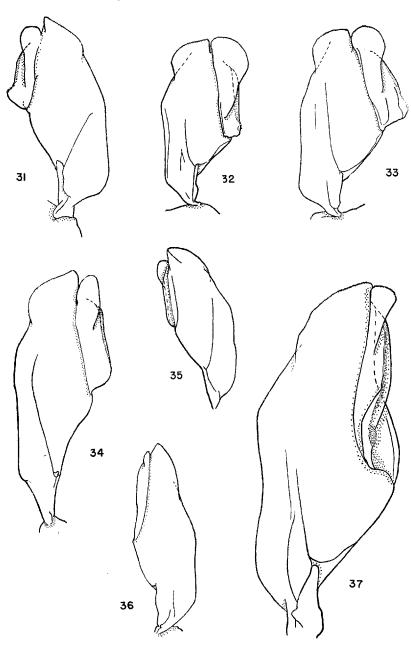
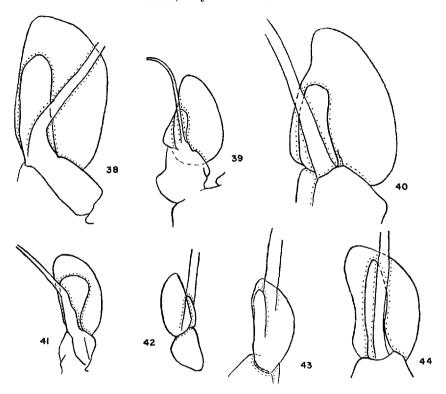


Genital sternites (XII, XIII and XIV, with third, fourth and fifth leg-bases). 26. Benthesicymus brasiliensis Bate (Specimen No. 7,  $\circ$ ),  $\times$  4.8. 27. B. strabus, n. sp. (No. 18, TYPE  $\sigma$ ),  $\times$  11. 28. B. cereus, n. sp. (No. 16,  $\circ$ ),  $\times$  4.8. 29. B. iridescens Bate (No. 23,  $\sigma$ ),  $\times$  4.8. 30. B. iridescens Bate (No. 22,  $\circ$ ),  $\times$  11.



which two forms are found together (the occurrence of B. brasiliensis with B. iridescens at Tristan da Cunha) may indicate that the fixation is not environ-



Appendix masculina (Figures 38, 39, 40, 41 and 44, left pleopod, posterior view of the appendix; Figure 42, left pleopod, anterior view; Figure 43, right pleopod, anterior view). 38. Benthesicymus brasiliensis Bate (Specimen No. 1, cotype), × 12. 39. B. urinator, n. sp. (No. 8, type), × 6.8. 40. B. urinator, n. sp. (No. 12), × 12. 41. B. strabus, n. sp. (No. 18, type), × 12. 42. ? B. cereus, n. sp. (No. 15), × 12. 43. B. iridescens Bate (No. 20), × 15.5. 44. B. iridescens Bate (No. 19, type), × 5.

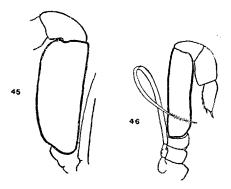
mental. The detailed identity of specimens from the north and the south Western Atlantic; from Torres Strait and the Hawaiian Islands; and from Tristan da Cunha and the Fiji Islands, seems evidence that if these similar forms are not to be regarded merely as direct reflections of similar environments,

Petasma (Figures 32, 33, 34 and 37, left half, anterior face; Figures 31 and 36, right half, anterior face; Figure 35, left half, posterior face). 31. Benthesicymus brasiliensis Bate (Specimen No. 1, COTYPE), × 4.8. 32. B. urinator, n. sp. (No. 8, TYPE), × 4.8. 33. B. urinator, n. sp. (No. 12), × 4.8. 34. B. strabus, n. sp. (No. 18, TYPE), × 11. 35. 7 B. cereus, n. sp. (No. 15), × 11. 36. B. iridescens Bate (No. 20), × 11. 37. B. iridescens Bate (No. 19, TYPE), × 4.8.

4 65

they must be regarded as more than simple geographical-genetic segregants, that is, as specifically rather than as racially distinct.

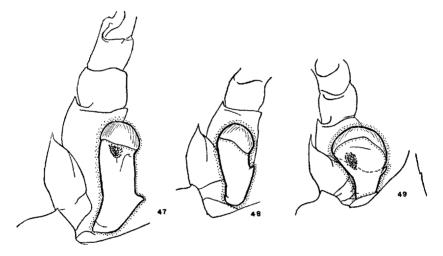
Specimen No. 18, here designated as <u>B. strabus</u> n. sp., is distinct in so many features not only from the other specimens with a single armed pleonic tergite, but from all the other material available, that I have been forced to conclude that specific differentiation exists in the <u>B. brasiliensis</u> complex even beyond the limits set by the possible variations in pleonic formula. As is shown by table and by illustrations, this specimen resembles <u>B. cereus</u> in rostrum (figure 10, p. 35) and in pleonic armature but falls well outside that group in position of proximal telson spine (figure 23, p. 37), in which it resembles <u>B. urinator</u>. The proximal spine (the only remaining) is, however, relatively very much



Second maxillipede, posterior view (showing degree of expansion of merus). 45. Benthesicymus urinator, n. sp. (Specimen No. 8, TYPE),  $\times$  4.4. 46. B. strabus, n. sp. (No. 18, TYPE),  $\times$  4.4.

longer than in other available specimens; and if in No. 18 (as in the others) the proximal is the shortest of the telson spines, the anterior ones must have been of excessive length. The antennal scale is relatively somewhat narrower than is the extreme among the other fifteen mensurable specimens. The genital sternites (figure 27, p. 39) differ from those of all other specimens in that the fourteenth bears a very large, strong, slender spine; while the thirteenth bears a similar spine in place of the more usual broad scute. The distal edge of the distoventral lobe of the petasma (figure 34, p. 40) is less oblique than in the other specimens, except B. urinator (where it is still less oblique) and the distolateral lobe differs from the B. brasiliensis type in the lesser narrowing of its proximal portion. The posterior blade of the appendix masculina (figure 41, p. 41) is unique in the great expansion of its distal part. In two further features, not considered in the table, in which the remainder of the material is rather uniform, No. 18 is highly distinct. The merus of its second maxillipede (figure 46, p. 42) is as little expanded as in Group II of Benthesicymus, being more than

three and one-half times as long as broad; whereas in other specimens this ratio seems never to be as much as three times. Its eye (figure 49, p. 43) is extremely short; the cornea very broad and extending considerably further down the peduncle on the ventral than on the dorsal surface; and the tubercle of the median margin is placed nearly at the level of the proximoventral margin of the cornea. Although the length of the peduncle varies somewhat in the other representatives of the complex (the subjoined figures representing the extremes of the series), it is always much longer than in *B. strabus*, and subcylindrical;



Left eye, dorsal view (Figures 47 and 48 representing the extremes of variation in the specimens of the complex other than B. strabus). 47. Benthesicymus cereus, n. sp. (Specimen No. 16),  $\times$  3.7. 48. B. iridescens Bate (No. 24),  $\times$  3.7. 49. B. strabus, n. sp. (No. 18, Type),  $\times$  3.7.

the cornea is never much broader than the main column of the peduncle, and does not extend further down the peduncle on the ventral than on the dorsal surface; and the tubercle is always placed far proximal to the cornea. In a fairly extensive experience with the shrunken, ill-preserved, or otherwise distorted eyes of museum specimens of deep-sea peneids, I have never observed any deformations suggestive of the features of the eye of No. 18; and am unable to conceive of its peculiarities as artificially produced. In consideration of the above differences, despite the uncertainties of specific differentiation in the whole complex and the fact that only a single juvenile male is available to serve as type, it seems best to consider No. 18 as specifically distinct from its congeners.<sup>1</sup>

<sup>1</sup> In view of the fact that B. strabus differs from other members of its complex and approaches Benthonectes in form of merus of second maxillipede and of eye, it

Specimens of the *Benthesicymus brasiliensis* complex equivalent in pleonic armature to *B. urinator*, *B. strabus*, and *B. cereus* have never been named or described as distinct; and indeed, none equivalent to the latter two have been described at all. I have therefore concluded that none of the names employed by previous students is applicable to these three forms. The two species of which type material has not been available to me, *B. armatus* MacGilchrist and *B. longipes* Bouvier, are said to lack pleonic armature completely, and I have therefore referred them to *B. iridescens*.

The description of the very large female type of *B. armatus* agrees very well with *B. iridescens*, and the relatively great breadth of its antennal scale is particularly suggestive of the identity of the two forms. I have observed the depth of the sixth pleonic somite to vary in the complex from .25 to .51 times the length, without any very apparent relation to size or species; in the available specimens of *B. iridescens*, this ratio ranges from .39 to .43, as compared to .49 for *B. armatus*. The pleonic carination in both *B. iridescens* and *B. cereus* is usually as described for *B. armatus*, although a carina is occasionally lacking on the eighteenth somite in both of the former, as it is in the single specimen of *B. strabus*.

As to B. longipes, Bouvier's statement that it differs from his specimens of B. moratus in that the posterior blade of the appendix masculina is nearly as long as the anterior, and distally attenuated, clearly corresponds to the difference in this organ between B. iridescens and B. brasiliensis (with the petasma of which the figure by Milne Edwards and Bouvier, 1909, is roughly in agreement). Bouvier is probably mistaken in thinking the submedian ridge of B. longipes to bear cincinnuli only at its proximal end; the spines are generally densest on this prominence, but in B iridescens are continued to the distal end of the ridge, which is, in Bouvier's figure, hidden behind the unarmed median margin of the petasma. That the rostrum of B. longipes is shorter than in Bouvier's B. moratus is quite compatible with the present determinations of these specimens; the figures which Bouvier presents are, however, hardly accurate. The antennal angle, said not to be in B. longipes, is armed in all of the available material, but the tooth is often much reduced. Bouvier says of his speries "Le telson est loin d'atteindre la longeur du segment abdominal précédient"; but since under B. moratus he says, "Le telson est notablement plus court que le sixième segment abdominal," what distinction he here wishes to make is not clear to me. From his figures, the finger of the second maxillipede of B. longipes would be relatively longer instead of shorter

seems well to emphasize its strict adherence to the mode of its complex in features in which *Benthonectes* is conspicuously different (carination of carapace, form of mandibular palp and molar, development of terminal segment of first maxillipede), according to supplementary notes on the type very graciously prepared by Dr. Gordon of the British Museum. The third maxillipedes of the type are missing.

than that of B. moratus. The "assez différentes" relative lengths of the dactyls of the chelipeds of B. longipes seem to me little different from what he describes on a preceding page for B. moratus. The penultimate article of the endoped of the first maxillipede of B. longines is much wider than that figured by Bouvier for B. moratus, but is not significantly wider than this joint as figured by Smith, 1884. The occurrence of three teeth on the incisor process of the mandible of B. longipes does not distinguish it, since in available specimens of the complex there seems to be an asymmetry not unusual in the family, two teeth occurring on the mandible of the left side, three on the right. Bouvier's statement that in B. moratus the incisor process "se termine par une dent aigue" seems erroneous. I can find no features in Bouvier's description which might encourage the opinion that B. longipes is not identical with B. iridescens.

Although the above revision is, in a sense, tentative, it seems well to clear the way of future investigators by the presentation of a diagnostic key to the species of the complex as at present determinable.

### KEY TO THE SPECIES OF THE B. BRASILIENSIS COMPLEX

p. 40; 38, p. 41.

- Posterior margin of the fourth pleonic tergite armed with a tooth. Posterior rostral tooth usually behind the level of the orbital margin.
- Posterior margin of the third pleonic tergite armed with a tooth; tooth of the fourth tergite not greatly enlarged. Interval between penultimate and antepenultimate lateral spines of the telson more than twice as great as that between penultimate and ultimate pairs. Anterior blade of appendix masculina not broadest at the base.

B. brasiliensis Bate Figures 2 and 3, p. 31; 14, 15 and 16, p. 36; 21, p. 37; 26, p. 39; 31,

IB. Posterior margin of the third pleonic tergite unarmed; tooth of the fourth much larger than that of the succeeding tergites. Interval between penultimate and antepenultimate less than one and onehalf times as great as that between penultimate and ultimate spines. Anterior blade of appendix masculina very wide at base.

B. urinator, n. sp.

Figures 4 and 5, p. 31; 9, p. 35; 17 and 18, p. 36; 32 and 33, p. 40; 39 and 40, p. 41; and 45, p. 42.

- Posterior margin of the fourth pleonic tergite unarmed. Posterior rostral tooth usually anterior to the level of the orbital margin.
- IIA, Merus of the second maxillipede more than three and one-half times as long as broad. Cornea nearly as broad as the ocular peduncle is long; ocular tubercle nearly at the level of the proximoventral corneal margin. Posterior blade of the appendix masculina distally much expanded.
  - Posterior margin of the sixth pleonic tergite armed with a tooth. Interval between the proximal lateral spine and the distalmost of the

basolateral emarginations of the telson less than the interval between the distal and the penultimate emarginations.

B. strabus, n. sp.

Figures 10, p. 35; 23, p. 37; 27, p. 39; 34, p. 40; 41, p. 41; 46, p. 42; 49, p. 43.

- IIB. Merus of the second maxillipede less than three times as long as broad. Cornea not nearly so broad as ocular peduncle is long; ocular tubercle far proximad the cornea. Posterior blade of the appendix masculina not considerably expanded at the tip.
- IIB 1. Posterior margin of the sixth pleonic tergite armed with a tooth.

  Breadth of antennal scale usually less than one-third the length.

  Interval between proximal lateral spine and the distalmost of the basolateral emarginations of the telson usually less than one and one-third times the interval between the distal and the penultimate emarginations.

  B. cereus, n. sp. For list of figures see p. 30.

IIB 2. Posterior margin of the sixth pleonic tergite unarmed. Breadth of antennal scale usually more than one-third the length. Interval between proximal spine and distal emargination usually more than one and one-third times the interval between the distal and the penultimate emarginations

B. iridescens Bate
Figures 7, p. 31; 13, p. 35; 20, p. 36; 25, p. 37; 29 and 30, p. 39; 36 and 37, p. 40; 43 and 44, p. 41; 48, p. 43.

# Benthesicymus carinatus Smith

Benthesicymus? carinatus, Smith, 1884; Sund, 1920. Gennadas carinatus, Alcock, 1901; Bouvier, 1906a; Kemp, 1910b; DeMan, 1911. Gennadas carinatus?, MacGilchrist, 1905. ? Gennadas A, Hanström, 1933 and 1934.

1 male, juvenile; carapace length 38 mm.; total length about 130 mm.  $B.\ O.\ C.$  150. Pawnee Station 54; N. 21° 15′ 40″ W. 71° 17′ 06″; April 12, 1927. Wire 7,500 feet (bottom struck at 900–945 fathoms).

The present specimen, from Turks Island Passage in the West Indies, provides the third Atlantic record, the fifth known individual, and the second known male. The type female, of considerably smaller size, was taken in approximately the same longitude, but more than 18° to the north. Sund's Atlantic female was taken still more to the northward and considerably farther east. The Indo-Pacific male and female were both taken, some years apart, in the Arabian Sea near the Laccadives. All records are from 900 to 1000 fathoms; but while that by Sund appears to refer to a pelagic capture, the other specimens were with more or less probability taken at the bottom, a supposition strengthened by the results of examination of the statolith (see p. 22).

The belief expressed by Kemp and by Sund that B. carinatus is intermediate between Benthesicymus and Gennadas is based on the degree of expansion of the

maxillipedal and pereiopodal meri, which in this species is no greater than in *Benthesicymus crenatus*, the genotype. Since in other characters *B. carinatus* approaches much less closely to *Bentheogennema* or *Gennadas* than do members of the *B. bartletti* group, in which the degree of expansion of the pereiopods is very slight, the emphasis attached to this feature by previous workers is seen to be misplaced.

The petasma of the present specimen is much as in the Indo-Pacific male figured by Kemp, except that the distolateral lobe is no higher than the distoventral (Kemp's is a posterior view of the petasma, the median margin being to the reader's left). It is a peculiar fact that, as in the other members of Group I, the median margin bears no trace of cincinnuli. A row of short, straight spinules, edging a ridge lateral to the median margin which extends up the anterior face of the endopod to the notch between distormedian and distolateral lobes, is probably functionally equivalent in adults to the cincinnuli of other peneids. The ridge may represent a lobus accessorius, such as occurs in more typical form in the B. bartletti group where, in B. altus, the accessory is denticulate although the median margin bears normal cincinnuli. Alcock believes the petasmal endopods of B, carinatus to be normally separate "when not in use," but it seems more probable that the available males are juvenile, the straight spinules being transformed into grapples in the adult (as in B. crenatus); and the endopods hooked together except just after the molt. The distomedian and distolateral lobes bear a few spinules at their apex similar to those of the lobus accessorius; and the distoventral lobe is likewise denticulate along its distal and outer margins.

According to Smith, Alcock and Kemp, the third tergum of the pleon is longitudinally carinated; this is not the case in the present specimen. The fourth, fifth and sixth terga are carinated in all known specimens; none of the carinae ends in a tooth. According to Kemp the postcervical sulcus is strongly marked; and the postrostral carina continued to the posterior margin; this is not the case in the present specimen. According to Smith, there is no conspicuous tooth on the first pleonic sternite; but a small tooth is present in the Indo-Pacific specimens according to Alcock and to MacGilchrist, and in the present male.

The complete lack of rostral armature is unique in the series; and indeed, in the family, although not in the tribe.

# GROUP II

## Benthesicymus bartletti Smith

Benthesicymus bartletti, Smith, 1882; Faxon, 1896; Alcock, 1901; Bouvier, 1906a, 1908, and 1922; Milne Edwards and Bouvier, 1909; DeMan, 1911. Benthoecetes bartletti, Smith, 1884, 1885 and 1887; Agassiz, 1888. Benthesicymus pleocanthus, Bate, 1888; DeMan, 1911. ? Benthesicymus bartletti, Hanström, 1933 and 1934.

1 female, carapace 24.5, total length about 85 mm. B.O.C. 151. Pawnee Station 54; N. 21/15/40, W. 71/17/06; April 12, 1927. Wire 7,500 feet (bottom struck at 900–945 fathoms).

In addition to this material, three females of carapace length 24.5 to 34 mm and a juvenile male of carapace 15 mm, in the collection of the Zoology Department of the Peabody Museum of Natural History, were available. These specimens are from "Albatross" dredgings off the Atlantic coast of the United States; one of the specimens, that from Station 2215, has been recorded by Smith, 1887. The extensive series of this species from the "Blake" operations in the collection of the Museum of Comparative Zoology at Harvard, including males of carapace length up to 21 mm has also been examined. Finally, through the very great kindness of Dr. Calman and Dr. Gordon of the British Museum, I have been enabled to examine Bate's material, described as B. pleocanthus: the type, an Atlantic male of carapace length 15.5 mm from "Challenger" Station 23; the two South Pacific males of carapace 18 and 13.4 mm from "Challenger" Station 250; and the Philippine male and female from "Challenger" Station 205. For comparison with B. bartletti, Faxon's Pacific American material of the related species B. altus Bate and B. tanneri Faxon, in the collection of the Museum of Comparative Zoology, has been available, as well as more than one hundred and fifty specimens of B. tanneri from off the Pacific coast of Central America, from the collections made by Dr. Beebe during the "Arcturus" Expedition. Of the related B. investigatoris Alcock and Anderson, two males and a female from Hawaii, recorded by Rathbun, 1906, have been loaned by the U.S. National Museum.

Bouvier, 1908, in differentiating *B. bartletti* Smith from *B. pleocanthus* Bate, makes the incorrect statement that the latter was taken by the "Challenger" only in the Indo-Pacific. The type of Bate's species was taken in the West Indies, a region where *B. bartletti* is abundant. Bouvier's opinion, that the cornea of *B. pleocanthus* is narrower and that its posterior pereiopods are much shorter than are those of *B. bartletti*, is evidently based on Bate's very unsatisfactory figure.

Bate has incorrectly stated that the type of *B. pleocanthus* is a female. The specimen is a juvenile male, of carapace length 15.5 mm, which seems to fall well within the range of variation of other Atlantic specimens of *B. bartletti*. The three "Challenger" males from the Pacific display no features by which they can be distinguished from the Atlantic form. The Philippine female, in which, as observed by Bate, the dorsal spine of the fifth pleonic somite projects from the posterior margin of the tergum, has acquired this anomaly by injury, as believed by Bate; the portion of its fifth tergum dorsal to the locking joint and posterior to the base of the spine having been torn away.

In many, but not in all specimens of B. bartletti, there is a small tooth at the distal end of the basis of the first leg. There is some variation in the height,

ŧ

breadth, and curvature of the distoventral projection of the petasma, and in the sculpture of the male genital sternites; and there is an appreciable amount of variation in the thelycum affecting more especially the strength of the protuberances at the anterolateral corners of the scute of the fourteenth sternite and the shape of the anterior margin of the scute of the thirteenth.

The three species related to B. bartletti have not been involved in very evident synonymic confusion. It seems extremely probable that the specimens from Hawaii referred to B. investigatoris Alcock and Anderson by Rathbun, 1906, are identical with those taken in the Indian Ocean. Benthesicymus tanneri Faxon is a well-defined species limited to the Pacific American region, from which it has been recorded by Faxon, 1895, Rathbun, 1910, and Schmitt, 1924. B. altus Bate, the fourth species of the group, seems to be a widely ranging form like B. bartletti, although its distribution is quite different from that of Smith's species. There seems no reason to doubt that the Pacific American specimens recorded by Faxon and by Schmitt are identical with the type female from Torres Strait. Whether Bate's extensive series, from various localities along the western front of Asia and from the South Atlantic, is completely homogeneous is uncertain, since he makes the puzzling remark that in the males, in contrast to the females, the dorsal carina of the fifth and sixth pleonic somites terminates in a minute tooth. Such a varietal form is difficult to accept, in view of the peculiar form of the sixth pleonic segment of B. altus, and I think it quite possible that Bate's material may include specimens of B. investigatoris.

The diagnostic distinctions between the species of Group II, given in a preceding paragraph, may be enlarged upon; and certain other differences between the forms may be considered, as follows:

Benthesicymus investigatoris, which is limited to the Indo-Pacific, is quite distinct from the other three species of the group, which form a very compact unit and all of which occur in American waters. In B. altus, B. tanneri, and B. bartletti the eye is rather similar to that found in species of Group I other than B. strabus. On the contrary, this structure in B. investigatoris is different from any type reported for the family by Hanström, 1933. Proximal to the normal pigmented visual area of the eye of B. investigatoris there can be seen a whitish grained area (rather inaccurately indicated in a figure by DeMan, 1911) lying beneath the weakly-facetted cuticular surface, which appears to represent an unpigmented continuation of the crystalline-cone layer of the normal part of the eye. If the entire area of crystalline cones is considered, rather than the extent of the normal pigmented part, the receptor area of the eye of B. investigatoris approaches the usual hemispherical shape; but if the normal region alone is considered, the receptor area is acutely reniform; it is, however, reniform in a plane the reverse of that found in littoral peneids with reniform eye, since the visual area extends down the median, rather than the lateral side of the peduncle. It seems a matter of note that in Benthonectes filipes according to Smith, 1885 and 1887, the eye is of similar reverse-reniform type, which is not known elsewhere in the tribe, and it would be of the greatest interest to know whether this shape has been attained in the same manner in *Benthonectes* as in *Benthesicymus investigatoris*: that is, by what appears to be an incomplete degeneration of a posterior part of the visual surface. The coincidence, that in *Benthonectes*, as in the present species, the peduncle differs from the form usual in the series by its shortness and by the situation of the tubercle at a point much nearer to the cornea than to the base of the peduncle, may be observed.

The petasma of the three species of Group II which occur in America very nearly resembles that of Bentheogennema intermedia (Bate) and Gennadas capensis Calman; while that of B. investigatoris differs in the lesser development of its distoventral projection. Superficially, the petasma of B. investigatoris is somewhat like that of B. altus, but in the latter the distoventral projection rises high above the distoventral flap (the distal margin of which is marked by the notch in the lateral edge of the petasma), the superficial similarity being caused only by shallowness in both forms of the emargination between distoventral projection and distolateral lobe. The figure of the petasma of B. investigatoris by Balss, 1927, clearly shows the complete lack of marginal distinction between distoventral projection and distolateral lobe (although the two are separated by a faint, short, longitudinal ridge on the distal part of the posterior face of the petasma, not visible in Balss' view); and the equality in height between distoventral projection and flap. For comparison with Balss' figure, some idea of the shape of the petasma of B. bartletti and of B. tanneri may be obtained from the sketches by Smith, 1882, and Faxon, 1895. The distoventral flap is in B. tanneri much more conspicuously separated from the projection than in Faxon's figure, and is more as in Smith's figure of B. bartletti. Group II as a whole is distinguished in petasmal structure from Group I by the fact that the cincinnuli by which the endopods are hooked together occur on the median edge of the appendage, rather than on a ridge extending up the anterior face of the endoped lateral to the median margin (and it is therefore obvious that the statement by Balss, 1927, anent B. investigatoris, "Durch das petasma is die form den B. moratus Smith . . . am nachsten verwandt," is quite incorrect). It seems possible that this cincinnulate submedian ridge of Group I is homologous with the true Lobus accessorius of which a trace at least is found in all members of Group II; and it is of interest in this connection that the fairly well-developed accessory of B. altus of Group II is edged with denticles, a feature not found in the conspicuous accessory lobe of Gennadas.

In the species of Group II, a sperm receptacle which may be termed enclosed, whether or not it functions as such, is formed by the exaggeration (relative to Group I) of the median projection of sternite XIII. It seems doubtful whether the thelycum of *B. investigatoris* can be considered as functionally of the enclosed type, since the scute of the thirteenth sternite projects free anteriorly only for

a slight distance at its anterolateral corners. This thelycum represents the nearest approach of Group II to the primitive open thelycum of Group I. The anteromedian emargination of the scute of XIII of B. investigatoris is extremely broad, instead of narrow and slit-like as in the other members of Group II. The posteriorly projecting hinder margin of the scute is narrower in the available Hawaiian female than in the figure by DeMan, 1911; and the median posterior margin of the twelfth sternite is thrown into three shallow projections instead of being smoothly curved. In the three species of the Group which occur in America the scute of the thirteenth sternite extends forward as a free projection over the anterior half of the sternite; its antero-lateral margins are bent dorsally, to abut against projections of the latero-posterior margins of the twelfth sternite; and its narrowly cleft antero-median margin abuts on the base of a triangular prominence of the twelfth sternite. A deep and wellenclosed cavity is thus formed, in which it seems possible that the spermmass may be stored. Whether this function is actually performed is not ascertainable, since impregnated females of the Group have not been discovered (unless the "orange-coloured, discoid mass between the coxae of the fourth pair of legs" seen by Bate in B. altus refers to a spermatophore, rather than, as is more probable, to the sternal scute. In specimens of B. tanneri long preserved in alcohol, traces of orange pigment still adorn the sternal skin, as well as the appendages). For its bearing on the question of the manner of sperm storage in Group II, the spermatophore of a male of B. tanneri has been removed from the vas deferens and examined. The spermatophore consists of an elongate ellipsoidal sheath, containing numerous small spheroidal aggregations of spermatozoa embedded in a gelatinous matrix, to which is attached a large wing-like mass of sperm-free material. The sheath, instead of being more or less detachable from the sperm-free accessory structure as in Gennadas, is rather firmly bound to it, although not so indissolubly as in Penaeus setiferus (Burkenroad, 1934a); and it is therefore uncertain whether the spermatophore is attached externally as in *Penaeus setiferus*, the female cavity functioning only as an anchoring surface; whether, as in Metapenaeus (Burkenroad, 1934b) the sperm mass is introduced into the receptacle while the accessory structure is employed in sealing the chamber; or whether, as in Gennadas, the sperm-mass is introduced into the receptacle and the accessory structure discarded. The sperm-mass alone of a single spermatophore of B. tanneri is larger than the cavity of the receptacle. In any case, there is no doubt but that the female structures found in Group II are intermediate between the purely external sculpture of Group I and the deeply invaginated receptacles found in Bentheogennema and Gennadas, in which the prominences of the thirteenth sternite play a relatively slighter part. The sequence of thelycal structure in Benthesicymae is entirely paralleled in the Penaeinae Penaeus and Parapenaeus. The anterior margin of the scute of the thirteenth sternite of the three species of Group II

which occur in America is deeply and rather narrowly cleft, so that externally, the thelycum somewhat resembles that found in section 1 of the penaeine Trachysalambria; in internal structure it is analogous to that of Penaeus brasiliensis, but since the enclosure is placed one segment in advance of that of the Penaeinae, the two cannot be homologous. It is a peculiar fact that in all three American forms of Group II, the adult thelycum is spotted with small circular depressions from the floors of which sprout clumps of setae. These depressions are absent in the juvenile, in which, also, the cleft at the anterior end of the scute is shallower, and the anterior breadth greater; so that the juvenile seems in these features to approach B. investigatoris. A rough idea of the appearance of the thelyca of B. bartletti and of B. tanneri may be obtained from the figures by Milne-Edwards and Bouvier, 1909, and by Faxon, 1895. The thelycum of B. altus differs slightly from these by the more constricted anterior end of the scute of XIII and of the median anterior projection on XIV, but these features are variable.

Of other differences between the species of Group II, the posterior dorsal margin of the fourth pleonic sternite of B. bartletti and B. tanneri is somewhat emarginated, although to a variable depth; while it is straight in B. investigatoris. The pleonic spine of B. bartletti seems homologous with that occurring at the posterior dorsal margin of the fifth pleonic somite in B. tanneri and B. investigatoris. Its peculiar position in the middle of the segment evidently has been produced by a forward shifting of the posterior dorsal mid-margin, followed by fusion of the lips of the deep emargination formed behind the spine by this recession. The posterior of the two cervical sulci is deeper, and the postcervical carina stronger in B. tanneri, and to a lesser degree in B. bartletti, than in B. investigatoris. Faxon is wrong in figuring the anteroinferior angle of the carapace as sharp in B. tanneri, and the distinction from B. investigatoris made by DeMan on this basis has no validity. Faxon's figure also errs in the omission of the strong pterygostomian spine. The "very small rudiment of a movable spine" noted by Rathbun, 1906, as occurring behind the posterior rostral tooth in B. investigatoris, and believed by DeMan, 1911, to have been present in his specimens, evidently refers to the minute lenticel found in most Aristaeinae and Solenocerinae in this position, which is not the origin of a spine, but the vestige of the larval anterior dorsal organ.

Some individual variation in the number of rostral teeth occurs in Group II. Alcock's type of *B. investigatoris* evidently bore three instead of the modal two teeth (although his figured specimen has the usual armature); Faxon observed one specimen of *B. tanneri* among 135 with but a single tooth; while I have found three among 152 of the same species with three teeth, the additional being a small distal one. The rostral length and height are quite variable. No variation in pleonic armature has heretofore been reliably reported; but in one male of *B. tanneri*, the posterodorsal margin of the fifth pleonic segment lacked a tooth, without any sign of injury being apparent.

The dactyl of the third maxillipede of Group II differs from that of Group I by its broad, diagonally truncated tip. Sexual dimorphism in the spiny armature of the same joint occurs; and in its shape as well, a spinose tubercle appearing on the outer proximal margin in adult males. This phenomenon seems worth consideration in greater detail, as follows:

It has been suggested by certain carcinologists that gross cyclical changes in structure of the accessory reproductive organs may occur in adult Penaeidea in correlation with changes in state of sexual activity. Such changes have been indicated to take place in other decapod groups; a classical example is furnished by Faxon's observation (1884) that two forms of male of adult dimensions occur in Cambarus, and that the sexually active form transforms at the end of the breeding season into an alternative form characterized by reduced copulatory appendages. It is assumed by Faxon that a reverse transformation will follow, since, he points out, the largest males are invariably of the active style. The population study of Cambarus by Creaser, 1933, seems confirmatory of Faxon's views, although Creaser interprets the data as signifying that Faxon's regressive-form is actually a juvenile stage preceding the assumption of the normally permanent breeding form. Kemp, 1925, suggests an analogous cyclical dimorph-

<sup>1</sup> My interpretation of the data graphically presented by Creaser is as follows: From September, 1931, until May, 1932, there is indicated a fairly distinct Form I young-of-1931 mode constant at about 16 mm. This mode; a second Form I mode at about 20 mm which is evidently composed of young-of-1930; and a possible third Form I mode at about 26 mm perhaps referring to young-of-1929, which the numbers involved are insufficient to define, fluctuate surprisingly little, in view of the relatively small numbers involved, through the entire cold season. In May, 1932, however, there is a sudden and virtually complete disappearance of the 16 mm mode; and at the same time the 20 mm mode is also greatly reduced. Considering now the fate of the Form II population, from September, 1931, through March, 1932, there is a single constant young-of-1931 mode at about 14 mm, the steep slopes of which curve remain steady with a minimum at about 10 mm and a maximum at about 17 mm. Between March 17 and May 24, 1932, however, the Form II mode advances to 16 mm, and the maximum, by the astonishing figure of 10 mm, to 26 mm; while the steep descending slope from 14 mm to the 10 mm minimum fails to advance at all from the position which it has occupied throughout the cold season. Therefore, while it is probable that some part of the May advance in Form II mode may derive from growth, the absence of an increase in the minimum seems suspicious, especially since according to Creaser's data its movement should not be retarded by any accession of fresh material. By contrast, the further advance of the Form II mode from 16 mm to 20 mm by June 29 is accompanied by the expected growth-indicating increase in the minimum, from 10 mm to 16 mm.

It is thus evident that a peculiar aggrandizement of the Form II population occurs in May simultaneously with a sudden impoverishment of the Form I stocks; and a comparison of the graphs for March and May suggests that the increases of the one group are very nearly commensurate with the losses of the other. I therefore con-

ism for females of the Pasiphaeoid Leptochela, but it may be noted that although lack of defined breeding season makes his interpretation probable, the possibility that one form is the juvenile is not completely excluded. A regressive change in males of Pandalus superficially somewhat resembling that in Cambarus was formerly interpreted as reversible dimorphism by certain workers; but it has now been proven by Berkeley, 1930, that Pandalus is regularly protandric, and that the regression is a prelude to the assumption of the female state. Edmondson, 1929, has presented evidence for a reversible dimorphism affecting both sexes, among the Atyidae; but it may be suggested that the mechanism here involved is by no means clear, and that the conversely unbalanced sex-ratios found in the Atya and the Ortmannia forms might be indicative of some complicated maturation phenomenon perhaps involving protandry.

The only specific suggestion of reversible dimorphism among the Penaeidea refers to the differences in structure of the dactyl of the third maxillipede found among males of the Benthesicymus bartletti group. Faxon, 1895, states that in some males of B. altus and B. tanneri the dactyl is of the female type, without a basal protuberance, the petasma being poorly developed in these males; while in others the dactyl bears a basal protuberance and there is a strongly developed petasma. Faxon suggests that this may be a case of reversible change such as he has described in Cambarus. Because the systematic value of the external genitalia of peneids seems to some degree suspect as long as it is believed that cyclical changes in the structure of adult individuals occur (and it may be noted that the suspicion has had practical effects, as witness Calman, 1925, p. 3), I have given special attention to the phenomenon described by Faxon in Benthesicymus tanneri, although the available data are insufficient for any definite conclusion. My observations completely coincide with his; the petasmal rami are unjoined in all males lacking the protuberance of the dactyl of the maxillipede; and are joined in almost all of those in which it is present. But there is an additional fact which Faxon overlooks, that the less highly developed males are the smaller, those with protuberance of the dactyl

sider that Creaser's figures, as far as they go, are interpretable as referring to a whole-sale spring regression (similar to the conversion in a reverse direction which he accepts, from changes analogous to the above, as taking place in late summer) of Form I males to Form II.

The above analysis forces me to regard with doubt (much as I should like, in view of my opinion that reversible dimorphism does not occur in the Penaeidae, to concur in it) Creaser's belief that Form II is "a developmental condition" and that regression of Form I males to Form II occurs rarely if at all; and to conclude that the results of this population survey are not in disagreement with the view of Faxon and others that breeding males of Cambarus normally revert after the season to a condition similar to that of the juveniles, subsequently regaining the active form. The possibility is of course not excluded that another explanation of the phenomena observed in Cambarus might be found.

the larger of the series. The accompanying table, which deals with the total catch of males at "Arcturus" Station 74, makes this size-form relationship apparent.

Table of the Relation of Carapace Length to Degree of Development of Secondary Sexual Organs in Males of Benthesicymus tanneri Faxon

| Carapace length in mm:              | < 20 | 20-22 | 22 - 24 | 24 - 26 | 26 – 28 | 28 - 30 | Total |
|-------------------------------------|------|-------|---------|---------|---------|---------|-------|
| Daetyl third mxpd. lacks basal pro- |      |       |         |         |         |         |       |
| tuberance; petasmata uncoupled.     | 10   | 15    | 18      | 8       | 0       | 0       | 51    |
| Dactyl of the third mxpd. bears ba- |      |       |         |         |         |         |       |
| sal protuberance; petasmal rami     | . 0  | 0     | 1       | 17      | 19      | 12      | 49    |
| coupled (with four exceptions).     |      |       |         |         |         |         |       |

The petasma increases in size and complexity rather regularly with increase in length of the individual, until the coupling of its halves; after which, within the size range of 22–30 mm carapace length, it seems to be nearly invariable. Four individuals, of from 24 to 26.5 mm in carapace length, were found in which, although the dactyl of the third maxillipede bore the rudiments of the adult protuberance, the petasmal rami were uncoupled. The petasmal endopods of the smaller of these were, as also in those individuals of more than 23 mm which completely lacked the maxillipedal protuberance, very nearly of the maximum size and development; but the cincinnuli were less numerous than in the coupled petasma, and were less strongly hooked at their free ends. It may be noted that some sporadic occurrence of individuals with fully formed but uncoupled petasmal endopods, just emerged from the molt or otherwise disarranged, is only to be expected.

As shown by the table, between the carapace lengths of 22 and 26 mm, individuals of Benthesicymus tanneri may be of either adult or juvenile form. This overlap is not at all incompatible with a reference of the changes in maxillipede and petasma to an irreversible metamorphosis of juvenile into adult, rather than to reversible changes in adult structure accompanying the phases of sexual activity; since such a degree of variation in the size at which the individual matures might be expected. The available sample, therefore, lends no support to Faxon's views. If, however, we compare Creaser's data for Cambarus, in which reversible dimorphism seems certainly to occur, it will be observed that during the periods when no change of one to the other male form seems to be going on (November, 1931 through March, 1932; and September, 1932), the overlap in size between the adult- (breeding-) and the juvenile- (regressive-) forms is no greater than is shown in the above figures for Benthesicymus. Only during the brief periods at which active change seems to be in progress (conversion, in August-September, 1931; and less clearly, in June-July, 1932; and regression in May, 1931) does the minimum size of the breeding-form individuals of Cambarus fail to be within a few mm of the maximum of the juvenile-form.

Therefore, since it cannot be assumed that the size-form relationship shown by the available sample of *Benthesicymus* is completely representative (especially since the unimpregnated state of all of the females indicates breeding to be seasonally limited), the available data are not adequate for refutation of Faxon's suggestion. They do, however, show that an explanation of the two male forms in *Benthesicymus* as merely the stages of an irreversible metamorphosis of juvenile into adult is perfectly adequate to account for the observed facts.

### BENTHEOGENNEMA, new name

Gennadas, Balss, 1927.

Gennadas, part, Bate, 1888; Bouvier, 1908; Kemp, 1909 and 1910b; DeMan, 1911; Calman, 1925.

Amalopenaeus, part, Sund, 1920.

Genotype, Bentheogennema intermedia (Bate). Species included, B. borealis (Rathbun) [with which B. calmani (Kemp), 1909 is synonymous] and B. pasithea (DeMan) [with which B. praecox (Kemp), 1910, is synonymous according to Balss, 1927].

Benthesicymae with a podobranch on somites VIII-XII; gill of VII large and richly plumose. Exopod of the first maxillipede without a constricted, segmented distal portion. Pleonic terga in advance of XX uncarinated. Telson with more than a single pair of mobile lateral spinules but without a posteromedian point.

It has been demonstrated by Balss that the genotype by monotypy of Bate's genus Gennadas, G. parvus (as restricted by Kemp, 1909), lacks podobranchs behind VIII. It is therefore evident that Gennadas cannot be applied, as by Balss, to the group with pereiopodal podobranchs; and that Amalopenaeus Smith, used by Balss for the group without posterior podobranchs, is a synonym of Gennadas. Thus, the new name Bentheogennema is necessary for the B. intermedia group.

# Bentheogennema intermedia (Bate)

Figure 50, p. 58.

Gennadas intermedius, Bate, 1888; Kemp, 1909; Calman, 1925; Balss, 1927, part (?).

Gennadas alicei, Bouvier, 1906a, 1908, 1922; Milne Edwards and Bouvier, 1909; Lenz and Strunck, 1914; Sund, 1920.

Gennadas sp., Rathbun, 1906.

## Tongue of the Ocean, Bahamas

1 male, juvenile. B.O.C. 206. Pawnee St. 16; March 9, 1927. Wire 7,000 feet.

<sup>1</sup>Since among the peneids sexual distinctions seem to become established early in the post-larval stages, it is unlikely that the possibility of protandry need be considered in dealing with members of the group.

1 female, juvenile. B.O.C. 211. Pawnee St. 18; March 10, 1927. Wire 7,000 feet.

## EXUMA SOUND, BAHAMAS

2 males, 1 female, juvenile. B.O.C. 207. Pawnee St. 25; March 18, 1927. Wire 8.000 feet.

1 male, juvenile. B.O.C. 208. Pawnee St. 33; March 22, 1927. Wire 8,000 feet.

#### BERMUDA

1 female, juvenile. B.O.C. 209. Pawnee St. 59; April 21, 1927. Wire 8,000 feet.

## PROVIDENCE CHANNEL, BAHAMAS

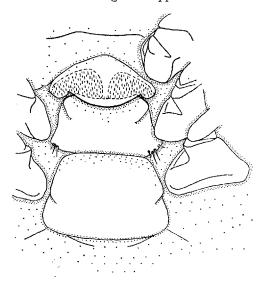
5 males, 8 females, juvenile to adult. B.O.C. 210. Atlantis St. 1478; February 20, 1933. Wire 5,250 feet.

### GULF OF MEXICO

- 2 subadult females and three fragments. B.O.C. 226. Atlantis St. 2427; April 10, 1935. Wire 3164 meters.
- 2 males (specimens utilized for chemical analysis). Atlantis St. 2410; April 4, 1935. Wire 2050 meters.

The present material is in agreement with Kemp's description of the types of B. intermedia rather than with Bouvier's description and figures of B. alicei, as regards the form of its infra-antennal angle and of the merus of its second maxillipede, but despite the differences it seems proper to follow Balss in synonymizing Bouvier's B. alicei with Bate's species. Balss is in error, however, in synonymizing B. calmani (Kemp) with B. intermedia; and the consequent uncertainty of his records (1927) is the more unfortunate in that aside from the single specimen from Hawaii (recorded as Gennadas sp. by Rathbun, 1906), Bentheogennema intermedia is definitely known only from the Atlantic. B. calmani is almost certainly identical with B. borealis (Rathbun). According to available descriptions B. borealis differs conspicuously from B. intermedia in that its cervical and postcervical sulci do not interrupt the postrostral carina; in its possession of a strong pterygostomian spine followed by a perceptible carina; in the convex ventral margin of its rostrum; in its broader telson tip; in the stronger distolateral lobe of its petasma, with truncated rather than gently rounded distal margin; in the weaker rudiment of the distoventral projection (proximad the notch in the lateral margin) and stronger rudiment of lobus accessorius of its petasma; in the occurrence of a pair of triangular projections on the anterior part of sternite XIII of the female, the median angles of which extend into a space between the median plates of sternites XIII and XII; and in other details. The known range of B. borealis is limited to the North Pacific, from Japan (Kemp) through the Aleutians and down the Pacific coast of North America to Southern California (Rathbun, 1902, 1910; Schmitt, 1924). It seems quite possible, since B. intermedia is known from the Cape of Good Hope and from Hawaii, that Balss' indeterminable records from the east coast of Africa, the Arabian Sea, and the Indian Ocean refer entirely to this predominantly Atlantic species and not to B. borealis.

The third species apparently referable to the genus, *Bentheogennema pasithea* (DeMan), differs conspicuously from its congeners, and resembles the species of *Gennadas*, in the considerable degree of approximation to one another dor-



Thelycum (with outline of sperm receptacles beneath scute of XII indicated by dashed areas). 50. Bentheogennema intermedia (Bate), Bahaman  $\circ$ ,  $\times$  11.

sally of its cervical and post-cervical sutures; and the strong development of the Lobus accessorius of its petasma. Balss is very probably correct in synon-ymizing with this species *Gennadas praecox* Kemp, 1910, although Kemp's description differs from DeMan's in two details: the English carcinologist finds the penultimate segment of the antennular peduncle to be two-thirds as long as the ultimate, rather than only one-half; and he describes the telson armature as similar to that of *Gennadas*, that is, with only a single pair of mobile lateral spines, rather than with three pairs as noted by DeMan.

Among nine of the available specimens of Bentheogennema intermedia, only six have any trace of pterygostomian spine. A second minute spine, weaker than the first and occupying a marginal position posteroventral to it, is present in two of these six specimens. There appears to be considerable variation in the distance separating the cervical and postcervical sulci in the dorsal line, the

interval ranging from one-half to two-fifths the distance between the postcervical and the posterior margin. The rostrum usually bears a post-terminal tooth, the telson four pairs of mobile lateral spines.

The sperm receptacles of the female of B. intermedia consist in a pair of large cavities, one on either side of the midline, beneath the elevated plate of sternite XII. These enclosed receptacles open at the posterior edge of the sternite, their broad mouths being guarded by the anterior edge of the elevated plate of sternite XIII. None of the available females are impregnated. Balss, 1927, states that the thelycum of Gennadas kempi Stebbing "vollkommen dem von . . . [Bentheogennema] intermedius Bate entspricht." Although it is true that there is some superficial resemblance between the thelyca of the two forms, that of Gennadas kempi is of a type essentially different from that of Bentheogennema intermedia, since the large sperm receptacles of the latter, which open broadly by contiguous apertures, are in the Gennadas replaced by a pair of minute cavities the narrow entrances to which are widely separated and are guarded posteriorly by triangular papillae.

#### **GENNADAS** Bate

Gennadas, Bate, 1881.

Gennadas, part; Bate, 1888; Alcock, 1901; Bouvier, 1908; Kemp, 1909 and 1910b; Stephensen, 1923; Calman, 1925.

Amalopenaeus, Smith, 1882, 1884 and 1887; Kemp, 1909 and 1910a; Balss, 1927; Sund, 1920, part.

Gennadas (Amalopenaeus), Bouvier, 1922.

Not Gennadas, Balss, 1927.

Benthesicymae lacking podobranchs behind VIII and with the gill of somite VII reduced to a vestige. Exopod of the first maxillipede without distal segmented prolongation. Pleon with the sixth somite only carinated in the dorsal midline. Telson without median terminal point and with only a single pair of mobile lateral spines.

It is probable that *Euphema H. Milne Edwards* refers to a mysis larva of *Gennadas* (cf. Stephensen, 1923; Gurney, 1924). However, since it is unlikely that *E. armata Edwards* can ever be identified with an adult and thereby given standing as a genotype, the name *Gennadas* Bate may be retained.

It is of interest that, in contrast to the conditions usual in other Penaeidae, the pleonic portion of the mature ovary of *Gennadas* is of very slight extent, while posterior carapacic lobes are enormously developed and extend far ventrally within the fourteenth somite, being perceptible through the coxa of the fifth leg as a conspicuous yellow mass. Also, it may be noted that the opening of the oviduct of females of *Gennadas*, which resembles that of Sergestidae, is a narrow transverse slit across the coxa of the third legs, unconnected with the group of projections of the leg base proximal to it.

As here defined, the genus includes thirteen species of which it seems that

both male and female are known; and one of which the male only is known. The six species from the Bingham Collection reported in the present paper include numerous males and females of G. capensis Calman, previously known only from two males taken off the Cape of Good Hope; as well as both sexes of G. bouvieri Kemp, the male of which has been known in the past as G. alcocki Kemp, and of which only a single specimen has heretofore been recorded from the Atlantic (Balss, 1927). In addition to material contained in the Bingham Oceanographic Collection, specimens of five other species have been available; a total of eleven out of fourteen species has therefore been studied at first hand for the ensuing review of the genus.

Through the work of Smith, Bouvier, Kemp, Stephensen, Calman, Balss, and others, a considerable amount of information as to the species of Gennadas is available. However, the extreme homogeneity of the genus has been responsible for an accumulation of detailed knowledge of individual forms without any corresponding increase in understanding of the relationships of the various forms to one another. Because of the considerable similarity of the species of Gennadas in other features than genital structure, and their great diversity in thelycum and petasma, not only have males and females of the same species been placed under different names, and the sexes of distinct species coupled under the same name, but no orderly arrangement of the genus¹ has been proposed by which the identification of undetermined material by other process than individual comparison with descriptions of previously known species is made possible.

An analysis of genital structure within the group indicates that beneath the very great and superficially chaotic interspecific diversity of genital details of both sexes, essentially similar organization distinguishes various groups of species. This analysis therefore provides a basis for the subdivision of the genus, although the features necessarily utilized are, for the females, recognizable only by careful scrutiny.

It is obvious that unless assurance is forthcoming that male and female associated under the same name actually represent the sexes of the same species, the statements in the foregoing paragraph are open to doubt. Correct association of male with female has in the past been based chiefly on the records of capture, which are by now sufficiently numerous to allow a fair degree of assurance for a majority of the species of the genus. To supplement this method, while interspecific variation in other than genital structures is too slight, and intraspecific variation is correspondingly too great to make convenient the use of nongenital differences either as specific criteria or in the erection of superspecific groups, the allocation of male to female may be accurately checked by means of comparisons in the characters which are not subject to great sexual

<sup>1</sup> The subdivision on the basis of relative length of the merus of the third legs, by Bouvier, 1908, may be discarded as neither practically satisfactory nor natural.

dimorphism, such as the relative proportions of the leg joints and of the segments of the antennular peduncle; the strength of the mid-dorsal carina of the carapace between the cervical and postcervical sulci; the shape of the distal segments of the endopod of the first maxillipede; the size and position of the pigment-fleck and rhabdome-outgrowth of the ocular peduncle; the relative size of the animal; and especially the shape of the extremity of the antennal scale.

As to the doubt of the taxonomic value of the thelycum of Gennadas expressed by Calman, 1925, while it is quite true that there may be considerable variation in thelycal structure between individuals of a species, and that there may be large changes in thelycum within a single individual during its development to adult stages, there is at present no evidence that in Gennadas or any other peneid there is any sort of gross seasonal or other cyclical change in an adult individual (excluding differences in superficial appearance caused by the presence or absence of spermatophores) such as has been suggested to be possible. Also, thirteen very distinct types of thelycum are known in Gennadas, and only fourteen types of petasma; it is therefore evident that the one structure is as constant as the other. The degree to which thelycal structure varies from individual to individual (if it is accepted that adult structure is fixed within any single individual) is of much less systematic importance than is the degree of separation between extremes of variation in related species. For example, there is considerably less individual variation in thelycum in any of the three species of Benthesicymus, B. bartletti Smith, B. tanneri Faxon, and B. altus Bate than occurs in Gennadas valens (Smith). Yet the thelycum is almost valueless in distinguishing the mentioned species of Benthesicymus because it is so similar in all three forms that the relatively slight individual variability permits intergradation. On the other hand, the thelycum of G. valens, with a great range of intergrading variations, is entirely distinct from any of twelve other types of thelycum within the genus and is therefore taxonomically useful.

The structure of the petasma of Gennadas is as follows: The distal margin of each endopod of the petasma, as in other Penaeidae, is divided into three major lobes which may be termed the distomedian, the distomedian lobe generally bears chitinous hooks, a continuation of the row of cincinnuli which effect the attachment of the two endopods; and rarely, the other lobes may be armed with spines. From the dorsomedian edge of the distolateral lobe springs a projecting lobule which is absent or of little importance in other peneids, but is here of

<sup>1</sup> The term distolateral is somewhat unfortunate in its application to the open petasma, where the lobe is in the middle of the distal margin, flanked laterally by the distoventral and medially by the distomedian lobes. The term was originated with reference to the semitubular petasma of *Penaeopsis*, where the free margin of the petasma is folded over ventrally almost to the midline, bringing the middle lobe into a lateral position (cf. Burkenroad, 1934b).

considerable dimensions. This structure may continue to bear the term accessory lobe originated by Balss, 1927. The other terms utilized by Balss, "Lobus medianus" and "Lobus externus" are replaced by distolateral and distoventral, respectively, inasmuch as Balss' terminology, designed for the petasma of Gennadas alone, neglects the distomedian lobe, important in other groups; and is therefore no more apt than the present terminology, which, unfortunately, had been applied to the littoral forms before Balss' paper had come to my attention. In the external margin of the petasma near its distal end a notch of variable depth occurs which seems to be homologous to the gape which in other peneids (as certain Solenocerinae and the series Parapeneae of Penaeinae) separates the distoventral lobe into two parts, the distoventral projection and the distoventral lobe consists of the homologue of the distoventral projection of Penaeopsis (Burkenroad, 1934b).

As to the female genitalia, it has been noticed in the general account of the Benthesicymae that the sperm receptacles of Gennadas (and of Bentheogennema and the B. bartletti group of Benthesicymus) are unique in the family in that they are invaginated from a transverse furrow lying between the twelfth and thirteenth instead of the thirteenth and fourteenth sternites as in other Penaeidae. It would appear that in Aristeae and Solenocerinae the thelycum is without enclosed receptacles of any kind, and the large spermatophores, in which the sperm mass is enclosed in an elaborate capsule of sperm-free material, are simply attached along the surface of the three posterior pereionic sternites. A similar primitive condition persists in certain members of the series Peneae of Penaeinae, but in the majority of that subfamily, and in the Eusicyoninae, an enclosed spermatheca has been produced by the deepening of the furrow between the posterior two sternites. Into the single or double spermatheca of Penaeinae-Eusicyoninae is introduced a pair of relatively small spermatophores, the dimensions of which have been decreased principally at the expense of the outer capsule so highly developed in the forms without enclosed receptacles. reduction characterizes the spermatophore as formed in the vas deferens of the male. In members of the series Trachypeneae the modification of the exposed type of spermatophore has progressed so far as to include secondary spermatophores, small encapsuled packages of sperm resulting from the subdivision of the unitary sperm-mass found in the exposed spermatophore (cf. Burkenroad, 1934 a and b), and the outer capsule may be represented only by an amorphous mass utilized by the females in sealing the entrances of the receptacle.

The modification of the open thelycum found at the opposite, Benthesicymine, end of the series Solenocerinae-Aristeae is completely parallel to that found at the Penaeine end, although probably independent in origin. Like certain of the series Penaeinae, some species of Benthesicymae maintain an

open thelycum; but in the majority of the maniple enclosed receptacles of varying complexity occur which, except for their nonhomologous position, are very similar to those of the Penaeinae. The spermatophores of Benthesicymae with enclosed receptacle have also been reduced in size at the expense of the outer capsule, but this has here been effected by a means quite different from that employed in Penaeinae. Whereas in the latter the remainder of the outer capsule is retained, as an integral part of the material transferred by the male to the female but in greatly reduced bulk, in Gennadas a fully developed outer capsule is produced by the male but is later discarded instead of being transferred to the female. In the ductus ejaculatorius of Gennadas a tremendous and complicated structure of sperm-free secretion, with well developed lamellate anterior and posterior lateral appendages such as anchor an exposed spermatophore to the genital area of the female, is found. Embedded in the massive main portion of this structure is a relatively small mass of spermatozoa surrounded by a thin envelope; and as in some Penaeinae, the sperm-mass of certain species of Gennadas is itself sub-divided into small secondary bundles. In impregnated females only the sperm-mass itself, with or without its special envelope, is found in the receptacles, which are physically incapable of receiving the enormous outer capsule. No trace of the capsule can be found adhering to the external surface of the thelycum (unlike those Penaeinae in which the vestiges of the capsule are employed to seal the receptacular orifices); and it therefore seems certain that it is lost. It seems probable that the capsule of Gennadas plays a part in the mechanics of sperm-transfer and that the retention of the open petasma in Aristaeinae with enclosed receptacles, in contrast to the conversion of the male organ into a semitubular syringe-like apparatus in Penaeinae with analogous enclosed spermathecae, is correlated with the difference in the means by which the necessary reduction in the bulk of the spermatophore is effected. In their great functional similarity, the two morphologically distinct modifications of the basic "open" method of sperm storage compared above seem to represent as remarkable a case of parallelism as is known among crustacea.

The structure of the receptacles themselves is relatively simple in Gennadas, the complexity of the thelycum being due to the elaborate sculpture of the adjacent sternal surfaces. In essence, the receptacles are a pair of invaginations of the sulcus between the twelfth and thirteenth sternites. The openings of these invaginations may lie widely separated and, by obliteration of the median part of the transverse sulcus, on the surface of the sternum; or they may be more or less closely approximated and enclosed together in the sinus between the raised posterior margin of the twelfth and anterior margin of the thirteenth sternites. In the first instance, the openings are usually closed by papilliform

<sup>1</sup> It may be observed that the differences between the two types of thelycal structure in *Gennadas* are strictly analogous to those between the Penaeinae *Trachysalambria* and *Parapenaeus* (Burkenroad, 1934b).

elevations of the thirteenth sternite; in the second, they are usually slit-like simple apertures. The invaginations themselves vary greatly in depth and shape in nearly related species.

It is found that in all species of *Gennadas* with independent spermathecal orifices the distolateral lobe of the petasma is entire, not subdivided; whereas in all species with orifices contained within a common atrium, the distolateral lobe is bifurcated. The subdivision of the genus here proposed is based upon this correlation.

A KEY TO THE ADULT PETASMA AND THELYCUM OF THE SPECIES OF Gennadas BATE<sup>1</sup>

Group I. Male. Distolateral lobe of the petasma undivided.

Female. Orifices of the seminal receptacles opening independently, not included in a common atrium.

IA. Male. Distoventral lobe of the petasma undivided.

Female. Orifices of the receptacles not guarded posteriorly by large and conspicuous prominences. Orifices widely separated, the distance between them as great or greater than that between the apertures and the anterior margin of sternite XIV.

IA 1. MALE. Distolateral lobe not so wide as the distoventral; accessory lobe of petasma projecting far above the distal margin.
FEMALE. Unknown.

1. G. sordidus Kemp; Balss, 1927. ♂.

- IA 2. Male. Distolateral lobe much wider than the distoventral; accessory lobe not reaching above the distal margin.
- IA 2a. Male. Both lobules of the distomedian lobe armed with truncated spines; accessory lobe slender and clavate, arising far mediad the lateral margin of the distomedian lobe.

Female. Transverse elevation of the posterior margin of XII w-shaped; XIII without a rectangular elevation.

2. G. capensis Calman, 1925, ♂ [♀, figure 53, p. 70].

- IA 2b. Male. Median lobule only of the distomedian lobe armed; accessory lobe broad, arising laterad the lateral margin of the distomedian lobe.
  - Female. Transverse elevation at the posterior margin of XII  $\land$  shaped; XIII with a conspicuous rectangular elevation, the anterolateral corners of which overlap the posterior lips of the orifices of the sperm-receptacles.
    - 3. G. kempi Stebbing, Balss, 1927, ♂ [♀, figure 54, p. 70].
  - IB. MALE. Distoventral lobe of the petasma divided.

Female. Orifices of the sperm receptacles guarded posteriorly by large and conspicuous prominences; orifices not widely separated, distance between them less than that between apertures and anterior margin of XIV.

<sup>1</sup> Dated references are to works of previous students containing satisfactory figures of the species in question. Bracketed references to numbered figures indicate illustrations in the present paper.

- IB 1. Male. Distormedian lobe not reaching so far distad as the distoventral; accessory lobe much less than half as broad as the distoventral.
  - Female. Posterior portion of XIII, behind the level of the posterior lips of the spermathecal orifices, without a shield-shaped median elevation with anteriorly directed apex.
    - 4. G. elegans (Smith), 1882, ♂ [♀, figure 55, p. 70].
- IB 2. Male. Distomedian lobe reaching farther distad than the distoventral; accessory lobe more than half as wide as the distoventral. Female. Posterior portion of XIII with strong anteriorly directed median elevation.
- IB 2a. MALE. Cleft between the lobules of the divided distoventral lobe extending farther proximad than the cleft between the distoventral and distolateral lobes.
  - Female. Apex of the median plate of XIV considerably overlapping the base of the median plate of XIII.
    - 5. G. brevirostris Bouvier; Balss, 1927, ♂ and ♀ (sub G. similis).
- IB 2b. Male. Cleft of the distoventral lobe not so deep as that between distoventral and distolateral.
  - Female. Median plate of XIV not overlapping that of XIII.
- IB 2b (1). Male. Distolateral lobe broader than the distoventral, and reaching as far distad as it does; accessory lobe smaller than the distolateral, and entire.
  - Female. XIV without a median longitudinal ridge.
    - 6. G. tinayrei Bouvier, 1908, ♂ [♀, figure 56, p. 70].
- IB 2b (2). Male. Distolateral lobe much narrower than the distoventral, and not reaching so far distad as does the latter; accessory lobe much larger than the distolateral, and tripartite.
  - Female. Elevation of XIV with a median longitudinal ridge.
    - 7. G. parvus Bate; Balss, 1927, ♂ and ♀.
- Group II. Male. Distoventral and distolateral lobes of the petasma both divided.
  - Female. Orifices of the sperm receptacles lying within a common atrium.
  - IIA. Male. Lobules of the distolateral lobe subequal in breadth.

    Female. A transverse pair of conspicuous tooth-like projections on
  - IIA 1. Male. Lobules of the distolateral lobe curved toward one another and acuminated.
    - Female. Posterior margin of XII produced backward over XIII, as a large free flap buttoned into place by the widely separated pair of projections of XIII.
      - 8. G. bourieri Kemp, 1909, ♀; Balss, 1927, ♂ (sub. G. alcocki).
  - IIA 2. MALE. Lobules of the distolateral lobe not hooked and acuminated. Female. Posterior lip of XII not much produced; projections of XIII extending to or nearly to the midline.
  - IIA 2a. Male. Lateral lobule of the distoventral lobe longer than the median;

lobules of the distolateral lobe short and stout, the cleft between them not half as deep as that between distoventral and distolateral lobes.

Female. Paired projections of XIII not meeting in the midline; not reaching nearly to the anterior margin of XIII.

9. G. valens (Smith) 1884, ♂ [♀, figure 57, p. 79].

IIA 2b. Male. Median lobule of the distoventral lobe longer than the lateral; lobules of the distolateral lobe long and slender, the cleft between them more than half as deep as that between distoventral and distolateral lobes.

Female. Paired projections of XIII meeting in the midline; reaching nearly to the anterior margin of XIII.

10. G. gilchristi Calman, 1925, ♂ [♀, figure 58, p. 79].

IIB. Male. Lobules of the distolateral lobe very unequal in breadth. Female. No transverse pair of toothlike projections on XIII.

IIB 1. Male. Distoventral lobe much longer than the distolateral.

Female. Interspace between the orifices of the sperm receptacles, within the atrium, not elevated as a conspicuous longitudinal ridge; XIII with a single elevation not separated into anterior and posterior

parts.

11. G. incertus Balss, 1927, ♂ (and ♀, sub G. gardineri).

IIB 2. Male. Distoventral lobe much shorter than the distolateral.

Female. Atrium between XII and XIII divided by a well-defined median longitudinal ridge; XIII with distinct anterior and posterior elevated areas.

IIB 2a. Male. Lateral lobule of the distolateral lobe much broader than the median one.

Female. Elevated area of XIII weakly separated into a short anterior and a long posterior portion by a shallow transverse sulcus. 12. G. talismani Bouvier; Balss, 1927, 3 [9, figure 60, p. 79].

IIB 2b. Male. Lateral lobule of the distolateral lobe much narrower than the median.

Female. XIII with distinct anterior and posterior elevations.

IIB 2b (1). Male. Lateral lobule of the distoventral lobe broader than the median; median lobule of the distolateral lobe not acuminated.

Female. A free flap projecting forward from the anterior margin of XIV nearly to the anterior margin of XIII.

13. G. scutatus Bouvier, 1908, ♂ [♀, figure 59, p. 79]. IIB 2b (2). Male. Lateral lobule of the distoventral lobe narrower than the median; median lobule of the distolateral lobe tapering to a narrow

Female. No free projection from XIV.

14. G. propinquus Rathbun; Balss, 1927, ♂ (sub G. scutatus indicus); Kemp, 1910b, ♀ (sub G. olcocki).

### GROUP I

## Gennadas capensis Calman

Figures 51, p. 68; 53, p. 70

Gennadas capensis, Calman, 1925.

## TONGUE OF THE OCEAN, BAHAMAS

- 3 males. B.O.C. 153. Pawnee St. 9; March 1, 1927. Wire 4000-7000 feet.
- 6 males, 5 females. B.O.C. 154. Pawnee St. 11; March 2, 1927. Wire 7000 feet.
  - 1 female. B.O.C. 160. Pawnee St. 16; March 9, 1927. Wire 7000 feet.
- 3 males, 1 female. B.O.C. 155. Pawnee St. 18; March 10, 1927. Wire 7000 feet.
- 2 males, 1 female. B.O.C. 156. Pawnee St. 22; March 12, 1927. Wire 7000 feet.
- 2 males, 2 females. B.O.C. 157. Pawnee St. 23; March 14, 1927. Wire 8000 feet.

# EXUMA SOUND, BAHAMAS

- 2 females. B.O.C. 158. Pawnee St. 25; March 18, 1927. Wire 8000 feet.
- 1 male. B.O.C. 159. Pawnee St. 27; March 18, 1927. Wire 8000 feet.
- 2 males, 1 female. B.O.C. 161. Pawnee St. 31; March 21, 1927. Wire 7000 feet.
- 3 males, 1 female. B.O.C. 162. Pawnee St. 33; March 22, 1927. Wire 8000 feet.
  - 2 males. B.O.C. 163. Pawnee St. 35, March 23, 1927. Wire 7500 feet.

### CROOKED ISLAND PASSAGE, BAHAMAS

- 3 males, 2 females. B.O.C. 164. Pawnee St. 39, March 29, 1927. Wire 8000 feet.
- 2 males, 1 female.  $\it B.O.C.~165$ . Pawnee St. 41; March 30, 1927. Wire 10,000 feet.

### CAICOS PASSAGE, BAHAMAS

- 1 female. B.O.C. 166. Pawnee St. 46; April 4, 1927. Wire 10,000 feet.
- 11 males, 8 females. B.O.C. 167. Pawnee St. 48; April 6, 1927. Wire 7000 feet.

### TURKS ISLAND PASSAGE, BAHAMAS

- 6 males, 3 females. B.O.C. 168. Pawnee St. 52; April 11, 1927. Wire 8000 feet.
- 1 female. B.O.C. 169. Pawnee St. 54; April 12, 1927. 900-945 fathoms (bottom).
  - 2 males. B.O.C. 170. Pawnee St. 56; April 13, 1927. Wire 6500 feet.

#### BERMUDA

1 female. B.O.C. 172. Pawnee St. 58; April 20, 1927. Wire 10,000 feet.

### PROVIDENCE CHANNEL, BAHAMAS

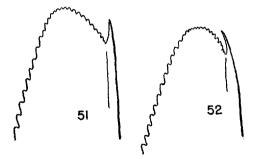
5 males, 4 females. *B.O.C.* 171. Atlantis St. 1478; February 20, 1933. Wire 5250 feet.

### Gulf of Mexico

- 2 females, 3 fragments. B.O.C. 226. Atlantis St. 2427; April 10, 1935. Wire 3164 meters.
- 2 males (utilized for chemical analysis). Atlantis St. 2410; April 4, 1935. Wire 2050 meters.

For comparison with *G. capensis* there have been available to me two adult females of *G. kempi* loaned from the collection of the Zoologischen Museums der Universität (D.T.E. St. 89, determined and recorded by Dr. Balss, 1927); and an adult male loaned from the collection of the British Museum (M.S.S.A. St. 87, determined and recorded by Dr. Calman, 1925), as well as three adult females (two of which are impregnated) and a juvenile male included among undetermined material from the same station and received through the courtesy of Dr. Calman.

Balss, 1927, is mistaken in synonymizing G. capensis with G. kempi Stebbing, 1914a. Although the two species bear a closer resemblance to one another in the essentials of genital form than they do to any other member of the genus;



Tip of left antennal scale from beneath. 51. Gennadas capensis Calman, Bahaman 9,  $\times$  35. 52. G. kempi Stebbing (D. T. E. St. 89),  $\times$  35.

and although their petasmae are superficially as well as essentially very similar, their thelyca are superficially highly distinct. In characters not affected by sexual dimorphism, the two species are readily distinguished by differences of shape of the antennal scale (figures 51 and 52, p. 68), the apex of the blade of this appendage in *G. kempi* being symmetrically placed in the center of the distal margin, rather than near the lateral edge as in Calman's species.

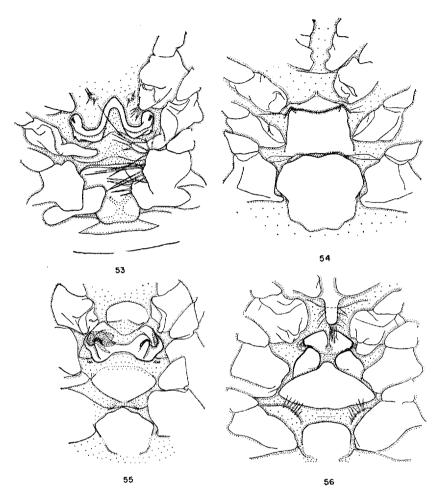
The resemblance of the petasma of *G. capensis* and *G. kempi* to that of *Bentheogennema intermedia*, which has been noted by previous workers, does not extend to details; since an accessory lobe is not developed in the latter form. The "complete correspondence" of the thelycum of *G. kempi* with that of *Bentheogennema intermedia* which is mentioned by Balss, does not extend beyond the most superficial features, as will be indicated below.

The genital sculpture of females of *G. capensis* does not correspond to any which has been previously described. It consists of an ill-marked rectangular plate on the fourteenth sternite; a strong w-shaped ridge on the thirteenth sternite; and a pair of setose knobs anterior to the ridge, on the twelfth sternite. The boundary between the twelfth and thirteenth sternites is not marked, save at the lateral edges of the outer legs of the w. At this point, on either side, a notch is perceptible in which lies the aperture of a small bilobed sperm receptacle. In impregnated females the receptacles are filled with an unorganized sperm mass which is devoid of a sheath such as encloses the sperm mass recoverable from females of *G. valens* or *G. bouvieri*. The outer capsule of the spermatophore as found in the ductus ejaculatorius of the male surrounds a thin, irregular envelope containing free spermatozoa, the volume of which seems much greater than the capacity of the female receptacle.

The enormous development of the projections of the inner sides of the coxae of the fourth and fifth legs in females of *G. capensis* is not matched elsewhere in the genus. On the fourth leg the projection has the form of a long, slender blade which nearly meets its fellow of the opposite side; while on the fifth leg the coxa bears proximally a subrectangular projection reaching well over toward the midline, and distally a shallowly bilobed prominence.

The thelycum of G. kempi (figure 54, p. 70), like its petasma, bears a greater essential resemblance to that of G. capensis than it does to the thelycum of any other species of the genus, in that the orifices of the extremely minute receptacles, which open independently of one another, are very widely separated. Beyond this essential resemblance, however, the genital sculpture of the two forms is entirely different. Corresponding to the w-shaped ridge of XII in G. capensis is a triangular ridge in G. kempi. Whereas the posterior lips of the spermathecal orifices of G. capensis are unaccentuated, the apertures are guarded posteriorly by distinct though small papillae in G. kempi. Whereas sternite XIII is without a conspicuous raised plate in G. capensis, this somite bears a large square elevation in G. kempi, the free anterolateral corners of which overlap the posterior lips of the spermathecal orifices, and thereby create a certain resemblance to the not very dissimilarly formed receptacular sinus of Group II. That the thelycum of G. kempi resembles that of Bentheogennema intermedia only in the most superficial manner must be obvious on comparison with the account of the latter form.

In the impregnated females of Gennadas kempi, the transverse sulcus between



Thelycum (with outline of right sperm receptacle of G. elegans, between XII and XIII, indicated by dashed areas, Figure 55). 53. Gennadas capensis Calman, Bahaman  $\circ$ ,  $\times$  11. 54. G. kempi Stebbing (D. T. E. St. 89),  $\times$  11. 55. G. elegans (Smith), Bahaman  $\circ$ ,  $\times$  11. 56. G. tinayrei Bouvier, Bahaman  $\circ$ ,  $\times$  23.

sternites XII and XIII is occupied by a horny bar composed of spermatozoa embedded in a gelatinous matrix. As in *G. capensis*, the sperm mass is not enclosed in a sheathing layer. At either end, where it extends into the minute invaginations representing the sperm receptacles proper, the bar is expanded, and is thus very securely anchored. Whether or not the bar is produced by the

fusing of two sperm masses supplied by the male is not known. Functionally, this method of sperm storage is quite distinct from that found in *G. capensis*, where two separate sperm masses are each completely enclosed in the minute receptacles; and it is interesting that organs of great structural similarity should be utilized in so distinct a manner.

The petasma of the present material of G. capensis is rather well represented by Calman's figure, except that the lateral portion of the distomedian lobe is more heavily armed; and the apex of the distoventral lobe rounded rather than acute. The petasma of G. kempi has been figured by Stebbing and by Balss; in the available two males the accessory lobe is shorter and broader than in Balss' figure, and the distormedian lobe supports a heavily armed median prominence. The petasmae of the two species are easily distinguished by the following features: The distoventral lobe is relatively much broader in G. capensis than in G. kempi and extends farther beyond the unproduced distolateral area of the petasma; in the middle of its median margin it constantly bears a stout tooth-like projection not represented in G. kempi. There are no notches at the median and the lateral margins of the distolateral area such as set off a free distolateral lobe in G. kempi. The distomedian lobe is broader than in G. kempi, and both of its lobules, instead of only the more median one, are heavily armed with truncated spinules. The accessory lobe of G. capensis is of peculiar form, its free part arising considerably mediad the lateral margin of the distomedian lobe, and forming a slender distally directed clavate rod. On the contrary, the square, flap-like accessory of G. kempi is attached along a line lateral to the lateral margin of the distomedian lobe.

It seems a most interesting matter, to be mentioned with reference to anomalies in the distribution of *Gennadas elegans*, that *G. capensis*, heretofore known only from two males taken off the Cape of Good Hope, occurs in great abundance in the Bahaman region and in the Gulf of Mexico.

Two males of *G. capensis* from "Pawnee" Station 11, and a female from Station 48 (as well as a male of *G. elegans* from "Albatross" Station 2724, and a female of *G. tinayrei* from "Pawnee" Station 39) were infested with an enormous Gordiacean roundworm, probably *Nectonema*, which nearly filled the thorax and anterior portion of the pleon. *Nectonema* has not been previously recorded from pelagic Natantia, although a specimen of *Gennadas* infested with what is probably this worm was figured by Bate in 1888.

# Gennadas elegans (Smith)

Figure 55, p. 70

Amalopenaeus elegans, Smith, 1882 and 1884; Smith, 1887, part; Kemp, 1910a; Balss, 1927.

Gennadas elegans, Bouvier, 1908; Hansen, 1908; Stephensen, 1923 and 1935.

Gennadas parvus, Bate, 1881 and 1888, part; Kemp, 1906.

NOT Gennadas elegans, Milne Edwards and Bouvier, 1909.

#### BERMUDA

6 males, 7 females. B.O.C. 187. Pawnee St. 58; April 29, 1927. Wire 10,000 feet.

3 males, 7 females. B.O.C. 188. Pawnee St. 59; April 21, 1927. Wire 8000 feet.

## PROVIDENCE CHANNEL, BAHAMAS

2 females. B.O.C. 189. Atlantis St. 1478; February 20, 1933. Wire 5250 feet.

Contributions to a knowledge of the geographical and bathymetric distribution of this often-discussed and abundant member of the genus have been provided by many workers; reference may be made to the extensive analysis of the "Thor," and other records presented by Stephensen, 1923 and 1935.

Gennadas elegans is exceedingly abundant, both absolutely and relative to other members of the genus, in the North Atlantic as far south as 30° North Latitude; and seems to be especially numerous in the northeastern North Atlantic, and in the Mediterranean. The only previous record of the species from the western North Atlantic south of 30° (of a female from St. Lucia by Milne Edwards and Bouvier, 1909) seems based on the mistaken identification as G. elegans of a related but distinct form since described as a new species, G. similis, by Stephensen. G. elegans has been sparingly recorded in the castern and central South Atlantic as far south as the Cape of Good Hope, in which latter region the results of Calman, and of Balss, seem to indicate that it is replaced as the most abundant form by other species of the genus. Of interest, especially by comparison with the similar phenomenon at the Cape of Good Hope, is the fact that whereas the "Pawnee" took sixteen specimens of G. elegans north of 30° north latitude, near the Bermudas, by comparison with seven of G. valens, one of G. bouvieri, and one of G. capensis; and the "Atlantis" took two specimens of G. elegans to none of G. valens, one of G. bouvieri, and nine of G. capensis in the Bahamas at 25° north latitude, not a single specimen of G. elegans was taken at the numerous "Pawnee" stations south of 25° among the Bahamas, which yielded a very abundant catch of G. valens, G. bouvieri, and especially of G. capensis. Depth of operation and season were comparable in all cases. The distribution of G. elegans, on the basis of these new records, seems anomalous (see also p. 3). What factors may determine its abundance in the northern North Atlantic and the Mediterranean as compared with its rarity in the southeastern South Atlantic and the Bahaman region; and its very wide Atlantic distribution as compared with an apparently complete absence from other oceans, is not obvious. Temperature and salinity, by the occurrence of G. elegans both to north of 60° N. Lat. and in the eastern Mediterranean (into which regions no other members of the genus penetrate), seem excluded as determining factors, and can hardly serve to explain the distribution even if the Mediterranean stock should turn out a racially distinct glacial relict. It is noteworthy that Gennadas capensis, a form as yet known, like G.

elegans, from the Atlantic alone, is recorded in that ocean only from the two widely separated regions where G. elegans seems very rarely to occur. The possibility, to which the distribution of G. capensis may be a clue, must therefore be considered, that the barriers to the spread of G. elegans operate at second-hand; and that it is not the inability of the species to exist in the chemical and physical environment which determines its absence from certain areas; but that these areas are suitable for other, more stenopotential organisms incompatible with G. elegans, which other organisms cannot exist at either extreme of the range of tolerance of the very eurypotential G. elegans.

In addition to material contained in the Bingham Collection, 5 females and 4 juvenile males from "Albatross" dredgings off the Middle Atlantic coast of the United States, contained in the collection of the Zoology Department of the Peabody Musuem, have been avialable. Of this material specimens from stations 2002, 2036, and 2116 have been listed by Smith, 1884. A specimen from "Albatross" station 2201, determined and published as "G. elegans" by Smith, 1887 is referable to G. valens.

The thelycum of *G. elegans* has not been previously described or figured with any accuracy. The external sculpture consists in a low shield-shaped elevation with anteriorly directed apex on sternite XIV, and a similar elevation, with posteriorly directed apex, on the posterior part of XIII. As in *G. capensis*, the juncture of sternites XII and XIII is defined only by the spermathecal orifices. A transverse elevation, which is probably the anterior margin of XIII, narrow in the middle and expanded laterally, bears upon its broader portions a pair of elongate papillae which guard the spermathecal apertures posteriorly. The anterior margins of the orifices are hooded by setose elevations. Anterior to the level of the openings of the sperm receptacles is an ill-defined median elevation of sternite XII. The receptacles are trilobate invaginations of moderate size, the anterior chambers of which are the largest.

### Gennadas tinayrei Bouvier

Figure 56, p. 70

Gennadas tinayrei, Bouvier, 1906a, 1908, 1922; Lenz and Strunck, 1914; Stephensen, 1923.

Amalopenaeus tinayrei, Sund, 1920; Balss, 1927.

CROOKED ISLAND PASSAGE, BAHAMAS

2 females. B.O.C. 215. Pawnee St. 39; March 29, 1927. Wire 8000 feet.

### BERMUDA

males. B.O.C. 192. Pawnee St. 58; April 20, 1927. Wire 10,000 feet.
 male. B.O.C. 194. Pawnee St. 59; April 21, 1927. Wire 8000 feet.

# ATLANTIC OFF ELEUTHERA ISLAND, BAHAMAS

1 male, 1 female. *B.O.C. 193*. Atlantis St. 1479A; February 26, 1933. Wire 450 feet.

The species has been taken chiefly in the temperate North Atlantic. One specimen is known from the middle of the South Atlantic, another is here recorded for the first time from South African waters, off the Cape of Good Hope, while two have been recorded from the Indian Ocean by Balss. The material of the Bingham collection, from Bermudan and Bahaman waters, was taken well to the south and westward of previous North Atlantic captures.

Of the species which are most nearly related to *G. tinayrei*, the distribution of *G. elegans* has already been discussed. *G. brevirostris* Bouvier (*G. similis* Stephensen, 1923) is known from the eastern North and South Atlantic and the West Indies; while *G. parvus* Bate, which has in the past been known only from the Indo-Pacific, where it is widely distributed, is here for the first time recorded from the Atlantic, off the Cape of Good Hope.

Material for comparison with *G. tinayrei* has been made available to me as follows: A male and a female of *G. brevirostris* loaned from the collections of the Zoologischen Museums der Universität [D.T.E. St. 41 and 66, respectively, determined (as *G. similis* Stephensen) and recorded by Dr. Balss, 1927]; and a male of *G. brevirostris*, B.O.C. 218, obtained by exchange from the Universitetets Zoologiske Museum ["Thor" St. 232, determined (as *G. similis* Stephensen) and recorded by Dr. Stephensen, 1923]. A female and two males of *G. parvus* loaned by the Zoologischen Museums der Universität (D.T.E. St. 221, determined and recorded by Dr. Balss, 1927); and a female of *G. parvus* and one of *G. tinayrei* from the British Museum (M.S.S.A. St. 87, included among undetermined material of the genus most generously put at my disposal by Dr. Calman).

The petasma of G. tinayrei differs from that of the three nearly related species G. elegans, G. brevirostris Bouvier, and G. parvus Bate in that its distoventral lobe is only very shallowly cleft, and is somewhat variably armed with small spinules. It resembles that of G. brevirostris more nearly than the other two species in the relatively great breadth of its distolateral lobe. The petasma of G. brevirostris differs from that of all other members of the first Group of Gennadas by the great length of the lobules of its bifurcated distoventral lobe. The petasma of G. parvus most nearly resembles that of G. elegans in the mode of furcation of its distoventral lobe and in the small size of its distolateral lobe, but is unique in the genus (perhaps most nearly resembling G. sordidus Kemp) in the large size and peculiar, lobulate form of its accessory lobe.

The thelyca of *G. tinayrei*, *G. brevirostris*, and *G. parvus* are very similar. All three forms differ from *G. elegans* in that the posterior part of XIII bears an elevated plate with anteriorly directed apex. *G. tinayrei* resembles *G. elegans* and differs from the other two species by lack of the two setose tubercles found

on sternite XIII of the latter just latered the prominences which guard the spermathecal orifices. Females of *G. tinayrei* are distinguished from all other members of the genus by the peculiar setose projection directed backward from the posterior margin of XI.

The South African female of *G. parvus* available to me differs from the Indo-Pacific ones in that the longitudinal carina of the plate of XIV ends abruptly in a sharp tooth, some distance behind the anterior margin of the segment; and also in the great length of the anteriorly directed median elevation of XIII, which considerably overlaps the high transverse ridge of XII.

The West Indian female figured and described as G. elegans by Milne Edwards and Bouvier, 1909, seems identical (by the fact that there is an anteriorly directed shield-shaped elevation on both XIII and XIV, the hinder of which overlaps the more anterior scute) with the form described by Stephensen, 1923, as G. chiasmifera, and later identified by Balss (1927) with the male simultaneously described by Stephensen as G. similis; which species has heretofore been known only from the Eastern Atlantic. Bouvier, 1905b, had previously named the West Indian specimen, without description, as a new species, G. brevirostris. Application to the Museum of Comparative Zoology and to the Museum National d'Histoire Naturelle indicates that the specimen in question has disappeared. Although it might be preferable to wait until actual records of G. similis from the western North Atlantic make positive its identity with G. brevirostris, in my opinion Bouvier's sketch of the type of the latter is diagnostic, and G. similis may be considered to be a synonym of Bouvier's species.

The sperm mass of *G. tinayrei* is contained within a thin-walled envelope embedded, as is usual in the genus, within a complex structure of sperm-free secretion. However, instead of forming an unorganized mass, as in *G. valens* and *G. bourieri*, the spermatozoa of *G. tinayrei* are aggregated as small eggshaped bundles containing several hundred sperm, each surrounded by a resistant envelope. A similar arrangement is found in *G. scutatus* Bouvier (as well as in *Benthesicymus tanneri* Faxon). The spermatozoa are peculiar short cylinders with an abrupt enlargement in the middle.

### GROUP II

## Gennadas valens (Smith)

Figure 57, p. 79

Amalopenaeus valens, Smith, 1884; Sund, 1920; Balss 1927.

Amalopenaeus valens?, Kemp, 1910a.

Gennadas valens, Bouvier, 1908 and 1922; Lenz and Strunck, 1914; Stephensen, 1923.

Gennadas bidentata, Stephensen, 1923.

Amalopenaeus elegans, part, Smith, 1887.

## TONGUE OF THE OCEAN, BAHAMAS

1 female. B.O.C. 186. Pawnee St. 9; March 1, 1927. Wire 4000-7000 feet.
1 male, 3 females. B.O.C. 173. Pawnee St. 11; March 2, 1927. Wire 7000 feet.

2 males, 1 female. B.O.C. 174. Pawnee St. 16; March 9, 1927. Wire 7000 feet.

2 males, 1 female. B.O.C. 175. Pawnee St. 18; March 10, 1927. Wire 7000 feet.

## Exuma Sound, Bahamas

1 male. B.O.C. 176. Pawnee St. 25; March 18, 1927. Wire 8000 feet.

# 1 male. B.O.C. 177. Pawnee St. 31; March 21, 1927. Wire 7000 feet.

CROOKED ISLAND PASSAGE, BAHAMAS
3 males, 2 females. B.O.C. 178. Pawnee St. 39; March 29, 1927. Wire 8000 feet.

## CAICOS PASSAGE, BAHAMAS

1 male. B.O.C. 179. Pawnee St. 46; April 4, 1927. Wire 10,000 feet.

5 males, 5 females. B.O.C. 180. Pawnee St. 48; April 6, 1927. Wire 7000 feet.

### TURKS ISLAND PASSAGE, BAHAMAS

1 male. B.O.C. 181. Pawnee St. 52; April 11, 1927. Wire 8000 feet.

1 male. B.O.C. 182. Pawnee St. 54; April 12, 1927. 900-945 fathoms (bottom).

9 males, 6 females. B.O.C. 183. Pawnee St. 56; April 13, 1927. Wire 6500 feet.

### BERMUDA

1 male, 4 females. B.O.C. 184. Pawnee St. 58; April 20, 1927. Wire 10,000 feet.

1 male, 1 female. B.O.C. 185. Pawnee St. 59; April 21, 1927. Wire 8000 feet.

#### Gulf of Mexico

2 males, juvenile. *B.O.C.* 227. Atlantis St. 2427; April 9-10, 1935. Wire 3164 meters.

For comparison with the Bingham material of *G. valens*, in addition to specimens contained in the collection of the Department of Zoology of Peabody Museum and referred to below, there have been available a female (B.O.C. 217) obtained by exchange from the Universitetets Zoogoliske Museum ["Thor" St. 71, determined (as *G. bidentata* Stephensen) and recorded by Dr. Stephensen, 1923]. A male and an unimpregnated female of the closely related *G. gilchristi* have been loaned by the Zoologischen Museums der Universität (D.T.E. St. 91,

determined and recorded by Dr. Balss, 1927); and a male syntype by the British Museum (M.S.S.A. St. 87, determined and recorded by Dr. Calman, 1925), as well as four females, one impregnated, included among undetermined material from the same station.

Gennadas valens has been previously recorded from the eastern half of the North Atlantic between 51° and 27° north latitude, and from the western corner of the Mediterranean (Sund, 1920); from the western half of the North Atlantic between 49° and 34° north latitude; and from the eastern half of the South Atlantic between 11° and 36° south latitude.

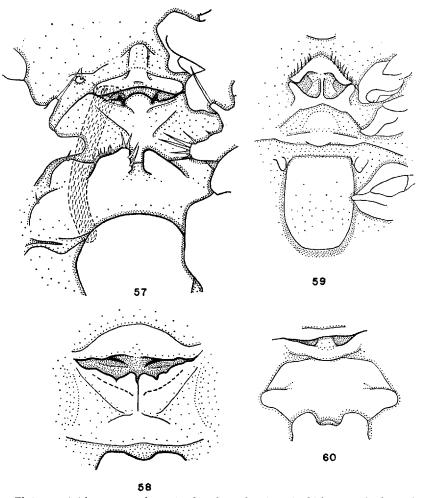
The type of G. valens, taken at 37° N, 74° W off the Middle Atlantic coast of the United States, represents the most southwesterly capture heretofore known. The record of "Amalopenaeus elegans" from "Albatross" station 2201, 39° N, 71° W, by Smith, 1887, also refers to A. valens, as determined by a reëxamination of the specimen which is contained in the collection of the Zoology Department of the Peabody Museum. An unrecorded female in the same collection was taken at "Albatross" Station 893, off Block Island. The present records from the Bermudas, the Bahamas, and the Gulf of Mexico therefore represent an expansion of the known range of the species. Over most of the recorded area, G. valens is less abundant than G. elegans, in company with which it is often taken; and it is not known from the inner parts of the Mediterranean and from high latitudes in the North Atlantic where G. elegans occurs; on the other hand, it is fairly abundant in Bahaman waters where G. elegans seems to be very rare or absent. It is a peculiar fact that according to the present records the frequency per haul of G. valens is in logarithmic inverse proportion to that of G. bouvieri Kemp.

There is no doubt but what the males of the present collection are identical with the type, and with the male figured by Bouvier, 1908. The petasma figured by Balss, 1927, seems to be that of an incompletely adult specimen. The relative length and the shape of the outer lobule of the distolateral lobe of the petasma are slightly variable in the twenty-five available males, but the differences are not of a sort to arouse any suspicion of the homogeneity of the material.

Assurance may be obtained from the station records that the females here attributed to *G. valens* are conspecific with the males. The sculpture of the thelycum is somewhat variable; these variations have been recognizably mentioned by Bouvier, 1908, although his figures are extraordinarily poor. The structure of the thelycum is as follows: The fourteenth sternite bears a large scute, the anterior margin of which varies from a smoothly rounded condition in some individuals to one in which the anterolateral margins of the scute are produced as two strong setose horns projecting forward over one-third or more of the length of the thirteenth sternite. In the middle of the thirteenth sternite are a pair of lamellate, setose teeth, of variable size, which are rarely almost absent as in one of the figures offered by Bouvier. Lateral to each tooth is a

ridge which varies from an independent, tooth-like setose projection to a state in which it forms an indistinguished lateral continuation of the more median tooth. Posterior to this ridge is another which in some cases is faintly connected with the more median tooth. An elevation at the anterior margin of XIII. posteriorly poorly defined, forms the posterior lip of the sinus between XII and XIII; while an anteriorly somewhat indefinite elevation of XII forms the anterior lip. The variations in different structures noted above show no obvious correlation one with another; and there seems to be no correlation between thelycal form and size of individual within the large range in carapace length of 7 to 12 mm. Females of any size within this range may be impregnated, and all are therefore adult. At the lateral ends of the sinus lie the orifices of the sperm receptacles, from which, in impregnated females, project the ends of the slender, dark-brown spermatophores. The receptacles are tubular invaginations of extraordinary length, which may reach back as far as the anterior third of the fourteenth sternite. The spermatophores, when separated from the outer capsule in which they are imbedded in the male vas deferens, are long, slender, somewhat flattened rods tapering at each end; and are encased in a double sheath. The spermatophore is longer than the receptacle, and one end usually projects from the orifice of the spermatheca, while the other is doubled back for a short distance in the blind end of the receptacle. Within the sheath, the spermatozoa lie in a homogeneous mass.

Stephensen, 1923, has described as a new species, G. bidentata, ten females taken west of Ireland and in Cadiz Bay, within the geographical range of G. valens, which Stephensen himself records from the same waters. The figure of the thelycum of the type seems to represent a specimen of G. valens, with which G. bidentata is not compared by its author. Balss, 1927, has noted the similarity of Stephensen's figure to that by Kemp of an Irish specimen doubtfully identified with G. valens. According to Stephensen, "apart from its thelycum, this species is characterized by the two powerful teeth on the inferior margin of 1. joint in p[ereiopod]. 4."; but this pair of projections is well developed in all of my material of G. valens. The examination of one of the smaller paratypes of G. bidentata obtained through the courtesy of Dr. Stephensen, permits me to state that this specimen is certainly a G. valens of the type in which the lateral ridges of XIII fuse with the more median pair of teeth, and the scute of XIV has a rounded anterior margin. Since, as indicated above, these two variations do not necessarily occur simultaneously, there seems to be no basis for separating specimens of this type from other variants. It seems probable that G. bidentata simply represents a selection of specimens of G. valens in which certain of the possible variations of two thelycal structures occur together. The ultimate segment of the endoped of the first maxillipede, in the paratype of G. bidentata and in our material of G. valens, is smaller than in Stephensen's figure, and the penultimate segment is narrower.



Thelycum (with spermatophores in G. valens, the tips of which protrude from the atrium; outline of receptacle of right side indicated by dashed area, Figure 57. Produced lamella of XIV in G. scutatus turned back to expose XIII and XII, Figure 59). 57. Gennadas valens (Smith), Bermudan 9,  $\times$  30. 58. G. gilchristi Calman (D. T. E. St. 91),  $\times$  30. 59. G. scutatus Bouvier, Caribbean 9,  $\times$  20. 60. G. talismani Bouvier (D. T. E. St. 67),  $\times$  30.

In thelycum, as in petasma, G. valens most nearly resembles G. gilchristi Calman (figure 58, p. 79). The figure of an impregnated thelycum by Balss, 1927, is incomplete and somewhat misleading. From the middle of sternite XIII of the female of G. gilchristi arises a transverse lamella the free margin of which reaches nearly to the front of the segment. The free margin of the lamella

is cut into a pair of large teeth, homologous to those of G. valens. The median margins of these teeth are appressed but are not fused. The crenellated free margin of the lamella laterad the pair of teeth is homologous to the lateral ridge of G. valens. The anterior margin of sternite XIII is not marked by a ridge forming the posterior margin of the receptacular sinus, such as occurs in G. valens. Instead, the transverse elevations at the middle of XIII, which in G. valens do not even extend far enough forward to overlap the posterior lip of the sinus, in G. gilchristi take on the function of the missing posterior lip. The anterior lip is fairly well developed, and just behind its lateral parts are a pair of shallow invaginations of the floor of the sinus. These are equivalent to the enormously elongated receptacles of G. valens. In the available impregnated female of G. gilchristi the entire depression anterior to the teeth of XIII is filled by a pair of large ellipsoidal sheathed spermatophores embedded in a dark-brown mass of secretion. The spermatophores are sunk for about twothirds of their length in the divergent shallow invaginations forming the receptacles proper.

## Gennadas bouvieri Kemp

Gennadas bouvieri, Kemp, 1909 and 1910b.

Amalopenaeus bouvieri, Balss, 1927.

Gennadas alcocki, Kemp, 1910b, part [3].

Amalopenaeus alcocki, Balss, 1927.

Gennadas elegans, part, Lenz and Strunck, 1914.

Gennadas parvus, part, Bate, 1881 and 1888; Alcock, 1901.

NOT Gennadas alcocki, Kemp, 1910b and 1913, part [ ].

### TONGUE OF THE OCEAN, BAHAMAS

1 female. B.O.C. 195. Pawnee St. 9; March 1, 1927. Wire 4000-7000 feet. 2 males, 1 female. B.O.C. 196. Pawnee St. 11; March 2, 1927. Wire 7000 feet.

1 male. B.O.C. 197. Pawnee St. 16; March 9, 1927.

2 males, 1 female. B.O.C. 205. Pawnee St. 18; March 10, 1927. Wire 7000 feet.

3 males, 1 female. B.O.C. 198. Pawnee St. 22; March 12, 1927. Wire 7000 feet.

2 males, 3 females. B.O.C. 199. Pawnee St. 23; March 14, 1927. Wire 8000 feet.

#### EXUMA SOUND, BAHAMAS

1 male. B.O.C. 200. Pawnee St. 33; March 22, 1927. Wire 8000 feet.

## CAICOS PASSAGE, BAHAMAS

? 1 male, juvenile. B.O.C. 214. Pawnee St. 46; April 4, 1927. Wire 10,000 feet.

# TURKS ISLAND PASSAGE, BAHAMAS

5 males, 3 females. B.O.C. 201. Pawnee St. 52; April 11, 1927. Wire 8000 feet.

2 males, 2 females. B.O.C. 202. Pawnee St. 56; April 13, 1927. Wire 6500 feet.

## BERMUDAS

1 male. B.O.C. 203. Pawnee St. 58; April 20, 1927. Wire 10,000 feet.

## Providence Channel, Bahamas

1 female. B.O.C. 204. Atlantis St. 1478; February 20, 1933. Wire 5250 feet.

### CARIBBEAN

? 1 male, juvenile.  $B.O.C.\ 213$ . Atlantis St. 1939; February 3, 1934. Depth between 50 and 200 m.

Seven females of *G. bouvieri* have heretofore been taken, in the Eastern Pacific and the Indian Ocean; seven males have been recorded from the Indian Ocean, and one male (Balss, 1927) in the South Atlantic. In none of these cases were male and female ever taken in the same haul; therefore it is understandable that the sexes should have been maintained until the present under distinct names, the females as *G. bouvieri* Kemp, the males as *G. alcocki* Kemp. It is a matter of considerable interest that seventeen males and ten females have been taken by the "Pawnee" in Bahaman and Bermudan waters; the present station records clearly indicate that the male of *G. alcocki* is correctly assigned to *G. bouvieri*. It may be noted that the female incorrectly paired with the male by Kemp is evidently attributable to *G. propinquus* Rathbun (*G. clavicarpus* DeMan; *G. scutatus indicus* Kemp). As Kemp seems to consider the female described by Alcock, 1901 (as *G. parvus*), as the type, *G. alcocki* is strictly speaking a synonym of *G. propinquus* rather than of *G. bouvieri*.

Between figures of the petasma of males from the Indian Ocean by Kemp, 1910b, and Balss, 1927, some differences are perceptible. According to Balss, the median lobule of the distolateral lobe has the form of a laterally directed hook opposing the medially directed, hook-like lateral lobule; and the distolateral lobe rises no higher than the distoventral. In Kemp's figure 5, the median lobule of the distolateral lobe is directed mediad; and the distolateral overtops the distoventral. My material agrees with Balss' figure in the first point (although the tips of the lobules do not nearly touch each other as shown by Balss); with Kemp's in the second. Both Balss and Kemp show the lateral lobule of the distolateral lobe produced as a tapering projection which overtops the distolateral lobe; and the accessory lobe as not reaching nearly to the tip of the distolateral lobe. In my material the distomedian is divided in two by a shallow median emargination, neither lobule extending nearly as far

under the name G. scutatus indicus. No females were attributed to G. s. indicus. Balss, 1927, notes the possible identity of G. scutatus indicus with the male of G. propinquus Rathbun, 1906. The type female of G. clavicarpus seems identical with the female of G. propinquus figured by Rathbun. The essentially close resemblance of the thelycum of G. propinquus to that of G. scutatus, to be discussed in an ensuing paragraph, provides strong presumption for the belief that Rathbun and DeMan make no error in joining this female to the male G. propinquus-clavicarpus (part)-indicus, the petasma of which is very similar to that of G. scutatus.

In both G. scutatus and G. propinquus the relative length and shape of the distal lobes of the petasma seem to be somewhat variable, but in all known specimens of G. scutatus the median lobule of the divided distoventral lobe is narrower than the lateral one; and the median lobule of the distolateral lobe is not conspicuously tapered from base to tip, while, conversely, the median lobule of the distoventral lobe is broader than the lateral one in G. propinquus, and the median lobule of the distolateral tapers conspicuously to its narrow distal end. The two forms therefore seem to be quite distinct.

The thelycum of G. scutatus consists of a somewhat hexagonal plate on the fourteenth sternite, from the anterior margin of which springs a large, free, tongue-shaped flap extending forward to the twelfth sternite. At the posterior margin of the thirteenth sternite is a low transverse ridge. At the anterior margin of XIII is another transverse, shallowly U-shaped elevation, from the median margin of which a longitudinal ridge runs forward, dividing the sinus between XII and XIII into halves. At the posterior edge of XII is a  $\land$ -shaped ridge the posterior ends of the arms of which abut against the anterior margin of XIII. In the space enclosed within the lips thus formed is a pair of depressions separated by the median longitudinal ridge, at the lateral ends of which lie the orifices of the sperm receptacles. In impregnated females the shallow receptacles are filled with a mass of sperm which protrudes them and covers the elevation of XII. This exposed sperm mass is, however, concealed by the anterior end of the free projection of the fourteenth sternite.

To judge from the figures by Rathbun, Kemp, and DeMan, the thelycum of G. propinquus differs chiefly in that the anterior edge of the plate of the fourteenth sternite is not produced as a free flap, and the transverse ridge of the posterior part of XIII is more strongly developed, with a conspicuous anterior convexity or projection. There are some differences in the details of the elevations surrounding the sperm receptacles, but on the whole the thelycum of G. propinquus seems to resemble that of G. scutatus much more closely than does that of any other species of the genus. It may be noted that males and females of G. propinquus have been found together in the same haul on several occasions; the types were taken together, and were unaccompanied by other representatives of the genus, and Balss records 4 males and 3 females at station 215, the genus

being otherwise represented in this haul by a single male of G. bouvieri Kemp and two of G. sordidus Kemp.

The spermatophore of *G. scutatus*, as freed from the accessary secretion-mass enveloping it in the male vas deferens, consists of a thin-walled slender cylinder containing numerous minute bean-shaped aggregations of sperm, each encased in a special envelope, as in *G. tinayrei*. The mass as deposited in the female receptacles seems to represent only the contents of the cylindrical sheath; and the walls of the bean-shaped aggregations are no longer definite, the clumps of spermatozoa being embedded in a gelatinous matrix.

Of other species of the genus, G. talismani Bouvier seems most nearly related to G. scutatus and to G. propinquus. A male and a female (B.O.C. 216), determined by Balss, have been obtained by exchange from the Zoologische Museum der Universität, Berlin. The thelyeum (figure 60, p. 79) differs from the figure by Balss, 1927, in that, as in G. scutatus, the posterior lip of the receptacular atrium is medially continued forward as a ridge dividing the atrium in half.

According to the figure by Balss, 1927, the petasma of *G. incertus* Balss, to which no female has been assigned, bears some resemblance to that of *G. scutatus*. *G. gardineri* Balss, to which no male has been assigned, likewise seems from Balss' figure of the thelycum to display more resemblance to *G. scutatus* than to other species of the genus. Since these two forms seem to belong to the same section of the genus, it seems possible that *G. gardineri* represents the female of *G. incertus*. The only other species of which the female is unknown, *G. sordidus* Kemp, undoubtedly belongs to a different section, and may be predicted with some confidence to have a thelycum with separated, independent spermathecal orifices.

## Series ARISTEAE Bouvier

Since the present collection does not include adult material of *Aristaeomorpha*, of *Aristaeus*, or of many of the species of other genera, a thorough-going revision of the series has not been attempted, although some modifications of the accepted generic groupings are suggested.

It may be mentioned in this place that Ortmann's subfamily Cerataspinae, which persists in the literature, may be discarded, since Cerataspis is composed of the mysis larvae of Aristaeomorpha and Plesiopenaeus. C. monstrosa Gray (C. affinis Kishinouye) and C. petiti Guérin are perhaps respectively attributable to the adults known as Aristaeomorpha foliacea (Risso) (with which Aristaeus japonicus Yokoya, 1933, is evidently synonymous) and A. wood-masoni Calman; while Cerataspis (Cerataspides Bonnier) longiremus Dohrn, Peteinura gubernata Bate and an undescribed third form in the Bingham Collection appear to represent the mysis stage of Plesiopenaeus. If the present allocations are confirmed, Aristaeomorpha is a synonym of Cerataspis; and A. wood-masoni, of C. petiti.

#### **HEPOMADUS** Bate

The genus is diagnostically distinguished from Hemipenaeus chiefly by the possession of an hepatic spine.¹ The branchial formula of Hepomadus and of Hemipenaeus has been believed (Bouvier, 1908) to resemble that of Aristaeus, and to differ from that of Aristaeomorpha and of Plesiopenaeus in the absence of podobranch from the twelfth and of epipodite from the thirteenth sternites. Bouvier's statements follow those of Alcock, 1901; but the latter author, although not mentioning the fact in his key, has observed that a rudimentary epipodite occurs in Hepomadus; I am able to confirm this statement, with the addition that the epipod is a small subrectangular lamella in available material, rather than the "tiny filament" found by Alcock in a Bengalese representative. I further observe that in a juvenile female, although not in the other available specimens, a vestigial podobranch is borne by the epipodite of the twelfth somite. Therefore, although a quantitative difference between the branchiae of Hepomadus and of Aristaeomorpha or Plesiopenaeus remains, the supposed qualitative difference seems to be elided.

It may be observed that the large spine of the third pleonic tergite in *Hepomadus tener* springs from the posterior margin of the segment, rather than from a point in advance of the posterior margin as in those species of *Hemipenaeus* in which such a spine occurs. It is interesting that this difference seems to have been brought about by a change in the position of the spine relative to the posterior margin of the tergite, not by a recession of the posterior margin, bearing the spine with it, as in *Benthesicymus bartletti*.

## Hepomadus tener Smith

Hepomadus tener, Smith, 1884 and 1887, Bouvier, 1908. ? Hepomadus tener?, Wood Mason and Alcock, 1891a; Alcock, 1901.

1 female, juvenile; carapace length 12.5 mm, rostrum 5.7 mm, total about 43 mm. B.O.C. 147. Pawnee Station 54; N. 21° 15′ 40″, W. 71° 17′ 06″; April 12, 1927. Wire 7,500 feet (Bottom struck at 900–945 fathoms).

In addition to this specimen three large individuals from the collection of the Zoology Department of the Peabody Museum have been available. These are, a female of carapace 53 mm (rostrum broken) from off the eastern coast of the United States in 843 fathoms, determined in 1885 by S. I. Smith although not mentioned in his papers; together with a female of carapace 47 mm and a

<sup>1</sup> The hepatic spine is acquired relatively late in the larval development of those Penaeidae in which it occurs. In all but a few Aristaeinae, the spine never appears; on the contrary it appears at some stage in all other members of the family, occasionally subsequently disappearing, as in adults of Funchalia villosa. Thus, in absence of hepatic, Hemipenaeus and Funchalia represent a convergent rather than a homologous condition.

male of carapace 44 mm with unattached petasmal endopods from the same region at 1239 fathoms, identified by A. E. Verrill.

The small female of the Bingham Collection is 4.5 mm less in carapace length than are the males reported as *Hepomadus tener* Smith by Bouvier, 1908, from the Sargasso Sea at 1723 fathoms and the male reported as *Hepomadus glacialis* Bate by Milne Edwards and Bouvier from the Gulf of Mexico west of the Tortugas, at 955 fathoms. The largest of the available females, with a total length of not less than 200 mm, is somewhat larger than Bate's *H. glacialis* from the northwest Pacific.

It seems highly probable that the juvenile of the present collection, the smallest known specimen of the genus, is identical with *Hepomadus tener*, although it differs from the three available adults of the latter in bearing the rudiment of a podobranch on the epipodite of XII, and in having only the faintest trace of a postrostral carina. What relationship the present small specimen may bear to Bouvier's specimen from the Mexican Gulf, and to Bate's species, is uncertain.

The length of the spine at the posterodorsal margin of the third pleonic somite, employed as a diagnostic character in Bouvier's key to the species of the genus, does not distinguish Bate's H. glacialis (according to the figure) from H. tener of comparable size. The accurate description of this spine in terms of its extent over the succeeding somite is not practicable, since its relative length then depends on the extension of the pleon. If bent as in Bate's figure, this tooth in the three large specimens of H. tener at hand does not attain more than two-fifths of the length of the fourth somite. In more accurate terms, the tooth in the present large specimens as compared to the distance between the transverse furrow and the posterior margin of the third tergite is respectively 13/7 mm, 11/6.5 mm and 11/7 mm. In Bate's figure this ratio is 15/6, somewhat but not greatly shorter. In Smith's figure (1887) of a specimen of carapace 32 mm, the proportion is 7/7 mm; in the present small female, it is 1.9/1.4 mm. The length of the spine is therefore intraspecifically variable; the available information suggests that it decreases in relative length with increasing size of the individual.

The postrostral carina in both of Bouvier's specimens is reported to become very indistinct posteriorly, as it does in the present small female. In the available large specimens, this carina is extremely high and sharp to within one-seventh of the posterior margin of the carapace. In Smith's description (1884) of a male of carapace 17.8 mm, the postrostral carina is said to be present only in front of the cervical sulcus; and in the large specimens later described (1887), the carapace is said to resemble that of *Plesiopenaeus armatus*, in which there is no postcervical middorsal carina. Bate describes his large female as without carina on the cardiac region. These differences in strength of postrostral carina appear to be interpretable as individual and growth variations.

In the small female of the present collection the stylocerite falls slightly short of the end of the first antennular segment; in the large specimens it extends to the end, or very slightly beyond. The antennal scale extends a variable distance beyond the antennular peduncle, from slightly more to slightly less than the length of the distal segment of the peduncle beyond its tip.

In the small female under discussion, the anterior lobe of the epistome lacks a conspicuous median carina. A carina in this region is present in the three large specimens, in which the outer margins of the epistome are also considerably elevated; this condition is perhaps due to differential shrinkage induced by the action of the preservative. In all four specimens the shape of the epistome is elongated and lanceolate, and the tip (which is the dorsal margin of an anterior vertical ridge) is a narrow obtuse projection.

In the present small female, the inner lobe of the second segment of the mandibular palp is not much produced, and is rather blunt; in the large specimens this lobe is produced, narrow, and acute at tip, somewhat as in Bate's figure. In available specimens the maxillary palp bears three strong and two weak spines on its posterior edge, two or three strong and one or two weak spines on its anterior edge. The palp of the first maxillipede bears five or six strong spines of which the distal four or five are stouter and more curved. According to Milne Edwards and Bouvier, 1909, there are eight such spines in the "Blake" specimen attributed to H. glacialis, but his figures indicate only seven.

There is no trace of a tooth or projection at the posterior margin of the dorsal carina of the fourth and fifth somites of any of the present specimens, and the posterior angle of the sixth somite is acute.

The rostral lengths and tooth intervals of known specimens of Hepomadus in order of size are as follows: (Present small female) rostrum less than half the carapace in length; interval between the two rostral teeth half the distance between the anterior tooth and the tip, and a little more than a third the distance between the posterior rostral tooth and the postorbital tooth. Bouvier, 1908 (small male) half the carapace (text); interval two-thirds distance to tip and more than half distance to postorbital (figure). Milne Edwards and Bouvier, 1909 (figure of a small male) nearly two-thirds carapace; interval one-third distance to tip and to postorbital. Smith, 1887 (figure of female of intermediate size) two-thirds or more of carapace; interval less than one-half distance to the incomplete tip, and more than one-half to postorbital. (Present medium large female) incomplete rostrum more than five-eighths of carapace, interval less than one-third distance to tip and one-half distance from postorbital. It may be noted that Smith's figure is very inaccurately reproduced by Bouvier, 1908, at much less than the stated "Gr. nat.", and that it does not represent the type, as is thought by the French author.

The small male from the "Blake" collection, according to the description by

Milne Edwards and Bouvier, seems as shown above to be distinguished from the present specimens in the relatively greater length of its rostrum; in the relative shortness in so small an individual of the spine of its third pleonic somite; in the small interval between its two rostral teeth; in the presence of teeth at the posterior ends of the dorsal carinae of its fourth and fifth pleonic somites; in the obtuseness of the posteroinferior angle of its sixth somite; and in the absence of spines from the anterior edge of its maxillary palp. These and other differences are believed by Bouvier to mark the "Blake" specimen as H. glacialis Bate and to distinguish it from H. tener Smith. Supposed differences, in form of epistome, armature of the palp of the first maxillipedes, shape of the inner lobe of the mandibular palp, and structure of antennulae, seem of doubtful significance. If Bouvier's description of the "Blake" specimen is accurate, it may, as he believes, belong to another species than H. tener. Whether or not it is identical with H. glacialis is uncertain. The strongest reason for identifying the "Blake" specimen with the latter form (and, indeed, for believing, in view of the rather obscure coordination of variations among known specimens, that they include more than one species) is supplied by the occurrence of teeth at the posterior dorsal margins of the fourth and fifth pleonic tergites in both. In the Benthesicymus brasiliensis complex a similar difference is of specific value; but on the contrary, in Hymenopenaeus laevis it seems to represent individual variation.

The lanceolate plate of the thirteenth somite of the available adult females differs slightly from Bate's figure. The petasma differs little from the same organ as found in Hemipenaeus, Plesiopenaeus and Aristaeus. The appendix masculina of the male consists of a very broadly lanceolate outer blade with twisted margins and a narrow inner blade as long as the outer. The tubercle of the carapace which represents the larval posterior dorsal organ has a sharp anterior edge. The cervical sulcus is complete and distinct, the postcervical faint. The dactyl of the third maxillipede of both sexes has its proximal inner margin excavate beneath, the emargination being edged with strong spines. There is a small tooth at the inner distal end of the ischium of the third maxillipede. The stout spine at the distal end of the merus of the first legs, noted by Smith, is mobile; a similar mobile spine occurs (as well as in many other Aristeae) in Hymenopenaeus diomedeae (Faxon) and Haliporus thetis Faxon, where it is accompanied by a fixed meral tooth such as is found (unaccompanied by the mobile) in Hymenopenaeus robustus and H. debilis. A similar mobile meral spine is also present on the second leg of Hepomadus. The basal segment of the antennular peduncle in the small female bears a minute parapeneid spine on its ventromedian margin, which is not present in the adults.

#### **HEMIPENAEUS** Bate

Hemipenaeus, Bate, 1881 and 1888, part; Wood Mason and Alcock, 1891 a and b; Faxon, 1895; Alcock, 1901; Bouvier, 1908; DeMan, 1911; Balss, 1925. Aristaeus, Wood Mason and Alcock, 1891b, part; Faxon, 1895, part.

The distinctions between Aristaeus and Hemipenaeus heretofore recognized, chiefly comprising the reduction of the pleurobranchs in advance of the last thoracic gill and the loss of the cervical sulcus of the former, are of rather slight value. Hemipenaeus is usually defined, after Alcock, as with small but plumose pleurobranchs in contrast to the vestigial dorsal gills of Aristaeus. But, although Alcock, 1901, and Kemp and Sewell, 1912, find the pleurobranchs of Aristaeus virilis Bate and A. semidentatus Bate to bear only a few simple pinnulae at most, according to DeMan these gills in specimens (certainly closely related) which he attributed to these two species bear numerous bi- or even tri-furcated pinnulae. On the contrary, Faxon reports the pleurobranch of XIII of Hemipenaeus spinidorsalis to lack pinnulae completely; and although this statement is not confirmed by reëxamination of the material (since this gill in all specimens bears pinnulae trifurcated at the least), the pleurobranchs of this species of *Hemipenaeus* do not appear to be a great deal stronger than are those of some specimens of Aristaeus. The usual statement that in Hemipenaeus the cervical sulcus is conspicuous by contrast with the indistinct one of Aristaeus, seems likewise to imply a sharper distinction between the two groups of forms in this respect than is justified; since the sulcus, in specimens of Hemipenaeus spinidorsalis contained in the collection of the Museum of Comparative Zoology, is extremely faint.

It seems possible, however, in view of the observations detailed below, that diagnostic characters not heretofore generally recognized may distinguish Hemipenaeus from Aristaeus. In the earliest description of members of the former group, Bate, 1888, correctly states that a podobranch occurs on the twelfth and a rudimentary epipodite on the thirteenth sternite. Faxon, 1895, also notes the occurrence of the podobranch; though not of the epipodite, in Hemipenaeus spinidorsalis Bate and H. triton Faxon. Succeeding workers, as Alcock, 1901, have denied the occurrence of these structures. I am able to confirm Bate's and Faxon's observations as to the podobranch, and Bate's statement of the existence of a rudimentary epipodite, in the two species of Hemipenaeus available to me. I have further observed the occurrence of small exopods in Hemipenaeus, the existence of which is denied by Bouvier, 1908.

In the only species of Aristaeus available to me, A. occidentalis Faxon, no trace of a podobranch on the twelfth sternite; of an epipod on the thirteenth; or of exopods on the walking legs can be found; in agreement with earlier observations. Thus, if the available form is representative of the genus, Aristaeus

<sup>1</sup> It may be observed in this place that contrary to Faxon's statements, pleuro-branchs of *Aristaeus occidentalis* posterior to IX bear a number of simple pinnulae.

is as clearly distinguished from *Hemipenaeus* as are any other of the superspecific groups of the series from one another. Unfortunately, however, *Hemipenaeus* (assuming the branchial structure here observed to be representavie) can no longer be distinguished from another superspecies, *Plesiopenaeus*, by branchial formula, but only by the quantitative difference in degree of development of the podobranch and epipodite.

It seems evident that keys to the genera of Aristeae presented by Alcock and by Bouvier are not compatible with the actual distribution of characters within the group; but in view of the lack of critical knowledge of many species, it seems best to postpone an extended review of the series until it is known whether the limiting characters indicated in this paper are constant throughout the genera involved. The known occurrence of individual variability in branchial development almost sufficient to obliterate generic distinctions, in *Hepomadus*, *Aristaeus*, and *Hemipenaeus*, seems to indicate an uncertain validity for definitions of the genera of Aristeae based in differences of branchial development, and it is possible that a further reconsolidation of the groups may be found necessary.

Balss, 1925, states that the genus *Hemipenaeus* contains six species, but whether by this he means to imply that of the seven described species *H. triton* is synonymous with *H. carpenteri*, as suggested by Faxon, 1895, and by DeMan, 1911, and below; or that either *H. sibogae* DeMan or *H. crassipes* Wood Mason and Alcock are synonymous with *H. gracilis* Bate, as suggested by DeMan, is not evident.

No evidence is available to confirm Alcock's suggestion (1901) that *Hemipenaeus carpenteri* is of bathypelagic rather than benthonic habit.

### ? Hemipenaeus carpenteri Wood Mason

? Hemipenaeus carpenteri, Wood Mason and Alcock, 1891 a and b; Alcock, 1901. Hemipenaeus triton, Faxon, 1893 and 1895; 1896.

3 males, juvenile. B.O.C. 149. Pawnee Station 54, N. 21° 15′ 40″; W. 71° 17′ 06″; April 12, 1927. 7500 feet wire.

Carapace lengths respectively 24, 23, and 16 mm; rostrum 4.2, 4 and 3 mm. Total length of the largest specimen about 88 mm.

The present material, of a species with spine on the third pleonic tergum nearly related to or identical with the Indo-Pacific *H. carpenteri* Wood-Mason is identical with *H. triton* Faxon, a species only once previously recorded from the Atlantic. In addition to the fresh Atlantic specimens, the female of carapace length 17 mm in the collection of the Museum of Comparative Zoology, from "Blake" St. 227, St. Vincent, listed by Faxon, 1896, as *H. triton*, has been available for comparison, as have the Pacific American types of *H. triton*; and also Faxon's material of *H. spinidorsalis*. The present material provides the fourth record of the genus from the Atlantic, from which ocean the only other species previously recorded are *H. speciosus* Bate and *H. spinidorsalis* Bate, both from

the southern South Atlantic. The former of these two belongs to the subgeneric group not equipped with a large spine springing from the third pleonic tergum; the latter species bears such a spine and is nearly related to the present form. If it be assumed that, as seems likely, the *H. spinidorsalis* of Faxon, from Pacific America, is identical with the species recorded under that name by Bate both from the South Atlantic and the Indo-Pacific, then the present material (as was observed by Faxon) is distinguished from *H. spinidorsalis* (Bate) by its shorter rostrum, which is not a fifth as long as its carapace, and does not reach the end of the eye (falling short of the base of the cornea in the two larger Atlantic specimens); by its more distinct cervical sulcus; and by the fact that the median blade of its bipartite appendix masculina is longer than the lateral one, the lateral blade being short and broad, with a roundedly truncate distal end.

The reexamination of Faxon's material of *H. spinidorsalis* permits the statement of certain additional differences: the postcervical sulcus and the cardiacobranchial carina are stronger in ? *H. carpenteri*; the lanceolate plate of sternite XIII is narrower in both males and females and in the females its anterior margin has a different shape; the median spines at the anterior margins of sternites XII-VIII are weaker; the antennular stylocerite fails to reach the base of the externodistal tooth of the proximal segment of the antennular peduncle, whereas in *H. spinidorsalis* it reaches to the tip of this tooth; the dactyl and pollex of the third cheliped are shorter and stouter; and the petasma differs somewhat, in that its short cincinnulated margin is more strongly set off from the lateral parts of the petasma, and that the spur of the external surface of the peduncle projects more extensively.

Comparison of the available Atlantic material with the types of *H. triton* Faxon reveals no significant differences in carapace or pleon; Faxon's figures are not entirely accurate. The posterior cervical sulcus is sometimes better marked in Pacific than in Atlantic specimens, reaching to and indenting the postrostral carina, but both in strength and in outline, the groove is inconstant. The middorsal carina of the sixth pleonic somite of both Atlantic and Pacific specimens ends in a small tooth omitted from Faxon's figure. The tooth of the third pleonic somite increases in relative length with decreasing size of the individual.

The eye and antennular stylocerite, which are too short as shown in Faxon's figure, are similar in all material. The antennal scale is shorter and broader in Pacific than in Atlantic specimens, being not so long as the interval between the orbital margin and the posterior of the cervical sulei of the carapace, and not two and one-half times as long as broad. These ratios are, however, variable with size; thus, in the three specimens of the present collection, the scale extends two-fifths of the distance between the posterior cervical sulcus and the posterior margin of the carapace behind the sulcus in the largest, while in the smallest it

extends to two-thirds this distance; similarly, the scale is in the largest Bingham specimen two and four-fifths times as long as broad, whereas in the smallest it is more than three times as long as broad. The third leg extends somewhat beyond the third maxillipede in Pacific specimens; not to its end in Atlantic ones. The dactyl of the third chela is in the Pacific specimens from one-fourth to two-fifths the palm longer than the palm; in Atlantic specimens the finger is an eighth or less longer. The entire chela is somewhat shorter in Atlantic material, not reaching from the orbital margin to the posterior cervical sulcus of the carapace, whereas in Pacific specimens it reaches to or behind this point.

The petasma of the juvenile Atlantic males is very nearly identical (save for smaller size and unattached halves) with that of the Pacific adults. The appendix masculina differs in the slightly reduced relative breadth of its anterior blade. The shield-shaped scute of sternite XIII in the Bingham males and the small "Blake" female closely resembles the same structure in Pacific adults.

The small podobranch of XII is in some Pacific specimens much larger than in Atlantic ones, and plumose, with richly branched pinnulae; but in others the gill is as small as in Atlantic material, and with as few as six pairs of simple pinnules.

It appears from the above that Faxon's determination of the small Atlantic female of the "Blake" is correct insofar as he considers Atlantic and Pacific American specimens to be conspecific. Whether the American form is identical with the Indo-Pacific H. carpenteri Wood Mason is uncertain, although it seems probable that it is, both by reason of evident similarities, and on a priori grounds (cf. Introduction). The known Indo-Pacific females (no males having been captured) are larger than the Atlantic American specimens, smaller than the Pacific ones. They appear to fall about midway between the two American groups of specimens in relative length of antennal scale and third leg. The dactyl of the third leg, according to Alcock, 1901, is twice the length of the palm, but his figure (Illustr. Zool. "Investigator") shows it to be no more than one-half longer. The rostrum, reaching to the end of the eye, is longer than in American material. The posterior cervical sulcus is not indicated in the figure. The presence of a rudimentary epipod on XIII and small podobranch on XII was not observed; however, the podobranch is often extremely inconspicuous and likely to be overlooked unless carefully searched for. The scute of sternite XIII of American females is hardly to be termed "pentagonal," its anterior margin, although bearing spine at the midpoint, being arched, and joining the lateral margins without an angle.

Further structural features of ? H. carpenteri may be noted as follows:

There is an extremely minute trace of a parapeneid spine in the middle of the ventromedian margin of the basal segment of the antennular peduncle of Atlantic specimens, which is largest in the smallest male. This spine is entirely absent in the Pacific adults. The superior antennular ramus is considerably

longer than the basal segment of the peduncle; it is flattened, and troughed beneath, the trough being pubescent. The exopod of the second maxillipede is longer than the endopod; that of the third maxillipede reaches beyond the base of the carpus. Pereiopodal exopods are minute but present. None of the epipods are furcate; that of XIII is a small but readily evident subrectangular lamella. The pleurobranch of XIII is the smallest, not half so large as that of XIV; the gill of VII is of similar structure to those on following somites, and is larger than any pleurobranch.

The chela of the third legs is about one and two-thirds as long as the carpus, which is less than three-quarters as long as the merus. The dactyl of all the chelae is conspicuously shorter than the pollex. The cutting faces of the chelae are set with a sharp edge of uncalcified chitin which, in the third chelae, is interrupted by three to five conspicuous chitinous teeth. The legs are unarmed at base, save for the tooth at the anterior inner edge of the coxa of the fifth legs (referred to by Faxon as on the "second segment"); and none bears a mobile meral spine.

The distoventral lobe of the petasma is a stiff, curved, flat rib with roundedly truncate tip, free from the membranous distolateral lobe for more than half its length. The distomedian lobe is not well marked. In Faxon's figure, a dorsal view, this lobe is concealed by the distolateral. The distomedian lobe is not sharply marked off from the distolateral. The distolateral is poorly represented in Faxon's figure; its lateral margin slopes regularly from the apex, and forms a line different from that represented. On the outer surface of the pedicel of the petasma is a pair of short free projections.

### PLESIOPENAEUS Bate

Plesiopenaeus, part, Bate, 1881; Faxon, 1895.

Plesiopenaeus, Alcock, 1901; Bouvier, 1908; DeMan, 1911.

Penaeus, Johnson, 1867, part.

Aristaeus, part, Miers, 1878; Bate, 1881 and 1888; Wood Mason and Alcock, 1891 b; Faxon, 1895.

Aristaeopsis, Wood Mason and Alcock, 1891b; Alcock, 1901; Bouvier, 1908; DeMan, 1911.

Aristaeinae of the series Aristeae, with a large epipodite on XIII, a large podobranch on XII, exopodites on the walking legs, no hepatic tooth, and a tridentate rostrum.

The provisional name *Plesiopenaeus* was suggested by Bate, 1881, for those relatives of *Aristaeus* with an epipodite on XIII. No type was named, but the only species discussed by Bate which are equipped with conspicuous epipodite on XIII were *Aristaeus armatus* Bate and *A. rostridentatus* Bate [*Aristaeomorpha foliacea* (Risso)]. The genus *Aristaeopsis* was established by Wood-Mason and Alcock, 1891, with *Penaeus edwardsianus* Johnson as the genotype;

to which genus Bate's Aristaeus armatus was also referred. Faxon, 1895, designated A. armatus the type of Bate's genus Plesiopenaeus, with which name he synonymized Wood Mason's Aristaeopsis (as well as Aristaeomorpha Wood Mason and Alcock, established for Aristaeus rostridentatus Bate). Alcock, 1901, transferred Penaeus edwardsianus to Plesiopenaeus Bate, making Aristeus armatus Bate the sole species of Aristaeopsis Wood Mason and Alcock. It seems evident that Alcock's action is the reverse of that necessitated by the history of the genotypes, and that the genus Aristaeopsis should refer to Penaeus edwardsianus Johnson, whereas the name Plesiopenaeus Bate as clearly refers to Aristaeus armatus Bate. Rather than create confusion by reversing the names at this late date, it seems preferable on consideration of the similarity of the two groups to synonymize Aristaeopsis with Plesiopenaeus. The distinctions given by Alcock are, that in "Aristaeopsis" armatus the exopods of the first and second maxillipede are shorter and slenderer than in "Plesiopenaeus" edwardsianus and "P." coruscans, and the pleurobranchs anterior to XIV are relatively longer. In these features, however, the three species appear to form a series without sharp breaks. Thus, according to Alcock, the pleurobranchiae in advance of XIV are in "Plesiopenaeus" "much reduced in size"; this probably refers to P. edwardsianus, since in our specimen of P. coruscans the richly plumose pleurobranch of XIII is 10.5 mm in length as compared with one of 18 mm on XIV, hardly a great reduction. In a female of Plesiopenaeus armatus tridens (Smith) with a carapace length of 41 mm, from the collection of the Zoology Department of the Peabody Museum, the pleurobranch of XIV measures 6, There seems to be more variation in development of that of XIII 5 mm. pleurobranchs within Aristaeus than between all three species of Plesiopenaeus. The exopod of the second maxillipede of *Plesiopenaeus edwardsianus* is nearly twice as long as the endopod, that of P. coruscans not much longer than the endopod, and that of P. armatus considerably shorter than the endopod. As for other differences between the three species, those distinguishing P. edwardsianus and P. coruscans seem quite as extensive as those between P. edwardsianus and P. armatus. The supposed difference between Aristaeopsis and Plesiopenaeus in occurrence of leg exopods given in the key by Bouvier, 1908, has no actual basis, inasmuch as small but distinct exopods are present in Plesiopenaeus coruscans. In so uniform a group as Plesiopenaeus-Aristaeopsis, within which there is no conspicuous grouping of the few species, it seems profitless to maintain the generic distinction, especially in view of the confusion of names which must ensue.

# Plesiopenaeus coruscans (Wood Mason)

Figure 61, p. 99

Aristaeus coruscans, Wood-Mason and Alcock, 1891b; Faxon, 1895. Aristaeus (Plesiopenaeus) coruscans, Alcock, 1901. Plesiopenaeus coruscans, Bouvier, 1908; DeMan, 1911. 1 male, juvenile; carapace 57 mm, rostrum 55 mm. B.O.C. 148. Pawnee Station 54; N. 21° 15′ 40″, W. 71° 17′ 06″; April 12, 1927, Wire 7,500 feet (Bottom, at 900-945 fathoms).

Only two specimens of *P. coruscans* have been taken in the past; a female from the Bay of Bengal at 561 fathoms, with a carapace and rostrum of 75 mm and a total of 150 mm, and a larger male from the Arabian Sea at 825 fathoms (Alcock, 1901). Whether the present male is completely identical with these is not, in the absence of material for direct comparison, determinable with certainty, although it seems probable that all are conspecific. The present specimen represents a new record for the Atlantic. A second species of *Plesiopenaeus*, *P. edwardsianus* (Johnson), has been taken in considerable abundance in the North Atlantic, and a form identified with it, although apparently not by direct comparison, in the Indian Ocean.

The typical species of the genus, Plesiopenaeus armatus (Bate) has been recorded from the Indo-Pacific (Bate, 1888; Alcock, 1901) and the South Atlantic (Bate); and as the variety, P. a. tridens (Smith) (Bouvier, 1908) from the North Atlantic. Sund, 1920, has replaced Smith's name in its original specific status, with the following remark: "As the species [P. tridens] is . . . . clearly distinguishable from A. armatus (Bouvier, 1909), there seems to be little reason to encumber its name by referring it as a variety of another distinct though nearly related species." Against this view, it may be urged that several of the distinguishing characters utilized by Bouvier are of no value: thus, in Bate's figure of A. armatus the stylocerite is indicated to overtop the second article of the antennular peduncle quite as considerably as in Smith's form; Bate's figure is probably incorrect in its failure to indicate a tooth at the posteroinferior corner of the sixth pleonic somite (since the presence of this tooth and of a pleural armature on the three preceding somites is noted by Alcock in Indo-Pacific material); the thickening of the tip of the antennal scale in Alcock's single male is of doubtful significance. Finally, in Smith's figure the exopod of the second maxillipede extends little beyond the middle of the merus of the endopod; the length of this ramus is evidently rather variable. The suggested differences from P. armatus are thus reduced to the item, of uncertain significance, that in Alcock's single male the exopod is "very much shorter than the merus." The difference in rostrum between Smith's and Bate's forms is established only on the basis of Bate's figure, that author being notably careless as to details. A possible difference between North Atlantic and other material, overlooked by Bouvier, may, however, be brought to contradict the indications of the above analysis, namely, that the exopod of the first pleopod is stated by Alcock and is figured by Bate as equal to not much more than the first four pleonic terga, whereas according to Smith, and in the available specimen, this appendage is as long as the first five terga. A direct comparison of Pacific and Atlantic specimens might perhaps reveal specific differences, but I should certainly not,

merely on the basis of the putative differences listed by Bouvier, follow Sund in regarding the North Atlantic material as a distinct species, or even as a variety. There is no clear evidence that Bate's South Atlantic material corresponds to the Indo-Pacific rather than the North Atlantic form, in case any real distinctions should be found between the latter two.

The present male of Plesiopenaeus coruscans agrees with Alcock's description of that species, except that the third legs do not extend beyond the third maxillipedes; and the fifth legs hardly beyond the end of the antennular peduncle, not to the end of the antennal scale. According to the figures of a female given by Wood Mason and Alcock, 1891b, and in the "Illustrations of the Zoology of the Investigator," the third leg should overtop the maxillipede by the length of the chela. In these figures, the chelae are shown as increasing in size from first to third, whereas in our specimen the reverse is conspicuously the case. Both Wood Mason's figure and the later one do not quite correspond to the present specimen in details of carapacic carinations; thus, the cervical sulcus is indicated to cross the dorsum, whereas in our specimen it fades before reaching the midline and does not indent the carina; a postcervical sulcus is indicated of which no trace is perceptible in the (somewhat battered) Atlantic specimen, and the carina which reappears "again in the interval between the gastrohepatic and cervical grooves" is in our specimen an arched, slanting ridge which originates just above the carina from the pterygostomian spine and well anterior to the level of the dorsal part of the cervical groove. This carina runs upward and backward, margining the lower end of the cervical sulcus and extending behind it on a lower level than that of the "postorbital crest [which] commences close behind the orbital margin," instead of above the level of the anterior ridge. In figures of the Indo-Pacific specimen, the line which should represent the anterior ventral portion of this ridge as found in our specimen is shown as forming the lower end of the cervical sulcus; while the posterior portion is indicated to be separate. Alcock mentions no differences in carapacic carination between P. coruscans and P. edwardsianus. According to various figures there is in the latter a posteroventrally-directed carina given off at the juncture of pterygostomian and cardiacobranchial carinae, which is indicated in P. armatus, but absent in our specimen of P. coruscans.

The postrostral carina of our specimen of *P. coruscans* is sulcate for a very short distance, behind the point where the cervical would cross if continued. There is a small dorsomedian tubercle just in front of the posterior margin of the carapace. There is a faint ridge on the posterior fifth of the third pleonic tergum, not terminating in a tooth. The teeth of the fourth and fifth terga do not surmount the apex of a cleft, but are projections of the posterior margin itself. The sixth pleonic somite is more than twice the length of the fifth, about 30 mm long by 17 mm in greatest height, as compared with a telson length of 29 mm. The telson extends to within one-fifth the length of the

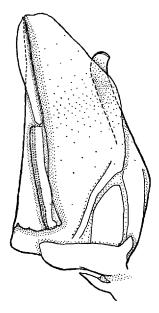
uropodal endopod from the tip of this ramus; it is armed with four pairs of minute mobile spinules of which the distalmost are 1.5 mm proximad the terminal point.

There is a high shield-shaped scute, anteriorly pointed, on the thirteenth sternite, a low elevation with a sharp slender tooth near its anterior end on the twelfth, and a low pyramidal projection on the fourteenth sternite.

The rather long ocular peduncles are flattened; the cornea is little wider than the stalk, and about one-half as long as wide; the eye reaches beyond the middle tooth of the rostrum. The antennular stylocerite reaches even beyond the tip of the tooth at the outer distal corner of the basal segment of the peduncle. The superior flagellum is given off from the middle of the upper surface of the third segment, the inferior flagellum meeting the peduncle squarely end-on. The superior flagellum is as long as the basal peduncular segment, very broad and flattened, hardly tapering; from its rounded distal margin springs a short and very slender filament.

There is hardly a trace of a tooth on the outer margin of the base of the antennal peduncle; the flagellum-bearing segment is extremely long, reaching the middle of the third segment of the antennular peduncle. The tip of the antennal scale reaches beyond the antennular peduncle by the length of the third segment of this last. The tooth of the outer margin of the scale lies beyond the tip of the antennular peduncle. There is a stout projection just anterior to the tubercle which bears the aperture of the antennal gland.

The mandibular palp is short, just reaching the opening of the excretory organ; its distal segment is two-thirds the length of the preceding one; there is an oblique suture separating a small, third, basal segment. The exopod of the second maxillipede is extremely stout, the diameter of its cylindrical proximal part being greater than the breadth of the dactyl of the endopod. The tooth at the inner distal end of the ischium of the third maxillipede is much smaller than in P. armatus. There is a mobile spine on the merus of the first legs; in P. armatus such a spine is present on both the first and the second legs. There is no fixed tooth on the basis or ischium of the chelipeds (in contrast to P. armatus, where there is a strong ischial tooth, unusual for the series, on the first legs), although the stout projection usual in males of this series and of the Solenocerinae exists on the coxa of the fifth. All the walking legs bear small but conspicuous exopods, about 1 mm in length. The legs are slenderer than the third maxillipedes, in which the ischium is extremely broad and flattened. The chelate legs are not greatly stouter than the fourth and fifth pairs. The first chela is 1 mm longer than the second, and the second the same amount longer than the third; the second leg reaches somewhat beyond the base of the dactyl of the third, and the first to one-third the palm of the third leg. The fingers of the chelae are slender, straight but meeting only at the tip, edged on the biting surface with close-set minute teeth. From protuberances on the inner and outer surfaces of the fingers spring scattered clumps of setae. The special setiferous organ of the first chelipeds is present on carpus and propodus, but very weak. The joints of the third leg, from ischium distally, measure respectively 6, 19.5, 36, 6 (palm) and 7 mm in length; the carpus is expanded at base, measuring 2 mm in diameter proximally against 1 mm distally. The joints of the fifth leg measure respectively 10, 26, 24.5, 15, and 10 mm (the styliform dactyl being not quite complete); the propodus is very conspicuously swollen at base.



Petasma, right half, anterior face (median part folded twice). 61. Plesiopenaeus coruscans Wood Mason and Alcock, North Atlantic  $\sigma$ ,  $\times$  4.4.

The exopod of the first pleopod is 60 mm long. The petasmal endopods are unjoined, but fairly well developed; they are quite similar to those of *Hemipenaeus carpenteri*, but the distoventral lobe is narrower at tip, and distally curved more strongly outward; the distolateral lobe is broader, does not reach so high above the lateral projection, and is pointed at its apex, which is in the middle. The anterior blade of the appendix masculina is subrectangular with roundedly truncate distal end, 5 mm long by 3 wide; the posterior or median blade is very minute, narrow, triangular, 1 mm long, and completely hidden behind the anterior blade.

Plesiopenaeus coruscans is described by Alcock, 1901, as throwing out luminous fluid "from, or from somewhere near, the openings of the green glands." Alcock

has observed similar behavior in a deep-sea Pandalid; and Beebe, 1934, p. 701, has described the discharge of luminous material by an Acanthephyrid observed under natural conditions at a great depth. I have seen jets of bright blue luminescence thrown out in the branchial current of an Acanthephyrid brought up alive in the trawl; the discharge did not appear to originate from the antennal gland. "Open" methods of luminescence somewhat similar to the above are found among many crustacea other than the Decapoda. On the other hand, compound photophores (which are here for the first time reported in one of the Penaeidae, *Hymenopenaeus debilis*) seem to be limited to the Eucarida; they are of very sporadic occurrence among Decapods, where they have been previously described in Sergestids, Acanthephyrids, and Pandalids (see Kemp, 1910c and 1925). It seems notable that the "open" and the "closed" systems of luminosity among Decapods are both limited, so far as is known, to the same groups, although both systems have not been observed to function together in the same species.

#### Solenocerinae Wood Mason

Solenocerina Wood Mason and Alcock, 1891b.
Solenocerinae Burkenroad, 1934a.
Parapenaeinae, part, Ortmann, 1901.
Penaeinae; part, Alcock, 1901; DeMan, 1911.
Penaeinae, series Haliporae, Bouvier, 1908; Balss, 1925.

In restoring the subfamily Solenocerinae to independent status, it was pointed out by Burkenroad, 1934a, that despite the presence of antennular and ocular scales, the group seems to be more closely allied to Aristaeinae than to Penaeinae. Although a number of characters were noted in the preceding paper as distinguishing adults of most Aristaeinae and Solenocerinae from most Penaeinae and Eusicyoninae, no completely diagnostic feature absent in all of the latter and common to all of the former were discovered. For example, the complete cervical sulcus and the epipodite of XIII do not occur in Aristaeus; a functional anterior arthrobranch is present on XIII in the penaeine Artemesia; the middle epipodites are furcated in some Solenocerinae, uncleft in the penaeine Trachypeneopsis. For this reason, the present observation that in the males of all known Aristaeinae and Solenocerinae the appendix masculina is composed of two blades, whereas it seems to be single in all Penaeinae and Eusicyoninae, is of considerable interest as establishing a diagnostic distinction between adults of the oceanic and the littoral subfamilies.

Of interest in the same connection is the fact that in *Haliporus thetis* Faxon, and, to judge from Bate's description of the nearly related genotype, in *Hali-*

<sup>1</sup> It is of course possible that the additional blade represents an appendix interna, which although perhaps taking part in the formation of the petasma, as the distomedian lobe, is otherwise absent in members of the family.

porus curvirostris, the prosartema of the inner edge of the basal segment of the antennular peduncle is no more than a rigid short projection, rather more as in Aristaeinae (or Eusicyoninae) than like the elongate flexible scale of adult Penaeinae (and other Solenocerinae). In these two species of *Haliporus* podobranchs occur on segments posterior to VIII, a characteristic otherwise limited to Aristaeinae, though not universal in that group. The telson bears several pairs of mobile lateral spines anterior to the distal fixed pair, a feature which is found in no other adult Solenocerinae; and which, although duplicated in some Penaeinae and Eusicyoninae, is here indicative of an approach to the Aristaeine type.

The Solenocerine genus Haliporus was established by Bate in 1881. The first species listed, H. curvirostris Bate, is the only one to which the generic definition elaborated by Bate in 1888 can apply. A second genus, Pleoticus, was established by Bate in 1888, the first described and typical species being P. mülleri Bate, a form congeneric with most of the species referred by Bate to Haliporus. The two genera, Haliporus and Pleoticus, have since been universally regarded as synonymous. Various forms placed in Haliporus by Bate differ from H. curvirostris (which may be regarded as the genotype) and resemble Pleoticus mülleri in their lack of podobranchs posterior to VIII, and of mobile lateral telson spines anterior to the fixed pair. Therefore Bate's separation into two genera of the forms included in *Haliporus* by recent authors is essentially correct, although his allocation of the species is inaccurate. S. I. Smith, in 1882, established the genus Hymenopenaeus for a species, H. debilis, congeneric with Bate's Pleoticus mülleri and P. lucasii. Therefore, Hymenopenaeus Smith takes precedence over *Pleoticus* Bate as a name for the score of species generically distinct from Haliporus curvirostris Bate.

The examination of *Haliporus thetis* Faxon has been made possible by the very great kindness of Dr. H. L. Clark and Mr. F. A. Chace, Jr. This species, because of its short posterior legs, is placed by Bouvier, 1906b and 1908, in Group III of his rather artificial subdivision of "Haliporus." Comparing H. thetis with the description of Bate's genotype, Haliporus curvirostris (a species placed by Bouvier in his Group I), it is found that the two resemble one another [in addition to those features mentioned above, the short prosartema; podobranchs behind VIII (VIII-XII in H. thetis, VIII-X in H. curvirostris); and several pairs of lateral spines on the telson in the possession (as in all Aristaeinae) of a pterygostomian but no branchiostegal spine; in the small size of the exopodite of the third maxillipedes; and in the posterior division of the cardiaco-branchial carina into two branches. The two species differ in podobranchial formula and proportions of posterior legs, and in rostral and postrostral armature, as well as in numerous other details. In spite of these differences, H. curvirostris and H. thetis bear a much stronger resemblance to each other than to any other Solenocerinae, and may therefore, in my opinion, be regarded as congeneric.

name Haliporus may be restricted to them; and the other species which have been included under the name, to the number of twenty or more, may be transferred to Hymenopenaeus Smith. It may be observed that a spine is present on the median margin of the basal segment of the antennular peduncle of H. thetis, near its distal end, which appears to be a persistent parapeneous spine such as is found in all larval Penaeidae. This spine has heretofore been known in adult stages only among the species of Parapeneae (Burkenroad, 1934a and b); and, as noted in a preceding paragraph, in Benthesicymus crenatus Bate.

The third genus of the subfamily, Solenocera Lucas, is closely related to Hymenopenaeus, and aside from the diagnostic character, expanded and canaliculate antennular flagella, is differentiable from it only by a few minor features to be discussed in a further paragraph. Bate, 1881 and 1888, confuses Solenocera with Hymenopenaeus (under the name Pleoticus), although he did not synonymize the two.

The three genera of Solenocerinae form a series ranging from species closely approaching the Aristaeinae to those somewhat resembling Penaeinae. In all, the scale at the external angle of the ocular somite otherwise found well developed only in Penaeinae, is present. In all except the uncertainly known Solenocera maldivensis Borradaile (for which the subgenus Transolenocera has been proposed by Burkenroad, 1934a) a postorbital spine, not represented in other Penaeidae (except in the Jurassic Aeger, which is quite possibly to be regarded as Solenocerine) is present.

It seems a matter of interest that the genotype of *Hymenopenaeus*, *H. debilis*, is provided with well-developed compound photophores, organs never before reported among Penaeidae, although known in *Sergestes*. The photophores of *H. debilis* differ in structure from all which have been previously described in *Eucarida*.<sup>1</sup>

### **HYMENOPENAEUS** Smith

Hymenopenaeus, Smith, 1882, 1884, 1886, 1887; Wood Mason and Alcock, 1891 a and b.

Pleoticus, Bate, 1888, part.

Philonicus, Bate, 1888, part.

Haliporus, Bate, 1881, part; Wood Mason and Alcock, 1891b; Alcock, 1901; Faxon, 1895, part; Rathbun, 1906; Bouvier, 1906b and 1908, part; Milne Edwards and Bouvier, 1909; DeMan, 1911, part.

Penaeopsis, Faxon, 1895.

Faxonia, Bouvier, 1905b.

Parartemesia, Bouvier, 1905b.

Haliporoides, Stebbing, 1915b.

<sup>1</sup> The detailed morphology of the luminescent organs of *H. debilis* is to be described in a forthcoming paper by Mr. M. Ramadan of the University of Cambridge.

Genotype, Hymenopenaeus debilis Smith. Solenocerinae without podobranchs behind VIII; with well-developed prosartema and only a single pair of lateral telson spines in adult stages, and with cylindrical filiform antennular flagella.

The branchial formula given by Bouvier, 1906b and 1908, is incorrect in that the seventh somite, as in *Haliporus*, bears a gill. This gill, as in Aristaeinae, has the compound form of those on succeeding somites; and although it may be relatively somewhat reduced in size, has little similarity to the lamella, generally fringed with simple filaments, occupying a similar position in Penaeinae.

The species of Hymenopenaeus are, although of rather uniform habit of life, quite diversified in structure. The genus has been subdivided by Bouvier. 1906b and 1908, chiefly after Alcock, 1901, on the basis of relative length of posterior legs. Aside from the fact that the groups thus constructed are not sharply distinguished from one another, and that the associated character used by Bouvier, relative diameter of the proximal portion of the carpus of the second and third legs, fails to be constantly correlative with a given length of posterior legs, these groups are not composed of forms more nearly related to one another than to members of other groups. The division established by Bouvier may therefore be termed artificial. Of secondary key characters employed by Bouvier, the relative dilation of the eyes is particularly misleading as used, since species otherwise barely differentiable may according to this feature be placed in separate categories, together with forms much more remotely related. It is noteworthy for the clarification of terminology that in his "Group III" Bouvier has lumped species with pterygostomian spine with forms having a branchiostegal spine, under the latter term.

A comparison of the nine species available to me with the literature indicates that *Hymenopenaeus* may be divided into four or more fairly well-defined superspecies, according to the presence or absence of branchiostegal or pterygostomian spines, and to the nature of the postrostral armature. The homogeneity of certain of these groups is doubtful, and their exact limits may therefore be regarded as only provisionally indicated; but it seems probable that the present arrangement is less artificial as well as more convenient than the previous system based on the relative length of the posterior legs.

## Synopsis of the Superspecies of Hymenopenaeus Smith

GROUP I. (Including the genotype of *Pleoticus* Bate).

Neither branchiostegal nor pterygostomian spine. Postrostral teeth not separated from the rostral series. *H. mülleri* (Bate), tropicalis (Bouvier), steindachneri (Balss).

Group II. [Including the genotype of Faxonia Bouvier (preocc. Faxonius Ortmann)]. Branchiostegal but no pterygostomian spine. Postrostral teeth not separated from the rostral series.

Section 1. Orbital angle dentiform. H. robustus Smith.

Section 2. Orbital angle not dentiform. H. lucasii Bate, [malhaensis Borradaile)], modestus Smith, [affinis (Bouvier)].

Group III. (Including the genotype of *Haliporoides* Stebbing). Pterygostomian but no branchiostegal spine. One postrostral tooth separated from the rostral series. *H. diomedeae* (Faxon), sibogae (DeMan), triarthrus (Stebbing). Group IV. Branchiostegal spine present, pterygostomian present or absent.

Two postrostral teeth separated from the rostral series.

Section 1. Pterygostomian present. H. laevis (Bate), doris (Faxon), nereus (Faxon).

Section 2. Pterygostomian absent. H. aequalis (Bate), obliquirostris (Bate), neptunus (Bate), propinquus (DeMan), debilis Smith, aphoticus n. sp. 4

Two further species of Hymenopenaeus, H. villosus (Alcock and Anderson) and H. taprobanensis (Alcock and Anderson), are difficult to relate to the above subdivisions by means of the information at hand. The former, which seems to be described as bearing both branchiostegal and pterygostomian spines, and in which no postrostral teeth are separated from the rostral series, perhaps merits an independent position. The latter, in which a pterygostomian but no branchiostegal spine is figured, seems by virtue of its well-developed cardiacobranchial sulcus, the armed posterodorsal median margin of its fourth and fifth pleonic somites, its undentiform orbital angle, and the lateral position of the externodistal tooth of the uropodal exopods, to approach Group III. From this compact superspecies, it seems to differ, however, by the lack of a postrostral tooth separated from the rostral series; the lack of a denticle at the cervical notch dorsad the hepatic spine; and the much longer exopod of the second maxillipedes.

As to the homogeneity of the defined groups, information of many species is insufficiently detailed for positive determination of affinity. Group IV is certainly homogeneous, and is quite distinct from any of the other series. Among other characteristic features, the distolateral lobe of its petasma is generally more or less deeply cleft, in addition to often bearing a lobule which springs from its proximolateral margin. The three species listed as Group III are very closely related, and the group is likewise clearly distinct from other series, especially from Group II. The statement by Bouvier, 1908, that H. robustus "présente des affinités particulièrement étroites avec" H. diomedeae is not correct. H. robustus differs from H. diomedeae in all the features mentioned in the preceding paragraph (with reference to H. taprobanensis) as characteristic of Group III. The petasma of H. diomedeae differs considerably from that of H. robustus in that its distoventral lobe does not bear a free distoventral projection; and that the median cincinnulated margin, terminating in the distomedian lobe, does not extend nearly to the distal margin of the distolateral lobe. In petasmal structure, Groups III and IV display some resemblance, as also in the occurrence of postrostral teeth separated from the rostral series; of

a well-developed cardiacobranchial carina; and of an unarmed orbital angle. It is of interest that the suprahepatic denticle of Group III reappears in Solenocera hextii Wood Mason and Alcock.

Whether Group II as here defined is homogeneous, is uncertain. It is probable that *H. modestus* and *H. lucasii* are nearly related. Both seem to resemble *H. robustus* in several details in addition to the characters utilized as diagnostic, but they differ from the type of the subgenus in their lack of a well-defined orbital angle.

Finally, Group I seems rather well distinguished from other series; but whether the obvious resemblances between H. mülleri and H. steindachneri are actually evidence of the homogeneity of the group is not known. In all three of the species here placed together, the orbital angle is dentiform; and, as in H. robustus, the cardiacobranchial carina is obsolescent, the tooth of the uropodal exopod is terminal rather than lateral, and there is a posterodorsal median tooth on the sixth pleonic somite only. In Balss' figure of H. steindachneri is indicated a peculiar longitudinal sulcus ventral to the remnants of the cardiacobranchial, such as occurs in P. mülleri. The sharp tooth in the dorsal midline behind the cervical sulcus indicated in the figure of H, steindachneri may be no more than an exaggeration of the projection present near the posterior border of the carapace in all Solenocerinae. The petasma of H. steindachneri seems to lack a free distoventral projection, but as in H. robustus, the cincinnulated margin rises as high as the distolateral lobe. Bate's figure of the petasma of H. mülleri is difficult of interpretation, but the organ appears to be very different from that of H. steindachneri. The merus of the first cheliped of H. mülleri, like that of Hymenopenaeus laevis and H. doris, lacks the peculiar immobile tooth which is present in H. robustus, in H. lucasii according to DeMan, in H. diomedeae, H. debilis and H. aphoticus, and in Haliporus thetis, and which so strongly recalls the meral armature observed by Balss, 1923, on all the walking legs of the Jurassic Aeger tipularius.

The published notices of capture of Solenocerinae establish with fair certainty their benthonic habit. The only previous record known to me of a member of the genus taken pelagically is provided by Balss, 1925, who notes a single specimen of Hymenopenaeus aequalis in a vertical tow supposed to have cleared the bottom by sixty fathoms. It is therefore surprising that in the horizontal bathypelagic hauls made during the third oceanographic expedition of the "Pawnee" at Stations 11, 52, 56, 58, and 59, a number of specimens of Hymenopenaeus laevis (Bate) and of H. aphoticus, n. sp. were taken. Other specimens were taken at station 54, for which clear evidence of bottom contact is given by the catch itself, Aristaeinae other than Gennadas and Bentheogennema being present in this haul alone. Only two specimens of Hymenopenaeus were taken at Station 54, fewer than were obtained in the other tows for which no trace of bottom contamination is at present discernible. According to Professor A. E. Parr,

the tow at Station 54 made bottom at 900 to 945 fathoms, while the other hauls in question were at no time on, though in general close to, bottom.

In an effort to ascertain precisely the habit of the above apparently nektonic specimens of Hymenopenaeus, the statocyst and hind gut contents were examined. In all specimens except one, the statolith consisted of a cemented mass of foraminifera and unrecognizable calcareous granules. In one specimen of P. aphoticus, from station 11, the statocyst contained only a small flat plate of cuticular material in which setae were embedded. The gut of all specimens save a juvenile female of H. aphoticus from Station 54 and a juvenile male of H. laevis from Station 58 was empty. In these two specimens the contained material included very rare sponge spicules, many shell fragments, and some rather heavy gastropod opercula, as well as some gastropod veligers; crustacean remains; foraminifera; minute, slender, siliceous spicules, possibly of Radiolaria; fragments of what appear to be hydroid perisarc; an algal stem, and peridinian tests, Two foraminiferan tests, one from the gut of the young H. laevis, the other from the young H. aphoticus, have been determined by Dr. Joseph A. Cushman, to whom I am very deeply indebted for this information, and from whose letter I quote: "These seem to be young stages of Cibicides pseudoungerianus (Cushman), a bottom-living species which occurs along the general Atlantic coast. The deepest records for this are around 2000 fathoms, but it comes up along the continental shelf into fairly shallow water." The feeding habits of these two specimens of Hymenopenaeus therefore seem definitely to have been those of bottom foragers. Although portions of the gut contents might within possibility have been derived by a pelagic animal from sinking objects, it is inconceivable that so many objects of a type to be found concentrated on the substratum should have been gathered together by this method. It seems very probably that the statoliths of other specimens than the H. aphoticus from Station 11, which are composed of calcareous fragments and foraminifera, had been collected from the bottom.

It being clear that the specimens of *Hymenopenaeus* in question have resorted to the bottom, it is possible that they had been entirely benthonic in habit, and that the nets at all the stations involved made inadvertent contact with the substrate; but another possibility remains: that certain species of *Hymenopenaeus* may swim up from the bottom at intervals, and may therefore be taken in pelagic hauls.

## GROUP IV

### Section 1

## Hymenopenaeus laevis (Bate)

Haliporus laevis, Bate, 1881 and 1888.

Hymenopenaeus microps, Smith, 1884 and 1887; Wood Mason and Alcock, 1891 a and b.

Haliporus microps, Alcock, 1901. Haliporus androgynus, Bouvier, 1906 b and c, 1908. ? Haliporus sp., Lenz and Strunck, 1914.

1 male, adult; carapace 15, rostrum 4, total length about 57 mm. B.O.C. 133. Pawnee station 56; N. 21/20/15; W. 71/13/20; April 13, 1927. 6500 feet wire.

2 females; adult, carapace 17 mm; juvenile, carapace 8 mm. 1 male, juvenile, carapace 12.5 mm. B.O.C. 134. Pawnee Station 52; N. 21/30; W. 71/11/04; April 11, 1927. Wire 8000 feet.

1 male, juvenile, carapace 8, total about 28 mm. *B.O.C.* 135. Pawnee Station 58; N. 32/24/15; W. 64/29; April 20, 1927. Wire 10,000 feet.

1 female, juvenile, carapace 13 mm. *B.O.C.* 136. Pawnee Station 59; N. 32/19/18; W. 64/32/30; April 21, 1927. Wire 8000 feet.

In addition to the above there has been available a very large female, carapace 23 mm, rostrum 6 mm, total length about 65 mm, from the collection of the Department of Zoology of the Peabody Museum, which was taken off the Middle Atlantic Coast of the United States, at Albatross Station 2566, on bottom, at 2620 fathoms, in 1885. Also, with the very kind permission of Dr. Calman and Dr. Gordon, I have examined the eastern North Atlantic females, types of H. laevis Bate, 1881; and the female from the Philippines later referred to the same name by Bate, 1888. The present records of H. laevis from the southeastern Bahamas and from southwest of Bermuda at depths of from 600 to 950 fathoms or less, extend the known western North Atlantic range somewhat to southward.

There appear to be nine valid species attributable to the Group IV of Hymenopenaeus. In all of these the fourth and fifth legs are long and slender, the body is more or less attenuated, and a branchiostegal spine is present. In some of the species a pterygostomian spine is present; in some absent, but a lamentable confusion, which cannot altogether be clarified, has surrounded this point. In H. debilis Smith, H. aphoticus n. sp., H. obliquirostris (Bate), and H. propinquus (DeMan), the pterygostomian is certainly absent. H. equalis (Bate) and H. neptunus (Bate) are described and figured by their author as lacking pterygostomian, and DeMan, 1911, concurs for H. aequalis; but Wood Mason and Alcock, 1891b, mention the presence of pterygostomian in H. neptunus, while Alcock, 1901, reports that H. equalis and H. neptunus are identical with H. microps Smith (= H. laevis Bate, in which a pterygostomian is present) save in a few characters among which are not included differences in occurrence of pterygostomian. DeMan, Alcock and Bate all seem to have dealt with the same species under the name H. aequalis, the first and last named being agreed that the pterygostomian is absent. H. neptunus is not noted by DeMan to differ from H. aequalis by possession of a pterygostomian. It will therefore be here assumed that these two species lack the spine; and with the four others mentioned above as of similar character, they will be discussed in greater detail in comparison with H. aphoticus.

Species in which a pterygostomian is present may now be considered. *H. nereus* (Faxon) and *H. doris* (Faxon) are figured as with the spine; and this is confirmed by examination of specimens in the collections of the Museum of Comparative Zoology and of the New York Zoological Society. Bouvier, 1908, and Milne Edwards and Bouvier, 1909, are therefore in error when they compare *H. doris* with *H. debilis* Smith. *H. laevis* is described by Bate as with pterygostomian spine, and an examination of the types shows this to be correct. The armature of the carapace of *H. microps* is not described by Smith; and the figure (1884) is obscure, although a pterygostomian seems to be indicated. The examination of a specimen identified by Smith makes it certain, however, that the spine is present. Bouvier is therefore incorrect in supposing that his *H. androgynus*, in which a pterygostomian occurs, is distinct in this feature from *H. microps*. Finally, the spine is described as present in *H.* species of Lenz and Strunck. As will be demonstrated below, the last four forms mentioned seem to be specifically identical.

No clear reasons have been given for the separation of H. species of Lenz and Strunck from H. laevis (with the fairly accurate descriptions of which under the names H. microps and H. androgynus, the authors fail to compare it); although there are some differences, according to the figure, in the proportions of the leg joints. In the Bingham material of H. laevis, in both an adult male of carapace 15 and a juvenile of carapace length 8 mm, the merus and carpus of the fourth legs are approximately equally long, the propodus being in the adult about one-fourth the carpus, in the juvenile about one-third of it. In the figure of Hymenopenaeus species given by Lenz and Strunck, the merus is much longer than the carpus, and the propodus slightly longer. It seems possible that Lenz and Strunck have misplaced the carpalpropodal joint, perhaps mistaking for it a break in the limb.

As to *H. androgynus* Bouvier, the deletion of the supposed difference in occurrence of pterygostomian spine leaves few distinctions from *H. microps* which seem of any importance. The material available to me agrees with Bouvier's description in thelycum; with Smith's somewhat imperfect figure (1887) in petasma. The very large petasmiform endopod of the first pleopoda, and appendix masculina of the second, which Bouvier reports in his females, probably represent an abnormality rather than a specific distinction. In the matter of exopod of the fifth leg, Smith's account is evidently erroneous, since in all available specimens including that determined by himself, this ramus is present. Also, in available material the terminal article of the endopod of the first maxillipede is considerably shorter than the preceding segment instead of "approximately equal" to it; the length of the telson relative to the uropods varies from a condition in which telson does not attain the tip of uropodal

endoped, to one in which the telson projects beyond by one-sixteenth or more of its length; the relative length of the leg-segments is rather variable; and the antennal scale extends slightly beyond the antennular peduncle. Finally, the posterodorsal pleonic armature, believed to distinguish H. and rogynus from H. microps, but which Bouvier notes to be somewhat variable in his material, seems not to be a feature upon which specific distinctions may be based. In available material, there is a tooth at the posterodorsal margin of the sixth pleonic somite only, in the large Peabody Museum female and in Bate's Pacific specimen; minute additional teeth on the fourth and fifth somites in the largest male of the Bingham Collection and in Bate's Eastern Atlantic females; and a strong tooth on all three posterior segments in the largest female of the Bingham Collection. Although it is true that Bate's Eastern Atlantic specimens, taken near the type locality of H. androgynus, agree with the latter in pleonic armature, the fact that some of the Western Atlantic specimens also agree with Bate's in this feature; and that no correlated character can be found in which specimens with strong teeth on the eighteenth and nineteenth somites are constantly different from those with a weaker armature or those without, seems to dispose of reasons for believing that "H. androgynus" may represent a species distinct from "H. microps."

The figure of H. laevis by Bate bears little resemblance to the specimen from which it was made, and it is therefore not surprising that the name has not attained currency. The two Atlantic females taken by the "Challenger" have a carapace length of about 18 mm, the Philippine one of 17.5 mm. The latter is the specimen treated as type, and figured, in 1888; but as it is not mentioned in 1881, the Atlantic females are necessarily the types of the species. The Pacific specimen differs from the two Atlantic ones in lacking pleonic dorsal armature in advance of the sixth segment, but in this agrees with certain other Atlantic specimens. It differs from Bate's two Atlantic specimens, but agrees with the four other Atlantic females available, in bearing a small tooth on the anterior margin of the coxal projection of the fifth legs. This tooth seems to be variable with age in certain other Solenocerinae in which it occurs. Finally, the Pacific specimen differs somewhat in thelycum from all Atlantic specimens including the types. The horizontal projections from the posterior margin of the twelfth sternite are shorter; and the pyramidal elevation of the fourteenth lower (falling far short of the tip of the projection of XIII) than has been observed to be the case in other females; but these proportions are not invariable in the Atlantic specimens. The "narrow, straight-sided, vertical projection" (to use Bate's words) which is erected from the posterior part of the thirteenth sternite is "broken at the apex," one prong of the fork in which it ends being lost; the remaining prong bears a small denticle on its median margin, which I have not observed in any Atlantic specimens. However, unless this denticle is shown to be of constant occurrence in Pacific females, I am inclined to agree

with Bate's and with Alcock's identification of the Pacific and the Atlantic stocks.

Between the descriptions and figures of *H.* "microps" by Smith, 1884 and 1887, and of *H.* "androgynus" by Bouvier, 1906c, considerable information of *H. laevis* is obtainable. A few additional points may here be mentioned, as follows:

The sculpture of the carapace consists in a carina and accompanying sulcus which run posteriorly from the branchiostegal tooth beneath the hepatic spine. dividing near the middle of the carapace into two branches, the upper of which forms the cardiacobranchial carina; while the lower slopes backward and downward to join the branchiostegal carina. A broad ridge dorsally bordered by a deep sulcus extends between the hepatic and the postorbital spine. carina runs from the branchiostegal to the pterygostomian spine. The cardiacobranchial carina gives off a faint dorso-posteriorly directed ridge at the top of its upward curve, which is probably homologous with the more vigorous tributary found in Haliporus. The cervical suture of Hymenopenaeus laevis is notched at a point somewhat dorsad the hepatic spine. From this notch a ridge runs downward and backward to near the point where the cardiaco-branchialis arises. This notch seems to become dentiform in the species of the Faxonia group, as well as in one species of Solenocera (S. hextii Wood Mason). The anterior of the two separated postrostral teeth is larger than the posterior, as in other species of Group IV, and behind the latter is a minute denticle of variable size, probably the remains of the larval anterior dorsal organ. The dorsal surface of the carapace is depressed at the level of the cervical sulcus. At the posterior end of the postrostral carina is a distinct obtuse tooth, evidently a vestige of the larval posterior dorsal organ. This tooth is perhaps homologous with one of those occurring in a similar position in Holiporus curvirostris. It is possible that the posteriormost dorsal carapacic tooth of the Eusicyoninae, the only other peneid group in which postrostral armature behind the level of the cervical sulcus occurs, may also be a derivative of the posterior dorsal organ, rather than a posteriorly shifted true rostral tooth. The sculpture of the carapace of H. laevis is reminiscent of that of such Aristaeinae as Benthesicymus. and of the Penaeine Funchalia as well.

All the epipods are unfurcated. The exopodites of the legs of IX through XIV are small, reaching little beyond the basis; that of VIII extends to the distal third of the merus. The carpus of the second and third legs is not expanded proximally.

The more lateral lobule of the distolateral lobe of the petasma bears a few very minute spinules on its median margin. On the more median lobule of one endopod only of an immature male, a very small third point is visible, mediad the pair of larger ones. Of this latter pair of spines the median is much larger than the lateral. The juvenile petasma is very much like that of the adult,

save that the protuberance and notch of the lateral margin, representing the distoventral projection, are much less marked. As in related species, the median margin is cincinnulate only to about halfway up the median edge of the endopod. The median of the two blades of the appendix masculina of the second pleopods of the juvenile male is proximally much less expanded than in the adult. In a still younger male of carapace length 8 mm, only the lateral blade, homologous to the single one of other peneids, is well developed, the median blade and the posterior spur being no more than short projections.

In a very young female of carapace 8 mm, the vertical lamella of sternite XIII is distally truncated, the V-shaped emargination having disappeared; and it is directed anteriorly instead of posteriorly, thus somewhat resembling the same structure in *H. nereus* (Faxon).

H. nereus and H. doris (Faxon) are closely related to H. laevis, from which, as well as from one another the Pacific American species are distinguished by details of the structure of the thelycum. The petasma of H. doris is unknown; that of H. nereus is somewhat similar to that of H. microps in shape and especially in that the median lobule of its bifurcate distolateral lobe bears a series of five strong teeth (only three of which are indicated in Faxon's figure). The Atlantic species carries only two teeth in this position. An apparent distinction from the other two forms indicated in the figure of H. doris, that a tooth is shown as occurring on the postrostral carina just behind the cervical suture, has no existence in fact.

## Section 2

## Hymenopenaeus debilis Smith

Figures 63, p. 113; 64, p. 114

Hymenopenaeus debilis, Smith, 1882 and 1887.

Haliporus debilis, Faxon, 1896; Bouvier, 1908; Milne Edwards and Bouvier, 1909; Boone, 1927.

Haliporus debilis var. africanus, Bouvier (teste Bouvier, 1908).

2 males, 4 females, juvenile to adult. B.O.C. 139. North of Glover Reef, Caribbean; April 20, 1925. Trawl, 484 fathoms.

31 males, 122 females, subadult to adult; 110 juveniles. B.O.C. 224. Atlantis St. 2381; N. 28/35, W. 89/46; March 26, 1935. 1-foot stramen ring-net on headrope of otter trawl; 165 fathoms.

B.O.C. 139, adult male, carapace length 9.7, total 43 mm; juvenile male, carapace 7 mm; females, carapace 7.1 to 9.7 mm. B.O.C. 224, largest male, carapace length 8.6 mm, total about 35 mm; largest female, carapace 11.4 mm, total about 46 mm.

In addition to the above, an adult female of carapace 13 mm (reported by Milne Edwards and Bouvier, 1909) from the collection of the Museum of Comparative Zoology, has been examined.

It is a most remarkable fact that in a single haul of half an hour with a net of one-foot aperture, more than twice as many specimens of H. debilis were taken as the total number which have been previously recorded, and for which more than twenty-five fruitful hauls, with much larger nets, were required. The Delta region, according to this catch, seems extremely rich. The species has been recorded from off the Middle Atlantic coast of the United States by Smith; the Eastern Atlantic as far north as N. 39/49 by Bouvier; the Gulf of Mexico (off the Tortugas and the Mississippi Delta) by Faxon and by Milne Edwards and Bouvier; and from the Caribbean by Boone (B.O.C. 139 above). The least depth previously reported, 100 meters, by Milne Edwards and Bouvier, 1909, is perhaps a misprint for 500 meters, given by Bouvier, 1908 (in which paper, however, Bouvier gives a specific reference to a catch at 454 m, at St. 234).

Both sexes of *H. debilis*, in all postlarval stages, bear six large photophores, arranged as follows: a pair in the elevated posterior margin of sternite XIII, just mediad the coxae of the fourth legs; a pair between the second pleopods, and two unpaired organs respectively placed between the bases of the fourth and of the fifth pleopods. The cellular portions of the photophores are conical in shape, their posteriorly directed basal surfaces abutting against a cuticular lens readily detectable even in long-preserved material. In the largest female, the photophores, including the lens, measure about .35 mm in length, .3 mm in greatest diameter.

Bouvier describes the color of *H. debilis*, from a sketch made at the moment of capture, as "d'un rouge-orange presque uniforme." The fresh material observed by me in the Gulf of Mexico was transparent, speckled with minute scarlet chromatophores which were concentrated at the bases of the pleopods and uropods and at the tip of the telson. The ocular peduncle at the base of the cornea, the mouthparts, and the tip of the second maxillipede were scarlet. The stomach was red, the pleonic gut and nerve-cord orange; the gastric gland brownish, the ovary creamy (as seen through the overlying tissues). The eyes were reddish brown. Finally, the six photophores, brilliant scarlet cones with glistening white basal surface applied to the faintly yellowish transparent cuticular lens, were a striking feature of the sternum. These organs are not very conspicuous in material bleached by alcohol, which probably accounts for the failure of those who have previously examined *H. debilis* to discover them.

## Hymenopenaeus aphoticus, new species

Figures 62, p. 113; 65, p. 114; 66 and 67, p. 115

1 male, adult, holotype; 1 female, juvenile. B.O.C. 137. Pawnee Station 54; N. 21° 15′ 40″; W. 71° 17′ 06″. March 12, 1927. 900–945 fathoms, bottom. 1 male, adult. Paratype. B.O.C. 138. Pawnee Station 11; N. 23° 57′ 45″; W. 77° 26′ 25″; March 2, 1927. Wire 7000 feet.

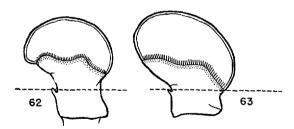
Type, carapace 18 mm, total length about 60 mm. Paratype, carapace 15

mm, total length about 55 mm. Juvenile female, carapace 10.2 mm, total length about 35 mm.

Hymenopenaeus aphoticus is very closely related to H. debilis Smith, from which it is distinguishable by its larger size; by its relatively longer and slenderer cephalothorax; by its much smaller eyes, of quite different shape; by its somewhat different petasma and appendix masculina; and by the fact that it completely lacks photophores.

The sculpture of the carapace of H. aphoticus is similar to that of H. debilis, except that the rostral and postrostral teeth are somewhat smaller. The rostrum is complete only in the juvenile female of the new species, in which it bears only seven dorsal teeth and does not display a ventral armature. In H. debilis the rostral armature is variable. Up to three ventral teeth may be present. Contrary to Bouvier's observations, I have not seen any specimens with fewer than nine dorsal teeth.

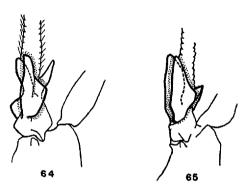
The depth of the carapace of the three specimens of H. aphoticus, measured with ocular micrometer vertically from the dorsal crossing of the cervical groove to the branchiostegal carina, varies with reference to carapace length (rostrum excluded) from 42 to 48.5%, average, 46%. In the six specimens of H. debilis from off Honduras the same proportion varies from 46.1 to 63%, average 52.1%. A clearer distinction is provided by the relation of distance between cervical crossing and posterior dorsal margin of carapace to total length of carapace (excluding rostrum). In H. aphoticus this distance varies between 46.5 and 49.5%, average 47.3%; in H. debilis between 42 and 45.5%, average 43.4%.



Right eye, dorsolateral view (showing differences in relative size of eye, shape of cornea and position of tubercle). 62. H. aphoticus, n. sp. paratype  $\sigma$  of carapace length 16 mm,  $\times$  12. 63. Hymenopenaeus debilis Smith, Honduran  $\circ$  of carapace length 9.8 mm,  $\times$  12.

The proportion of the greatest diameter of the eye of H. aphoticus to the carapace length is between 10.7 and 12.5%, average 11.7%. The same proportion in H. debilis (in the six Honduran specimens) varies between 19.3 and 26.9%, average 22.3%. The cornea in H. debilis is subreniform, while in H. aphoticus it is hemispherical, as in H. laevis. The difference in size, as well as

in shape of eye is so marked as to be perceptible at a casual glance. Correlated with the difference in corneal shape, and removing any doubt as to its actuality (since the chitinous peduncle is little subject to distortion) is a striking difference in the shape of the cornea-bearing segment of the ocular peduncle. In *H. debilis*, the dorsal margin between peduncle and cornea slants diagonally in a posterior direction from its median to its lateral edges; and a line from the tubercle on the median margin of the peduncle, parallel to the proximal margin of the segment, crosses the outer posterior corner of the cornea. In *H. aphoticus*, on the contrary, the sinuous dorsal margin between cornea and peduncle runs transverse to the long axis of the peduncle, and a line from the tubercle parallel to the base of the segment cuts the outer margin of the peduncle at a point two-fifths the length of the segment from the outer posterior corner of the cornea.



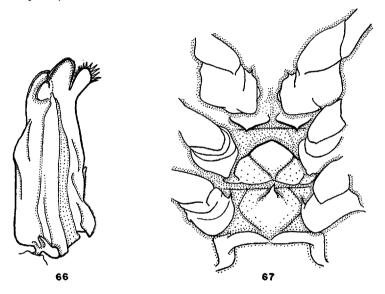
Appendix masculina of right pleopod, anterolateral view. **64.** Hymenopenaeus debili<sup>3</sup> Smith, Honduran  $\sigma$ ,  $\times$  17. **65.** H. aphoticus, n. sp., type,  $\times$  17.

The appendix masculina of the two species differs as follows: in *H. aphoticus* the posterior spur of the appendix is considerably less than half as long as the anterior blades; while in *H. debilis* it is nearly three-quarters as long as the longest of the anterior blades (the lateral one). In *H. aphoticus* the median blade is broadly lanceolate; in *H. debilis* the median blade has a much expanded proximal part distal to which it narrows suddenly, the median margin of the blade thus being deeply concave.

The petasma of the two species differs as follows: The lateral part of the divided distolateral lobe of the petasma of H. aphoticus is shorter and fleshier than that of H. debilis and bears at the base of its ventrolateral edge a large free lobule, fringed with spinules, which is represented in H. debilis only by a very small and inconspicuous naked projection.

The thelycum of the juvenile female of H. aphoticus bears the rudiments of

structures characterizing H. debilis, and does not differ conspicuously from that of juvenile females of the latter species, save that the anterior face of the median elevation of XIII is nearly vertical, instead of sloping anteriorly at a gentle angle as in H. debilis; and its posterior face is longer than in the genotype. The structures of XIII in H. debilis are poorly represented by Bouvier's figure. It seems significant that females of H. debilis of length considerably less than that of the available juvenile of H. aphoticus have a fully-developed thelycum which is of adult form. It is probable that the adult thelycum of H. aphoticus, like its petasma, will display more resemblance to that of H. debilis than to other known species, but will differ in detail.



Petasma, left half, anterior face. 66. Hymenopenaeus aphoticus, n. sp., type, × 17. Thelycum. 67. H. aphoticus, n. sp., cotype, × 17.

In both H. debilis and H. aphoticus the first legs bear a long and slender ischial spine in addition to the basisal present on both first and second legs. In the juvenile females of both species there is a sharp tooth at the anterointernal corner of the coxa of the fifth legs, and a small tooth in a similar position on the third; the former of these persists in adults, while the latter becomes inconspicuous, or disappears, in adults of H. debilis. There is no trace of a similar armature on the coxae of the fourth legs, such as DeMan describes for H. obliquirostris.

No significant differences in the mouth parts are ascertainable. In both species there is a faint trace of the postrostral carina posterior to the cervical

sulcus; and the pleon is carinate on the fourth, fifth and sixth somites, faintly compressed on the third; a posterodorsal spine being present only on the sixth somite. In both species, as in *H. laevis*, there is a very small spine on the ventral margin of the sixth pleonic somite just anterior to the rounded posteroventral corner.

It is possible that some of the extensive material which has been attributed to H. debilis by Bouvier may be of the present species, in which case the name " $[Haliporus\ debilis]$  var. africanus, E. L. Bouvier (1906), Visite de sa Majeste Carlos I<sup>er</sup>, roi de Portugal . . . au Museum, p. 41," listed by Bouvier, 1908, may conceivably have been applied to material including H. aphoticus. I am unable to locate the paper referred to, and it is evidently not a scientific publication. The name H. d. africanus Bouvier seems in any case to be a nomen nudum. Therefore, even should it be shown to have been applied to material including H. aphoticus, I do not believe that there would be any justification for applying Bouvier's name (which was, as in a number of similar cases, later retracted by its author) to the present species.

H. aphoticus and H. debilis are distinguished from the four related Indo-Pacific species in which a pterygostomian spine may with more or less certainty be stated to be absent, as follows:

The six species of the group appear to be very similar in sculpture of carapace and pleon. Some variation in strength of postrostral carina occurs, according to descriptions by Alcock, 1901, and DeMan, 1911. In *H. neptunus* (Bate) this ridge is rather strong, in *H. aequalis* (Bate) it is weak, posterior to the cervical sulcus; while the other species range between these two. *H. propinquus* (DeMan) seems to differ from all the others by the carination of the third, and even the first and second, somites of its pleon. According to Wood-Mason and Alcock, 1891, there is a posteromedian dorsal tooth on the fourth and fifth as well as the sixth pleonic somites of *H. neptunus*, but it is possible that this armature may be inconstant, as in *H. laevis*.

Differences in the relative size (and probably also differences in the shape) of the eye occur, the organ being rather large in H. propinquus, H. aequalis, H. obliquirostris and H. debilis, small in H. neptunus and H. aphoticus. There are some differences in the armature of the leg-bases; in H. aequalis (after the figure by Balss, 1925) and in H. propinquus the basis of the first legs is unarmed, although the ischium bears a spine; in H. obliquirostris and H. aphoticus both joints are armed; in H. debilis the ischium is sometimes unarmed. There are indications in the literature of individual variation in leg-base armature of other species besides H. debilis; thus according to Bate the "basis and merus" are in H. obliquirostris unarmed.

<sup>&</sup>lt;sup>1</sup> As an addition to previous synonymic lists for this species, it may be observed that the "Challenger" specimen referred by Bate, 1881, to *Solenocera crassicornis* H. Milne Edwards is evidently the type of *H. aequalis* Bate, 1888.

# U.S. DEPARTMENT OF COMMERCE National Oceanic and Atmospheric Administration

To: 1 m/ miles / miles / miles

From:



The sharpest distinctions between the six species seem to be supplied by differences in petasma and thelycum. In *H. aequalis* and *H. propinquus*, the distolateral lobe of the petasma is only very shallowly cleft, instead of being divided into two subequal lobules (like those of *H. laevis*) as in *H. aphoticus* and *H. debilis*. In *H. neptunus* the lobe is bifurcate, but the tips of both its lobules, and of that of the distoventral lobe as well, are described by Bate and by Alcock as somewhat sharply pointed, rather than rounded as in *H. debilis* and *H. aphoticus*. The petasma of *H. obliquirostris* is unknown.

The thelyca of H. aegualis, H. propinguus, H. obliquirostris, and H. neptunus seem according to the descriptions to differ from those of H. debilis and the juvenile of H. aphoticus (as well as from those of the species with pterygostomian spine, H. laevis, H. doris, and H. nereus), in that they lack a pair of posteriorlydirected projections from the posterior margin of the twelfth sternite. These projections are extremely long and conspicuous in adults of H. debilis, though no larger in juveniles than in the available female of H. aphoticus. In females of H. aequalis and H. propinguus, after DeMan, there is a median projection (which is flanked posteriorly by the paired elevations of the lateral portions of the posterior margin of the segment) with a scutate posterior face which meets the anterior face of the projection in a wide transverse ridge, not conspicuously elevated in the middle, on the thirteenth sternite; and a broad elevation, not rising to an anterior peak, on the fourteenth. In H. obliquirostris according to Bate's figures and to DeMan's description, the elevation of XIII projects strongly, forming a "sharply pointed, compressed tooth"; and there is a tubercle with a marked median longitudinal carina on XIV. In H. neptunus according to Bate and to Alcock, the sculpture of the thirteenth sternite seems similar to that figured by DeMan for H. propinguus; but the ridge of XIV is narrow. In H. debilis the median elevation of XIII is rather like that figured by DeMan for H. aequalis; but sternite XIV bears a broad elevation narrowing anteriorly to a conspicuous, sharp-pointed free projection which overlaps the preceding segment. In the available female of H. aphoticus sternite XIV is as in H. debilis, and the projection is not carinated, while the median elevation of XIII, although rising to a slight median point, is hardly tooth-like.

It therefore appears that H. aphoticus is distinguished by its petasma, as well as by certain other details, from other species than H. obliquirostris, of which the male is unknown. In the lack of an adult female of the new species, the diagnostic distinctions from H. obliquirostris are not perfectly ascertainable, but the eye of the latter seems to be considerably larger; and its thelycum seems to lack the posterior projections of XII, the rudiments of which are present in the juvenile female of H. aphoticus, and there is a tooth on XIII rather than the transverse elevation clearly indicated in H. aphoticus. It is not known whether H. obliquirostris or the other Indo-Pacific forms exhibit the stout meral spine on the first chelipeds which, although absent in H. laevis and H. doris, is present

in *H. debilis* and in *H. aphoticus*. Whether or not photophores occur in any of the Indo-Pacific species is also not known. If the large eye of *H. debilis* is a correlate of its illuminant ability, it seems indicated that *H. obliquirostris* may also be found to be equipped with photophores.

### GROUP II

## Section 1

## Hymenopenaeus robustus Smith

Hymenopenaeus robustus, Smith, 1885.

Penaeopsis ocularis, (A. M. Edw. MS) Faxon, 1895.

Faxonia ocularis, Bouvier, 1905b.

Haliporus robustus, Bouvier, 1906b; Milne Edwards and Bouvier, 1909.

Parapeneus paradoxus, part, Boone, 1927.

8 adult males, carapace about 32, total length about 134 mm; 2 adult females, one of carapace 45 mm, the other, impregnated, of carapace 47, total length 175 mm. B.O.C. 140. North of Glover Reef; April 20, 1925. 366 fathoms.

8 juvenile females, carapace of the largest 5.3 mm in length; total lengths from 21.5 to 12 mm. B.O.C. 229. Atlantis St. 2377; N. 29° 16′; W. 87° 54′. March 24, 1935. 120–130 fathoms.

1 juvenile female. B.O.C. 230. Atlantis St. 2381; N. 28° 35′; W. 89° 46′. March 26, 1935. 165 fathoms.

Adults of *Hymenopenaeus robustus* have been previously recorded among the lesser Antilles; on the north coast of Venezuela behind Curacao; and in the Gulf of Mexico off the Mississippi Delta, in depths from 208 to 321 fathoms, on bottom. The present adult material is from off the coast of British Honduras in slightly deeper water.

The present minute specimens, taken on bottom in the Gulf of Mexico in depths somewhat less than those from which the adults have been recorded, are found to agree almost perfectly with the mature individuals ranging up to more than fourteen times as long. Various slight differences in proportion may be found, but the juveniles have already lost all larval features such as the mobile lateral armature of the telson and the parapeneid spine of the antennule; and rudiments of the thelycal structures are distinguishable.

There is a strong postorbital spine, well dorsal to the level of the antennal, which has been omitted from Bouvier's figure. The orbital angle is dentiform. A cardiaco-branchial ridge is faintly indicated. The branchiostegal carina is marginal; that is, the portion of the carapace ventral to it forms a flexible branchiostegal membrane. The posteroventral angle of the sixth pleonic somite bears a spine. The epipodites of the second and third legs are clearly forked; the others mitten-shaped. As noted by Smith, the first legs are armed,

in addition to basisal and ischial, with a fixed meral spine, while the second legs are completely unarmed.

The petasma is not very clearly figured by Milne Edwards and Bouvier; in their ventral view, the lateral margins are bent into an abnormal position, so that the exposed faces of the endopods appear convex instead of concave. The edge of the distoventral lobe bears a short, rigid, free, distoventral projection, such as is present in Solenocera agassizii Faxon, but not in other species of Hymenopenaeus of which the petasma is known. The distolateral lobes have a very small projection from their lateral edge, such as occurs in H. laevis or H. aphoticus. The distomedian lobe is cincinnulated along its median edge nearly to the distal end, in distinction to the related Solenocerinae (except Hymenopenaeus steindachneri), in which the line of cincinnuli is discontinued far short of the median end of the lobe. The distal margin of the distoventral projection is armed with a series of short, stout, but minute spines. The margin of the distoventral flap itself bears an armature very much more minute than is suggested by Bouvier's figure.

In the impregnated female a conjoined pair of large spermatophores cover the thirteenth and fourteenth sternites, and project well above the coxae of the legs. In general arrangement, though not in details of structure, they are similar to the exposed spermatophores of *Penaeus setiferus* (Linnaeus), described by Burkenroad, 1934a.

The coloration of freshly caught, though dead, juveniles, was as follows: Eyes deep reddish-brown with greenish reflections; gastric gland grayish-brown with light yellow-green flecks, stomach red; body pale orange-red, with a band of deeper salmon on the posterior part of each pleonic tergum; an iridescent bluegreen area on the dorsum of each pleonic segment and of the telson.

In despite of Faxon and of Bouvier, it is improbable that H. robustus stands in close relationship to H. diomedeae (Faxon). The two species are, however, not distinguished by branchial formula, as stated by these two authors, a very well-developed gill being present on VII in H. robustus.

It seems probable that *H. robustus* is more closely related to *H. modestus* Smith than to any other member of the genus. *H. lucasii* (Bate) and the perhaps synonymous *H. malhaensis* (Borradaile) are evidently nearly related to *H. modestus* Smith [probably not identical with the *Haliporus modestus* of Rathbun, 1906] and the very doubtfully distinct *H. affinis* (Bouvier).

## Hymenopenaeus mülleri (Bate)

Pleoticus mülleri, Bate, 1888; Berg, 1898.
Philonicus mülleri, Bate, 1888.
Haliporus carinata, Bouvier, 1906b.
Parartemesia carinata, Bouvier, 1905b.
Haliporus mülleri Milne Edwards and Bouvier, 1909.

4 females, adult. B.O.C. 124. Rio de Janeiro, Brazil; May (?), 1934.

The present seems to be the most completely littoral member of the Soleno-cerinae, aside perhaps from one or two of Solenocera. The present material was taken in the coastal commercial fishery of Rio, together with Penaeus brasiliensis and an undescribed species, discussed in a forthcoming paper, which is the southern representative of Penaeus setiferus. Previous records all refer to a locality more than ten degrees to southward, the Plata estuary, where, according to Berg, 1898, H. mülleri is abundant and attains a very large size, being one of the chief commercial crustaceans of the region. For the present specimens I am deeply indebted to Mr. M. W. Feingold and his associates, and to Dr. Carlos Moreira.

The following differences from the description by Milne Edwards and Bouvier may be stated: There is a trace of a tubercle on the median distal surface of the ocular peduncle; the inferior antennular flagella is little shorter than the superior, this last being about one and two-thirds times the carapace without the rostrum; the antennal scale extends well beyond the antennular peduncle (in which point Bouvier's figure contradicts his text); a special setiferus organ is well developed on propodus as well as carpus of the first legs; the fifth legs are of variable length, in some specimens failing to extend beyond the antennal scale or beyond the third chelipeds, and the merus scarcely or not at all beyond the hepatic spine (the fourth legs are much stouter and shorter than the fifth, not reaching to more than two-thirds of the propodus of the latter); the pleon differs from that of *H. robustus* in that the first and second somites carry a middorsal longitudinal ridge; the relative length of the telson is variable, and the structure may not reach as far as the tips of the uropodal endopods. The "lames saillantes obliquement inclinées" between the fourth legs are not sternal, but coxal.

There is a deep, suture-like, longitudinal sulcus, the homologies of which are doubtful, between the faint cardiacobranchial and the branchiostegal carinae.

Hymenopenaeus tropicalis (Bouvier) seems as described to be distinct from H. mülleri, but a few of the differences pointed out by Milne Edwards and Bouvier are invalid: thus, a complete setiferus organ is present in H. mülleri; the fifth legs may be as short as in H. tropicalis, and the paired protuberances of the anterior part of sternite XIII are present in H. mülleri, and are even indicated in Bouvier's figure. It may be noted that whereas the epipods of VIII and IX are figured as furcated in H. tropicalis, all the epipods are unfurcated in H. mülleri.

## SOLENOCERA Lucas

Solenocera, Lucas, 1850; Wood Mason and Alcock, 1891 a and b; Bouvier, 1908; DeMan, 1911; Burkenroad, 1934a.

Pleoticus, part, Bate, 1888.

Philonicus, part, Bate, 1888.

Parasolenocera, Wood Mason and Alcock, 1891b; Bouvier, 1908; DeMan, 1911.