The three characters—relative lengths of the rostrum, petasma, and third pereopod—which Burkenroad (1934) indicated might prove to be different in the two stocks, vary with increasing size, and the first also with attainment of sexual maturity in the female. The proportional length of the rostrum $\frac{(\text{r.l.})}{(\text{c.l.})}$ is variable and decreases as the adult shrimp grow longer; but it

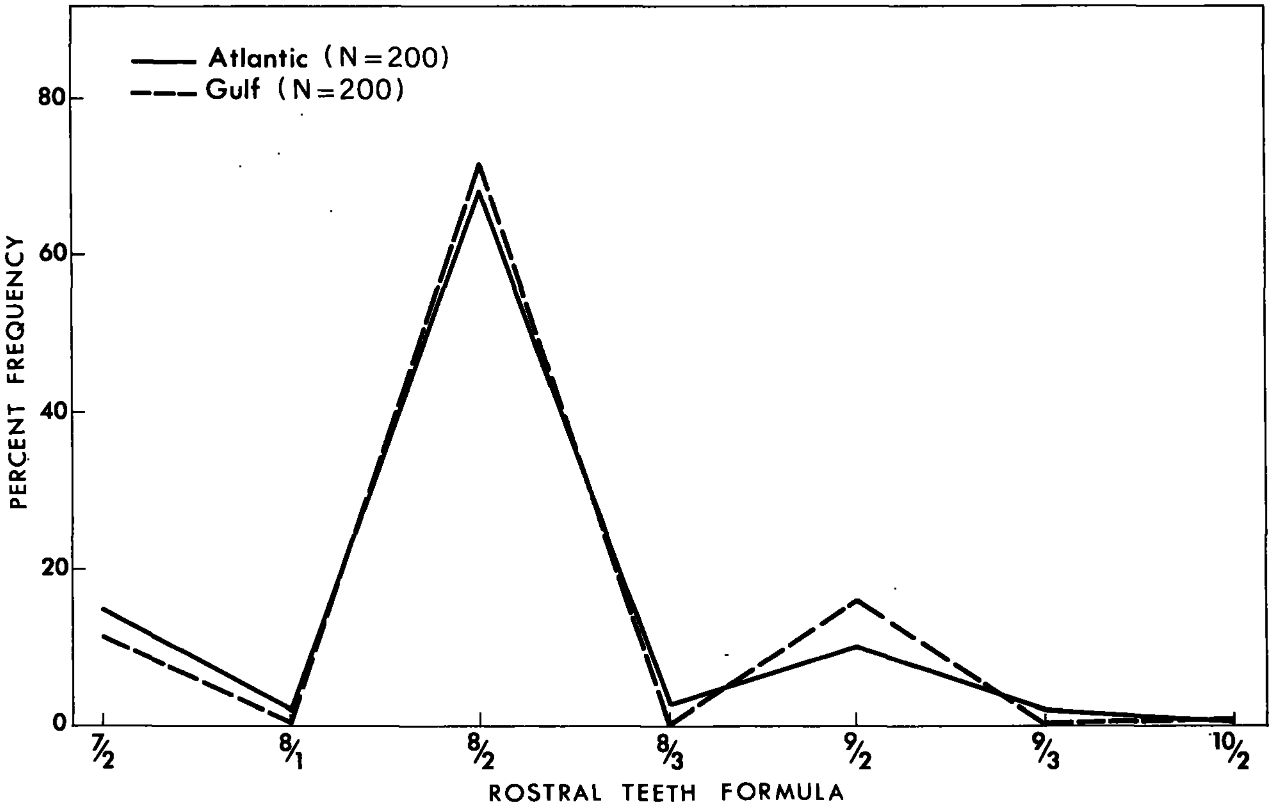

FIGURE 13.—Percentage frequency of the different combinations of rostral teeth in *Penaeus* (*L.*) *setiferus* (L.) from the Atlantic Ocean and the Gulf of Mexico.

exhibits a range of variation that is about the same in both stocks. The range of relative length of the petasma in shrimp with the same total length in the two areas also overlaps. In both stocks the third pereopod, believed to be shorter in the Atlantic individuals, increases with increasing size, and, thus, its relative length depends on the size of the shrimp; no significant difference has been observed among shrimp of the same length in the two populations. To be sure, the largest females examined in this study came from the Gulf of Mexico, and their third pereopods were comparatively longer than those of the largest females that were available from the Atlantic; however, the Atlantic females were smaller than the Gulf females. It now seems clear that the apparent differences in the two populations are not real if shrimp of the same size are compared.

Burkenroad (1934) mentioned that the median sulcus might be used to distinguish the two stocks. The median sulcus of *P. setiferus* from the Atlantic Coast usually consists of two shallow depressions joined by a groove—the anterior one attenuated anteriorly as a line—but this type of median sulcus also occurs in some specimens from several localities in the northern Gulf of Mexico and in many from Campeche. White shrimp from the Gulf often have a median sulcus consisting of two isolated shallow concavities, the anterior one blunt. The rostral tooth formula is almost the same in the two populations as is indicated in figure 13.

Rioja (1939) described the median flagellum of this species as having "16 articles bearing one long central and two small lateral spines [processes]." In contrast, I found that the number of articles armed with processes varies, and that each article almost always has two processes, one long and one short; only in one instance was an article observed to bear three processes. Articles bearing two processes are typical throughout the range of the species—in the Atlantic as well as in the Gulf of Mexico.

## Relationships

*P. setiferus* closely resembles *P. schmitti*, the white shrimp from the Antilles, Central America, and South America; the external genitalia, however, allow the two species to be separated readily. The pair of fleshy, closely set, anteriorly produced posterior lobes and the medially turned anterolateral ridges on sternite XIV set female *P. setiferus* apart from females of *P. schmitti*. Also, the posterior ridge of sternite XII has only two small lateral convexities. The diagonal ridge and conspicuous fold on the interior surface of the distal portion of the lateral lobe of the petasma are typical of *P. setiferus* males.

Serological tests by Leone and Pryor (1952) indicated that, although *P. setiferus* is more closely related to *P. d. duorarum* than to *P. a. aztecus*, the latter two are more closely allied than either is to *P. setiferus*. Their results, thus, confirm conclusions reached through a study of the external morphology of the three shrimps.

## Reproduction

### SUBADULT STAGE-SEXUAL MATURITY

Males have been found with petasmal endopods joined (animals in subadult stage) at a minimum size of 22 mm. c.l., 105 mm. t.l. The joining of the petasmal endopods occurs within the size range 22 to 27 mm. c.l., 105 to 127 mm. t.l. The minimum size at which females are impregnated is not known.

According to Burkenroad (1934), males have spermatophores fully developed, of maximum dimensions they will attain throughout the life of the shrimp, at a minimum of about 35 mm. c.l., about 155 mm. t.l., but ripe sperm first appear at 25 mm. c.l., about 118 mm. t.l. The smallest ripe females recorded (Burkenroad, 1939) had a carapace length of 30 mm. (about 135 mm. t.l.).

### COPULATION

Copulation in *P. setiferus* is believed to take place between hard-shelled individuals (Burkenroad, 1939). Mating in this condition is contrary to that in the species of *Penaeus* with a closed thelycum, in which females are impregnated immediately after molting.

During copulation the male attaches the spermatophore to the female. The spermatophore remains anchored on the thelycum by various attachment structures and a glutinous material that accompanies it when it is extruded. The coxae of the fourth and fifth pereopods of the female are produced into platelike projections bearing long bristles directed medially which press the spermatophore against the thelycum and also help it to adhere to the thelycum. Despite the various devices that help to hold the spermatophore anchored, it seems to be rather easily dislodged because few females are found with spermatophores. The spermatozoa have generally been thought to be released from the spermatophore simultaneously with the expulsion of the ova. Harry L. Cook (personal communication), however, observed in the laboratory that mature females that did not bear a spermatophore spawned eggs that developed normally; the eggs were reared to subadult stages.

### OVARY DEVELOPMENT

The female reproductive system consists, as in other *Penaeus*, of two partly fused ovaries, which in mature animals extend for much of the length of the body. Each ovary has a long, slender anterior lobe that extends to the level of the anterior portion of the gastric mill and bears lateral projections (usually 6–8) in the cephalothorax, and a posterior lobe running the length of the abdomen dorsolateral to the midgut.

The five ovary stages recognized by King (1948) and now generally accepted are:

1. Undeveloped. Found in young shrimp; ovaries are small and translucent.
2. Developing. Ovaries larger, opaque, and yellowish, with scattered melanophores over surface.
3. Nearly ripe or yellow. Ovaries are still larger than in previous stage and are yellow to yellowish-orange.
4. Ripe. Ovaries reach maximum size, occupy practically all space among other organs, and are drab olive-brown. Diameters of ova range from 0.192 to 0.300 mm. (Gutsell MS.[3]). According to Pearson (1939), eggs measure 0.28 mm.
5. Spent. Recently spawned ovaries are flaccid, muddy green, not so deeply colored as in the ripe stage. As they regress the ovaries become yellowish or milky and resemble the "developing" stage. Only through microscopical examination can the stage of the opaque ovary be accurately determined, although the length and weight of the gland often permit a distinction between the two stages.

The eggs are spherical and opaque, and possess a chorion with purplish-blue coloration in reflected light under a microscope (Pearson, 1939). The spermatozoa have a large, subspherical head, a short and narrow middle piece, and a relatively thick, short tail (King, 1948).

The number of eggs produced by a female is not known with certainty. Burkenroad (1934) indicated that a female white shrimp produces an average of about 500,000 eggs, whereas Anderson, King, and Lindner (1949) stated that the ovary of a 172-mm. female contained about 860,000 eggs and that a female could be expected to lay between 500,000 and a million eggs at a single spawning. For the present, this range of fecundity of one-half to almost a million eggs in a single spawning must be accepted.

### SPAWNING

Spawning is in oceanic waters. On the basis of the presence of ripe and recently spent females, Lindner and Anderson (1956) concluded that in Louisiana waters most spawning takes place in depths of 4.5 to 17 fm. Their finding has been confirmed by a number of authors for the entire northern Gulf of Mexico. Pearson (1939) and Lindner and Anderson (1956) indicated that in some areas of the Atlantic Coast spawning may occur near shore.

The beginning of spawning varies slightly in different areas, but even within an area it seems to vary from year to year and with depth. Lindner and Anderson (1956) stated that spawning probably begins late in March or early in April and may extend into November, though probably it is completed by the end of September. Renfro and Brusher (1964) concluded that in the northern Gulf of Mexico the onset of spawning is in mid-April or early in May at 7½ fm., but takes place several weeks earlier at 15 fm. Recently, Temple and Fischer (1967), as a result of their studies in the Gulf of Mexico, near Galveston, Tex., stated that "The occurrence of larvae at 14 m. (about 7¾ fm.) stations in April to August reflects, we believe, the spawning of white shrimp in shallow waters." In northeast Florida spawning seems to begin at about the same time as in Texas; Joyce (1965) suggested that spawning probably begins in April and lasts until October. In South Carolina and North Carolina it apparently starts later. Lindner and Anderson (1956) stated that in South Carolina they found spawning to start in May and extend into September; they believed that no more than 2 weeks separated the onset of spawning in South Carolina and Texas. Williams (1955a) gathered evidence that spawning starts in May in North Carolina.

Lindner and Anderson (1956) concluded that in the northern Gulf of Mexico, spawning appears to increase to a single peak in June or July, but the number of shrimp in inshore waters did not follow this trend. On the basis of frequency distribution of the catches, two main broods appeared annually in certain localities and three in others.

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[3] Gutsell, James S. A study of the ovaries of the common shrimp *Penaeus setiferus* with reference to the life history. In the files of the Gulf Investigations, U.S. Fish and Wildlife Service, New Orleans, La. (Unpublished manuscript, 1936).

Gunter (1950) and Kutkuhn (1962) in the same region and Joyce (1965) in northeast Florida found two main broods annually.

Temperature is a major factor controlling spawning. Lindner and Anderson (1956) stated that spawning seems to be started more by rapid changes in temperature than by attainment of an optimum temperature; sudden warming in the spring apparently triggers spawning, which appears to end when the temperature declines abruptly in the fall, even though the water is warmer at this time than at the beginning of the spawning season.

Evidence is considerable that *P. setiferus* may spawn more than once during its life span. King (1948) found that immediately after the first spawning the spent ovaries grow considerably. He suggested that females which spawn early in the season may develop a second crop of eggs and spawn again the same season. Studies of ovary development in the northwestern Gulf by William C. Renfro and Robert F. Temple (personal communication) indicate that recovery and redevelopment are fairly rapid, at least during the summer; recently spent ovaries contained large numbers of rapidly developing ova together with ripe ova in the process of being absorbed. According to Lindner and Anderson (1956), the percentage of females with spent ovaries is very low in Louisiana waters from June through August. They suggested shrimp could spawn four times in a season.

### SEX RATIO

The general male-female ratio appears to be about 1:1; considerable variation has been observed, however. I have examined many offshore samples that contained but one sex, so some segregation by sexes may occur.

## Postembryonic Development

### LARVAE, POSTLARVAE, AND JUVENILES

Eggs hatch within a few hours after spawning, and the young emerge as nauplii, the first of 11 larval stages. Pearson (1939) was the first to study the larval development of white shrimp through material found in plankton samples and by rearing experiments. So accurate were his observations that subsequent studies by Heegaard (1953) and Johnson and Fielding (1956) have proved his series of stages almost faultless, except that one mysis stage was not recognized. Harry L. Cook (personal communication) observed in the laboratory that *P. setiferus* has five nauplial, three protozoeal, and three mysis stages. After the last mysis comes the first mastigopus or first postlarva.

Some investigators doubt the existence of diagnostic characters that distinguish the larvae of western Atlantic *Penaeus*, whereas others maintain that they can be separated. Pearson (1939) and Heegaard (1953) described the main characteristics of various larvae of *P. setiferus*.

The whole larval cycle of the white shrimp was found by Johnson and Fielding (1956) to extend 10 to 12 days, but these authors stated that "the duration of the metamorphic period is not fixed, but depends to some extent on local conditions of food and habitat." At the end of this period the planktonic larvae have reached the postlarval stage. Early postlarvae are planktonic and live offshore. As they grow they move toward and finally enter inshore waters.

Williams (1959) distinguished postlarvae under 12 mm. t.l. of *P. setiferus*, *P. a. aztecus*, and *P. d. duorarum* on the basis of two characters recognized by Pearson (1939)—the relative lengths of the rostrum and third pereopod—as well as by body size and shape of the distal end of the antennal scale. These characters have proved to be helpful, although it seems that sometimes their range of variation in the various species overlaps. According to Baxter and Renfro (1967), those features allow the identification of white shrimp postlarvae up to 10 mm. t.l. in the Galveston area.

Recently, Zamora and Trent (1968) reported that in postlarval white shrimp the keel of the sixth abdominal somite is smooth, lacking setae, whereas that of postlarval brown and pink shrimps bears setae. The presence or absence of setae on the keel considerably facilitates the separation of the postlarvae of white shrimp from those of the pink and brown shrimps.

Small *Penaeus* are considered juveniles when they have attained the ultimate rostral tooth formula. Freshly caught juveniles of the white shrimp often have widely spaced body chromatophores and, thus, have a lighter color than those of sympatric pink and brown shrimps; this character, however, has only limited diagnostic value since shrimp collected from dark substrates tend to be dark. Juveniles 18 mm. t.l. have no long adrostral sulci and so are easily separated from the grooved *Penaeus*.

In the development of individuals sex can be determined easily when they reach 6 mm. c.l., 28 mm. t.l. At this length females can be distinguished from males by the endopods of the first pair of pleopods, which are relatively shorter and narrower, and by the presence of two protuberances on sternite XIV, which are minute but clearly distinct. At 18 mm. c.l., 86 mm. t.l., the median flagellum of the male bears a few long processes, at 21 mm. c.l., 96 mm. t.l., it has small processes, and at 23 mm. c.l., 109 mm. t.l., its longer and shorter processes are well developed. The sizes given above are the minimum at which the antennular processes, in males, have attained the respective stages of development.

### GROWTH

Growth studies in *Penaeus* shrimps are difficult because of the variation in rate of increase according to size and sex of individuals as well as during the different seasons of the year. After rearing shrimp in ponds, Johnson and Fielding (1956) estimated that white shrimp attain a total length of about 80 mm. 2 months after hatching. Gunter (1950) had previously reported a growth rate of 25 to 40 mm. per month from 28 to 100 mm. t.l. in inshore water adjacent to the Gulf of Mexico, and Viosca (1920) estimated a monthly growth of about 25 mm. for shrimp with 30 to 150 mm. t.l. In Mobile Bay, Ala., Loesch (1965) found that white shrimp increase 12 to 27 mm. a month in winter, 18 to 31 mm. in summer, and the "very young" may grow as much as 65 mm. per month in summer. Williams (1955a) calculated that inshore white shrimp in North Carolina grow about 36 mm. per month during the summer, and Joyce (1965) estimated that white shrimp in northeast Florida grow an average of 35 mm. per month. Lindner and Anderson (1956) concluded that individuals 100 mm. long reached 141 mm. in 2 months—an average increase of 20.5 mm. per month. Lindner and Anderson (1956) also showed that shrimp grow rapidly through the spring to early fall. Klima (1964) estimated that in Louisiana waters during the fall white shrimp grow from 120 mm. to 159 mm. in 2 months, an average of about 19.5 mm. per month, whereas larger shrimp grow very little. Growth is negligible during the winter, a conclusion reached by Lindner and Anderson (1956) for all populations, by Kutkuhn (1962) for the Louisiana offshore population, and by Joyce (1965) for the northeast Florida population.

Kutkuhn (1962) estimated that the rate of weight increase is relatively low in small shrimp, reaches a maximum in the middle of the size range, and then decreases progressively with further increase in size. He found that growth also varies considerably from year to year; one age class showed a 30-percent increase from November through April, whereas the corresponding age class in the previous year showed a 150-percent increase during the same period.

### SEX DIFFERENCES IN SIZE

The largest female examined, collected off mouth of Sabine River, Tex., is 60 mm. c.l., 200 mm. t.l.; the largest male, collected off Bayou Scolfield, La., is 41 mm. c.l., 175 mm. t.l.

Sizes of females and males differ little inshore, as shown in the length frequency distribution of the shrimp in North Carolina (Williams, 1955a) and in northeast Florida (Joyce, 1965). A sex-size disparity occurs offshore, where females are larger than males (Weymouth et al., 1933). In my samples the differences in length between sexes do not appear to be so pronounced as those shown by the grooved shrimps.

## Ecology

### FOOD

Juvenile and adult white shrimp were reported to be omnivorous by Viosca (1920), Weymouth et al. (1933), Darnell (1958), and Broad (1965). Their digestive tracts have been found to contain, in addition to inorganic detritus and organic debris, fragments of many different animals, particles of higher plants, and a variety of diatoms and other algae.

Studies by Flint (1956) of the stomach contents of "shrimp" (some of which were probably white shrimp) from Louisiana showed they were scavengers. He found a great variety of fragments of bryozoa, sponges, and corals and also sand grains. He stated that filaments of blue-green algae, lithophytic algae, and diatoms were present in such quantities as to indicate that algae may often serve as an important element of their diet. This worker assumed that the presence of diatoms "was incidental to the intake of other structures to which they were adherent or attached." Flint also noted that the contents of the intestinal tract of small shrimp about 10 mm. t.l. "consisted almost

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entirely of cropped filaments of blue-green algae and such diatoms as ordinarily in the natural habitat would have been found adherent to them."

Studies by Zein-Eldin (1964) emphasized the importance of an abundance of food during the postlarval–juvenile period in the life of the shrimp and indicated the ultimate value of the estuarine waters in providing the vast amount of food required for the rapid growth of the shrimp before it returned to the sea.

## SUBSTRATE

*P. setiferus* inshore live mostly on muddy or peaty bottoms that have large quantities of decaying organic matter or vegetation for protection. Occasionally they occur on bottoms of sand or clay (Williams, 1955a, 1955b). Laboratory experiments by Williams (1958) indicated that the young white shrimp prefer softer substrates than do the young pink or brown shrimps.

Adult white shrimp are most abundant in offshore waters on soft muddy and silt bottoms. They also live on bottoms of clay or sand with fragments of shells (Springer and Bullis, 1954; Hildebrand, 1954, 1955).

*P. setiferus* burrows in the bottom but apparently not as regularly as do the brown or pink shrimps. Williams (1958) observed that it leaves the long antennae lying on the surface of the bottom, whereas the other two shrimps often bury their antennae (which are shorter than those of the white shrimp).

## DIEL CYCLE

Although *P. setiferus* has been thought to be a diurnal species, Williams (1958) found that in the laboratory it is also active at night. Fishing for white shrimp, inshore as well as offshore, is usually carried out during the day, but some successful catches are made at night. Joyce (1965) considered white shrimp to be diurnal, but stated that in certain inshore localities during the summer, sample catches at night equaled or even exceeded those made during the day. He suggested that migration could have been a factor in the abundance of shrimp in these instances.

## MOVEMENTS

Most scientists believe that favorable currents transport the larvae and early postlarvae toward inshore waters.

Many studies have been made on the movements of the postlarvae of white shrimp. As stated earlier, shrimp reach the nursery grounds as postlarvae, 6 to 7 mm. long (Weymouth et al., 1933; Anderson, King, and Lindner, 1949; Bearden, 1961; Baxter and Renfro, 1967). There they adopt a benthic existence (Anderson, King, and Lindner, 1949; Williams, 1955a) either immediately or, as indicated by Joyce (1965), after having traveled some distance inland. Williams (1955a) also stated that postlarvae, as well as juveniles, are able to move many miles before finding a suitable nursery area. In the northern Gulf of Mexico they arrive in coastal waters from May to November (Christmas et al., 1966; Baxter and Renfro, 1967). According to Baxter and Renfro (1967), peak postlarval immigration into Galveston Bay, Tex., occurs in the summer. In South Carolina (Bearden, 1961) and in North Carolina (Williams, 1955a) postlarvae begin to arrive in early June, and the period of influx extends throughout the summer to mid-August or September. Postlarval abundance appears to show two peaks in the area, one in early June and the other in mid-August.

In the nursery grounds, the size of juveniles often shows a gradient; the smaller individuals are farther inland. White shrimp may be found in rivers as far from the coast as about 160 km. (Burkenroad, 1934) and 210 km. (Joyce, 1965)—farther than the brown or pink shrimps. Shrimp grow rapidly, and as they grow they move back to water nearer the sea and shrimp return to the sea when they have attained a modal length between 100 and 120 mm. t.l. (Weymouth et al., 1933; Gunter, 1950; Lindner and Anderson, 1956). The seaward migration takes place from spring through summer and early winter. In some areas two migrations are typical, one in spring and the other at the onset of winter. The first seems to be undertaken by shrimp hatched late in the previous spawning season, and the second migration is by shrimp spawned early in spring. Lindner and Anderson (1956) and Joyce (1965) believe that the stage of maturation of the gonads is the main determinant of this migration, although fall and winter temperatures also influence it.

Adult shrimp may migrate long distances parallel to the shoreline. On the Atlantic Coast, the tagging experiments by Lindner and Anderson (1956) indicated that white shrimp move south during the fall and early winter and northward in late winter and early spring. The longest migration recorded was made by a shrimp that moved south from near Beaufort, N.C., where it was tagged, to the east coast of Florida, covering a distance of about 580 km. in 95 days. The longest northward migration was made by a shrimp that moved from south of Cape Kennedy, Fla., north to the coast of South Carolina, a distance of about 419 km. in 168 days.

McCoy and Brown (1967) also reported that some shrimp migrate southward from North Carolina. The greatest distance known to have been traveled by the animals they released was 555 km.; two individuals were recaptured off St. Augustine, Fla. That all of the North Carolina population does not leave the area during the winter, however, is attested by the limited white shrimp fishery off Cape Fear during the coldest months of the year (Williams, 1955a).

The limited information gathered by Lindner and Anderson (1956) through tagging in the northeastern Gulf indicated that during the fall and winter white shrimp tend to move into deeper water and toward the mouth of the Mississippi River. The population from the northwestern Gulf, west of the Mississippi River to central Texas, also exhibits only offshore and inshore movements associated with temperature changes and spawning. The marine shelf off the mouth of the Mississippi River seems to be a natural barrier because this area was not crossed apparently in either direction.

Along the coast from south-central Texas to northern Mexico, white shrimp seem to move southward during the fall and early winter and northward in the spring. These coastwise movements compare with those observed for white shrimp on the Atlantic Coast and were first documented by Lindner and Anderson (1956) and later by Gunter (1962c), who based his conclusions on evidence that catches of white shrimp increased during the winter southward along the Coast.

## EFFECTS OF TEMPERATURE

As stated earlier, spawning seems to be greatly influenced by temperature, which by its sudden changes apparently initiates and later terminates the ovulation. Temple and Fischer (1967) found that along the coast of Texas white shrimp larvae were present from May through September and that a close correlation appears to exist between temperature and abundance of larvae.

The rate of growth is directly related to temperature, for it reaches its maximum during the warmer months, becomes very slow or negligible during winter, and resumes or increases with the advent of higher temperatures in late winter or early spring.

Laboratory experiments by Zein-Eldin and Griffith (1965) indicated that temperature affected the growth and molting of postlarvae. Animals tested at 18°, 25°, and 32° C., at a salinity of 25 p.p.t., showed that molting frequency and growth increased with temperature, although the increase in total length per molt was independent of temperature. This finding suggests that temperature influences growth through a change in molting rate but has no effect on the increase in size per molting. Their studies indicated further that, at a given salinity, postlarval white shrimp are more sensitive to low temperatures than are postlarval brown shrimp, but that, conversely, white shrimp postlarvae can better withstand high temperatures. Another experiment by Zein-Eldin (1966) confirmed this result.

Lindner and Anderson (1956) gathered evidence that white shrimp moved from shallow to deeper water during cold periods and that the smaller shrimp returned to shallower water when the temperature of the water increased.

There is also some information on how extremes of temperature affect white shrimp. Lunz (1956) reported that *P. setiferus*, 51 to 95 mm. t.l., had survived 36° C. in a pond in South Carolina. Reports of mortality of white shrimp during cold waves have been given by Gunter (1941), Gunter and Hildebrand (1951), Lunz (1958), and Joyce (1965), all of whom have found white shrimp dead after near freezing (4° and 4.5° C.) or freezing temperatures. Joyce found shrimps in a state of decay, which suggested that they had died during the first days of freezing temperatures. Sudden changes of temperature often may be responsible for the mortality of the shrimp rather than the temperature itself, although both the rate of change and the duration of high or low temperatures doubtlessly affect mortality.

## EFFECTS OF SALINITY

Conclusions about the influence of salinity on the life and distribution of white shrimp inshore vary widely. High concentrations of young individuals in low-salinity waters (less than 10 p.p.t.) have been reported by a number of authors—Gunter (1950), Gunter and Shell (1958), Gunter (1961a), Gunter et al. (1964), and H. Loesch (in unpublished data, the conclusions of which were included in the paper by Gunter et al., 1964). Williams (1955a) pointed out that in North Carolina young white shrimp are most abundant in the areas of lowest salinity and that in general they live in waters of lower salinity than do the brown or pink shrimps. Gunter (1961a) suggested that the low salinity of Louisiana nursery grounds may be optimal for juvenile white shrimp. Joyce (1965) reported that white shrimp made up by far the largest percentage of shrimp in localities of lower salinities and that no white shrimp were caught in the high-salinity waters of the Edgewater-Oak Hill (Fla.) area. The fact that white shrimp move farther upriver and grow to a greater size in inshore waters seems to indicate that the young have a higher tolerance to low salinity over a longer period of their development than the sympatric *Penaeus.*

Gunter and Hildebrand (1954) are of the opinion that in Texas there is a direct correspondence between rainfall of the State and production of white shrimp. Gunter et al. (1964) pointed out that the drought from 1947 to 1957 was accompanied by a remarkable decline in production of white shrimp, and when the long drought was over the annual production increased 331 percent from 1957 to 1958.

The lowest salinities at which the young of *P. setiferus* have been recorded are 0.42 p.p.t. in the northern Gulf of Mexico (Gunter and Shell, 1958) and 0.26 p.p.t. in northeast Florida (Joyce, 1965).

Although the field studies mentioned above indicate that white shrimp prefer low-salinity water, other studies show that they are not affected adversely by high salinity and are rather insensitive to large fluctuations in salinity. Lindner and Anderson (1956), as a result of their investigation in the waters of Louisiana, and Hoese (1960a, 1960b) who worked in various localities along the coast of Texas, concluded that within certain areas at least, young shrimp are indifferent to varying salinity. In Laguna Madre small white shrimp have been found at salinities of 47.96 p.p.t. (Hildebrand, 1958) and 41.3 p.p.t. (Gunter, 1961a). Lunz (1956) reared juveniles at 17.6 to 33.2 p.p.t., and Johnson and Fielding (1956) found that white shrimp could be reared successfully in ponds at salinities of 18.5 to 34 p.p.t. Laboratory experiments by Zein-Eldin (1963a) showed that, under constant temperature and rather restricted diet, postlarval shrimp can survive and grow within a wide range of salinity. She stated that "it would appear that salinity tolerance *per se* may not play a direct role in the growth and survival of postlarval and juvenile shrimp in the estuarine environment." Joyce (1965) observed a temperature-salinity relation in the distribution of inshore shrimp and stated that apparently these shrimp remained away from areas of low salinity during cold weather. This finding agrees with the laboratory findings of Zein-Eldin and Aldrich (1965), who observed that postlarvae of *P. a. aztecus*, at temperatures below 15° C., exhibited decreased tolerance to low salinity. Burkenroad (1939) suggested that the general geographic distribution of the species possibly depends on a temperature-salinity correlation and that temperature might limit the occurrence of white shrimp within an extreme range of salinity.

### ENEMIES AND DISEASES

*P. setiferus*, like *Penaeus* in general, constitute part of the diet of many carnivorous teleost and some elasmobranch fishes (Gunter, 1945; Darnell, 1958). Cannibalism, common among *Penaeus* as soon as they reach the postlarval stage, makes their maintenance in aquariums difficult for laboratory experiments if they are not well fed.

White shrimp appear to suffer from a number of diseases, some of them caused by parasites. Telosporidians, cnidosporidians, trematodes, cestodes, and nematodes have been recorded from white shrimp (Sprague, 1950, 1954; Kruse, 1959; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959; Hutton et al., 1962; Hutton, 1964; Aldrich, 1965). Dawson (1957) and Joyce (1965) reported *Balanus* on white shrimp.

### HARDINESS

According to De Sylva (1954), *P. setiferus* is more delicate and short lived than *P. d. duorarum* and *P. a. aztecus*. Apparently, it is also the most susceptible to low temperatures. Broad (1965) too considers *P. setiferus* less hardy than *P. a. aztecus.*

## Commercial Importance

This species is fished in several areas along the eastern coast of the United States, the most important of which are Georgia and the northeast coast of Florida. The most northern fishery is in the vicinity of Pamlico Sound, North Carolina.

The largest production by far is in the Gulf of Mexico, where the waters of Louisiana and eastern

Texas yield the highest catches. This species was the only shrimp fished in the estuarine waters along the northern coast of the Gulf of Mexico until about 1937–38, when offshore stocks began to be fished. The resource then declined while landings of brown and pink shrimps increased. By mid-1950, catches of those two species far exceeded catches of white shrimp. During 1956–59, white shrimp constituted only 20 percent of all Gulf shrimp produced by U.S. fishermen, but landings in recent years have risen again. According to Lyles (1967), annual landings of white shrimp in the United States during 1965 were 30,865,840 kg. (whole weight), or about 31 percent of all shrimp landed.

Along the Gulf coast of Mexico the white shrimp is caught commercially on the northeast coast of Tamaulipas and off Cabo Rojo, Veracruz, where it is fished in small quantities. The most important white shrimp grounds in Mexico are between Laguna Mecoacán and Paso Real, in Golfo (Bahía) de Campeche. *P. setiferus* contributes substantially to the shrimp landings from the Gulf coast of Mexico—20,224,000 kg. in 1966 (Croker, 1968)—but the actual composition of the landings, which also include *P. d. duorarum* and *P. a. aztecus*, is not known.

## *Penaeus (Litopenaeus) schmitti* BURKENROAD

Figures 14 to 19

Cuba, Honduras, Nicaragua, Venezuela: camarón blanco. Cuba: camarón casquiazul. Venezuela: longostino blanco. Brazil: camarão legítimo, camarão verdadeiro, camarão branco, camarão lixo, vilafranca, caboclo. United States: white shrimp, blue shrimp, green shrimp. British Honduras: white shrimp.

*Cancer setiferus:* Gmelin, 1790: 2990 [part]; [fide] Gunter, 1962a: 108; Gunter, 1962b: 119; Gunter, 1963: 104, 105, 107, 108; Gunter, 1964: 229–231. Not *Cancer setiferus* L., 1767.

*Astacus setiferus:* Olivier, 1791: 343. Not *C. setiferus* L., 1767.

*Palaemon setiferus:* Olivier, 1811: 660; [fide] Gunter, 1962a: 108. Not *C. setiferus* L., 1767.

*Penaeus setiferus:* H. Milne Edwards, 1837: 414, 415 [part]; de Saussure, 1858: 471 [part]; Heller, 1865: 121; Bate, 1881: 176–178, pl. 11, fig. 1; Kingsley, 1882: 107 [part]; Sharp, 1893: 110 [part]; Guppy, 1894: 115; Rathbun, 1897: 45, 46; Rathbun, 1900: 151; Moreira, 1901: 7, 72, 73; Johnson and Lindner, 1934: 68; Burkenroad, 1934: 77, 86 [part]; Burkenroad, 1939: 19, 20 [part]; von Ihering, 1940: 194, 871, fig.; de Oliveira, 1940: 141; Magalhães Filho, 1943: 12, 24; Magalhães Filho, 1944: 100, 101; de Oliveira, 1944: 133; de Oliveira, 1950: 371, 386; Sánchez Roig and Gómez de la Maza, 1952: 162, 163, fig. 5; Devold, 1958: 20; Gunter, 1962a: 107–112; Gunter, 1962b: 119–121; Gunter, 1963: 103, 105–108; Gunter, 1964: 229, 230; Gunter, 1966: 78. Not *P. setiferus* (L.), 1767.

*Penaeus setifer:* von Martens, 1872: 141, 142; von Martens, 1876: 38; Doflein, 1900: 126, 127 [part].

*Peneus setiferus:* von Ihering, 1897: 156. Not *P. setiferus* (L.), 1767.

*Penaeus schmitti* Burkenroad, 1936: 313–318, figs. 1a, 2, 3 (lectotype, here designated, ♂, YPM 4396–BOC 128–Kingston, Jamaica, February 1, 1934; paralectotypes, YPM); Burkenroad, 1939, 19, 20; Anderson and Lindner, 1945: 304; Whiteleather and Brown, 1945: 25, 27; Carlson, 1953: 34; Pérez Farfante, 1953: 232–235, 238, 241; Pérez Farfante, 1954a: 97; Voss, 1955: 8, 10, fig. 10a, b; Gunter, 1956: 100; Dall, 1957: 142; Lindner, 1957: 11–14, 16, 21–23, 34–36, 65–67, 69, 70, 129–131, 153, 154, 160–165; Suárez Caabro, 1957: 137; U.S. Fish and Wildlife Service, 1958a: 11, 13; Lindner, 1858: 31–33; Suárez Caabro, 1958: 5, 7; Bullis and Thompson, 1959a: 41; Bullis and Thompson, 1959b: 7, 9; Higman, 1959: 8, 10, 13; Holthuis, 1959: 42–44, 61–63, 66, fig. 6a; Eldred and Hutton, 1960: 91, 98, 99, 101, 104, 108; Sadowski and Radasewski, 1960: 1–5; Anonymous, 1961: 34; Pérez Farfante, Acosta, and Alemany, 1961: 33, 36–38, 50; Gunter, 1962a: 110, 111; Holthuis, 1962: 115, 117, 118; Idyll, 1962: 184; Kutkuhn, 1962: 343; Loesch, 1962: 172–177; Miles, 1962: 189, 193; Boschi, 1963: 5, 6, 13, 17–20, 29, figs. 5 (1–7), 11; Davant, 1963: 9–11, 26–29, 34, 35, 66, 67, 82–85, 87, 88, 90, 91, figs. 4, 5, and 4, 5, bis; Gunter, 1963: 103, 104, 106; Simpson, 1963: 22, 23; Boschi, 1964: 39, 41; Ewald, 1964: 20, 22, 24, 25, table, figs. 10, 11; Gunter, 1964: 230, 231; Holthuis, 1964a: 227–229; Neiva and Wise, 1964: 132, 133; Tremel, Wise, Mistakidis, and Jonsson, 1964: 6, 7, 12, 20, 24; Ewald, 1965a: 26, 29, 30; Ewald, 1965c, 51, 52, 59, 65, 69, 72–74, 80, 81, 83, 84, 86, 88–99, 103–114, 5 figs., pls. 3–5; García Pinto, 1965: 131–134; Holthuis and Rosa, 1965: 6; Mistakidis, 1965: 9, 11, 18, 28; Pericchi López, 1965: 23; da

Silva, 1965: 1, 3; Simpson, Griffiths, and Atilano, 1965: 77; Tremel and Mistakidis, 1965: 2, 4; Alves Coelho, 1966: 162, 168; Mistakidis and Neiva, 1966: 434; Neiva and Mistakidis, 1966: 1, 2, 5, 6, figs. 9a, b; Croker, 1967: 63, 67, 68, 73–75, 78–80, 84, 86, 87, 89, 94, 95, 98, 106; International Commission on Zoological Nomenclature, 1967: 151, 152; Instituto de Fomento Nacional, 1967: 5, 8.

*Penaeus setiferus:* Magalhães Filho, 1944: 101, fig. 4B.

*Penaeid schmitti:* Anonymous, 1962: 56.

*Penaeus schimitti:* Boschi, 1964: 40.

*Penaeus schmitt:* Gunter, 1964: 230.

White shrimp: Carlson, 1953: 34.

Camarão legítimo: Richardson and Moraes, 1960: 8, 9, 18, 34, 36, 42, 43, 48; Braga, 1962: tables 1, 2.

### Taxonomic Remarks

Burkenroad (1936), in his description, cited two "types," one a male and the other a female. I here designate the male as the lectotype of *Penaeus schmitti* Burkenroad; the remaining specimens in the type series are paralectotypes.

### Study Material

**CUBA**

4 ♂ 3 ♀, CIP, Cojímar, La Habana, 1954, J. A. Suárez Caabro. 3 ♂ 2 ♀, CIP, Jaruco, La Habana, 1954, A. de la Torre. 1 ♂ 2 ♀, USNM, Bahía de Matanzas, 1954, C. Sánchez. 5 ♂ 6 ♀, CIP, Nuevitas, Camagüey, 1953, J. A. Suárez Caabro. 1 ♂ 1 ♀, USNM, estuary Río Cacoyugüín, Bahía de Gibara, Oriente, C. G. Aguayo. 2 ♂ 3 ♀, CIP, Banes, Oriente, 1953, A. R. Quiñones. 6 ♂ 4 ♀, CIP, Antilla, Oriente, 1953, H. Martínez. 5 ♂ 5 ♀, CIP, Bahía de Nipe, Oriente, 1953, J. Fernández Pardo. 12 ♂ 1 ♀, CIP, Niquero, Oriente, T. Sánchez. 5 ♂ 2 ♀, USNM, Manzanillo, Oriente, J. Saavedra. 22 ♂ 19 ♀, CIP, Manzanillo, Oriente, 1954, T. Sánchez. 50 ♂ 50 ♀, CIP, Golfo de Guacanayabo, Oriente, 1959, I. Pérez Farfante. 42 ♂ 38 ♀, CIP, off Santa Cruz del Sur, Camagüey, 1954, I. Pérez Farfante and G. Canet. 18 ♂ 15 ♀, CIP, Júcaro, Las Villas, 1954, G. Canet and T. Sánchez. 20 ♂ 22 ♀, CIP, Tunas de Zaza, Las Villas, 1954, G. Canet and T. Sánchez. 3 ♂ 5 ♀, CIP, Casilda, Las Villas, 1954, G. Canet and T. Sánchez. 1 ♂ 1 ♀, USNM, Bahía de Cienfuegos, Las Villas, 1954, G. Muñoz.

**JAMAICA**

29 ♂ 29 ♀, USNM, March 1–11, 1884, *Albatross*. 10 ♂ 15 ♀, YPM, Kingston market, February 26, 1937, *Atlantis* in port.

**HAITI**

3 ♀, USNM, Port au Prince, March 10, 1944, A. Curtis. 1 ♂, USNM, Port au Prince, August 22, 1945, A. Curtis. 1 ♂, USNM, Port au Prince, September 14, 1945, A. Curtis. 1 ♀, USNM, Port au Prince, 1946, A. Curtis. 1 ♂ 1 ♀, USNM, Montet, May 17, 1930, W. Parish.

**BRITISH HONDURAS**

1 ♀, UMML, Belize, April 15, 1954, E. P. Bradley.

**NICARAGUA**

1 ♀, UMML, off Nicaragua, 1959. 2 ♂ 2 ♀, UMML, S. of Puerto Cabezas, August 8, 1958. 2 ♂ 1 ♀, USNM, Bluefields, 1965, A. Flores.

**COSTA RICA**

4 ♂ 1 ♀, USNM, Puerto Limón, November 1966, Ex. M. C. Filippi.

**PANAMA**

1 ♀, USNM, Fox Bay, Colón, March 31, 1911, S. E. Meek and S. F. Hildebrand. 1 ♀, USNM, Fox Bay, Colón, February 23, 1935, S. F. Hildebrand. 2 ♀, USNM, Mindi Cut, Canal Zone, February 3–4, 1911, S. E. Meek and S. F. Hildebrand. 15 ♂ 8 ♀, USNM, Colón, January 27, 1912, S. E. Meek and S. F. Hildebrand. 2 ♂ 2 ♀, YPM, Limón Bay, Canal Zone, October 1934, *Atlantis* in port.

**COLOMBIA**

6 ♂ 10 ♀, USNM, off Tucuracas, Departamento de la Guajira, 12 fm., October 6, 1965, *Oregon* Sta. 5674.

**VENEZUELA**

3 ♂ 2 ♀, UMML, Lake Maracaibo, December 1963, J. J. Ewald. 9 ♂ 15 ♀, USNM, Curarire, Lake Maracaibo, July 9, 1964, J. J. Ewald. 12 ♂ 3 ♀, USNM, Barranquita, Lake Maracaibo, April 23, 1964, J. J. Ewald. 2 ♀, USNM, Tacarigua de la Laguna, Miranda, March 1, 1949, Hno. Ginés. 4 ♂ 2 ♀, USNM, Gulf of Venezuela, May 3, 1964, J. J. Ewald. 1 ♀, USNM, Castilletes, Gulf of Venezuela, 10 fm., October 6, 1965, *Oregon* Sta. 5669. 1 ♀, UMML, Carenero, 1962, Tovar. 1 ♂, USNM, off Isla Mariusa 13 to 15 fm., August 26, 1958, *Oregon* Sta. 2211. 1 ♂ 1 ♀, USNM, off Punta

Araguapiche, 15 fm., August 26, 1958, *Oregon* Sta. 2210. 2 ♀, USNM, off Boca Araguao, 9 to 10 fm., August 27, 1958, *Oregon* Sta. 2215.

### TRINIDAD

1 ♀, UWI, Caroni Swamp, October 1965, P. R. Bacon. 1 ♀, USNM, Cocorite Swamp, August 31, 1966, P. R. Bacon. 1 ♂ 2 ♀, USNM, Maturin Bar, Gulf of Paria, 6 fm., April 26, 1944, R. J. Whiteleather and H. H. Brown.

### GUYANA

2 ♂ 2 ♀, USNM, pond of Fisheries Laboratory, Department of Agriculture, 1960, W. H. L. Allsop. 1 ♀, USNM, off Guyana, 12 fm., May 30, 1957, *Coquette* Sta. 155. 5 ♂ 3 ♀, USNM, off Guyana, 10 fm., March 25, 1963, *Oregon* Sta. 4306.

### SURINAM

1 ♂, USNM, NE. of mouth of Surinam River, 13 1/5 fm., June 11, 1957, *Coquette* Sta. 203. 1 ♀, USNM, off mouth of Surinam River, 13⅕ fm., June 11, 1957, *Coquette* Sta. 208. 1 ♂, USNM, off mouth of Surinam River, 14 3/10 fm., June 28, 1957, *Coquette* Sta. 293. 5 ♀, UMML, off Surinam, summer 1960, H. Lijding.

### BRAZIL

**Pará-Maranhão:** 1 ♂ 2 ♀, USNM, June–July 1965, P. Paiva.

**Maranhão:** 1 ♂ 2 ♀, USNM, June 30, 1965, J. Fausto Filho.

**Ceará:** 2 ♂ 1 ♀, USNM, Fortaleza, April 6, 1965, J. Fausto Filho.

**Pernambuco:** 2 ♂ 2 ♀, USNM, Recife, August 10, 1964, P. Alves Coelho. 2 ♂ 1 ♀, USNM, Recife, H. von Ihering.

**Alagoas:** 1 ♂, USNM, Maceió, July 22, 1899, Branner-Agassiz Exped.

**Bahia:** 1 ♂ 2 ♀, USNM, Mapelle, Hartt Exped. 1 ♂, YPM, Lagoon in Caravelas, Hartt Exped. 17 ♂ 14 ♀, USNM, Taperoá, March 3, 1966, E. Luz. 14 ♂ 1 ♀, USNM, Maragogipe, 1966, A. Barbosa de Oliveira.

**Sergipe:** 4 ♂ 5 ♀, USNM, mouth of Agua Azeda River, Nossa Senhora do Socorro, March 9, 1966, do Condese.

**Espírito Santo:** 1 ♂ 1 ♀, MNHNP, Villa d'Anchieta, November 30, 1961, *Calypso* Sta. 92.

**Rio de Janeiro:** 2 ♂ 2 ♀, USNM, Baía de Sepetiba, 1 fm., SUDEPE. 2 ♂ 1 ♀, USNM, Rio de Janeiro, Ex. Museo Paulista. 1 ♂, USNM, Rio de Janeiro, H. von Ihering.

**São Paulo:** 1 ♂, USNM, Santos, 1949, J. de P. Carvalho. 1 ♀, USNM, Santos, September 12, 1925, W. L. Schmitt. 7 ♂ 12 ♀, USNM, Santos, September 6, 1964, G. Vazzoler. 1 ♂, USNM, Santos, June 1913, H. Leuderwaldt. 2 ♂ 2 ♀, USNM, Farol de Moela, October 29, 1964, G. Vazzoler. 5 ♂ 4 ♀, USNM, Cananéia, September 1965, V. Sadowsky. 1 ♀, USNM, Cananéia, November 1955, E. E. Boschi. 1 ♂, USNM, Cananéia, Mar do Cubatas, 1950, J. de P. Carvalho.

**Paraná:** 2 ♀, USNM, Paranaguá, 1965, W. Romanzini.

**Santa Catarina:** 1 ♀, CPPSC, Armação da Piedade, January 3, 1965, E. Tremel.

## Diagnosis

Adrostral carina and sulcus short, ending at epigastric tooth. Petasma with inner surface of distal portion of lateral lobe smooth, lacking diagonal ridge and fold, and with distoventral corner produced, forming subrectangular projection; emargination median to inner lappet deep. Thelycum with pair of subparallel anterolateral almost straight ridges followed posteriorly by two rounded and rigid protuberances on sternite XIV; posterior margin of sternite XII bearing two pairs of rather large projections.

## Description

### ROSTRUM (fig. 14)

Teeth $\frac{7\text{–}10}{1\text{–}3}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—55, 9/2—26, 7/2—15, 7/1—2, 8/1—1, 10/2—0.66, 9/3—0.33; N=300) + epigastric; ventral teeth relatively far apart, first tooth usually opposite or anterior to last dorsal tooth; rostrum slender and long, in juveniles extending to base of distal ¼ of thickened portion of lateral antennular flagellum; maximum length in relation to carapace length obtained at 13 to 16 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.95); decreasing progressively with increasing length of shrimp, reaching distal end of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.54); rostrum straight, slightly concave posteroventrally; highest portion of blade usually at level of second, occasionally of third dorsal tooth, and at level of first tooth in some young; third dorsal tooth level with anterior margin of carapace; tip slender and long, almost one-half of length of rostrum.

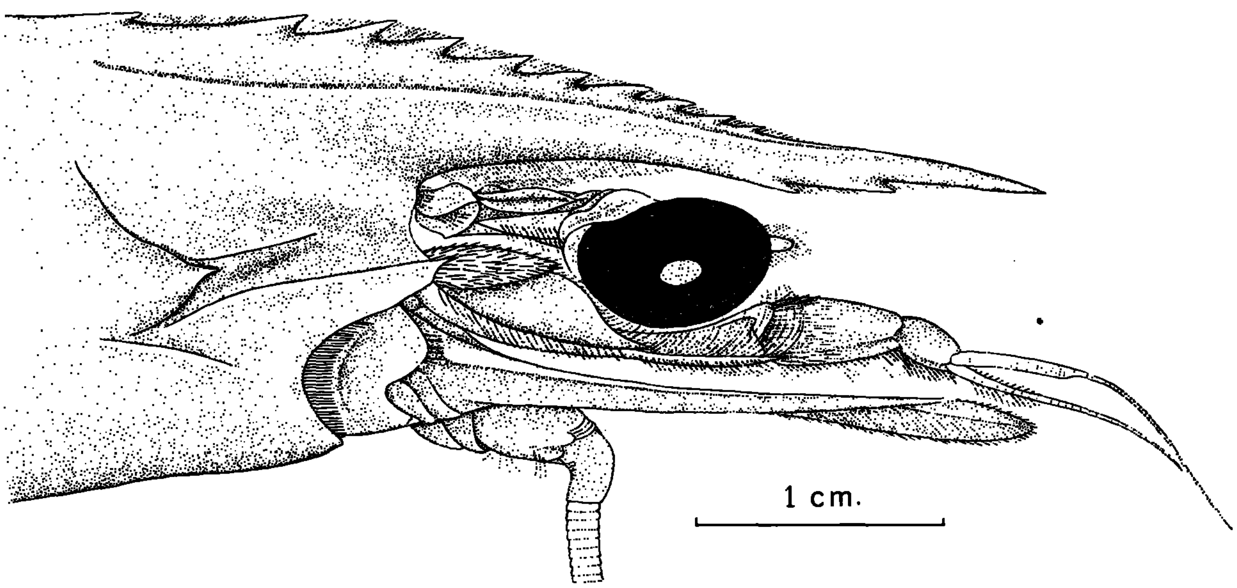

FIGURE 14.—*Penaeus* (*L.*) *schmitti* Burkenroad. Rostrum, ♀ 39 mm. c. l., Santos, Brazil.

Postrostral carina narrow and relatively short, ending 1/7 to 1/13 c.l. from posterior margin of carapace, shorter in larger individuals. Median sulcus shallow, sometimes extremely so, interrupted, often appearing as two elongated depressions followed posteriorly by series of three to six minute pits. Adrostral carina rounded and short, ending at level of epigastric tooth. Adrostral sulcus shallow, and short, same length as adrostral carina.

### CARAPACE (fig. 15)

Length in proportion to total length smaller in juveniles, according to my data increasing suddenly at about the size at which subadult stage is reached. Gastrofrontal sulcus and carina absent, except for a short, almost imperceptible rib subparallel to first two rostral teeth. Orbito-antennal sulcus wide anteriorly and narrowing posteriorly to below apex of hepatic spine, there widening into base of spine. Gastro-orbital carina pronounced, sharp and relatively short, occupying posterior 3/5 to 2/3 distance between postorbital margin of carapace and hepatic spine. Antennal carina very prominent. Cervical sulcus deeper at its lower half and extremely shallow above, ending at about two-fifths c.l. from postorbital margin of carapace. Hepatic carina 1/6 to 1/5 c.l., sharp, sloping slightly anteroventrally to end 1/11 to 1/14 c.l. from anterior margin of carapace. Antennal spine acute and relatively short; hepatic spine prominent.

### ANTENNULES

Lateral flagellum long, its length seven-tenths to almost same length as antennular peduncle, slightly longer than median flagellum, with articles shorter than those of median flagellum. Median flagellum exhibiting sexual dimorphism: in adult males markedly flattened dorsoventrally, with two closely set rows of stout processes of unequal sizes along midportion of internal margin, and with long setae along proximal one-fifth of external margin; in females processes lacking but long setae present along proximal two-fifths of external margin. Anterolateral spine small, sharp. Stylocerite reaching slightly beyond midlength of first antennular segment. Prosartema extending to proximal fifth of second antennular segment.

### ANTENNAE

Scaphocerite 2½ to 2⅔ times maximum width; spine reaching three-quarters of length of third antennular segment to one-fifth of length of thickened portion of antennular flagellum. Carpocerite about 1¼ times longer than wide, its distal end reaching base of eye. Antennal flagellum very long, 2½ to 2⅔ times body length.

### THORACIC APPENDAGES

Third maxilliped reaching at least distal end of proximal five-sixths of first antennular segment, and at most distal end of proximal five-sixths of second antennular segment; length of dactyl ⅔ to ¾ of propodus. First pereopod extending to distal

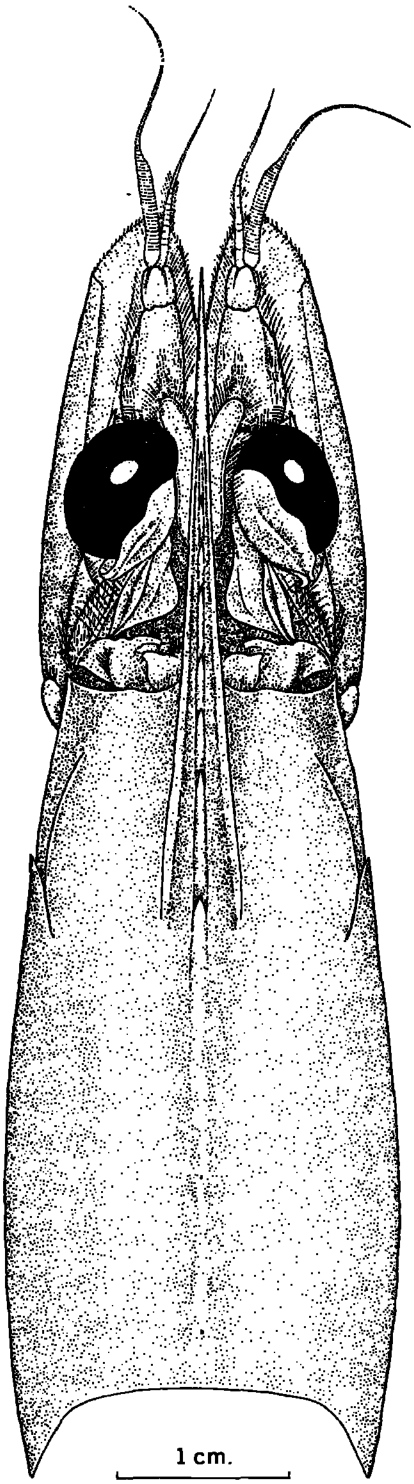

**Figure 15.**—*Penaeus* (*L.*) *schmitti* Burkenroad. Cephalothorax, ♀ 42 mm. c.l., Farol de Moela, Santos, Brazil.

end of carpocerite or surpassing it as much as five-sixths length of dactyl. Second pereopod reaching from seven-ninths of first antennular segment to one-third of second antennular segment. Third pereopod exceeding antennular peduncle from ⅔ to ⅞ of propodus. Fourth pereopod exceeding carpocerite from one-fifth to entire length of dactyl. Fifth pereopod surpassing fourth pereopod only by about one-half length of dactyl. Exopods on all pereopods; long ischial and basial spines on first pereopod; and rather long basial spine on second pereopod.

#### ABDOMEN

Carinate dorsally from midlength of third or from fourth somite posteriorly, carina gradually increasing in height forming keel on sixth somite, and ending in sharp spine on posterior margin of somite. Dorsolateral sulcus very narrow, shallow, and without lips. Sixth abdominal somite with three cicatrices on each side, anterior one longest; fifth somite with one cicatrix and diagonal series of minute pits anterior to sinus on posterior margin of somite; fourth somite with similar series of pits dorsal to sinus on posterior margin of somite. Ventral margin of pleuron of first somite moderately to deeply indented. Telson unarmed, with deep median sulcus and acuminate tip.

#### PETASMA (fig.16 a–c)

Lateral lobe with distal portion of inner surface smooth, lacking diagonal ridge and fold; distoventral corner of lateral lobe typically produced medially in subrectangular projection; anterior half of ventral border with two narrow ribs joined at both ends. Emargination median to inner lateral lappet relatively deep. Outer surface of lateral lobe armed with broad band of very closely set spines, as many as seven rows abreast distally and decreasing to two proximally. Crests distally on each side of band of spines, the one close to median lobe more prominent and sharp than that near free ventral margin, latter crest bifurcate. Lateral lobe often extending conspicuously beyond median lobe.

#### APPENDIX MASCULINA (fig. 16 d, e)

Subtriangular, its length twice or slightly greater than width at base, armed with short spines along median margin and with long ones on distal portion; distal spines slightly less than half length of appendix. Anterior surface subplane, posterior surface strongly concave, concavity bordered by arch-shaped ridge.

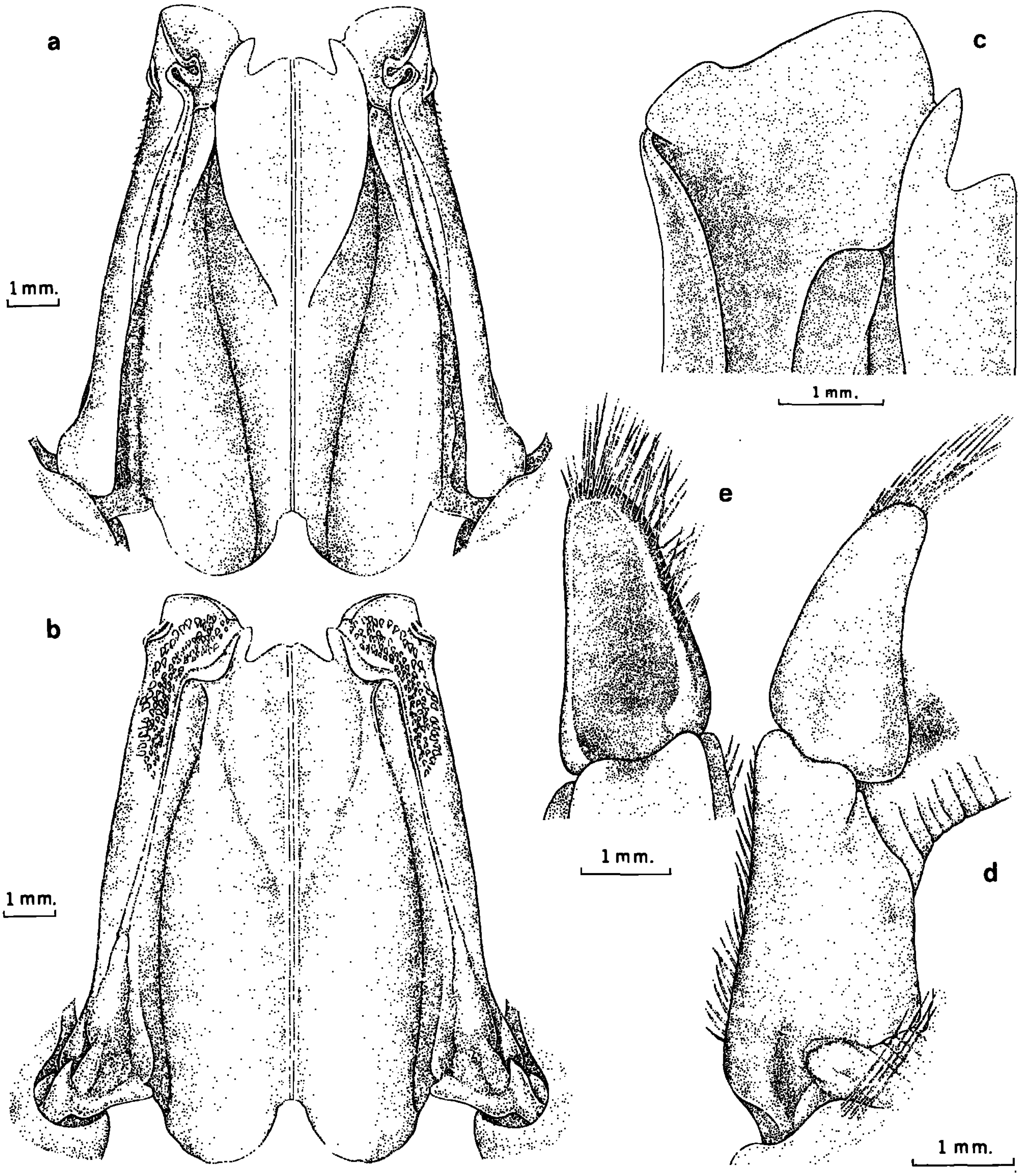

FIGURE 16.—*Penaeus* (*L.*) *schmitti Burkenroad.* a. Petasma, interior surface, ♂ 33 mm. c.l., off Tucuracas, Colombia. b. Petasma, exterior surface, ♂ 33 mm. c.l., off Tucuracas, Colombia. c. Petasma, interior surface of distal portion of left half, ♂ 36 mm. c.l., Punta Araguapiche, Venezuela. d. Appendix masculina, ♂ 36 mm c.l., Farol de Moela, Santos, Brazil. e. Appendix masculina, posterior surface, ♂ 36 mm. c.l., Farol de Moela, Santos, Brazil.

**SPERMATOPHORE**

Elongate and podlike, actually consisting of two spermatophores; in mature males each lying completely formed in paired terminal ampullae and joined when discharged. Anterior end, when attached to female, bearing pair of winglike lateral processes, each armed with short triangular projection at posterior edge. Posterodorsal portion extended into horizontal plate.

**THELYCUM (figs. 17 and 18)**

Open type. Sternite XIV with two subparallel anterolateral ridges running posteriorly without turning medially; ridges followed posteriorly by two protuberances, either rounded or subconical with rather inconspicuous apices; very narrow groove bordered by ribs, running along midline of sternite between anterior portion of protuberances. Strong median plate of sternite XIII with emarginated, shelflike projection overhanging sternite XIV; ridge on posterior margin of plate prominent; on anterior portion of sternite XIII fleshy tonguelike lamella bordered by minute setae forming the floor of cavity roofed by strong transverse ridge on posterior margin of sternite XII; ridge of sternite XII (hidden by the structures surrounding the gonopores and coxae of third pair of pereopods) with two pairs of strong projections, lateral pair often more prominent.

**COLOR**

*P. schmitti* is most frequently translucent white, having an almost glasslike appearance, with predominantly dark blue chromatophores and a bluish, grayish, greenish, or yellowish cast. Freshly caught juveniles are variable in color but most often light, with blue chromatophores rather sparsely distributed over the body and tail-fan; however, brownish or reddish-brown animals are not uncommon inshore.

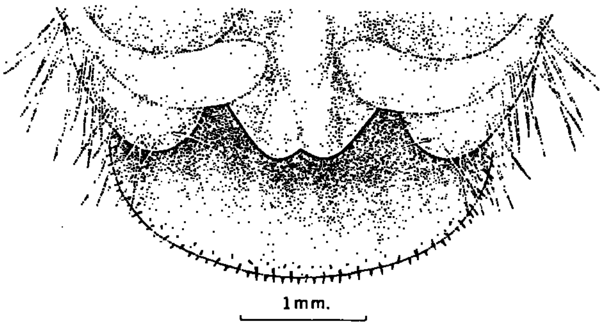

FIGURE 17.—*Penaeus* (*L.*) *schmitti* Burkenroad. Posterior portion of sternite XII and tonguelike lamella of sternite XIII, ♀ 50.5 mm. c.l., off Guyana.

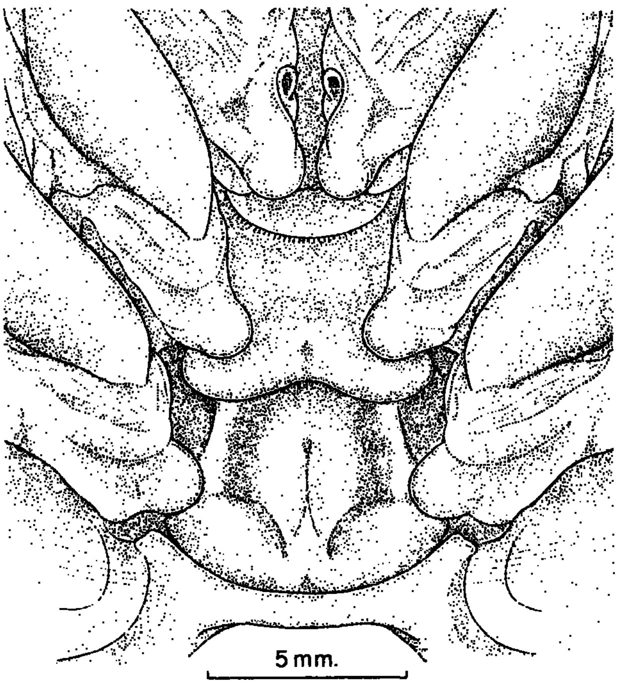

FIGURE 18.—*Penaeus* (*L.*) *schmitti* Burkenroad. Thelycum, ♀ 43.5 mm. c.l., off Guyana.

## Distribution and Morphological Variations

*P. schmitti* ranges from Cuba throughout the Greater Antilles and the Virgin Islands, apparently reaching the Lesser Antilles; it is also found in Trinidad. On the Continental Shelf, white shrimp are found from Belize, British Honduras, along the Caribbean Coast of Central America and northern South America and throughout the Atlantic Coast of South America to Laguna (lat. 28°29′ S.), Brazil (fig. 19). *P. schmitti* vicariates, or occupies the same kind of habitat, as the allopatric northern white shrimp *P. setiferus.*

Eldred and Hutton (1960) reported *P. schmitti* from off Cape Kennedy, Fla. This record is based on the statement by Harvey R. Bullis that during exploratory trips aboard the *Oregon* in 1956 and 1957, a number of specimens of this species were caught but not preserved. I have examined collections of *Penaeus* from the same area and found no *P. schmitti.*

The Lesser Antilles have a single record of white shrimp. According to Bate (1881), the description of "*P. setiferus*" by H. Milne Edwards (1837) was based on one specimen from the Island of

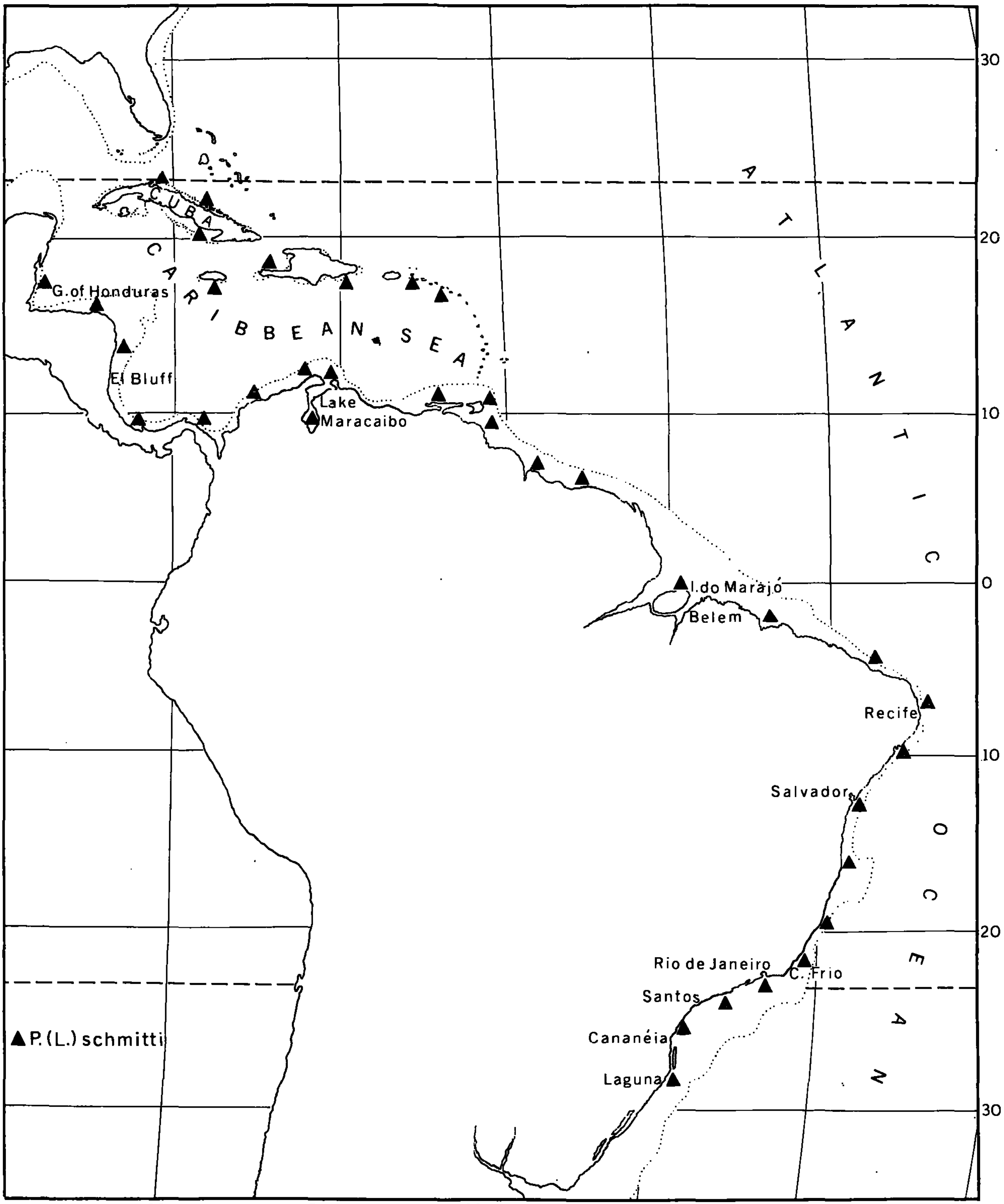

FIGURE 19.—Distribution of *Penaeus* (*L.*) *schmitti* Burkenroad.

Guadeloupe. The white shrimp is extremely rare in that general area; scarcity of brackish waters, or high salinity and unsuitable bottom may be responsible for the failure of the species to establish around those islands, where *P. a. subtilis* and *P. brasiliensis* are common.

This white shrimp is rather restricted within its range. Not only are there broad stretches where it seems to be absent; it also exhibits a disjunct distribution within rather small areas. In my intensive sampling for *Penaeus* in the waters around Cuba, both *P. schmitti* and *P. duorarum notialis* were found to be rather abundant. The latter lives in many localities around Cuba, but the white shrimp is restricted to certain areas. On the south shore, for instance, white shrimp is absent west of Bahía de Cienfuegos, and from the entire Golfo de Batabanó to the westernmost tip of Cuba. The dense concentrations of this species that are fished intensively are in relatively shallow water. In Cuba, white shrimp are found in large numbers to depths of 12 fm., and in the waters of the Gulf of Venezuela, they are abundant as deep as 10 to 14 fm. Although *P. schmitti* in most areas is found in water not deeper than 15 fm., off the coast of Honduras it is fished in depths between 11 and 20 fm. (Loesch, 1962), and Bullis and Thompson (1959b) caught a few specimens in water 15 to 26 fm. deep, off the northeast coast of South America. The reported (Anonymous, 1961) catches in 150 to 200 fm. off the western edge of Great Bahama Bank have not been authenticated; if this species does live in that area it is likely that the shrimp that appeared in this deepwater haul entered the net as it approached the surface.

My detailed studies of representative samples from many areas indicate little geographic variation in the diagnostic characters of *P. schmitti* throughout its range. I have been unable to recognize any significant differences between the population of the Caribbean Sea and that of the Atlantic, or throughout the latter population.

Although my data (fig. 19) and those of Ewald (1965c) seem to indicate that a change in the relation between carapace length and total length occurs at the time the white shrimp reaches about 21 to 22 mm. c.l., García Pinto (1965) found two discontinuities instead of one in that relation—one at a smaller and the other at a larger size.

## Relationships

*P. schmitti* has close affinities with *P. setiferus*. Females, however, may be distinguished by the two rigid, rounded posterior protuberances on somite XIV and the two anterolateral ridges that are almost parallel. The ridge at the posterior margin of somite XII also has typical shape, bearing two pairs of large convexities on each side, the lateral being the larger. Males of *P. schmitti* have the distomedian corner of the lateral lobe of the petasma produced in a characteristic subrectangular projection, with the inner surface lacking a diagonal ridge. The crest located nearer the ventral margin on the outer surface of the lateral lobe is also typically bifurcate instead of plain. In the original description of *P. schmitti*, Burkenroad considered the contour of the margin of the pleuron of the first pleonic somite a diagnostic character, but I have found the contour unreliable, for its shape varies over a wide range.

## Reproduction

### SUBADULT STAGE-SEXUAL MATURITY

The minimum size of males with joined petasmal endopods is 21 mm. c.l., 100 mm. t.l.—apparently the smallest size at which males reach the subadult stage. The joining of the petasmal endopods occurs, however, within the size range 21 to 27 mm. c.l., 100 to 126 mm. t.l. In both *P. schmitti* and *P. setiferus* the petasmal endopods join at a larger size than in the grooved *Penaeus*.

Thus far, it has not been possible to determine accurately the minimum size at which females are capable of being impregnated, although, according to my observations, the thelycum seems fully developed at 21 mm. c.l., 100 mm. t.l. The minimum size at which females of this species reach sexual maturity is not known.

### COPULATION

As it seems to be true in other *Penaeus* with an open thelycum, copulation in *P. schmitti* is believed to take place between hard-shelled individuals. The smallest females that have been found impregnated were 30 mm. c.l. The spermatophores are attached to the thelycum by means of the anterolateral wings, the triangular structure on the posterior margin of each wing, and the posterodorsal extensions. The glutinous material that surrounds the spermatophores when extruded aids in holding them temporarily to the thelycum. The coxae of the fourth and fifth pereopods of the female are produced into a platelike projection bearing long bristles directed medially which press the spermatophore against the thelycum, and help it adhere to the thelycum.

Few females have been found carrying spermatophores. I caught impregnated females in southern Cuba from February to June. In western Venezuela, between April and September Ewald (1965c) found a number of females with spermatophores attached, and off Tucuracas, Departamento de la Guajira, Colombia, at *Oregon* Sta. 5674, a female with a spermatophore attached was caught in October.

### OVARY DEVELOPMENT

The reproductive system of *P. schmitti* is similar to that of *P. setiferus*. In mature females two partly fused ovaries extend almost the entire length of the body, from the cardiac region of the stomach to the posterior end of the abdomen. The development of the ovary in *P. schmitti* has not been studied in detail. Five stages have been recognized by external characters similar to those described for *P. setiferus:*

1. Undeveloped. Ovaries very narrow and translucent.
2. Developing. Ovaries rather opaque and yellowish with chromatophores on the surface.
3. Nearly ripe or yellow. Ovaries larger than in the previous stages, and yellow-orange.
4. Ripe. Ovaries greatly distended, and drab olive or brownish.
5. Spent. Ovaries flaccid, from light green to whitish.

### SPAWNING

Spawning is in oceanic waters. Ewald (1965c) reported sexually mature females from water about 10 to 15 fm. deep in the Ensenada de Calabozo, Gulf of Venezuela, where maximum spawning occurs in April through June. In southern Cuba I found ripe females in March through June and in water 8 to 12 fm. deep.

The presence of white shrimp 20 mm. t.l. in Cuban waters during March seems to indicate that *P. schmitti* may spawn there also in late February. Da Silva (1965) in Baía de Sepetiba, Brazil, took advanced larvae and juveniles in March and April, which suggests that spawning takes place until late summer in those waters.

### SEX RATIO

The general male-female ratio is about 1 : 1. Ewald (1964) reported that in samples of sizes larger than 20 to 25 mm. c.l. from commercial catches, the percentage of females was slightly higher than that of males, but these samples were from areas where females seemed to be larger than males and, thus, more easily caught by the nets employed.

## Postembryonic Development

### LARVAE, POSTLARVAE, AND JUVENILES

To date, the larvae and postlarvae of this species have not been studied. Juveniles 18 mm. t.l. have short adrostral sulci, and, thus, may be separated from those of the grooved *Penaeus*. Juvenile *P. schmitti* frequently can be separated also by their light coloration.

In the development of individuals sex can be determined easily when they reach 6 mm. c.l., 28 mm. t.l. At this length the endopods of the first pair of pleopods in males are much wider than those in females, and the appendix masculina, although minute, is well formed.

Development of the petasma and median antennular flagellum in the males proceeds as follows: at 16 mm. c.l., 80 mm. t.l., the petasma has two rows of spines but lacks crests in the outer surface. At 17 mm. c.l., 83 mm. t.l., the petasma is still unjoined and the median flagellum bears long processes. At 21 mm. c.l., 100 mm. t.l., the petasmal endopods first join, the lateral lobes have three or four rows of spines, and the median flagellum has good numbers of long and a few short processes. Shrimp as small as 23 mm. c.l., 108 mm. t.l., have the petasma with the outer bands of spines fully developed and the median flagellum with both series of processes in large numbers.

Progressive changes in the thelycum occurs as follows: in females 10 mm. c.l., 48 mm. t.l., the thelycum bears low but distinct anterolateral ridges on sternite XIV. At 17 mm. c.l., 83 mm. t.l., the posterior protuberances, as well as the shelf overhanging from sternite XIII, are clearly formed and the ridges are prominent. At 21 mm. c.l., 100 mm. t.l., the thelycum seems to be fully developed and capable of holding the spermatophores in place; only females with a carapace length greater than 29 mm., however, have been found bearing spermatophores.

An incomplete investigation on the southern shores of Camagüey Province, Cuba, by Pérez Farfante et al. (1961) provided some data on juveniles of *P. schmitti*. Individuals 20 to 50 mm. t.l. were taken in estuarine water ⅓ to ½ fm.

deep from March to July, but were absent in August, scarce in September, and absent again in October and December. According to de Oliveira (1950), juveniles are abundant in Baía de Guanabara, Brazil, in January and February (during the summer) and da Silva (1965) collected larvae and juveniles in Baía de Sepetiba, Brazil, in March and April, or in late summer and early fall.

### GROWTH

Little information is available on growth of this species. It has been stated (Anonymous, 1962) that in Guyana individuals kept in ponds grew from 25 mm. t.l. to 200 to 225 mm. t.l. through a period of 7 to 8 months. Ewald (1965c) estimated that in Lake Maracaibo—where juveniles and subadults live—shrimp increase up to 50 mm. monthly. Finally, Khandker (in press) found that in Laguna de Unare, Venezuela, *P. schmitti* grew an average of 1 mm. per day from July through October.

### SEX DIFFERENCES IN SIZE

Females attain a greater length than males. The maximum reported female length is 235 mm. t.l. (Davant, 1963). The largest male measured was 43 mm. c.l. (about 175 mm. t.l.); it was taken in the Gulf of Venezuela by Ewald (1965c).

In inshore samples males and females are about the same size, whereas in the offshore material some of the females are larger than the largest males. This sex-size disparity in the white shrimp was noticed in material obtained by Loesch (1962) and in the material I examined.

## Ecology

### FOOD

White shrimp are omnivorous. They ingest algae, organic debris and sand, as well as a variety of animals. Among the animal remains found in their digestive tract are those of nematodes, annelids, mollusks, and crustaceans.

### SUBSTRATE

*P. schmitti* offshore lives on soft bottoms of mud and silt, often mixed with coral sand and small fragments of mollusk shells. Although not numerous, these shrimp also occur in patches predominantly of sand on rock bottoms. In estuarine water, late postlarvae and juveniles live on muddy bottoms where there is abundant vegetation or organic debris.

### DIEL CYCLE

In some areas—Gulf of Venezuela (Ewald, 1965c) and southern Cuba (Pérez Farfante, 1954b; Pérez Farfante et al., 1961)—the capture of adults day and night indicates that they are active at all hours, but in Honduras and Nicaragua they are caught almost exclusively during the day. In Cuba, juveniles and subadults of *P. schmitti* are fished in estuarine waters mostly at dawn or during the morning. According to Ewald (1964), white shrimp are fished commercially in Lake Maracaibo during the last hours of the night, and Boschi (1963) stated that they are taken in the lagoons of Cananéia, Brazil, in the first hours of the morning. It, thus, seems as if the young shrimp are more active at dawn and the hours immediately after.

### MOVEMENTS

The larvae of *P. schmitti* move from the sea, where hatching occurs, to brackish waters where they arrive as postlarvae. Khandker (in press) reported that postlarvae appear at the seashore near Laguna de Unare, Venezuela, in June and July and begin to enter the Laguna in July at an average length of 8.5 mm. t.l. Ewald (1965c) collected thousands of postlarvae up to 10 mm. t.l. in the Estrecho de Maracaibo, and the occurrence of these postlarvae indicates a movement from the Ensenada de Calabozo, where mature females are found, toward Lake Maracaibo, one of the most important nursery grounds of the white shrimp.

The juveniles grow rapidly in the rich estuarine waters, reaching a size and abundance that makes commercial fishing highly profitable. At the end of a few months—6 to 9 in Lake Maracaibo (Ewald, 1965c)—they move back to sea where the life cycle is completed. An indication of the seaward migration of *P. schmitti* was given by Ewald (1965c), who found that the largest as well as the average sizes of both males and females in Lake Maracaibo were smaller than those in the Gulf of Venezuela. This observation suggests that as the shrimp grow they move from the almost fresh waters of the lake to waters of higher salinity in the Gulf. With regard to size distribution in sea waters, Pérez Farfante (in press) in Cuba found a gradient from shallow to deep water; the largest specimens were farthest from shore and in the deepest water.

### EFFECTS OF TEMPERATURE

No studies have been made on the influence of temperature on the life and distribution of this white shrimp. The geographical distribution and the fact that the densest population is in the Gulf of Venezuela-Lake Maracaibo complex indicate that *P. schmitti* is a warm-water species. White shrimp, however, are found as far south as Laguna (lat. 28°29′ S.), Brazil, in water influenced by the Falkland Current.

### EFFECTS OF SALINITY

Among the sympatric *Penaeus*, the young *P. schmitti* seems to have the greatest preference for low-salinity water. Da Silva (1965) stated that the white shrimp is by far the most abundant species in Baía de Sepetiba, Brazil, where the salinity is very low because about a dozen rivers flow into it. In western Venezuela, white shrimp are most abundant in the low-salinity water of Lake Maracaibo and in the southwestern part of the Gulf of Venezuela, which has the lowest salinity in the area. In contrast, white shrimp within the Gulf of Venezuela are absent from the Golfete de Coro, where the salinity is extremely high because of intense evaporation.

### ENEMIES AND DISEASES

No detailed study of *P. schmitti* predators has been undertaken. It is, however, well established that *Penaeus* shrimp in general are an important food of various species of carnivorous fishes and various other animals. My examination of the stomach contents of different snappers (Lutjanidae) showed that white shrimp made up a high percentage of their food. Nikolić and Ruíz (in press) reported white shrimp in the stomach of a stingray "lebisa," and also in stomachs of porpoises. White shrimp are also cannibalistic, like other *Penaeus*.

Specimens have been found with black coloration, apparently suffering from "black spot" caused by a microsporidian sporozoan (Ewald, 1964, 1965c).

## Commercial Importance

*P. schmitti* is commercially important in Cuba, the Caribbean waters of Central America, Colombia, and especially in Venezuela. It is also extensively fished commercially along the coast of Brazil. Cuba has a fishery for white shrimp in the Gulf de Guacanayabo and along the southern coast of Camagüey and Las Villas to Bahía de Cienfuegos. In Guatemala, small quantities of white shrimp are caught at Lago Izabal (Lindner, 1957) and in the western portion of Bahía de Amatique (Croker, 1967). The only important fisheries for white shrimp in Central America are in Honduras and Nicaragua. In 1965, Honduras shrimp exports to the United States (which represent almost the entire production) amounted to 740,270 kg. (heads-off);[4] practically all shrimp in Honduras are caught on the Caribbean Coast, and Loesch (1962) estimated that *P. schmitti* accounts for about half of the catches made there. In Nicaragua fishing for white shrimp, although seasonal, is highly productive; the composition of the production is not known. In Colombia the young are taken commercially in the lagoons near the mouth of the Río Magdalena, and adults are caught in the vicinity of Cartagena (Alejandro Londoño, personal communication).

The greatest fishery by far is in western Venezuela. According to Ewald (1965c), in 1964 the total shrimp production in Lake Maracaibo-Bahía de Tablazo, Gulf of Venezuela, amounted to 4,249,531 kg., and white shrimp made up 70 percent of the shrimp caught in Lake Maracaibo and 50 percent of that caught in Bahía de Tablazo. In 1965 catches in this area amounted to 7,242,130 kg. (according to Croker, 1967, "weights are mostly in heads-off equivalents although shrimp for the domestic market are probably recorded as heads-on"). In the coastal lagoons to the east, white shrimp support several small fisheries (Davant, 1963; Khandker, in press) and appear to be scarce in the shallow waters of Guyana, Surinam, and French Guiana, where only small quantities are caught.

*P. schmitti*, as stated earlier, is abundant in the waters of Brazil. It is taken commercially in or when leaving the estuarine nursery grounds from Belém along the coast to São Luis, and also at Parnaiba, Natal, Recife, and in Salvador. In eastern Brazil, camarão legítimo makes up part of the commercial catches from Rio Doce to Cabo Frio and Baía de Guanabara. The most important fisheries for this shrimp in Brazil are those in Baía de Sepetiba (da Silva, 1965) and in the lagoons along the coast of the States of São Paulo (Sadowski and Radasewski, 1960; Braga, 1962), Paraná and Santa Catarina (Richardson and Moraes, 1960;Tremel et al., 1964; Tremel and Mis-

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[4] All exports figures cited here for Latin America should be understood to include only "heads-off" estimates.

takidis, 1965). In Rio de Janeiro landings of camarão legítimo during 1965–66 reached an all-time high, averaging 754,200 kg. (SUDEPE). At São Paulo landings averaged 119,900 kg. (Instituto de Pesca Marítima) during the same two-year period and in Santa Catarina they increased sharply in 1966, to 69,700 kg., after extremely poor landings during 1965, when only 4,500 kg. were reported (Centro de Pesquisas de Pesca).

### *Penaeus (Melicertus) duorarum duorarum* BURKENROAD

Figures 20 to 31

United States: pink shrimp, spotted shrimp, pink-spotted shrimp, brown-spotted shrimp, grooved shrimp, green shrimp, pink night shrimp, red shrimp, hopper, skipper, pushed shrimp. Mexico: camarón rosado.

*Penaeus brasiliensis:* Gibbes, 1850: 198 [part]; Stimpson, 1871: 132 [part]; ? Smith, 1874: 642; Rathbun, 1884: 821–823 [part]; Ives, 1891: 194, 200 [part]; Evermann, 1892: 90 [part]; Rathbun, 1893: 821–823 [part]; Sharp, 1893: 108, 109 [part]; A. Milne Edwards and Bouvier, 1909: 235–238, figs. 64–67, pl. 6, figs. 11, 12; Andrews, 1911: 420, 422–424, figs. 3, 4; de Man, 1911: 96; Boone, 1927: 78 [part]; Cowles, 1930: 355, 356, 358 [part?]; Weymouth, 1931: 11 [part?]; Burkenroad, 1934: 61, 75, 77, 78, 93, 94 [part]; Johnson and Lindner, 1934: 4, 5 [part]; Myers and Gowanloch, 1934: 12 [part?]; Pearson, 1935: 172 [part]; Lindner, 1936: 155 [part?]; Pearson, 1939: 2, 30–39, 50, 51, 53, 59, 71, 72 [part]; Anderson, 1948: 1 [part]. Not *P. brasiliensis* Lat., 1817.

*Peneus braziliensis:* Coues, 1871: 124 [part?]; Kingsley, 1878: 69 [part]; Kingsley, 1879: 330 [part?]; Kingsley, 1880: 427 [part].

*Penaeus braziliensis:* Kingsley, 1882: 106 [part]; Verrill, 1922: 41–43 [part], pl. 13, figs. 1, 2 (?), pl. 16, figs. 1, 2, 2a (?), pl. 17, fig. 10d–f; Williams, 1959: 281, 285, 286, 288 [part].

*Paneus brasiliensis:* Collins and Smith, 1892: 102 [part].

*Peneus brasiliensis:* Faxon, 1896: 162 [part]; Hay and Shore, 1918: 377, 378 [part], pl. 26, fig. 6(?); Boone, 1930: 14, 15, 101–105 [part], pl. 30.

*Penaeus duorarum* Burkenroad, 1939 [part, "Form A"]: 4, 21, 27, 30, 31–34, 36, 39–45, 51, figs. 23, 25 ("holotype and cotypes", 1 ♂ 2 ♀, YPM 4806–BOC 255 and 256, off Mobile Bay, Ala., 20 fm., March 20, 1937, *Atlantis* Sta. 2813, lat. 29°45′ N., long. 88°11′ W. [1 of the ♂ types "taken abroad," see below]); Anderson, Lindner, and King, 1949: 16; Burkenroad, 1949: 688; Broad, 1950: 1–4, 2 figs.; Gunter, 1950: 22–27, 40, 46, 47, 49; Holthuis, 1950: 27; Idyll, 1950: 7, 9, 10, 14, 15, 17, 19, 22, fig. 1; Broad, 1951: 27, 28, 30–32, 34, 35; Burkenroad, 1951: 26; Sánchez Roig and Gómez de la Maza, 1951: 113; Gómez de la Maza, 1952: 167, 169–171, fig. 1b; Leone and Pryor, 1952: 27–31; Springer and Bullis, 1952: 9, 10, 12, fig. 9; Hedgpeth, 1953: 159, 160, 210; Hildebrand and Gunter, 1953: 152, 155; Pérez Farfante, 1953: 229, (238, 241 [part]); Williams, 1953: 156–160, figs. 1, 2; De Sylva, 1954: 10, 18, 19, 23, 24, 26, 29, 33, fig. 1; Hildebrand, 1954: 233, 241, 245, 247, 266, 267, 350; Springer and Bullis, 1954: 3, 4, 6–8, 12, 16, fig. 10c; Hildebrand, 1955: 172, 174–179, 220, 224–227; Parker, 1955: 205; Voss, 1955: 5, 8, 10, figs. 11, 14, 15; Williams, 1955a: 116–118, 129, 133–136, 137, 140–142, 144; Williams, 1955b: 200, 204, 206, fig. 2; Anderson, 1956: 2, 4; Darnell and Williams, 1956: 844–846; Guest, 1956: 6, 12, 14, 18, figs. 2, 3; Gunter, 1956: 99–105; Springer and Bullis, 1956: 9; Anderson, 1957: 399; Carranza, 1957: 147; Ingle, 1957: 10, 13, 16, 17; Lindner, 1957: 83, 84, 92; Simmons, 1957: 178, 191, 199; Viosca, 1957: 12, 20, 1 fig.; Woodburn et al., 1957: 5–7, 12–14, 18, 20–24, 31, fig. 1; Anderson, 1958a: 1–3, fig. 3; Anderson, 1958b: 2; Darnell, 1958: 385, 388; Eldred, 1958: 2–13, 15–21, 23–25, figs. 2–15; Hildebrand, 1958: 159; Hutton and Eldred, 1958: 27; Lindner, 1958: 29–33; U.S. Fish and Wildlife Service, 1958b: 1, 6, 8, 12, 15, 18, 20–22, 24–26, 33, 34, fig. I–5b; Williams, 1958: 283–290; Collier, Gunter, Ingle, and Viosca, 1959: 1; Costello, 1959: 1–5; Costello and Allen, 1959: 13–18; Eldred, 1959a: 75, 76; Eldred, 1959b: 2–6; Hutton, Sogandares-Bernal, and Eldred, 1959: 490; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959: 6–13, 15–17, 19–25, 27, fig. 22; Ingle, Eldred, Jones, and Hutton, 1959: 1–45; Iversen and Manning, 1959: 130–132; Kruse, 1959: 123, 124, 126, 128, 130–132, 134, 136, 137, 139, 142, 144; Sogandares-Bernal and Hutton, 1959: 362; Williams, 1959: 282, 288, 289, figs. 1–3, 5–7; Chin, 1960: 135, 136, 140; Costello and Allen, 1960: 5–9; Eldred, 1960: 164, 165; Eldred and Hutton, 1960: 91, 97–99, 101, 103, 104, 106, 108, figs. 3, 4, 8; Hoese, 1960a: 592, 593; Hoese, 1960b: 330, 331; Hutton and Sogandares-Bernal, 1960: 290; Iversen and Idyll, 1960: 1–8; Iversen, Jones, and Idyll, 1960: 1–62; Kutkuhn, 1960: 11–15; Renfro, 1960b: 63, 64, 1 fig.; Williams, 1960: 560, 561, 565, 567, 569, 570; Anonymous, 1961: 34; Bearden, 1961: 3, 4, 6–8; Costello and Allen, 1961: 18–21; Cummings, 1961: 462–468, figs. 3, 5a, b; Dobkin, 1961: 321–348, figs. 2–20; Eldred, Ingle, Woodburn, Hutton, and Jones, 1961: 5–136; Gunter, 1961a: 599; Ingle, 1961: 22–27; Iversen and Jones, 1961: 1–28; Renfro, 1961: 11; Tabb and Manning, 1961: 594; Anderson, 1962: 1, 2, fig. 3; Gunter, 1962a: 107, 108; Gunter, 1962c: 216–223, 226; Hutton, Ball, and Eldred, 1962: 327–332, fig. 4; Kutkuhn, 1962: 343, 355, 369–378, 383, 388, 397, 398, 401; Tabb, Dubrow, and Jones, 1962: 6–28; Tabb, Dubrow, and Manning, 1962: 12, 42, 44, 52, 60, 61, 63, 74; Baxter, 1963: 80; Boschi, 1963: 5, 6, 13, 20–23, 26, 29, 35, fig. 6 (1–5); Gunter, 1963: 108; Gunter and Hall, 1963: 295, 297, 304; Kutkuhn, 1963: 66–77; McFarland and Lee, 1963: 391, 392, 394, 406, 408–410; Renfro and Brusher, 1963: 15, 16; Zein-Eldin, 1963a: 188–196 [part]; Aaron and Wisby, 1964: 121–130; Costello and Allen, 1964: 30, 31; Fuss, 1964: 62–73, figs. 1, 3; Gunter et al., 1964: 182, 184; Hutton, 1964: 440, 444, 445; Jones, Dimitriou, Ewald, and Tweedy, 1964: 1–3, 9, 10, 16–75; Renfro, 1964: 95; Anderson and Lunz, 1965: 1, 4–6; Broad, 1965: 86–89; Bullis and Thompson, 1965: 6; Copeland, 1965: 11, 13, 14, figs. 2, 3; Eldred, Williams, Martin, and Joyce, 1965: 1–4, 7–25; Ewald, 1965b: 436–448; Holthuis and Rosa, 1965: 4 [part]; Idyll and Jones, 1965: 25–27; Joyce, 1965: 14, 19, 20, 24, 29, 30, 34, 39, 40, 44, 49, 50, 53, 58, 59, 62, 67, 68, 70, 75, 76, 79, 80, 83, 84, 88, 91, 93, 96, 98, 99, 102–104, 115, 121–128, 132, 134, 154–161, 170, 173, 177–192, 219, 221; Loesch, 1965: 42–56; Saloman, 1965: 1–13; Simpson et al., 1965: 77; Temple and Fischer, 1965a: 59; Van Engel, 1965: 38; Williams, 1965: 21–24, 26, 27, figs. 10, 11; Zein-Eldin and Aldrich, 1965: 199, 212; Christmas et al., 1966: 196, 197, 200, 201, 204–206, 209, 211, 212, fig. 5; Cook, 1966: 438; Copeland and Truitt, 1966: 65, 68–70, 72, 73; Costello and Allen, 1966: 449–459; Fuss and Ogren, 1966: 170–189; Hughes, 1966: 504; Joyce and Eldred, 1966: 8, 9, 11–13, 16, 19–21, 23, 25, 32–34; Kutkuhn, 1966a: 19, 20, 26; Kutkuhn, 1966b: 313–338; Sykes and Finucane, 1966: 372–376; Baxter and Renfro, 1967: 151, 152; Lyles, 1967: 315–317, 371–376; McCoy and Brown, 1967: 1–3, 8–11, 14, 15, 18, 21, 22, 25–27; Temple and Fischer, 1967: 323, 325; Saloman, 1968: 1–5; Zamora and Trent, 1968: 17, 19.

*Penaeus duoarum:* Anderson and Lindner, 1945: 306 [part]; Gunter, 1945: 77; Dall, 1957: 142, 226 [part].

*Penaeus ducrarum:* Viosca, 1957: 10.

*Penaeus duorarium:* Broad, 1965: 87.

*Penaeus duorarum duorarum:* Pérez Farfante, 1967: 98.

Pink shrimp: Renfro and Brusher, 1964: 13; Cook, 1965: 11; Idyll, Iversen, and Yokel, 1965: 28, 29; Idyll and Jones, 1965: 25, 27; Idyll, Iversen, and Yokel, 1966: 19, 20; Lindner, 1966: 18–26.

Shrimp: Higman, 1952: 1–4; ?Flint, 1956: 11, 12.

## Taxonomic Remarks

I have examined 1♂ and 2♀ of the 2♂ 2♀ BOC "301" ("Holotype and Cotypes") mentioned by Burkenroad (1939) in the original description. They are together in a single bottle accompanied by two labels, on one of which is written "Holotype" and on the other "Cotypes," both with complete information on locality, depth, and date they were caught by the *Atlantis.* Neither label, however, shows the sex of the specimens. The label for the holotype is numbered 255 and the other 256; neither is numbered 301, the BOC catalog number given by Burkenroad. In addition to the two labels, there is in the bottle a slip of paper on which is written "smaller ♂ taken abroad" in Burkenroad's handwriting. It was not possible for me to determine which of these specimens is the holotype.

Several erroneous records for this subspecies occur in the literature. I have examined the male of "*P. brasiliensis*" from west of Whale Rock, northwest end of Arrecife Alacrán, MCZ 7211, described and illustrated by Milne Edwards and Bouvier (1909). I found it to be *P. d. duorarum.* Burkenroad (1934) pointed out that their illustrations show unusual features of the rostrum, carapace, and fifth and sixth abdominal somites. I believe that the first maxilla is not shown correctly either. These structures were undoubtedly misrepresented by the artist. I also examined material from Turtle Harbor, Fla., described by Boone (1930) and deposited in the Vanderbilt Marine Museum, Long Island, N.Y. The specimen figured in her plate 30 under the name "*P. brasiliensis*" is a female of *P. d. duorarum*, and although it is in a jar with a male of the same species (from the Marquesas Keys), it was easily identified because the object—a spermatophore—which appears in the photograph between the fifth pair of pereopods and the first pair of pleopods still remains attached.

## Study Material

### UNITED STATES

**Maryland:** 1 ♂ 1 ♀, CBL, Holland Strait to Smith Island, July–September 1964, E. Harrison. 3 ♂ 3 ♀, CBL, around Smith and Bloodsworth Islands, summer 1965, E. Harrison.

**Virginia:** 1 ♂, USNM, Cape Charles, August 18, 1897, W. H. Stirling. 2 ♂ 6 ♀, USNM, Cape Charles, September 1890, W. P. Seal. 3 ♂, USNM, Cape Charles, October 25, 1897, W. H. Stirling. 1 ♂, USNM, James Fishery, Norfolk, September 30, 1921, W. C. Schroeder.

**North Carolina:** 1 ♂, USNM, off Cape Hatteras, 14 fm., October 19, 1884, *Albatross* Sta. 2283. 1 ♂ 2 ♀, USNM, off NE. Cape Hatteras, 13 fm., October 19, 1884, *Albatross* Sta. 2285. 1 ♀, YPM, off Cape Hatteras, 11 fm., October 19, 1884, *Albatross* Sta. 2286. 1 ♀, USNM, off Cape Lookout, 15 to 16 fm., February 18, 1950, *Albatross III* Sta. 1. 2 ♂ 3 ♀, USNM, off Cape Lookout, 8 to 7 fm., August 27, 1959, *Silver Bay* Sta. 1312. 4 ♀, USNM, SE. of Lookout Lighthouse, 17 fm., January 25, 1949, *Willi Bross.* 4 ♂ 10 ♀, USNM, Beaufort Bar, 7 to 8 fm., October 6, 1949, A. Williams. 2 ♂ 1 ♀, USNM, off Beaufort, October 11, 1941, *Madelena*, W. W. Anderson. 14 ♂ 20 ♀, USNM, Bogue Sound, Morehead City, September 5, 1964, B. B. Collette and D. M. Cohen. 1 ♂, USNM, Middle Sound, Wilmington, April 18, 1880, R. E. Earll. 12 ♂ 21 ♀, USNM, Bogue Inlet Sea Buoy, 7 fm., June 7, 1949, *Perry E. Meyers*, W. W. Anderson. 7 ♂ 2 ♀, YPM, Fort Macon. 1 ♂, YPM, Fort Macon, H. C. Yarrow. 1 ♀, YPM, Fort Macon, J. E. Coues.

**Georgia:** 1 ♂, USNM, Doboy Sea Buoy, October 3, 1941, *Perry E. Meyers*, W. W. Anderson.

**Florida:** 1 ♂, YPM, off Matanzas Inlet, 8 to 10 fm., April 2, 1934, M. B. Bishop. 1 ♀, USNM, off Flagler Beach, 35 to 38 fm., June 2, 1957, *Combat* Stas. 345, 346. 1 ♂, USNM, off New Smyrna Beach, 27 fm., November 8, 1963, *Silver Bay* Sta. 5228. 1 ♂ 1 ♀, USNM, off Edgewater, 9 fm., January 21, 1960, *Silver Bay* Sta. 1562. 1 ♂, USNM, off Cape Kennedy, 20 fm., September 20, 1961, *Silver Bay* Sta. 3360. 1 ♀, off Cape Kennedy, 180 fm., January 26, 1962, *Silver Bay* Sta. 3710. 1 ♂ 1 ♀, USNM, off Cape Kennedy, 30 fm., November 8, 1963, *Silver Bay* Sta. 5231. 2 ♂, USNM, off Cape Kennedy, 20 fm., November 9, 1963, *Silver Bay* Sta. 5241. 2 ♂ 5 ♀, USNM, off Cocoa Beach, 10 to 11 fm., January 13, 1965, *Oregon* Sta. 5181. 5 ♂ 3 ♀, USNM, off Melbourne Beach, 11 fm., January 13, 1965, *Oregon* Sta. 5182. 7 ♂ 4 ♀, USNM, off Melbourne Beach, 30 fm., January 14, 1965, *Oregon* Sta. 5200. 7 ♂ 8 ♀, USNM, off Melbourne Beach, 30 to 29 fm., January 14, 1965, *Oregon* Sta. 5201. 5 ♂ 6 ♀, USNM, off Melbourne Beach, 30 to 31 fm., January 15, 1965, *Oregon* Sta. 5202. 4 ♂ 5 ♀, USNM, off Sebastian, 31 to 28 fm., January 15, 1965, *Oregon* Sta. 5203. 1 ♂ 1 ♀, USNM, Lantana, February 12, 1892, H. M. Smith. 1 ♀, USNM, Lemon City, E. J. Brown. 3 ♂ 2 ♀, YPM, mouth of Indian River, March 21, 1874, E. Palmer. 2 ♂ 2 ♀, YPM, off Miami Beach, February 21, 1927, *Pawnee* II. 23 ♂ 24 ♀, USNM, Biscayne Bay, February 2, 1966, D. M. Allen. 1 ♂ 1 ♀, USNM, off Elliott Key, 36 fm., October 24, 1960, *Silver Bay* Sta. 2351. 1 ♂, USNM, off Key Largo, Florida Keys, 40 fm., November 10, 1961, *Silver Bay* Sta. 3523. 5 ♂ 10 ♀, USNM, off Key Largo, 30 fm., October 26, 1960, *Silver Bay* Sta. 2380. 14 ♂ 4 ♀, USNM, off Key Largo, 40 fm., November 10, 1961, *Silver Bay* Sta. 3523. 8 ♂ 4 ♀, USNM, off Key Largo, 40 to 45 fm., November 9, 1961, *Silver Bay* Sta. 3521. 2 ♂ 2 ♀, USNM, Card Sound, February 13, 1889, USFC. 1 ♂ 1 ♀, USNM, Upper Jewfish, Bush Lake, 1½ fm., January 30, 1903, *Fish Hawk*. 13 ♂ 6 ♀, USNM, off Sombrero Key, Florida Keys, 32 to 30 fm., October 28, 1960. 4 ♂, USNM, Newfound Harbor Key, December 7, 1906, *Arian*, B. A. Bean. 57 ♂ 57 ♀, USNM, Florida Bay, February 1962, D. C. Tabb and D. Dubrow. 1 ♂ 2 ♀, USNM, Key West, 1884, *Albatross*, W. Nye. 17 ♂ 19 ♀, USNM, Key West, 1886, *Albatross*. 18 ♂ 29 ♀, USNM, off Marquesas Keys, 9 to 7 fm., July 19, 1957, *Silver Bay* Sta. 78. 1 ♂, VMM, Marquesas Keys. 20 ♂ 15 ♀, USNM, Tortugas grounds, 11 fm., September 18–23, 1961, *George Bowers*, C. H. Saloman. 11 ♂ 10 ♀, USNM, Tortugas grounds, February 1966, R. Benton. 4 ♂ 3 ♀, USNM, off Tortugas, 37 fm., April 13, 1954, *Oregon* Sta. 1004. 1 ♀, VMM, Turtle Harbor, January 10, 1923, *Ara*. 1 ♀, VMM, Turtle Harbor, April 10, 1923, *Ara*.

2 ♂ 1 ♀, USNM, 48 km. NE. of Loggerhead Key, Tortugas, 19 fm., December 3, 1954, G. H. Eubank. 1 ♀, YPM, Double Headed Shot Cays, 3 fm., March 7, 1925, *Pawnee II*. 3 ♂, USNM, off Cape Sable, 3 fm., December 18, 1902, *Fish Hawk* Sta. 7358. 1 ♀, USNM, Cape Romano, 6 fm., April 7, 1954, *Oregon* Sta. 993. 1 ♂ 3 ♀, USNM, Marco, February 25, 1889, USFC. 16 ♂ 12 ♀, USNM, SW. of Naples, July 18, 1957, *Silver Bay* Sta. 67. 4 ♂ 8 ♀, USNM, Sanibel grounds, 6 fm., March 19, 1962, D. M. Allen. 3 ♂ 8 ♀, USNM, Sanibel grounds, 6 fm., March 19, 1962, *Silver Bay*, D. M. Allen. 20 ♂ 5 ♀, YPM, Sanibel Island, shore, June 1935, M. Storey. 1 ♂ 2 ♀, USNM, Charlotte Harbor, March 1887, W. H. Dall. 6 ♂ 10 ♀, YPM, off Englewood, 4 fm., January 7, 1936, Bass Biol. Station. 76 ♂, USNM, St. Petersburg, Tampa Bay, October 3, 1938, V. E. Springer and K. D. Woodburn. 13 ♂ 11 ♀, USNM, Tampa Bay, March 29, 1901, *Fish Hawk* Sta. 7109. 4 ♂ 3 ♀, USNM, Tarpon Springs, November 5, 1896, USFC. 2 ♀, USNM, Anclote Keys, 6¼ fm., January 24, 1902, *Fish Hawk* Sta. 7239. 1 ♂ 3 ♀, USNM, Cedar Keys, October 6, 1949, G. K. Reid. 3 ♂ 1 ♀, USNM, Pensacola, February 9, 1885, *Albatross*. 2 ♂ 1 ♀, USNM, Pensacola Bay, 2½ fm., September 1929, W. C. Schroeder.

**Alabama:** 2 ♀, USNM, off Mobile, 7 fm., January 28, 1962, *Oregon* Sta. 3475. 1 ♂ 2 ♀, YPM, off Alabama, 19 fm., March 20, 1937, *Atlantis* Sta. 2813.

**Mississippi:** 7 ♂ 5 ♀, GCRL, Mississippi Sound, off Horn Island, May 13, 1964, J. Y. Christmas. 16 ♀, USNM, off Pascagoula, 17 to 18 fm., January 23, 1958, *Oregon* Sta. 2374.

**Louisiana:** 3 ♂, USNM, off Louisiana, 12 fm., February 6, 1938, *Pelican*. 33 ♂, USNM, Cat Island, November 15, 1931, J. C. Pearson.

**Texas:** 4 ♂ 5 ♀, USNM, off Texas, 12 fm., April 28, 1938, *Pelican* Sta. 49–5. 4 ♂ 8 ♀, USNM, off mouth of Sabine River, 10 fm., May 19, 1965, BCFBLG. 4 ♂ 6 ♀, USNM, off Galveston, 15 fm., March 26 to April 2, 1966, BCFBLG. 4 ♂ 4 ♀, USNM, off Freeport, 15 fm., September 22, 1966, BCFBLG. 3 ♀, USNM, off western Texas, Gulf of Mexico, April 1965, BCFBLG. 2 ♀, USNM, off western Texas, Gulf of Mexico, April 1965, BCFBLG. 2 ♂ 3 ♀, USNM, S. of Padre Island 12 fm., January 27, 1964.

### MEXICO

**Tamaulipas:** 7 ♂ 4 ♀, USNM, N. of Hut's Bayou, 8 to 10 fm., March 17, 1947, *Pelican* hauls 7 to 12, Mexican tagging trip. 4 ♂ 4 ♀, INIBP–USNM, Tampico, May 14, 1963, S. García. 3 ♀, INIBP, off Tampico, June 30, 1959, E. Ramírez and G. Aguilar.

**Veracruz:** 1 ♂ 2 ♀, INIBP–USNM, Bocaina, Laguna de Tamiahua, June 9, 1964, R. Márquez and C. Tovar. 4 ♂ 3 ♀, INIBP–USNM, Tuxpan, August 29, 1963, S. Basulto. 1 ♂ 1 ♀, INIBP–USNM, Tuxpan, off La Bocana, March 7, 1964, A. Mendoza and R. Márquez.

**Campeche:** 8 ♂ 5 ♀, INIBP–USNM, shore, Campeche, November 1963, fishermen. 2 ♀, INIBP–USNM, Golfo de Campeche, 7 fm., May 2, 1959, R. Ramírez and M. Flores. 2 ♂, USNM, off Campeche, 26 fm., November 21, 1958, *Silver Bay* Sta. 846. 3 ♂ 2 ♀, INIBP–USNM, NW. of Campeche, 26 fm., April 30, 1959, R. Ramírez and M. Flores. 5 ♀, INIBP–USNM, Morro to Ceybaplaya, 7 fm., May 3, 1959, R. Ramírez and M. Flores. 2 ♂ 5 ♀, USNM, off Cayo Arcos, 20 fm., December 11, 1952, *Oregon* Sta. 720.

**Yucatán:** 8 ♂ 10 ♀, INIBP–USNM, between Dzilam de Bravo and Yalkubul, October 10, 1961, M. Solís. 2 ♂ 1 ♀, MCZ, NW. of Arrecife Alacrán, 6 km. off Whale Rock, 35 fm., *Blake* Sta. 37.

**Quintana Roo:** 1 ♂, INIBP, 90° NNW. of Isla Mujeres, 21 fm., July 17, 1967, H. Chapa Saldaña, D. Fuentes, and J. M. de la Garza.

### BERMUDA ISLANDS

1 ♂, YPM, Mullet Bay, ½ fm., January 27–29, 1935. 1 ♂, YPM, Gibbet Island Bay, September 19, 1905. 1 ♀, YPM, Fairyland Creek, September 30, 1915. 2 ♀, YPM, Ferry Beach, 1936.

## Diagnosis

Adrostral sulcus broad posteriorly and long, almost reaching posterior margin of carapace. Median sulcus long, ending immediately anterior to posterior end of adrostral sulcus, and deep along its entire length. Dorsolateral sulcus narrow, sometimes almost closed. Petasma with distal portion of ventral costa broadening and turning proximally rather abruptly, armed with minute spines along free border and with compact group of large teeth on attached border; apex of ventral costa adnate to adjacent wall; distal fold small, unarmed or with few submarginal spinules. Thelycum with anterior process relatively large, and with prominent undivided median carina on posterior process; carina exposed owing to slight divergence of anteromedian corners of lateral plates.

## Description

**ROSTRUM (fig. 20 a, b)**

Teeth $\frac{7\text{–}10}{1\text{–}3}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—67, 9/2—21, 8/3—5, 7/2—4, 9/3—2, 7/1—1; N=300) + epigastric; position of ventral teeth variable, first tooth situated from well anterior to slightly posterior to distal dorsal tooth; rostrum relatively short in larger juveniles, reaching at most to base of lateral antennular flagellum; attaining maximum length in relation to carapace length at 8 to 13 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.75); decreasing progressively with increasing length of shrimp, rostrum reaching distal end of first antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.35); rostrum straight apically or directed downward, occasionally upturned, convex proximally; highest portion of blade at level of third dorsal tooth; latter level with anterior margin of carapace; rostrum tip 1/5 to 1/4 r.l. Postrostral carina strong, prominent, uniform in width or slightly wider in anterior half, and long, extending almost to posterior margin of carapace. Median sulcus deep throughout, long, ending near posterior margin of cara-

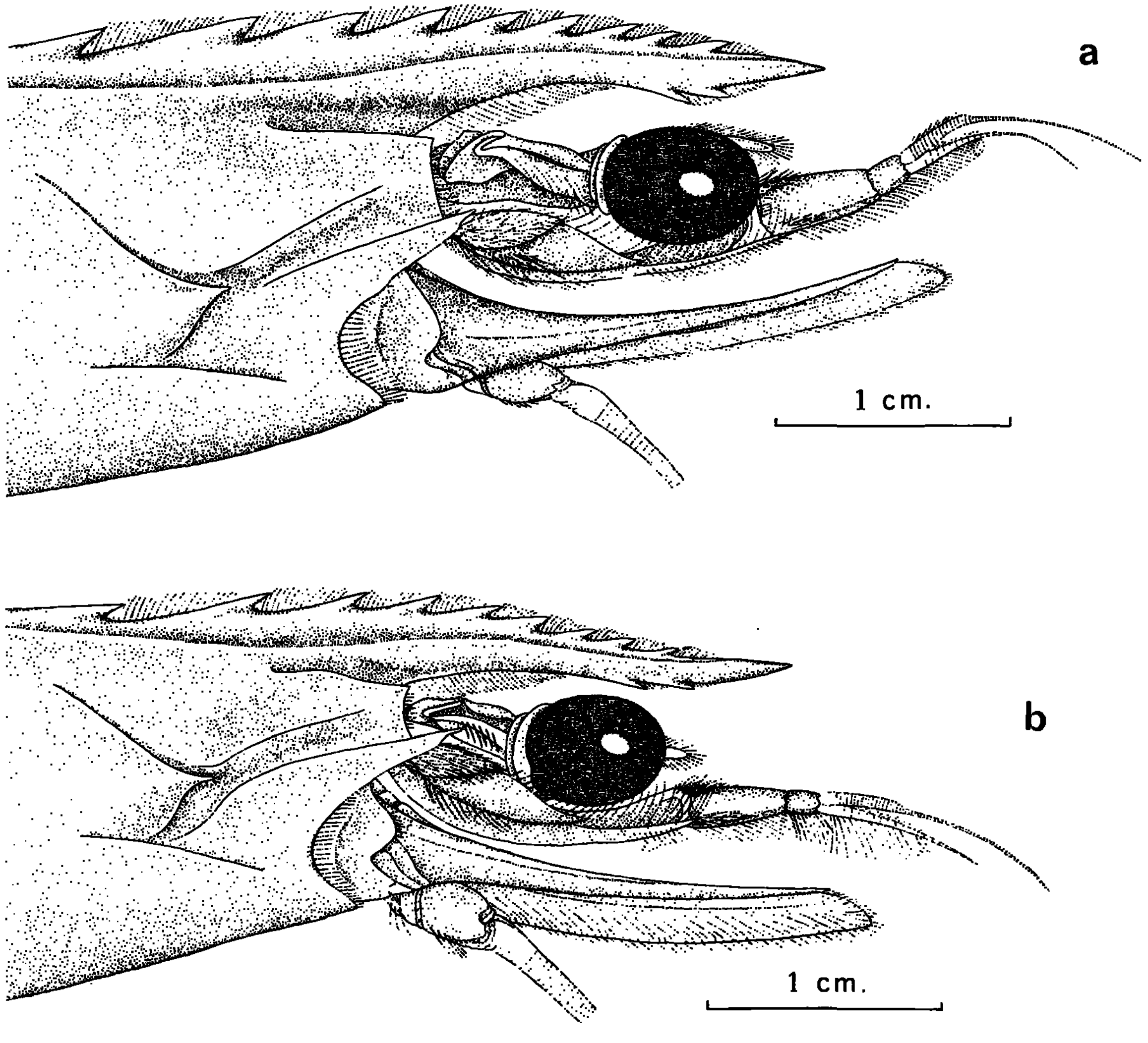

FIGURE 20.—*Penaeus* (*M.*) *duorarum duorarum* Burkenroad. a. Rostrum, ♀ 37 mm. c.l., off Sebastian, Fla. b. Rostrum, ♂ 35 mm. c.l., off Melbourne Beach, Fla.

pace. Adrostral sulcus deep, broad posteriorly, 3/5 to 1½ width of postrostral carina, measured at level of one-eighth distance from its posterior end to epigastric tooth, and long, ending 1/13 to 1/20 c.l. from posterior margin of carapace. Adrostral carina prominent, sharp along carapace, and long, same length as adrostral sulcus.

### CARAPACE (fig. 21)

Length in proportion to total length smaller in juveniles, according to my data increasing slightly at subadult stage. Gastrofrontal sulcus broad, extending to about one-fifth c.l.; gastrofrontal carina sharp, turning slightly toward dorsal margin posteriorly, ending in acute orbital angle anteriorly. Orbito-antennal sulcus wide anteriorly, narrowing posteriorly to below apex of hepatic spine. Gastro-orbital carina high and sharp, occupying approximately posterior four-fifths of distance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus 1/5 to 1/4 c.l., ending slightly anterior to midlength of carapace. Hepatic carina 1/5 to 1/4 c.l., sharp, sloping slightly anteroventrally to end 1/13 to 1/20 c.l. from anterior margin of carapace. Antennal spine prominent and acute; hepatic spine pronounced.

### ANTENNULES

Lateral flagellum ½ to 3/5 length antennular peduncle, slightly longer than median flagellum and with articles shorter than those of median flagellum. Anterolateral spine small, sharp. Stylocerite acuminate, reaching slightly beyond midlength of first antennular segment. Prosartema extending to distal end of proximal fifth of second antennular segment.

### ANTENNAE

Length of scaphocerite 2½ times maximum width, its length relative to carapace length decreasing slightly with growth; spine reaching at least distal end of antennular peduncle and at most distal end of proximal one-fourth of thickened portion of lateral flagellum. Carpocerite length 1¼ width, reaching distal end of optic peduncle. Antennal flagellum relatively short, about 1⅓ body length.

### THORACIC APPENDAGES

Third maxilliped reaching at least proximal one-fifth but not beyond distal end of second antennular segment; length of dactyl 3/5 to 2/3 that of propodus. First pereopod reaching base of carpocerite and at most exceeding it by seven-eighths

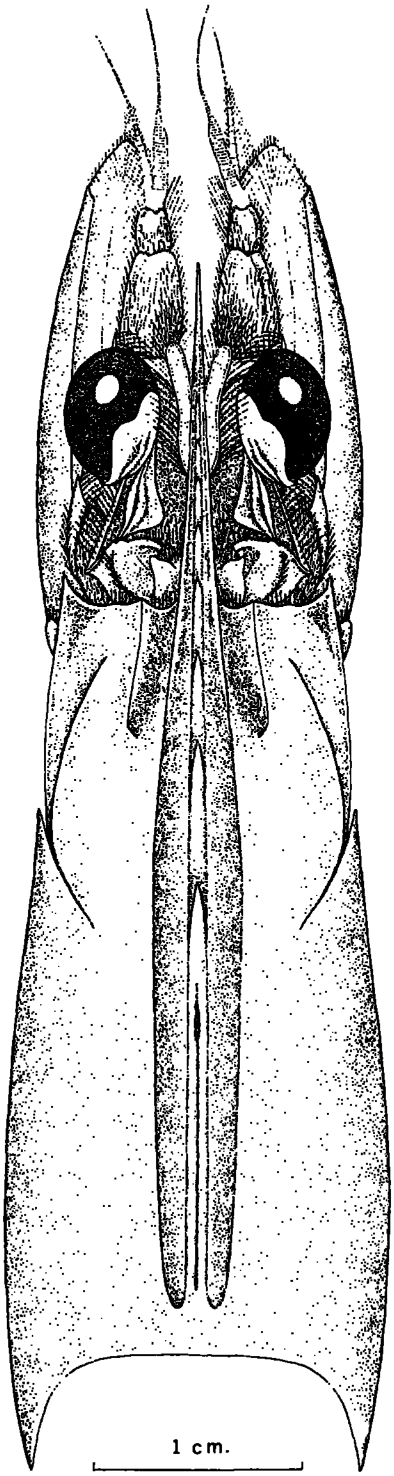

FIGURE 21.—*Penaeus (M.) duorarum duorarum* Burkenroad. Cephalothorax, ♀ 37.5 mm. c.l., off Melbourne Beach, Fla.

of propodus. Second pereopod surpassing carpocerite by one-half of length of dactyl to entire propodus. Third pereopod extending to distal end of second or at most surpassing third antennular segment by entire dactyl. Fourth pereopod reaching base of carpocerite or exceeding it by entire length of dactyl. Length of fifth pereopod subequal to that of fourth. Exopods on all pereopods; long ischial and basial spines on first pereopod; rather long basial spine on second pereopod.

**ABDOMEN**

Carinate dorsally from posterior half of fourth somite, posteriorly carina gradually increasing in height to form keel on sixth somite, ending in sharp spine on posterior margin. Dorsolateral sulcus (fig. 22) very narrow, ratio between height of keel and width of sulcus (at about one-third length from posterior margin of somite) varying from about 2.5 to 15.5 (modally 4.5, fig. 23); in some specimens sulcus almost entirely closed. No significant difference in K/S (ratio of the height of the keel to the width of the sulcus) between males and females at any size. Figure 24 shows K/S also has a modal value of 4.5 in size classes to 22 mm. c.l. and in the largest class, whereas K/S mode increases slightly in intermediate classes. Lips sharp, bordering sulcus to near posterior end, there sulcus widens slightly in nearly oval depression. Sixth abdominal somite with three prominent cicatrices on each side, anterior one longest; fifth somite with one cicatrix and series of minute pits anterior to sinus on posterior margin of somite; fourth abdominal somite with similar series of pits dorsal to sinus on posterior margin of somite. Telson unarmed, with deep median sulcus and sharp pointed tip.

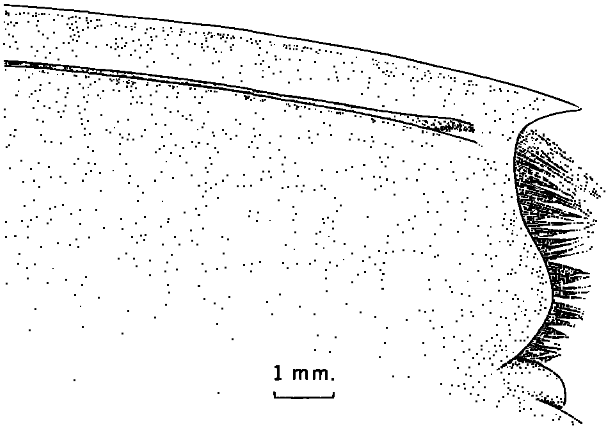

FIGURE 22.—*Penaeus* (*M.*) *duorarum duorarum* Burkenroad. Sixth abdominal somite, posterodorsal portion, ♀ 42.5 mm. c.l., off Long Key, Florida Keys.

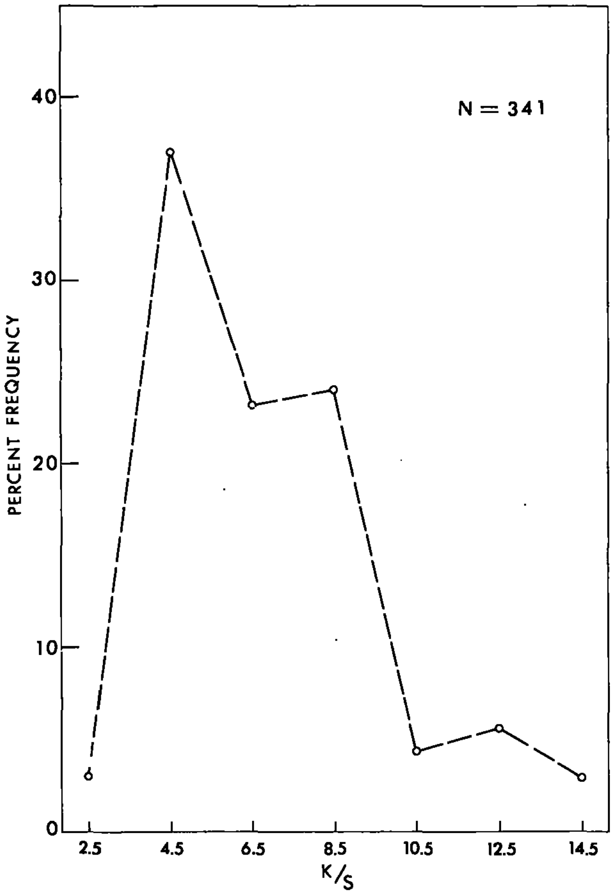

FIGURE 23.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *duorarum duorarum* Burkenroad.

**PETASMA (fig. 25 a–d)**

Ventral costa broadening and turning proximally rather abruptly, with apex adnate to membranous side of ventrolateral lobule, distal portion armed along free margin with a series of 1 to 12, usually 4 to 7, minute spines clearly distinct (even in rather small juveniles 9 mm. c.l., about 42 mm. t.l.), and on attached margin with compact group of 6 to 16 prominent, often curved teeth. Ventrolateral lobule with narrow band of minute spines consisting of single series distally, pair of series proximally followed by three or four longer, closely set series. Distal fold of free margin of lateral lobe small, intruding little inside petasma, unarmed or with few spinules near free edge. Distomedian projections rather thick and relatively short, forming hood overhanging distal portion of ventral costae.

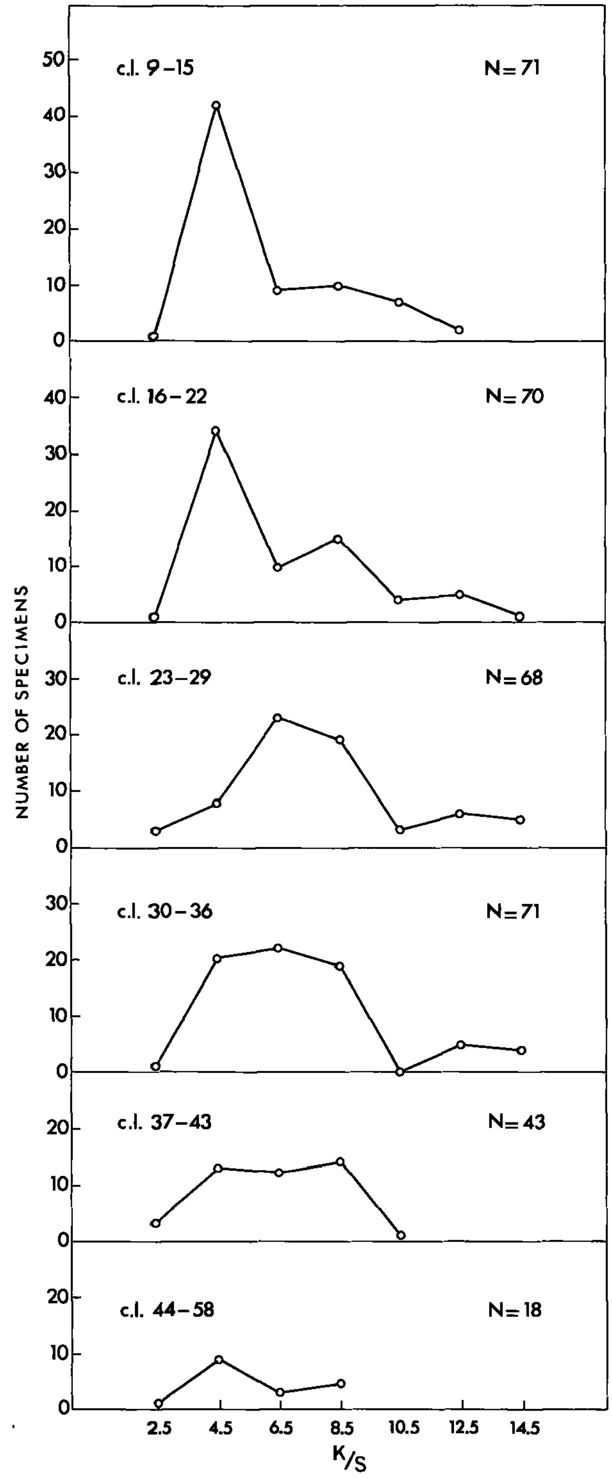

FIGURE 24.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus (M.) duorarum duorarum* Burkenroad of different size classes.

### APPENDIX MASCULINA (fig. 25 e–f)

Broad, its length 1⅒ to 1⅕ maximum width, armed with single row of strong spines along distal two-thirds of concave lateral margin, and with three rows of longer spines along distal and median margins. Anterior surface slightly convex, posterior surface strongly concave, with sharp ridge projecting from median margin.

### THELYCUM (figs. 26 and 27)

Anterior process relatively large, bordered by strongly convex, sharp ridge, surrounding rather strongly concave ventral surface. Posterior process bearing single, prominent, median carina, extending anteriorly toward anterior process. Lateral plates with median appressed border raised as a ridge or lip; rounded or slightly projecting anteromedian corners diverging, leaving median carina exposed. Seminal receptacle dorsal to lateral plates provided with median slitlike opening; latter corresponding to fissure between plates.

### COLOR

Color of *P. d. duorarum* is variable. Specimens from the Tortugas and Campeche commercial grounds are generally pink, and fishermen in those areas refer to this subspecies as "pink shrimp" and "camarón rosado," respectively. Large individuals from the northern Gulf of Mexico frequently have a grayish color, and brownish specimens are also common in inshore waters. Young shrimp are also of a clear gray, whitish, green, or pink coloration, and some are almost colorless. The pink coloration is often deep, and the live-bait shrimp dealers along both coasts of Florida call this subspecies "red shrimp." Williams (1953) described freshly caught juveniles from North Carolina as having the uropods with chromatophores scattered uniformly, reddish brown distally and blue along the creases. The uropods of the subadult are almost transparent, with a light blue margin.

*P. d. duorarum* very often has a reddish or purplish brown spot on each side at the juncture of the third and fourth abdominal somites—hence, the common names pink-spotted, brown-spotted, or simply spotted shrimp. Many specimens, however, lack abdominal spots, and, when present, the spots usually fade and become invisible after death. This shrimp also shows concentrations of chromatophores that darken certain areas, like narrow bands anterior to the posterior margin of the carapace and abdominal somites, as well as

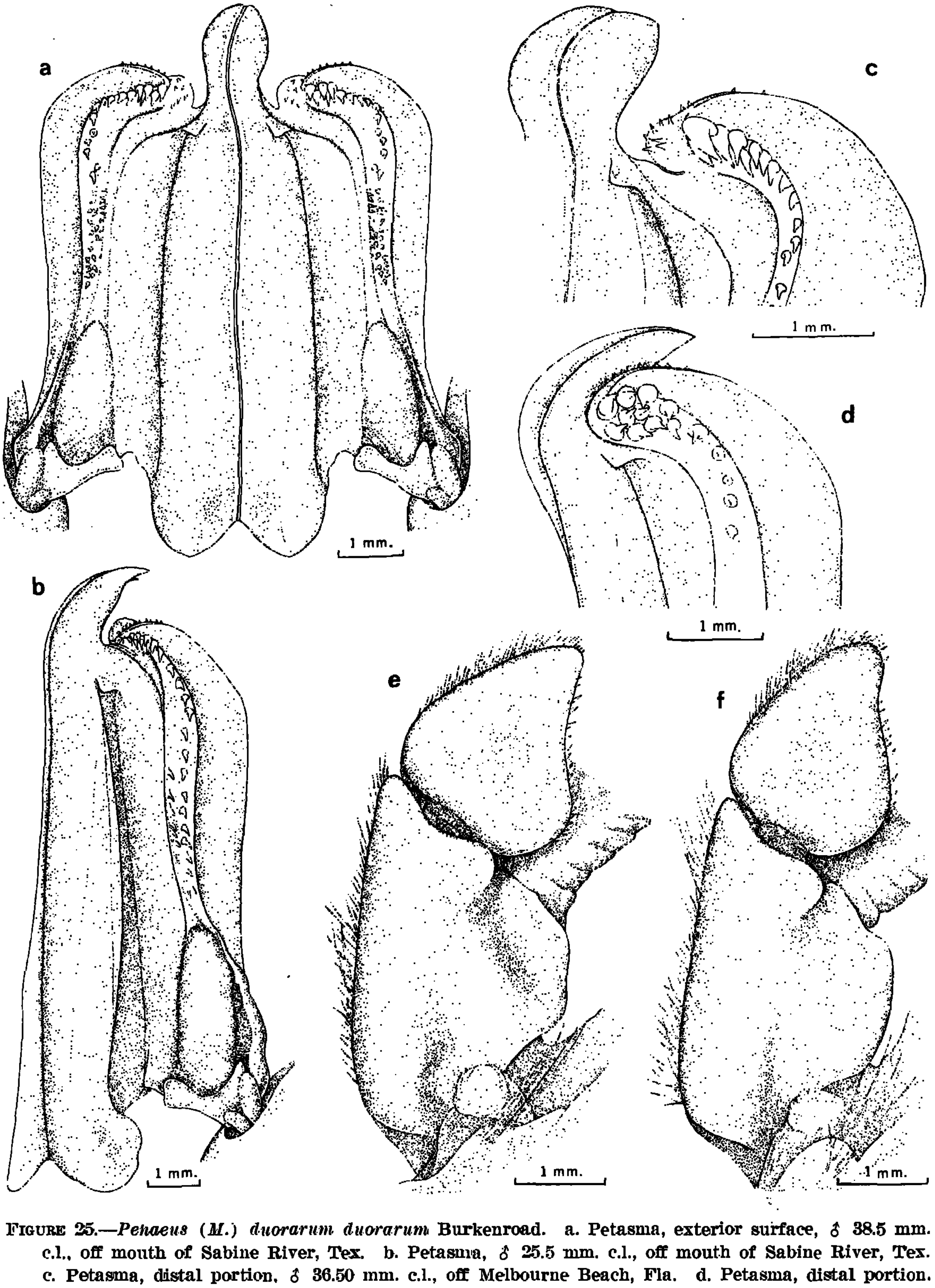

FIGURE 25.—*Penaeus* (*M.*) *duorarum duorarum* Burkenroad. a. Petasma, exterior surface, ♂ 38.5 mm. c.l., off mouth of Sabine River, Tex. b. Petasma, ♂ 25.5 mm. c.l., off mouth of Sabine River, Tex. c. Petasma, distal portion, ♂ 36.50 mm. c.l., off Melbourne Beach, Fla. d. Petasma, distal portion. ♂ 33.5 mm. c.l., off Sebastian, Fla. e. Appendix masculina, ♂ 38.5 mm. c.l., off Edgewater, Fla. f. Appendix masculina, ♂ 39 mm. c.l., off mouth of Sabine River, Tex.

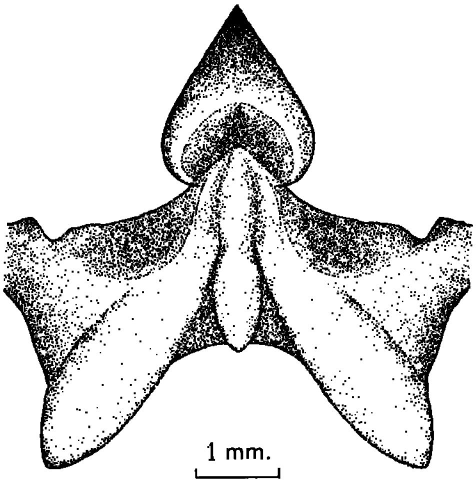

**FIGURE 26.**—*Penaeus (M.) duorarum duorarum* Burkenroad. Median protuberance with horns on posterior margin of sternite XIII, ♀ 47.5 mm. c.l., northwestern Gulf of Mexico.

roundish patches at the center of each pleuron. Gunter and Hall (1963) described the pink shrimp as having a saddle-shaped mark extending from the prominent abdominal spot forward and diagonally across the second abdominal somite and over the posterior end in the spot on the third somite.

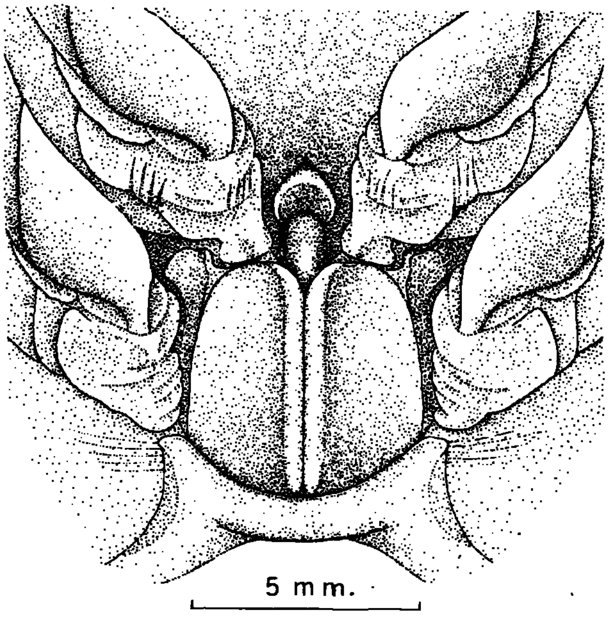

**FIGURE 27.**—*Penaeus (M.) duorarum duorarum* Burkenroad. Thelycum, ♀ 38 mm. c.l., Sanibel grounds, Fla.

## Distribution and Morphological Variations

The range of *P. d. duorarum* extends from lower Chesapeake Bay southward along the Coast to the Florida Keys and Gulf of Mexico. In the Gulf it ranges from the Tortugas Islands along the Gulf Coast of the United States and through the coastal waters of Mexico to Cape Catoche and south to Isla Mujeres. It is also found in the Bermuda Islands (fig. 28). This paper carries the first report of pink shrimp from the northern coast of Yucatán and beyond Cape Catoche.

The densest populations of pink shrimp are off southwestern Florida and in the southeastern portion of Golfo de Campeche. The Gulf of Mexico, thus, is considered the center of distribution of the subspecies.

The greatest concentrations of pink shrimp are between 6 and 20 fm. but in some localities pink shrimp are abundant at depths of as much as 35 fm. A few specimens were collected at 180 fm. (*Silver Bay* Sta. 3710) off Cape Kennedy, Fla., and it has been reported (Anonymous, 1961) that catches of "*P. duorarum*" were taken at 150 to 200 fm. off the western edge of the Great Bahama Bank. These shrimp could have been either *P. d. duorarum* or *P. d. notialis* because which of the two subspecies occupies the area is not known.

*P. d. duorarum* shows some degree of variation throughout its range: the keel–dorsolateral sulcus ratio ranges rather widely, the breadth of the adrostral sulcus varies, the number of external spines at the distal end of the ventral costa of the petasma varies considerably, and the distal fold of the petasma may or may not be armed with submarginal spinules. None of the variations, however, are restricted to portions of the range.

## Relationships

*P. duorarum duorarum* has the dorsolateral sulcus narrower than *P. duorarum notialis* from the Caribbean Sea, the Atlantic Coast of South America, and Africa. Burkenroad (1939) was the first to point out this difference between the two and called the former "Form A," and the latter "Form B." Biometric studies have indicated a statistically significant difference in the ratio (K/S) of K (height of the keel) to S (width of the sulcus) between those populations. In *P. d. notialis* from the southern region, K/S varies from about 0.25 to 3, modally 1.75 (fig. 34). Overlapping is so

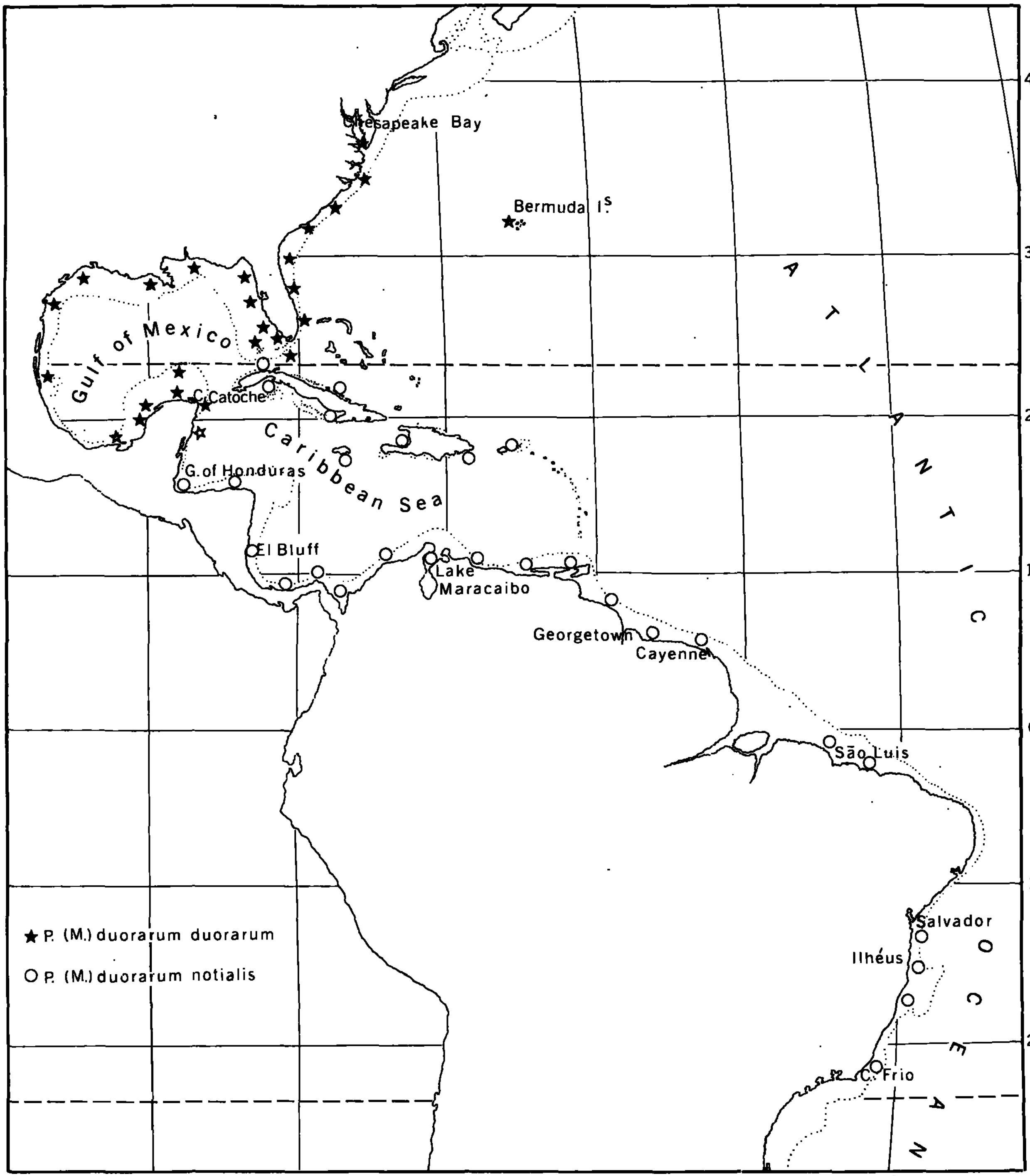

FIGURE 28.—Distribution of *Penaeus* (*M.*) *duorarum duorarum* Burkenroad and *Penaeus* (*M.*) *duorarum notialis* Pérez Farfante.

small that I consider each population to represent a geographical subspecies; thus, the name *P. duorarum duorarum* applies to the typical shrimp (Pérez Farfante, 1967). The two subspecies also differ in the length of the third pereopod, which is proportionately shorter in *P. d. duorarum* than in *P. d. notialis.*

Adult *P. d. duorarum* can be separated readily from the closely related *P. a. aztecus* and *P. brasiliensis.* Females may be recognized by the undivided median carina on the posterior process and the slightly divergent anteromedian corners of the lateral plates. Males may be distinguished by the shape, the external spination, and the compact group of very large, pointed teeth of the ventral costa; the small, and either plain or sparsely armed distal fold of the petasma, and also by the appendix masculina, which is stubby and broader at the base than in *P. a. aztecus* and *P. brasiliensis.* The shape of the ventral costa, which I recognized as a diagnostic character for the first time, is a striking feature by which the grooved species of *Penaeus* from the western Atlantic and the Gulf of Mexico may be distinguished.

*P. d. duorarum* also can be separated from *P. a. aztecus* by its comparatively higher keel and narrower dorsolateral sulcus; as stated above, the ratio K/S in the former is usually over 3 (fig. 23); in only about 5 percent of my sample was K/S smaller. Pink shrimp also have a higher rostrum which is usually straight rather than sinuous; the shape of the rostrum varies, however, and occasionally specimens of *P. d. duorarum* have the tip of the rostrum upturned (fig. 20b), and some *P. a. aztecus* have a straight rostrum (fig. 39b). In addition, pink shrimp have a proportionately shorter rostrum than *P. a. aztecus*, the ratio $\frac{\text{r.l.}}{\text{c.l.}}$ varying from a maximum of 0.75 in the young to about 0.35 in individuals of 50 mm. c.l.; the rostrum reaching to the base of the thickened portion of the lateral antennular flagellum in the young and to the distal end of the first antennular segment in specimens of 50 mm. c.l. The rostrum provides a useful but not an entirely reliable character for separating the two subspecies.

The third pereopod is stouter and much shorter in *P. d. duorarum* than in *P. a. aztecus*, reaching only to the distal end of the second and at most exceeding the third antennular segment by the entire dactyl. The merus and, particularly, the carpus (fig. 29) are responsible for the shorter length in *P. d. duorarum*, for the differences in the lengths of the other podomeres of the third pereopod are small (table 3). Tables 1 and 2 show the lengths of the five distal podomeres (dactyl to ischium) of the third maxilliped and of the first pereopod for three carapace-length intervals in *P. a. aztecus*, *P. d. duorarum*, and *P. brasiliensis;* no significant differences in these characters are evident. Another difference between the pink and brown shrimps is the ratio between the lengths of the carapace and abdomen, adult *P. d. duorarum* has a shorter abdomen.

The dark-colored spot on each side between the third and fourth abdominal somites is generally characteristic of *P. d. duorarum;* but many specimens lack abdominal spots, and similar spots are present not only in the other subspecies of *P. duorarum* from the Antilles and Central and South America, but also in *P. brasiliensis* and occasionally in *P. a. aztecus.* Throughout much of its range, *P. d. duorarum* lives in close proximity with *P. a. aztecus*, and the presence of abdominal spots cannot be used reliably to separate the two

TABLE 1.—*Ranges of lengths of distal five podomeres of third maxilliped in* P. a. aztecus, P. d. duorarum, *and* P. brasiliensis *of indicated intervals of carapace length*

[Based upon a minimum of 30 specimens for each subspecies and species]

| Carapace length in mm. | Dactyl | | | Propodus | | | Carpus | | | Merus | | | Ischium | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. |
| | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* |
| 20.0–30.0: | | | | | | | | | | | | | | | |
| Minimum | 2.0 | 2.0 | 2.0 | 3.0 | 3.0 | 3.0 | 4.5 | 4.5 | 4.5 | 5.0 | 5.0 | 5.0 | 5.5 | 6.5 | 5.5 |
| Maximum | 3.0 | 3.0 | 3.0 | 4.5 | 4.5 | 4.5 | 6.0 | 6.0 | 6.0 | 6.5 | 6.5 | 6.5 | 8.0 | 8.0 | 8.0 |
| 30.1–40.0: | | | | | | | | | | | | | | | |
| Minimum | 3.0 | 3.0 | 3.0 | 4.5 | 4.5 | 4.5 | 6.0 | 6.0 | 6.0 | 6.5 | 6.5 | 6.5 | 8.0 | 8.0 | 8.0 |
| Maximum | 3.5 | 3.5 | 3.5 | 5.5 | 5.5 | 5.5 | 8.5 | 8.5 | 8.5 | 9.0 | 8.5 | 8.5 | 11.0 | 11.0 | 11.0 |
| 40.1–50.0: | | | | | | | | | | | | | | | |
| Minimum | 3.5 | 3.5 | 3.5 | 5.5 | 5.5 | 5.5 | 8.5 | 8.5 | 8.5 | 9.0 | 8.5 | 8.5 | 11.0 | 11.0 | 11.0 |
| Maximum | 4.0 | 4.0 | 4.0 | 7.0 | 6.5 | 6.5 | 9.5 | 9.5 | 9.5 | 11.5 | 11.5 | 10.5 | 14.5 | 14.0 | 14.0 |

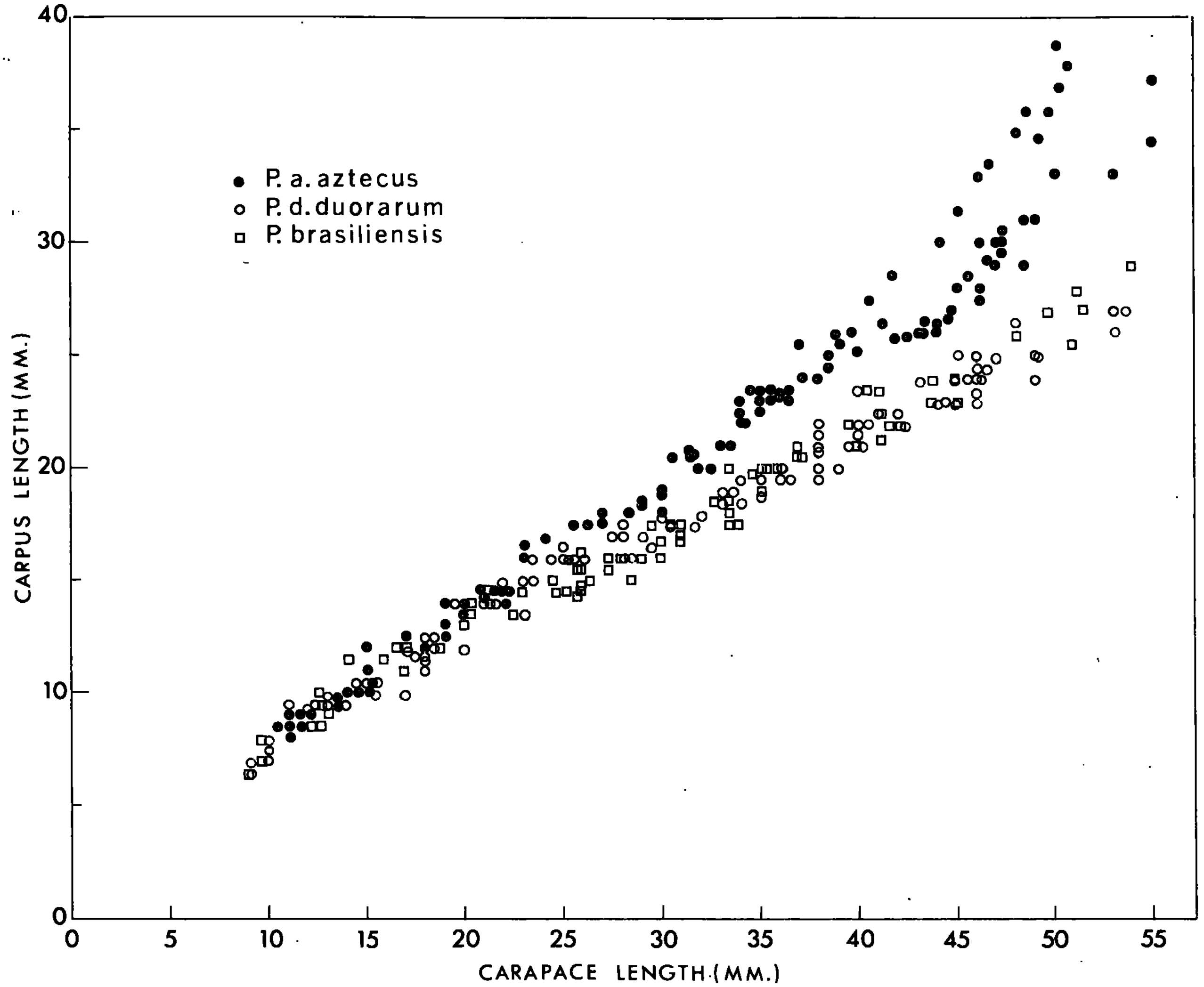

FIGURE 29.—Carpus length-carapace length relation in *Penaeus (M.) aztecus aztecus* Ives, *Penaeus (M.) duorarum duorarum* Burkenroad, and *Penaeus (M.) brasiliensis* Lat.

TABLE 2.—*Ranges of lengths of distal five podomeres of first pereopod in* P. a. aztecus, P. d. duorarum, *and* P. brasiliensis *of indicated intervals of carapace length*

[Based upon a minimum of 30 specimens for each subspecies and species]

| Carapace length in mm. | Dactyl | | | Propodus | | | Carpus | | | Merus | | | Ischium | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. |
| | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* |
| 20.0–30.0: | | | | | | | | | | | | | | | |
| Minimum | 3.0 | 3.0 | 3.0 | 5.0 | 4.5 | 4.5 | 5.0 | 5.0 | 5.0 | 5.0 | 5.0 | 5.0 | 3.5 | 3.5 | 3.5 |
| Maximum | 4.0 | 4.0 | 4.0 | 6.5 | 6.5 | 6.0 | 6.5 | 6.5 | 6.0 | 7.0 | 7.0 | 6.5 | 5.0 | 5.0 | 4.5 |
| 30.1–40.0: | | | | | | | | | | | | | | | |
| Minimum | 4.0 | 4.0 | 4.0 | 6.5 | 6.5 | 6.0 | 6.5 | 6.5 | 6.0 | 7.0 | 7.0 | 6.5 | 5.0 | 5.0 | 4.5 |
| Maximum | 5.5 | 5.5 | 5.0 | 8.5 | 8.5 | 7.5 | 8.5 | 8.5 | 8.0 | 8.5 | 8.5 | 8.0 | 6.0 | 6.0 | 5.5 |
| 40.1–50.0: | | | | | | | | | | | | | | | |
| Minimum | 5.5 | 5.5 | 5.0 | 8.5 | 8.5 | 7.5 | 8.5 | 8.5 | 8.0 | 8.5 | 8.5 | 8.0 | 6.0 | 6.0 | 5.5 |
| Maximum | 7.0 | 7.0 | 6.0 | 11.0 | 11.0 | 9.5 | 11.0 | 11.0 | 10.0 | 11.0 | 11.0 | 10.0 | 8.0 | 8.0 | 7.0 |

**Table 3.**—*Ranges of lengths of distal five podomeres of third pereopod in* P. a. aztecus, P. d. duorarum, *and* P. brasiliensis *of indicated intervals of carapace length*

[Based upon a minimum of 30 specimens for each subspecies and species]

| Carapace length in mm. | Dactyl | | | Propodus | | | Carpus | | | Merus | | | Ischium | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. | P.a.a. | P.d.d. | P.b. |
| | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* | *Mm.* |
| 20.0–30.0: | | | | | | | | | | | | | | | |
| Minimum | 3.5 | 3.0 | 3.0 | 6.5 | 6.0 | 6.0 | 14.5 | 12.0 | 13.5 | 8.5 | 7.0 | 8.0 | 4.5 | 4.5 | 4.5 |
| Maximum | 4.5 | 4.0 | 4.0 | 8.5 | 8.0 | 8.0 | 19.0 | 17.5 | 17.5 | 12.0 | 11.0 | 11.0 | 6.0 | 6.0 | 6.0 |
| 30.1–40.0: | | | | | | | | | | | | | | | |
| Minimum | 4.5 | 4.0 | 4.0 | 8.5 | 8.0 | 8.0 | 18.0 | 17.5 | 16.0 | 11.5 | 11.0 | 10.5 | 6.0 | 6.0 | 6.0 |
| Maximum | 5.5 | 5.0 | 5.0 | 10.5 | 9.5 | 9.5 | 26.0 | 22.0 | 22.0 | 15.5 | 13.0 | 13.5 | 8.0 | 8.0 | 8.0 |
| 40.1–50.0: | | | | | | | | | | | | | | | |
| Minimum | 5.5 | 5.0 | 5.0 | 10.5 | 9.5 | 9.5 | 25.0 | 21.0 | 21.0 | 15.0 | 13.0 | 13.5 | 8.0 | 8.0 | 8.0 |
| Maximum | 7.0 | 6.0 | 6.0 | 14.0 | 13.0 | 13.0 | 39.0 | 26.5 | 26.5 | 19.5 | 16.5 | 16.5 | 9.5 | 9.0 | 9.0 |

subspecies, as has been done to identify freshly caught specimens.

Juveniles of the grooved *Penaeus* from the western Atlantic and the Gulf of Mexico are difficult to identify. A number of characters, however, allow the separation of those of *P. d. duorarum* from most of those of *P. a. aztecus*. The former have a narrower dorsolateral sulcus, usually a shorter rostrum, a stouter body, and often external genitalia that are better developed than those of *P. a. aztecus* at the same length. In addition, male juveniles of *P. d. duorarum* may be separated from those of *P. a. aztecus* by the ridge on sternite XIV which is higher and pointed anteriorly (fig. 30). Being usually better developed than males of *P. a. aztecus*, they also have the petasmal endopod larger at the same carapace length. At 11 mm. c.l., 51 mm. t.l.—occasionally at 9 mm. c.l., 42 mm. t.l.—the petasma frequently has spines on the distal margin of the ventral costa. Small females of pink shrimp may be distinguished by characters of the thelycum. At 10 mm. c.l., 47 mm. t.l., they lack a knob on the midline at the posterior margin of sternite XIII, whereas brown shrimp of comparable length possess such a knob; and at 12 mm. c.l., 55 mm. t.l., the posterior margin of sternite XIII in the pink shrimp is smooth, whereas that of the brown shrimp bears a small spine projecting posteriorly. Finally, in *P. d. duorarum* the median carina is simple, whereas in *P. a. aztecus* of at least 14 mm. c.l., 65 mm. t.l., it has two anterior arms.

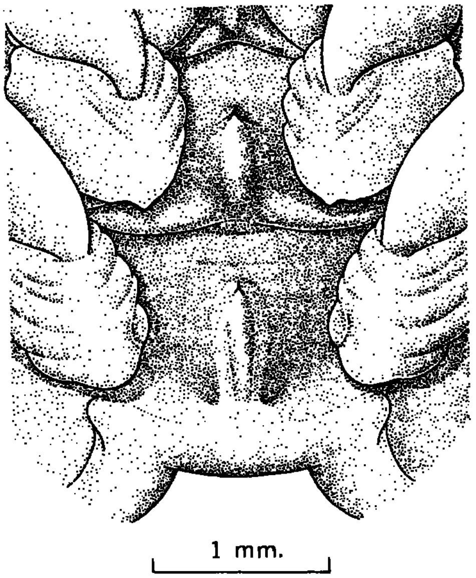

**Figure 30.**—*Penaeus* (*M.*) *duorarum duorarum* Burkenroad. Sternites XIII and XIV, ♂ 10 mm. c.l., Cat Island, La.

Juveniles of *P. d. duorarum* can often be distinguished from those of *P. brasiliensis* by having the adrostral carina markedly convex dorsally on the posterior two-thirds of the rostrum, rather than straight along the entire length of the rostrum. This character varies, however, and the variations in its shape seem to intergrade with those shown by *P. brasiliensis*. Differences in the external genitalia are discussed under the latter species.

## Reproduction

### SUBADULT STAGE-SEXUAL MATURITY

In males, I found the petasmal endopods to be first joined at 14 mm. c.l., 65 mm. t.l. This length seems to be the smallest at which copulation can be carried out by male pink shrimp. The petasma, however, can remain unjoined to 19 mm. c.l., 86 mm. t.l.; thus, males attain the subadult stage within the range of 14 to 20 mm. c.l. Small males 8 mm. c.l., 34 mm. t.l., were found with developed spermatophores within the terminal ampullae.

Females are considered subadults when the thelycum is sufficiently developed to permit impregnation; in the grooved *Penaeus* this occurs when median borders of lateral plates meet. The minimum length at which I found females with a functional thelycum is 15 mm. c.l., 69 mm. t.l., but in some individuals the lateral plates do not become contiguous until the shrimp attain 20 mm. c.l., 89 mm. t.l. Therefore, pink shrimp females attain the subadult stage within the range of 15 to 20 mm. c.l., 69 to 89 mm. t.l. The minimum length at which they have been found with well-developed ovaries is 92 mm. t.l.; ripe females of this length were reported by Eldred et al. (1961) off Tampa Bay, Fla. This size is larger than that at which females can be first impregnated.

Eldred (1958) discussed the statement by Burkenroad (1939) that the smallest impregnated females of *P. duorarum* he found were 23 mm. c.l. and the smallest males with joined petasmal endopods were 15 mm. c.l. The smallest impregnated females she had found in Florida waters were considerably larger (31 mm. c.l.), and suggested that Burkenroad (who did not mention locality) could have referred to *P. duorarum* from the Caribbean Sea, that is to say, to *P. d. notialis*. Individuals of the latter subspecies, however, do not seem to attain the subadult stage at smaller size than do those of *P. d. duorarum*. Whatever the locality of Burkenroad's specimens, the discrepancy was caused by a difference in technique—Burkenroad measured the length of the carapace from postorbital margin to posterior margin of carapace (see Burkenroad, 1936) while Eldred included the rostrum. Addition of the length of the rostrum to Burkenroad's measurements greatly reduces the discrepancy.

### COPULATION

Copulation in *P. d. duorarum* seems to take place (as in all *Penaeus* with a complicated thelycum) between a hard-shelled male and a soft-shelled female soon after the female molts. The reasons for this assumption are many: for transfer of the spermatophores into the thelycum the petasma must have its two valves firmly joined (soft newly molted males have the petasma unjoined or partially joined); only hard-shelled males have been seen with extruding spermatophores; females kept in aquariums were apparently impregnated shortly after molting while in soft-shelled condition, and their exoskeletons carried the spermatophores to the following ecdysis; finally, even in live specimens, it is difficult to open the thelycum of hard-shelled females (Eldred, 1958).

Copulation takes place several times during the growth and development of the females and is not directly associated with maturation and spawning. This conclusion is based on the facts that spermatophores are cast off at each ecdysis and impregnated females are found with ovaries in different stages of development, from undeveloped to ripe.

Impregnated females of *P. d. duorarum* carry the spermatophores inside the seminal receptacle and can usually be detected by the strongly convex shape of the lateral plates of the thelyca. The lateral plates may remain convex after spawning, however, and, thus, their bulging appearance cannot be taken as a certain indication of impregnation.

There seems to be evidence that offshore *P. d. duorarum* mate throughout the year; in the Tortugas area, Ingle et al. (1959) found the largest percentage of impregnated females in May and June, but also some in all months of the year.

### OVARY DEVELOPMENT

In *P. d. duorarum*, as in all its congeners, the ovaries extend from the anterior end of the cephalothorax to the posterior end of the abdomen. Each ovary consists of one anterior lobe and six to eight lateral lobes in the cephalothorax and one long lobe in the abdomen. The size, color, and texture of the ovaries vary with the degree of maturity. The development of the ovary in *P. d. duorarum* has been studied by Cummings (1961), who identified the following stages:

1. Undeveloped. Ovaries very slender, translucent, flaccid, and invisible through the exoskeleton. Ova transparent, small, modal size less than 0.137 mm.
2. Developing. Ovaries still flaccid, but larger, opaque, white to pale olive-buff. Modal size of ova 0.137 to 0.274 mm.
3. Nearly ripe. Ovaries larger, relatively light bluish green at the beginning and darker at the end, somewhat turgid, and visible throughout the exoskeleton. Modal size of ova 0.274 to 0.342 mm.
4. Ripe. Ovaries dark grayish green, very similar in appearance to the previous stage from which they can be distinguished only microscopically by the presence around the nucleus of a peripheral layer of rodlike bodies with apices directed toward the center of the ova. According to Cummings, the modal size of the ova is slightly less than 0.37 mm. Dobkin (1961), however, reported that eggs spawned at the laboratory measured 0.31 to 0.33 mm., and Eldred et al. (1965) found that eggs

ranged from about 0.23 to 0.33 mm. in diameter.

5. Spent. Ovaries are flaccid and their color fades, becoming milky as the regression proceeds.

Eggs of pink shrimp, like those of other *Penaeus*, are demersal. According to Dobkin (1961), "eggs are yellow brown in color and opaque, although when light is reflected in a certain way, the chorion shows the blue hue reported by Pearson (1939) for the eggs of *P. setiferus*."

### SPAWNING

Spawning takes place in oceanic waters at 2 to 26 fm. and probably at greater depths also. In laboratory experiments by Ewald (1965b) spawning occurred in the early morning.

Field work by Cummings (1961), Tabb, Dubrow, and Jones (1962), and Jones et al. (1964) gave some indications that on the Tortugas grounds spawning continues throughout the year. Evidence is also strong that spawning is more intense during spring, summer, and fall (Ingle et al., 1959; Cummings, 1961; Jones et al., 1964). On the basis of analysis of fishery statistics Kutkhun (1962) indicated two peaks of spawning, one in the spring and the other in the summer. Farther north spawning is thought to be restricted to certain months; Joyce and Eldred (1966) stated that at the St. Petersburg and St. Augustine latitudes in Florida, spawning does not begin until early spring, and Williams (1955a, 1965) reported that in North Carolina postlarvae enter inshore water only from May to November.

The northernmost breeding population of *P. d. duorarum* seems to be that off North Carolina where Burkenroad (1949), Broad (1950), and Williams (1955a) reported mature females.

In regard to the relation of spawning to water temperature in *P. d. duorarum*, Eldred et al. (1965) stated that rising temperatures seem to be the most important factor inducing spawning, whereas Idyll and Jones (1965) indicated that spawning intensity is affected mostly by absolute temperature and changes in temperature. The minimum temperature at which Jones et al. (1964) found hours-old larvae was 19.6° C. Spawning has been recorded up to 30.1° C. (Eldred et al., 1965) and 30.6° C. (Jones et al., 1964).

*P. d. duorarum* probably spawns more than once as is believed to be true for various other *Penaeus*. This assumption is based on the evidence that large females about 180 mm. t.l. and longer are found with their ovaries in a developing stage, which suggests that preparation for a second spawning was taking place. Cummings (1961) found one ripe female with large ova in addition to a group of undeveloped ova, which also suggests the development of two successive batches of eggs by an individual.

### SEX RATIO

The general ratio of males to females is about 1:1 in inshore populations (Tabb, Dubrow, and Jones, 1962; Eldred et al., 1961; Saloman, 1965). The sex ratio in offshore populations has not been definitely established. Studies by Iversen et al. (1960) on the Tortugas grounds showed that the percentage of females does not increase with size. Kutkuhn (personal communication), however, found that the percentage does increase, and Ingle et al. (1959) and Eldred et al. (1961), on the basis of their sampling in a restricted area on the same grounds, also found a predominance of females at greater lengths. Sexes appear to segregate because many samples contain but one sex.

## Postembryonic Development

### LARVAE, POSTLARVAE, AND JUVENILES

By maintaining eggs that had been spawned in the laboratory, Dobkin (1961) ascertained that *P. d. duorarum* goes through five nauplial stages preceding the first protozoea. He also tried to work out the rest of the larval development by assembling stages obtained in plankton tows. This investigation produced a second and a third protozoea and three mysis stages before the postlarvae developed. The studies by Jones et al. (1964) and the rearing experiment by Ewald (1965b) seem to corroborate that pink shrimp pass through 11 larval stages. The larval cycle in the laboratory occurred in a minimum of 15 days, during which time the animal grew from a first nauplius to first postlarva.

Dobkin (1961) described the larval stages of *P. d. duorarum* and found them slightly larger than, and different from, those of *P. setiferus*. Some larval specialists question the validity of the diagnostic characters given, maintaining that observable distinguishing features between the corresponding larvae of the two shrimps have not been found. First and second postlarvae were closely similar to those of *P. setiferus* and had about the same size range. In *P. d. duorarum* first postlarvae ranged from 3.8 to 4.8 mm. t.l. (Ewald, 1965b, obtained somewhat smaller first postlarvae, 2.9 to 4.6 mm. t.l.), the second 4.7 to 6.6 mm. In the first postlarva, however, the supra-orbital spine was almost always absent in *P. d. duorarum* but still present, although reduced, in *P. setiferus*. The first ventral teeth appeared when the number of dorsal teeth had increased to 7, at about 10 to 11 mm. t.l.; postlarvae with 8 to 10 dorsal and 2 ventral teeth were 12.5 to 13.7 mm. long. The variation in length of the postlarvae within a single dentition stage has been corroborated by Tabb, Dubrow, and Jones (1962) in the population of Florida Bay. Pink shrimp having six dorsal and no ventral rostral teeth had a carapace from 1.7 to 2.3 mm. long; the relation of length to dentition is most variable in the seven-to-nine tooth stages when the ventral teeth are being formed.

Postlarvae of *P. d. duorarum* under 12 mm. t.l. were distinguished by Williams (1959) from those of *P. setiferus* and *P. a. aztecus* (see under the latter subspecies).

Juvenile *P. d. duorarum* 18 mm. t.l. have shallow but distinctly long adrostral sulci and at 20 mm. t.l. the sulci are well developed. This character allows for a rapid separation of early juveniles of pink shrimp from those of the nongrooved *P. setiferus* and *P. schmitti.*

It is difficult to differentiate between the sexes in small specimens but, at a minimum of about 20 mm. t.l., males and females can be distinguished by the shape and position of the endopods of the first pair of pleopods. In the male the endopod is located more proximally on the basis and is a little longer than in the female. Small males can also be distinguished by the ridge on the midline of sternite XIV (fig. 31a); in females sternite XIV is drawn ventrally to a median point (fig. 31b). Males 11 mm. c.l., 51 mm. t.l., with the petasmal endopods still unjoined, usually have the ventral costa with minute distomarginal spines and a few teeth near the apex. (See also under Relationships.)

## GROWTH

A number of studies on growth of *P. d. duorarum* at various phases of its life cycle have been conducted. Among those concerned with larval development, that of Ewald (1965b) is the most complete. In the laboratory the larval phase was completed in 15 to 25 days, during which time the animals grew from a first nauplius (about 0.4 mm. t.l.) to a first postlarva (2.9 to 4.6 mm. t.l.). Ewald also found in the laboratory that specimens from 6.9 to 9.4 mm. t.l. grew from 0.35 to 0.51 mm. t.l. per day for 25 days.

There are various estimates of growth rate in juvenile and subadult pink shrimp. Tabb, Dubrow, and Jones (1962), in length-frequency studies of shrimp of northern Florida Bay, found that individuals of 6 mm. average c.l. increased at a monthly rate of 2 mm. average c.l., and that the rate increased to a maximum of 3 to 4 mm. monthly until an average size of 20 mm. c.l. was reached. Through mark-recapture studies, Costello and Allen (1960) estimated that pink shrimp 16.7 mm. mean c.l. in Florida Bay and adjacent waters grew at a rate of 3.5 mm. mean c.l. per month. Kutkuhn

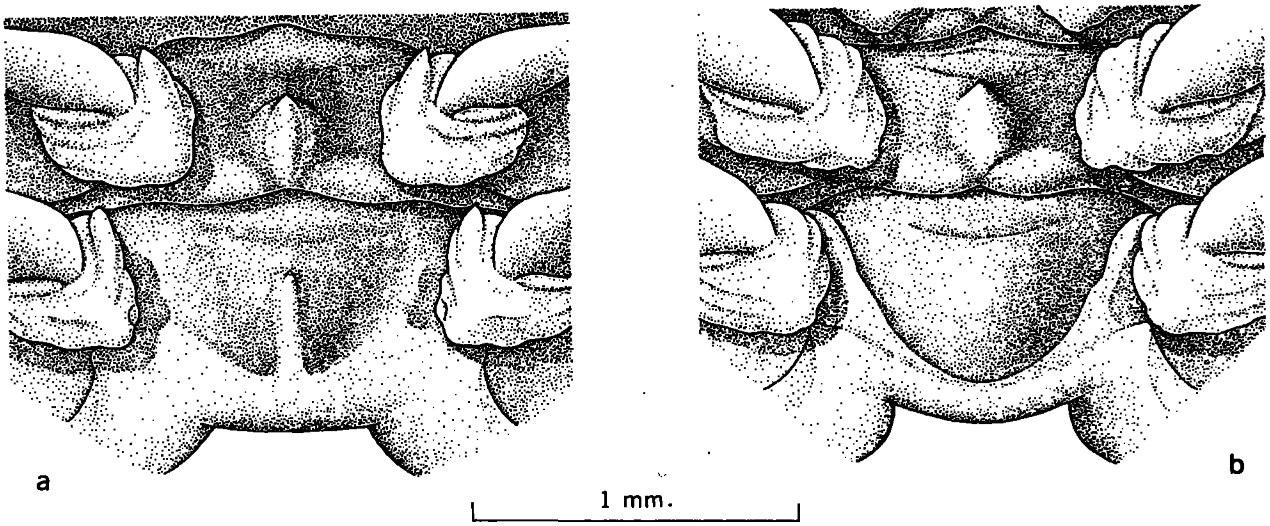

FIGURE 31.—*Penaeus (M.) duorarum duorarum* Burkenroad. a. Sternites XIII and XIV, ♂ 5.5 mm. c.l., Tampa Bay, Fla. b. Sternites XIII and XIV, ♀ 5 mm. c.l., Tampa Bay, Fla.

(1966b), on the basis of a mark-recapture experiment, estimated that in the Tortugas area shrimp 17.9 to 20.2 mm. c.l., 84.2 to 94.1 mm. t.l., at the beginning of the experiment grew an average of about 3.4 mm. t.l. per week. He also demonstrated that in shrimp above 30 mm. c.l. weight increases rapidly in relation to increase in carapace length. Williams (1955a), using upper extremes of size distribution, calculated that juvenile shrimp in North Carolina grew at a mean rate of 52 mm. t.l. in July, and 7.5 mm. t.l. per month in winter and early spring.

Growth rate in adult pink shrimp has attracted the attention of a number of investigators. Iversen and Idyll (1960) studied the shrimp on the Tortugas grounds and showed that females 31 mm. c.l. grew an average of about 2 mm. c.l. per month, and males 26 mm. c.l. grew an average of about 1 mm. c.l. per month. Growth studies on the same grounds by Iversen and Jones (1961) indicated, for both sexes combined, an average monthly increase of 1.8 mm. c.l. in "small shrimp" (25 mm. c.l.), 1 mm. c.l. in "medium shrimp" (33 mm. c.l.), and very little (0.5 mm. c.l.) or no growth in "large shrimp" (40 mm. c.l.).

### SEX DIFFERENCES IN SIZE

The females of *P. d. duorarum* reach a maximum length of 280 mm. t.l.; a truly giant specimen of this size from the Campeche fishing grounds is in the collection of the St. Petersburg Marine Laboratory, Fla. The males are usually much smaller, although Thomas J. Costello (personal communication) measured one of 269 mm. t.l.

In North Carolina, Williams (1955a) observed that the size disparity between sexes in *P. d. duorarum* is statistically significant at mean total length slightly exceeding 100 mm. [no less than 21 mm. c.l.]. In Tampa Bay, Saloman (1968) found that small females with a mean carapace length of 13.7 mm. were larger than the juvenile males collected with them. The disparity in length between larger females and males has been reported for many localities by various authors. Because the females are larger than the males, a sample containing both sexes produces a bimodal distribution. On the average, the large males and females are found at the greater depths throughout the subspecies range.

## Ecology

### FOOD

*P. d. duorarum* is mostly a bottom and a nocturnal feeder. Omnivorous like other penaeids, it ingests algae and fragments of higher plants, as well as sand, mud, and organic debris. It also feeds on a larger variety of animals, including foraminiferans, hydroids, nematodes, mollusks, polychaetes, crustaceans, tunicates, and fish larvae (Williams, 1955a, 1958; Flint, 1956; Woodburn et al., 1957; Eldred et al., 1961).

### SUBSTRATE

*P. d. duorarum* prefers rather firm bottoms of mud and silt with coral sand containing a mixture of mollusk shells, as has been shown by investigations in the Gulf of Mexico by Springer and Bullis (1954), Hildebrand (1954, 1955) and Gunter (1956), and by laboratory experiments by Williams (1958). Pink shrimp also live on hard sand bottoms. The distribution of the subspecies in the northern Gulf of Mexico may be explained by its preference for firm bottoms. Whereas it is scarce on the soft muddy bottoms from Mississippi to middle Texas, it is very abundant on the firmer bottoms off the Tortugas Islands and the southeastern part of the Golfo de Campeche. Its presence north of Ciudad Campeche, Mexico, where *P. setiferus* is absent, also could be attributed to the firm bottoms there.

### DIEL CYCLE

Adult pink shrimp are nocturnal and are fished at night in all areas. They seem, however, to be somewhat active on cloudy days and during days when the water is turbid (Hildebrand, 1955; Eldred et al., 1961). Several observations indicate that they normally remain buried during daytime.

Larvae seem to be as nocturnal as adults. Jones et al. (1964) made by far the largest catches after dark and concluded that larvae move vertically, gathering near the surface at night and descending in the water during the day. Postlarvae, however, apparently are active day and night, because Eldred et al. (1965) captured 54 percent of the postlarvae taken over 24 hours in the daytime in Tampa Bay.

Juveniles and subadults seem to be mostly nocturnal but capable of diurnal activity. Higman (1952) and Tabb, Dubrow, and Jones (1962) collected large numbers of specimens leaving estuaries in southern Florida at night but few or none during the day. In Tampa Bay, Saloman (1968) made larger catches during darkness, and Joyce (1965) noted that his sampling in northeast Florida yielded a larger percentage of young *P. d. duorarum* at night, but because of the size composition of sample catches he concluded that the very small shrimp were mainly nocturnal whereas the larger individuals were more diurnal.

In the laboratory, Williams (1958) noted that several groups of shrimp, with mean total length of 50 to 60 mm., were active at night, and, during the day, remained almost or completely hidden in the substrate. In contrast, Eldred et al. (1961) reported that in aquariums, individuals smaller than 55 mm. t.l. were active during the day or when exposed to bright light, whereas large specimens remained buried in the sand. Aaron and Wisby (1964) stated that in their laboratory experiments, more than half of the shrimp, 55 to 105 mm. t.l. "between the leading edge of the blades and the spine of the telson," showed positive phototaxis when exposed to 3.23 lumens per 1 m.$^2$, those 75 mm. showed the greatest. Studies by Fuss and Ogren (1966) indicated that larger shrimp are more sensitive to light than smaller shrimp, although most individuals within the size ranges (80 to 180 mm. t.l.) observed showed a negative photic response: burrowed in the presence of daylight or artificial light. They are of the opinion that light is apparently the most important single factor in shrimp diel activity.

Availability of pink shrimp offshore seems to vary with the phases of the moon. Fishermen say, and many others have observed, that offshore catches show a sharp decrease during the full moon. The activity of shrimp inshore through the lunar cycle has not been clearly determined. Eldred et al. (1965) recorded a higher percentage of postlarvae during the full-moon spring tides. Idyll et al. (1965) are of the opinion that moon phase and speed of ebbing current are two of the more important factors responsible for the variation in the size of the catch of shrimp at the mouth of the estuaries. At Buttonwood Canal, Fla., they consistently obtained higher numbers of shrimp moving on the ebb tide during or near the new and full moon than during the other moon phases. Copeland (1965) reported peak seaward migrations at the time of the full moon, whereas Saloman (1968) caught greater numbers of shrimp during the dark phases of the lunar cycle than during the full moon.

In the laboratory, Aaron and Wisby (1964) found evidence that the moon phase has a significant effect on the activity of shrimp; they observed that maximum photoactivation occurred during the full moon, and the minimum during the new moon. Fuss and Ogren (1966), in turn, reported that in aquariums, direct correlations between lunar cycles per se and pink shrimp nocturnal activity were not well defined. Size of animals and light intensity—as Fuss and Ogren have suggested—could be responsible for the differences in behavior in relation to lunar changes.

### MOVEMENTS

The larvae of *P. d. duorarum* move from the spawning sites toward inshore waters and, thus, have the same migratory pattern as the sympatric *Penaeus*. The larvae are thought to be carried by currents, but, as stated earlier, the larvae probably are not entirely passive during their onshore movement.

Larvae develop at sea and the young shrimp arrive in the nursery grounds usually as postlarvae. Postlarval shrimp are predominantly transported inshore by flood tides (Tabb, Dubrow, and Jones, 1962; Copeland and Truitt, 1966; Hughes, 1966). Hughes (1966) stated that the movement of the postlarvae into the nursery areas is apparently effected largely by their passive displacement by the tide. Although most postlarvae reach estuarine waters, some pink shrimp may complete their entire life cycle in oceanic waters. Ingle et al. (1959) and Eldred et al. (1961) have advanced the view that the extensive shallows from Key West, Fla., west through the Marquesas Keys to Rebecca Shoal, are nursery grounds for pink shrimp.

The studies by Williams (1959) in North Carolina, Bearden (1961) in South Carolina, and Tabb, Dubrow, and Jones (1962) in Florida Bay showed that most postlarvae enter the inshore waters at the six-to-seven-rostral-tooth stages, although in Florida Bay a few were at the four-rostral-tooth stage. In Tampa Bay, Eldred et al. (1965) found that the postlarvae arrive when younger—when the rostrum possesses a minimum of two and a mode of four teeth.

The period of postlarval movement of pink shrimp varies with the range of the subspecies. In North Carolina, Williams (1955a, 1965) reported that influx takes place from late May to November. Bearden (1961) showed similar movement in South Carolina. Joyce (1965) on the basis of the presence of individuals 40 mm. t.l. and smaller, concluded that in northeast Florida major inshore movement appears to take place from June through December.

The extensive sampling data from southwest Florida suggest that postlarvae enter inshore water throughout the year, but that peaks of abundance occur, which vary from one year to another. In Florida Bay a large peak was reported from April to June by Tabb, Dubrow, and Jones (1962) and from July through October by Jones et al. (1964). A secondary peak of abundance is known to take place late in the fall or during the winter. In Tampa Bay an extremely large peak was recorded in July by Eldred et al. (1965). In Mississippi, Christmas et al. (1966) found pink shrimp postlarvae from May through December, but only a few before July. In the Aransas Pass, Tex., inlet, Copeland and Truitt (1966) observed a maximum peak of postlarval *P. d. duorarum* in August and September.

Small pink shrimp grow rapidly in the nursery areas and move toward the sea as they approach maturity. They leave mostly on the ebb tides since sample catches are usually much larger then than during flood tides, and largest when the tidal current is strongest. Costello and Allen (1966) estimated that shrimp remain in the estuaries of southwest Florida for a period ranging from about 2 to 6 months.

Hughes (in press) has suggested that the displacement of the postlarvae inshore on flood tides and the emigration of the "juveniles" offshore on ebb tides appear to be effected by the respective responses of the two stages to changes in salinity. Juveniles usually exhibit a positive rheotaxis; however, when the salinity of the water decreases downstream swimming ensues. This ensures that in nature juveniles will swim against the current and, thus, resist displacement in an inshore direction by the flood tide but will swim offshore with the ebb tide. Postlarval shrimp respond to a decrease in salinity by dropping to the substrate; when the salinity increases they become active in the water column. Consequently, postlarvae are moved inshore on the flood tide and evade displacement seaward on the ebb tide.

A number of studies have been carried out in different localities to follow the migration of pink shrimp as they leave the estuaries. Tabb, Dubrow, and Jones (1962) and Idyll et al. (1966) investigated the emigration from the estuaries to Florida Bay. The former authors observed that many shrimp move to the Bay at about 18 to 20 mm. c.l. (about 82 to 90 mm. t.l.) and practically all before attaining a carapace greater than 25 mm. (about 105 mm. t.l.). Idyll et al. (1966) estimated that the monthly mean size of the migrating shrimp ranged from 9.9 mm. c.l. (about 46 mm. t.l.) to 18 mm. c.l., and averaged 14 mm. c.l. (about 65 mm. t.l.). The relative abundance of shrimp moving to Florida Bay fluctuates seasonally. Numbers are greatest in late summer and early fall, and abundance reaches a peak in September. A second peak occurs from January to April. Eldred et al. (1961) in Tampa Bay found that shrimp began their seaward movement at 85 mm. t.l. in April and continued to leave through July. Mass migration to offshore waters did not seem to occur during the fall and winter. Copeland (1965) stated that most shrimp leave through Aransas Pass, Tex., inlet, at 70 to 90 mm. t.l., from April through October. Joyce (1965) gathered evidence that in northeast Florida the young leave the nursery grounds at a length of 85 to 90 mm.

Williams (1955a) in North Carolina observed that pink shrimp that arrive at the nursery grounds in spring grow rapidly and after having reached the subadult stage move back to the ocean, where as young adults they are harvested in late summer and fall. Individuals that overwinter in the estuaries migrate to the sea in May and June and become the object of a spring fishery.

Several investigations have been made to establish the movements of pink shrimp leaving the nursery areas of southwest Florida for the spawning grounds. Costello and Allen (1966) concluded that: (a) some pink shrimp from shallow coastal waters of southwest Florida follow broad migratory routes in moving to offshore grounds; (b) shrimp from each nursery area seem to assume "a distinct pattern of distribution on the offshore grounds," that is, those found in the Tortugas come from shallow waters ranging from northeast to east of the grounds, whereas those taken on the Sanibel grounds are immigrants from the adjacent coastal waters; (c) ranges of the stocks from which the Sanibel and Tortugas populations are derived overlap along the southwest coast of Florida and in the offshore water between the two trawling grounds; (d) shrimp enter the Tortugas grounds from the north, east, and southeast. Furthermore, it seems that the Tortugas shrimp do not migrate to the Sanibel fishing areas, and south Sanibel shrimp seldom migrate to the Tortugas grounds or to the northwest Sanibel grounds. The above conclusions were based on various mark-recapture experiments by Costello and Allen (1960, 1961, 1964, 1966); Iversen and Idyll (1960), Iversen and Jones (1961), and the sampling studies in the area by Ingle et al. (1959), Iversen et al. (1960), and Eldred et al. (1961). The investigation of Iversen et al. (1960) on the size distribution of shrimp suggested that they leave the Tortugas grounds in a northwesterly direction and move toward deeper water.

Evidence suggests that hurricanes markedly influence the movement of shrimp. Massive offshore migration takes place in response to abnormalities brought about by the storms. In 1960 after hurricane "Donna" struck southern Florida, the catches on the Tortugas grounds included a much higher percentage of small individuals, and the average size of shrimp was smaller than in previous years (Eldred et al., 1961). These changes indicated that hurricanes can cause the shrimp to move offshore earlier and at a smaller size than normal. Also, hurricanes in the nursery areas are known to cause high mortality among the young (Tabb, Dubrow, and Jones, 1962).

In contrast to our rather clear understanding of migrations of *P. setiferus*, almost nothing is known about coastal migrations of *P. d. duorarum*. Neither seasonal migrations nor movements in response to temperature changes in the latter have been adequately investigated. Recent data acquired by McCoy and Brown (1967) from release and recapture procedures indicated that pink shrimp migrated southward from Beaufort Inlet, N.C., from May through August; however, the greatest distance traveled was only 193 km. in 5 weeks.

## EFFECTS OF TEMPERATURE

*P. d. duorarum* is the only *Penaeus* that overwinters in the estuaries of North Carolina. There Williams (1955a) found them at 6° C. and suggested that they may survive the severe winter cold by burrowing deeply into the substrate. The laboratory experiments of Williams (1960) showed that *P. d. duorarum* was better able to withstand a combination of low salinity and temperature than *P. a. aztecus*. This discovery may help to explain the occurrence of pink shrimp in the northern inshore waters of North Carolina during the winter and even in those of Virginia, where, according to Van Engel (1965), specimens are taken in almost all months. On the basis of our present knowledge, there is no explanation for the fact that even though the pink shrimp is more tolerant of low temperatures than are white and brown shrimps, the northern limit of its range is some 2°30′ and 3°25′, respectively, south of that of the others; obviously, some factor other than temperature has prevented their spreading farther north.

Local movements of young shrimp in response to sudden changes in temperature have been observed. In southwest Florida, Tabb, Dubrow, and Jones (1962) noted that the shrimp moved out of the shallows to deeper, warmer water during cold periods and returned again as soon as the water began to warm. They indicated that if the descent in temperature occurred gradually, the shrimp seemed to remain in the inshore waters.

Temperature is one of the principal factors governing growth (see above) and survival of pink shrimp as it is known to be for the closely allied *Penaeus*. The maximum temperature at which *P. d. duorarum* has been recorded is 35.5° C., at which Eldred et al. (1961) collected them in Tampa Bay. In general, it seems that the lower temperature limit for pink shrimp activity is about 14° to 16° C. (Williams, 1955a; Fuss and Ogren, 1966). Complete cessation of activity occurs below about 10° C. (Williams, 1955a; Eldred et al., 1961; Fuss and Ogren, 1966). The lowest temperature at which pink shrimp have been found is 3.5° C.; a single specimen was collected in Lower Chesapeake Bay (Thimble Shoal Light) in February (W. A. Van Engel, personal communication).

## EFFECTS OF SALINITY

Larval and early postlarval stages, large subadults, and adults abound in oceanic waters of high salinity. On the Tortugas fishing grounds Iversen et al. (1960) reported bottom salinities (10-15 fm.) of 36.15 p.p.t. to 37.73 p.p.t.

Postlarvae, juveniles, and early subadults live in inshore water within a wide range of salinities. Tabb, Dubrow, and Jones (1962) have recorded salinities of zero to 47 p.p.t. in the nursery areas of south Florida. Joyce (1965) found specimens 80.5 km. up the St. Johns River, Fla., in almost fresh water. Gunter et al. (1964) indicated that salinity seems to be a limiting factor in the abundance of *P. d. duorarum* as well as of *P. setiferus* and *P. a. aztecus*. Their investigations in inshore water adjacent to the Gulf of Mexico showed that pink shrimp were more abundant at salinities of 18 p.p.t. and above, whereas brown shrimp were more abundant in water of 10 to 20 p.p.t. and white shrimp in water of salinity lower than 10 p.p.t.

They also pointed out that the greatest abundance of adult pink shrimp occurs in areas where the salinity is high.

### ENEMIES AND DISEASES

Predation by fishes is very probably the most important cause of natural mortality among pink shrimp, as it is for most *Penaeus*. Several workers have demonstrated that the pink shrimp is an important food for some fishes. Aquatic birds are also possibly among their enemies.

Parasites of the pink shrimp include protozoans, trematodes, cestodes, and nematodes, and even an insect (Sprague, 1950, 1954; Hutton and Eldred, 1958; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959; Hutton, Sogandares-Bernal, and Eldred, 1959; Kruse, 1959; Hutton et al., 1962). The microsporidian *Thelohania duorara* Iversen and Manning causes what is commonly known as "milk" or "cotton" shrimp, because of the opaque whitish discoloration shown by infected individuals.

## Commercial Importance

*P. d. duorarum* is one of the most valuable species of commercial shrimp in the Gulf of Mexico fisheries. The areas of maximum productivity are the Tortugas-Sanibel and Obregón-Campeche grounds. Annual catches from the former are about 8,000,000 kg. (whole weight) and from the latter are even higher. In the Tortugas-Sanibel grounds at least 80 percent of the catches are made during winter-spring, but in the Obregón-Campeche beds pink shrimp production shows little seasonal variation. Throughout the rest of the Gulf region, pink shrimp are taken in moderate quantities in northern Florida and western Texas, but catches in other areas are rather insignificant.

Pink shrimp make up part of the occasional commercial catches made at the southernmost portion of the range, between Isla Contoy and Isla Mujeres, Mexico. They are fished commercially also along the southeastern coast of the United States. Moderate catches are taken off North Carolina and small ones off the other southern Atlantic States.

Lyles (1967) reported that in 1965 landings of pink shrimp in the United States were 19,760,132 kg. (whole weight) which represents about 20 percent of all *Penaeus* shrimp landed in the Gulf and Atlantic States.

## *Penaeus (Melicertus) duorarum notialis* PÉREZ FARFANTE

Figures 32 to 38

Cuba: camarón acaramelado, camarón cocinero, camarón carbonero. Nicaragua: camarón rojo. Venezuela: langostino amarillo, langostino rosado, camarón rosado sin mancha.

*Penaeus brasiliensis:* Miers, 1878: 299, 306 [part]; Ives, 1891: 199 [part]; Rathbun, 1897: 46 [part]; Rathbun, 1901: 100, 101 [part]; Pesta, 1915: 113 [part]; Boone, 1927: 78 [part]; Boone, 1930: 14, 15, 101–105 [part]; Burkenroad, 1934: 88, 93, 94 [part], 109; Schmitt, 1935: 128, 129 [part?]. Not *P. brasiliensis* Lat., 1817.

*Penaeus duorarum:* Burkenroad, 1939 [part, "Form B"]: 29, 31–34, 40–45, figs. 18, 19, 26, 27; Sánchez Roig and Gómez de la Maza, 1951: 113; Pérez Farfante, 1953: 232–234, 236, 237, (238, 241 [part]); Pérez Farfante, 1954a: 97, 98; Pérez Farfante, 1954b: 9, 13, 20, 26–30; Pérez Farfante, 1955: 180; Lindner, 1957: 11, 14, 25, 66, 69–72, 159, 160, 165; Suárez Caabro, 1957: 137; Eldred, 1958: 5, 23; Suárez Caabro, 1958: 5, 7; U.S. Fish and Wildlife Service, 1958a: 11; Holthuis, 1959: 67, 68; Eldred, 1960: 164, 165; Eldred and Hutton, 1960: 91, 98, 101, 106, 108, fig. 7a; Eldred et al., 1961: 87, 90, 91; Pérez Farfante et al., 1961: 18, 22, 33–55, 60, 63; Anonymous, 1962: 56, 1 fig.; Idyll, 1962: 184; Loesch, 1962: 172–177; Rossignol and Repelin, 1962: 157–174; Davant, 1963: 9, 11, 15–17, 31–35, 65, 67, 71–73, 86–91, figs. 6b, 11–14, and bis; Simpson, 1963: 22, 23; Boschi, 1964: 39–41; Ewald, 1964: 10, 20–23, 24, 28, tables [part]; Ewald, 1965a: 29; Ewald, 1965c: 52, 59, 65, 67, 69, 72–74, 80, 81, 83, 84, 86, 87, 91, 93–96, 114, (80, 88–90, 92, 97–99, 113, fig. 13 [part]); Holthuis and Rosa, 1965: 4 [part]; Joyce, 1965: 132, 135, 220, 221; Pericchi López, 1965: 24; da Silva, 1965: 3, 4; Simpson et al., 1965: 77; Williams, 1965: 22, 23; Neiva and Mistakidis, 1966: 5, 6, fig. 11a, b; Croker, 1967: 63, 67, 68, 72–74, 79–81, 84, 87, 98, 110; Instituto de Fomento Nacional, 1967: 5, 8.

*Penaeus duoarum:* Anderson and Lindner, 1945: 306 [part]; Dall, 1957: 142, 226 [part].

*Penaeus duorarum* Burkenroad "var. *cameronensis*" Rossignol and Repelin, 1962: 159.

*Penaeus duorarum notialis* Pérez Farfante, 1967: 94–98, fig. 4a–d; (holotype, ♂, USNM 119132, off Las Piedras, Gulf of Venezuela, 26 fm., October 5, 1965, *Oregon* Sta. 5664, lat. 11°44′ N., long. 70°22′ W.).

### Taxonomic Remarks

Questions have arisen concerning the identity of *P. duorarum* from tropical West Africa. Burkenroad (1939) identified the specimens from that region as *P. duorarum* "Form B," the same as "candied shrimp" from the Caribbean region and the Atlantic Coast of South America. My studies also indicate that the specimens of *P. duorarum* from both regions should be referred to *P. d. notialis*. On the basis of biometric studies Rossignol and Repelin (1962) concluded that there are two different populations of this shrimp in West Africa: one population along the coast of Cameron has shrimp with the third pair of pereopods longer than they are in the other population that ranges along "la côte du Congo et du Sud Gabon." They considered the northern population a different variety and named it "cameronensis." This varietal name does not have priority over *notialis* because under the International Rules of Zoological Nomenclature, a new name published after 1960 as a variety is to be regarded as of infrasubspecific rank. In the eastern Atlantic *P. d. notialis* ranges both west to Cap Blanc and south to Angola beyond the areas considered by Rossignol and Repelin.

### Study Material

For a list of records see Pérez Farfante, 1967. Additional records follow.

**MEXICO**

**Quintana Roo:** 2 ♂, USNM, Punta Nicchehabin, Bahía de la Ascensión, less than ⅓ fm., April 13, 1960, F. C. Daiber, Smithsonian- Bredin Exped. Sta. 65–60.

**COLOMBIA**

1 ♂, USNM, off Punta Broqueles, 400 fm., *Oregon* Sta. 4902, May 28, 1964.

### Diagnosis

Adrostral sulcus broad posteriorly, and long, reaching almost to posterior margin of carapace. Median sulcus long, ending immediately anterior to posterior end of adrostral sulcus, and deep along its entire length. Dorsolateral sulcus broad. Petasma with distal portion of ventral costa broadening and turning proximally rather abruptly, armed with minute spines along free border and with compact group of large teeth on attached border; apex of ventral costa adnate to adjacent wall; distal fold small, unarmed or with few submarginal spinules. Thelycum with apical process relatively large, and with prominent, short, undivided median carina on broad posterior process; carina exposed owing to slight divergence of anteromedian corners of lateral plates.

### Description

**ROSTRUM**

Teeth $\frac{7\text{–}9}{0\text{–}2}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—61, 9/2—30, 8/1—4, 7/2—3, 7/1—1, 9/1—0.33, 7/0—0.66; N=300)+epigastric; position of ventral teeth variable, first tooth situated from well anterior to slightly posterior to last dorsal tooth; rostrum relatively short in larger juveniles and subadults, reaching at most to distal end of antennular peduncle; attaining maximum length in relation to carapace length at 12 to 18 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.75); decreasing progressively with increasing length of shrimp, rostrum reaching distal end of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.40); rostrum straight apically, occasionally upturned, convex proximally; highest portion of blade at level of third dorsal tooth; latter level with anterior margin of carapace; rostrum tip ⅕ to ¼ r.l. Postrostral carina strong, prominent, and uniform in width or slightly wider in anterior half, and long, extending almost to posterior margin of carapace. Median sulcus deep throughout, long, ending near posterior margin of carapace. Adrostral sulcus deep, broad posteriorly, ⅘ to 1½ width of postrostral carina, and rather long, ending $1\frac{1}{11}$ to $1\frac{1}{6}$ c.l. from posterior margin of carapace. Adrostral carina prominent and long, same length as adrostral sulcus.

**CARAPACE (fig. 32)**

Length in proportion to total length smaller in juveniles, increasing abruptly at about subadult stage. Gastrofrontal sulcus broad, extending posteriorly to about one-fifth c.l.; gastrofrontal carina sharp, turning slightly posterodorsally and ending in acute orbital angle anteriorly. Orbito-antennal sulcus wide anteriorly, narrowing posteriorly to below apex of hepatic spine, there widening into base of spine. Gastro-orbital carina high and sharp, occupying posterior ¾ to ⅘ of distance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus 1/5 to 1/4 c.l., ending slightly anterior to midlength of carapace. Hepatic carina 1/5 to 1/4 c.l., sharp, sloping anteroventrally to end 1/15 to 1/20 c.l. from anterior margin of carapace. Antennal spine prominent and acute; hepatic spine pronounced.

### ANTENNULES

Lateral flagellum about three-quarters of length of antennular peduncle, slightly longer and with articles shorter than median flagellum; anterolateral spine sharp; stylocerite acuminate, reaching slightly beyond midlength of first antennular segment. Prosartema reaching distal end of proximal fifth of second antennular segment.

### ANTENNAE

Length of scaphocerite 2½ times maximum width, its length relative to carapace length decreasing slightly with growth; spine reaching distal end of antennular peduncle or to distal end of proximal quarter of thickened portion of dorsal flagellum. Carpocerite 1¼ times longer than wide, reaching distal end of optic peduncle. Antennal flagellum relatively short, about 1⅓ body length.

### THORACIC APPENDAGES

Third maxilliped reaching at least distal one-third of second and, at most, distal end of third antennular segment; longer in larger individuals. Length of dactyl 3/5 to 3/4 that of propodus. First pereopod surpassing carpocerite by half length of dactyl or by entire length of propodus. Second pereopod surpassing carpocerite at least by entire length of propodus and, at most, by one-half length of carpus. Third pereopod exceeding antennular peduncle by one-half length of dactyl or by one-eighth length of carpus. Fourth pereopod surpassing carpocerite by one-half length of dactyl to three-quarters length of propodus. Fifth pereopod subequal in length to fourth. Exopods on all pereopods; long ischial and basial spines on first pereopod; rather long basial spine on second pereopod.

### ABDOMEN

Carinate dorsally from posterior half of fourth somite posteriorly, carina increasing in height progressively from base to keel on sixth somite, there ending in sharp spine on posterior margin. Dorsolateral sulcus characteristically broad (fig. 33), ratio between height of keel and width of sulcus ranging from about 0.25 to 3, modally 1.75 (fig. 34); K/S mode 1.75 in size classes 16 to 36

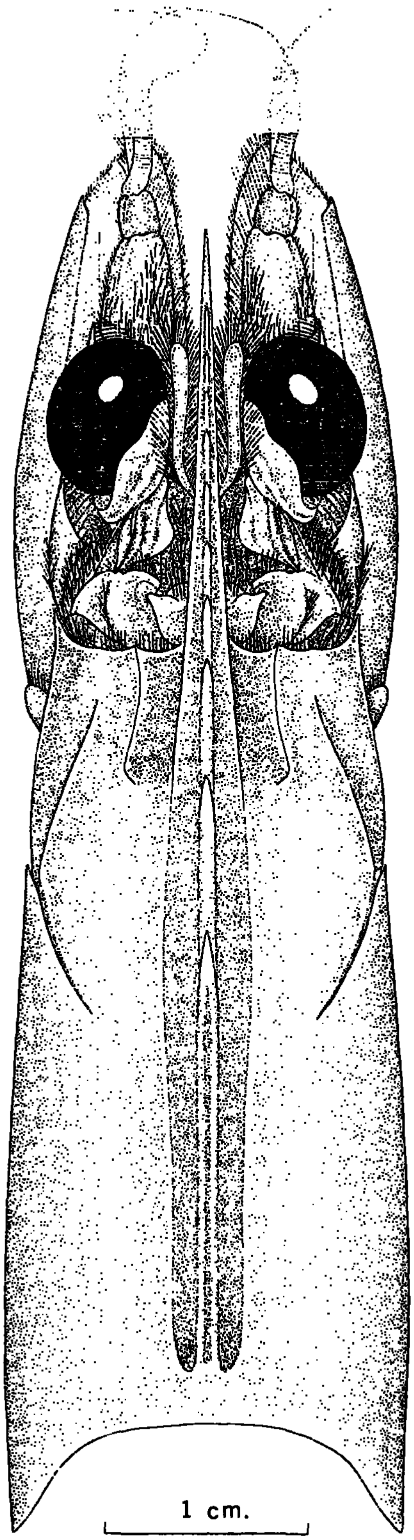

FIGURE 32.—*Penaeus (M.) duorarum notialis* Pérez Farfante. Cephalothorax, holotype, ♂ 41.5 mm. c.l., off Las Piedras, Gulf of Venezuela.

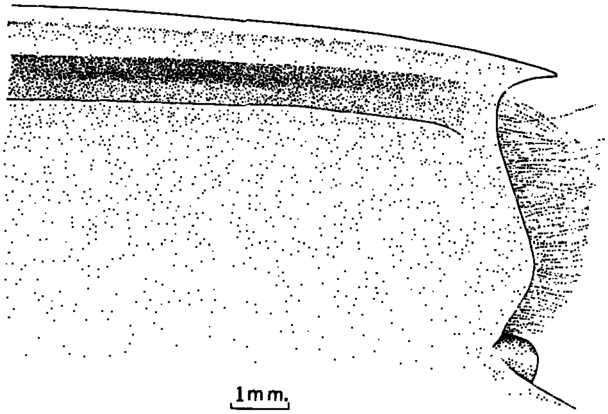

FIGURE 33.—*Penaeus (M.) duorarum notialis* Pérez Farfante. Sixth abdominal somite, posterodorsal portion, ♀ 42 mm. c.l., off Great Pedro Bluff, Jamaica.

mm. c. l., and less in smaller and larger size classes (fig. 35); both lips sharp. Sixth abdominal somite with three prominent cicatrices on each side, anterior the longest; fifth somite with one cicatrix and series of minute pits anterior to sinus on posterior margin of somite; fourth abdominal somite with similar series of pits dorsal to sinus on posterior margin of somite. Telson unarmed, with deep median sulcus and sharp pointed tip.

**PETASMA (fig. 36)**

As in *P. d. duorarum*.

**APPENDIX MASCULINA**

As in *P. d. duorarum*.

**THELYCUM (fig. 37)**

Similar to that of *P. d. duorarum*.

**COLOR**

Although variable, color of *P. d. notialis* is most frequently light brown; thus, the name camarón acaramelado (candied shrimp) in Cuba and langostino amarillo in Venezuela. In certain areas it is pink and is known as camarón rosado (pink shrimp), whereas in other areas it is very dark brown and is called camarón carbonero (coal-carrying shrimp) or camarón cocinero (cook shrimp).

In the Antilles, this subspecies has a large, dark, reddish-brown spot on each side at the junction of the third and fourth abdominal somites, whereas in northern South America, it consistently seems to lack these large spots.

## Distribution and Morphological Variations

In American waters, *P. d. notialis* ranges from Cuba through the Greater Antilles to the Virgin Islands and from Bahía de la Ascensión, Quintana Roo, Mexico, along the Caribbean Coast of Central America and South America and the Atlantic Coast of South America to São Luis, Brazil. It is apparently absent from northeastern Brazil, but appears again in Ilhéus and extends south to Cabo Frio (fig. 28). Here, for the first time, *P. d. notialis* is recorded from the Caribbean Coast of Mexico, north of the Gulf of Honduras. It is also found in the eastern Atlantic, along the coast of Africa, from Cap Blanc to Angola.

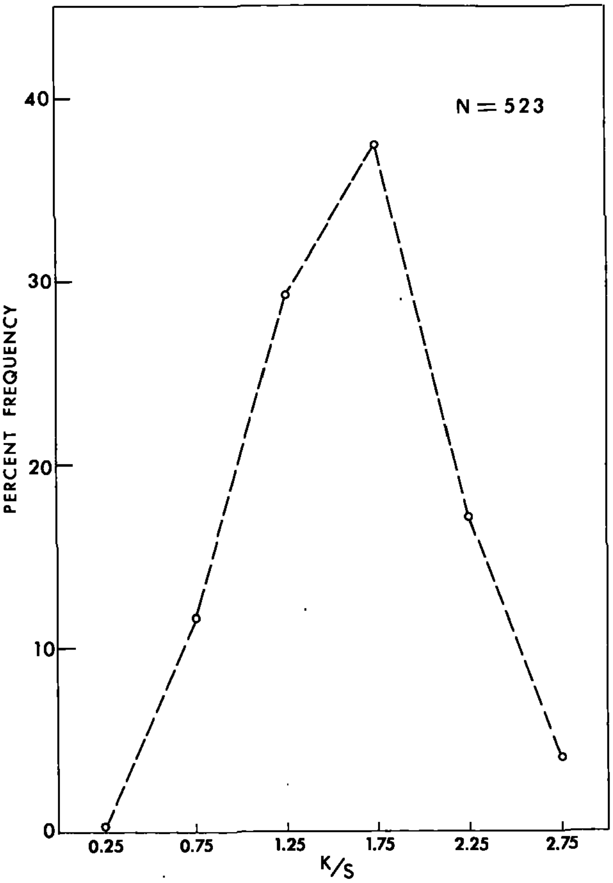

FIGURE 34.—Percentage of distribution of keel-sulcus (K/S) in *Penaeus (M.) duorarum notialis* Pérez Farfante.

A few specimens of this subspecies have been reported beyond the northern and southern limits of its range in the western Atlantic as given here. I believe that those from northeast Florida recorded by Joyce (1965) are most likely members of the small percentage of *P. d. duorarum* that have a rather broad dorsolateral sulcus, as figure 23 shows. Although camarón acaramelado has been mentioned from Baía de Guanabara, Brazil (da Silva, 1965), it is doubtful that it reaches so far south. I have examined specimens from that

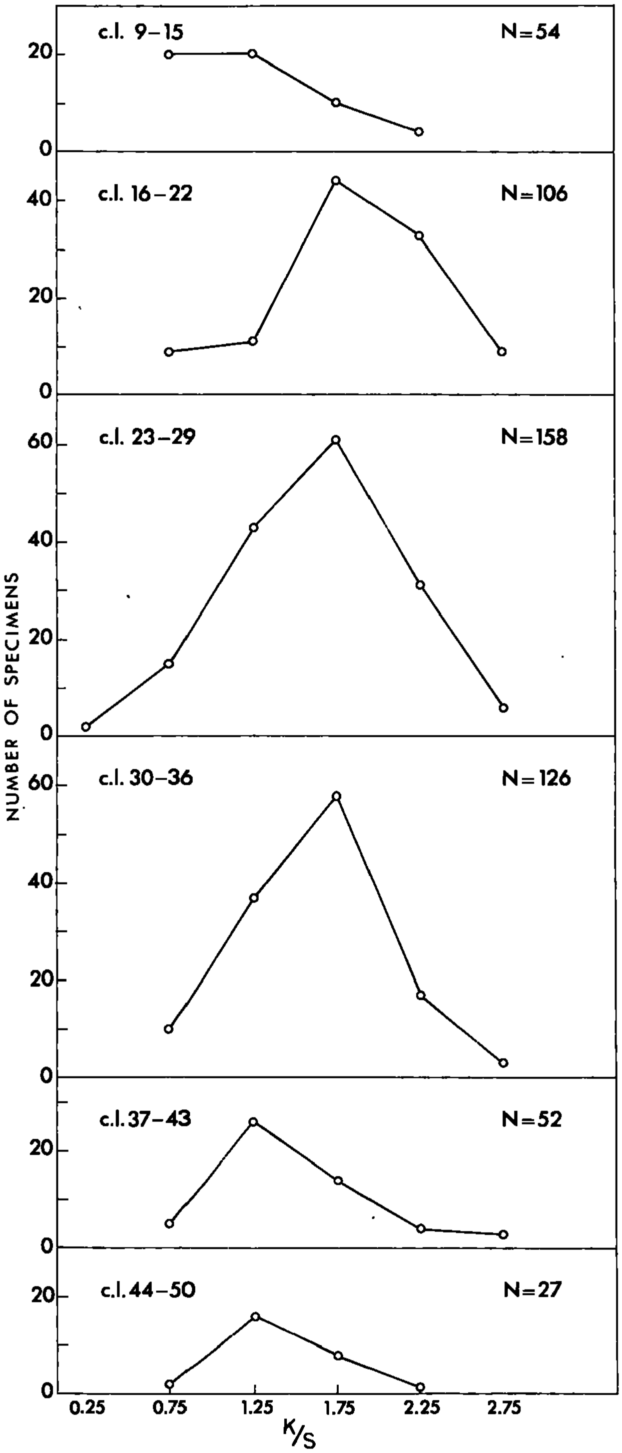

FIGURE 35.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *duorarum notialis* Pérez Farfante.

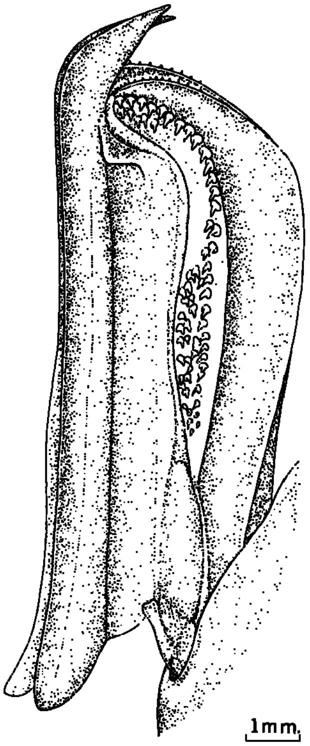

FIGURE 36.—*Penaeus* (*M.*) *duorarum notialis* Pérez Farfante. Petasma, ♂ 34 mm. c.l., off Las Piedras, Gulf of Venezuela.

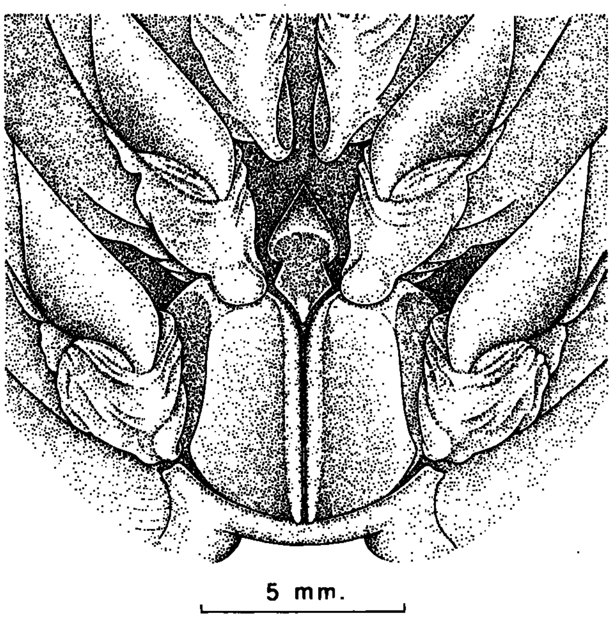

FIGURE 37.—*Penaeus* (*M.*) *duorarum notialis* Pérez Farfante. Thelycum, ♀ 38 mm. c.l., off Las Piedras, Gulf of Venezuela.

locality identified as "*P. duorarum*," but they were actually *P. paulensis*.

The bathymetric distribution of *P. d. notialis* seems to extend to water much deeper than has been previously reported. The greatest depths at which this subspecies was known to live were 60 to 65 fm. (Pérez Farfante, 1967), but a single male was caught at 400 fm. off Punta Broqueles, Colombia, *Oregon* Sta. 4902. It was taken with other penaeids—*Hymenopenaeus robustus* Smith, *Aristaeomorpha foliacea* (Risso), *Plesiopenaeus edwardsianus* (Johnson), and *Aristeus antillensis* Bouvier—which occupy water deeper than that in which *Penaeus* usually live. On the basis of this record, it seems possible that camarón acaramelado occasionally may wander into water as deep as 400 fm. Moderately large concentrations of *P. d. notialis* are found in the Greater Antilles in 2 to 15 fm., in the Gulf of Venezuela in 20 to 25 fm., and off Honduras, Nicaragua, and the northeast coast of South America higher densities are found in deeper water, 34 to 35 fm.

*Penaeus d. notialis* is remarkably uniform throughout its range in American waters. Among the few variations that exist is the relative length of the third pereopod. Although its length varies rather considerably, it seems to me that little systematic importance can be attached to this character in the western Atlantic. For example, in a single locality I found females with a carapace of 40 mm. in which the length of the carpus—which is indicative of the length of the third pereopod—ranges from 26 to 29 mm.; in turn, females with 36 and 40.5 mm. c.l. have a carpus of 29 mm. (fig. 38). Furthermore, in large females from the Golfo de Darién to Islas San Bernardo, Colombia, the carpus is considerably longer than in the females of the same size from neighboring

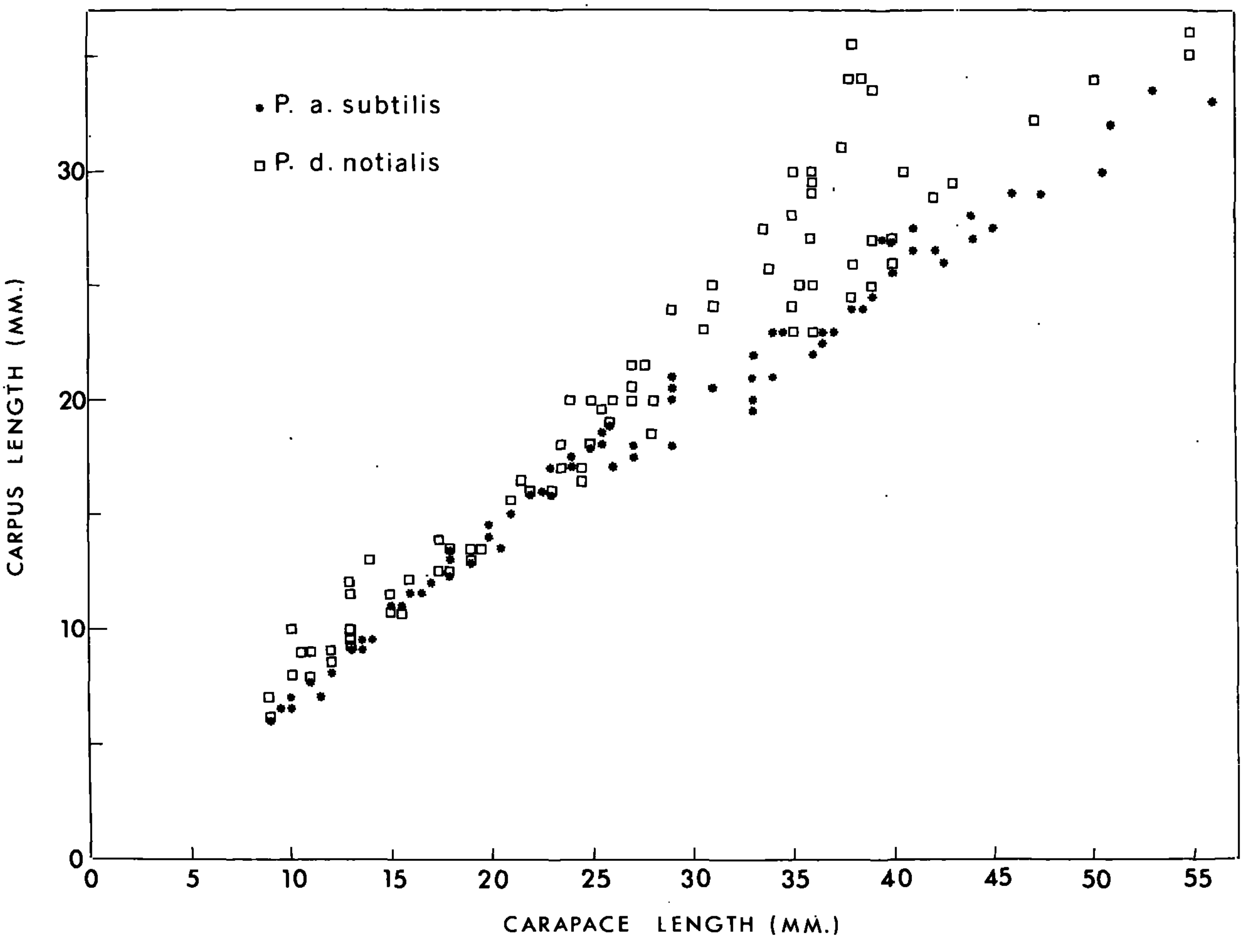

FIGURE 38.—Carpus length-carapace length relation in *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante and *Penaeus* (*M.*) *duorarum notialis* Pérez Farfante.

Central America and the Gulf of Venezuela; no other apparent differences exist between the specimens examined. The discontinuity in the range of variation in this character in the western Atlantic is in contrast to the observations by Rossignol and Repelin (1962) who were working with this subspecies along the west coast of Africa (see above).

## Relationships

(See under *P. duorarum duorarum.*)

## Reproduction

### SUBADULT STAGE-SEXUAL MATURITY

The number of small specimens examined was not sufficient to permit a conclusion as to the size range at which they become subadults. Males were found with petasmal endopods first joined at 16 mm. c.l., 73 mm. t.l. The minimum size at which females had the thelycum fully developed was 16 mm. c.l., 73 mm. t.l.

### COPULATION

Copulation has not been observed, but it most probably takes place between a soft-shelled female and a hard-shelled male for the same reasons that were mentioned earlier for *P. d. duorarum*. Information on impregnation is too meager to allow conclusions.

### OVARY DEVELOPMENT

My observations show that in *P. d. notialis* the ovaries go through five basic stages that are similar to those described for *P. d. duorarum* and can be recognized by the same characters of size and color.

### SPAWNING

The presence of very small juveniles in shallow coastal waters of southern Camagüey, Cuba, as well as in Laguna Doctor, Playa de Baracoa, Cuba, throughout most of the year seems to indicate that spawning is probably continuous around the island. The preliminary investigation of specimens from Cuban waters by Pérez Farfante et al. (1961) showed that mature females were present in the waters south of Camagüey from March through May.

### SEX RATIO

In inshore waters and coastal waters to 12 fm., the ratio of males to females seems to be approximately 1:1. Pérez Farfante et al. (1961) found the entire sample from Laguna Doctor, Playa de Baracoa, Cuba, contained 54 percent males and 46 percent females, and a sample from the southern coast of Cuba had 51 percent males and 49 percent females.

## Postembryonic Development

### LARVAE, POSTLARVAE, AND JUVENILES

No studies have been conducted on either larval or postlarval stages of this shrimp.

My studies of small shrimp showed that the adrostral sulci are only faintly indicated in juveniles 18 mm. t.l., but are clearly distinct in specimens 19 mm. t.l.

In the development of "candied shrimp" sex can be determined when they reach about 20 mm. t.l. At this length the endopods of the first pair of pleopods in the males are situated more proximally on the bases and are a little longer than in the females. In addition, males have a sharp ridge along the median line of sternite XIV, which increases slightly in height anteriorly and forms a sharp angle at its anteroventral extremity. Females have no ridge along the median line of sternite XIV, which instead is produced to a median point.

The following discussion on the development of juveniles consists largely of a summary of progressive changes occurring in the petasma and the thelycum. In males 9 mm. c.l., 42 mm. t.l., the ventral costae of the petasma may be armed with at least one distomarginal spine, and 12 mm. c.l., 55 mm. t.l., the ventral costae possess several distomarginal spines and relatively strong subapical teeth. At 16 mm. c.l., 73 mm. t.l., males may have the petasma joined.

Progressive changes in the thelycum occur as follows. In females with a 5 mm. c.l., 24 mm. t.l., the lateral plates are distinct, and at 9 mm. c.l., 42 mm. t.l., their anterior margins touch or almost touch the apex of the horns of the median protuberance. At 12 mm. c.l., 55 mm. t.l., the posterior process often bears a small posteromedian carina, which does not project caudally, and the lateral plates partially cover the horns of the median protuberance. Larger females exhibit this typically undivided median carina. As stated earlier, some females 16 mm. c.l., 73 mm. t.l. have the lateral plates contiguous along median borders, and, thus, the thelycum with functional form.

### GROWTH

The only information available comes from the laboratory experiment by Pérez Farfante et al. (1961) during which juveniles 25 mm. t.l. grew to

42 mm. t.l. in 48 days, or at an average daily rate of 0.36 mm.; and individuals 75 to 90 mm. t.l. grew 10 mm. t.l. in 30 days—an average daily increase of 0.33 mm.

### SEX DIFFERENCES IN SIZE

The largest female I examined was 48 mm. c.l., 192 mm. t.l., and the largest male 41 mm. c.l., 175 mm. t.l., from off Las Piedras, Gulf of Venezuela. Ewald (1965c) reported females 55 mm. c.l. in the lower Gulf of Venezuela. Although the females of *P. d. notialis* attain a much larger size than the males, both increase in length with increasing depth (Pérez Farfante et al., 1961).

## Ecology

### SUBSTRATE

"Candied shrimp" live on a variety of bottom types—very soft to firm mud, sand and mud, and predominantly sand patches among rocks.

### DIEL CYCLE

Juveniles as well as adults are mostly nocturnal in habit. In Cuba, however, they constitute a small percentage of the commercial catches taken during the day.

The only data available on the behavior of "candied shrimp" in relation to moon phases are statements by fishermen that these shrimp become extremely scarce during the full moon.

### MOVEMENTS

The sampling by Pérez Farfante et al. (1961) in Cuba showed that the young remain in estuarine waters until they are about 85 mm. t.l., at which length they seem to move seaward. In Laguna Doctor, Playa de Baracoa, Cuba, however, larger specimens were caught (to 130 mm. t.l.).

### EFFECTS OF TEMPERATURE

No studies have been made.

### ENEMIES AND DISEASES

Only a few enemies and diseases of "candied shrimp" are known. Undoubtedly, this is because so little attention has been accorded them. Carnivorous fishes are probably their most important enemies. They are also victims of their brethren, particularly the young. "Candied shrimp" suffer an infection that causes them to become opaque white, a malady similar to that found in *P. d. duorarum* called "cotton shrimp" or "milk shrimp" in the United States. This condition is rather common in shrimp from southern Cuba.

## Commercial Importance

*P. d. notialis* and *P. schmitti* are the most important commercial shrimps in the Greater Antilles and the Caribbean Coast of Central America. It makes up about half of Honduran shrimp catches (the rest consists mostly of *P. schmitti* and small quantities of *P. a. subtilis*); as stated earlier, practically the entire production is exported to the United States and in 1965, amounted to 740,270 kg. In Nicaragua, *P. d. notialis* and *P. brasiliensis* account for a large percentage of the shrimp taken along the Caribbean Coast; exports to the United States from eastern Nicaragua in 1964 amounted to 1,049,623 kg. (catches by U.S. vessels off Nicaragua are not included). Most of the rather small catches of grooved shrimps in the Gulf of Venezuela (Ewald, 1965c) consist of *P. d. notialis*. This shrimp also occurs in the enormous catches made along the northeastern Atlantic Coast of South America, from Guyana to Baía de Marajó, Brazil. Croker (1967) stated that because it is not distinguished from *P. brasiliensis* by the fisherman, it is not possible to say what proportion of the catches it constitutes. Finally, according to Lindner (1957), *P. d. notialis* is taken commercially along the southernmost portion of its range, from Ilhéus to Cabo Frio, Brazil.

## *Penaeus (Melicertus) aztecus aztecus* Ives

Figures 39 to 50

United States: brown shrimp, brownies, green lake shrimp, red shrimp, redtail shrimp, golden shrimp, native shrimp. Mexico: camarón café, camarón moreno.

*Penaeus brasiliensis:* Gibbes, 1850: 198 [part]; Stimpson, 1871: 132; Verrill, Smith, and Harger, 1873: 551; Smith, 1874: 642; Smith, 1880: 267; Rathbun, 1884: 821–823 [part]; Herrick, 1887: 47; Ives, 1891: 199 [part]; Evermann, 1892: 90 [part]; Rathbun, 1893: 821–823 [part]; de Man, 1911: 96 [part]; Fowler, 1913: 314–316, 542; Cowles, 1930: 355, 356, 358 [part]; Weymouth, 1931: 11 [part]; Weymouth et al., 1932: 108 [part]; Weymouth et al., 1933: 2, 4, 6, 8, 12, 21, figs. 3b, 4b; Burkenroad, 1934: 81, 82, 89–93, 138, (61, 75, 77, 78, 88, 94, 134 [part]), figs. 8, 9; Johnson and Lindner, 1934: 4, 57 [part]; Myers and Gowanloch, 1934: 12 [part]; Lindner, 1936: 155 [fig. 2 middle?]; Pearson, 1939: 2, 28, 30–39, 50, 51, 53, 59, 71, 72 [part], figs. 21–31; Anderson, 1948: 1 [part]; U.S. Fish and Wildlife Service, 1958b: 13 [part]. Not *P. brasiliensis* Lat., 1817.

*Peneus braziliensis:* Coues, 1871: 124 [part]; Kingsley, 1878: 69 [part]; Kingsley, 1879: 330 [part]; Kingsley, 1880: 427 [part].

*Penaeus brasiliensis*, var. *aztecus* Ives, 1891: 190, 191, 199 [part] (lectotype, here designated, ♀, PANS 4764, Veracruz, Mexico, Heilprin Expedition, 1890; paralectotypes, PANS); de Man, 1911: 95, 96; Burkenroad, 1934: 94.

*Paneus brasiliensis:* Collins and Smith, 1892: 102 [part].

*Penaeus brasiliensis aztecus:* Sharp, 1893: 109; Burkenroad, 1939: 27, 34.

*Peneus brasiliensis:* Faxon, 1896: 162; Sumner, Osburn, and Cole, 1913: 665; Hay and Shore, 1918: 377, 378, fig. 6 [part ?].

*Penaeus braziliensis:* Tulian, 1920b: 107, 108; Williams, 1959: 281, 282, 285–288 [part]; Dobkin, 1961: 347 [part].

*Penaeus aztecus:* Burkenroad, 1939 [part, "Form A"]: 5, 20, 21, 23, 25–27, 29, 30, 33, 46, figs. 20, 21, 24, 30, 31; Pearson, 1939: 30; Gunter, 1941: 203; Anderson and Lindner, 1945: 306 [part]; Gunter, 1945: 69, 77, 87, 113, 115, (178?); Anderson et al., 1949: 16; Burkenroad, 1949: 688; Knapp, 1949: 139; Broad, 1950: 1–4, 3 figs.; Gunter, 1950: 13, 15, 20–27, 40, 42, 43, 46–49; Hedgpeth, 1950: 106–108, 110–113, 118; Idyll, 1950: 7, 9, 10, 14, 17, 19, 22, 25, fig. 1; Sprague, 1950: 2; Whitten et al., 1950: 78; Broad, 1951: 27–29, 31–35; Gunter and Hildebrand, 1951: 733; Sánchez Roig and Gómez de la Maza, 1951: 113; Gómez de la Maza, 1952: 167, 170, 171, fig. 1a; Leone and Pryor, 1952: 27–31; Springer and Bullis, 1952: 8–10, 12; Heegaard, 1953: 76, 78, 102; Hedgpeth, 1953: 159–161, 210; Hildebrand and Gunter, 1953: 152, 155; Pérez Farfante, 1953: 229, 230 (238, 241 [part]); Williams, 1953: 156–160, figs. 1, 2; De Sylva, 1954: 10, 18, 19, 23, 24, 26, 27, 29, 31, 33; Hildebrand, 1954: 233, 234, 241–248, 261–267, 324–326, 349–351, 362–366; Sprague, 1954: 248, 251; Springer and Bullis, 1954: 3–6, 13–16; Hildebrand, 1955: 172–179, 190, 220, 224, 226, 227; Parker, 1955: 193, 197, 211; Voss, 1955: 5, 8, 11, figs. 11, 16, 17; Williams, 1955a: 116, 118, 127, 138–141, 144; Williams, 1955b: 200, 203, 204, 206; Guest, 1956: 6, 12, 14, 18, figs. 2, 3; Gunter, 1956: 99, 105; Springer and Bullis, 1956: 9; Anderson, 1957: 399; Carranza, 1957: 147; Dall, 1957: 142, 226, 227; Ingle, 1957: 10–12, 14–17; Lindner, 1957: 72, 73, 83, 84; Pearse and Gunter, 1957: 139; Simmons, 1957: 178, 191, 199; Viosca, 1957: 12, 20, 1 fig.; Woodburn et al., 1957: 6, 7, 11; Anderson, 1958a: 1–3, fig. 2; Anderson, 1958b: 2; Darnell, 1958: 369, 385, 388, 400, 405; Gunter and Shell, 1958: 17, 23; Hildebrand, 1958: 159; Lunz, 1958: 47; U.S. Fish and Wildlife Service, 1958b: 1, 6, 8, 12, 13, 15, 18–22, 24–28, 30, 32, fig. I–5c; Williams, 1958: 283–290; Collier et al., 1959: 1–5; Eldred, 1959a: 75; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959: 6, 7, 9, 10, 12, 14–16, 19–24; Iversen and Manning, 1959: 130; Kruse, 1959: 123, 124, 126, 128, 130, 134, 136, 137, 140–142, 144; Williams, 1959: 281–283, 285–289, figs. 4, 8; Young, 1959: 7, 8; Chin, 1960: 135–141; Eldred, 1960: 164, 165; Eldred and Hutton, 1960: 91, 97, 98, 101, 103, 104, 106, 108, figs. 5–9; Hoese, 1960a: 592, 593; Hoese, 1960b: 330, 331; Inglis, 1960: 66–69; Renfro, 1960a: 9, 10; Renfro, 1960b: 63, 64, 1 fig.; Wheeler, 1960: 7, 8; Williams, 1960: 560–570; Bearden, 1961: 3–8; Costello and Allen, 1961: 21; Eldred et al., 1961: 69, 80, 86–88, 97, 98, 109; Gunter, 1961a: 599; Gunter, 1961b: 184; Renfro, 1961: 11, 12; Tabb and Manning, 1961: 594, 595; Anderson, 1962: 1, 2, fig. 2; George, 1962: 160–163; Gunter, 1962a: 107, 108; Gunter, 1962c: 216–226; Hutton et al., 1962: 327, 330, 331; Kutkuhn, 1962: 343, 355, 361–370, 385, 388, 394–396, 401; Tabb, Dubrow, and Jones, 1962: 7, 11, 12, 28; Baxter, 1963: 79, 80, 82–87; Boschi, 1963: 5, 6, 13, 20, 23, 26–29 [part], fig. 8 (1, 2, 3 [right], 4–6); Gunter and Hall, 1963: 295, 296, 304; Gunter, 1963: 108; Kutkuhn, 1963: 66–77; McFarland and Lee, 1963: 391, 392, 394–397, 399, 401–415; Renfro and Brusher, 1963: 13–17; St. Amant, Corkum, and Broom, 1963: 14–22, 25; Zein-Eldin, 1963a: 188–196; Costello and Allen, 1964: 31; Gunter et al., 1964: 182–184; Hutton, 1964: 440, 445; Jones et al., 1964: 1; Klima, 1964: 52–60, 63, 64; Renfro, 1964: 94–97; Aldrich, 1965: 370–375; Anderson and Lunz, 1965: 1, 4–6; Broad, 1965: 86–90; Bullis and Thompson, 1965: 6, 7; Cook, 1965; 12, 13; Copeland, 1965: 9, 13, 14; Eldred et al., 1965: 2, 17, 26; Holthuis and Rosa, 1965: 4 [part]; Joyce, 1965: 14, 17, 18, 24, 27, 28, 34, 37, 38, 44, 47, 48, 53, 56, 57, 62, 65, 66, 70, 73, 74, 79–82, 88, 90, 93, 95, 99, 101, 103, 114–121, 128, 132, 134, 145–154, 170–173, 176–180, 184, 185, 191, 192, 220, 221; Loesch, 1965: 42, 45, 47, 49–51, 53, 54, 56, 57; Temple and

Fischer, 1965a: 59, 60; Temple and Fischer, 1965b: 16; Van Engel, 1965: 38; Williams, 1965: 22–27, fig. 12; Zein-Eldin and Aldrich, 1965: 199–216; Zein-Eldin and Griffith, 1965: 77–81; Anderson, 1966: 1, 3; Christmas et al., 1966: 186, 196–198, 201, 202, 205, 212, figs. 2, 3; Cook, 1966: 438; Copeland and Truitt, 1966: 65, 68–70, 72, 73; Joyce and Eldred, 1966: 8, 9, 11–13, 16–19, 22, 25, 31, 32, 34, 35; Kutkuhn, 1966a: 19, 20, 26; Parker, 1966: 32, 34, 35; St. Amant et al., 1966: 1, 2, 4, 5, 7, 8, 10–14, 16; Sykes and Finucane, 1966: 374; Aldrich et al., 1967: 80; Baxter and Renfro, 1967: 149–158, figs. 2, 3; Lyles, 1967: 315–317, 371–376; McCoy and Brown, 1967: 1–3, 8, 10, 12, 14, 16, 19, 21, 23, 25–27; Temple and Fischer, 1967: 323, 325, 328, 329, 332, 333; Trent, 1967: 7–16; Villalobos-Figueroa, Suárez Caabro, Gómez, de la Lanza, Aceves, Manrique, and Cabrera, 1967: 75, 85; Zamora and Trent, 1968: 17–19.

*Penaeus axtecus:* Gunter, 1950: 40.

*Palaemonetes aztecus:* Lunz, 1956: 93.

*Penaeus aztecus aztecus:* Pérez Farfante, 1967: 84, 87.

Brown shrimp: Loesch, 1957: 40, 41; Zein-Eldin, 1963b: 61, 62; Aldrich, 1964: 61–64; Baxter and Furr, 1964: 28, 29; Renfro and Brusher, 1964: 13, 14; Klima and Benigno, 1965: 38–40; Renfro and Brusher, 1965: 10; Ringo, 1965: 68–70; Parker, 1966: 32, 34, 35; Zein-Eldin, 1966: 41, 42.

?Shrimp: Flint, 1956: 11, 12.

## Taxonomic Remarks

Burkenroad (1939) cited 11 ♂ and 7 ♀ in Ives' syntypes series, and named them "Holotypes and Cotypes" of *P. aztecus* Ives. He mentioned a "Holotype female, 'Form A,' carapace 11.2 mm." I examined the syntypes, which are in the Academy of Natural Sciences of Philadelphia, and found that Burkenroad had selected a female which he labeled "lectotype" (PANS No. 4764). This female is here designated as lectotype of *Penaeus aztecus* Ives. The specimen actually has 21.2 mm. c.l., and on the label that accompanies it the locality is not given, but since 7 ♀ were cited by Burkenroad, and I found that there are now but 6, I assume that the lectotype was removed from Ives' lot. It should be mentioned, however, that this lot has 12 instead of 11 males.

## Study Material

UNITED STATES

**Massachusetts:** 1 ♀, USNM, Tisbury Pond, Martha's Vineyard, October 18, 1906, V. N. Edwards. 1 ♂, UMML, Great Pond, W. Tisbury, Martha's Vineyard, November 1, 1957, A. J. Provenzano. 1 ♀, USNM, Katama Bay, Martha's Vineyard, September 8, 1900, V. N. Edwards.

**New York:** 2 ♀, USNM, Shinnecock Bay, Long Island, September–October 1957, F. H. Low. 2 ♂ 2 ♀, NYCD, Harts Cove, Moriches Bay, September 10, 1962, R. L. Wigley.

**New Jersey:** 1 ♀, USNM, Brigantine Refuge, Oceanville, August 17, 1949, P. F. Springer. 1 ♂, USNM, Beesley's Point, September 9, 1887, T. H. Bean. 6 ♂ 1 ♀, USNM, Beesley's Point, September 10, 1887, T. H. Bean. 1 ♀, USNM, Lousy Harbor, Great Egg Harbor, August 18, 1887, T. H. Bean. 2 ♂ 1 ♀, YPM, Delaware Bay, 4 fm. or less, September 1932, A. E. Parr. 1 ♀, PANS, Ventnor, summer 1949, C. B. Atkinson. 4 ♀, YPM, Mispillion River, 4 fm. or less, August 26, 1932, A. E. Parr.

**Maryland:** 1 ♂ 10 ♀, CBL, Holland Straits to Smith Island, July–September, 1964, E. Harrison. 1 ♀, USNM, Tred Avon River, 3 km. from Easton, B. E. McHale. 1 ♂, CBL, Drum Point, Chesapeake Bay, 2½ fm., August 8, 1953, R. Robinson. 2 ♂ 1 ♀, CBL, Smith and Bloodsworth Island, summer 1965, E. Harrison.

**Virginia:** 1 ♂, USNM, Mobjack Bay, July 16, 1892, *Grampus* Sta. 5.

**North Carolina:** 2 ♀, AMNH, S. of Pamlico Sound. 6 ♂ 10 ♀, USNM, off Beaufort Inlet, October 1964, A. B. Williams. 6 ♂ 8 ♀, USNM, Neuse River at mouth of Adams Creek, August 30, 1949, A. B. Williams.

**South Carolina:** 1 ♀, YPM, off Charleston Harbor, October 1935, G. R. Lunz and Y. H. Olsen.

**Georgia:** 2 ♀, USNM, N. end of St. Catherines Island, July 16, 1931, W. W. Anderson. 7 ♂ 12 ♀, USNM, off Brunswick, 3 to 4 fm., August 26, 1965, BCFBL-Brunswick.

**Florida:** 1 ♂, USNM, N. of Jacksonville, 6 to 8 fm., October 2, 1957, *Combat* Sta. 504. 1 ♂ 3 ♀, USNM, S. of Cape Kennedy, 22 fm., March 23, 1956, *Pelican* Sta. 14. 1 ♂, USNM, off Cape Kennedy 9½ fm., January 26, 1962, *Silver Bay* Sta. 3710. 1 ♂, USNM, off Cape Kennedy, 20 fm., November 9, 1963, *Silver Bay* Sta. 5241. 3 ♂ 2 ♀, USNM, off Cocoa Beach, 10 to 11 fm., January 13, 1965, *Oregon* Sta. 5181. 2 ♂ 2 ♀, USNM, off Melbourne Beach, 11 fm., January 13, 1965, *Oregon* Sta. 5182. 13 ♂ 18 ♀, USNM, off Melbourne Beach, 30 fm., January 14, 1965, *Oregon* Sta. 5200. 7 ♂ 37 ♀, USNM, off Melbourne Beach, 30 to 31 fm., January 15, 1965, *Oregon* Sta. 5202. 7 ♂ 28 ♀, USNM, off Sebastian, 31 to 28 fm., January 15, 1965, *Oregon* Sta. 5203. 4 ♂ 4 ♀, USNM, off Sebastian, 34 to 35 fm., March 14, 1965, *Oregon* Sta. 5350. 1 ♂, USNM, off Fort Pierce, 50 fm., November 11, 1961, *Silver Bay* Sta. 3529. 2 ♀, USNM, off Stuart, 30 fm., November 11, 1963, *Silver Bay* Sta. 5268. 5 ♂ 4 ♀, AMNH, W. side Destin Bridge, Pompano Beach, 2½ fm., July 29, 1948, L. A. Burry. 3 ♂ 3 ♀, USNM, off Key Largo, 50 fm., November 10, 1961, *Silver Bay* Sta. 3524. 2 ♂ 1 ♀, USNM, off Matacumbe Key, 50 fm., November 10, 1961, *Silver Bay* Sta. 3524. 1 ♂, USNM, off Lower Matacumbe Key, 60 fm., October 27, 1960, *Silver Bay* Sta. 2391. 22 ♂ 10 ♀, USNM, Pilot Cove, Apalachicola Bay, November 12, 1958, R. M. Ingle. 1 ♂ 2 ♀, USNM, off Apalachicola Bay, 6 fm., October 31, 1953, *Oregon* Sta. 863. 3 ♂ 8 ♀, YPM, Pensacola Bay, September 9–15, 1932, M. D. Burkenroad. 16 ♂ 20 ♀, YPM, Pensacola Bay, 5 fm., March 3, 1935, *Atlantis* in port.

**Alabama:** 10 ♂ 5 ♀, USNM, off Mobile Bay, 7 fm., January 28, 1962, *Oregon* Sta. 3475. 2 ♂ 5 ♀, USNM, off Mobile Bay, 29 fm., February 1, 1962, *Oregon* Sta. 3486.

**Mississippi:** 3 ♂, USNM, off Pascagoula, 22 fm., August 21, 1962, *Oregon* Sta. 3713. 5 ♂ 11 ♀, GCRL, Mississippi Sound, June 4, 1964, J. Y. Christmas. 4 ♂ 2 ♀, GCRL, Mississippi Sound, September 30, 1964, J. Y. Christmas. 7 ♂ 10 ♀, USNM, off Mississippi, 29 fm., February 4, 1962, *Oregon* Sta. 3489. 10 ♂ 17 ♀, GCRL, Biloxi Bay, June 18, 1965, BCFFS-Pascagoula.

**Louisiana:** 2 ♂ 3 ♀, YPM, off Louisiana, 17 fm., March 21, 1937, *Atlantis* Sta. 2814. 1 ♂ 10 ♀, YPM, off Louisiana, 51 to 63 fm., April 10, 1931, *Atlantis* Sta. 2853–I. 5 ♂ 6 ♀, USNM, Lake Pontchartrain, 1954, R. M. Darnell. 1 ♂, YPM, off Pass a Loutre, 12 fm., January 31, 1931, M. D. Burkenroad. 4 ♂ 1 ♀, USNM, off Mississippi Delta, 33 fm., October 23, 1953, *Oregon* Sta. 845. 7 ♀, USNM, off Mississippi Delta, 40 fm., February 3, 1938, *Pelican*. 4 ♂ 1 ♀, USNM, off Mississippi Delta, 33 fm., October 23, 1953, *Oregon* Sta. 845. 2 ♂ 1 ♀, YPM, 48 km. S. of Barataria Pass, 16 fm., August 6, 1930, M. D. Burkenroad. 7 ♀, AMNH, S. of Barataria Pass, August 6, 1930, M. D. Burkenroad. 29 ♂ 33 ♀, USNM, lower Barataria Bay, May 21, 1959, E. Schrader and P. Landry.

**Texas:** 23 ♂ 23 ♀, USNM, Fort Livingston, May 14, 1934, M. J. Lindner and W. W. Anderson. 7 ♂ 7 ♀, off mouth of Sabine River, 10 fm., May 19, 1965, BCFBLG. 3 ♂ 9 ♀, USNM, Galveston Bay, March-May 1965, BCFBLG. 8 ♂ 2 ♀, USNM, Galveston Bay, April 1965, BCFBLG. 2 ♂ 9 ♀, USNM, off Galveston, 4½ fm., September 8, 1965, BCFBLG. 3 ♀, USNM, northwestern Gulf of Mexico, May 2, 1963, BCFBLG. 7 ♂ 8 ♀, USNM, northwestern Gulf of Mexico, May 6, 1963, BCFBLG. 3 ♂ 3 ♀, USNM, off Matagorda Bay, 25 fm., May 31, 1965, BCFBLG. 1 ♀, USNM, Port Aransas, April 28, 1948, J. W. Hedgpeth. 4 ♂ 1 ♀, USNM, Corpus Christi, November 27–30, 1891, B. W. Evermann. 2 ♂ 3 ♀, USNM, off Padre Island, 19 fm., January 27, 1964, *Oregon* Sta. 4643. 3 ♀, USNM, off Puerto Isabel, 18 fm., June 3, 1954, *Oregon* Sta. 1086.

### MEXICO

**Tamaulipas:** 2 ♀, INIBP, N. of Tampico, November 7, 1962, U. Barron and A. Macías. 2 ♂ 4 ♀, INIBP–USNM, off Tampico, June 10, 1959, E. Ramírez and F. Aguilar. 4 ♂ 1 ♀, USNM, off Tampico, September 12, 1963, U. Barron. 12 ♂ 3 ♀, INIBP–USNM, Villa Cuauhtémoc, Tampico, August 4, 1962, J. García.

**Veracruz:** 3 ♂ 1 ♀, INIBP-USNM, Canal del Chijol, Laguna de Tamiahua, July 21, 1963. 2 ♂ 4 ♀, INIBP-USNM, Bocaina, Laguna de Tamiahua, June 9, 1964, R. Márquez and C. Tovar. 4 ♂ 2 ♀, INIBP-USNM, Túxpan, August 29, 1963, S. Basulto. 1 ♂, INIBP, Tuxpan, August 29, 1963, S. Basulto. 3 ♂ 2 ♀, INIBP-USNM, La Bocana, Tuxpan, March 7, 1964, A. Mendoza and R. Márquez. 5 ♂ 3 ♀, INIBP-USNM, Estero Tabasco, Río Tuxpan, March 24, 1964, A. Mendoza. 9 ♂ 9 ♀, INIBP-USNM, Laguna de Pueblo Viejo, March 1, 1959, E. Ramírez and F. Aguilar. 8 ♂ 2 ♀, INIBP, Laguna de la Mancha, June 21, 1964, F. Lachica and A. Morales. 1 ♂ 1 ♀, INIBP, Laguna de Buen País, 12 km. W. of Alvarado, April 1965, F. Lachica and F. Carmona.

**Campeche:** 1 ♂ 5 ♀, INIBP-USNM, Laguna de Términos, February 1, 1964, F. Lachica and

F. Carmona. 3 ♀, INIBP-USNM, off Ciudad del Carmen, April 29, 1959, R. Ramírez and M. Flores. 2 ♂ 4 ♀, INIBP-USNM, NW. of Ciudad del Carmen, 16 to 20 fm., April 29, 1959, R. Ramírez and M. Flores. 1 ♂, MCZ, NW. of Arrecife Alacrán, 6.5 km. of Whale Rock, 35 fm., *Blake* Sta. 37.

### Diagnosis

Adrostral sulcus broad posteriorly, and long, reaching near posterior margin of carapace. Median sulcus long, ending immediately anterior to posterior end of adrostral sulcus, and deep along its entire length. Dorsolateral sulcus broad. Petasma with distal portion of ventral costa increasing gradually in width and turning proximally in arc, unarmed along free border and with elongated group of closely set, small teeth on attached border; apex of costa adnate to membranous portion of ventrolateral lobule, latter bearing extensive armature of closely set spines; distal fold small, usually with numerous spinules but sometimes unarmed. Thelycum with anterior process relatively broad and with anteriorly bifurcate median carina on posterior process; carina exposed owing to wide divergence of anteromedian angles of lateral plates.

### Description

#### ROSTRUM (fig. 39 a, b)

Teeth $\frac{5\text{–}10}{0\text{–}3}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—47, 9/2—44, 10/2—5, 9/3—1, 7/2—1.50, 6/2—0.50, 6/0—0.50, 5/2—0.50; N=200) + epigastric; position of ventral teeth variable, first tooth situated from well anterior to slightly posterior to last dorsal tooth; rostrum long, in juveniles and subadults reaching as far as base of distal ⅓ of thickened portion of lateral antennular flagellum, attaining maximum length in relation to carapace length at 13 to 20 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.80); decreasing progressively with increasing length of shrimp, rostrum reaching at least three-quarters of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.50); rostrum slender, sinuous, with apical portion usually upturned, posteroventral margin concave; highest portion of blade at level of second or third dorsal tooth; latter level with anterior margin of carapace; tip of rostrum narrow, long, ¼ to ⅓ r.l. Postrostral carina strong, prominent, uniform in width or slightly wider in anterior half, and long, extending to posterior margin of carapace. Median sulcus deep throughout, often slightly wider in anterior half, and long, ending near posterior margin of carapace. Adrostral sulcus broad posteriorly, four-fifths to twice width of postrostral carina, usually long, ending 1/11 to 1/20 c.l. from posterior margin of carapace. Adrostral carina prominent, sharp on carapace, long, same length as adrostral sulcus, and parallel to postrostral carina or inclined obliquely mesially at posterior end.

#### CARAPACE (fig. 40)

Length in proportion to total length apparently changing little, if at all, after juvenile stage is reached (fig. 40). Gastrofrontal sulcus broad, extending to about one-sixth c.l. Gastrofrontal carina sharp, turning slightly toward dorsal margin posteriorly, ending anteriorly in acute orbital angle. Orbito-antennal sulcus wide anteriorly, narrowing posteriorly to below hepatic spine, there widening again into base of spine. Gastro-orbital carina sharp, occupying approximately posterior four-fifths of distance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus ⅕ to ¼ c.l., ending slightly anterior to middle of carapace. Hepatic carina ⅕ to ¼ c.l., sharp, sloping slightly anteroventrally to end 1/18 to 1/23 c.l. from anterior margin of carapace. Antennal spine very prominent and acute; hepatic spine strong.

#### ANTENNULES

Lateral flagellum about two-thirds length of antennular peduncle, slightly longer than median flagellum and with articles shorter than those of median flagellum. Anterolateral spine small, sharp. Stylocerite acuminate, extending to or slightly beyond midlength of first antennular segment. Prosartema reaching to distal end of proximal one-fifth of second antennular segment.

#### ANTENNAE

Scaphocerite length 2½ times maximum width, its length relative to carapace length decreasing slightly with growth; spine reaching base of antennular flagellum. Carpocerite length 1⅓ times width, extending slightly beyond base of eye. Antennal flagellum relatively short, 1⅖ c.l. (fig. 41).

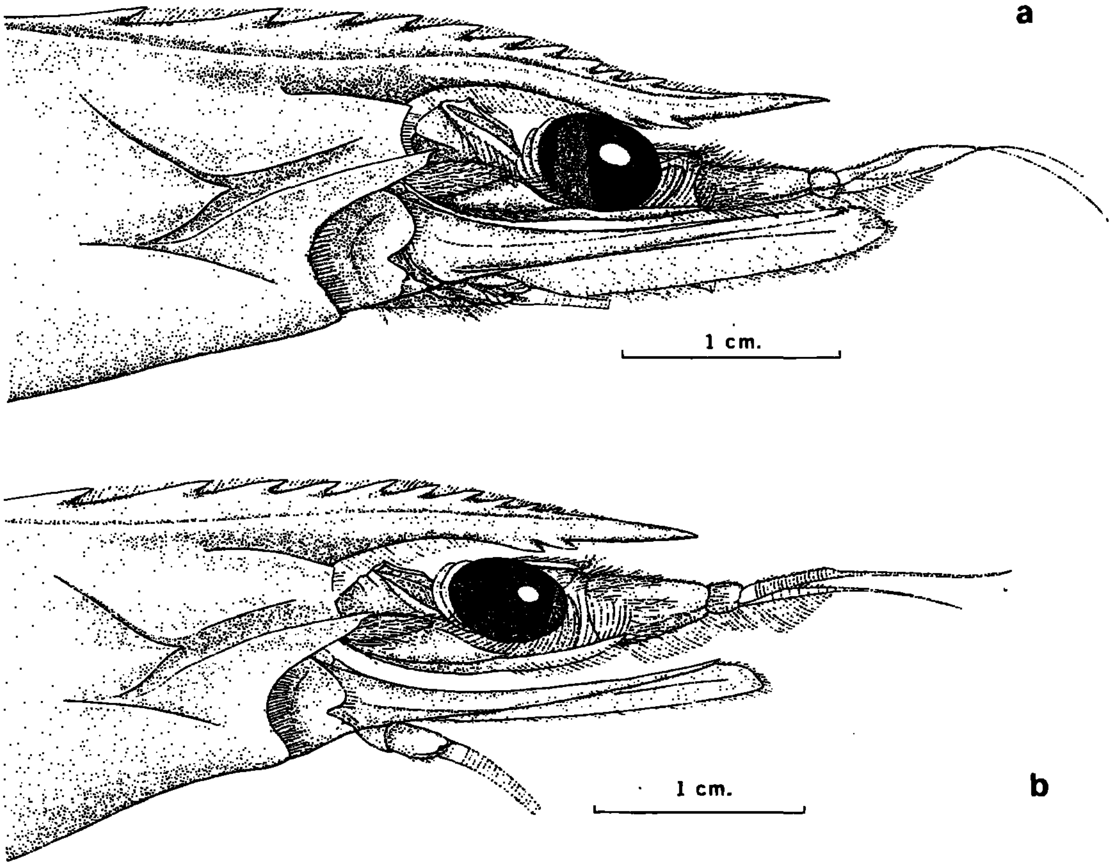

FIGURE 39.—*Penaeus* (*M.*) *aztecus aztecus* Ives. a. Rostrum, ♀ 35 mm. c.l. off Tampico, Mexico, b. Rostrum, ♂ 31 mm. c.l., off Tampico, Mexico.

### THORACIC APPENDAGES

Third maxilliped reaching at least to base and, at most, to distal end of second antennular segment; length of dactyl about two-thirds that of propodus. First pereopod surpassing carpocerite by one-third length of dactyl to seven-eighths of propodus. Second pereopod exceeding carpocerite by one-half length of dactyl to entire length of propodus. Third pereopod reaching at least distal end of antennular peduncle, and, at most, exceeding it by as much as one-tenth length of carpus, proportionately longer in larger individuals. Fourth pereopod reaching at least distal end of carpocerite and, at most, exceeding it by length of dactyl. Length of fifth pereopod subequal to that of fourth pereopod. Exopods on all pereopods; long ischial and basial spines on first pereopod; rather long basial spine on second pereopod.

### ABDOMEN

Carinate dorsally from posterior half of fourth somite posteriorly, carina increasing in height posteriorly to form median keel on sixth somite, there ending in sharp spine on posterior margin. Dorsolateral sulcus (figs. 42, 43) broad, ratio K/S ranging from 0.50 to 3.50, modally 1.25 (fig. 44), varying within same limits in males and females; in small size classes to 29 mm. c.l. (fig. 45), modal value of K/S higher than in larger individuals; dorsal lip of sulcus rounded, ventral lip sharp. Sixth abdominal somite with three conspicuous cicatrices on each side, first longest; fifth abdominal somite with one cicatrix and series of minute pits anterior to sinus on posterior margin of somite, on rib in larger specimens. Fourth abdominal somite with series of minute pits dorsal to sinus on posterior margin of somite, also on rib in larger specimens. Telson unarmed, with deep median sulcus and sharp pointed tip.

### PETASMA (fig. 46 a–d)

Width of ventral costa increasing uniformly proximally, mesiodistal portion forming gentle arc; distal portion unarmed along free border but attached border with elongated, narrow patch of 14 to 25 small, closely set teeth arranged in two or three series; apex of costa not projecting free but tightly joined to adjacent membranous portion. Ventrolateral lobule with extensive armature of rather closely set spines. Distal fold relatively small, armed with 2 to 33, perhaps more, spinules, occasionally unarmed. Distomedian projections rather thick and short, slightly overhanging distal portion of ventral costae.

### APPENDIX MASCULINA (fig. 46 e)

Rather elongated, its length 1⅖ to 1⅗ width at base, armed with single row of short, strong spines along distal four-fifths of lateral margin, and with longer spines along median margin. Anterior surface slightly convex, posterior surface with rather deep excavation flanked by sharp longitudinal ridge projecting from median margin.

### THELYCUM (figs. 47, 48)

Anterior process terminating ventrally in sharp semicircular to nearly triangular ridge, surrounding concave surface usually plain, although sometimes with knob or short rib at center; posterior process with median carina typically bifurcate anteriorly, forming two ribs; ribs turning mesially and almost coming together at anterior process, giving rise to diamondlike or ovate-acuminate structure; depression thus formed deep when ribs are high or very shallow, when ribs are low, usually plain but sometimes bearing median rib along anterior or posterior half, rarely along entire length. Lateral plates with anteromedian angles widely divergent leaving posterior process, including median carina, exposed.

### COLOR

Although of variable color, *P. a. aztecus* is most frequently brown. Thus, the commercial name of brown shrimp or brownies in the United States and camarón café or camarón moreno in Mexico. Large offshore individuals often have an orange or lemon coloration, deeper on pereopods and around tailfan; the latter often has a darker edge which may be purple or reddish purple. Juveniles and subadults are frequently light grayish brown or brown with darker speckles on the sides; red and green specimens also occur and are commonly called red shrimp and green shrimp. *P. a. aztecus* occasionally has a lateral spot at the junction of third and fourth abdominal somites, in this character it resembles both subspecies of *P. duorarum* and also *P. brasiliensis*. Fishermen believe that brown

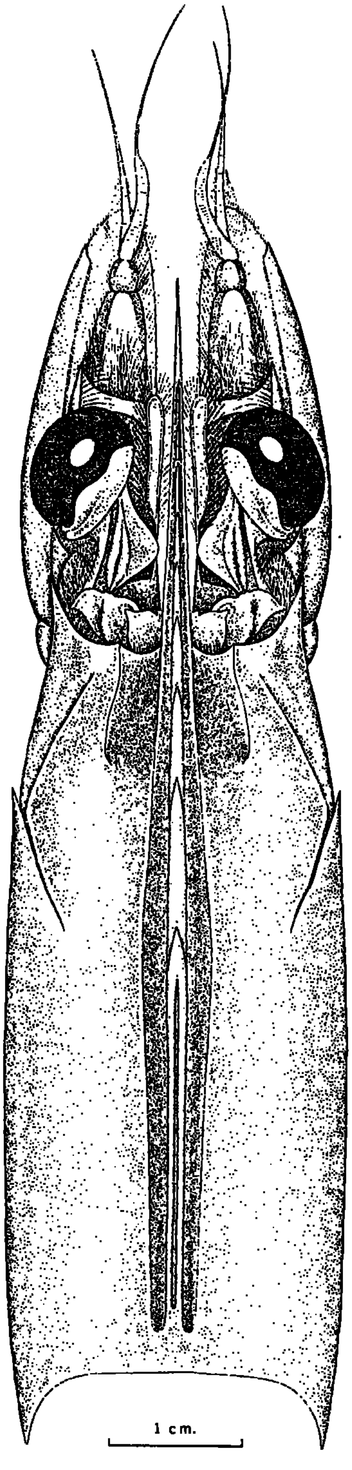

FIGURE 40.—*Penaeus* (*M.*) *aztecus aztecus* Ives. Cephalothorax, ♀ 47.5 mm. c.l., off Tampico, Tamaulipas, Mexico.

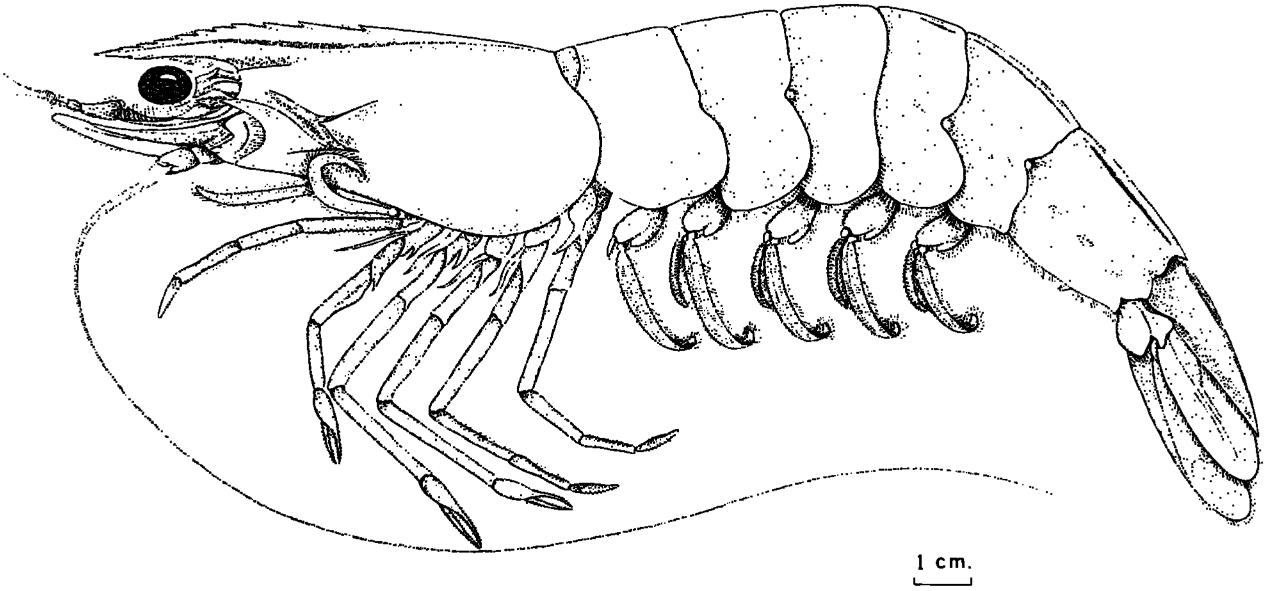

FIGURE 41.—*Penaeus* (*M.*) *aztecus aztecus* Ives. Lateral view, ♀ 54.5 mm. c.l., off Corpus Christi, Tex.

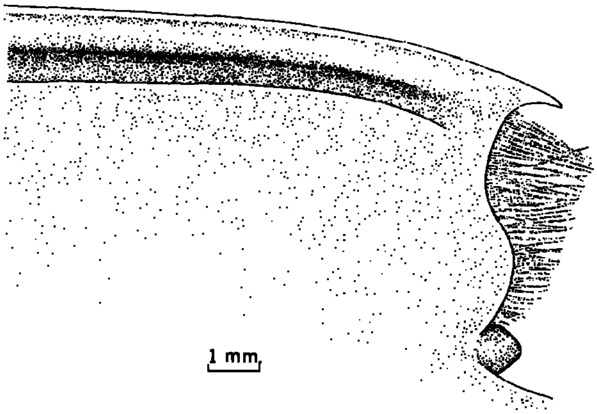

FIGURE 42.—*Penaeus* (*M.*) *aztecus aztecus* Ives. Sixth abdominal somite, posterodorsal portion, ♀ 33.5 mm. c.l., Ciudad del Carmen, Campeche, Mexico.

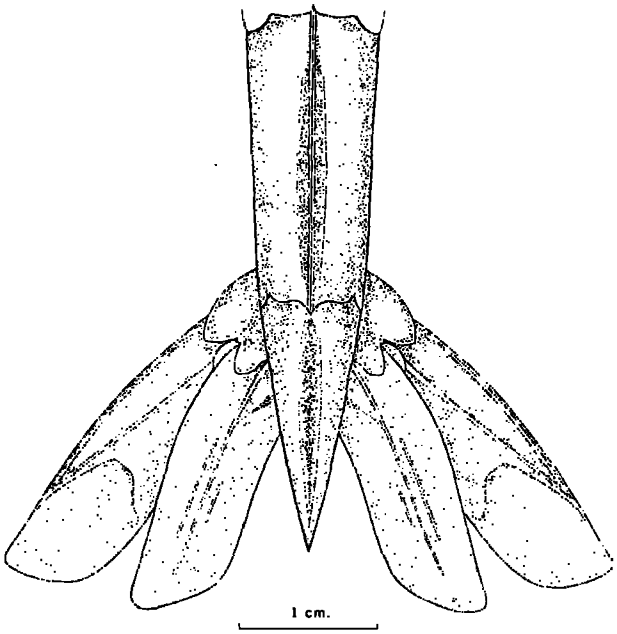

FIGURE 43.—*Penaeus* (*M.*) *aztecus aztecus* Ives. Dorsal view of sixth abdominal somite, telson, and uropods, ♂ 37.5 mm. c.l., off Matagorda Bay, Tex.

shrimp change color while moving, becoming reddish, especially on the pleopods.

Variations in the color of shrimps have been attributed to several factors, such as temperature, nature of bottom, and food.

## Distribution and Morphological Variations

*P. a. aztecus* ranges from Martha's Vineyard south to the Florida Keys and north on the west coast of Florida to the northwest Sanibel grounds. Apparently, it is absent north of these grounds to the vicinity of Apalachicola Bay, where it appears again, ranging along the northern and western coasts of the Gulf of Mexico and the northwestern coast of Yucatán (fig. 49). The brown shrimp is found farther north than other species of the genus *Penaeus* occurring in the western Atlantic, but it rarely reaches the northernmost waters of its range. It seems to be a summer and early fall visitor from Chesapeake Bay northward to Martha's Vineyard; the northernmost breeding population lives along the coast of North Carolina.

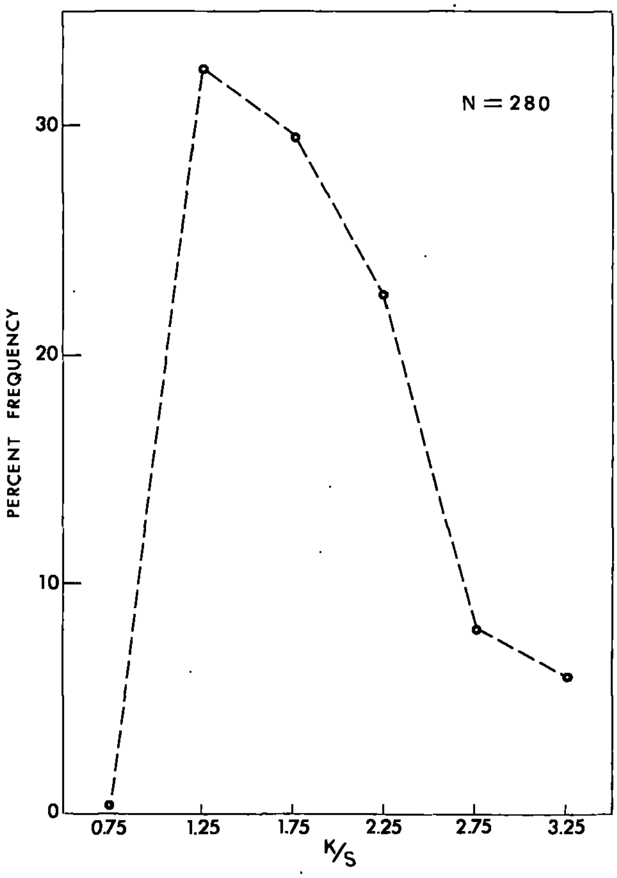

**FIGURE 44.**—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *aztecus aztecus* Ives.

The range of *P. a. aztecus* is somewhat similar to that of *P. setiferus*. *P. a. aztecus*, however, wanders farther north and also farther south along eastern United States, reaching the Florida Keys. Both are absent along most of the Gulf Coast of peninsular Florida, and neither of the two shrimps reaches Cuba. The female *P. aztecus* from Cuba waters identified by Burkenroad as *P. aztecus* "Form A" is most likely one of the specimens of *P. a. subtilis* that show relatively long and broad adrostral sulci.

Brown shrimp are only moderately abundant from North Carolina to northeast Florida and are scarce in southern Florida. In spite of the extensive sampling in the area, only a small population has been found south of the Florida Keys, and very few specimens have been reported from Florida Bay (Tabb and Manning, 1961). Recently the brown shrimp was recorded for the first time (Costello and Allen, 1964) from the northwest Sanibel grounds, offshore from Fort Myers, in

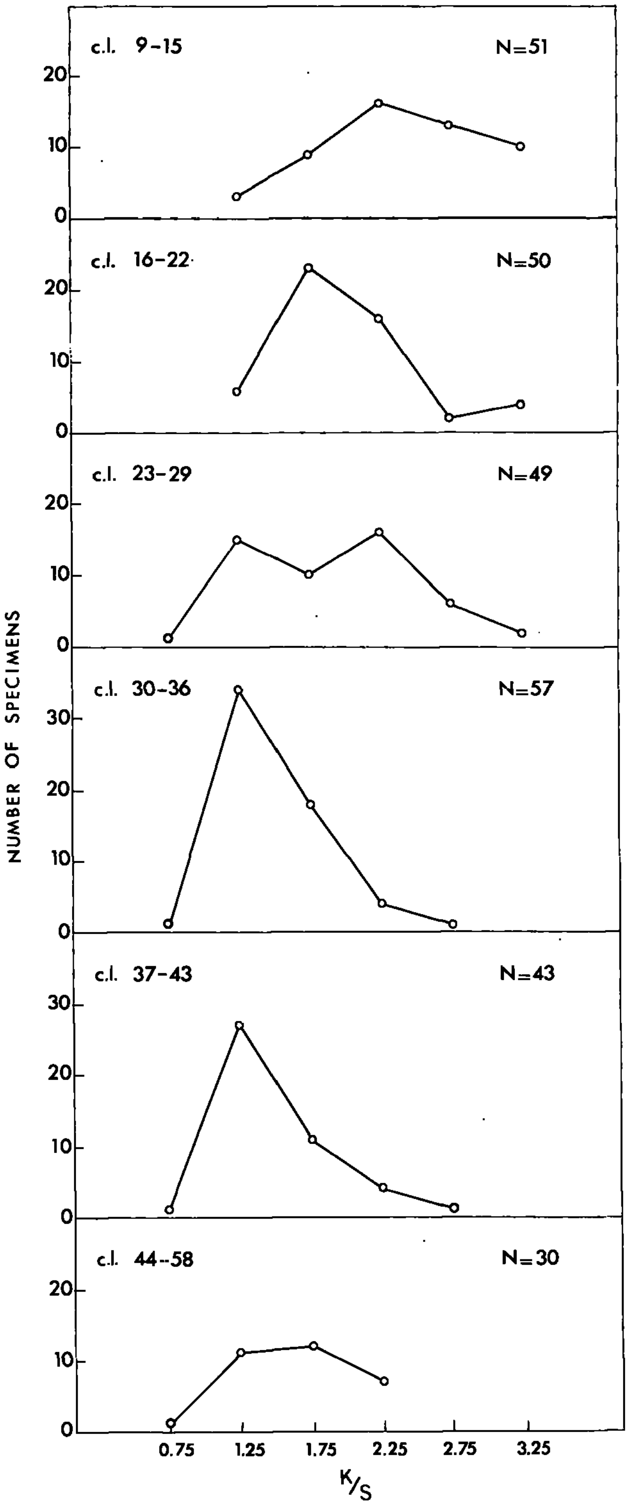

**FIGURE 45.**—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *aztecus aztecus* Ives of different size classes.

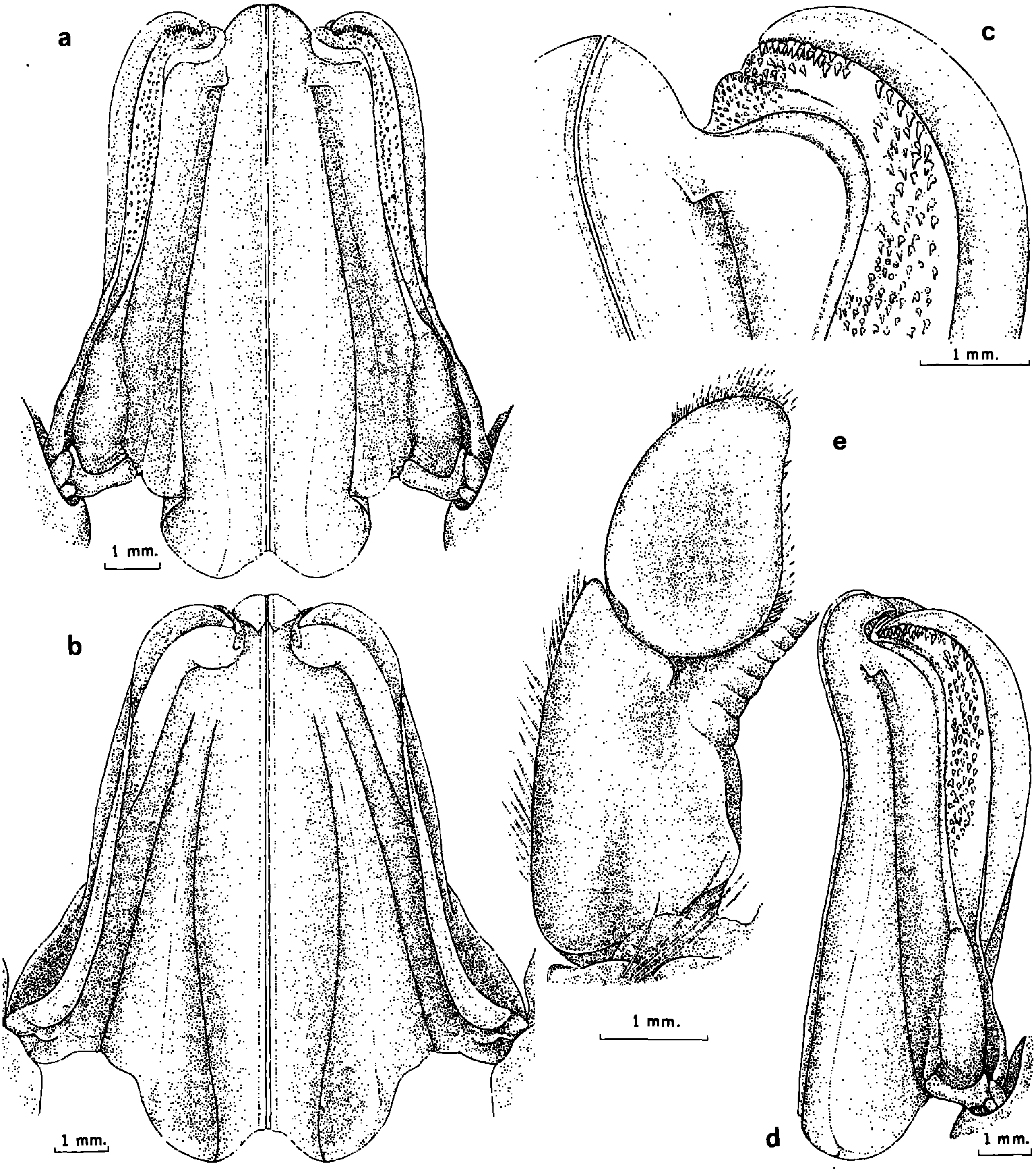

FIGURE 46.—*Penaeus* (*M.*) *aztecus aztecus* Ives. a. Petasma, exterior surface, ♂ 36 mm. c.l., off Matagorda Bay, Tex. b. Petasma, interior surface, ♂ 36 mm. c.l., off Matagorda Bay, Tex. c. Petasma, distal portion, ♂ 37 mm. c.l., off Matagorda Bay, Tex. d. Petasma, lateral view, ♂ 35 mm. c.l., off Sebastian, Fla. e. Appendix masculina, ♂ 37 mm. c.l., off Matagorda Bay, Tex.

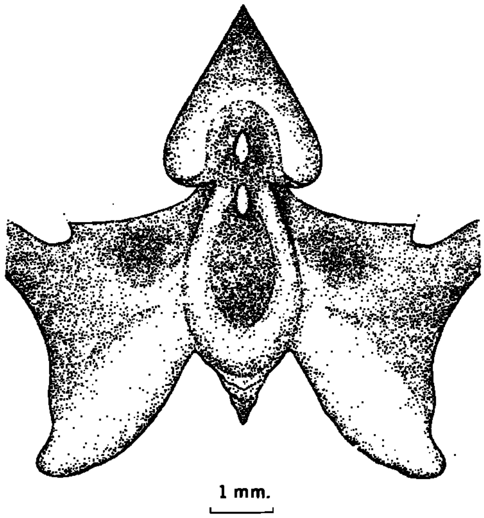

FIGURE 47.—*Penaeus* (*M.*) *aztecus aztecus* Ives. Median protuberance with horns on posterior margin of sternite XIII, ♀ 55.5 mm. c.l., off Matagorda Bay, Tex.

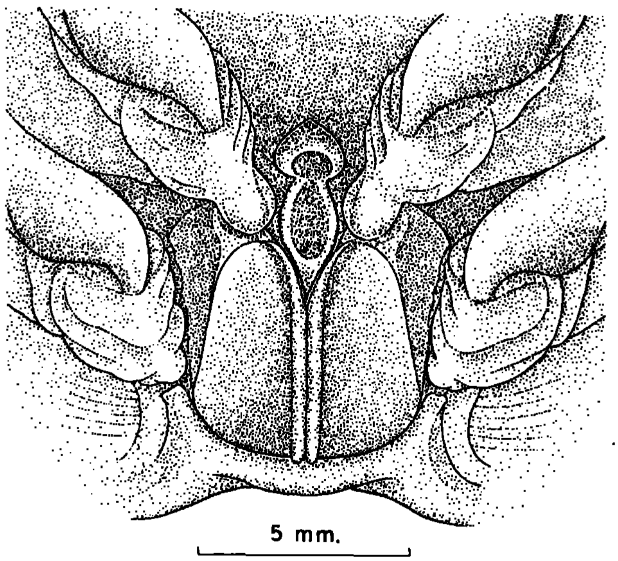

FIGURE 48.—*Penaeus* (*M.*) *aztecus aztecus* Ives. Thelycum, ♀ 39 mm. c.l., northwestern Gulf of Mexico.

5 fm. The only reference to the presence of *P. a. aztecus* farther north on Florida's west coast is that by Eldred et al. (1965), who reported two postlarvae 145 km. off the mouth of Tampa Bay (also one postlarva about 96 km. off Fort Myers). This subspecies attains its maximum density along the coast of Texas but is also relatively abundant off the northeast coast of Mexico south to Veracruz, and a dense concentration exists in Campeche in the area west of Carmen.

Highest densities of brown shrimp are between 15 and 30 fm., but they are commercially abundant down to 60 fm. At depths less than 10 fm. they are immature and relatively small and move to deeper waters as they grow. Although most individuals stay in water shallower than 30 fm., some go three times as deep. At *Pelican* Sta. 114–4 (lat. 26°56.5′ N., long. 96°27′ W.) off Armstrong, Tex., two females were caught in 90 fm. These specimens were identified by Lipke B. Holthuis and are now at Tokyo University of Fisheries. *P. a. aztecus* was also found at *Pelican* Sta. 11 (lat. 29°11′ N., long. 88°30′ W.) off Mississippi in 88½ fm., and at Sta. 115–1 (lat. 26°55′ N., long. 96°27′ W.) off Armstrong, Tex., in 90 fm. The specimens taken at these latter stations were tentatively identified by Milton J. Lindner (personal communication).

*P. a. aztecus* shows no significant morphological variations within its range.

## Relationships

*P. a. aztecus* differs rather strikingly from the southern subspecies *P. a. subtilis* in having a long and deep median sulcus and a long and broad adrostral sulcus. Figure 59 shows that, despite some overlapping in the length of the adrostral sulcus in the two subspecies, the adrostral sulcus reaches $\frac{1}{12}$ to $\frac{1}{20}$ c.l. from the posterior margin of carapace in the higher percentage of specimens of *P. a. aztecus*, whereas in the higher percentage of *P. a. subtilis* it reaches from $\frac{1}{5}$ to $\frac{1}{12}$ c.l. Furthermore, *P. a. aztecus* usually has a broader dorsolateral sulcus and its K/S has a modal value of only 1.25 (fig. 44), whereas in *P. a. subtilis* K/S has a modal value of 3.5.

Adult *P. a. aztecus* can be separated readily from the closely related *P. d. duorarum* and *P. brasiliensis*. Females may be distinguished by the anteriorly bifurcate median carina on the posterior process and the widely divergent anteromedian corners of the lateral plates. Males of *P. a aztecus* differ from those of *P. d. duorarum* by the shape and armature of the ventral costa of the petasma (turning proximally in an arc, lacking spines on free margin, and with a patch of small, closely set teeth on the distal portion of the attached margin) and the relatively elongated—rather than broad—appendix masculina. The compact patch of teeth on the attached margin of the ventral costa also distinguishes male brown shrimp from male *P. brasiliensis*, which

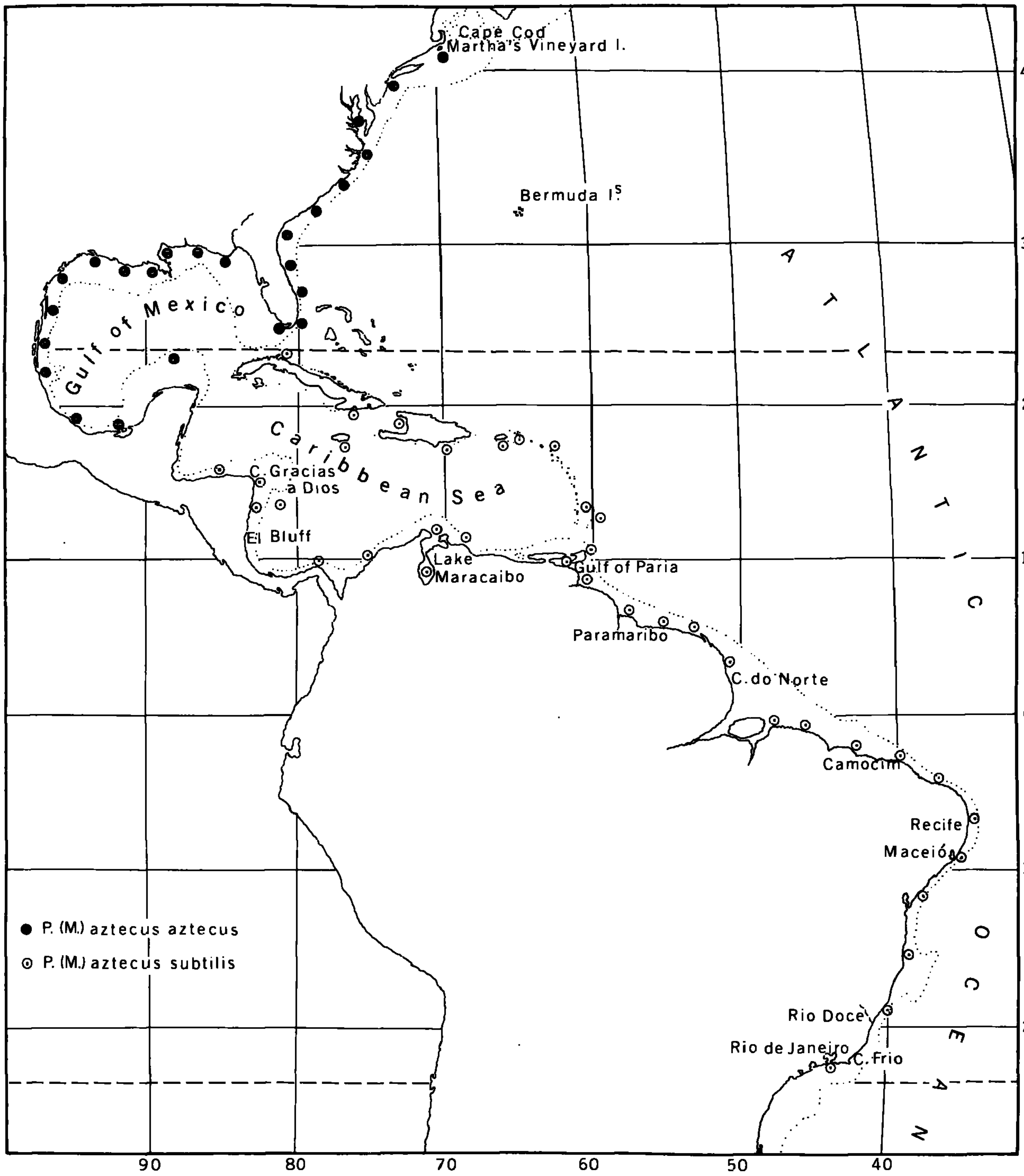

FIGURE 49.—Distribution of *Penaeus* (*M.*) *aztecus aztecus* Ives and *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante.

instead have slightly larger and fewer teeth. The shorter distomedian projection and the distal fold, however, are the most striking characters that set the males of *P. a. aztecus* apart from those of *P. brasiliensis*. In the former the distal fold is relatively small and unarmed, or, more frequently, armed with small spines on the outer surface, whereas in *P. brasiliensis* the fold protrudes inward to form a large auriclelike projection that bears strong spines on the inner surface.

*P. a. aztecus* also differs from *P. d. duorarum* and *P. brasiliensis* in northern waters by the broad dorsolateral sulcus and the often sinuous rostrum. Large brown shrimp also differ from the other two in having a proportionately longer abdomen. Furthermore, in *P. a. aztecus* the third pereopod is thinner and longer—reaching at least to distal end of the antennular peduncle and in large individuals exceeding it by as much as one-tenth length of carpus—than in *P. d. duorarum* and *P. brasiliensis*. The relatively longer length of the third pereopod in brown shrimp is illustrated in table 3, which includes the lengths of various podomeres (dactyl to ischium) for the three carapace-length intervals, and in figure 29, which shows the length of the carpus at various carapace lengths in *P. a. aztecus*, *P. d. duorarum*, and *P. brasiliensis*.

As stated earlier, it is difficult to distinguish small juvenile *P. a. aztecus* from *P. d. duorarum* and *P. brasiliensis*. Many juvenile brown shrimp, however, have a broad dorsolateral sulcus and, thus, may be readily identified. Also, small brown shrimp are usually more slender and their external genitalia are proportionately less well developed than those of the other two shrimps. Juvenile males of *P. a. aztecus* may also be recognized by having a low, rounded midrib on sternite XIV surrounded by a very shallow, horseshoe-shaped groove (fig. 50). Furthermore, in males of *P. a. aztecus* 11 mm. c.l., 51 mm. t.l. and larger, the ventral costa of the petasma lacks distomarginal spines, which are present in *P. d. duorarum*. Juvenile females of *P. a. aztecus* may be recognized by characters of the thelycum. Among females with a carapace length of 10 to 11 mm. c.l., 47 to 51 mm. t.l., those of *P. a. aztecus* may be distinguished by the presence of a knob on the midposterior margin of sternite XIII. In females 12 mm. c.l., 55 mm. t.l., a small triangular projection extends caudad from the midposterior margin of sternite XIII, and when attaining 14 mm. c.l., 64 mm. t.l., the anterior arms of the median carina are clearly distinct on the posterior process. At 16 mm. c.l., 73 mm. t.l., the posterior process has assumed its typical diamond-like shape. At 17 mm. c.l., 77 mm. t.l., the two ribs projecting from the median carina are strongly developed. The thelycum also attains the adult form at a greater size in females of *P. a. aztecus* than in *P. d. duorarum* and *P. brasiliensis*.

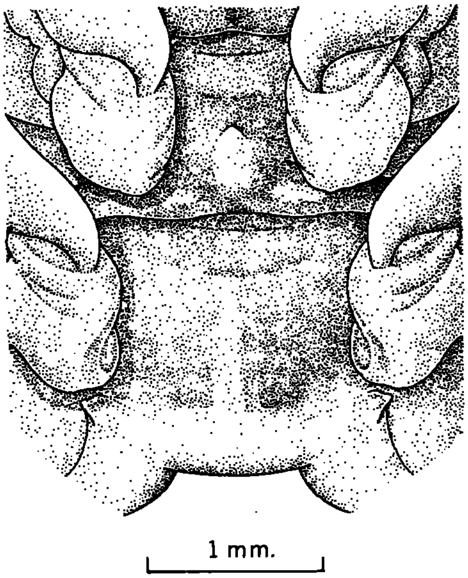

FIGURE 50.—*Penaeus* (*M.*) *aztecus aztecus* Ives. Sternites XIII and XIV, ♂ 10 mm. c.l., Laguna de la Mancha, Veracruz, Mexico.

The length of the rostrum also aids in distinguishing juveniles of *P. a. aztecus* from those of *P. d. duorarum*. Brown shrimp, some as small as 8 mm. c.l., 36 mm, t.l., have rostrum proportionately longer than those in *P. d. duorarum;* the rostrum of the brown shrimp extends anteriorly as far as distal one-third of the thickened portion of the lateral antennular flagellum.

*P. a. aztecus* is separable from the closely allied *P. paulensis* by the broader dorsolateral sulcus, with its rounded rather than sharp dorsal lip. Females of brown shrimp have wider anterior and posterior processes, and in males the distal portion of the ventral costa is strongly arched and the attached margin is armed with numerous contiguous teeth.

## Reproduction

### SUBADULT STAGE-SEXUAL MATURITY

The smallest male I found with joined petasmal endopods was 19 mm. c.l., 85 mm. t.l., but individuals up to 22 mm. c.l., 97 mm. t.l., may have the petasma unjoined. Thus, males seem to attain the subadult stage at a carapace length of 19 to 23 mm., or 85 to 101 mm. t.l. It is possible, however, that some males attain this stage at a smaller size.

The smaller females I found to have reached the subadult stage were 18 mm. c.l., 82 mm., t.l. Individuals up to 22 mm. c.l., 97 mm. t.l., however, may have the thelycum with lateral plates noncontiguous; thus, the subadult stage is attained between 18 and 23 mm. c.l., 82 to 101 mm. t.l.

Burkenroad (1939) reported that female brown shrimp reach sexual maturity or gonadal ripeness at about 30 mm. c.l. or about 145 mm. t.l., and Renfro (1964) found that sexual maturity is usually first attained at a total length of about 140 mm.

### COPULATION

Burkenroad (1939) was the first to suggest that copulation in *P. a. aztecus* takes place between a soft-shelled female and a hard-shelled male, as is now thought to be true for all *Penaeus* with a closed thelycum. Copulation occurs without respect to the developmental stage of the ovaries.

Impregnated females can usually be detected macroscopically, like those of the other *Penaeus* with a closed thelycum, by the bulging of the lateral plates and the tumid appearance—the "lip" of their borders. These criteria are not infallible however, because the lateral plates remain strongly convex in recently spent females.

### OVARY DEVELOPMENT

Like many of its congeners, *P. a. aztecus* possesses ovaries consisting of one anterior lobe from which project six to eight lateral lobules and one posterior lobe that extends to the base of the telson. The size, color, and texture of the ovaries change with the degree of maturity.

Burkenroad (1939) distinguished three stages in the development of the ovary, which correspond approximately to the last three stages recognized by Cummings (1961) in *P. d. duorarum.* Five stages of ovarian development are now generally accepted.

1. Undeveloped. Ovaries slender, flaccid, and translucent. Ova small and translucent.
2. Developing. Ovaries opaque, yellowish with numerous heavily granular ova; diameter of ova 0.10 to 0.18 mm.
3. Nearly ripe. Ovaries large, yellowish brown, becoming darker brown. Diameter of ova 0.19 to 0.25 mm.
4. Ripe. Ovaries golden brown. Diameter of ova 0.26 to 0.28 mm.
5. Spent. Ovaries greatly reduced in diameter, flaccid, light brown to yellowish.

### SPAWNING

The information on spawning—depths, seasons, and peaks—of brown shrimp has been largely deduced from records of the occurrence of females with ripe or spent ovaries and the distribution and abundance of larvae and postlarvae. *P. a. aztecus* spawns at sea, usually in water deeper than 10 fm. and down to at least 60 fm. (Renfro and Brusher, 1965). Laboratory experiments by Cook (1965) indicated that spawning takes place at night. Spawning activity varies through the range of the shrimp and with depth. According to studies on ovary development by Renfro and Brusher (1965) in the northwestern Gulf of Mexico, spawning is continuous in depth between 25 and 60 fm. and appears to be most intensive during the fall. At 15 fm., however, spawning is restricted, taking place from March–April through November–December, and maximum spawning activity apparently occurs in late summer. Recently, Temple and Fischer (1967) indicated from the seasonal abundance of larvae that the maximum peak of spawning was from September to November. Studies on abundance of juveniles (Gunter, 1950) and those on population dynamics, including general knowledge of maximum aggregations of postlarvae in the nursery grounds (Kutkuhn, 1962) indicated that two annual peaks of spawning occur in the northern Gulf of Mexico, one in early spring and the other in the fall.

Along the southeastern Atlantic Coast of the United States a single peak of spawning activity seems to occur in February or March (Williams, 1955a, 1959; Bearden, 1961; Joyce, 1965). In North Carolina, Williams' (1965) collection of postlarvae in the sounds from October to May indicates a protracted spawning season including fall and winter, but the postlarvae that reach inshore waters are apparently killed by low temperatures because no juveniles were found until mid-April.

In the northern Gulf of Mexico and the southeastern Atlantic Coast of the United States, the first peak of brown shrimp spawning occurs earlier in the year than do those of *P. setiferus* and *P. d. duorarum;* the postlarvae of the latter do not appear until May or June, after those of

*P. a. aztecus* have passed their peak of abundance. In the northern Gulf of Mexico the second peak of brown shrimp spawning occurs later in the fall than those of the white and pink shrimps.

Burkenroad (1939) indicated that because females first spawn at sizes only a little above 30 mm. c.l., the largest females may spawn more than once. He also observed that the ovaries of large females contained ripe ova together with young ova, which suggests preparation of the ovary for a second spawning. Studies by Renfro and Temple (personal communication) indicated that recovery and redevelopment are fairly rapid at least during the warmer months. They found in recently spent ovaries that the immature ova present at spawning were developing rapidly while remnants of ripe ova from a previous spawning were being reabsorbed. This finding is taken also as evidence of more than one spawning by one individual.

### SEX RATIO

The sex ratio in inshore as well as offshore waters is about 1:1 (Renfro and Brusher, 1963; Joyce, 1965).

## Postembryonic Development

### LARVAE, POSTLARVAE, AND JUVENILES

Wheeler (1960) reared *P. a. aztecus* from eggs spawned in the laboratory through five nauplial stages to the first protozoea. Later Cook (1965) succeeded in rearing brown shrimp to postlarvae. The entire larval cycle was completed in a minimum of 12 days at about 29° C. Harry L. Cook (personal communication) found that the larval cycle of brown shrimp is similar to that of the white and pink shrimps, and includes, in addition to five nauplial stages, three protozoeal and three mysis stages. To date, no distinctive characters have been observed which will allow specific identification of the different larval stages of the various grooved *Penaeus* from the western Atlantic and the Gulf of Mexico.

Various investigations have been conducted on the morphology of the postlarvae of *P. a. aztecus*, *P. d. duorarum*, and *P. setiferus*.

Pearson (1939) described various postlarvae of *P. brasiliensis* (*P. a. aztecus* and *P. d. duorarum*) and distinguished them from those of *P. setiferus*. Williams (1959) separated the postlarvae under 12 mm. t.l. of *P. a. aztecus*, *P. d. duorarum*, and *P. setiferus* on the basis of two of the diagnostic characters pointed out by Pearson (length of rostrum and third pereopod) plus body size and shape of distal portion of antennal scale. Baxter and Renfro (1967) found that those morphological and morphometric characters, combined, allowed the identification of brown and white shrimp postlarvae below 10 mm. t.l. in the Galveston Bay area. Christmas et al. (1966), however, as a result of the examination of extensive collections from Mississippi, concluded that intraspecific variation among the postlarvae of the brown, white, and pink shrimps is wide. They found that during spring postlarvae of brown shrimp have a larger size than those of the pink and white shrimps, but that the differences disappear in summer when postlarval brown shrimp have more nearly the same size as the other two. Baxter and Renfro (1967) also reported an overlap in length distribution of the postlarvae of brown and white shrimps during the summer, but the mean length of the brown shrimp always exceeded that of the white shrimp.

Juvenile *P. a. aztecus* 18 mm. t.l. have very shallow but distinctly long adrostral sulci and at 20 mm. t.l., the sulci are well developed. Brown shrimp of this size and larger can, therefore, be readily separated from *P. setiferus*, as well as from *P. schmitti*, the only other nongrooved *Penaeus* in the western Atlantic.

In juveniles sex can be determined when they reach about 20 mm. t.l. Males can be distinguished by the shape and position of the endopods of the first pair of pleopods, which are lower on the bases and longer than in females. Small males can also be recognized by having a low rib on the midline of sternite XIV, whereas in females the sternite XIV is produced ventrally, often bearing a minute knob at its extremity. (See also under Relationships.)

### GROWTH

There are various estimates of the rate of growth of *P. a. aztecus* at different sizes and under different environmental conditions. Pearson (1939) reported that postlarvae of "*P. brasiliensis*," which most probably were *P. a. aztecus*, held in the laboratory grew at a maximum rate of 0.56 mm. per day. Zein-Eldin and Aldrich (1965) studied in the laboratory the growth of postlarvae 12.1 mm. t.l. at temperatures ranging from 7° C. to 35° C. through a 28-day period. They concluded that growth increased with temperature, with significant growth beginning at some temperature above 11° C. but below 18° C. The most marked increase in growth rate occurred in the temperature region between 11° C. and 25° C., and the maximum increase was 1.4 mm. per day at 32° C. and 1.1 mm. per day at 25° C. Almost no growth occurred at 11° C.

Ringo (1965), using the difference in size between the largest shrimp in successive collections, calculated that in Galveston Bay, Tex., young brown shrimp grew an average of 0.1 mm. t.l. per day from March to early April; as temperature rose the rate of growth increased to an average of 1.7 mm. per day and reached a maximum of 3.3 mm. per day during late May. This growth rate is the highest reported for any *Penaeus* from the Gulf of Mexico and the western Atlantic.

Loesch (1965) estimated that in Mobile Bay, Ala., very young shrimp (20 mm. mean t.l. at the beginning of the investigation) grew at an average rate of as much as 50 mm. t.l. per month in spring, and juveniles and subadults increased 24 to 43 mm. t.l. per month during summer and 12 to 35 mm. t.l. in winter. St. Amant et al. (1966) studied the growth of *P. a. aztecus* in the Barataria Bay, La., area during March, April, and May from 1962 to 1965. Growth varied, the range of variation was from no growth to 2.5 mm. per day. They stated that "There appeared to be a trend, though not completely evident in these data, for the growth of brown shrimp to be less than 1.0 mm per day when the water temperature was below 20C and less than 1.5 mm per day when the water temperature was below 25C. Little or no measurable growth was noted at cumulative average water temperatures below 16C."

Klima and Benigno (1965), through a mark-recapture experiment in Mississippi, estimated that during a 4-week period in summer, nearshore, male brown shrimp grew from 104 mm. in total length to 132 mm., and females from 104 mm. to 135 mm.—monthly increases of about 28 mm. and 31 mm., respectively. Chin (1960), on the basis of length-weight relation, assumed that in Galveston Bay, Tex., the growth rate for the sexes is almost identical.

Williams (1955a), taking the upper extremes of size distribution, estimated that in North Carolina the mean length of juveniles increases at a rate of 45.7 mm. per month from April to June. This growth is slightly less than that of *P. d. duorarum*, but still extremely rapid. Joyce (1965) estimated a similar growth rate of 45 mm. per month for brown shrimp in northeast Florida.

### SEX DIFFERENCES IN SIZE

The largest female on record, 236 mm. t.l., was reported by Renfro (unpublished data) from south of Morgan City, La., in 60 fm. The largest males, also reported by Renfro, were 195 mm. t.l.—one from off Galveston, Tex., in 60 fm. and one from southeast of Morgan City, La., in 45 fm. The survey of the northern Gulf of Mexico population by Renfro and Brusher (1964) indicated that size of shrimp varies with depth and, to some extent, distance from shore. Regardless of time of the year, the mean length of brown shrimp increased with increasing depth.

Brown shrimp exhibit a sex-size difference (females are larger than males) which becomes evident upon attainment of a length of about 100 mm. (Williams, 1955a). Burkenroad (1939) attributed the difference in size in offshore individuals to a longer life among females.

## Ecology

### FOOD

Brown shrimp are omnivorous, feeding upon different plants and animals as well as organic debris. (See also under Food in the discussion of *Penaeus setiferus*.)

### SUBSTRATE

Juveniles of *P. a. aztecus* prefer muddy or peaty bottoms, but they also live on sand, silt, or clay frequently mixed with fragments of shells and rocks. They usually abound in areas covered with vegetation and plant debris (Williams, 1959). The adults prefer a substrate softer than the sympatric *P. d. duorarum* (Hildebrand, 1954; Kutkuhn, 1962). They are abundant on mud or silt bottoms and, occasionally, where the bottom consists of mud, sand, and shell.

### DIEL CYCLE

Adult brown shrimp are mostly nocturnal and are usually taken at night, but, according to Springer and Bullis (1952), "The difference in the catch rate between day and night fishing is not so well marked in deeper parts of the range." Juveniles are more active diurnally than adults and can be highly active during the daytime—a fact clearly established by the sampling carried on by Joyce (1965), who took about 71 percent of his *P. a. aztecus* juveniles by day.

Information on the diel activity of postlarvae in approaching inshore waters appears to be somewhat conflicting. St. Amant et al. (1966) found no discernible difference between nocturnal and diurnal catches of postlarvae moving into the greater Barataria Bay, La., area, whereas Copeland and Truitt (1966) captured most of the postlarvae at night at Aransas Pass, Tex., inlet, and Baxter and Furr (1964) estimated that 70 percent of the postlarvae in their samples at the entrance of Galveston Bay, Tex., were caught between 9 p.m. and 6 a.m. Copeland and Truitt (1966) also reported that during the day no significant difference could be detected between surface and bottom samples and suggested that "Perhaps, penaeid postlarvae actively pursue the upper layers (even during the day) to take advantage of faster currents on the surface." Rearing experiments by Cook (1965) indicated that larvae are positively phototropic, for when reared under an overhead light they swim to the surface.

The effects of phases of the moon on the behavior of brown shrimp have not been well established. Hildebrand (1954) stated that some shrimpers maintain that fishing for brown shrimp is most successful during the full moon, but that others believe that catches do not change substantially at any moon phase. Copeland (1965) found that peak seaward migrations of brown shrimp through Aransas Pass, Tex., inlet occurred at times of full moon.

### MOVEMENTS

The larvae of *P. a. aztecus* move from the high-salinity waters of the spawning grounds toward brackish waters where they arrive as postlarvae.

It was generally believed that larvae and postlarvae moved toward estuaries and that the latter entered them directly. Temple and Fischer (1967), however, have gathered evidence that in the northwestern Gulf of Mexico "brown shrimp larvae and postlarvae, or both, overwinter in waters of the Continental Shelf."

Postlarvae enter the nursery grounds at 8 to 14 mm. t.l. (Baxter and Renfro, 1967). They move into the estuaries on flood tides (St. Amant et al., 1966; Copeland and Truitt, 1966). Major postlarval brown shrimp influx into the nursery areas occurs earlier—in late winter or early spring—than do those of the sympatric *Penaeus*. Studies by Baxter and Renfro (1967) showed that postlarvae were scarce in the entrance of Galveston Bay and in Galveston Island Beach, Tex., throughout most of the winter. Their number increased rapidly and reached a peak between mid-March and mid-April. After the spring peak few postlarvae were caught until mid-June when their number increased again and reached a second peak in August and September. Copeland and Truitt (1966) in Aransas Pass, Tex., inlet observed two similar peaks of postlarval abundance. St. Amant et al. (1966) reported that in Barataria Bay, La., peak catches of postlarvae occurred in April in 1962 and 1963, in February in 1964, and in March in 1965. Christmas et al. (1966) first took postlarvae of brown shrimp in Louisiana in February. They observed that the period of inshore movement lasted through September and that few individuals were present during October and November.

Studies by Villalobos et al. (1967) in Laguna de Alvarado, Veracruz, Mexico, showed that postlarval stages of *P. a. aztecus* were abundant in March (dry season); in contrast, none were found during August (rainy season). In South Carolina, Bearden (1961) found the greatest abundance of postlarvae in February and March. Williams (1955a, 1965) collected postlarvae in the sounds of North Carolina from October to May and reported the peak of abundance from late March to early April.

The postlarvae molt to the juvenile stage 4 to 6 weeks after they arrive in estuaries (Parker, 1966). A number of investigators have studied the occurrence of juveniles and subadults in the nursery grounds of the United States adjacent to the Gulf of Mexico (Gunter, 1950; Ingle, 1957; Chin, 1960; St. Amant et al., 1966; Trent, 1967). Brown shrimp juveniles begin to appear in small numbers in the estuarine waters of Texas and Louisiana late in March or early in April. Their numbers increase to a maximum in May and June. They are abundant in July and August, become increasingly scarce from September to the end of October, and are almost absent during late fall and winter. Seaward migration begins and rapidly intensifies in May or June through August. Tabb, Dubrow, and Jones (1962) found that *P. a. aztecus* is extremely rare in the estuaries adjacent to Florida Bay, because only a few young specimens were taken during their extensive sampling from April through August.

Several investigations have also been conducted on the seasonal abundance of juveniles in the nursery grounds of the eastern United States. In St. Lucie estuary, eastern Florida, Gunter and Hall (1963) found the smallest specimens of brown shrimp in January, February, May, and October and suggested that summer and fall were the periods of least abundance. Joyce (1965) concluded that in northeast Florida juveniles first appear in the nursery grounds in early May, or probably earlier; their number increases considerably in June to reach a maximum in July. In August, as subadults, they migrate toward the sea, few remain in September and October, and almost none from November to March. In North Carolina, Williams (1955a, 1959) found juveniles from mid-April throughout the summer [to November, according to a graph in his 1955a publication]; peak abundance was in the first half of May. The information above strongly suggests that in the brackish waters of North Carolina to northeast Florida juveniles appear in large numbers in April, reach a peak of abundance during the period May through July, and their numbers decline from August through October.

Brown shrimp leave inshore waters at different sizes. Copeland (1965) reported that brown shrimp move out to sea at 70 to 80 mm. t.l. Sampling by Joyce (1965), in turn, indicated that brown shrimp emigrate offshore at an average size 100 to 105 mm. t.l. Recently, Trent (1967) reported that the length of shrimp leaving the estuaries ranges from 60 to 130 mm. t.l., and that the size of those moving out of Galveston Bay, Tex., in 1966 increased as the season of emigration progressed.

Evidence is strong that shrimp migrate from inshore waters to sea during ebb tides. Copeland (1965) reported peak abundance of shrimp leaving through Aransas Pass, Tex., inlet on the ebb tide and usually during the full moon.

Information on migrations of brown shrimp after they leave estuaries is rather meager. Mark-recapture experiments by Klima (1964) indicated that in Texas most individuals moved parallel to the coast and remained within 48 km. of the release site in waters 16 to 30 fm. deep. In Texas and Louisiana, a large proportion of the marked small shrimp were recovered also within 48 km. of the release area. One individual, however, was caught about 314 km. away, the longest distance known to have been traveled by a brown shrimp. Studies by Klima and Benigno (1965) suggested that along the Mississippi Coast shrimp did not move great distances from the release site, at least during the summer; the most rapid migration observed was at a rate of 4.32 km. per day. These experiments, as well as a previous one by Inglis (1960), also indicate that at least part of the annually recruited population in the northern Gulf moves from east to west. There are also indications that brown, like white shrimp, migrate southward along the northeast coast of Mexico, from late summer through winter. This movement was first suggested by Gunter (1962c), who pointed out that the average monthly production from Texas waters suggested a southward drift, and later Klima and Benigno (1965) found that some of the shrimp marked off Port Aransas, Tex., in August moved south; one individual traveled 104 km. in a southerly direction.

Along the Atlantic Coast of the United States some brown shrimp move northward during the summer, apparently from the northernmost spawning grounds off North Carolina. In the lower portion of Chesapeake Bay juveniles and subadults are caught during summer and fall; information gathered from different laboratories suggests that only occasionally do brown shrimp move farther north along the coast. Such a movement seems to have taken place during the sampling reported by Burkenroad (1939) in Delaware Bay and southern New Jersey. Brown shrimp were first taken at the end of August (minimum of 13 mm. c.l. in males and 17 mm. c.l. in females), and they were no longer there at the end of October. Because no small juveniles were collected through the sampling period and because 2 months before shrimp arrived the water had reached higher temperatures than were registered when they were presumably leaving the area, Burkenroad concluded that juveniles had migrated from southern waters where spawning and larval development occurred. Small individuals have been caught as far north as southern Martha's Vineyard, Mass., but the small number of records strongly suggests that only rarely do stragglers reach that latitude. As a result of their mark-recapture experiment in North Carolina, McCoy and Brown (1967) stated that brown shrimp leaving Beaufort Inlet moved southward from June through October. The record migration was about 241 km. in 5 weeks.

## EFFECTS OF TEMPERATURE

Temperature greatly influences survival and growth of brown shrimp. Laboratory experiments by Zein-Eldin and Aldrich (1965) indicated that postlarvae can tolerate wide fluctuations in temperature and salinities, but are adversely affected by extreme temperatures. Postlarvae survived temperatures from 11° C. to 30° C., at salinities of 21 to 40 p.p.t.; at temperatures below 15° C., however, their tolerance to low salinities (below 10 p.p.t.) decreased, and near 35° C. survival was reduced regardless of salinity. The authors suggested that the combined effect of low temperature and low salinity could be partly responsible for the time of postlarval influx into estuarine waters because they do not seem to enter estuaries until the temperature has increased to a degree that low salinities are not harmful. They further suggested that temperature may have a decisive effect on survival of postlarvae in estuaries because if the temperature becomes lower in an environment of intermediate temperature (18° C.) and low salinity, the survival rate will be adversely affected.

Experiments by Aldrich et al. (1967) showed that postlarval *P. a. aztecus* regularly burrowed into a silty clay substrate as temperature fell to 12° to 17° C., and emerged as temperature rose to 18° to 22° C. The postlarvae of brown shrimp, thus, may "hibernate" in burrows for a portion of the winter.

Williams (1960) investigated the influence of temperature on osmotic regulation in young brown and pink shrimps. He found that the brown shrimp have a less efficient osmoregulatory mechanism in low temperatures than do pink shrimp; at temperatures of 8.7° to 8.8° C. the brown shrimp's ability to regulate is impaired and its blood tends toward isotonicity. This difference may explain, in part, why brown shrimp do not winter in the estuaries of North Carolina whereas pink shrimp do. On the other hand, the brown shrimp seems to have a greater tolerance to lower temperatures than does the white shrimp. *P. a. aztecus* ranges farther north; intensive spawning seems to begin in late winter or early spring in the cold waters of North Carolina, at least 2 months earlier than that of *P. setiferus;* and postlarval movement into inshore waters begins earlier and ends later than that of *P. setiferus.*

Temperature also has a pronounced effect on growth. The studies by Zein-Eldin and Aldrich (1965) indicated that postlarvae were able to grow in a wide range of salinity, but that growth was arrested at low temperatures. Postlarvae survived but did not grow at 11° C. and 15 p.p.t. salinity, whereas growth rate increased with rises in temperature, the maximum occurred between 18° and 25° C. Experiments by Zein-Eldin and Griffith (1965) indicated that temperature affects growth of postlarvae of brown shrimp, as it does those of white shrimp, by hastening molts rather than by increasing the increment per molt. Cook (1965) determined that temperature also greatly affects the growth of larvae; the optimum range was 28° to 30° C. (see also under Growth).

Although the precise effects of extreme temperatures are largely unknown, shrimp exposed to 30° C. and above become flaccid and perish rapidly when handled. Zein-Eldin and Aldrich (1965) estimated that the maximum tolerable temperature for postlarvae is probably only slightly above 35° C. The lowest temperature that they can tolerate is not known, but Gunter and Hildebrand (1951) reported a mass narcosis of the young at 4.4° C. and below.

### EFFECTS OF SALINITY

Field observations indicate that juvenile and subadult brown shrimp, like pink shrimp and white shrimp, are able to withstand a wide range of salinity. Gunter and Hall (1963) reported that small juveniles (28–38 mm. t.l.) were taken in St. Lucie estuary, Fla., at salinities of 0.22 p.p.t. and 0.36 p.p.t.; Loesch (*In* Gunter et al., 1964), found *P. a. aztecus* in Mobile Bay, Ala., at 0.0 to 1.00 p.p.t., the lowest range of salinity at which this subspecies has been reported. At the other extreme, Simmons (1957) in Laguna Madre, Tex., collected specimens in salinity of 69 p.p.t. Experiments by Zein-Eldin (1963a) showed that at constant temperatures of 24.5° to 26° C., postlarval *P. a. aztecus* survived and grew over a range of salinities of 27 to 40 p.p.t. Later, Zein-Eldin and Aldrich (1965) demonstrated that postlarval brown shrimp withstand a wide range of salinity-temperature combinations except at extreme temperatures (see above).

Although juveniles of *P. a. aztecus* tolerate a wide range of salinity, their optimum seems to be higher than that of *P. setiferus.* In North Carolina, Williams (1955b) found only small populations of brown shrimp juveniles on low-salinity nursery grounds, where *P. setiferus* was most abundant. Gunter et al. (1964) stated that in the bays of Texas, young brown shrimp "are found in the greatest abundance within the salinity range 10 to 30, and with considerably higher concentrations at salinities above 20 than at salinities below 10. This is in considerable contrast to the white shrimp in the same bodies of water, which are found at the greatest abundance below 10." Joyce (1965) concluded that although in northeast Florida the nursery grounds of *P. a. aztecus* overlap those of *P. setiferus*, the former are generally more saline than those of the white shrimp.

### ENEMIES AND DISEASES

Like *Penaeus* in general, brown shrimp are prey to many carnivorous teleost fishes (Gunter, 1945; Knapp, 1950; Darnell, 1958). They are also infested by a number of parasites (Sprague, 1950, 1954; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959; Kruse, 1959; Hutton et al., 1962). Aldrich (1965) reported that brown shrimp, like white shrimp, serve as intermediate hosts for *Prochristianella penaei*, a trypanorhynchan cestode, which as an adult lives in the Atlantic stingray, *Dasyatis sabina.*

## Commercial Importance

*P. a. aztecus* is fished along the Atlantic Coast of the United States from North Carolina to about Cape Kennedy, Fla. In North Carolina it ranks first among the three important commercial *Penaeus* found in the region, but farther south *P. setiferus* is taken in larger quantities than is *P. a. aztecus* (Anderson and Lunz, 1965; Lyles, 1967). Along the northern Gulf of Mexico, brown shrimp are taken commercially from Apalachicola, Fla., to northeast Tamaulipas, Mexico. The largest catches made in the region are along the Texas Coast. Farther south in Mexican waters, brown shrimp are caught from the southeasternmost end of Tamaulipas, along the coast of Veracruz, Tabasco, and the southwestern part of the coast of Campeche. The grounds off the latter two States are by far the most important.

According to Lyles (1967), the brown shrimp was the most valuable shrimp in the United States in 1965, as it was from 1956 to 1963 (in 1964 white shrimp landings exceeded those of brown shrimp). In 1965, of a total landing of 99,890,237 kg. (whole weight) of *Penaeus* shrimps, *P. a. aztecus* made up 49,264,265 kg. or about 49 percent of the landings.

## ***Penaeus* (*Melicertus*) *aztecus subtilis*** **PÉREZ FARFANTE**

Figures 51 to 59

Nicaragua: camarón café. Venezuela: camarón marrón, langostino amarillo. Guyana: short feelered prawn. Brazil: camarão lixo, camarão vermelho, camarão branco. United States: brown shrimp, dark shrimp.

*Penaeus brasiliensis:* Rathbun, 1897: 46 [part]; Rathbun, 1901: 100, 101 [part]; Pesta, 1915: 113 [part]; Burkenroad, 1934: 92 [part]; Schmitt, 1935: 128, 129 [part?]; ?Magalhães Filho, 1943: 12–26, figs. 1–6. Not *P. brasiliensis* Lat., 1817.

*Penaeus braziliensis:* Moreira, 1901: 6, 7, 72 [part].

*Penaeus aztecus:* Burkenroad, 1939 [part "Form B"]: 20, 27, 34–45, figs. 28, 29, 34; Anderson and Lindner, 1945: 305 [part]; Whiteleather and Brown, 1945: 25; Holthuis, 1948: 1104, 1105; Holthuis, 1950: 27; Sánchez Roig and Gómez de la Maza, 1951: 113; Pérez Farfante, 1953: 233, 234, 237 (238, 241 [part]); Pérez Farfante, 1954a: 97; Pérez Farfante, 1954b: 29; Lindner, 1957: 11–15, 21, 22, 65, 153, 154, 162, 165; Lindner, 1958: 33; U.S. Fish and Wildlife Service, 1958a: 11, 13; Bullis and Thompson, 1959a: 33–35, 41; Bullis and Thompson, 1959b: 1, 6, 9; Holthuis, 1959: 42–44, 47, 63–67, fig. 6b; Eldred and Hutton, 1960: 91, 106, 108; Pérez Farfante et al., 1961: 40, 48, 56, 57, 61, 64; Anonymous, 1962: 56; Miles, 1962: 189, 193; Boschi, 1963: 26–29 [part], figs. 8 (3, left), 11; Davant, 1963: 9, 12, 18–20, 32, 34, 35, 68, 74–76, 85–89, 91, figs. 6, 15, 16a, b, 17a, b, 18, and bis; Simpson, 1963: 22, 23, fig. 15; Boschi, 1964: 39 (40, 41 [part]); Ewald, 1964: 10, 20–23 (24, 28, and tables [part]); Cervigón, 1965: 21; Ewald, 1965a: 29; Ewald, 1965c: 52, 59, 65, 67, 70, 72, 74, 80, 82, 84–87, 91, 93–96, 114 (72, 80, 88–90, 92, 97–99, 113, fig. 13 [part]); Holthuis and Rosa, 1965: 4 [part]; Pericchi López, 1965: 23; Simpson et al., 1965: 77; Williams, 1965: 25, 26; Croker, 1967: 63, 68, 73, 74, 79–81, 84, 87, 95, 98, 105, 106; Instituto de Fomento Nacional, 1967: 5, 8.

*Penaeus astecus:* Whiteleather and Brown, 1945: 27.

*Penaeus aztecus subtilis* Pérez Farfante, 1967: 87–94, fig. 2a, b (holotype, ♂, USNM 119130, off Gallinas Point, Departamento de la Guajira, Colombia, 95 fm., October 9, 1965, *Oregon* Sta. 5685, lat. 12°29′ N.; long. 71°54′ W.)

Brown shrimp: Higman, 1959: 8, 10, 12–14.

## Study Material

For list of records see Pérez Farfante, 1967.

## Diagnosis

Adrostral sulcus relatively short, narrow posteriorly, either tapering to a point or turning laterally and broadening slightly at the end. Median sulcus short, ending well anterior to posterior end of adrostral sulcus, shallow, and often interrupted. Dorsolateral sulcus usually narrow. Petasma with distal portion of ventral costa increasing gradually in width proximally and turning in arc; unarmed along free border and with elongated group of closely set small teeth on attached border; apex of costa adnate to membranous portion of ventrolateral lobule; latter rather extensively covered with spines; distal fold small, usually with numerous spinules, but sometimes unarmed. Thelycum with anterior process relatively broad, and with anteriorly bifurcate median carina on posterior process; lateral plates with anteromedian angles widely divergent, leaving median carina exposed.

## Description

### ROSTRUM

Teeth $\frac{6\text{–}10}{1\text{–}2}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—57, 9/2—27, 7/2—7, 10/2—5, 8/1—1, 9/1—1, 7/1—1, 6/1—1, N=200)+ epigastric; position of ventral teeth variable, first tooth situated from well anterior to slightly posterior to last dorsal tooth; rostrum long, in larger juveniles and subadults reaching to base of distal one-third of thickened portion of lateral antennular flagellum, attaining maximum length in relation to carapace length at 18 to 23 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.85); decreasing progressively with increasing length of shrimp, rostrum reaching midlength of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.50); rostrum usually strongly sinuous, proximal half convex, distal half with dorsal margin strongly concave; highest portion of blade at level of second or third dorsal tooth; latter level with anterior margin of carapace; rostrum tip $\frac{1}{4}$ to almost $\frac{1}{3}$ r.l. Postrostral carina strong, usually expanded in anterior half, and usually short, ending well anterior to posterior margin of carapace. Median sulcus shallow, usually interrupted, short, ending well anterior to posterior margin of carapace. Adrostral sulcus typically narrow posteriorly, $\frac{1}{5}$ to $\frac{3}{4}$ width of postrostral carina, tapering to point posteriorly or turning laterally and broadening slightly at end; sulcus usually short, ending $\frac{1}{6}$ to $\frac{1}{14}$ c.l. from posterior margin of carapace, occasionally ending $\frac{1}{15}$ to $\frac{1}{19}$ c.l. from carapace margin. Adrostral carina prominent anteriorly, sharp on carapace, same length as adrostral sulcus.

### CARAPACE (fig. 51 a, b)

Length in proportion to total length smaller in juveniles, increasing slightly at about subadult stage. Gastrofrontal sulcus broad, extending to about one-fifth c.l. Gastrofrontal carina sharp, turning slightly posterodorsally, ending in acute orbital angle anteriorly. Orbito-antennal sulcus wide anteriorly, narrowing posteriorly to below apex of hepatic spine, there widening again into base of spine. Gastro-orbital carina very pronounced, occupying approximately posterior four-fifths of distance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus deep along entire length, $\frac{1}{5}$ to $\frac{1}{4}$ c.l., ending slightly anterior to midlength of carapace. Hepatic carina $\frac{1}{5}$ to $\frac{1}{4}$ c.l., sharp, sloping anteroventrally to end $\frac{1}{22}$ to $\frac{1}{18}$ c.l. from anterior margin of carapace. Antennal spine very prominent; hepatic spine pronounced and acute.

### ANTENNULES

Lateral flagellum relatively long, two-thirds length of antennular peduncle, slightly longer than median flagellum and with articles shorter than those of median flagellum. Anterolateral spine small, sharp; stylocerite acuminate, reaching slightly beyond midlength of first antennular segment. Prosartema reaching distal end of proximal one-fifth of second antennular segment.

### ANTENNAE

Length of scaphocerite $2\frac{1}{2}$ times maximum width; its length relative to carapace length decreasing slightly with growth; spine reaching basal thickened portion of antennular flagellum. Carpocerite about $1\frac{1}{3}$ times longer than wide. Antennal flagellum relatively short, $1\frac{1}{2}$ times total length.

### THORACIC APPENDAGES

Third maxilliped reaching at least end of first antennular segment and at most two-thirds length of second antennular segment; length of dactyl three-fifths that of propodus. First pereopod reaching only to midlength of carpocerite and at most exceeding it by entire length of dactyl. Second pereopod exceeding carpocerite by at least length of dactyl and at most by one-quarter length

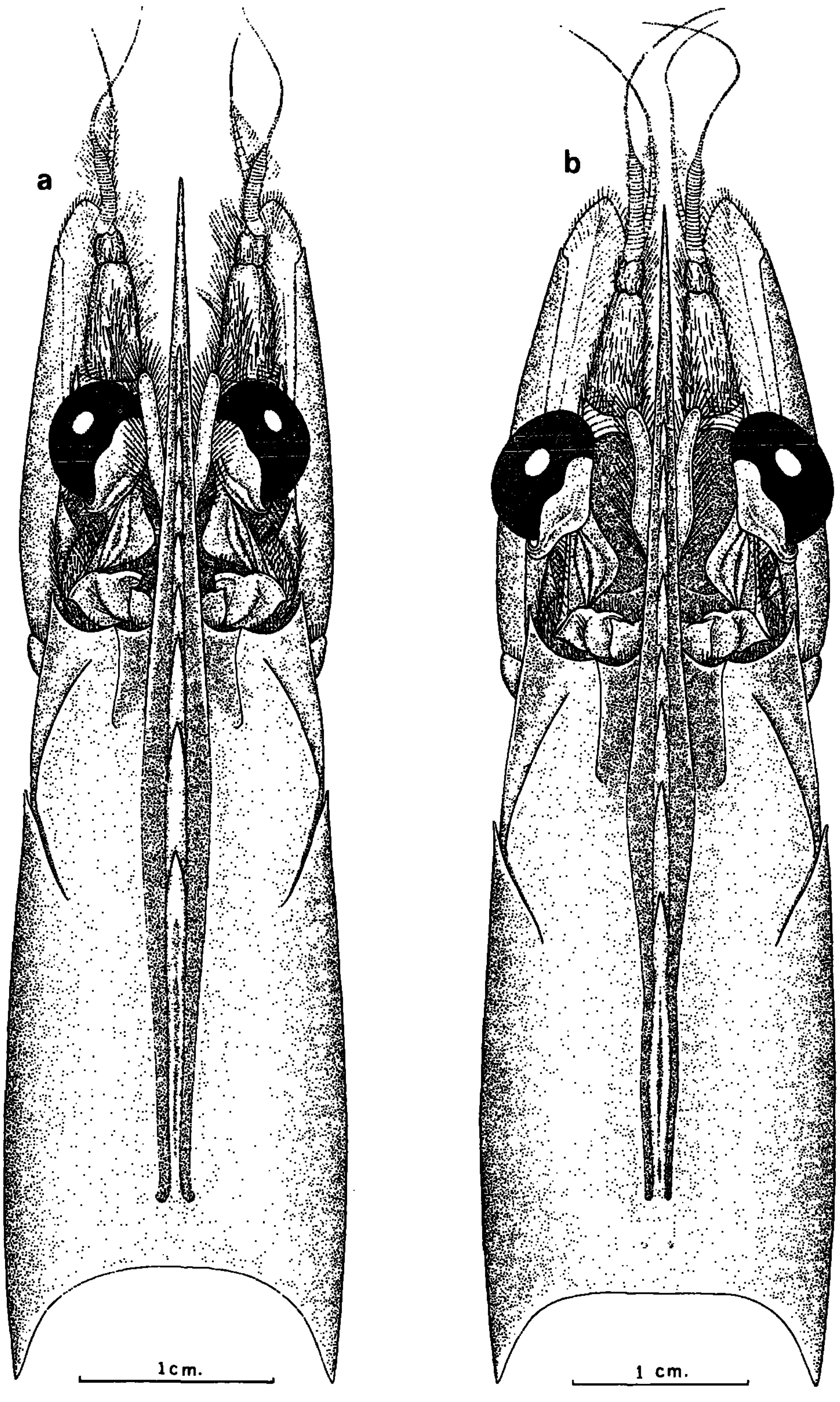

**Figure 51.**—*Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante. a. Cephalothorax, ♀ 36 mm. c.l., Gulf of Venezuela, Venezuela. b. Cephalothorax, ♀ 35 mm. c.l., off mouth of Surinam River, Surinam.

of carpus. Third pereopod reaching at least to distal half of second antennular segment and at most exceeding peduncle by entire length of dactyl. Fourth pereopod reaching at least midlength of carpocerite and at most exceeding it by entire length of dactyl. Fifth pereopod equal in length to fourth or surpassing it by ⅕ to ½ length of dactyl. Exopods on all pereopods. Long ischial and basial spines on first pereopod; rather long basial spine on second pereopod.

### ABDOMEN

Carinate dorsally from posterior half of fourth somite posteriorly, carina gradually increasing in height posteriorly to form median keel on sixth somite, ending in sharp spine on posterior margin. Dorsolateral sulcus (fig. 52) usually narrow, ratio of height of keel to width of sulcus from 2 to 8.5, modally 3 in the Caribbean region and eastern Brazil (fig. 53), and 3.5 from the Gulf of Paria to Camocim, Brazil (fig. 55); in the Caribbean region and eastern Brazil modal value of K/S is 3 or less in all size classes (fig. 54) whereas in the Gulf of Paria to Camocim modal values of K/S range from 2 to 8 in the various size classes, although figure 56 shows a strong tendency toward a grouping of these values around 4; range of K/S is same in males and females; dorsal lip of dorsolateral sulcus rounded, ventral lip sharp. Sixth abdominal somite with three prominent cicatrices on each side, anterior one the longest; fifth abdominal somite with one cicatrix and series of minute pits anterior to sinus on posterior margin of somite; fourth abdominal somite with similar series of pits dorsal to sinus on posterior margin of somite. Telson unarmed, with deep median sulcus and sharp pointed tip.

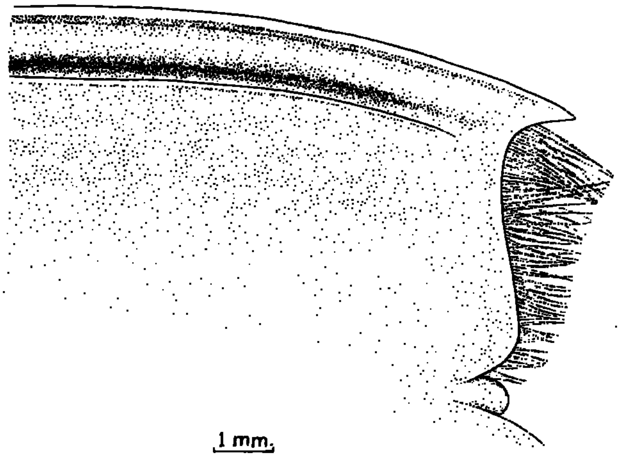

FIGURE 52.—*Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante, sixth abdominal somite, posterodorsal portion, ♀ 36 mm. c.l., Gulf of Venezuela.

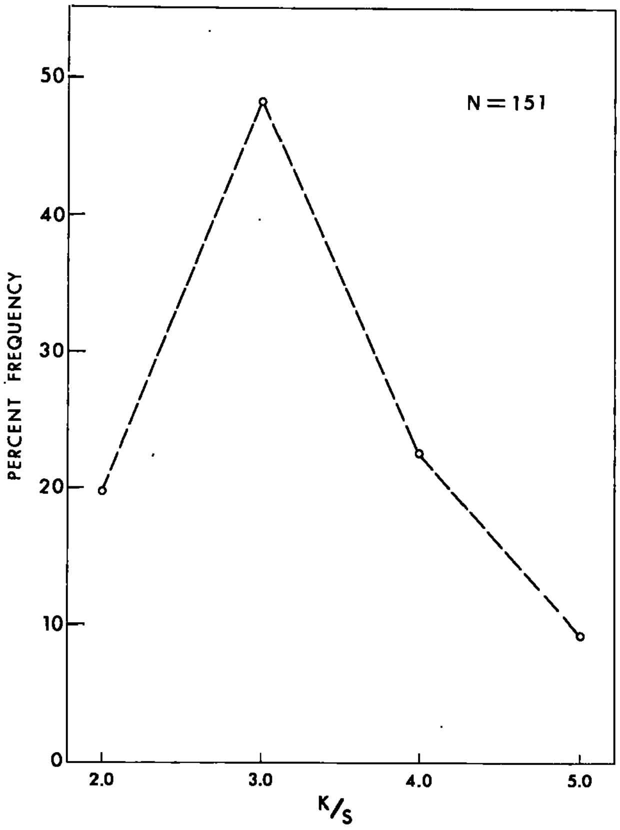

FIGURE 53.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante from the Caribbean region and eastern Brazil.

### PETASMA (fig. 57)

Ventral costa increasing uniformly in width proximally, mesiodistal portion forming gentle arc, distal portion unarmed along free border—rarely with two or three widely spaced spinules—and with two to four series of small teeth arranged in elongate, narrow patch on attached border; apex of costa adnate to adjacent membranous portion of ventrolateral lobule, latter with extensive armature of thickly set spines. Distal fold rather small, usually armed with spinules, often in large numbers, but occasionally plain. Distomedian projections rather thick, and short, overhanging slightly distal portion of ventral costae.

### APPENDIX MASCULINA

Relatively elongate, length 1⅖ to 1⅗ times maximum width, armed with strong, short spines along slightly concave outer margin and with longer

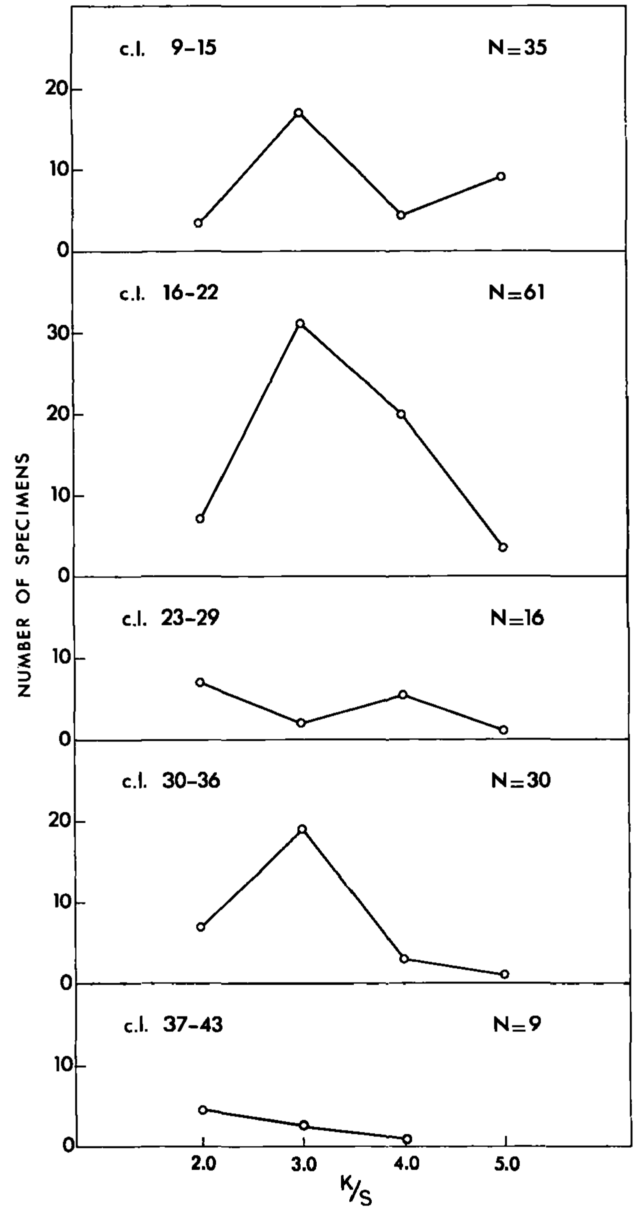

FIGURE 54.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante of different size classes from the Caribbean region and eastern Brazil.

spines along distomedian margin. Anterior surface subplane, posterior surface strongly concave, with sharp longitudinal ridge projecting from median margin.

### THELYCUM (fig. 58)

Anterior process projecting ventrally in sharp, relatively low, marginal arc-shaped ridge, often expanding on both sides, and surrounding shallow depression with knob usually present at center.

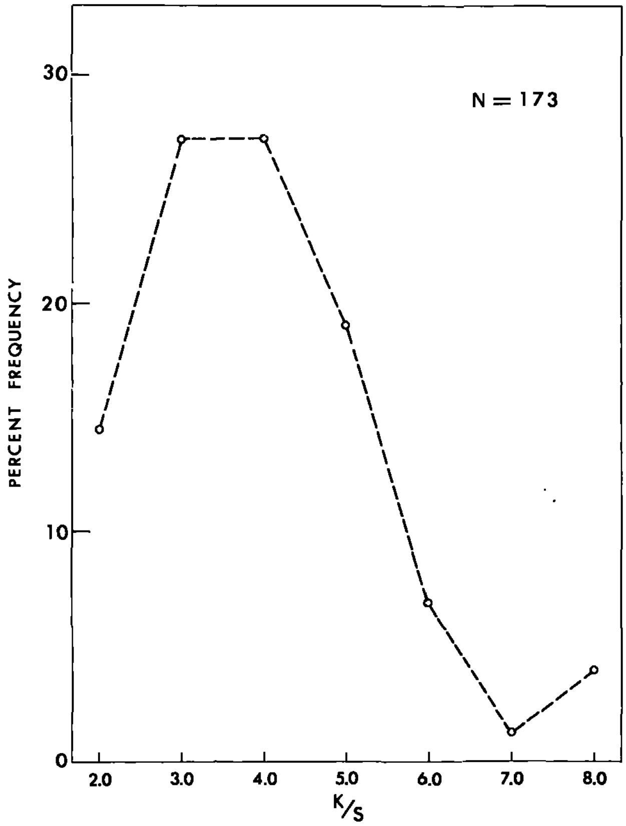

FIGURE 55.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante from the Gulf of Paria to Camocim, Brazil.

Posterior process broad, with anteriorly bifurcate median carina, resulting ribs turning medially and converging at base of anterior process, giving rise to diamondlike structure; enclosed area deeply concave or almost flat, plain, or, more often, bearing median rib anteriorly, posteriorly, or along entire length.

### COLOR

*P. a. subtilis*, although variable in color, is most often brown—thus, the name camarón marrón (brown shrimp) in Venezuela, and camarão lixo (dirty shrimp) in Brazil. Grayish brown or yellowish specimens are rather common, and in some localities individuals are translucent pale yellow and are called camarão branco (white shrimp) in Brazil.

According to Holthuis (1959) and Davant (1963), no large dark spots have been observed on the sides, at the junction of the third and fourth abdominal somites, in this shrimp, at least in those along the northern and northeastern coasts of South America.

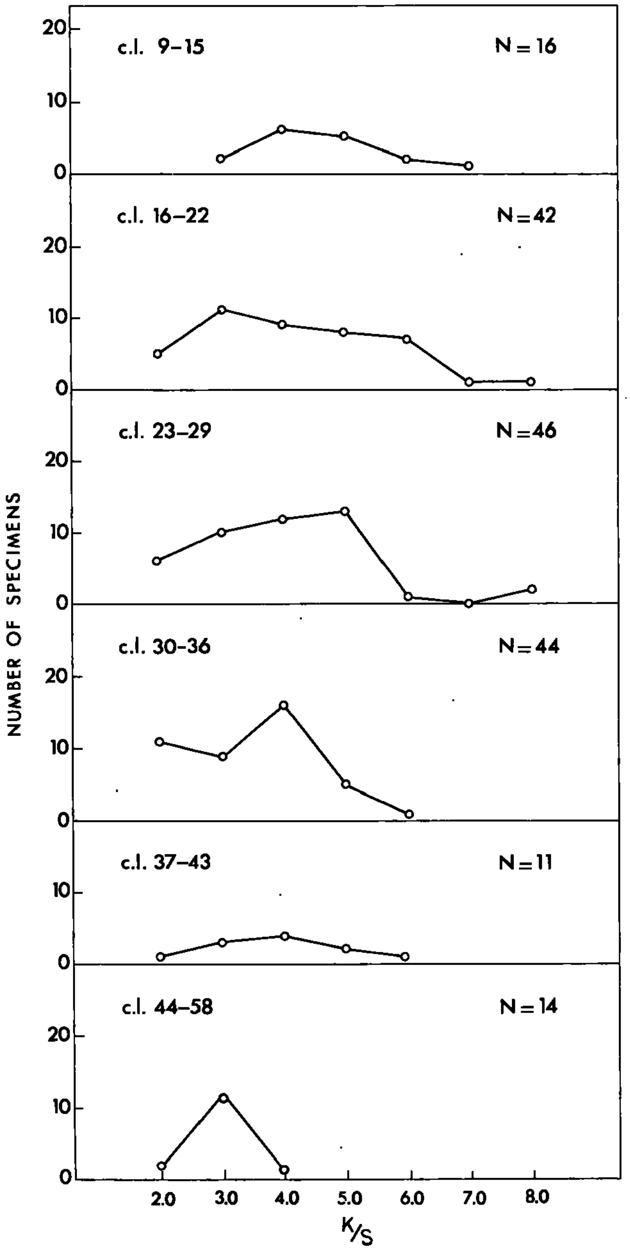

FIGURE 56.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante of different size classes from the Gulf of Paria to Camocim, Brazil.

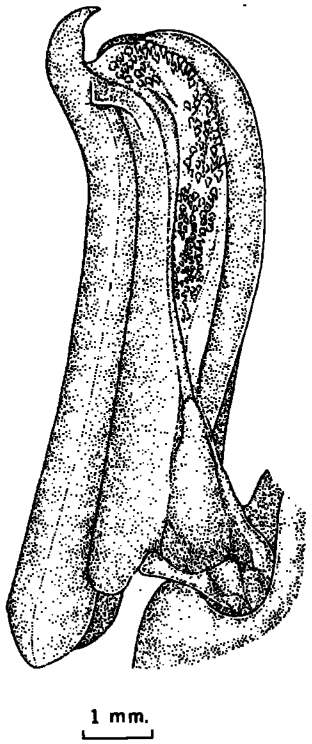

FIGURE 57.—*Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante. Petasma, lateral view, ♂ 34 mm. c.l., off Punta Gallinas, Departamento de la Guajira, Colombia.

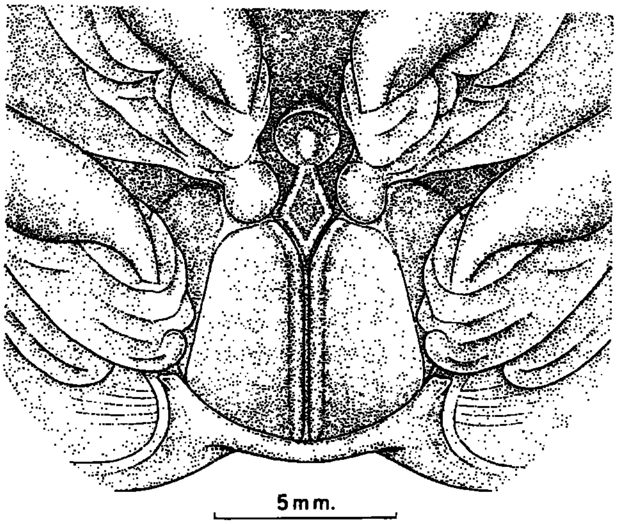

FIGURE 58.—*Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante. Thelycum, ♀ 45.5 mm. c.l., off Isere Point, French Guiana.

## Distribution and Morphological Variations

*P. a. subtilis* ranges from Cuba through the Antilles and from Honduras throughout the Caribbean Coast of Central and South America and the Atlantic Coast of South America to at least Cabo Frio, Brazil. Burkenroad (1939) reported and illustrated specimens of this subspecies from "Rio de Janeiro" (fig. 49). The distribution of the dark shrimp is far from uniform, because population densities differ greatly over its range. It is scarce on the northern coast of Cuba and rare on the southern coast, except in Oriente province, where I collected many specimens in the bays of Guantánamo and Santiago de Cuba. It is not common in the rest of the Greater Antilles, the Virgin Islands, and the Lesser Antilles. *P. a. subtilis* is moderately abundant in some areas along the coast of Central America.

Croker (1967) did not cite this subspecies as constituting part of the commercial catches in the northeast coast of South America, but collections from that region identified by Holthuis (1959), Bullis and Thompson (1959a, b), and me show that *P. a. subtilis* is not only present, but is apparently rather abundant in the area. Curiously enough, whereas Croker reported *P. d. notialis* as present in the commercial catches, Holthuis recorded but a single female of *P. d. notialis* from Surinam, and Bullis and Thompson did not find it along the northeast coast of South America. *P. a. subtilis* abounds along the southernmost part of its range.

*P. a. subtilis* has a rather wide bathymetric range; it has been caught in waters as deep as 105 fm., NE. of Punta de Gallinas, Departamento de la Guajira, Colombia (*Oregon* Sta. 5684, lat. 12°30′ N., long. 71°48′ W.), at 100 fm., west of Cabo de la Vela, Colombia (*Oregon* Sta. 4913, lat. 12°09′ N., long. 72°47′ W.), and at 95 fm. off Punta de Gallinas, Departamento de la Guajira, Colombia (*Oregon* Sta. 5685, lat. 12°29′ N., long. 71°54′ W.), the type locality.

The population of *P. a. subtilis* from the Gulf of Paria to the neighborhood of Camocim, Brazil, as discussed by Pérez Farfante (1967), is distinguishable from the populations at both ends of the range of the subspecies. In the Paria-Camocim population, the adrostral sulci are shorter (fig. 59) (ending ⅕ to $\frac{1}{11}$ of the length of the carapace from its posterior margin), shallower and acuminate posteriorly, and the rostrum is longer and more sinuous. Many individuals, however, show feeble indications of the posterior portion of longer adrostral sulci as well as isolated pits where these sulci would seem to have terminated. In addition, at both ends of the range of this intermediate population, in the Gulf of Paria, and near Camocim, individuals with the above characters were found intermingled with individuals possessing the characters typical of the shrimp found to the north and south. Also, in Colombia and Venezuela, the ranges of variations of the length and width of the adrostral sulci and the length of the rostrum overlap those of specimens from the Gulf of Paria to northeastern Brazil; figure 59 shows the overlapping in length of adrostral sulci. Furthermore, the ratio K/S is not significantly different throughout the range: in the samples from the Caribbean region and eastern Brazil the ratio K/S is modally 3 and in those from the Gulf of Paria-Camocim, 3.5. In the Caribbean and eastern Brazil areas, K/S ranges from 2 to 5 and at Gulf of Paria-Camocim K/S ranges from 2 to 8, but in only a small percentage of the samples does the K/S reach values above 5. It appears as if the observed differences could be due to environmental conditions, because the intermediate population occupies the area receiving the discharge of the Orinoco and Amazon Rivers.

## Relationships

*P. a. subtilis* differs from all the other grooved *Penaeus* in the western Atlantic by the narrower, shorter, and peculiarly shaped posterior portion of the adrostral sulci and (except from *P. paulensis*) by the shallower, usually interrupted, and shorter median sulcus. It may also be distinguished from typical *P. a. aztecus* by the K/S ratio, which is modally 3.5 (dorsolateral sulcus narrow), whereas in *P. a. aztecus* it is 1.25. Also, females of *P. a. subtilis* tend to have the anterior and posterior processes wider and often the anterior process flat instead of deeply concave. In both subspecies the third pereopod has about the same lengths for each carapace length to 40 mm. c.l.; in larger individuals of *P. a. aztecus* it is longer (compare figures 29 and 38, which show the lengths of the carpus—indicative of the lengths of the third pereopod—for various carapace lengths in *P. a. aztecus* and *P. a. subtilis*, respectively). The third pereopod of *P. a. subtilis* less than 40 mm. c.l. appears shorter than that of *P. a. aztecus* for, at most, it exceeds the antennular peduncle by only the length of the dactyl, whereas in *P. a. aztecus* it exceeds the peduncle by the entire length of the propodus. This apparent difference in length is due to the shorter antennular peduncle in *P. a. aztecus*.

*P. a. subtilis* may be distinguished from its close relative *P. paulensis* (which has a similar ill-defined median sulcus) by the broader dorsolateral sulcus with a rounded dorsal lip and by the sinuous rather than straight rostrum. Moreover, in *P. a. subtilis* males the ventral costa of the petasma has a different shape, and its attached border is

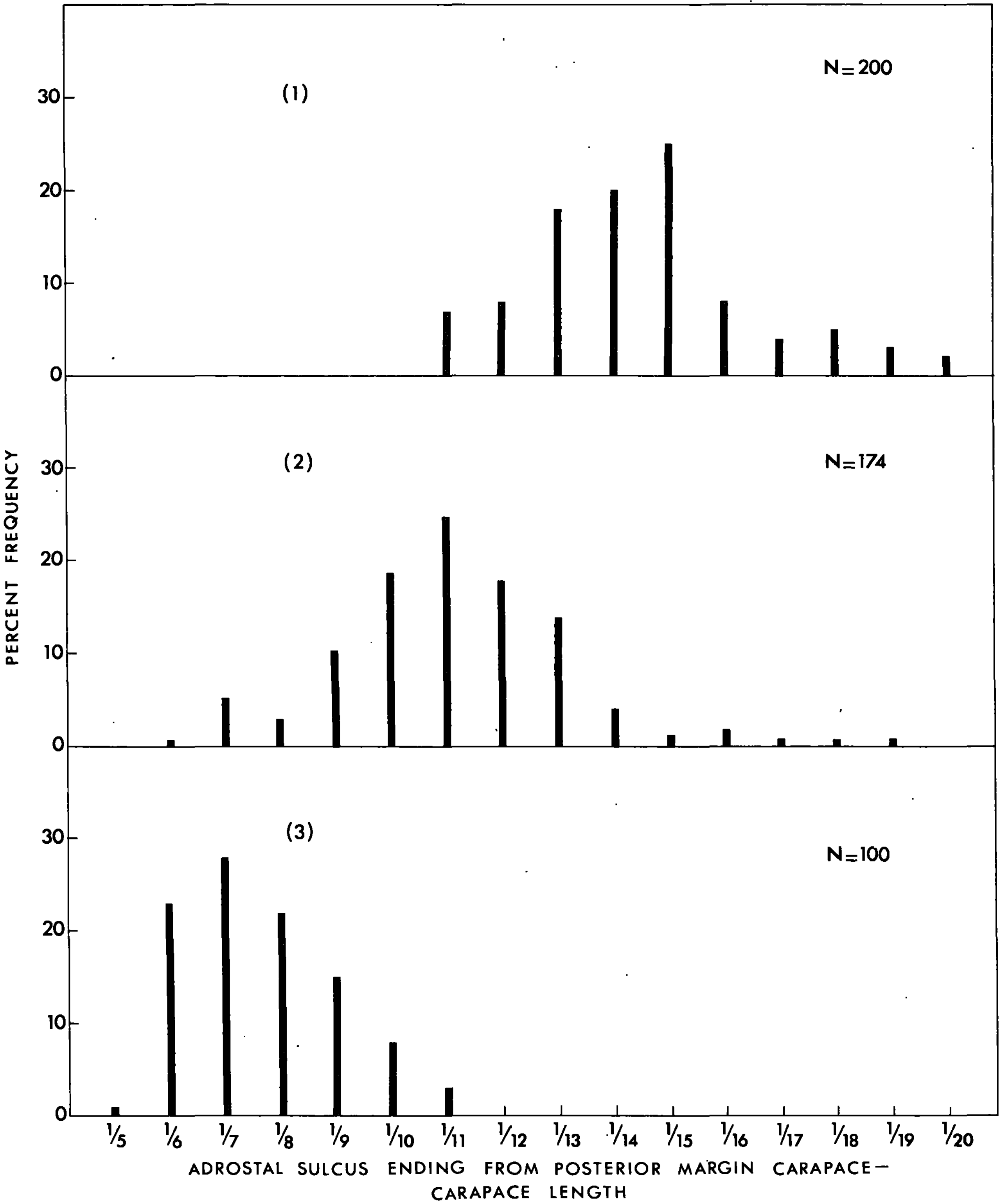

FIGURE 59.—Percent frequency of ratio of postsulcal carapace length to carapace length in 1. *Penaeus* (*M.*) *aztecus aztecus* Ives; 2. *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante, from the Caribbean region and eastern Brazil; 3. *Penaeus* (*M.*) *aztecus subtilis* Pérez Farfante, from the Gulf of Paria to Camocim, Brazil.

differently armed (with a narrow patch of closely set teeth). In females the anterior and posterior processes are much broader than those of *P. paulensis.*

## Reproduction

### SUBADULT STAGE-SEXUAL MATURITY

The smallest size at which males were found with the petasma joined was 16 mm. c.l., 72 mm. t.l. and the smallest size at which females were found with a functional thelycum was 18 mm. c.l., 83 mm. t.l. The size at which *P. a. subtilis* reaches sexual maturity is not known.

### OVARY DEVELOPMENT

The studies by Magalhães Filho (1943) of the external genitalia and gametogenesis of "*P. brasiliensis*," as he identified his material, seem to me to have been taken on *P. aztecus subtilis.* His illustrations of the thelycum with widely gaping lateral plates leaving exposed a broad posterior process and of a petasma with apparently short distomedian projections indicate that the specimens were probably dark shrimp.

## Postembryonic Development

### LARVAE, POSTLARVAE, AND JUVENILES

No studies have been made on the larval and postlarval stages of this shrimp.

My studies of small individuals showed that the adrostral sulci are distinctly developed in *P. a. subtilis* juveniles 18 mm. t.l. Because the sulci are shorter than in other grooved *Penaeus* from the western Atlantic, the juveniles can be readily distinguished from those of the nongrooved shrimps. Small males may be distinguished from females by the larger size of the petasmal endopod and its more proximal position on the basis. Males also have a low rib on the midline of sternite XIV, whereas females have sternite XIV ventrally produced to a midpoint.

Females with a 10.5 mm. c.l., 47 mm. t.l., bear a small spine projecting caudad from the posterior margin of sternite XIII. This conspicuous character also makes it possible to distinguish them at that small size from the grooved sympatric *Penaeus.*

### GROWTH

It has been reported (Anonymous, 1962) that in Guyana *P. a. subtilis* kept in ponds grew from 25 mm. t.l. to 200 to 225 mm. t.l. in 7 or 8 months.

### SEX DIFFERENCES IN SIZE

The largest female examined, caught off Surinam in 50 fm., *Oregon* Sta. 2016, had 55 mm. c.l., 205 mm. t.l.; the largest male, caught off Isère Point, French Guiana, in 34 fm., *Oregon* Sta. 2322, measured 36 mm. c.l., 152 mm. t.l. Boschi (1963) cited under *P. aztecus* an unusually large male, 200 mm. long, but no locality was given; neither was reference given as to which "Form" it belonged. It is not possible to ascertain if the specimen was typical *P. a. aztecus*, *P. a. subtilis*, or *P. paulensis.*

Offshore dark shrimp show a sex-size disparity: females are larger than males; the difference in size between sexes increases with depth.

## Ecology

### FOOD

No studies have been made on the food of this shrimp. I found a tentacle of the squid *Doryteuthis plei* Blainville hanging from the mouth of a specimen from off Departamento de la Guajira, Colombia.

### SUBSTRATE

Juvenile as well as adult *P. a. subtilis* prefer muddy substrates. Holthuis (1959) reported that in Surinam it was taken on bottoms of soft and hard mud, and mud with shells. Bullis and Thompson (1959a) stated that on the Continental Shelf of South America, from off Trinidad to the Amazon River, camarón marrón was found predominantly on muddy bottoms. It also lives on bottoms consisting of a mixture of mud and sand and on those which consist predominantly of coral sand, where I collected specimens in northern Cuba.

### DIEL CYCLE

No information is available on the diel activity of camarón marrón inshore. Bullis and Thompson (1959a) noted that in the Atlantic Coast of northeastern South America sizes of the catches were approximately the same day and night, whereas Croker (1967) stated that off Nicaragua this subspecies is fished at night.

### MOVEMENTS

Postlarvae of *P. a. subtilis* move into inshore waters where the young are known to live. Most of the specimens I examined from the Antilles came from bays. Ewald (1965c) reported that in Venezuela juveniles are found in abundance in lagoons and mouths of rivers and are taken commercially in Lake Maracaibo. Davant (1963) had previously reported specimens up to 100 mm. long from various estuarine waters of Venezuela. Farther along the

Atlantic Coast, juveniles and subadults are fished in brackish water in Surinam and Brazil.

Little is known of the seasonal abundance of the young. According to Lijding (1956, fide Holthuis 1959), inshore catches in Surinam are higher during July and August; Lindner (1957) reported that in northern Brazil they are caught the year round, but reach a peak of abundance from May to October.

### EFFECTS OF TEMPERATURE

No information is available on the effects of temperature on *P. a. subtilis*. Its distribution, however, seems to indicate that it requires relatively high temperatures because it is restricted to the Caribbean Sea and the warmest waters of the western Atlantic.

### EFFECTS OF SALINITY

The young, from late postlarvae to subadults, can live within a considerable range of salinities—from estuarine waters to small lagoons of high salinity, for example in Laguna Doctor, Playa de Baracoa, Cuba, and in pools in Surinam which have a salinity higher than sea water because of strong evaporation (Holthuis, 1959).

### ENEMIES AND DISEASES

No investigations on camarón marrón predators and enemies have been undertaken. Like its congeners, it most probably constitutes an important component of the diet of various carnivorous animals, particularly fishes. Holthuis (1959) reported one specimen from the stomach of the kingfisher *Chloroceryle americana* (Gmelin).

## Commercial Importance

*P. a. subtilis* is fished commercially in some areas throughout its range. It is taken in small numbers in many Antillean islands, usually along with the other abundant *Penaeus*. The fact that often no common name identifies this subspecies, whereas the other *Penaeus* are known by a variety of descriptive names, indicates that it is not frequent in the catches here. Camarón marrón contributes to the commercial catches in Honduras (Loesch, 1962; Croker, 1967), Nicaragua (Croker, 1967; Instituto de Fomento Nacional, 1967), Colombia and Venezuela. Ewald (1965c) reported that young are caught in the northern portion of Lake Maracaibo and adults in the Gulf of Venezuela; Lindner (1957) mentioned a fishery for adults at Puerto Cabello. Sampling by the *Oregon* along the coast of both Venezuela and Colombia has suggested that large adults of this subspecies are found throughout the region at depths beyond the present range of fishing. Lindner (1957) and Lijding (1956, fide Holthuis, 1959), reported that the young are fished in the estuarine waters of Surinam, and, in recent years, adults have been caught off the Guianas.

Camarón marrón is also commercially exploited in Brazil. In inland waters and off beaches along the northern coast, from the eastern shore of Baía de Marajó through São Luis to Parnaiba, fishing is very active; the young are also caught in Salvador. Finally, for many years, a fishery for adults has existed along the eastern coast, from Rio Doce to Cabo Frio.

## *Penaeus (Melicertus) paulensis*
### PÉREZ FARFANTE

Figures 60 to 67

Brazil: camarão rosa. Uruguay: langostino.

*Penaeus setiferus:* Heller, 1865: 121 [part]. Not *P. setiferus* (L.), 1767.

*Penaeus braziliensis:* Kingsley, 1882: 106 [part?]; Moreira, 1901: 6, 7, 72 [part]; Moreira, 1905: 130 [part?].

*Penaeus brasiliensis:* Ortmann, 1890: 446, 447, 449 [part], pl. 36, fig. 1 a–c; Sharp, 1893: 109 [part]; Pesta, 1915: 113 [part]; Lindner, 1957: 15; Devold, 1958: 20 [part]; ?Lindner, 1958: 32; Barattini and Ureta, 1960: 49. Not *P. brasiliensis* Lat., 1817.

*Penaeus aztecus:* Burkenroad, 1939 [part, "Form C"]: 20, 27, 35, 36, 38, 39, 41, figs. 32–34; Lindner, 1957: 11, 12, 14; Lindner, 1958: 33; Eldred and Hutton, 1960: 91, 106, 108; Miles, 1962: 193 [part]; Boschi, 1963: 26–29, fig. 11 [part]; Boschi, 1964: 40, 41 [part]; Mistakidis and Neiva, 1964: 472; Neiva and Wise, 1964: 132, (133 [part]); Tremel et al., 1964: 6, 7, 12, 14, 15, 19, 24, 30, 32, 34, 36, 38, 40, 42 [part]); Holthuis and Rosa, 1965: 4 [part]; Mistakidis, 1965: 9, 11–13, 38 (4, 8, 35 [part]); da Silva, 1965: 3, 4 (7 [part]); Tremel and Mistakidis, 1965: 2, summary (4, table 3 [part]); Williams, 1965: 25, 26; Mistakidis and Neiva, 1966: 434; Neiva and Mistakidis, 1966: 2, 5, 6, fig. 10 a–d; [fide] Pérez Farfante, 1967: 84, 87. Boschi, 1968: 222–223. Not *P. aztecus* Ives, 1891.

*Penaeus paulensis* Pérez Farfante, 1967: 84, 86, 87, 93, fig. 1 a–d (holotype, ♂, USNM 119128, Santos, São Paulo, Brazil, April 1964, M. Vannucci); Boschi, 1968: 223.

Camarão rosa: Richardson and Moraes, 1960: 8, 10–12, 16–18, 32–34, 42, 48, 53, 70, 71, 80, 81 [part]; Braga, 1962: 48, 49, 51, tables 1, 2 [part].

### Taxonomic Remarks

The specimens at the Academy of Natural Sciences of Philadelphia (No. 69) collected at Rio de Janeiro by W. S. Ruschenberger and recorded by Sharp (1893) as *P. brasiliensis* are actually two female *P. paulensis*.

### Study Material

For list of records see Pérez Farfante, 1967.

### Diagnosis

Adrostral sulcus broad posteriorly and long, almost reaching posterior margin of carapace. Median sulcus short, ending well anterior to posterior end of adrostral sulcus, shallow, continuous or interrupted, often limited to anterior concavity. Dorsolateral sulcus very narrow. Petasma with ventral costa extending proximally in slight curve, or almost straight line, broad and blunt at distal end, with free distal border even or with faintly undulating flange and bearing group of medium-size, irregularly set teeth close to apex; distal fold relatively small, usually armed with spinules. Thelycum with anterior process small, posterior process very narrow and bearing anteriorly bifurcate median carina; lateral plates with anteromedian angle markedly divergent, leaving median carina exposed.

### Description

**ROSTRUM (fig. 60)**

Teeth $\frac{6\text{–}8}{1\text{–}2}$, mode $\frac{7}{2}$ (percentage distribution: 7/2—50, 8/2—47, 7/1—1, 8/1—1, 6/2—1; N=100) + epigastric; position of ventral teeth variable, first tooth situated well anterior to slightly posterior to last dorsal tooth; rostrum relatively short, longer in larger juveniles and subadults, reaching at most to distal end of antennular peduncle: maximum length in relation to carapace length apparently obtained at about 20 to 25 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.75); decreasing progressively with increasing length of shrimp, rostrum reaching distal half of second antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.50); rostrum straight apically, often along entire length, occasionally with tip upturned; highest portion of blade at level of third dorsal tooth; latter level with anterior margin of carapace; rostrum tip about ¼ r.l. Postrostral carina strong, prominent and long, extending almost to posterior margin of carapace. Median sulcus shallow, continuous or interrupted, often limited to anterior concavity and minute posterior pit, and short, end-

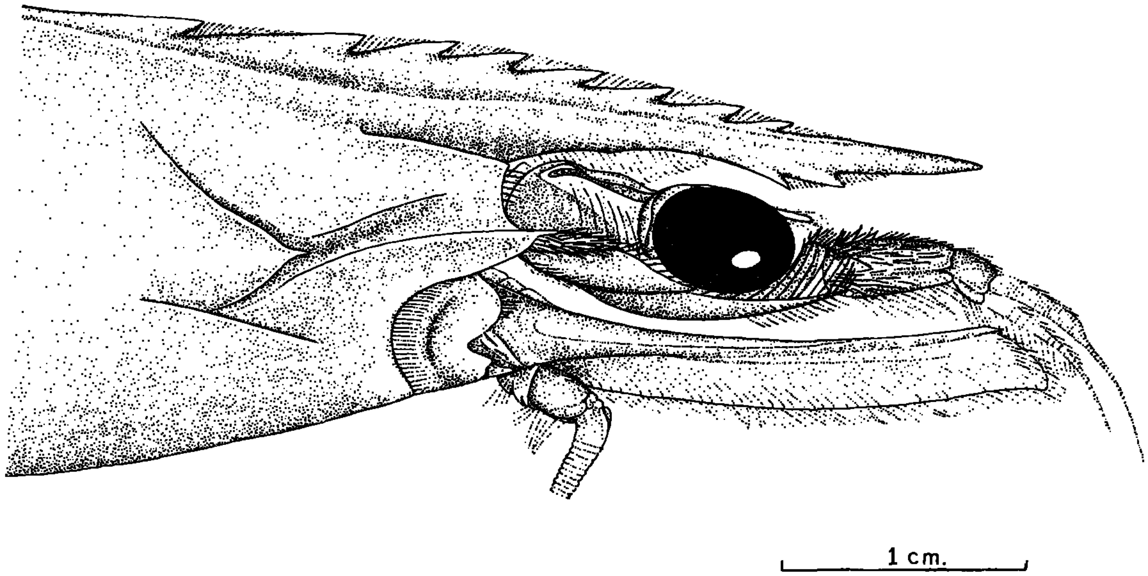

FIGURE 60.—*Penaeus* (*M.*) *paulensis* Pérez Farfante. Rostrum, ♀ 37.5 mm. c.l., off southernmost end Rio Grande do Sul, Brazil.

ing well anterior to posterior margin of carapace. Adrostral sulcus broad posteriorly from same to twice width of postrostral carina, and long, ending 1/12 to 1/20 c.l. from posterior margin of carapace. Adrostral carina prominent and long, same length as adrostral sulcus.

### CARAPACE (fig. 61)

Gastrofrontal sulcus broad, rather deep, extending to about one-fifth c.l.; gastrofrontal carina pronounced. Orbito-antennal sulcus slightly less than one-third c.l., wide anteriorly, narrowing posteriorly to below apex of hepatic spine, there widening again into base of spine. Gastro-orbital carina pronounced, sharp and long, occupying ⅘ to 6/7 distance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus ⅕ to ¼ c.l., ending slightly anterior to midlength of carapace. Hepatic carina sharp, sloping anteroventrally to end 1/16 to 1/20 c.l. from anterior margin of carapace. Antennal spine prominent and acute; hepatic spine very pronounced.

### ANTENNULES

Lateral flagellum relatively long, two-thirds length of antennular peduncle, slightly longer than median flagellum and with articles shorter than those of median flagellum; anterolateral spine sharp; stylocerite very acute, reaching midlength of first antennular segment. Prosartema reaching proximal one-sixth of second antennular segment.

### ANTENNAE

Scaphocerite length 2½ times width at base; spine reaching distal end of antennular peduncle. Carpocerite length 1⅓ width, its distal end reaching base of eye. Antennal flagellum short, 1⅖ body length.

### THORACIC APPENDAGES

Third maxilliped reaching approximately distal end of first antennular segment; length of dactyl ⅗ to ⅔ that of propodus. First pereopod reaching at least to distal end of carpocerite, but not exceeding it by more than three-quarters length of dactyl. Second pereopod surpassing carpocerite by entire length of dactyl or four-fifths that of propodus. Third pereopod reaching at least to distal third of second but not beyond distal end of third antennular segment. Fourth pereopod reaching distal end of carpocerite or surpassing it by one-half length of dactyl. Fifth pereopod extending anteriorly one-quarter dactyl length beyond

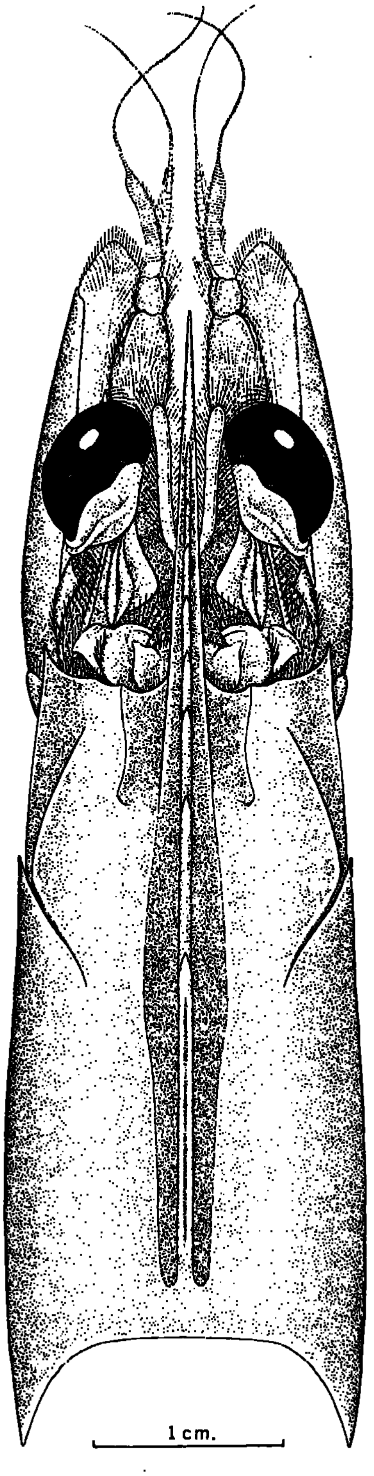

FIGURE 61.—*Penaeus* (*M.*) *paulensis* Pérez Farfante. Cephalothorax, holotype, ♂ 35 mm. c.l., Santos, São Paulo, Brazil.

fourth pereopod. Exopods on all pereopods. Long ischial and basial spines on first pereopod; rather long basial spine on second pereopod.

### ABDOMEN

Carinate dorsally from posterior half of fourth somite posteriorly, carina gradually increasing in height to form keel on sixth somite, ending in sharp spine on posterior margin. Dorsolateral sulcus (fig. 62) extremely narrow, ratio between height of keel and width of sulcus from about 3 to 16, modally 6 (fig. 63); K/S ratio showing same modal value of 6 for all sizes of both sexes (fig. 64); dorsal and ventral lips both sharp. Sixth abdominal somite with three cicatrices on each side, anterior the longest, posterior very small. Fifth abdominal somite with one cicatrix and row of minute pits anterior to sinus on posterior margin of somite. Fourth abdominal somite with similar row of minute pits dorsal to sinus on posterior margin of somite. Telson unarmed, with deep median sulcus and sharp pointed tip.

### PETASMA (fig. 65 a, b)

Ventral costa slightly curved with distal portion blunt, bearing group of 6 to 12 (modal 6) irregularly set teeth close to apex, its free distal margin even or with faintly undulating flange, apex adnate to ventrolateral lobule. Ventrolateral lobule with band of spines consisting of single row or pair of rows distally, with three to six series of spines extending proximally to about midlength of lobule. Dorsolateral lobule often with single row of widely spaced minute spines along midline. Distomedian projections relatively short, slightly overhanging distal portion of ventral costae.

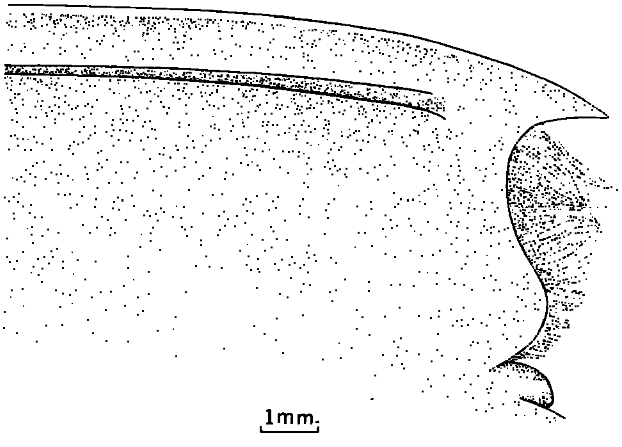

FIGURE 62.—*Penaeus* (*M.*) *paulensis* Pérez Farfante. Sixth abdominal somite, posterodorsal portion, holotype, ♂ 35 mm. c.l., Santos, São Paulo, Brazil.

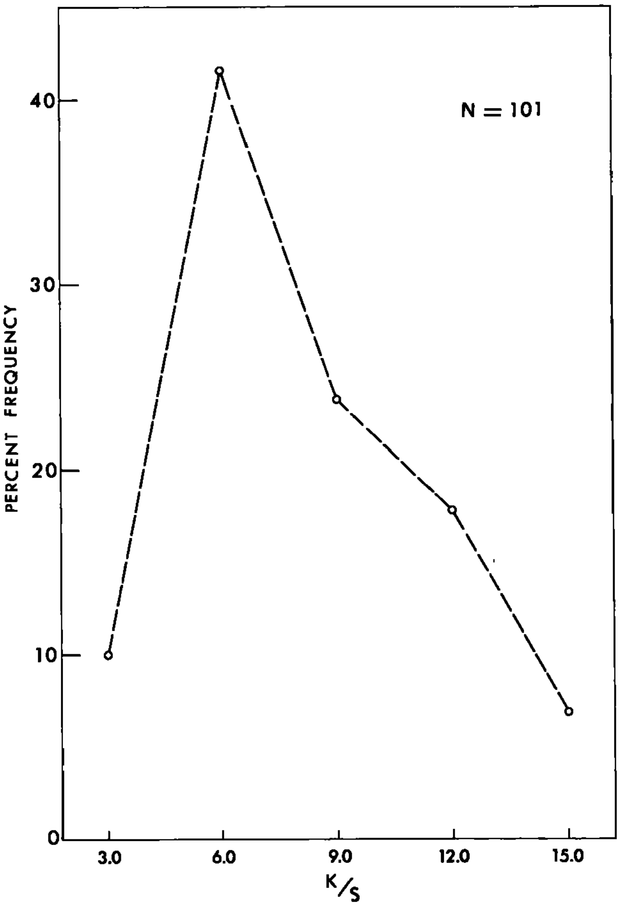

FIGURE 63.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *paulensis* Pérez Farfante.

### APPENDIX MASCULINA (fig. 65c)

Slightly elongated, length 1¼ to 1⅓ maximum width, with long spines projecting from distomedian margin and with slightly concave lateral margin armed with short, strong spines. Anterior surface subplane or slightly convex, posterior surface strongly concave, with sharp longitudinal ridge along median margin.

### THELYCUM (fig. 66)

Anterior process narrow, projecting ventrally in subtriangular or highly arched ridge, surrounding shallow depression with minute knob usually present at center. Posterior process with median carina bifurcate anteriorly, resulting ribs turning medially and converging at base of anterior process, giving rise to very narrow diamondlike structure. Lateral plates with anteromedian corners divergent, leaving posterior process exposed.

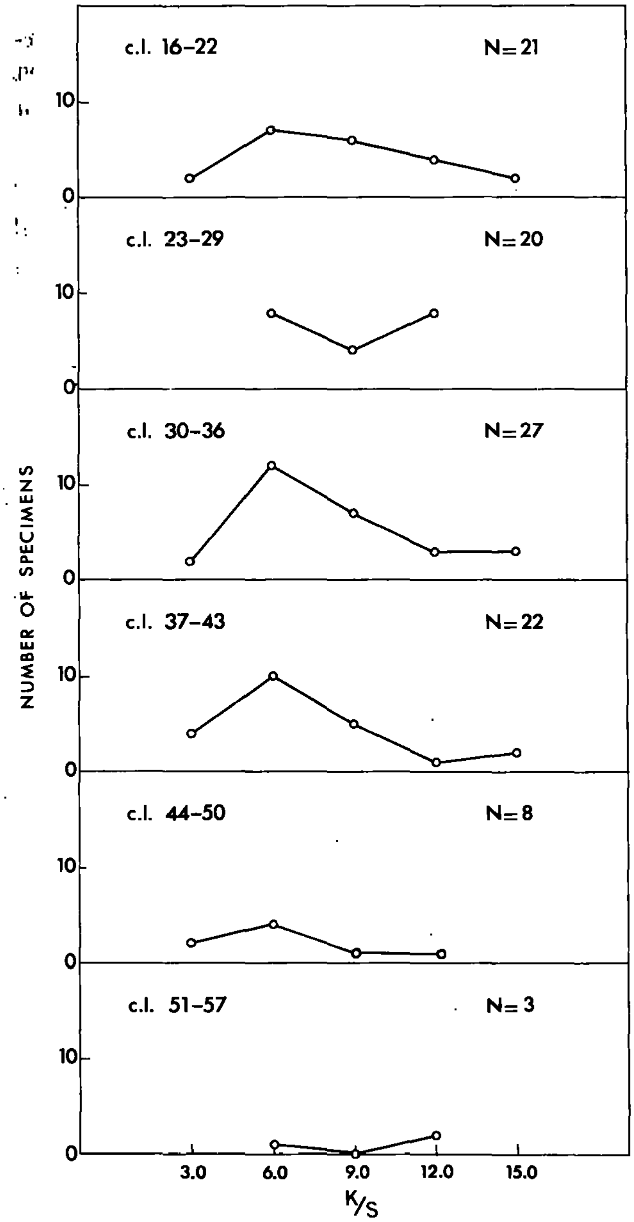

FIGURE 64.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *paulensis* Pérez Farfante of different size classes.

## COLOR

Like other *Penaeus*, *P. paulensis* is variable in color, but most often is pinkish; thus, the name camarão rosa (pink shrimp) applied to it in Brazil.

## Distribution and Morphological Variations

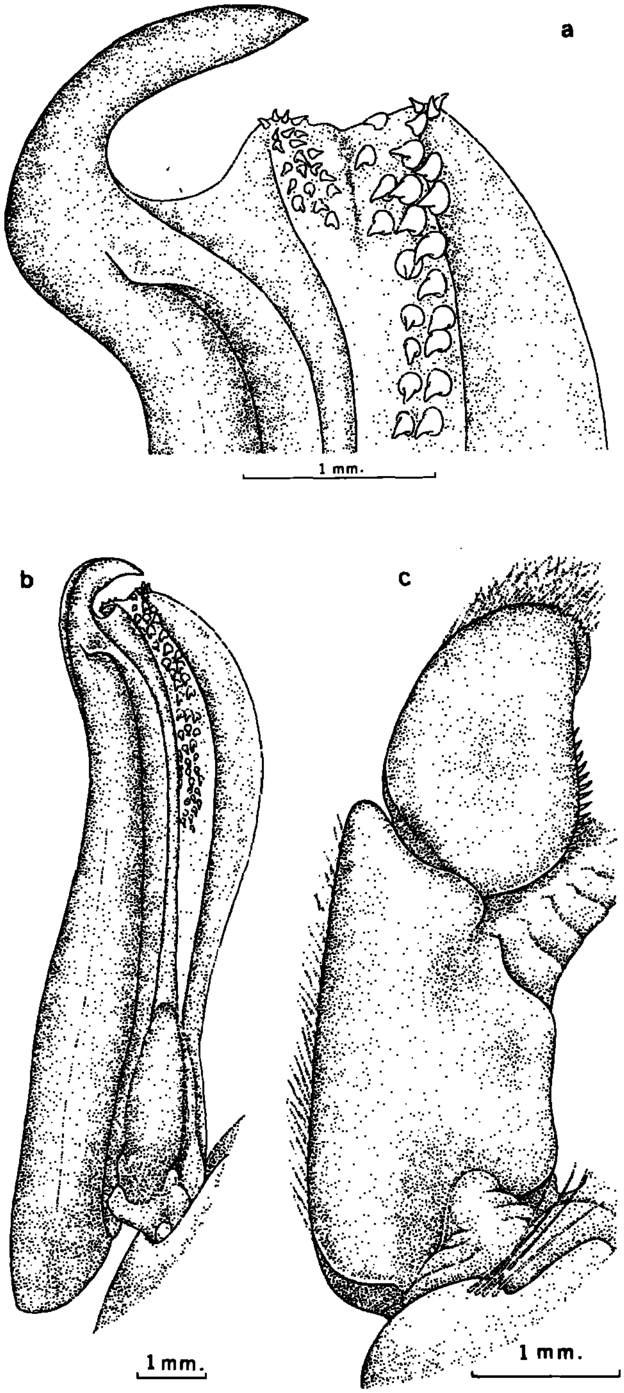

FIGURE 65.—*Penaeus* (*M.*) *paulensis* Pérez Farfante. a. Petasma, distal portion, ♂ 39 mm. c.l., Ponta do Boi, São Paulo, Brazil. b. Petasma, ♂ 39 mm. c.l., Ponta do Boi, São Paulo, Brazil. c. Appendix masculina, ♂ 39 mm. c.l., Santos, São Paulo, Brazil.

The range of *P. paulensis* extends from south of Cabo Frio along the coast of southern Brazil and Uruguay as far as northeast Argentina (fig. 67). Boschi (1968) has found *P. paulensis* along the eastern coast of Buenos Aires Province (lat. 38°30′ S; long. 57°20′ W.) and has, thus, confirmed the belief (Pérez Farfante, 1967) that the species ex-

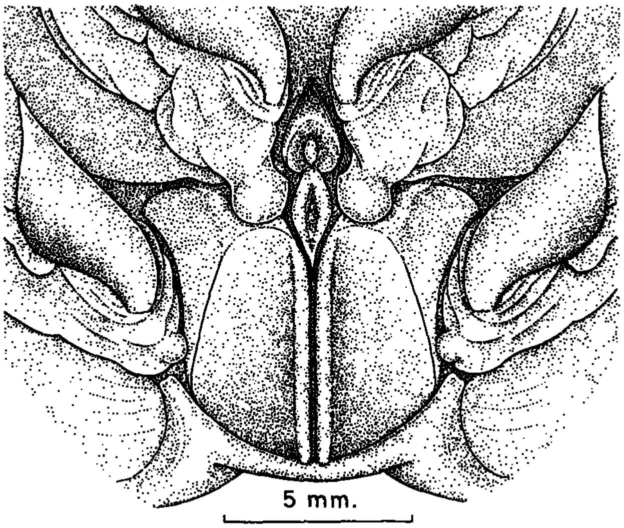

**FIGURE 66.**—*Penaeus* (*M.*) *paulensis* Pérez Farfante. Thelycum, ♀ 49.5 mm. c.l., Santos, São Paulo, Brazil.

tends farther south than the previously generally accepted southernmost limit of its range, Montevideo. It is abundant along the northern portion of its range and the coastal waters of Santa Catarina. Farther south, the young are very numerous in Lagoa dos Patos and the coastal lakes of Uruguay, but adults are rare along the southernmost portion of the range. Mistakidis (1965) reported having caught but one adult during exploratory fishing between Rio Grande and Cabo Polonio. Possibly the breeding populations extend only to the neighborhood of Rio Grande. The young seem to be able to invade waters that the larger adults cannot tolerate.

These shrimp live as deep as 65 fm.; large concentrations are found between 20 and 30 fm.

My studies indicate little variation in the diagnostic characters of *P. paulensis*. The only rather striking variation is that shown by the median sulcus, which is usually interrupted but occasionally continuous. Both types of sulcus were observed in specimens from the same locality.

## Relationships

*P. paulensis* is closely related to *P. a. aztecus* and *P. a. subtilis*. It differs from both by having the rostrum usually almost straight and shorter; by having a K/S ratio with a modal value of 6, which indicates a very narrow dorsolateral sulcus; and by having both lips of the sulcus sharp. The external genitalia are also distinct. In males, the ventral costa of the petasma is almost straight or only slightly curved instead of markedly convex distally and is armed with a group of medium-size, irregularly set teeth almost at the apex. In females, the anterior process is smaller and the posterior process narrower than in *P. a. aztecus* and *P. a. subtilis*. *P. paulensis* also differs from *P. a. aztecus* by the shorter, shallower, and often interrupted median sulcus and the shorter third pereopod and from *P. a. subtilis* by the broader adrostral sulci.

*P. paulensis* tends toward a smaller number of rostral teeth than any other species of *Penaeus* from the western Atlantic; the mode of the rostral teeth formula is $\frac{7}{2}$ instead of $\frac{8}{2}$. Also, specimens with a formula greater than $\frac{8}{2}$ must be uncommon because no specimen in the samples examined had more than 8 dorsal and 2 ventral teeth.

## Reproduction

### SUBADULT STAGE-SEXUAL MATURITY

The series of small specimens available was too small to permit a determination of the size range at which males and females become subadults.

No studies have been made on the size at which females attain sexual maturity.

### OVARY DEVELOPMENT

No studies have been made.

### SPAWNING

No studies are known on the spawning characteristics of *P. paulensis*. The information available on stages inshore, however, gives some indication of the spawning season through the range of this shrimp.

According to Tremel (1965), fishing for the young in Conceição and Imaruí Lagoons, Santa Catarina, Brazil, is carried out from August to April (peak from December to February). This timing appears to indicate that some spawning occurs from mid-fall through early winter, but that mass spawning probably takes place through late winter and early spring. Mistakidis (1965) reported that in Lagoa dos Patos, southeast Brazil, small shrimp are found from September to November, that postlarvae have been taken in the lakes of Uruguay in October and November, and that fishing for young in both areas is carried out from March to May, with a peak in March. The young, thus, arrive on these nursery grounds later than those that arrive in the lagoons of Santa Catarina. Because large adults are apparently rare off southern Brazil and Uruguay, the difference in time of arrival may be due to the longer dis-

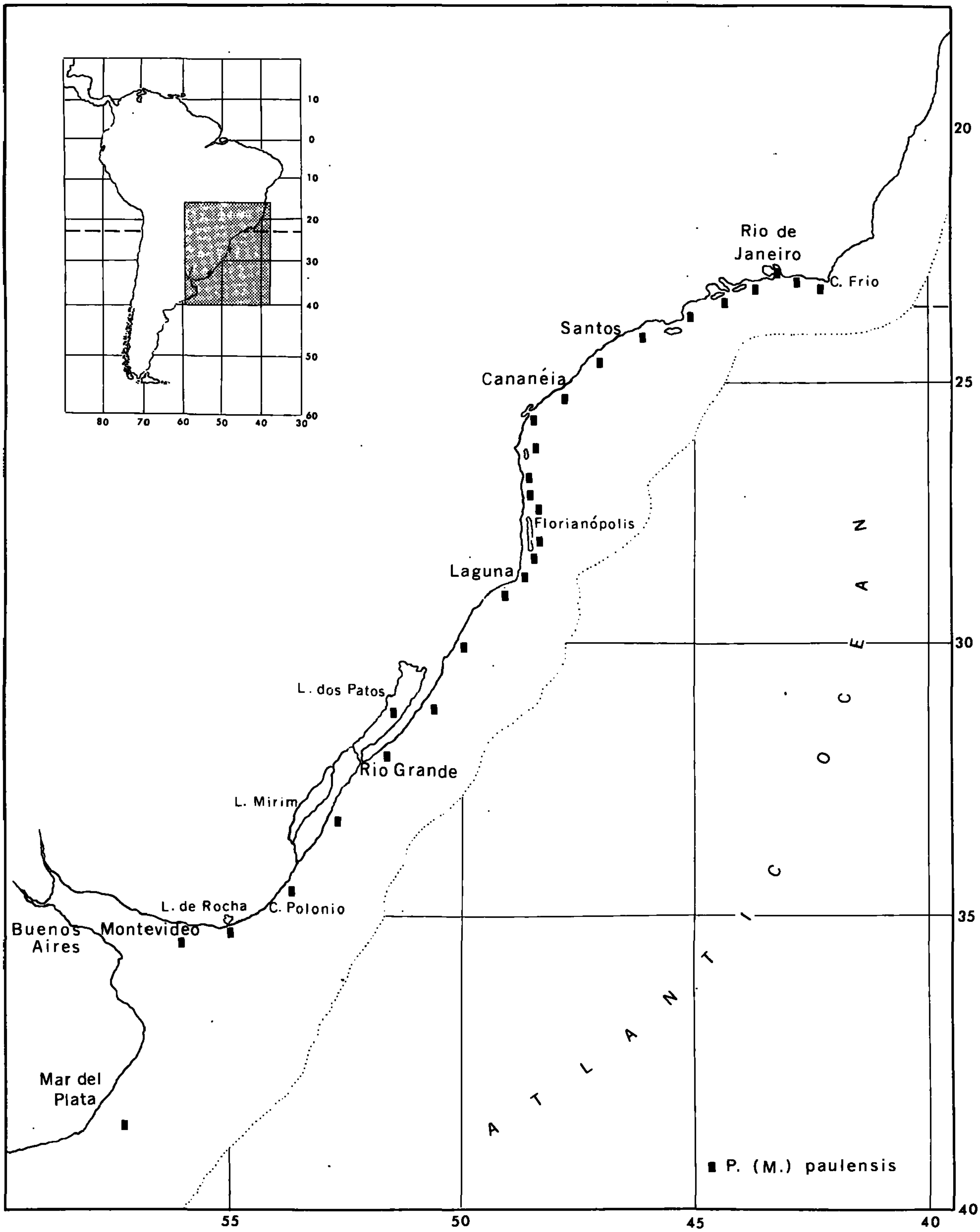

FIGURE 67.—Distribution of *Penaeus* (*M.*) *paulensis* Pérez Farfante.

tance larvae must travel from the spawning grounds to the southern areas.

## Postembryonic Development

### LARVAE, POSTLARVAE, AND JUVENILES

No studies have been conducted on either larval or postlarval stages of *P. paulensis*. The number of juvenile specimens available to me was too small to permit conclusions.

### GROWTH

No studies have been made.

### SEX DIFFERENCES IN SIZE

The largest female I examined was 54 mm. c.l., 215 mm. t.l., from off Rio de Janeiro; the largest male was 40 mm. c.l., 171 mm. t.l., from off Ponta do Boi, São Paulo, Brazil. Offshore the females are larger than males, and the size of both sexes increases with depth.

## Ecology

### SUBSTRATE

Little is known of the habits of this shrimp. Juveniles and subadults occupy soft muddy bottoms, but the largest concentrations of adults are on bottoms of firm mud.

### DIEL CYCLE

*P. paulensis* is mostly nocturnal; fishing for young on the nursery grounds and for adults offshore is carried on at night.

### EFFECTS OF TEMPERATURE

*P. paulensis* has a wide range of temperature tolerance since it occupies the waters of southeastern Brazil, where temperature is highly variable, and penetrates into the coast of northeast Argentina, where the water is relatively cold.

### EFFECTS OF SALINITY

There is little information on the effect of salinity on *P. paulensis*.

According to Closs (*In* Mistakidis, 1965), salinities in the southern portion of Lagoa dos Patos, the single largest nursery area for the species, vary from 1 p.p.t. to 29 p.p.t., and Mistakidis (1965) reported that in the coastal lakes of Uruguay salinities range from 2 p.p.t. to 26 p.p.t. This shrimp, thus, seems to be able to withstand a rather wide range of salinity during the inshore phase of its life cycle. Production from the nursery areas, however, shows large fluctuations from year to year, and it has been suggested by Lindner (1957) and Mistakidis (1965) that in Lagoa dos Patos, at least, declines in production are probably caused by excessive rainfall. Lindner states that "excessive quantities of fresh water in Lagoa dos Patos might restrict the area of shrimp nursery grounds." The reduced production could be due also to swift currents following heavy rainfalls which might prevent the shrimp from gaining access to inshore water.

## Commercial Importance

This species is not locally distinguished from *P. brasiliensis*. Both are known and classified in statistical studies as camarão rosa. Consequently, it is not possible to ascertain the quantities of *P. paulensis* that are caught.

The young of *P. paulensis* are commercially taken in Baía de Guanabara, Brazil, and from numerous lagoons and coastal lakes as far south as Laguna de Rocha, Uruguay. Offshore fishing is more restricted and is carried out only in the northern portion of the range, from off Baía de Guanabara to the neighborhood of Rio Grande.

It seems that the majority of the camarão rosa landed at Santos, São Paulo, is *P. paulensis* (Mistakidis, 1965). The Instituto de Pesca Marítima of São Paulo, Brazil, calculated that landings of camarão rosa in Santos—the most important port for landings from the ocean fishery—were 891,000 kg. in 1964, 1,868,000 kg. in 1965, and 2,157,300 kg. in 1966.

Landings of camarão rosa in the State of Rio Grande do Sul—almost entirely *P. paulensis* (Mistakidis, 1965)—present large annual fluctuations as shown by the landings from 1963 to 1966. The Centro de Pesquisas Oceanograficas do Rio Grande reported that the production reached 4,913,700 kg. in 1963, decreased to 1,568,600 kg. in 1964, rose to an all-time high of 5,844,400 kg. in 1965, and amounted to only 648,300 kg. in 1966.

## *Penaeus (Melicertus) brasiliensis*

### LATREILLE

Figures 68 to 77

United States: pink spotted shrimp, spotted pink shrimp, brown shrimp, Caribbean brown shrimp. Nicaragua: camarón rojo. Venezuela: langostino rosado con manchas, camarón rosado con manchas, langostino amarillo. Brazil: camarão rosa, camarão lixo.

*Penaeus brasiliensis* Latreille, 1817: 156 (neotype, designated by Burkenroad, 1939, ♀, British Museum (Natural History), Brazil); H. Milne Edwards, 1837: 415; Stimpson, 1871: 132 [part]; Miers, 1878: 299, 306 [part]; Bate, 1881: 175; Smith, 1885: 170; Doflein, 1899:

185; ?Doflein, 1900: 127; Young, 1900: 452; Moreira, 1901: 6, 7, 72; Rathbun, 1901: 100, 101 [part]; Moreira, 1905: 130; de Man, 1911: 95 [part]; Pesta, 1915: 113 [part]; Bouvier, 1918: 6; Burkenroad, 1934: 61, 75, 77, 78 [part]; Schmitt, 1935: 128, 129 [part?]; Schmitt, 1936: 364; Johnson and Lindner, 1934: 68; Wheeler, 1937: 325, 326, 329–332, 343, 344; Burkenroad, 1939: 26–31, 34, 39, 42–45, 50, figs. 16, 17, 22, 34; von Ihering, 1940: 194, 871; de Oliveira, 1940: 141; Magalhães Filho, 1944: 100, 101, fig. 4A; de Oliveira, 1944: 133; Anderson and Lindner, 1945: 305; Holthuis, 1948: 1104, 1105; Anderson et al., 1949: 16; Gunter, 1950: 22; Holthuis, 1950: 27; de Oliveira, 1950: 371, 386; Sánchez Roig and Gómez de la Maza, 1951: 113–119; Gómez de la Maza, 1952: 167, 169; Sánchez Roig and Gómez de la Maza, 1952: 153, fig. 6; Pérez Farfante, 1953: 232, 233, 238; Pérez Farfante, 1954b: 30, 31; Voss, 1955: 5, 8, 10, figs. 12–13; Anderson, 1956: 4, 12, 13 [part?]; Dall, 1957: 142, 226, 227; Lindner, 1957: 11–15, 34–36, 159, 160, 165; ? Rossignol, 1957: 111; Woodburn et al., 1957: 24; Devold, 1958: 20; Lindner, 1958: 31, 33; Suárez Caabro, 1958: 7; Bullis and Thompson, 1959a: 33–35, 41; Bullis and Thompson, 1959b: 1, 4–6, 9; Higman, 1959: 8, 10, 14; Holthuis, 1959: 43, 66, 67, fig. 6c; Young, 1959: 15; Eldred, 1960: 164, 165; Eldred and Hutton, 1960: 91, 98, 99, 101, 106, fig. 7b; Anonymous, 1961: 34; Costello and Allen, 1961: 21; Eldred et al., 1961: 87, 89, 101, 107, 109; Pérez Farfante et al., 1961: 40, 52, 58, 59, 61, 65; Gunter, 1962a: 108; Hutton et al., 1962: 327; Kutkuhn, 1962: 343; Tabb, Dubrow, and Jones, 1962: 11, 28; Boschi, 1963: 5, 6, 13, 20, 23, 25, 26, 29, 35, 37, figs. 7 (1–5), 11; Davant, 1963: 9–15, 29–31, 33, 35, 65–71, 85–89, 91, figs. 6a, 7a, b, 8a, b, 9a, b, 10 and bis; Simpson, 1963: 22, 23; Costello and Allen, 1964: 31; Ewald, 1964: 20–23, (24, 28, tables, [part]); Hutton, 1964: 440, 445; Iversen and van Meter, 1964: 549–552; Jones et al., 1964: 1; Mistakidis and Neiva, 1964: 472; Neiva and Wise, 1964: 132, 133 [part]; Tremel et al., 1964: 7, 24, (6, 12, 14, 15, 19, 30, 32, 34, 36, 38, 40, 42, fig. 2 [part]); Broad, 1965: 89; Bullis and Thompson, 1965: 6; Cervigón, 1965: 21; Ewald, 1965a: 29; Ewald, 1965c: 52, 59, 63, 67, 70, 72, 74, 80, 82, 84–86, 91, 93–96, 114 (80, 88–90, 92, 97–99, 113 [part]); Holthuis and Rosa, 1965: 4; Joyce, 1965: 115, 116, 132, 134, 170, 220, 221; Mistakidis, 1965: 9, 11, 13, 38 (4, 8, 35 [part]); Pericchi López, 1965: 24; da Silva, 1965: 3, 4, (7 [part]); Simpson et al., 1965: 77; Tremel and Mistakidis, 1965: 2, summary (4, table 3 [part]); Williams, 1965: 26; Alves Coelho, 1966: 163, 168, 171; Costello and Allen, 1966: 450, 452; Joyce and Eldred, 1966: 11, 25, 33; Neiva and Mistakidis, 1966: 1, 2, 5, 6, fig. 9a–d; Croker, 1967: 63, 72, 73, 78, 80, 81, 87, 95, 98; Instituto de Fomento Nacional, 1967: 5, 8; Pérez Farfante, 1967: 84, 94.

*Penæus brasiliensis:* H. Milne Edwards, 1837: 414.

*Penaeus setiferus:* Heller, 1865: 121 [part]. (According to Pesta, 1915.) Not *P. setiferus* (L.), 1767.

*Peneus brasiliensis:* Smith, 1869a: 27; Smith, 1869b: 390; von Martens, 1872: 140, 141 [part?]; von Ihering, 1897: 156; ? Torralbas, 1917: fig. 69; Rathbun, 1919: 319; Schmitt, 1924: 61; Boone, 1930: 15, 101–105 [part?].

*Penaeus braziliensis:* Kingsley, 1882: 106 [part]; Verrill, 1900: 580; Moreira, 1901: 6, 7, 72 [part]; Moreira, 1905: 130 [part]; Verrill, 1922: 41–43 [part], pl. 13, fig. 3, pl. 14, fig. 2, 2a (?); Idyll, 1950: 10; Ingle et al., 1959: 6; Anonymous, 1962: 56; Lyles, 1967: 371.

*Penaeus* sp. (*brasiliensis*): Scholander, Flagg, Walters, and Irving, 1953: 72, 75, 79, 80.

Camarão rosa: Richardson and Moraes, 1960: 8, 10–12, 16–18, 32–34, 42, 48, 52, 53, 70, 71, 80, 81 [part]; Braga, 1962: 48, 49, 51, tables 1, 2 [part].

## Taxonomic Remarks

The specimens cited by Pérez Farfante (1967) from Antigua, Lesser Antilles, as *P. a. subtilis* were actually two juvenile *P. brasiliensis* (see under Study Material).

## Study Material

### UNITED STATES

**North Carolina:** 1 ♂, YPM, off Cape Hatteras, October 19, 1884, *Albatross* Sta. 2285. 1 ♀, USNM, between Cape Hatteras and Cape Lookout, 32 fm., October 18, 1885, *Albatross* Sta. 2605.

**Florida:** 1 ♀, USNM, off St. Augustine, 12 fm., January 12, 1965, *Oregon* Sta. 5158. 1 ♂, USNM, N. of Oak Hill, July 4, 1963, E. A. Joyce. 1 ♀, USNM, S. of Cape Kennedy, 22 fm., March 23, 1956, *Pelican* Sta. 14. 1 ♀, USNM., off Melbourne, 38 fm., January 16, 1966, *Oregon* Sta. 5860. 4 ♂ 4 ♀, USNM, off Sebastian, 20 fm., November 11, 1961, *Silver Bay* Sta. 3529. 1 ♂

1 ♀, USNM, off Sebastian, 31 to 28 fm., January 15, 1965, *Oregon* Sta. 5203. 2 ♂, USNM, Biscayne Bay, 1⅝ fm., February 6, 1962, J. Y. Christmas. 1 ♂ 1 ♀, USNM, Matheson Hammock, Biscayne Bay, July 10, 1960, R. Still. 1 ♀, USNM, S. of Key Largo, 36 to 25 fm., October 25, 1960, *Silver Bay* Sta. 2364. 4 ♂ 7 ♀, USNM, off Key Largo, 40 fm., November 10, 1961, *Silver Bay* Sta. 3523. 1 ♂, USNM, off Key Largo, 50 fm., November 10, 1961, *Silver Bay* Sta. 3524.

### BERMUDA ISLANDS

1 ♂, YPM, Hayward's Bay, David's Island, September 6, 1905. 1 ♀, USNM, off Harrington Sound, February 12, 1888, C. M. Allen. 1 ♂ 1 ♀, YPM, Port Royal Bay, September 21, 1905. 1 ♀, YPM, St. Georges, January 27–29, 1935. 1 ♀, YPM, Bermuda, April 1898. J. M. Jones. 1 ♀, AMNH, Bermuda, W. Beebe. 1 ♀, YPM, Bermuda, 1936. 1 ♀, AMNH, Bermuda, August 31, 1935, W. Beebe. 1 ♀, USNM, Harrington Sound, February 17, 1881, C. M. Allen. 1 ♀, YPM, Mullet Bay, St. Georges Island, January 27–29, 1935.

### BAHAMAS

18 ♂ 7 ♀, USNM, 79 km. W. of Andros Island, 150 fm., November 11, 1960, *Silver Bay* Sta. 2471. 1 ♂ 1 ♀, USNM, Little Bahama Bank, November 1953, *Antilles*.

### CUBA

1 ♂, USNM, Dimas, Pinar del Río, May 17, 1915, *Tomas Barrera* Sta. 5. 1 ♂, USNM, off Puerto Esperanza, Pinar del Río, 1924, M. Sánchez Roig. 1 ♂, USNM, Laguna Doctor, Playa de Baracoa, La Habana, J. Mayor. 1 ♀, USNM, Laguna Doctor, Playa de Baracoa, La Habana, G. Mayor. 1 ♂, YPM, La Habana, February 1, 1932. 6 ♂ 8 ♀, CIP, S. of Cayo Cruz del Padre, Matanzas, March 1954, L. Howell Rivero. 15 ♂ 15 ♀, CIP, Bahía de Cárdenas, Matanzas, August 1955, G. Canet and I. Pérez Farfante. 15 ♂ 16 ♀, CIP, Bahía de Santa Clara, Las Villas, August 1955, G. Canet and I. Pérez Farfante. 8 ♂ 9 ♀, CIP, Bahía de Santa Clara, Las Villas, March 1954, L. Howell Rivero.

### JAMAICA

1 ♂ 1 ♀, USNM, Salt Pond, Montego Bay, August 1, 1910, E. A. Andrews. 1 ♂ 1 ♀, USNM, off Portland Point, May 14, 1962, 14 fm., *Oregon* Sta. 3538.

### PUERTO RICO

1 ♂, USNM, Bahía de Boquerón, January 26–27, 1899, *Fish Hawk*. 1 ♂ 1 ♀, USNM, off Bahía de Boquerón, January 27, 1899, *Fish Hawk*. 6 ♂ 3 ♀, USNM, Bahía de Boquerón, January 26–27, 1899, *Fish Hawk*. 1 ♀, USNM, off La Parguera, winter 1957–58, D. E. Erdman. 2 ♂ 4 ♀, USNM, off Hucares, February 13–14, 1899, *Fish Hawk*.

### VIRGIN ISLANDS

**St. Thomas:** 3 ♂ 1 ♀, USNM, Submarine Dock, October 2–3, 1959, H. R. Bullis. 4 ♂ 5 ♀, USNM, N. of St. Thomas, 42 fm., April 19, 1960, *Oregon* Sta. 2607. 1 ♂ 3 ♀, USNM, S. of St. Thomas, 26 fm., September 27, 1959, *Oregon* Sta. 2618. 2 ♂ 8 ♀, USNM, off St. Thomas, 40 fm., September 29, 1959, *Oregon* Sta. 2625.

**St. Croix:** 16 ♂ 6 ♀, USNM, Kranse Lagoon, H. A. Beatty.

### LESSER ANTILLES

**Antigua:** 1 ♂, USNM, English Harbor, April 4–9, 1956, Smithsonian-Bredin Exped., Sta. 83–56, F.A. Chace and D. V. Nicholson. 1 ♂, USNM Tank Bay, English Harbor, April 3, 1956, Smithsonian-Bredin Exped., Sta. 74–56, W. L. Schmitt, F. A. Chace, D. V. Nicholson, and Jackson.

**Aruba–Curaçao:** 1 ♂ 3 ♀, USNM, off Aruba, 40 fm., October 3, 1965, *Oregon* Sta. 5656. 4 ♂ 5 ♀, USNM, off Aruba, 38 fm., October 3, 1965, *Oregon* Sta. 5654. 1 ♂ 1 ♀, USNM, Riftwater, Curaçao, ½ fm., July 26, 1905.

### MEXICO

**Quintana Roo:** 1 ♂ 1 ♀, INIBP, "90° NNE." of Isla Contoy, July 17, 1967, H. Chapa Saldaña, D. Fuentes, and J. M. de la Garza. 1 ♂ 1 ♀, INIBP, "90°NNW." of Isla Mujeres, 21 fm., July 17, 1967, H. Chapa Saldaña, D. Fuentes, and J. M. de la Garza. 1 ♀, USNM, Isla de Cozumel, June 29, 1885, *Albatross*. 1 ♀, USNM, halfway point between Punta Nicchehabin and Vigía Chico, N. end of Bahía de la Ascensión, Smithsonian-Bredin Exped., Sta. 93–60. 18 ♂ 13 ♀, USNM, Punta Nicchehabin, Bahía de la Ascensión, less than ⅓ fm., April 13, 1960, F. C. Daiber, Smithsonian-Bredin Exped., Sta. 65–60.

### NICARAGUA

1 ♂ 2 ♀, USNM, N. of Bluefields, 1965, A. Flores.

### PANAMA

3 ♂ 8 ♀, YPM, Limón Bay, N. of Sweetwater River, Colón, February 12, 1934. 7 ♂ 11 ♀, USNM, Fox Bay, Colón, March 22, 1912, S. E. Meek and S. F. Hildebrand. 2 ♀, USNM, Fox Bay, Colón, January 12, 1912, S. E. Meek and S. F. Hildebrand. 1 ♀, USNM, Fox Bay, Colón, January 27, 1912, S. E. Meek and S. F. Hildebrand. 4

♂ 3 ♀, USNM, off Toro Point, Canal Zone, May 11, 1911, S. E. Meek and S. F. Hildebrand.

### COLOMBIA

2 ♂ 1 ♀, USNM, Isla de S. Andrés, June 6, 1964, H. R. Bullis. 1 ♀, Golfo de Urabá, 34 fm., October 17, 1965, *Oregon* Sta. 5728. 2 ♂ 3 ♀, USNM, Golfo de Morrosquillo, 23 fm., May 25, 1964, *Oregon* Sta. 4886. 3 ♂ 3 ♀, USNM, off Puerto Colombia, 15 fm., May 23, 1964, *Oregon* Sta. 4866. 1 ♂ 2 ♀, YPM, Sabanilla, March 16–22, 1884, *Albatross*. 4 ♀, USNM, off Punta Faro, 13–14 fm., May 18, 1964, *Oregon* Sta. 4849. 2 ♂, USNM, off Tucuracas, Departamento de la Guajira, 15 fm., October 12, 1965, *Oregon* Sta. 5704, 1 ♂ 7 ♀, USNM, off Carrizal, Departamento de la Guajira, 19 fm., October 12, 1965, *Oregon* Sta. 5703. 1 ♀, USNM, off Carrizal, Departamento de la Guajira, 28 fm., October 12, 1965, *Oregon* Sta. 5702. 2 ♀, USNM, off Carrizal, Departamento de la Guajira, 10 fm., June 1, 1964, *Oregon* Sta. 4919. 1 ♂ 1 ♀, USNM, off Cabo de la Vela, Departamento de la Guajira, 38 fm., October 12, 1965, *Oregon* Sta. 5700. 1 ♀, USNM, off Cabo de la Vela, Departamento de la Guajira, 26 fm., October 12, 1965, *Oregon* Sta. 5697. 1 ♀, USNM, off Cabo de la Vela, Departamento de la Guajira, 15 fm., October 12, 1965, *Oregon* Sta. 5695. 1 ♀, USNM, NE. of Departamento de la Guajira, 53 fm., September 6, 1963, *Oregon* Sta. 4400. 3 ♂ 13 ♀, USNM, NE. of Departamento de la Guajira, 40 fm., September 25, 1963, *Oregon* Sta. 4392.

### VENEZUELA

2 ♂ 3 ♀, USNM, Gulf of Venezuela, February 28, 1964, J. J. Ewald. 1 ♂ 3 ♀, USNM, Gulf of Venezuela, 32 fm., October 5, 1965, *Oregon* Sta. 5665. 3 ♂ 3 ♀, USNM, off Las Piedras, Gulf of Venezuela, 26 fm., *Oregon* Sta. 5664. 3 ♂, USNM, off La Guaira, 40 fm., October 17, 1963, *Oregon* Sta. 4466. 1 ♂, USNM, off Isla de Margarita, 30 fm., September 22, 1963, *Oregon* Sta. 4481. 12 ♂ 9 ♀, USNM, off Península de Paria, 31 to 34 fm., September 23, 1964, *Oregon* Sta. 5034. 2 ♂ 2 ♀, USNM, off Güiria, Gulf of Paria, 10 fm., October 24, 1963, *Oregon* Sta. 4493.

### TRINIDAD

1 ♀, USNM, Caroni Swamp, August 6, 1965, P. R. Bacon. 1 ♀, USNM Cocorite Swamp, August 31, 1966, P. R. Bacon.

### TOBAGO

1 ♂, USNM, off Crown Point Hotel, July 8, 1959, Smithsonian-Bredin Exped. 3 ♂ 4 ♀, USNM, off Plymouth, 34 fm., March 14, 1966, *Oregon* Sta. 5964. 1 ♂, USNM, S. of Plymouth, 34 fm., March 14, 1966, *Oregon* Sta. 5970. 9 ♂ 10 ♀, USNM, N. of Tobago, 36 fm., March 14, 1966, *Oregon* Sta. 5971.

### GUYANA

4 ♂ 3 ♀, USNM, off Guyana, 50 fm., August 28, 1958, *Oregon* Sta. 2221. 2 ♀, USNM, off Guyana, 28 to 46 fm., August 29, 1958, *Oregon* Sta. 2232. 1 ♂ 1 ♀, USNM, off Guyana, 23 fm., August 29, 1958, *Oregon* Sta. 2235. 1 ♂ 1 ♀, USNM, E. of Georgetown, 26 fm., February 19, 1963, *Oregon* Sta. 4168. 1 ♂ 1 ♀, USNM, off Guyana, 24 fm., June 28, 1957, *Coquette* Sta. 297. 2 ♂ 4 ♀, USNM, off Guyana, 75 fm., November 4, 1957, *Oregon* Sta. 1993. 1 ♂ 1 ♀, USNM, off Guyana, 45 fm., November 5, 1957, *Oregon* Sta. 2000.

### SURINAM

1 ♀, USNM, off Surinam, 50 fm., November 8, 1957, *Oregon* Sta. 2016. 1 ♂ 1 ♀, USNM, NE. of mouth Surinam River, 25 fm., May 12, 1957, *Coquette* Sta. 28. 1 ♂ 1 ♀, USNM, NE. of mouth Surinam River, 27 fm., May 12, 1957, *Coquette* Sta. 31. 1 ♂, USNM, NE. of mouth Surinam River, 28 fm., May 12, 1957, *Coquette* Sta. 33. 3 ♂ 4 ♀, USNM, between mouths of Coppename and Surinam Rivers, 13 fm., June 19, 1957, *Coquette* Sta. 251. 1 ♂, USNM, between mouths of Coppename and Surinam Rivers, June 26, 1957, *Coquette* Sta. 279. 9 ♂ 5 ♀, USNM, off mouth of Surinam River, 24 fm., June 28, 1957, *Coquette* Sta. 297. 1 ♀, UMML, off Surinam, summer 1960, H. Lijding.

### FRENCH GUIANA

2 ♂, USNM, off French Guiana, 34 fm., September 14, 1958, *Oregon* Sta. 2322. 2 ♂ 2 ♀, USNM, off French Guiana, 38 fm., November 12, 1965, *Oregon* Sta. 2045.

### BRAZIL

**Maranhão:** 2 ♀, USNM, off Ilha do Caju, 20 fm., March 11, 1963, *Oregon* Sta. 4241.

**Ceará:** 2 ♂ 3 ♀, USNM, off Camocim, 15 fm., March 12, 1963, *Oregon* Sta. 4247. 1 ♂, USNM, off Camocim, 18 fm., March 12, 1963, *Oregon* Sta. 4250.

**Bahia:** 1 ♂ 1 ♀, MCZ–USNM, Salvador.

**Espírito Santo:** 2 ♂ 3 ♀, MNHNP–USNM, off Itaúnas, 21 fm., November 29, 1961, *Calypso* Sta. 89.

**Rio de Janeiro:** 5 ♂ 6 ♀, USNM, off Baía de Guanabara, 3⅘ fm., da Silva. 3 ♂ 4 ♀, MNHNP–USNM, off mouth Baía de Guanabara, 12 ⅗ fm., December 8, 1961, *Calypso* Sta. 115. 1 ♀, YPM, Rio de Janeiro. 1 ♂ 1 ♀, YPM, Rio de Janeiro Market, M. W. Feingold. 26 ♂ 29 ♀, YPM, Rio de Janeiro, M. W. Feingold and C. Moreira. 5 ♂ 3 ♀, MNHNP–USNM, Baía de Sitio Forte, Ilha Grande, December 9, 1961, *Calypso* Sta. 119.

**São Paulo:** 1 ♂, USNM, Santos, September 12, 1925, W. L. Schmitt. 11 ♂ 5 ♀, USNM, Cananéia, December 16, 1963, V. Sadowsky. 1 ♂ 6 ♀, USNM, Cananéia, April 1965, V. Sadowsky.

**Santa Catarina:** 1 ♀, USNM, Lagoa da Conceição, Ilha de Santa Catarina, November 11, 1965, E. Tremel. 2 ♂ 4 ♀, USNM, Lagoa da Conceição, Ilha de Santa Catarina, November 19, 1965, E. Tremel. 1 ♀, USNM, Armação da Piedade, Ilha de Santa Catarina, November 19, 1965, E. Tremel. 2 ♂ 2 ♀, USNM, Arvoredo, Ilha de Santa Catarina, October 9, 1964, C. de Jesús.

## Diagnosis

Adrostral sulcus broad posteriorly and long, almost reaching posterior margin of carapace. Median sulcus long, ending immediately anterior to posterior end of adrostral sulcus, and deep along its entire length. Dorsolateral sulcus variable in width, broad to almost closed, narrower in northern portion of range of species. Petasma with distal portion of ventral costa increasing gradually in width proximally and turning proximally in arc, unarmed along free border and with elongate group of sharp teeth on attached border; apex of costa free; distal fold forming large auricle with prominent spines; distomedian projection long. Thelycum with anterior process small, posterior process with median carina, if present, located deep between horns of median protuberance; lateral plates with anteromedian corners produced to form projections covering posterior process.

## Description

### ROSTRUM (fig. 68)

Teeth $\frac{7\text{–}11}{0\text{–}3}$, mode $\frac{8}{2}$ (percentage distribution: 8/2—44, 9/2—43, 7/2—4, 10/2—3, 11/2—3.50, 9/1—1, 8/0—0.50, 7/0—0.50, 8/1—0.50; N=200) +epigastric; position of ventral teeth variable, first tooth situated from well anterior to slightly posterior to last dorsal tooth; rostrum in larger juveniles reaching base of distal one-third of thickened portion of lateral antennular flagellum; attaining maximum length in relation to carapace length at 11 to 15 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ as high as 0.78); decreasing progressively with increasing length of shrimp, rostrum reaching distal end of first antennular segment in shrimp 50 mm. c.l. (ratio $\frac{\text{r.l.}}{\text{c.l.}}$ reduced to about 0.50); rostrum straight apically, often along entire length, occasionally with tip upturned; highest portion of blade at level of third dorsal tooth, latter level with anterior margin of carapace; rostrum tip about ¼ r.l. Postrostral carina strong, prominent, and long, extending almost to near posterior margin of carapace. Median sulcus deep, sometimes widening either in anterior or posterior half; long, ending near posterior margin of carapace. Adrostral sulcus deep, expanded at level of epigastric tooth, broad, ¾ to 1½ width of postrostral carina, and long, continuing posteriorly to end 1/13 to 1/15 c.l. from posterior margin of carapace. Adrostral carina prominent and long, same length as adrostral sulcus.

### CARAPACE (fig. 69)

Length in proportion to total length smaller in juveniles, increasing slightly at about subadult stage. Gastrofrontal sulcus broad, extending to about one-sixth c.l.; gastrofrontal carina sharp. Orbito-antennal sulcus wide anteriorly, narrowing posteriorly to below apex of hepatic spine, there widening again to base of spine. Gastro-orbital carina pronounced, sharp, occupying approximately posterior four-fifths distance between postorbital margin and hepatic spine. Antennal carina very prominent. Cervical sulcus about one-quarter c.l., ending slightly anterior to midlength of carapace. Hepatic carina sharp, ⅓ to ¼ c.l., sloping anteroventrally to end 1/15 to 1/18 c.l. from anterior margin of carapace. Antennal spine slender, acute, and long; hepatic spine prominent.

### ANTENNULES

Lateral flagellum almost three-quarters length of antennular peduncle, slightly longer than median flagellum and with articles shorter than those of median flagellum. Anterolateral spine very prominent, long, slender, and sharp. Stylocerite acute, reaching slightly beyond midlength of first antennular segment. Prosartema reaching distal end of proximal fifth of second antennular segment.

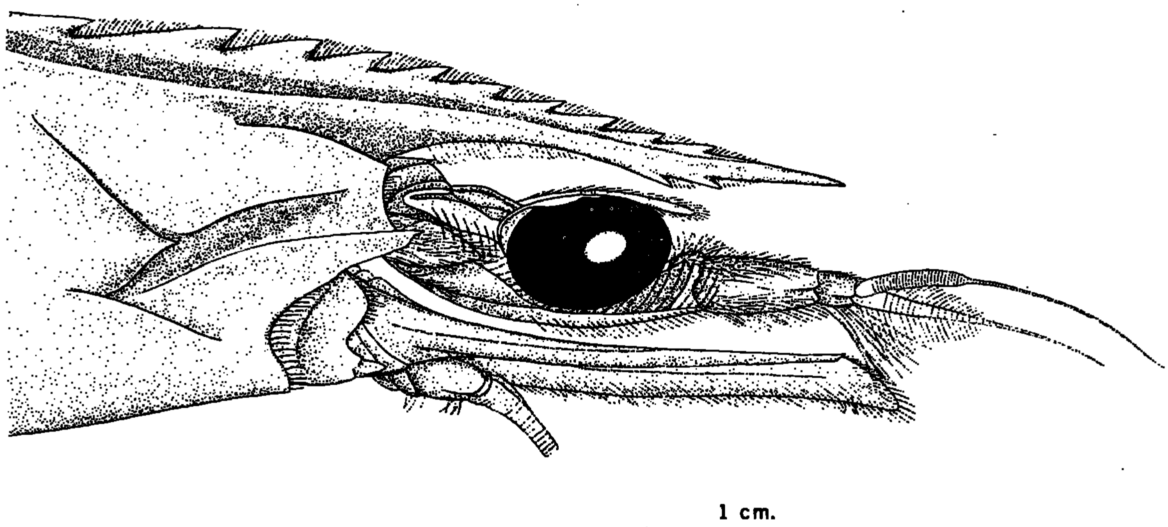

Figure 68.—*Penaeus* (*M.*) *brasiliensis* Lat. Rostrum, ♂ 38 mm. c.l., Arvoredo, Santa Catarina, Brazil.

### ANTENNAE

Scaphocerite length 2½ to 2¾ times maximum width, its length, relative to carapace length, decreasing slightly with growth; spine reaching distal end of antennular peduncle. Carpocerite length 1⅓ width. Antennal flagellum about 1⅖ t.l. of shrimp.

### THORACIC APPENDAGES

Third maxilliped reaching at least one-half of first, but not beyond distal half of second antennular segment; length of dactyl ⅗ to ⅔ that of propodus. First pereopod reaching at least three-fifths length of carpocerite or exceeding it by dactyl. Second pereopod surpassing carpocerite by half length of dactyl to one-tenth that of carpus. Third pereopod reaching at least base of second antennular segment and, at most, exceeding third antennular segment by entire length of dactyl; proportionately longer in juveniles. Fourth pereopod reaching at least base of carpocerite and at most surpassing it by length of dactyl. Fifth pereopod subequal to fourth.

### ABDOMEN

Carinate dorsally from posterior half of fourth somite, posteriorly carina gradually increasing in height to form keel on sixth somite, ending in sharp spine on posterior margin. Dorsolateral sulcus (fig. 70 a, b) with both lips sharp, variable in width, broad in populations from South America, ratio between height of keel and width of sulcus (K/S) ranging 1 to 4.5, modally 2 (fig. 71), narrower in specimens from the West Indies northward, K/S ranging from 3 to 9, modally 5 (fig. 73). In South America, K/S is also modally 2 in all size classes except 16 to 22 mm. c.l. with K/S modally 2.75 (fig. 72). In West Indies-Central America region and northward, K/S mode varies in different size classes—5 in the smallest class and at 23 to 29 mm. c.l.; 3 in the class intermediate between these two, and 3 in the largest (fig. 74). It does not seem that any significance could be attached to such a variation that does not show a trend. Sixth abdominal somite with three cicatrices on each side, posterior the smallest; fifth abdominal somite with one cicatrix and series of minute pits anterior to sinus on posterior margin of somite; fourth abdominal somite with similar series of pits dorsal to sinus on posterior margin of somite. Telson unarmed, with deep median sulcus and sharp pointed tip.

### PETASMA (fig. 75 a–c)

Ventral costa broadening and curving gradually from apex to distal end of ventromedian flap, extending almost straight proximally; distal portion unarmed along free border and with 6 to 12 pointed teeth set in two irregular rows on attached border; apex free from distal margin of ventrolateral lobule. Distal fold intruding considerably inside petasma, forming large, rounded auricle with numerous prominent spines arranged distally in half moon on inner surface. Ventrolateral lobule with external armature consisting of single or pair of series abreast distally, increasing in number proximally. Distomedian projections long, fingerlike in appearance, extending well over distal portion of ventral costae.

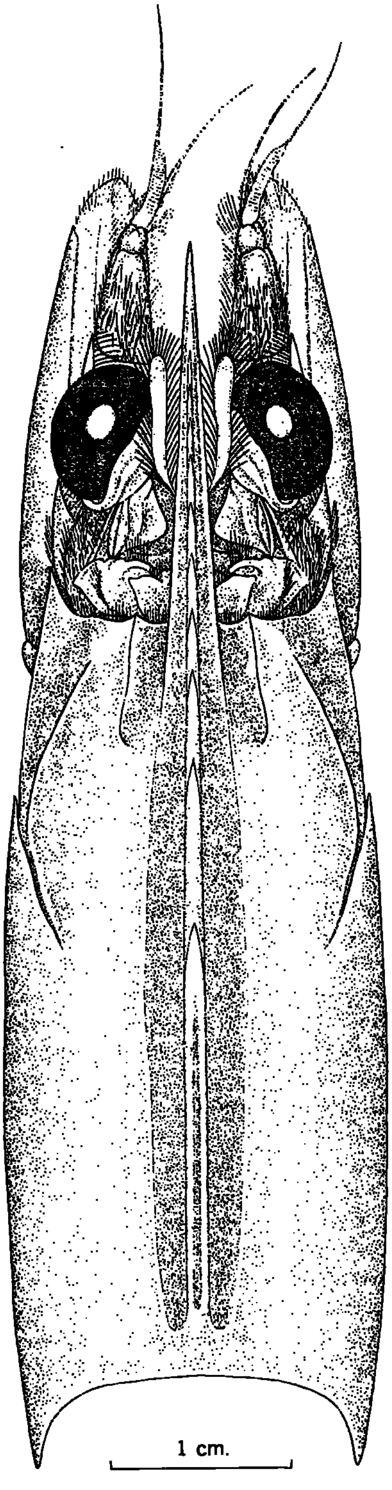

FIGURE 69.—*Penaeus* (*M.*) *brasiliensis* Lat. Cephalothorax, ♀ 43 mm. c.l., off Itaúnas, Espírito Santo, Brazil.

**APPENDIX MASCULINA (fig. 75 d)**

Relatively broad, its length 1⅕ to 1¼ maximum width, lateral margin with short spines reaching apex, median margin with long spines (almost half length of appendix) on distal half. Anterior surface slightly concave, posterior surface concave, with sharp longitudinal ridge projecting from median margin.

**THELYCUM (fig. 76 a–c)**

Anterior process typically small, projecting ventrally in subtriangular ridge, enclosed surface slightly to deeply concave. Posterior process rather weakly developed, often (not always) with short median carina situated deeply between horns of median protuberance, delimited by narrow sulcus on each side. Lateral plates with anteromedian corners extended anteriorly forming projections meeting along midline, and reaching base of anterior process, thus covering posterior process. Projections pointed or rounded anteriorly; if rounded, overlapping.

**COLOR**

The range of colors varies considerably. The usual pink or brownish-red specimens are designated camarão rosa in Brazil, and langostino or camarón rosado in Venezuela, both meaning pink shrimp. Yellow individuals, also common, are called camarón amarillo (yellow shrimp) and brown ones are not infrequent. The young are usually brownish and are called camarão lixo (dirty shrimp) in Brazil. *P. brasiliensis* usually possesses a roundish, dark reddish-brown spot on each side at the juncture of third and fourth abdominal somites, similar to that in *P. d. duorarum* and *P. d. notialis.* Davant (1963) and Holthuis (1959) pointed out that individuals of *P. brasiliensis* from Venezuela and Surinam-French Guiana, respectively, always seem to have the two spots, but that *P. a. subtilis* and *P. d. notialis* lack them. The two spots were also observed in individuals from Baía de Guanabara, Brazil, by da Silva (1965).

## Distribution and Morphological Variations

*P. brasiliensis* ranges from off Cape Hatteras south to the Florida Keys and, although rarely, reaches the Tortugas grounds. It also ranges from the Bermudas through the Bahamas and Antilles and along the Atlantic Coast of South America, to Rio Grande-Lagoa dos Patos, Brazil. It also occurs

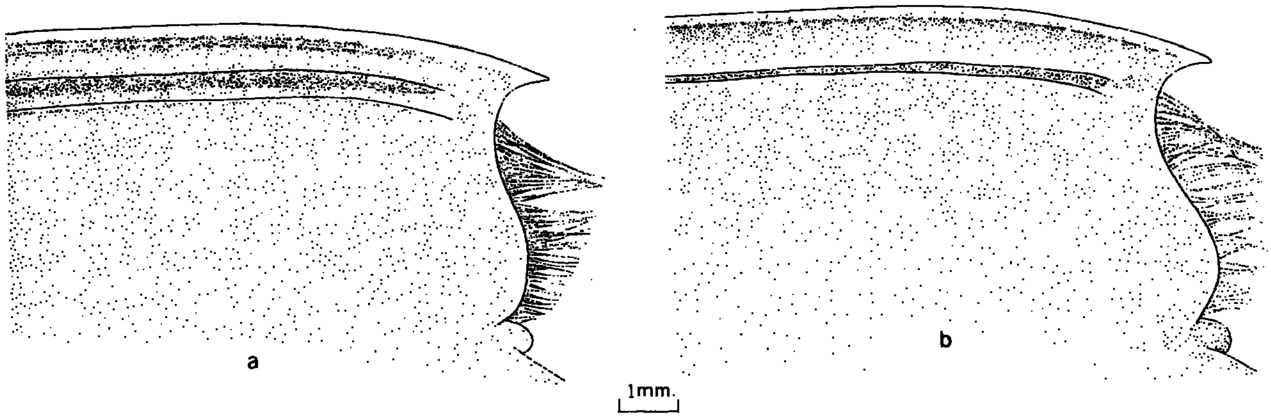

FIGURE 70.—*Penaeus* (*M.*) *brasiliensis* Lat. a. Sixth abdominal somite, posterodorsal portion, ♀ 37 mm. c.l., off Camocim, Brazil. b. Sixth abdominal somite, posterodorsal portion, ♀ 39.5 mm. c.l., Little Bahama Bank.

from the Isla Contoy along the Caribbean Coast of Mexico, Central America, and South America (fig. 77). It is absent from the Gulf of Mexico, north of Tortugas-Florida Bay to the vicinity of Cabo Catoche. Lindner (1957) indicated that it might be present in the coastal lakes of Uruguay. This probably erroneous assumption was based on the observation of specimens in the commercial catches at Rio Grande do Sul (Milton J. Lindner, personal communication); however, as implied above, no specimens have been collected so far south.

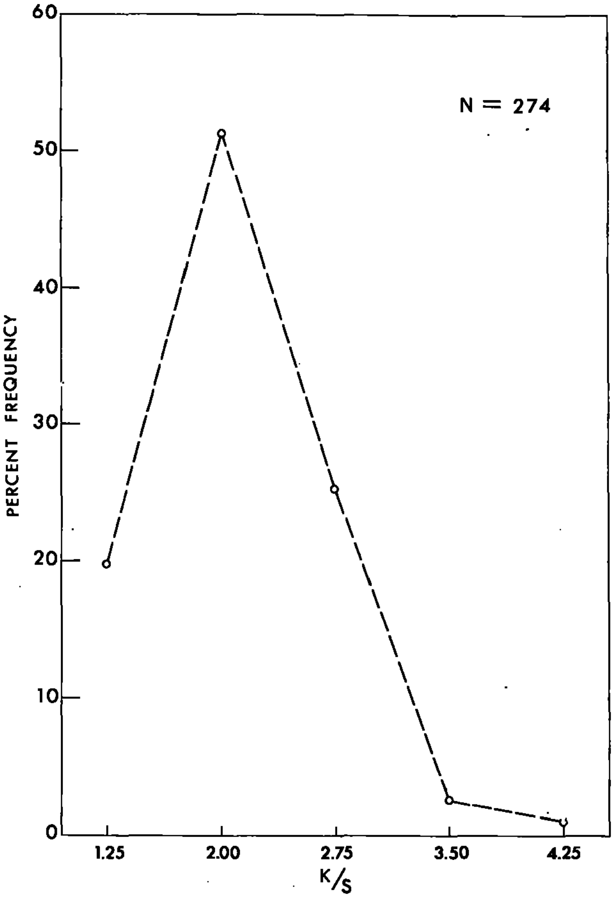

FIGURE 71.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *brasiliensis* Lat. from the coast of South America.

*P. brasiliensis* is generally very scarce in the northernmost portion of its range. The record from off Cape Hatteras given by Burkenroad (1939) was the first positive evidence of the presence of the species, as restricted by him, in the waters of the United States. Previous references of the occurrence of *P. brasiliensis* along the Atlantic Coast of the United States were based on collections of *P. a. aztecus* and *P. d. duorarum*, which were previously identified as *P. brasiliensis*. It may be that specimens of *P. brasiliensis* were represented in the collections. Eldred and Hutton (1960) stated that the range of the species included the Caribbean and Atlantic Coasts of South America and indicated the possibility (probably based on Burkenroad's only record) that it also occurs along the North American coast. Eldred (1960) found *P. brasiliensis* in Biscayne Bay, Fla., and, thus, corroborated its presence in the southeastern United States. Recently, Costello and Allen (1964) collected this species in eastern Florida Bay; and Joyce (1965) recorded it from northeast Florida. I have also examined specimens from other localities in Florida, north of Fort Pierce and off Key Largo (see Study Material). The presence of this species in the Tortugas is based on a single male specimen deposited in the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex. It was taken in a commercial catch made at approxi-

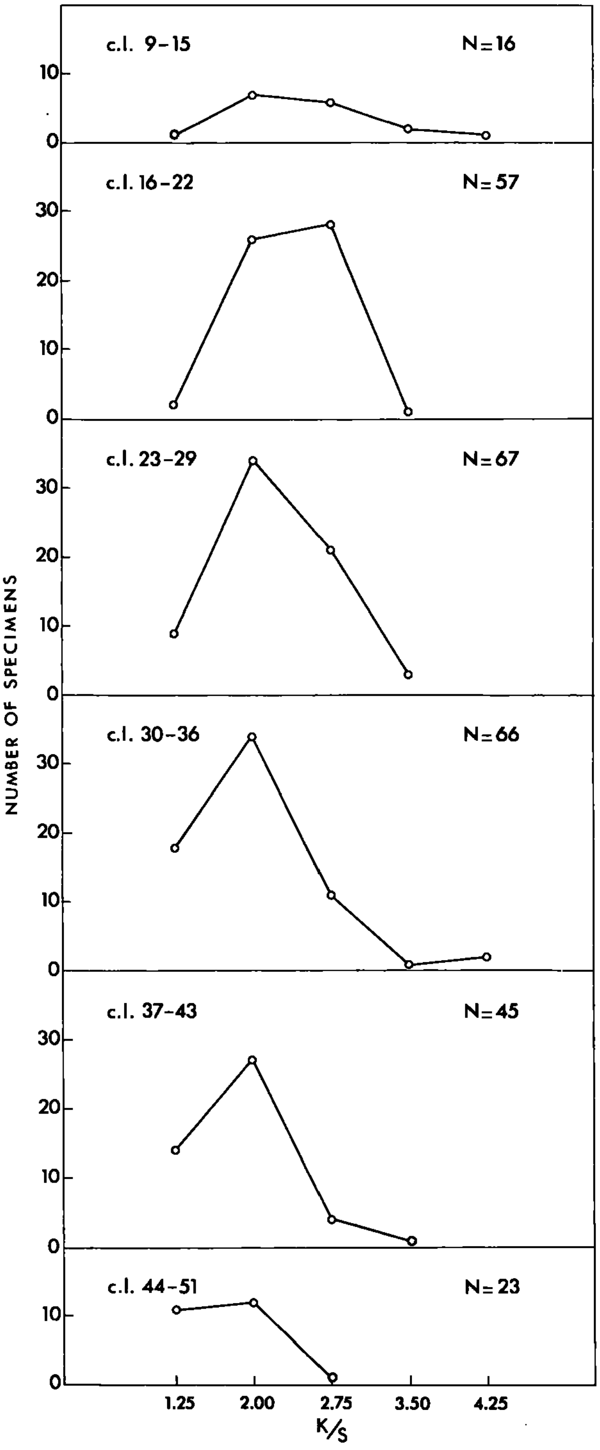

FIGURE 72.—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *brasiliensis* Lat. of different size classes from the coast of South America.

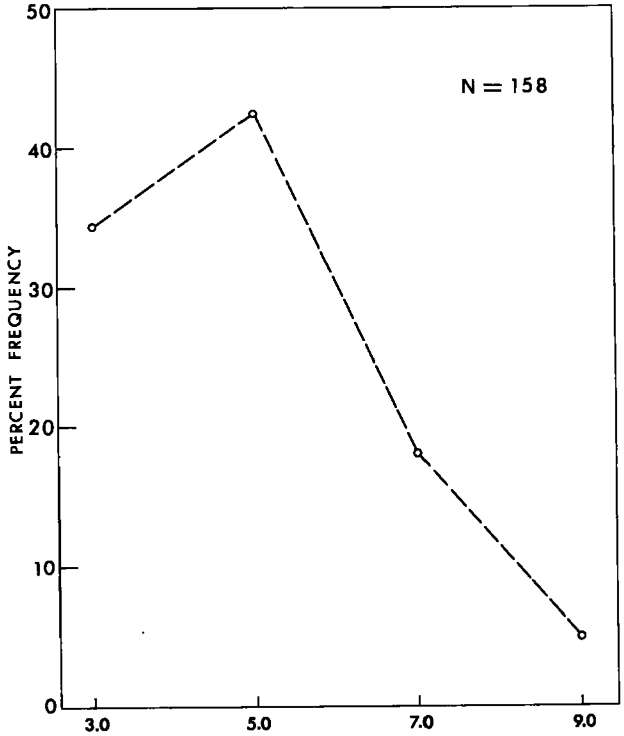

FIGURE 73.—Percentage of distribution of keel-sulcus (K/S) values in *Penaeus* (*M.*) *brasiliensis* Lat. from the West Indies, Central America, eastern United States, and the Bermudas.

mately lat. 24°54′ N., long. 82°15′ W., in water 13 fm. deep (Milton J. Lindner, personal communication).

*P. brasiliensis* apparently is not abundant in the Greater Antilles, although it is taken with *P. a. subtilis* through the Lesser Antilles, whereas *P. schmitti* seems to be extremely rare and *P.d. notialis* has not been recorded. The 1-year sampling carried out by Pérez Farfante et al. (1961) at Laguna Doctor, Playa de Baracoa, Cuba, showed that *P. brasiliensis* is the least common among the shrimp living in this body of water, making up only 10 percent of the total sample. This percentage seems to be representative of the relative abundance of the species, at least in northern Cuba. Although present along the southern coast of the island, P. *brasiliensis* is extremely scarce. I found only a very few individuals in the stomach of snappers (Lutjanidae). The three specimens listed by Boone (1930) as "*P. brasiliensis*" from Cuba, two from the "south coast" and a third from Guantánamo, I found to be *P. d. notialis*.

Holthuis (1959) reported that in Surinam *P. brasiliensis* is far less common in shallow water

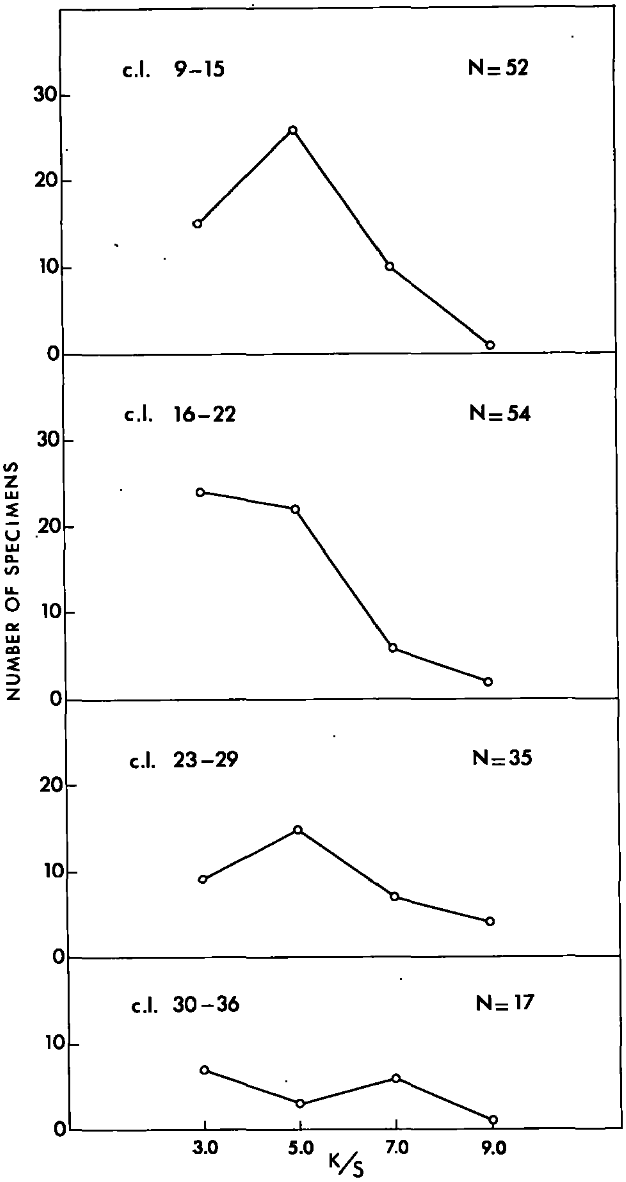

**Figure 74.**—Frequency distribution of keel-sulcus (K/S) values (both sexes included) in *Penaeus* (*M.*) *brasiliensis* Lat. of different size classes from the West Indies, Central America, eastern United States, and the Bermudas.

than *P. a. subtilis*, although it is more frequent in deeper water (20 to 30 fm.). He also indicated a similar finding in French Guiana, where most *P. brasiliensis* were caught between 22 and 38 fm. Bullis and Thompson (1959a) stated that commercial quantities of this species are present off the Guianas, and that maximum catches were taken near the 30-fm. curve. The same depth distribution seems to persist along the coast to Brazil, where it is also abundant.

The bathymetric range of *P. brasiliensis* while broad, is not so great as that of *P. d. notialis*. The greatest depth at which it has been collected is 150 fm. At this depth a collection was made west of Andros Island, Bahamas, at *Oregon* Sta. 2475. Other deep water records (see Study Material) include depths of 95, 100, and 105 fm.

Rossignol (1957) reported *P. brasiliensis* from West Africa. It seems probable that the specimens were actually *P. duorarum notialis*, and that the author identified them using the old name *P. brasiliensis*, a name employed before Burkenroad (1939) recognized that three species were included under the latter name.

In *P. brasiliensis* both the petasma and the thelycum vary, but none of the variations may be correlated with a restricted portion of the range. In the petasma the number of teeth on the attached edge of the ventral costa vary in number, and the band of spines along the membranous portion of the ventrolateral lobule may be narrow or relatively broad. The thelycum, in turn, may or may not have a median carina projecting caudad from the posterior process; the protracted anteromedian corners of the lateral plates may taper anteriorly or may be expanded into disklike projections that overlap. Neither of the characters mentioned, however, is typical of shrimp from a limited region.

As stated above, the keel-sulcus ratio increases progressively (the dorsolateral sulcus narrows) from northern South America northward; no distinct break occurs in the range of this ratio anywhere within the range of the species. The length of the rostrum also shows a south-north cline, a tendency to increase from south northward, reaching a maximum in the populations from the Bahamas, the United States, and the Bermudas.

## Relationships

Adults of *P. brasiliensis* are readily separable from adults of the other species of *Penaeus* from the western Atlantic. Females can be identified by the small anterior process and the anteromedian corners of the lateral plates, which are produced anteriorly and completely cover the posterior process, and by the lack of a median carina on the latter or the possession of a short one which is situated at the posterior end, sunk between the horns of sternite XIII. Males may be recognized by the free apex of the ventral costa, the distal fold that forms a large auricle armed with strong

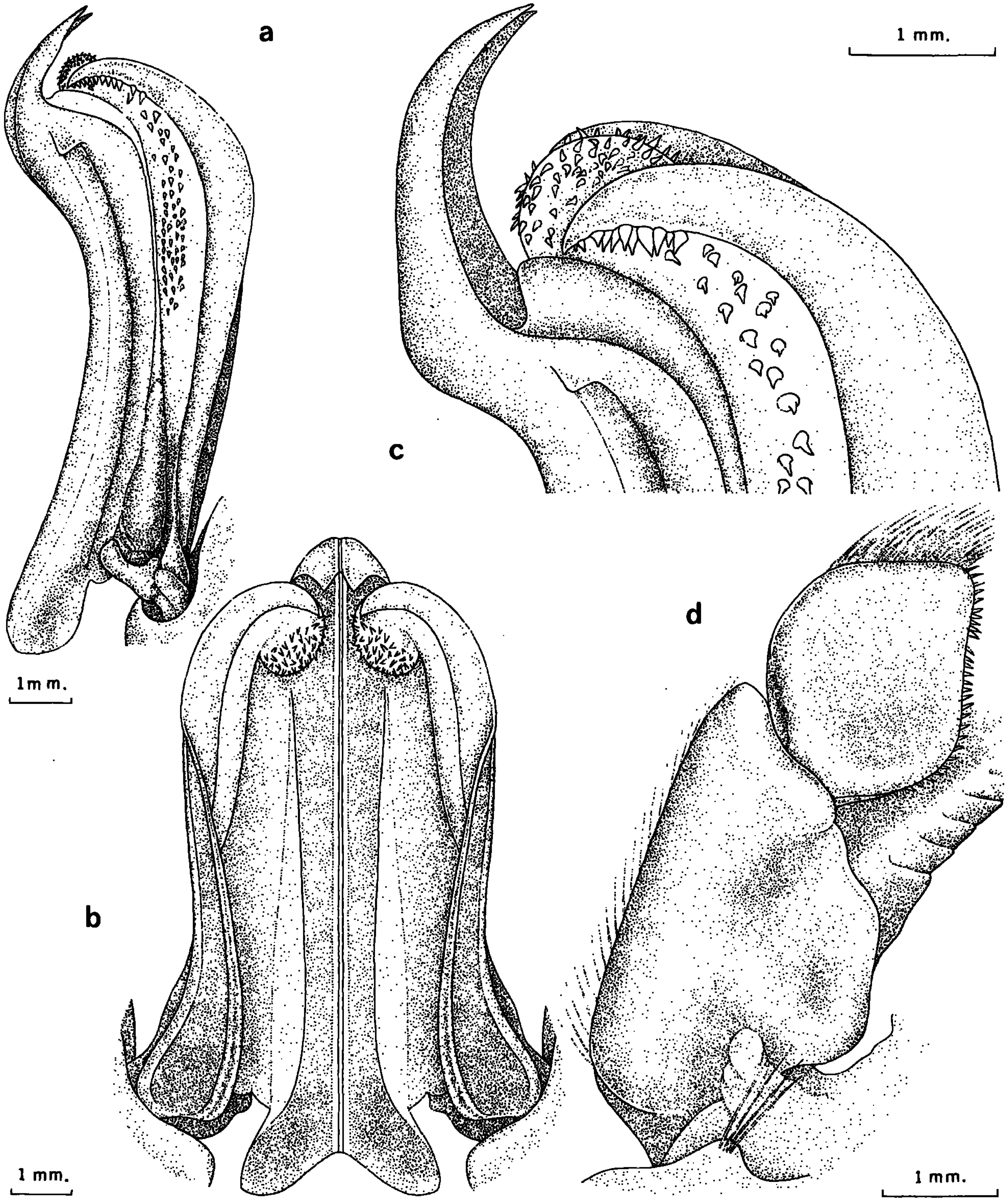

FIGURE 75.—*Penaeus* (*M.*) *brasiliensis* Lat. a. Petasma, ♂ 36 mm. c.l., N. of Península de Paria, Venezuela. b. Petasma, interior surface, ♂ 36 mm. c.l., N. of Península de Paria, Venezuela. c. Petasma, distal portion, ♂ 36 mm. c.l., N. of Península de Paria, Venezuela. d. Appendix masculina, ♂ 42 mm. c.l., off Guyana.

spines on its inner surface, and the long distomedian projections of the petasma.

*P. brasiliensis* also often has the cicatrices on the sixth abdominal somite conspicuously smaller, particularly the posterior one, than those of any other *Penaeus* from the entire region.

*P. brasiliensis* juveniles closely resemble those of *P. d. duorarum* and *P. d. notialis;* in *P. brasiliensis* males, however, the median ridge on sternite XIV is higher, particularly in the anterior portion which is produced in a triangle (as seen in lateral view), and the groove surrounding the ridge is deeper than that found in the two subspecies of *P. duorarum*. Furthermore, in males 10 to 11 mm. c.l., 47 to 51 mm. t.l., the ventral costa of the petasma lacks distomarginal spines. Males 12 mm. c.l., 55 mm. t.l., usually have the distomedian projections of the petasma longer and more slender than those of *P. d. duorarum* and *P. d. notialis* of corresponding size. In females, 12 mm. c.l., 55 mm. t.l., the anterior process is smaller; the lateral plates have the anteromedian corners angular or pointed anteriorly rather than rounded, and if the posterior process bears a median carina, it is located between the horns. In addition, in the Caribbean region, the dorsolateral sulcus in *P. brasiliensis* is usually narrower than in *P. d. notialis.*

Juveniles of *P. brasiliensis* are distinguished from those of *P. a. aztecus* and *P. a. subtilis* by the usually almost straight rostrum which is also shorter than in *P. a. subtilis* through their common range; males may also be distinguished by the sharp median ridge on the ventral surface of sternite XIV, and females by the posterior process, which is less prominent, is not produced caudally, and often lacks a median carina, which, if present, is situated more dorsally. The median sulcus is also deeper and longer, and the adrostral sulcus much wider and longer than in juveniles of *P. a. subtilis*. The typical characters of the external genitalia mentioned above also distinguish *P. brasiliensis* juveniles from those of *P. paulensis*. Furthermore, the dorsolateral sulcus is usually broader in *P. brasiliensis* throughout their common range.

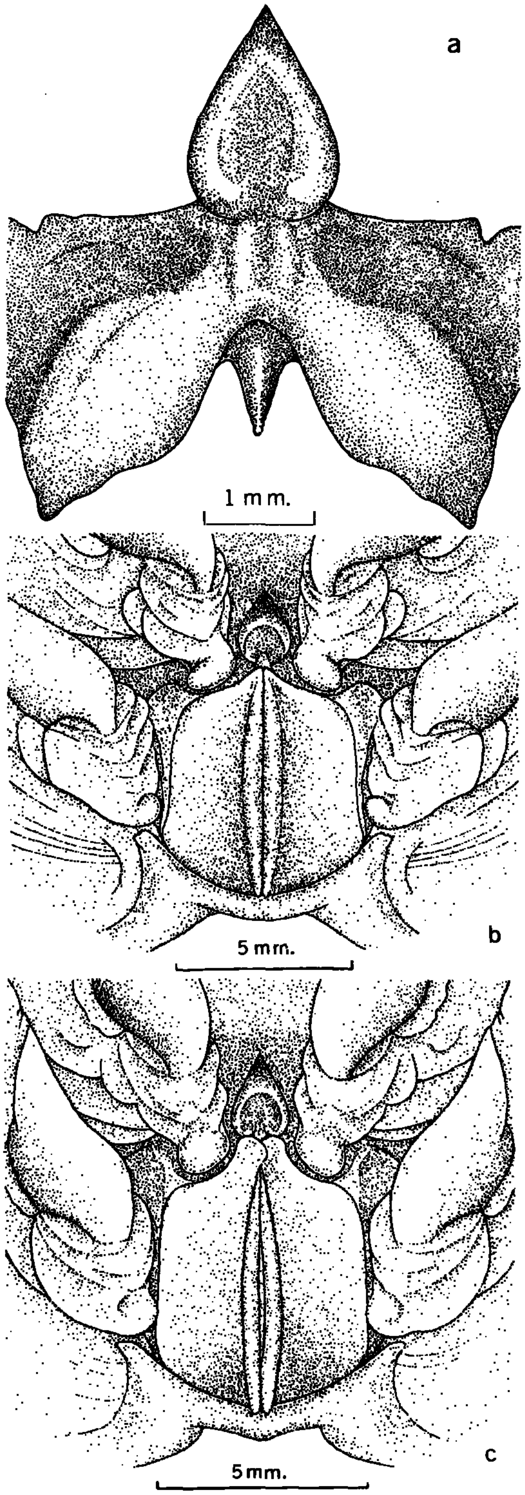

FIGURE 76.—*Penaeus* (*M.*) *brasiliensis* Lat. a. Median protuberance with horns on posterior margin of sternite XIII, ♀ 43.5 mm. c.l., E. of Georgetown, Guyana. b. Thelycum, ♀ 41 mm. c.l., off Surinam. c. Thelycum, ♀ 42 mm. c.l., off Surinam.

## Reproduction

### SUBADULT STAGE-SEXUAL MATURITY

The smallest males observed with joined petasma were 15 mm. c.l., 69 mm. t.l.; many individuals to 22 mm. c.l., 97 mm. t.l., however, had unjoined petasmal endopods. It, therefore, appears that males reach the subadult stage within the

FIGURE 77.—Distribution of *Penaeus* (*M.*) *brasiliensis* Lat.

size range 15 to 23 mm. c.l., 69 to 101 mm. t.l. The smallest females with functional thelyca were 15 mm. c.l., 70 mm. t.l., but in many females 19 mm. c.l., 86 mm. t.l. the lateral plates were non-contiguous. Thus, they reach the subadult stage within the size range 15 to 20 mm. c.l., 70 to 90 mm. t.l. No studies have been made to allow conclusions as to the size at which females first reach maturity.

### COPULATION

As it seems to be true in other *Penaeus* with a closed thelycum, copulation in *P. brasiliensis* is believed to take place between a hard-shelled male and a soft-shelled female.

### OVARY DEVELOPMENT AND SPAWNING

No studies have been conducted.

### SEX RATIO

No intensive sampling has been carried out to determine the male-female ratio.

## Postembryonic Development

### LARVAE, POSTLARVAE, AND JUVENILES

No studies have been made on either larval or postlarval stages of this shrimp.

My studies showed that juvenile *P. brasiliensis* of 18 mm. t.l. have distinctly long adrostral sulci. This character allows for the separation of early juveniles of this as well as those of the other grooved *Penaeus*, from those of the nongrooved *P. setiferus* and *P. schmitti*. At a minimum of about 20 mm. t.l. males and females are distinguished, as are those of the other grooved *Penaeus* in the western Atlantic, by the endopods of the first pair of pleopods, which in the males are longer and are located more proximally on the bases than in the females. In addition, males have a sharp, high ridge on the midline of sternite XIV, whereas in females the sternite XIV is produced on the midline where a knob is frequently present. (See also under Relationships.)

### GROWTH

No studies have been made.

### SEX DIFFERENCES IN SIZE

The largest females on record were 250 mm. t.l., reported from eastern Venezuela by Davant (1963), whereas the largest I measured was 58.5 mm. c.l., 214 mm. t.l., from off Guyana. The largest male recorded was 191 mm. t.l., reported by Holthuis (1959) from Surinam waters. Offshore samples indicate that, as in other *Penaeus* from the western Atlantic, *P. brasiliensis* females become larger than males.

## Ecology

### SUBSTRATE

*P. brasiliensis* juveniles are more abundant where the bottom consists of soft mud. Laguna Doctor, Playa de Baracoa, Cuba, where Pérez Farfante et al. (1961) carried on their sampling, has a bottom of very soft mud covered with vegetation, a habitat typical of most nursery grounds for *Penaeus* shrimp. Adults seem to prefer rather firm bottoms. According to Bullis and Thompson (1959a), along the Continental Shelf of South America, from Trinidad to the Amazon River, this species is most abundant on bottoms consisting chiefly of a mixture of mud and sand.

### DIEL CYCLE

*P. brasiliensis* has mostly nocturnal habits; the young in inshore water are fished at night. Tremel and Mistakidis (1965) described in detail the night fishing for camarão rosa (*P. brasiliensis* and *P. paulensis*) in the coastal lagoons of the State of Santa Catarina, Brazil. Adults are also active at night; Bullis and Thompson (1959a) stated that during their exploratory fishing, "catches fell off at or before daylight, and daytime trawling was unproductive for this species."

The only information available concerning the influence of the lunar phases on the behavior of this species is that given by Wheeler (1937); his observations were made in the Bermudas. This author stated that *P. brasiliensis* showed a rhythmic pattern of activity and quiescence over the new and full moon, respectively, and concluded that the most probable cause of periodic swarming is the cyclic absence of light. He also indicated that the effect of light is occasionally subject to interference by such factors as the opacity of the water.

### MOVEMENTS

No information is available regarding migrations of *P. brasiliensis* at any stage of its life cycle. The only data gathered are a few records of the time juveniles and subadults occupy inshore waters in different areas throughout the range. Eldred (1960) reported juveniles and subadults in Biscayne Bay, Fla., in July, December, and February. Later this species was found to form a large percentage of the shrimp that live in the Bay during the summer. I have identified specimens from inshore waters of Florida taken during both summer and winter.

It appears that in the Caribbean region *P. brasiliensis* occupy the nursery grounds at least from December to June. The sampling carried out by Pérez Farfante et al. (1961) in Laguna Doctor, Playa de Baracoa, Cuba, showed that small individuals to 95 mm. t.l. were present during two periods each year, March–June and September–December. Individuals up to 110 mm. t.l. were collected in January and February, and larger shrimp, 126 to 130 mm. t.l., from March through May. No specimens were taken in July or August. According to Lindner (1957), fishing for the young is usually carried out in the marshes of northern Colombia from January through May; farther east, in the Gulf of Venezuela, Ewald (1964, 1965c) found specimens 18 to 23 mm. c.l. from December to June.

Tremel and Mistakidis (1965) reported that in the State of Santa Catarina, Brazil, *P. brasiliensis* and *P. paulensis* are caught in the coastal lagoons from August to April.

### EFFECTS OF TEMPERATURE

*P. brasiliensis* seems to prefer waters of relatively high temperatures. It is the only one of the four *Penaeus* in the southeastern Atlantic Coast of the United States that does not invade the colder waters north of Cape Hatteras, and in the Southern Hemisphere only stragglers seem to wander south of Laguna, Brazil. Furthermore, the densest concentrations of *P. brasiliensis* are found in the warmest portion of its range. Experiments by Scholander et al. (1953) showed that "*Penaeus* sp. (*brasiliensis*)" could not tolerate temperatures lower than 8° to 12° C., nor those above 35° C.

### EFFECTS OF SALINITY

*P. brasiliensis*, like other species of *Penaeus*, appears to have a wide range of salinity tolerance during the inshore phase of its life. The meager information available, however, suggests that at least the young have a high optimum salinity. Lindner (1957) reported that although the young are fished intensively during the dry season— January through May—in Ciénaga Grande de Santa Marta, Colombia, the extensive marsh area in northern Colombia between Barranquilla and Santa Marta, they are caught during the entire year when rainfall is not heavy and the marsh waters are not greatly diluted. During floods fishermen are unable to locate shrimp in the area.

### ENEMIES AND DISEASES

Iversen and van Meter (1964) published the first record of a parasite in *P. brasiliensis*. In Biscayne Bay they found this shrimp infested with *Thelohania duorara* Iversen and Manning, the microsporidian that causes the condition known as "cotton" or "milk" shrimp. Infestations of this parasite in *P. d. duorarum* are common.

## Commercial Importance

*P. brasiliensis* is important to the fisheries of several Latin American countries, although it ranks lowest among the commercial *Penaeus* from West Indies northward. In Biscayne Bay, the only area in the United States where it is known to be significantly represented in the catches, this species may contribute to 41 percent of the shrimp caught during July (Costello, 1963; Joyce and Eldred, 1966). It abounds there in summer and fall.

This species forms only a very small percentage of the catches in the Greater Antilles. Milton J. Lindner has informed me that the U.S. boats have been taking spotted pink shrimp in numbers off Contoy, Mexico, for several years. *P. brasiliensis* contributes substantially to the catches made off Nicaragua (Croker, 1967; Instituto de Fomento Nacional, 1967). Lindner (1957) reported that the young are taken in Ciénaga Grande de Santa Marta, Colombia. Ewald (1964, 1965c) stated that it is the least important of the commercial species of *Penaeus* in western Venezuela, where it is caught only seasonally in the northeastern portion of the Gulf of Venezuela and outside the Gulf proper, north of Cabo San Ramón. *P. brasiliensis* supports the fishery of Isla Margarita, which, according to Croker (1967), probably accounts for most of the 236,757 kg. of shrimp taken along the coast of Venezuela, east of the Gulf.

*P. brasiliensis* makes up most of the gigantic catches made along the Atlantic Coast of South America, from Guyana to Baía de Marajó, Brazil. In 1965, exports to the United States from that area amounted to about 7 million kg.

This species apparently has limited commercial value throughout the coastal waters of northeastern Brazil, but it is important to the fisheries in the neighborhood of Cabo Frio and southward. Da Silva (1965) stated that the young of *P. brasiliensis* are the most abundant shrimp in Baía de Guanabara; offshore the adults make up a relatively large percentage of the shrimp catches. Landings of camarão rosa (*P. brasiliensis*, *P. paulensis*, and perhaps *P. a. subtilis*) in Rio de Janeiro during 1965 amounted to 63,900 kg., but in 1966 to only 10,700 kg. (SUDEPE).

The estimates by Braga (1962) indicate that *P. brasiliensis* together with *P. paulensis* make up a large percentage of the landings at Santos, São Paulo. The majority of the shrimp landed there under the name camarão rosa, however, seems to be *P. paulensis*. According to Tremel and Mistakidis (1965), camarão rosa (*P. brasiliensis* and *P. paulensis*) is fished in the State of Santa Catarina in the lagoons and the ocean throughout the year. The production in that State during 1965 amounted to 248,600 kg., and during 1966 reached an all-time high of 688,500 kg. (Centro de Pesquisas de Pesca).

Mistakidis (1965) found, contrary to previous information, that *P. brasiliensis* is very scarce in Lagoa dos Patos, where *P. paulensis* is responsible for the large commercial catches in that vast body of water.

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# SYSTEMATIC INDEX

[Limited to names related to western Atlantic shrimps]

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