

CRUSTACEA LIBRARY
SMITHSONIAN INSTITUTION
RETURN TO W-119

BULLETIN
OF
THE BINGHAM OCEANOGRAPHIC COLLECTION
PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY

VOL. V, ART. 2

THE ARISTAEINAE, SOLENOCERINAE AND
PELAGIC PENAEINAE OF THE BINGHAM
OCEANOGRAPHIC COLLECTION

MATERIALS FOR A REVISION OF THE OCEANIC PENAEIDAE

BY MARTIN D. BURKENROAD
Bingham Oceanographic Laboratory

Issued February, 1936
New Haven, Conn., U. S. A.



PUBLISHED BY
BINGHAM OCEANOGRAPHIC FOUNDATION

"Founded for the Purpose
of Oceanographic Research"

A. E. PARR
Curator and Editor

C. M. BREDER
Research Associate

G. E. PICKFORD
Research Assistant

M. D. BURKENROAD
Assistant Curator

Y. H. OLSEN
Assistant

THE ARISTAEINAE, SOLENOCERINAE AND
PELAGIC PENAEINAE OF THE BINGHAM
OCEANOGRAPHIC COLLECTION

MATERIALS FOR A REVISION OF THE OCEANIC PENAEIDAE

BY MARTIN D. BURKENROAD

Bingham Oceanographic Laboratory

INTRODUCTION

The present paper aims at concluding the preliminary review of the Penaeidae begun in two papers dealing chiefly with the littoral members of the family. Since habit and structure run parallel within the group, the previous studies have dealt chiefly with Penaeinae and Euscicyoninae, which are for the most part inhabitants of shallow water. These two littoral subfamilies (the latter of which may perhaps be considered the equivalent of a fixed penaeine larva) are structurally and ontogenetically more similar to one another than they are to the closely bound pair of subfamilies Aristaeinae and Solenocerinae now to be considered, which are largely oceanic.

Some overlap in range between the littoral and the oceanic subfamilies of course occurs; thus the nektonic Penaeinae *Funchalia* are oceanic (it is, however, noteworthy that the species of *Funchalia* seem usually to inhabit the upper water layers, at depths no greater than those common to the benthonic littoral members of the subfamily; whereas the nektonic Aristaeinae *Gennadas*, although sometimes found in the upper layers, are usually bathypelagic); the Penaeinae *Penaeopsis* (s. str.) and *Parapenaeus* are chiefly found at fair depths along the outer continental margins; and a few species of Euscicyoninae range far out on the continental shelves. In the oceanic groups, most of the species of *Solenocera* (which are probably burrowing forms), and many of the Solenocerinae *Hymenopenaeus* range above the hundred fathom line, one of the latter, *H. mülleri* Bate, being truly littoral. The Aristaeinae are without exception oceanic,¹ but certain

¹ Balss, 1923, has suggested that a genus of peneids of the Jurassic littoral, *Aeger* Münster, is referable to the subfamily Aristaeinae. However, according to Balss' own description, *Aeger* displays many striking differences from all living forms (enlargement and spination of third maxillipedes, peculiar rostral armature, sculpture

species of *Gennadas* are sometimes found in the upper water layers, and may thus occasionally be taken above bottoms on which Penaeinae or Eusicyoninae occur.

The nektonic habit occurs sporadically throughout the family, although most adult Penaeidae, whether littoral or oceanic, are benthonic. It is possible that both types of behavior are found together in certain species of abyssal Solenocerinae and Aristaeinae, which although frequenting the bottom, may at times occur at a considerable distance above it. Among littoral forms, *Penaeus setiferus* and *P. brasiliensis*, as well as species of such other genera as *Penaeopsis* (*Leptopenaeus*), may be taken swimming at the surface during the night. The larval stages of benthonic Aristaeinae and Solenocerinae are known from the surface in the open sea. In many littoral Penaeinae there seems to be a migration of the adults to deeper continental bottoms with the approach of sexual maturity, larval development as far as postmysis stages taking place pelagically in the offshore water layers.

The geographical no less than the bathymetric distribution of

of carapace) which seem to me to make difficult the acceptance of its inclusion within a modern subfamily; and in any case it seems to display most resemblance to the Solenocerinae, some members of which occupy a littoral range at the present. Balss, in stating that the "beide gleich lang" antennular flagella of *Aeger* resemble those of the Benthescyidae, overlooks the fact that the basal part of the superior flagellum of both series of Aristaeinae is thickened, a character not found in *Aeger*, the antennular flagella of which more nearly resemble those of certain Solenocerinae. The carapacic tooth figured by Balss for *Aeger tipularius*, and termed by him "Hepaticstachel," seems from its position far anterodorsad the cervical sulcus to be equivalent to the postorbital uniquely characteristic of Solenocerinae among recent Penaeidae; this interpretation seems confirmed by the observation of Van Straelen, 1925, that a true hepatic is simultaneously present in some members of the genus at least. Lack of hepatic is characteristic of living Aristaeinae (see footnote to p. 86). Ventral rostral teeth are unknown among modern Aristaeinae, although they are found in species of the other three recent subfamilies. The tooth observed by Balss at the distal ends of the meri of all the walking legs of *Aeger* is reminiscent of the stout fixed tooth in a similar position on the first leg in certain Solenocerinae (although it is of course possible that the homology is with the mobile meral spines found in both Aristaeae and Solenocerinae).

It might theoretically be expected that Aristaeine-like peneids, either before their restriction to the abyss or in process of colonizing the littoral waters with derivative groups, would at some period in history have occurred in the neritic zone; but it is also possible that the Aristaeinae have always been an oceanic group; and that the Aristaeine-like intermediaries between ocean and shallow were in ancient times, as they are still, Solenocerinae.

Aristaeinae and Solenocerinae is of a sort quite different from that characterizing the littoral peneids; it may on the whole be termed cosmopolitan, if this word is accepted as without any connotation of universal occurrence. Many abyssal and pelagic forms are known from all oceans, yet within this great range they are generally much, and quite irregularly, localized or concentrated. Other oceanic forms are not cosmopolitan in any sense, being limited, so far as is known, to a single ocean—despite the relatively great uniformity of their environment, the lack of any very apparent barriers to their spread, and the fact that related forms overlapping their range may spread far beyond it. As an example, *Gennadas elegans*, the most widespread and abundant Atlantic species of the genus, is known from Davis Straits (and from the Cape of Good Hope), certainly sometimes in water of less than 1° C., and from the Mediterranean, certainly sometimes at temperatures of more than 15° C.; is regularly found between 200 and 2000 meters depth, and performs daily vertical migrations of considerable extent; in short, occurs over a range of temperatures, salinities and localities which seem sufficiently varied to permit its easy access to all regions, and yet is completely unknown from the Indo-Pacific, as well as from certain extensive areas, seemingly not uninhabitable, within the Atlantic itself (see p. 72).

It is interesting to observe that although the oceanic peneid faunas of the eastern and western basins of the North Atlantic are, relative to the littoral faunas, very similar (and although it seems doubtful that any of the species of the Eastern North Atlantic are not also to be found in the western basin) some records, chiefly new, obtained from the Bermudan and Bahaman region indicate that an Indo-Pacific and extreme southeastern Atlantic component not represented on the northeastern side is comprised in the fauna of the western basin. The apparent absence of such species (*Gennadas capensis*, *G. bowieri*, *Cerataspis petiti*, *Hemipenaeus carpenteri*, *Plesiopenaeus coruscans*) from Pacific America (with the exception of the *Hemipenaeus*) seems to imply that this difference between the oceanic faunas of the eastern and western North Atlantic is dependent upon a continuity of the Bahaman with the Indo-Pacific population by way of the Cape of Good Hope, rather than on the other possible contact across Middle America during past geological time; a view for which further evidence is presented below.

Before proceeding to a detailed comparison of the geographical

distribution of the oceanic with that of the littoral American peneids, it seems necessary to justify a taxonomic definition of the terms *oceanic* and *littoral*. Data relating to the normal environment and to the extremes of range of most of the species to be considered are very slight, consisting chiefly in records of locality and depth of water or of capture. An ecologically acceptable definition, based on chemical and physical tolerances of the species is, then, obviously impracticable. Depth-and-locality, as a basis for the definition of groups the geographical distribution of which is to be compared, is for several reasons likely to permit confusion. Thus the chemical and physical conditions to which a given depth and locality refer are often uncertain, and if they are not, depth of capture of the organism is likely to be. At the same time, the available records are usually insufficient to establish the tolerances (or even the optima) of a majority of the peneids in even the better known sexually active phases; and such records are almost lacking for the larvae; yet it seems quite probable that Penaeinae and Solenocerinae ordinarily taken as adults in the same locality may nevertheless differ considerably, one from the other systematic group, in both adult and larval tolerances, a difference which should strongly affect distributional capacity. The present state of knowledge no more than permits the general statement that most of the Aristaeinae and Solenocerinae are usually taken as adults at some depth and in non-neritic waters, while most of the Penaeinae and Eusicyoninae are usually taken as adults (but sometimes not as larvae) in shallow, neritic areas. Therefore, *oceanic peneid* will here be systematically defined as referring to the Aristaeinae and Solenocerinae; a procedure which may conceivably be found to correspond to a more realistic grouping of the organisms as regards their essential environmental dependences than would an ecological grouping based upon known habit without systematic reference. Those cases in which there are littoral records of members of oceanic subfamilies, and the reverse, may according to the present system best be regarded as representing invasions which may range in type from accidental or temporary penetrations of another life-zone to a more or less complete exchange of habitat. For instance, an exceptional member of the littoral subfamily Penaeinae, *Funchalia*, is according to all records pelagic. Yet the fact that it is an inhabitant of surface waters of the ocean indicates its maintenance of the outstanding characteristic of a neritic organism; and it would not be surprising to find that its

inclusion according to the present definition with the *littoral peneids* is to some degree justified by its possession, either in adult or larval stages, of a greater tolerance for neritic conditions than characterizes the also nektonic Aristaeinae *Gennadas*. In fact, the available records of *Funchalia balboae*, limited to the two sides of America, might indicate according to a hypothesis to be set forth below that *Funchalia* does possess such tolerance, to the extent of being able to traverse previously existent transcontinental channels too shallow to permit the passage of most Aristaeinae and Solenocerinae. Taking the opposite case, an exceptional member of the oceanic subfamily Solenocerinae, *Hymenopenaeus mülleri*, has not been recorded from depths greater than a few fathoms. Yet I think it possible that an investigation of the life-history of this organism might reveal a seaward spawning migration, with a larval dependence upon oceanic conditions such as would prevent (as in the analogous case of terrestrial pagurids) any penetration of the neritic zone beyond a limit imposed by the capacity for dispersal of a single individual.

The question involved in the above working definition, as to the relation between the structural characters of peneids and their bathymetric habits, is one of great interest.¹ Critical evidence as to this relationship (i. e., as to which of the various structures that are different in oceanic and littoral peneids do not display modifications correlable with differences in habit within either group, and are therefore presumably without affective relation to environment-selection) should be supplied by peneids which have adopted a manner of life different from that modal for their systematic group. For instance, the gills of peneids decrease in number from subfamily to subfamily in direct ratio to decrease in depth inhabited. However, in the littoral *Hymenopenaeus mülleri* there is no decrease from the number of gills found in other members of the genus (which occur at much greater depths); and similarly there is no increase in the deep-living Penaeinae *Penaeopsis* (s. s.) as compared with the related littoral subgenus *Metapenaeopsis*. One might therefore suspect that the obvious differences in branchial equipment between the Aristaeine-Solenocerine and the Penaeine-Eusicyonine groups are not causally

¹ An investigation of the structural distinctions between deep and shallow-water peneids, by Mr. M. Ramadan of the University of Cambridge, now in progress, should provide a factual basis for considerations of the sort outlined below; and the results of this study may be awaited with interest.

related to adult bathymetric range, although critical investigation might reveal modifications other than in number, such as in gill-area, by which a littoral Solenocerine might obtain gill-equivalence with the Penaeinae without gross modification of the structural pattern proper to its own group. On the other hand, considering the ocular tubercles (organs suggested by Hanström to function as pressure receptors), which decrease in size with considerable regularity from Aristacinae to Euscicyoninae, it is found that in *Hymenopenaeus mülleri* these structures are more reduced than in deeper-living congeners; and similarly, the tubercles of *Penaeopsis* are more prominent than those of *Metapenaeopsis*. The cornea of the eye of the Aristacinae and Solenocerinae is generally hemispherical, the ocular peduncle solid; the cornea of Penaeinae and Euscicyoninae reniform with the major portion of the visual surface directed laterally, the peduncle usually longitudinally divided into two elements (which peduncular arrangement apparently functions in maintaining the non-visual area of the unilateral reniform eye constantly in the median plane, so that anterior vision is not impaired when the peduncle is swung laterally). In the Solenocerinae living at least depths, the eye is often reniform and the peduncle may display some evidence of divided structure; similarly, the oceanic Penaeine *Funchalia* shows some shift toward hemispherical eye, although the peduncle is still divided. One might therefore suspect that differences in ocular structures are causally related to adult bathymetric range, although critical investigation might, for instance, reveal that degree of development of the sensory complex of the ocular tubercle has no relation to the external form of the tubercle. Also, very striking exceptions to the generalizations made above are known; for instance, in certain of the abyssal Benthescyma, above all, in *Benthonectes*, the ocular tubercle is small; and the cornea in a sense reniform, although the major visual surfaces, contrary to the condition found in littoral forms, are directed medially rather than laterally.

The distributional relation between the oceanic penaeid faunas of the Atlantic and Pacific American regions, to return to the original question, seems to be of a different sort from that between the littoral penaeids of the two coasts, although the incompleteness of our knowledge of the deep-water faunas, and especially of that of the American Pacific, is too great to permit any but the most tentative generalization.

Approximately thirty Atlantic American Aristacinae and Soleno-

cerinae are known, as compared to only twelve from Pacific America. Of the Pacific American forms, one, the sublittoral *Solenocera agassizi*, bears a much closer relation to the Atlantic American *S. vioscai* than to members of the genus found in other parts of the world. Four species, *Benthesicymus crenatus*, *B. altus*, *Hemipenaeus spinidorsalis* and *H. carpenteri*, also occur in both the Atlantic and the Indo-Pacific. Four limited to Pacific America find close relatives in the Atlantic and the Indo-Pacific; of these *Benthesicymus tanneri* and *Hymenopenaeus doris* and *H. nereus* are represented by the very nearly related *B. bartletti* and *H. laevis* in both the Atlantic and the Indo-Pacific; while *Aristaeus occidentalis* is represented in the Atlantic by *A. antillensis* and in the Indo-Pacific by *A. semidentatus*, species which seem to be of approximately equal closeness of relationship to the Pacific American form. Finally, three species find much closer relatives in the Indo-Pacific than in the Atlantic; of these *Bentheogennema borealis* occurs on the Asiatic as well as on the American side of the Pacific; and *Haliporus thetis* and *Hymenopenaeus diomedea* find near representatives respectively in the exclusively Indo-Pacific *H. curvirostris* and *H. sibogae* and *triarthrus*. Comparing the corresponding portion of the Atlantic population, it is found that *Hymenopenaeus laevis*, *Bentheogennema intermedia* and *Benthesicymus bartletti*, which are replaced by related forms in the American Pacific, possess conspecific Indo-Pacific representatives. Of the remaining Atlantic forms a large majority are known to have nearly related or identical Indo-Pacific representatives, so that their discovery in Pacific American waters would constitute only an increase in the number of cosmopolitan groups; while if it should appear that any of these Atlantic forms are actually absent from Pacific America, rather than merely unrecorded, they would represent an increase in the Atlantic category of species with closer Indo- than American-Pacific relatives.

The relations between the Atlantic and Pacific American Penaeinae and Eusicyoninae may now be considered by way of comparison with the oceanic groups: On either American coast one unique form occurs which has no near relatives in any other region. On each coast a few forms (five in the Atlantic, one or two in the Pacific) occur for which there are no equivalents in the opposite American region, but which are represented by nearly related forms in other waters. On the Atlantic coast there are four species with closely related or identical Pacific American congeners, which also have representatives as closely

related in other regions. Finally, twelve Atlantic American species are very much more closely related to fourteen Pacific American species than they are to those of any other region. Thus, while a portion of either littoral American fauna has a closely related equivalent in other regions, the majority of forms are identical with or nearly related to those of the opposite American coast and lack representatives of anything like equal affinity in other regions.

It has been pointed out above that a portion of either American oceanic fauna has an Indo-Pacific but no American equivalent; while in strong contrast to the littoral forms, when identical or nearly related forms are found on opposite sides of the continent, the same or as nearly related a species usually occurs in the Indo-Pacific. It may therefore fairly be said that, as far as can at present be determined, the American oceanic faunas, in complete contrast to the littoral ones, have less resemblance to each other than they do to the fauna of any other region.

As to the significance of the above contrast in mode of distribution, I am informed by Professor Charles Schuchert that a communication of oceanic depth between the Atlantic and Pacific across Middle America probably existed until some time during the Cretaceous, but that the various interoceanic channels which pierced the upraised land-mass from that time through the Pliocene were very probably of continental nature. The similarity between the littoral peneids of Atlantic and Pacific America is readily accounted for by the existence until a late date of shallow interoceanic channels. On the other hand, although the available evidence is admittedly tenuous, it is possible to believe that the neritic character of the post-Cretaceous channels effectively placed the American oceanic peneids at opposite ends of the world; and therefore, that any identities which exist between them have been brought about or maintained by communication around the world.¹ This view would make possible a useful generalization:

¹ The possibility, as to which there is no direct information, of Antarctic communication between the American oceanic faunas, around Cape Horn, must be considered. Available data seem to indicate that the abyssal peneids, though inhabitants of water of low temperature, are most abundant in the warmer geographical regions of the world. There is evidence that larval stages of the oceanic peneids are normally passed at the surface of the sea; therefore it may well be that the existence of an oceanic species is dependent on the accessibility of warm water during the developmental period. In this case, the conditions for communication around the Horn would in recent times be much less favorable than would those for contact by the

that an oceanic species occurring on both sides of America will also exist in the Indo-Pacific. As an example of its application, one might maintain *a priori* that *Hemipenaeus triton* Faxon is identical with *H. carpenteri* Wood-Mason.

Professor Schuchert (1935), in his published discussion of the facts presented above, emphasizes that prior to the Cenozoic, the oceanic faunas of Atlantic and Pacific America could have maintained free communication. It must be admitted that the occurrence in the Jurassic of peneids closely related to living species (see footnote to p. 127) may be evidence that the evolutionary rate of the group is sufficiently slow that oceanic species common to the two sides of America in the Cretaceous could have maintained their specific identity until the present in the face of segregation, without the necessity of circumferential continuity. But it is on the other hand true that most of the littoral peneids of the two sides of America have diverged appreciably from one another since the cutting of all communication after the Pliocene; and although the presumably slower generation-rate of abyssal organisms living at lower temperatures might be expected to lower their rate of evolution relative to the littoral ones (assuming an equal rate of mutation in both),¹ there is no reason to believe that segregated stocks of oceanic peneids would remain specifically identical through the tremendous interval between the Cretaceous and the present.²

ACKNOWLEDGEMENTS

The bulk of material discussed in the present paper was obtained during Bermudan and Bahaman operations of the "Pawnee," under the direction of Mr. HARRY PAYNE BINGHAM, in 1927. Certain Solenocerinae were taken during the Pacific American Expedition of

much longer way of the Cape of Good Hope. The possibility that conditions more favorable than at present for polar communication around the American land mass may have existed subsequent to the closure of the Middle American deep-water sinus, can, of course, not be excluded.

¹ As suggested by Professor A. E. Parr (*in litt.*).

² The present hypothesis necessarily rests upon the assumption, which seems for the present purposes justified, that the stocks from which the living species of oceanic peneids are descended were of similar oceanic habit by the beginning of the Cenozoic, and were therefore unable to maintain communication through the shallow post-Cretaceous Central American waterways. The possibility that ancestral forms related to the Aristaeinae once occupied a littoral habitat has already been discussed (see footnote to p. 1).

the "Pawnee" in 1926, and the first Atlantic American Expedition in 1925. Some pelagic material from the Bahamas was obtained by use of the triangular trawl, as well as by ordinary bathypelagic gear, during the first joint expedition of the Woods Hole Oceanographic Institution and the Bingham Oceanographic Foundation aboard the "Atlantis" in 1933; and in the Caribbean by bathypelagic hauls and by the surface dredge employed for Sargassum collection during the second joint expedition in 1934; while both pelagic and benthonic materials were obtained in the Gulf of Mexico during the third joint expedition in 1935. Material of *Hymenopenaeus mülleri* (Bate) representing an important extension of the known range has been obtained from the markets of Rio through the kind mediation of Mr. M. W. FEINGOLD. Valuable material of *Gennadas* has been added to the Bingham collection through exchanges made possible by the generosity of Dr. A. SCHELLENBERG of the Zoologische Museum der Universität, Berlin; of Dr. K. STEPHENSEN of the Universitets Zoologiske Museum, Copenhagen; and of Dr. W. T. CALMAN and Dr. I. GORDON of the British Museum (Natural History). The enormous collection of peneids of the Department of Tropical Research of the New York Zoological Society, made under the direction of Dr. W. BEEBE, has yielded information of critical importance that is incorporated in the present paper; the bulk of this material will, however, be considered in a separate study. Material studied by Smith, in the collections of the Zoology Department of the Peabody Museum of Natural History and of the American Museum of Natural History, has been made available through the kindness of Dr. S. C. BALL and of Dr. R. W. MINER and Dr. W. J. VANNAME. Examination of the important collections reported by Faxon has been permitted by Dr. H. L. CLARK and his associates of the Museum of Comparative Zoology at Harvard, and their provision of facilities for work during visits to the institution is deeply appreciated. Dr. A. SCHELLENBERG has arranged the loan of a number of specimens of *Gennadas* from the collection of the Zoologische Museum der Universität, and has been so extremely good as to supply detailed notes on the types of the species of *Funchalia* described by Lenz and Strunck. Various Pacific specimens have been loaned by the U. S. National Museum, through the courtesy of Dr. W. L. SCHMITT. Dr. CALMAN and Dr. GORDON, to whom I am deeply grateful for the opportunity, have permitted the examination not only of South African specimens taken by the "Pickle," but of "Challenger"

materials described by Bate. Fossil penaeids from the collections of the Department of Invertebrate Paleontology of Peabody Museum have been made available through the kindness of Dr. C. O. DUNBAR. I have been greatly benefited by the advice of Dr. C. SCHUCHERT on questions pertaining to the geological history of Middle America. Deductions as to the previous history of certain specimens of *Hymenopenaeus* have been made possible by information generously supplied by Dr. J. A. CUSHMAN as to foraminifera extracted from the gut. To all, whose good will has made this study possible, and in the highest degree to Professor A. E. PARR, I wish to express my thanks. For most careful preparation of the typescript, acknowledgment is due to Mrs. S. H. Donahue; and for assistance in making the manuscript and figures ready for the press, to Mr. D. T. Pitcher.

LIST OF NEW SPECIES AND NEW NAMES

- Bentheogennema*, n. nom.
Benthesicymus urinator, n. sp.
Benthesicymus cereus, n. sp.
Benthesicymus strabus, n. sp.
Hymenopenaeus aphoticus, n. sp.

LIST OF STATIONS¹

OCEANOGRAPHIC EXPEDITIONS OF THE "PAWNEE" THIRD EXPEDITION, 1927

- STATION 9. III/1/27. N. 23° 55', W. 77° 09'. 4000-7000 feet wire.
 3 *Gennadas capensis* Calman.
 1 *G. valens* (Smith).
 1 *G. bowieri* Kemp.
- STATION 11. III/2/27. N. 23° 58', W. 77° 26'. 7000 feet wire.
 11 *Gennadas capensis* Calman.
 4 *G. valens* (Smith).
 3 *G. bowieri* Kemp.
 1 *Hymenopenaeus aphoticus*, n. sp.
- STATION 16. III/9/27. N. 23° 49', W. 76° 58'. 7000 feet wire.
 1 *Bentheogennema intermedia* (Bate).
 1 *Gennadas capensis* Calman.

¹ For a description of the operations carried out during 1927, reference may be made to Parr, 1928, and for an account of experiments with the triangular trawl in 1933, to Parr, 1934. Gear used by the "Pawnee" was the fourteen-foot stramin ring-net, in general towed within 200 fathoms of bottom.

3 *G. valens* (Smith).

1 *G. bowieri* Kemp.

STATION 18. III/10/27. N. 23° 42', W. 76° 43'. 7000 feet wire.

1 *Bentheogennema intermedia* (Bate).

4 *Gennadas capensis* Calman.

3 *G. valens* (Smith).

3 *G. bowieri* Kemp.

1 *Funchalia villosa* (Bouvier).

STATION 22. III/12/27. N. 23° 31', W. 77° 15'. 7000 feet wire.

3 *Gennadas capensis* Calman.

4 *G. bowieri* Kemp.

STATION 23. III/14/27. N. 24° 29', W. 77° 29'. 8000 feet wire.

4 *Gennadas capensis* Calman.

5 *G. bowieri* Kemp.

1 *G. scutatus* Bouvier.

STATION 25. III/17/27. N. 24° 51', W. 76° 37'. 8000 feet wire.

3 *Bentheogennema intermedia* (Bate).

2 *Gennadas capensis* Calman.

1 *G. valens* (Smith).

STATION 27. III/18/27. N. 24° 45', W. 76° 21'. 8000 feet wire.

1 *Gennadas capensis* Calman.

STATION 31. III/21/27. N. 24° 29', W. 75° 53'. 7000 feet wire.

3 *Gennadas capensis* Calman.

1 *G. valens* (Smith).

STATION 33. III/22/27. N. 24° 11', W. 75° 37'. 8000 feet wire.

1 *Bentheogennema intermedia* (Bate).

4 *Gennadas capensis* Calman.

1 *G. bowieri* Kemp.

STATION 35. III/23/27. N. 24° 11', W. 75° 35'. 7500 feet wire.

2 *Gennadas capensis* Calman.

STATION 39. III/29/27. N. 22° 43', W. 74° 23'. 8000 feet wire.

5 *Gennadas capensis* Calman.

5 *G. valens* (Smith).

2 *G. tinayrei* Bouvier.

STATION 41. III/30/27. N. 22° 31', W. 74° 26'. 10,000 feet wire.

3 *Gennadas capensis* Calman.

STATION 46. IV/4/27. N. 21° 46', W. 72° 50'. 10,000 feet wire.

1 *Gennadas capensis* Calman.

1 *G. valens* (Smith).

1 *G. bowieri* Kemp ? juvenile.

STATION 48. IV/6/27. N. 21° 44', W. 72° 43'. 7000 feet wire.

19 *Gennadas capensis* Calman.

10 *G. valens* (Smith).

1 *Funchalia villosa* (Bouvier).

STATION 52. IV/11/27. N. 21° 30', W. 71° 11'. 8000 feet wire.

9 *Gennadas capensis* Calman.

1 *G. valens* (Smith).

8 *G. bouvieri* Kemp.

2 *Hymenopenaeus laevis* (Bate).

STATION 54. IV/12/27. N. 21° 16', W. 71° 18'. Bottom struck at 900-945 fathoms.

1 *Benthesicymus bartletti* Smith.

2 *B. cereus*, n. sp.

1 *B. carinatus* Smith.

1 *Gennadas capensis* Calman.

1 *G. valens* (Smith).

1 *Hepomadus tener* Smith.

1 *Plesiopenaeus coruscans* Wood-Mason.

3 *Hemipenaeus carpenteri* Wood-Mason.

2 *Hymenopenaeus aphoticus*, n. sp.

STATION 56. IV/13/27. N. 21° 20', W. 71° 13'. 6500 feet wire.

2 *Gennadas capensis* Calman.

15 *G. valens* (Smith).

4 *G. bouvieri* Kemp.

1 *Hymenopenaeus laevis* (Bate).

STATION 58. IV/20/27. N. 32° 24', W. 64° 29'. 10,000 feet wire.

1 *Gennadas capensis* Calman.

5 *G. valens* (Smith).

1 *G. bouvieri* Kemp.

13 *G. elegans* (Smith).

1 *G. tinayrei* Bouvier.

1 *Hymenopenaeus laevis* (Bate).

STATION 59. IV/21/27. N. 32° 19', W. 64° 33'. 8000 feet wire.

1 *Bentheogennema intermedia* (Bate).

2 *Gennadas valens* (Smith).

10 *G. elegans* (Smith).

1 *G. tinayrei* Bouvier.

1 *Hymenopenaeus laevis* (Bate).

1 *Funchalia balboae* (Faxon).

COOPERATIVE CRUISES ON THE RESEARCH SHIP "ATLANTIS"
 SPONSORED JOINTLY BY WOODS HOLE OCEANOGRAPHIC
 INSTITUTION AND BY YALE UNIVERSITY (BINGHAM
 OCEANOGRAPHIC LABORATORY)

FIRST JOINT CRUISE, 1933

STATION 1478. II/20/33. N. 25° 29', W. 77° 18'. 5250 feet wire. Triangular trawl.

- 13 *Bentheogennema intermedia* (Bate).
- 9 *Gennadas capensis* Calman.
- 1 *G. bowieri* Kemp.
- 2 *G. elegans* (Smith).

STATION 1479A. II/26/33. N. 25° 30', W. 74° 30'. 450 feet wire. 2-m. ring-net.

- 2 *Gennadas tinayrei* Bouvier.
- 1 *G. scutatus* Bouvier.

SECOND JOINT CRUISE, 1934

STATION 1939. II/3/34. N. 16° 10', W. 76° 28'. Depth between 50 and 200 m. 2-m ring-net.

- 1 *Gennadas bowieri* Kemp ? juvenile.
- 38 *G. scutatus* Bouvier.
- 1 *Funchalia villosa* (Bouvier).

SARGASSUM-HAUL 77. II/6/34, night. N. 10° 20', W. 79° 15'. Surface. Sargassum collector.

- 1 *Funchalia balboae* (Faxon).

SARGASSUM-HAUL 111. II/28/34, night. N. 21° 04', W. 84° 11'. Surface. Sargassum collector.

- 1 *Funchalia balboae* (Faxon).

THIRD JOINT CRUISE, 1935

STATION 2377. III/24/35. N. 29° 16', W. 87° 54'. Depth 120-130 fathoms, on bottom. 1-foot stramin ring-net on head-rope of otter-trawl.

- 8 *Hymenopenaeus robustus* Smith.
- 1 *Solenocera vioscai* Burkenroad.

STATION 2381. III/26/35. N. 28° 35', W. 89° 46'. Depth 165 fathoms, on bottom. 1-foot stramin ring-net on head-rope of otter-trawl.

- 1 *Hymenopenaeus robustus* Smith.
- 263 *H. debilis* Smith.

STATION 2410. IV/4/35, 2:43 to 5:08 P.M. N. 25° 05', W. 93° 10'. 2050 meters wire, estimated depth, 1000 meters. Sounding, 2050 fathoms. 2-meter closing net.

- 2 *Bentheogennema intermedia* (Bate).

STATION 2427. IV/9-10/35, 4:00 P.M. to 6:00 A.M. N. 25° 53', W. 87° 53'; to N. 26° 19', W. 87° 30'. 3164 meters wire at 60°. Triangular trawl (cod-end lost).

5 *Bentheogennema intermedia* (Bate).

2 *Gennadas capensis* Calman.

2 *Gennadas valens* (Smith).

SYSTEMATIC DISCUSSION

PENAEIDAE Bate

For benefit of those enquiring into the relationship of this to other families of decapod crustacea, it may be mentioned that, much needed as is such an effort "d'en poursuivre l'homologie à travers tous les groupes," the homologies of the carapacic sulci suggested by Van Straelen, 1925, seem (to judge all by his diagrams of Penaeidae) unacceptable. Van Straelen's dependence on the sulci alone of the sculptured landmarks of the carapace is evidently responsible for certain of his difficulties; thus, a consideration of the positions of the hepatic spines would have prevented the comparison of "b" [the "sillon antennaire"] in his figure of *Aristaeomorpha foliacea* (Risso) (figure 1, "*Aristeus antennatus*") with that portion of the cervical sulcus designated as "b" in his figure 2 of *Benthesicymus iridescens*. A lack of the specialists's acquaintance with the normal sculpture of Aristeae is probably to blame for the description as cervical of a delineated sulcus evidently derived from the postcervical of *Aristaeomorpha*. The attribution to the Penaeinae of *Plesiopenaeus edwardsianus* weakens Van Straelen's textual generalizations as to the distribution of the sulci among the sub-families of Penaeidae.

ARISTAEINAE Alcock

Series *BENTHESICYMAE* Bouvier

Sharp distinctions between adults of the maniple Benthesicymae and the maniple Aristeae are somewhat difficult to draw, although the subdivision of the subfamily is natural and convenient. Only one of the key characters employed by Bouvier, 1908, to distinguish the two series (extensive development of the distal, filamentous portion of the superior antennular ramus in Benthesicymae) seems diagnostic. Bouvier's statements as to the second of his key characters (relative dimensions of the basal article of the mandibular palp) are confusing. On page 15, the basal article in Benthesicymae is "distinctement foliacé, . . . beaucoup plus long et plus large que le second"; on page 16 it is "plus large que le second, mais de longueur peu différente." On page 15, the basal article in Aristeae "qui peut être large, mais non foliacé, est plus long que le suivant"; on page 51, it is "plus étroit et notablement plus court . . ." I do not believe that the variations which occur in this

structure are of much significance. Of the other differences noted by Bouvier in his definitions of the maniples, none seems completely diagnostic; even though the extremes of the two series are quite distinct, some member of either maniple falls within the range of variation of the other. Thus, *Hemipenaeus triton* Faxon has a rostrum quite as short as that of many Benthescyinae.

Four features in which the Benthescyinae are generally distinct from the Aristeae, not mentioned by Bouvier, are of considerable significance: the median point of the telson is usually much less strongly developed in Benthescyinae than in Aristeae; the antennal flagellum is sharply inflected at some distance from its base in most Benthescyinae; the distoventral lobe of the petasma is not free from the median portion for much of the length of the organ (whereas in Aristeae it may be free for half the length of the petasma); and whereas the sperm receptacle of the Aristeae seems universally open, that of the Benthescyinae is often of an enclosed type which differs from that found in other Penaeidae in that it is formed from an invagination originating between the twelfth and thirteenth rather than between the thirteenth and fourteenth sternites. These four characters, which reach their most complete expression in those Benthescyinae which lack posterior podobranchs, are strikingly reminiscent of conditions obtaining among the Sergestidae. A discussion of the possible significance of this resemblance will be deferred until the completion of a study of the second family of Penaeidea, but it may be pointed out that these similarities may represent convergence, since whereas the spermatheca of Sergestidae opens between or in advance of the third legs, that of Benthescyinae opens posterior to the genital apertures.

The series Benthescyinae includes about twenty-five or -six probably valid species, which have been variably divided among the four generic names *Benthescyimus* Bate, 1881; *Gennadas* Bate, 1881; *Amalopenaeus* Smith, 1882; and *Benthonectes* Smith, 1885. No material of the last, monospecific genus, is available to me.¹ The limits of the other three genera have been confused in the

¹ According to Smith's description and figures (1885 and 1887), *Benthonectes* agrees with *Benthescyimus* in the features in which that group is distinct from the remainder of the series. In form of exopod of first maxillipede and in degree of development of the exopodites of the walking legs, it agrees with Group I of *Benthescyimus* (to be defined below); in the slight expansion of the maxillipedal meri and in the form of the petrygostomian spine and carina, with Group II. In the possession of an hepatic spine, *Benthonectes* differs from all Benthescyinae other than *Benthescyimus brasiliensis* and related species. A tendency to proximal extension of the cornea down the median surface of the ocular peduncle, and to reduction of the ocular tubercle, which may be observed in certain species of *Benthescyimus* (notably in *B. strabus* of the *B. brasiliensis* complex; and still more conspicuously in *B. investigatoris*), is expressed in the highest degree in *Benthonectes*. The genus seems unique in the subfamily (being paralleled by the littoral penaeine *Xiphopeneus*) in that the dactyls of the fourth and fifth legs are very long and are multiarticulated; and is also distin-

past, as witness the lack of agreement between previous workers in their placing of *Benthesicymus* ? *carinatus* Smith, 1884, regarded as a species of *Gennadas* by Alcock, 1901, Kemp, 1910b, and DeMan, 1911; the attribution to that genus of *Gennadas pectinatus* Schmitt, 1924, a species very closely related to or identical with the genotype of *Benthesicymus*; the variable use of *Amalopenaeus* Smith, employed by Kemp, 1909 and 1910a, and Balss, 1927, to distinguish those species lacking podobranchs behind VIII; and the abandonment of any formal distinction of the pelagic forms with from those without posterior podobranchs, by Calman, 1925. Alcock, 1901, having brought together a heterogeneous group under the name *Gennadas*, suggests that this assemblage may be no more than a subgenus of *Benthesicymus*. Bouvier, 1908, overlooks Smith's observation that certain of the pelagic forms lack podobranchs, and in distinguishing two genera, *Benthesicymus* and *Gennadas*, devotes his attention principally to nondiagnostic characters. Calman, 1925, and Balss, 1927, have clarified the knowledge of branchial formulae within the series by correction of Kemp's attribution of posterior podobranchs to many species which lack them; however, Balss, having shown that *Gennadas parvus* Bate (the genotype) lacks podobranchs behind VIII and is therefore certainly congeneric with *Amalopenaeus elegans* Smith, nevertheless restricts the name *Gennadas* to the pelagic species with podobranchs exemplified by *G. intermedius* Bate. Also, in referring the pelagic forms to *Gennadas* or *Amalopenaeus* by the single criterion, presence or absence of posterior podobranchs, Balss fails to discuss the problem of the relationship of the pelagic group with podobranchs to *Benthesicymus*.

A careful examination of the *Benthesicymae* available to me, and of the literature, indicates that three major groups in addition to *Benthonectes* (which is probably to be regarded as an offshoot of *Benthesicymus*) are recognizable. The distribution of certain characters among species of the series is shown in table on page 18.

The two key characters employed by Bouvier, 1908, in separating *Benthesicymus* from "*Gennadas*" (including both *Gennadas* s. s. and *Bentheogennema*) are given as 8 and 9 of the table. These characters seem of little value; indeed, it is only in the *Benthesicymus bartletti* group (and in *B. strabus* of the *B. brasiliensis* complex) that the merus of the second maxillipedes, more than three times as long as broad, cannot be termed expanded. The degree of expansion of the meri of the legs likewise grades from a state in which the breadth in the first leg is considerably less than one-fourth of the length, in *B. bartletti*, through the expanded condition in *B. carinatus* to the broadly expanded state in *Bentheogennema* and *Gennadas* where the breadth is one-third or more of the length.

guished from the species which on the whole it most nearly resembles (*Benthesicymus*, Group I) by the broader proximal and shorter distal segments of its mandibular palp, its differently shaped mandibular crown, the completely obliterated terminal segment of the endopod of its first maxillipede, and the slender, tapering and multi-spinose dactyl of its third maxillipede.

TABULAR COMPARISONS OF CERTAIN BENTHESICYMAE

Character (see explanation below)	1.	2.	3.	4.	5.	6.	7.	8.	9.
<i>Benthesicymus</i> Bate crenatus carinatus	+	+	+	+	+	+	+	+	O
brasiliensis	+	+	+	+	+	+	⊖	⊖	⊖
bartletti investigatoris	+	+	+	+	+	+	+	⊖	+
tanneri	+	+	+	+	+	⊖	+	⊖	+
altus	+	+	+	+	+	O	+	⊖	+
<i>Bentheogennema</i> , n. nom. intermedia	+	+	O	O	+	O	O	⊖	O
<i>Gennadas</i> Bate 11 spp.	O	O	O	O	O	O	O	O	O

EXPLANATION OF CAPTIONS AND SYMBOLS

+ indicates the condition to be as stated under the heading in question; O indicates the condition to be the reverse of that stated; ⊖ indicates the condition to be intermediate.

Character 1. Podobranchs are present on somites behind VIII.

Character 2. The gill of VII is larger and more richly plumose than the following maxillipedal pleurobranchs.

Character 3. The exopod of the first maxillipede has a slender, segmented tip.

Character 4. Pleonic segments in advance of the sixth are carinated in the dorsal midline.

Character 5. The telson is armed with more than a single pair of lateral spines.

Character 6. The telson terminates in a distinct median point.

Character 7. The infra-antennal angle of the carapace is not perceptible.

Character 8. The diameter of the second and third segments of the antennular peduncle nowhere much exceeds their articular diameter.

Character 9. The merus of the second maxillipedes is not expanded.

Of the points brought forward in Bouvier's generic definition, the thirteenth feature noted as characteristic of *Gennadas* is of great value, and is introduced in the fourth line of the foregoing table. The first feature, degree of development of infra-antennal angle, is of some value and is employed in the sixth line of the table; the angle, not marked in any species of *Benthesicymus*, although indicated as a low convexity in the *B. brasiliensis* complex, is in *Bentheogennema intermedius* conspicuous, but not sharp-pointed as in *B. borealis* (Rathbun) and *B. pasithaea* (DeMan), and in all the species of *Gennadas*. A number of other characters employed in Bouvier's generic definition seem to be of no

value whatever; these are the second (length of distal articles of antennular peduncle); the fourth, the fifth, and the seventh (distal article of endopod of first maxillipede). In the only specimen of *Benthesicymus* with unbroken antennal flagellum available to me (*B. bartletti*), the Sergestid-like geniculation occurs. The distal segment of the endopod of the first maxillipede is present in all available members of the series; in *Gennadas bouvieri* and *G. scutatus* it is as strong as in any species of *Benthesicymus*; in *Bentheogennema intermedia* as weak as in many species of *Gennadas*. Bouvier's third differential feature is hardly of diagnostic value; in *B. carinatus* the expanded portion of the flagellum is shorter than the peduncle; in *Bentheogennema intermedia* much shorter but longer than in available species of *Gennadas*. The eleventh, twelfth and fourteenth differentials are of slight interest; leg exopods, relatively strong in *B. crenatus*, *B. carinatus*, and the *B. brasiliensis* complex, are present but very minute in the *B. bartletti* group and in *Bentheogennema intermedia*, and occur as hardly discernible vestiges in *Gennadas elegans*. The relative length of the exopod of the second maxillipede, utilized as a diagnostic character by Alcock, 1901, seems to grade from the state found in *B. brasiliensis* and *B. bartletti*, in which it is longer than the endopod, through *B. carinatus* and *B. crenatus* where it is shorter than the endopod, to *Bentheogennema* and *Gennadas* where it never reaches beyond the propodus.

Among features of systematic interest not considered by previous investigators, the thelycum of the species of *Benthesicymus* which are segregated below as Group I displays no recesses for sperm storage and is quite probably utilized for anchorage of large external spermatophores such as seem to be employed among Aristeae (as in the figure of *Aristaeus antennatus* by Bouvier, 1908). It is of interest that in Group I, male and female genital sternites are very similar. On the other hand, the thelycum of the *B. bartletti* group is of somewhat similar form to that of *Gennadas* and *Bentheogennema*, since it includes more or less well enclosed receptacles between the twelfth and thirteenth sternites. Various types of petasma occur in the maniple; they are somewhat irregularly distributed. The petasma of *Gennadas* always includes the *LOBUS ACCESSORIUS* of Balss, 1927. In *Gennadas kempfi* Stebbing and *G. capensis* Calman the petasma is otherwise rather simple and closely resembles that of the *Benthesicymus bartletti* group. The lobus accessorius is fairly well developed in *Benthesicymus altus*, where it is armed with denticles; in *B. bartletti*, *B. tanneri*, and *B. investigatoris* it is only very weakly developed, and the petasma is hardly differentiable from that of *Bentheogennema intermedia* and *B. borealis*, in which there is no trace of lobus accessorius. In *Bentheogennema pasithaea*, on the contrary [assuming Balss to be correct in synonymizing with it *Gennadas praecox* Kemp, and Kemp to have rightly identified male with female], the accessory lobe is strongly developed. The accessory lobe seems to be absent from the curiously elongated petasma of

Benthesicymus crenatus, *B. carinatus*, and the *B. brasiliensis* complex; however, the homologies are difficult to interpret, and it is possible that the cincinnulated ridge lateral to the unarmed median margin of the petasma in these forms represents the accessory. In all available specimens of *Bentheogennema intermedia* the telson bears four pairs of mobile lateral spines; which are figured, although not mentioned by Bouvier, 1908 (sub *Gennadas alicei*); and the distal two pairs of which are described and figured by Kemp, 1909. In *Bentheogennema borealis* (Rathbun) 1910, the telson bears "a small lateral spine at its posterior fourth, two spines at the tip"; Kemp, 1909, notes the two distal pairs in one of his specimens (sub *Gennadas calmani*). In *Bentheogennema pasithaea*, DeMan finds a small proximal pair of spines as in *B. borealis*; these are not noted by Kemp, 1909 (sub *Gennadas praecox*). It seems probable that more than one pair of mobile lateral spines is actually present in all specimens of *Bentheogennema*. Only a single, distal, pair is known to occur in any species of *Gennadas*. The telson has a small median terminal spine in *Benthesicymus crenatus*, *B. carinatus*, *B. brasiliensis* and *B. bartletti*; in *B. tanneri* this spine is very minute and inconstant; in *B. altus* it is absent and the lateroterminal mobile spines enclose between them a wide distal margin which is, however, convex rather than straight or concave as in *Gennadas*. In *Bentheogennema intermedia* the distolateral mobile spines are placed close together, but the margin between is not produced as a median spine.

A character which might from the discussion seem of value for more than specific differentiation has been described by Hanström, 1933 and 1934, who finds that there occurs in some but not all *Benthesicymae* a pigment fleck lying in the ocular peduncle proximal to the corneal region. This fleck is believed by Hanström to represent cells which have migrated from the position of the tapetum layer of other decapods. The extra-ocular pigment fleck is stated to be present in "*Benthesicymus bartletti*," "*B. longipes*," "*B. A.*," "*B. B.*," "*Amalopenaeus A.*," and "*A. B.*" [which last Hanström thinks may be identical with *Gennadas elegans* (Smith)]; but absent in "*Gennadas A.*" A peculiar outgrowth of the proximolateral region of the rhabdome layer is also described in "*Benthesicymus B.*" and "*Amalopenaeus B.*" which is absent or little developed in the other form. Since it is difficult to judge which genera or species may be represented by the above references, an examination in optical section and by dissection of the eyes of available material of *Benthesicymae* has been resorted to with the following results:

The pigment fleck is absent only in *Benthesicymus carinatus*, in which the "Wucherung der Rhabdomschicht" likewise seems not to occur. This species is therefore likely to be Hanström's "*Gennadas A.*" In *Benthesicymus bartletti* and species of the *B. brasiliensis* complex; and in *Bentheogennema intermedia*, to which it is likely that Hanström's "*Amalopenaeus A.*" refers, no "Wucherung" is clearly perceptible, and the pigment fleck is small, situated just laterad the

distal part of the optic nerve and considerably median and ventral to the main muscle-strand of the peduncle. In *Gennadas tinayrei* and *G. kempfi* alone of available species of that genus does the "Wucherung" seem to be absent; and it is possible that Hanström's "*Amalopenaeus* A" may refer to the former species; unfortunately Hanström's use of the term "*Amalopenaeus*" in reference to descriptions by DeMan does not make clear whether his application is to forms with or to those without posterior podobranchs, although the evidence seems to favor the former intention. The pigment fleck of *G. tinayrei* is relatively large. In *G. elegans* and *G. scutatus*, the "Wucherung" is very large, the pigment fleck relatively small and placed near the proximomedian end of the "Wucherung," between the main muscle-strand and the optic nerve, nearly in the middle of the peduncle. Since in Hanström's "*Amalopenaeus* B" there is a "sehr grossen Pigmentfleck" which "grenzt unmittelbar an die Hypodermis der Lateralseit des Augenstiels," it seems possible that this species is not, as he thinks it to be, *Gennadas elegans*. In *Gennadas bowieri*, *G. valens*, and *G. capensis*, there is a moderately large "Wucherung," with a moderately large pigment mass at its proximal end which is almost in contact with the ventrolateral surface of the peduncle; it is therefore possible that Hanström's "*Amalopenaeus* B," taken south of Iceland, may refer to *Gennadas valens*.

A peculiar variation in distribution of the pigment mass in *G. capensis*, which is perhaps attributable to imperfect fixation, may here be described. In some specimens the fleck is very compact, and is localized ventromedian to the distal end of the main muscle-strand. In others, a varying degree of diffusion toward the proximal end of the peduncle occurs, in which the pigment is not scattered through the cavities of the peduncle, but is deposited on the surface of the muscle-strand, in some cases completely enwrapping it. A similar but much less extensive diffusion is seen in a few specimens of *G. valens* and *G. bowieri*. In *G. scutatus* and *G. elegans*, on the other hand, the fleck is occasionally diffused, but in a distal direction, along the median surface of the "Wucherung." A peculiarity of the eye of *Benthescymus investigatoris* not previously described will be discussed in a later paragraph.

The above analysis indicates that the regularity in distribution of pigment-fleck among Benthescymae suggested by Hanström's account, is actually based in the author's method of application of the generic names. It is, however, true that in absence of "Wucherung" and position of pigment fleck *Bentheogennema* more nearly resembles the condition usual in *Benthescymus* than that found in available material of *Gennadas*, a circumstance in agreement with other morphological data. However, the absence of "Wucherung" in *Gennadas tinayrei* and *G. kempfi*, its presence in Hanström's indeterminate "*Benthescymus* B," indicates that these structures, like so many other interspecifically variable features of the Benthescymae, have an irregular distribution. The absence of pigment-fleck in *Benthescymus carinatus*, instead of characterizing "*Gennadas*" is seen to represent an individual divergence from the norm of *Benthescymus*.

The above review of the distribution of significant characters among Benthescymae seems to show that the series is very closely knit, intergrading in most of the characters previously emphasized, or, where breaks occur, showing little correlation between different features in position of the break. However, in the presence, absence, or combination of the first six characters listed in the table, a means of distinguishing between three natural groups of Benthescymae of generic importance seems indicated. It is clearly shown above that *Bentheogennema* possesses no unique characters, and that it occupies a position intermediate between *Benthescymus* and *Gennadas*. Should future studies break down the balance of characters distinguishing the intermediate group from the two extremes, it is not probable that *Gennadas* can be considered a group naturally distinguished from *Benthescymus*.

It is believed by Kemp, 1910b, that structural differentiation among Benthescymae is paralleled by differences in habit, the species of *Benthescymus* being benthonic, those of "*Gennadas*" pelagic. This conception may receive a qualified confirmation, although in its practical application Kemp has fallen into error. According to him, Smith's *Benthescymus* ? *carinatus*, with limb joints greatly expanded as in *Bentheogennema* and *Gennadas*, is probably like them pelagic, and should therefore be referred to "*Gennadas*." The foregoing analysis of structural characters has clearly shown "*G.*" *carinatus* to be a typical member of the genus *Benthescymus*. An examination of the literature indicates that on four occasions *B. carinatus* has been taken by apparatus working on bottom, while once, by Sund (1920), it has been recorded from a pelagic haul. One other pelagic record of *Benthescymus* is known, two specimens of "*B. longipes* Bouvier" (a member of the *B. brasiliensis* complex with weakly expanded leg-joints), being reported by Sund, 1920, as having been taken at a point calculated to be not less than 800 meters above bottom. While there are many records of *Bentheogennema* and *Gennadas* from bottom hauls, a great mass of catch data makes it practically certain that the species of these two genera are pelagic in habit, and are taken with bottom apparatus by accident. Hanström, 1934, has called attention to the fact that in species of "*Amalopenaeus*" the open statocyst contains a self-secreted statolith rather than a concretion of foreign particles; and has suggested that a similar statolith may be expected to characterize pelagic shrimp in general. In agreement with Hanström's suggestion, a hypodermal concretion is present in specimens of *Bentheogennema* and of *Gennadas* (as well as in the Penaeine *Funchalia*). On the contrary, I find that in specimens of the *Benthescymus brasiliensis* complex, in *B. carinatus*, and in *B. bartletti*, presumably captured on bottom, the statocyst contains a loose rubble of foraminifera and indeterminable bottom-debris, more or less consolidated by amorphous hypodermal material. Therefore, although the records by Sund indicate that the species of *Benthescymus* are not limited to a benthonic existence (a probability mentioned by Bouvier, 1906a, in connection with

other species of the genus than "*Gennadas*" *carinatus*), it is certain that they resort to the bottom. As in the similar case of certain species of the Solenocerine *Hymenopenaeus*, I would suggest that some members of *Benthesicymus* may be quasipelagic, although the contrast in habit between *Benthesicymus* including *B. carinatus* on the one hand, and *Bentheogenmema* and *Gennadas* on the other remains, as reflected in the nature of the statolith, a sharp one.

BENTHESICYMUS Bate

Benthesicymus, Bate, 1881 and 1888; Smith, 1882, 1884 and 1887; Faxon, 1895;

Alcock, 1901; Bouvier, 1908; DeMan, 1911; Schmitt, 1924.

Benthoecetes, Smith, 1884 and 1887.

Gennadas, part, Alcock, 1901; Kemp, 1910b; DeMan, 1911; Schmitt, 1924.

? *Gennadas*, Hanström, 1933 and 1934.

Benthesicymae with a podobranch on somites VIII–XII. Gill of VII larger than pleurobranch of VIII. Exopod of the first maxillipede distally constricted and segmented. Pleonic terga in addition to that of XX carinated. Telson with four pairs of mobile lateral spinules; a small posteromedian point usually present. Dactyls of the fourth and fifth legs not subdivided.

Sixteen species of the genus (not including the three added in the present paper) have been described, the validity of only seven of which is certain. Aside from the lack of exact knowledge of intraspecific variation which is responsible for the difficulties of synonymy, scant information has been available even as to the differences between the seven clearly distinct species or super-species. Disregarding for the present the question, whether the *Benthesicymus brasiliensis* and *B. crenatus* groups contain one or many species, the structural relationships within the genus may be described as follows:

SYNOPSIS OF THE GENUS BENTHESICYMUS

- Group I.* Thelycum without well-defined receptacles between the twelfth and thirteenth sternites, the scutes of the twelfth and thirteenth sternites being simple and unexpanded. Distoventral lobe of the petasma separated from the distolateral by a deep notch. Median margin of the petasma unarmed, the cincinnuli being borne on a ridge extending up the anterior face of the organ. Exopod of the first maxillipede narrowing abruptly to the segmented distal portion. Merus of the second maxillipede expanded, less than three times as long as broad (except in *B. strabus*, n. sp.). Dactyl of third maxillipede triangular, with no more than one strong spine at the tip. Exopodites of the walking legs small but easily perceptible. Pterygostomial spine, in lateral view, placed at the margin of the carapace. Pterygostomial carina not sharp.
- 1A. Posterolateral margins of the fourth pleonic tergite without a comb-like series of strong serrae. Antennal carina strong. Cardiacobranchial carina turning ventrally in its posterior part, ending below

the posterolateral shoulder of the carapace. First chelipeds without a slender, well-defined tooth at distal ends of basis and ischium.¹

- IA 1. Hepatic tooth present. Pterygostomian carina very weak, and not extending posteriorly as far as the level of the hepatic buttress. A moderately strong tooth on the ventrolateral margin of the sixth pleonic segment, just anterior to the postero-ventral angle. Tooth of the first pleonic sternite small or absent. Merus of second maxillipede only moderately expanded, more than two and one-half times as long as broad.² *B. brasiliensis* Bate and related forms (cf. *B. cereus*)
- IA 2. Hepatic tooth absent. Pterygostomian carina obtuse but well-defined, and extending far behind the level of the hepatic buttress. No tooth on the ventrolateral margin of the sixth pleonic segment. Tooth of the first pleonic sternite very strong. Merus of second maxillipede considerably expanded, only about twice as long as broad.

B. carinatus Smith.

- IB. Posterolateral margins of the fourth pleonic tergite with a comb-like series of strong serrae. Antennal carina absent. Cardiac-branchial carina not turning ventrally at its posterior end, terminating at the level of the posterolateral shoulder of the carapace. First cheliped armed on basis and ischium.

Hepatic tooth absent. Pterygostomian carina very weak, and not extending posteriorly as far as the level of the hepatic buttress. A strong tooth on the ventrolateral margins of the sixth pleonic segment. Tooth of the first pleonic sternite very strong. Merus of second maxillipede strongly expanded, less than twice as long as broad.

B. crenatus Bate³ and related forms.

- Group II. Thelycum with well-defined cavities between the twelfth and thirteenth sternites, the scute of the thirteenth sternite being broadly expanded to overlap the sternal surface proper. Distoventral and distolateral lobes of the petasma not sharply separated. Median margin of the petasma cincinnulated. Exopod of the first maxillipede tapering gently to the tip. Merus of the second maxillipede unexpanded, not less than three and one-half times as long as broad. Dactyl of third maxillipede subrectangular, the distal margin bearing more than one strong spine. Exopodites of the walking legs very minute. Pterygostomian spine, in lateral view, set behind the margin of the carapace. Pterygostomian carina very sharply defined.

¹ In all of these features the two species of Section IA agree with Group II, except that the antennal carina is there weaker, though variable (ranging in strength from moderate in *B. bartletti* to absent in *B. investigatoris*).

² In all of these features, the *B. brasiliensis* complex differs from the species of Group II, although in degree of expansion of merus of second maxillipede it approaches Group II more closely than do the other species of Group I.

³ Diagnosis derived from an Hawaiian male, which differs from Bate's description in several of the features mentioned (see succeeding paragraphs).

- IIA. Ocular peduncle not much longer than the cornea is broad; ocular tubercle situated near distal end of median margin of peduncle. Scute of the thirteenth sternite of the female posteriorly overlapping the fourteenth sternite, anteriorly not projecting free in the midline. Distoventral *projection*¹ of the petasma not rising much above the distoventral *flap*.²
 Accessory lobe of the petasma rudimentary. Fifth and sixth pleonic tergites with a short strong tooth at the posterior midmargin.
B. investigatoris Alcock and Anderson.
- IIB. Ocular peduncle about twice as long as the cornea is broad; ocular tubercle at or proximal to the middle of the median margin of the peduncle. Posterior margin of the scute of thirteenth sternite of the female not overlapping the fourteenth; anterior part projecting free in the midline. Distoventral projection of the petasma rising considerably above the distoventral flap.
- IIB 1. Distoventral lobe of the petasma not rising very high above the distolateral; accessory lobe fairly well developed and with denticulate margin. Fifth and sixth pleonic tergites not terminating in a tooth; posterior margin of the sixth tergite upturned. *B. altus* Bate.
- IIB 2. Distoventral lobe of the petasma rising conspicuously above the distolateral as a slender projection; accessory lobe very weak.
- IIB 2a. Fifth and sixth pleonic tergites with a short, strong tooth at the posterior midmargin. *B. tanneri* Faxon.
- IIB 2b. Fifth pleonic tergite with a long slender tooth springing from the middle of its length; sixth pleonic tergum armed very weakly or not at all. *B. bartletti* Smith.

Tracing the distribution throughout the series of features distinguishing the various groups of *Benthesicymus*, it is found that in form of thelycum and petasma, in slight development of exopods of the walking legs, and perhaps in slight differentiation of distal end of exopod of first maxillipede, Group II resembles *Bentheogennema* and *Gennadas* more closely than does Group I; while in form of merus of second maxillipede and of dactyl of third maxillipede, Group I resembles *Bentheogennema* and *Gennadas* more closely than does Group II. The pterygostomial spine and carina are generally well developed in *Gennadas*, but are weak or absent in *Bentheogennema intermedia*. The spine anteroventral to the posteroinferior corner of the sixth pleonic somite is sometimes present but always of microscopic dimensions. The sixth pleonic segment bears a trace of posterodorsal tooth in *Bentheogennema intermedia*, which is absent in *Gennadas*.

¹ The more median part of the distoventral lobe, which in the *Benthesicymae* surmounts the more lateral portion of the lobe.

² The distal end of the lateral margin of the petasma, in *Benthesicymae* separated from the distoventral projection by a more or less conspicuous notch; in *Metapenaeopsis* greatly produced to form a spiral coil (cf. Burkenroad, 1934b).

It may be observed that the three species or superspecies of Group I are much more strongly distinguished one from another than are the four species of Group II. The question of degree of specific differentiation within the sections of Group I is a difficult one. As no specimens of Section IB are contained in the Bingham Collection, the synonymy of this complex will be discussed under the present general heading.

The first species of IB, *Benthesicymus crenatus*, the genotype, was described by Bate, 1881 and 1888. A second Indo-Pacific species, *B. laciniatus*, was differentiated from Bate's form by Rathbun, 1906. A third species, *B. hjorti*, described from the North Atlantic by Sund, 1920, was distinguished by its author from *B. crenatus* alone, without recognition of Rathbun's observations. A fourth species, *B. pectinatus* (Schmitt), 1924, from the American Pacific, has been set up without consideration of the preceding descriptions, since it was referred to *Gennadas* on the basis of a nondiagnostic definition apparently derived from Alcock, 1901, which utilized the characters supplied by relative length of the exopods and degree of expansion of the meri of the endopods of the second maxillipedes.

Through the great kindness of Dr. W. L. Schmitt of the U. S. National Museum, I have been enabled to examine an adult male of *B. laciniatus* Rathbun of carapace length about 33 mm, presumably a paratype, from "Albatross" Station 4183. It is from this specimen that the definition of the *B. crenatus* group given in preceding paragraphs has been derived. The present specimen differs from Bate's account in several essential features, but the uncertainty always attaching to Bate's observations makes caution in employing them a necessity. Careful comparison of the available specimen with the literature results as follows:

The type of *B. crenatus* is a female of 200 mm total length which differs from all other known members of the group, according to the description, in that an hepatic spine is said to be present; the cardiaco-branchial carina is figured as extending to the posterior margin of the carapace, which it strikes at a point below the level of the shoulder; the merus of the second maxillipede is figured as only slightly expanded; a tooth is said to occur on the dorsal midline of the carapace posterior to the orbital margin; and there are three rostral teeth, which are borne on a high crest. As to the first three of these characters, it may be suggested that a reexamination of the type might indicate that the statements are not accurate. As to the fourth point, it seems possible that Bate has mistaken the lenticular vestige of the larval anterior dorsal organ for the remains of a tooth, and has "restored" the tooth in description and figure. In the fifth character, Bate may well be correct, but it may be noted that the occurrence of a third rostral tooth is known as an occasional variation in other species of the genus. Whether Bate's paratypes are identical with the type in rostral armature is not known. Bate's illustrations of the appendages of his

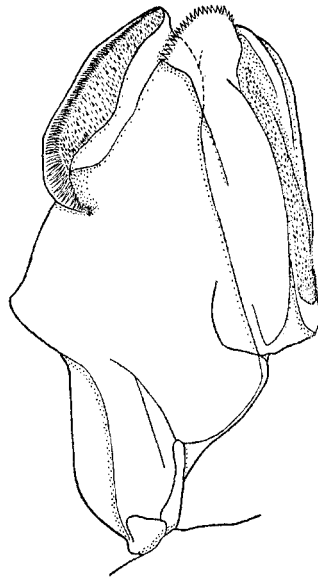
form are doubtfully correct; thus whereas the antennular flagella are described in the text as broken, they are figured as complete. Special mention of the differences from subsequent descriptions seems necessary only for the figure of the dactyl of the third maxillipede, which shows no resemblance to the highly characteristic form (a sub-rectangular basal part narrowing suddenly to a slender terminal portion nearly as long as the base, and tipped with a very long and slender spine) found in the Hawaiian male. As Sund's figure of the third maxillipede of a female also displays little resemblance to that structure in the available male, it seems possible that sexual dimorphism, as in the species of Group II, may occur.

Turning now to Sund's account of Atlantic and to Schmitt's of Pacific American material, it is found that in the illustrations by both, the cardio-branchial carina is shown as sloping upward in a straight line in its posterior part; whereas in the present male, the carina is slightly but definitely bent in this region, so that in its entirety it displays a sigmoid curvature. Sund's specimen seems to agree with the Hawaiian one and to differ from Schmitt's photograph in the shallowness of the anterior cervical sulcus, especially in its dorsal portion. In the Hawaiian specimen the posterior cervical sulcus, though nearly obsolete ventrally, is deeper cut dorsally than is the anterior cervical. The posterior rostral tooth of Sund's specimen is shown as placed well in advance of the orbital margin, and the eye as not extending beyond the rostrum, as in the Hawaiian specimen rather than in Schmitt's. The antennal scale is figured as shorter relative to the antennular peduncle in the Atlantic specimen, and its blade as extending much less far beyond the external tooth than in Schmitt's specimen and in the Hawaiian one. Sund's figure of the second maxillipede differs from Schmitt's photograph and from the Hawaiian specimen in the claw-like form of the dactyl and the lack of a large triangular projection at the inner distal edge of the propodus. The merus, propodus, and especially the dactyl of the second maxillipede of Schmitt's female seem shorter than in the Hawaiian male; the meri of the fourth and fifth legs are of the same lengths proportional to the carpi in both, but seem much shorter relative to sixth pleonic segment and to telson in Schmitt's specimen. The posterodorsal margin of the epimeron of the fifth pleonic somite in the Hawaiian specimen seems to have borne a large projection (of which, however, only the base remains) such as Schmitt describes for his Pacific American specimen. Rathbun's figure, photograph and brief description of the type female of her Hawaiian form are in agreement with the present male.

If Bate's account of the carapacic sculpture of *B. crenatus* corresponds to reality, this species is highly distinct from the other forms with spinous posterior margin of the eighteenth somite; but the relative proximity of the Low Archipelago to the Hawaiian Islands, and the uniformity of other material, engenders some doubt of Bate's accuracy. The distinctness of *B. hjorti* and *B. pectinatus*

from *B. laciniatus*, with which neither has been previously compared, seems doubtful, in spite of the divergences mentioned above (such as the deep cervical sulcus indicated by Schmitt's photograph) between the various accounts.

The petasma of the *B. crenatus* has not been previously described. In the available Hawaiian male (figure 1, p. 28), the organ differs from that of *B. carinatus* and the *B. brasiliensis* complex by its much greater breadth, especially that of its distoventral lobe, the free edge of which is thickened and armed with



Petasma, left half, anterior face. 1. *Benthescyrmus laciniatus* Rathbun, $\times 3.6$.

a double series of spines (a long, curved, marginal row in single file and a more anterior group of numerous straight short spinules). The distolateral lobe is large and is distally expanded like that of the *B. brasiliensis* group, but like the distoventral lobe it is armed with a conspicuous row of long spines, instead of minute denticles. The distomedian lobe is a well-defined projection somewhat like that of *B. carinatus*. The two endopods are rather insecurely attached by hooked spines arming a submedian ridge which may be homologous with the accessory lobe of certain *Benthescyrmæ*; it is therefore uncertain that these spines are homologues of the cincinnuli which perform the coupling function elsewhere in the family.

The anteroventral slope of the median projection of the coxa of the second, third and fourth legs is armed with a conspicuous slender tooth. A similar but

much smaller tooth is found in males of *B. carinatus* and the *B. brasiliensis* complex. This armature seems to be absent in the males of Group II. It is interesting to observe the persistence of a small parapeneid spine on the basal segment of the antennular peduncle of the present adult male of *B. laciniatus*.

GROUP I

As has already been discussed in detail under the generic heading, Group I includes three distinct species or complexes of species which center respectively

SYNONYMY OF THE *B. BRASILIENSIS* COMPLEX

Author's Name	Author	Locality	No. of specimens	Revised determination
<i>brasiliensis</i>	Bate, 1881 and 1888	Buenos Aires	4	<i>B. brasiliensis</i> Bate ¹
<i>brasiliensis</i>	Bate, 1888	Torres Strait	4	<i>B. urinator</i> , n. sp. ¹
<i>brasiliensis</i>	Bate, 1888	Fiji Islands	1	<i>B. iridescens</i> Bate ¹
<i>brasiliensis</i>	Bate, 1888	Between Australia and the Solomons	1	<i>B. iridescens</i> Bate ¹
<i>brasiliensis</i>	Bate, 1888	New Zealand	2	<i>B. cereus</i> , n. sp. ¹
<i>brasiliensis</i>	Bate, 1888	South Pacific	1	<i>B. strabus</i> , n. sp. ¹
<i>iridescens</i>	Bate, 1881 and 1888	Tristan da Cunha	2	<i>B. iridescens</i> Bate ¹ <i>B. brasiliensis</i> Bate ¹
<i>mollis</i>	Bate, 1888	Tristan da Cunha	3	<i>B. iridescens</i> Bate ¹
<i>moratus</i>	Smith, 1887	Middle Atlantic coast of the U. S.	5	<i>B. brasiliensis</i> Bate ¹
<i>armatus</i>	MacGilchrist, 1905	Arabian Sea	1	<i>B. iridescens</i> Bate
<i>moratus</i>	Rathbun, 1906	Hawaiian Islands	2	<i>B. urinator</i> , n. sp. ¹
<i>longipes</i>	Bouvier, 1906b and 1908	Cape Verde Islands	2	<i>B. iridescens</i> Bate
<i>moratus</i>	Bouvier, 1908	Morocco and the Cape Verde Islands	2	<i>B. brasiliensis</i> Bate
<i>moratus</i>	Milne-Edwards and Bouvier, 1909	Gulf of Mexico	1	<i>B. brasiliensis</i> Bate
<i>brasiliensis</i>	Sund, 1920	Canary Islands	1	<i>B. brasiliensis</i> Bate (?)
<i>longipes</i>	Sund, 1920	Canaries, Central North Atlantic	3	<i>B. iridescens</i> Bate (?)
<i>longipes</i>	Bouvier, 1922	Atlantic Spain	1	<i>B. iridescens</i> Bate
<i>longipes</i>	Hanström, 1933 and 1934	Madeira	—	<i>B. iridescens</i> Bate (?)

¹ Responsible revised determinations, based on direct examination.

about *Benthesicymus crenatus* Bate, (p. 26) *B. carinatus* Smith (p. 46) and *B. brasiliensis* Bate. The latter complex especially has been greatly in need of revision, a summary of the results of which is presented in the following list of the specimens which have been previously described. Detailed morphological comparisons of the forms are given below under the heading, *Benthesicymus cereus*.

***Benthesicymus cereus*, new species**

Figure 6, p. 31; 11 and 12, p. 35; 19, p. 36; 24, p. 37; 28, p. 39; 35, p. 40; 42, p. 41; and 47, p. 43.

1 subadult female, holotype; carapace length 25 mm., total about 76 mm. *B. O. C. 152*. Pawnee St. 54; N. 21° 15' 40'', W. 71° 17' 06''; April 12, 1927. Wire 7500 feet (bottom struck at 900-945 fathoms).

A fragment of a juvenile male, probably of the same species, of carapace length 18 mm. was taken in the same haul; it is referred to below as ? *B. cereus*. Two females taken by the "Challenger" have also been examined.

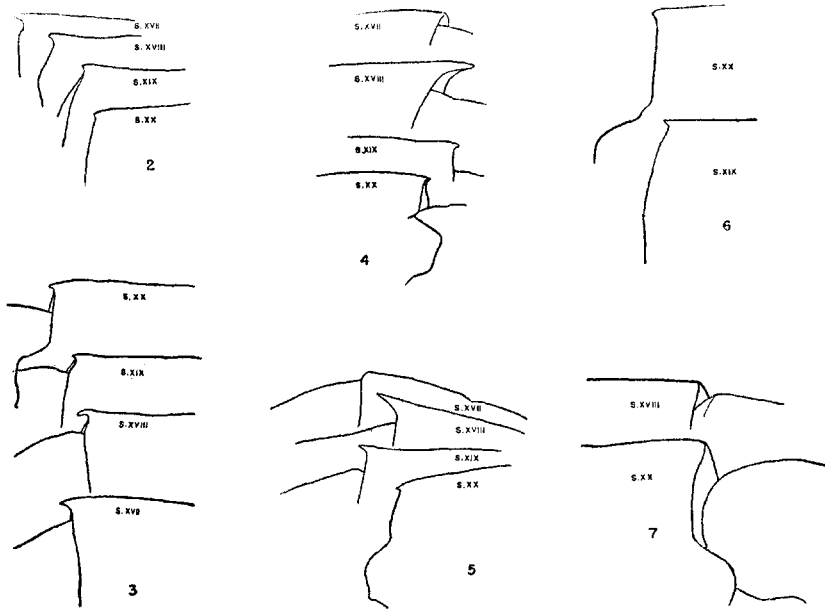
As five specific names are already available for the forms related to *Benthesicymus brasiliensis*, the description of *B. cereus* must be preceded by a revision of the complex. I have been enabled, through the great kindness of Dr. Calman and Dr. Gordon of the British Museum, Dr. Schmitt of the U. S. National Museum, and Dr. Ball of the Peabody Museum at Yale, respectively, to examine all of Bate's material, both of Rathbun's Hawaiian specimens, and the two females reported by Smith from "Albatross" Stations 2174 and 2222. Of a total of about 39 known specimens (including the two contained in the Bingham Collection), 24 have therefore been available for the present revision, including four of the six lots of type material. The types of *B. armatus* and *B. longipes* have not been examined.

The history of differentiation of the complex is as follows:

Benthesicymus moratus was described by Smith at a time when Bate had published only the unrecognizable preliminary diagnosis of *B. brasiliensis*. Bate's final account of *B. brasiliensis*, *B. iridescens*, and *B. mollis* is extremely poor, and these names have consequently never attained currency. MacGilchrist, with some justification, fails to compare his *B. armatus* with *B. iridescens*, and in noting that *B. moratus* (and *B. armatus*) differs from the description of *B. brasiliensis* by possession of an hepatic spine, clears the ground for an attribution of subsequent material of *B. brasiliensis* to Smith's rather than to Bate's name. Bouvier, having overlooked MacGilchrist's description, distinguishes *B. longipes* only from *B. moratus*. Meanwhile, Rathbun, with the mistaken statement that her specimens agree with Smith's description, attributes Hawaiian material to *B. moratus*. Finally, Sund revives the name *B. brasiliensis*, disused for more than thirty years, for a specimen which is possibly quite properly so designated. If Sund's specimen actually agrees with Bate's de-

scription of *B. brasiliensis*, except for the differences which he remarks, its affinities are doubtful; but it seems more probable that Sund has simply overlooked Smith's and Bouvier's accounts of *B. moratus*, the name to which specimens of *B. brasiliensis* have usually been referred.

A comparison of the few specimens of the *B. brasiliensis* complex included in the Bingham Oceanographic Collection and in that of the Department of



Tergites of posterior pleonic somites, lateral view (showing posterodorsal armature). 2. *Benthescymus brasiliensis* Bate (Specimen No. 3, TYPE), $\times 3.1$. 3. *B. brasiliensis* Bate (No. 6), $\times 3.1$. 4. *B. urinator*, n. sp. (No. 8, TYPE), $\times 4.3$. 5. *B. urinator*, n. sp. (No. 12), $\times 3.1$. 6. *B. cereus*, n. sp. (No. 16), $\times 3.1$. 7. *B. iridescens* Bate (No. 19, TYPE), $\times 3.1$.

Zoology of Peabody Museum with the literature had indicated that the named species were very poorly distinguished by their authors, and had inclined me to the opinion that the complex represented a single species, highly variable, especially in character of the armature of the pleonic tergites. This assumption seemed reasonable enough by analogy with the variation found in such forms as *Hymenopenaeus laevis* Bate; although it was recognized as peculiar that very little tendency to similar variation in pleonic armature could be discovered in other species of *Benthescymus*. Upon examination of the "Challenger" and Hawaiian material, however, it became clear that specimens from widely separated localities with similar pleonic armature display comparable simi-

STRUCTURAL CHARACTERS OF AVAILABLE SPECIMENS OF THE

Species and Locality	Reference #	Sex	Carapace Length (mm)	Armature of Pleonic Tergites ¹			
				XVII	XVIII	XIX	XX
<i>B. brasiliensis</i> Bate (TYPE, #3) Buenos Aires "Chall." St. 323	1	♂	35	+	+	+	+
	2	♂	22.5	+	+	+	+
	3	♀	48.5	+	+	+	(+)
	4	♀	24.8	+	+	+	+
Tristan da Cunha "Chall." St. 133	5	♀	16	+	+	+	+
Atlantic U. S. A. "Alb." St. 2174	6	♀	33.2	+	+	+	+
Atlantic U. S. A. "Alb." St. 2222	7	♀	32	+	+	+	+
<i>B. urinator</i> n. sp. (TYPE, #8) Torres Strait "Chall." St. 184	8	♂	22	0	+	+	+
	9	♂	16	0	+	+	+
	10	♀	19.5	0	+	+	+
	11	♀	13.5	0	+	+	+
Hawaii "Alb." St. 4185	12	♂	25	0	+	+	+
	13	♀	14	0	+	+	+
<i>B. cereus</i> n. sp. (TYPE, #14) Bahamas "Pawnee" St. 54	14	♀	25	0	0	0	+
	15 ⁹	♂	18	—	—	—	—
New Zealand "Chall." St., 168	16	♀	25.1	0	0	+	+
	17	♀	16.2	0	0	0	+
<i>B. strabus</i> n. sp. (TYPE, #18) South Pacific "Chall." St. 285	18	♂	17.5	0	0	0	+
<i>B. iridescens</i> Bate (TYPE, #19) Tristan da Cunha "Chall." St. 133	19	♂	47	0	0	0	0
	20	♂	22	0	0	0	0
	21	♂	20	0	0	0	0
	22	♀	15	0	0	0	0
Fiji "Chall." St. 173	23	♂	45	0	0	0	0
Australia-Solomons "Chall." St. 181	24	♂	18.5	0	0	0	0

B. *BRASILIENSIS* COMPLEX (EXPLANATORY FOOTNOTES ON PAGE 34)

Rostral Armature ^e	Telson Ratios		Antennal Scale ⁵	Armature of Genital Sternites ⁶			Appendix masculina ⁷		Petasma ⁸	
	A ³	B ⁴		XII	XIII	XIV	Ant. blade	Post. blade	Disto- ventral lobe	Disto- lateral lobe
P	.46	.75	.30		br. Δ	0	o	sl.	Δ	n.
P	—	.79	.28		br. Δ	0	o	sl.	(juv.)	(juv.)
P	.47	.94	.31		br. Δ	0	—	—	—	—
O	.27	.84	.28		br. Δ	sm. Δ	—	—	—	—
A	—	.69	—		br. Δ	sm. Δ	—	—	—	—
P	—	.72	—		br. Δ	0	—	—	—	—
P	.44	.88	.30		br. Δ	0	—	—	—	—
P	—	1.15	.26		sl. Δ	o	br. Δ	sl. sh.	\square	br.
P	.75	1.28	.29	lr. Δ	sl. Δ	o	br. Δ	sl. sh.	\square	br.
P	—	.97	.30		br. Δ	0	—	—	—	—
P	—	1.12	—		br. Δ	0	—	—	—	—
P	.67	.98	.27	h.	sh. Δ	0	br. Δ	sl. sh.	\square	br.
P	—	1.10	—	0	br. Δ	o	—	—	—	—
A	.19	.88	—	h.	br. Δ	0	—	—	—	—
P	—	—	.29	0	0	0	n. Δ	sl. sh.	Δ	n.
A	—	.92	.33	sp.	br. Δ	0	—	—	—	—
A	—	.73	.26		br. Δ	0	—	—	—	—
A	—	1.15	.24	0	sl. Δ	lr. Δ	o	spat.	interm.	interm.
O	—	—	—	o	sh. Δ	0	n. Δ	sl. l.	Δ	n.
A	—	.58	—		br. Δ	o	n. Δ	sl. l.	(juv.)	(juv.)
A	—	—	—	Δ	sh. Δ	o	n. Δ	sl. l.	Δ	n.
A	—	.59	.31	sl. Δ	sh. Δ	sh. Δ	(juv.)	(juv.)	(juv.)	(juv.)
—	—	—	.37	sp.	br. Δ	o	n. Δ	sl. l.	Δ	n.
A	.25	.68	.37	0	sh. Δ	sh. Δ	o	sl. sh.	(juv.)	(juv.)

larities in other features; which seems to indicate that the armature is a clue to specific distinctions, and is intra-, as opposed to inter-, specifically variable only within narrow limits.

A table of the chief characters of the available specimens of the *B. brasiliensis* complex is presented below. The specimens are arranged in order of pleonic spination.

The degree of intergradation between the various groups of specimens is somewhat less than is indicated by the tabular exposition. To begin with the pleonic armature itself (figures 2 through 7, p. 31), the shapes and relative dimensions of the spines are quite different in the forms with four (*brasiliensis*) than in those with three armed tergites (*urinator*). In all of the former, from three rather widely separated localities (western North Atlantic, western South Atlantic, and central South Atlantic), the spines diminish in size from the third through the sixth tergite; none is greatly enlarged; and that of the fourth is rather definitely hooked. In all of the latter, from two far removed localities (western South Pacific, central North Pacific), the tooth of the fourth tergite is an enormous projection, while those of the fifth and sixth are small and subequal. Some anomalies are found; in the type female of *B. brasiliensis*, the tooth of the sixth tergite is very small (an individual variation which Bate assumed to be the mode among his specimens); and in the larger New Zealand female of *B. cereus*, the fifth and sixth, instead of only the sixth, tergites are armed.

The next character listed in the table, position of posterior rostral tooth with reference to the orbital margin (figures 8 through 13, p. 35) is not of diagnostic value; but despite a range of variation sufficient to cause overlapping, the tooth may certainly be described as placed farther forward in *B. brasiliensis* and *B. urinator* than in *B. iridescens* and *B. cereus*. The rostrum seems usually to have a longer, slender tip in *B. brasiliensis* and *B. urinator* than in the other forms, but is variable in this respect as well as in height. The number of rostral

EXPLANATION OF CAPTIONS AND SYMBOLS

¹ Presence or absence of tooth of posterodorsal median margin of hinder four pleonic tergites. (SYMBOLS: + present, (+) minute, 0 absent.)

² Position of posterior rostral tooth with reference to orbital margin. (SYMBOLS: P posterior to, O over, A anterior to.)

³ Ratio A, of interval between penultimate and antepenultimate lateral spines of telson to that between ultimate and penultimate.

⁴ Ratio B, of interval between ultimate notch of lateral margin of the base of the telson and proximal of the lateral spines to that between ultimate and penultimate notches.

⁵ Ratio of breadth to length.

⁶ Size and shape of the median projection of the three posterior pereionic sternites. (SYMBOLS: 0 completely absent, ○ blunt protuberance, | longitudinal ridge, Λ spine, Λ scute, br. broad, h. high, lr. large, sh. short, sl. slender, sm. small, sp. anteriorly spinose.)

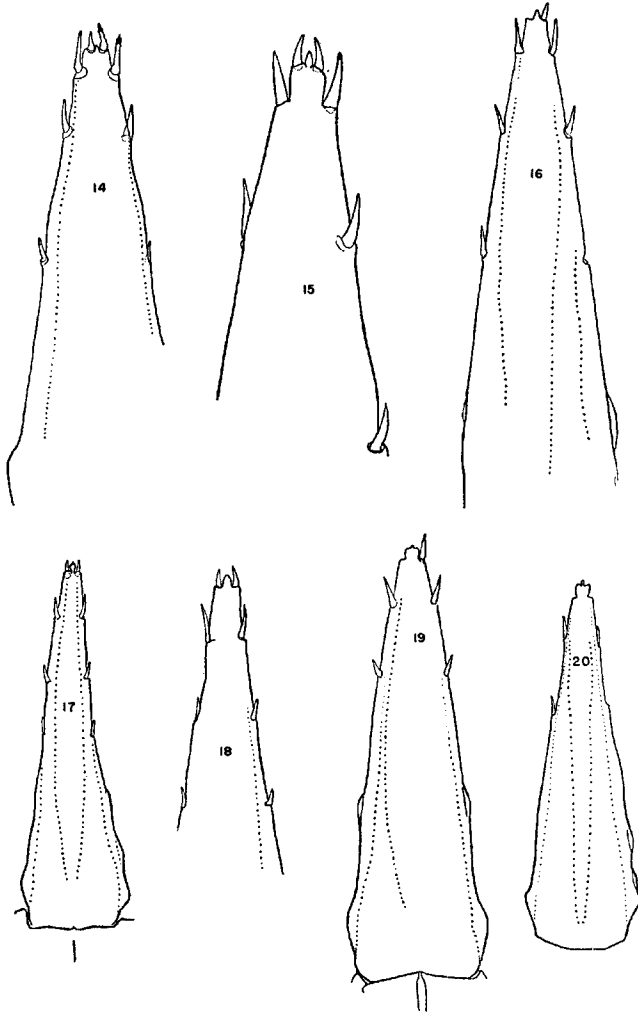
⁷ Shape of the anterior and posterior blades of the appendix masculina. (SYMBOLS: ○ elliptical, Δ triangular, br. broad, (juv.) juvenile, l. long, n. narrow, sh. short, sl. slender, spat. spatulate.)

⁸ Shape of the distal lobes of the petasma. (SYMBOLS: □ rectangular, Δ triangular, br. broad, interm. intermediate between Δ and □ or br. and n., (juv.) juvenile, n. narrow.)

⁹ Specimen damaged; determination uncertain. See p. 30.



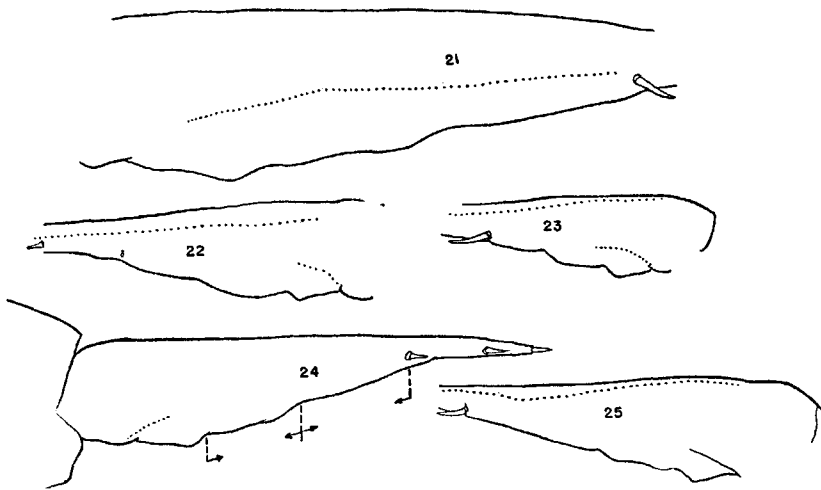
Anterior part of carapace, lateral view. **8.** *Benthescymus urinator*, n. sp. (Specimen No. 8, TYPE), X 3.6. **9.** *B. urinator*, n. sp. (No. 12), X 3.6. **10.** *B. strabus*, n. sp. (No. 18, TYPE), X 3.6. **11.** *B. ceruus*, n. sp. (No. 14, TYPE), X 3.6. **12.** *B. ceruus*, n. sp. (No. 17), X 3.6. **13.** *B. iridescens* Bate (No. 21), X 3.6.



Telson, dorsal view (showing lateral and terminal spines). 14. *Benthescycymus brasiliensis* Bate (Specimen No. 1), $\times 4.8$. 15. *B. brasiliensis* Bate (No. 4), $\times 11$. 16. *B. brasiliensis* Bate (No. 7), $\times 4.8$. 17. *B. urinator*, n. sp. (No. 9), $\times 4.8$. 18. *B. urinator*, n. sp. (No. 12), $\times 4.8$. 19. *B. cereus*, n. sp. (No. 14, TYPE), $\times 4.8$. 20. *B. iridescens*, Bate (No. 24), $\times 4.8$.

teeth is not completely constant. There are three teeth in both New Zealand specimens, and in the larger male from Buenos Aires. According to Bate, there is only a single tooth in the type of *B. iridescens*, and Bouvier, 1922, has reported a similar anomaly in another specimen (sub *B. longipes*).

The form of the telson, and especially of its lateral armature, seems to supply a very clear distinction between *B. urinator* and the other members of the complex (except possibly *B. strabus*), as may be even more readily perceived in the illustrations than from the numerical expressions. In the case of the degree



Telson, lateral view (showing distal basolateral crenellation, and proximal lateral spine; measured intervals indicated in Figure 24). 21. *Benthosicymus brasiliensis* Bate (Specimen No. 3, TYPE), $\times 4.4$. 22. *B. urinator*, n. sp. (No. 8, TYPE), $\times 4.4$. 23. *B. strabus*, n. sp. (No. 18, TYPE), $\times 4.4$. 24. *B. cereus*, n. sp. (No. 14, TYPE), $\times 4.4$. 25. *B. iridescens* Bate (No. 20), $\times 4.4$.

of separation of the ultimate from the penultimate spines, as compared with the interval between the penultimate and antepenultimate, only six individuals with entire telson are available (figures 14 through 20, p. 36). The close approximation of the two distal pairs of spines in the smaller of the female types of *B. brasiliensis*, as compared with the other specimens of that species, indicates that this ratio does not provide a diagnostic distinction between *B. brasiliensis* and *B. iridescens*, but it seems likely that a larger series would prove the modes to be different in all four forms. The subequal spacing of the spines in *B. urinator* gives the telson of that species a highly distinctive appearance. In the case of the relative distance by which the anteriormost lateral spine of the telson is separated from the crenellations of the proximolateral margin of the telson (figures 21 through 25, p. 37) a fairly complete series of measurements is avail-

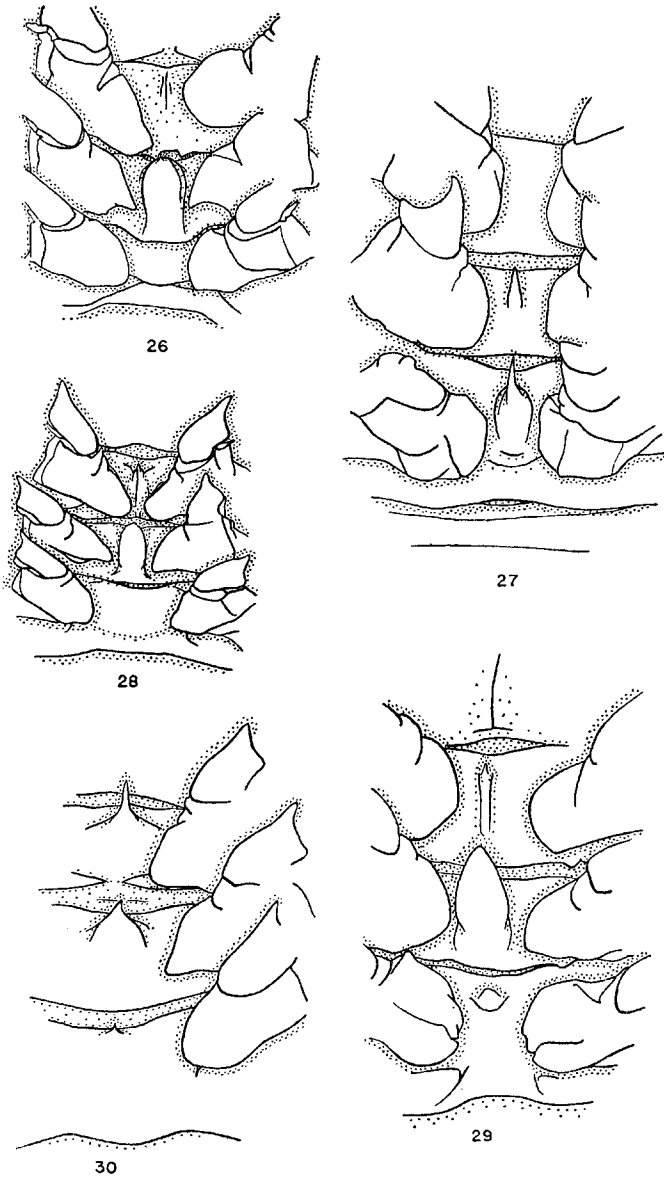
able. There is no sharp correlation between the length of this interval and that between the distal spines, although in general, the closer the proximal spine to the base of the telson, the farther the penultimate spine seems to be from the ultimate (i.e., the series seems to shift forward or backward more or less in unison). The range of variation of this ratio in any group is much greater than the interval between the extremes of the various groups (and in fact, the ratios in *B. cereus* are completely comprised within the extremes of variation in *B. brasiliensis*). There is, however, a difference in the averages between the groups as defined by differences in pleonic armature (*B. brasiliensis*, four tergites armed, 0.80; *B. urinator*, three tergites armed, 1.10; *B. cereus*, one (or two) tergites armed, 0.85; *B. iridescens*, no tergites armed, 0.62), probably sufficient to indicate that the differences in pleonic and in telson armature are correlated and do not represent random individual variations.

Differences in the relative breadth of the antennal scale are indicated by the present measurements to be of no diagnostic value; but here again it seems possible that the modes are distinct in the various groups; and in particular, it seems possible that *B. iridescens* may be characterized by a scale modally broader than that of the other groups, as suggested by MacGilchrist in the description of his specimen (0.40 for his *B. armatus*, as compared, presumably, with the measurements given by Smith for *B. moratus*, which are reducible to 0.30 and 0.28).

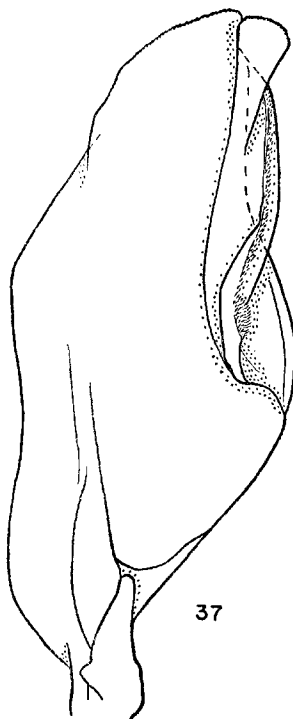
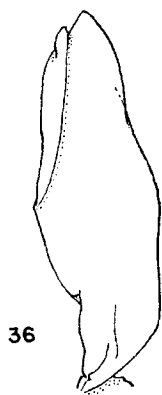
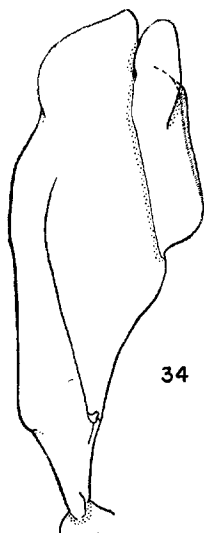
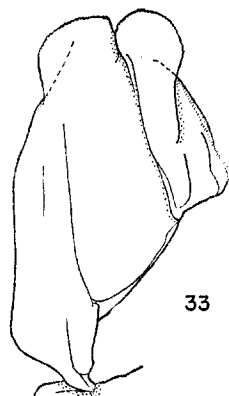
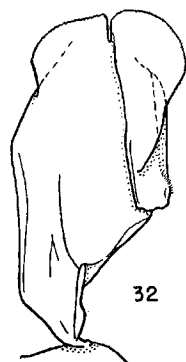
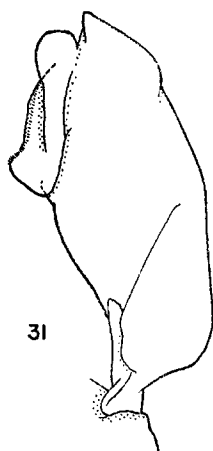
The sculpture of the genital sternites (figures 26 through 30, p. 39) is rather similar in males and females and seems subject to considerable, apparently random, variation in both. The descriptions are included in the table in order to emphasize that the sculpture in the anomalous specimen, *B. strabus*, is very different from that found in any other of the available individuals.

Finally, with regard to petasma (figures 31 through 37, p. 40) and appendix masculina (figures 38 through 44, p. 41) males of *B. urinator* from both localities are similar, and are quite distinct from the other four forms, which, with the exception of *B. strabus*, resemble one another rather closely in these features. The transverse rather than oblique distal margin of the distoventral lobe of the petasma; the larger size of the distolateral lobe; and the much broader base of the external blade of the appendix masculina in *B. urinator* are clearly indicated in the figures. Whether or not the less narrowed tip and less concave median margin of the anterior, and the lesser length of the posterior, blade of the appendix masculina of *B. brasiliensis* and *B. cereus* will be found diagnostic of these two forms as compared with *B. iridescens*, is not certain.

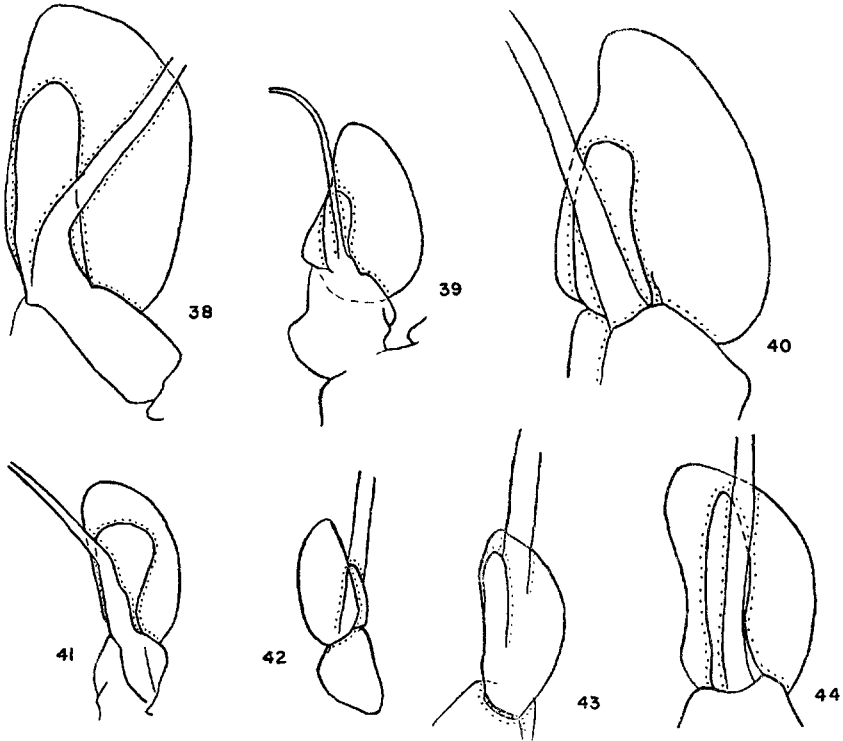
The distribution of the four forms known from more than a single specimen seems compatible with the belief that they represent distinct species. In all but one case, the material derived from a single area is homogeneous, which may be considered as evidence that the characters of variant forms within the complex are either genetically or environmentally fixed. The single case in



Gonital sternites (XII, XIII and XIV, with third, fourth and fifth leg-bases). 26. *Benthescymus brasiliensis* Bate (Specimen No. 7, ♀), × 4.8. 27. *B. strabus*, n. sp. (No. 18, TYPE ♂), × 11. 28. *B. cereus*, n. sp. (No. 16, ♀), × 4.8. 29. *B. iridescens* Bate (No. 23, ♂), × 4.8. 30. *B. iridescens* Bate (No. 22, ♀), × 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-



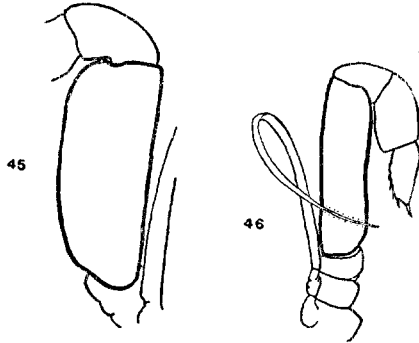
Appendix masculina (Figures 38, 39, 40, 41 and 44, left pleopod, posterior view of the appendix; Figure 42, left pleopod, anterior view; Figure 43, right pleopod, anterior view). 38. *Benthescycymus brasiliensis* Bate (Specimen No. 1, COTYPE), $\times 12$. 39. *B. urinator*, n. sp. (No. 8, TYPE), $\times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

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. *Benthescycymus brasiliensis* Bate (Specimen No. 1, COTYPE), $\times 4.8$. 32. *B. urinator*, n. sp. (No. 8, TYPE), $\times 4.8$. 33. *B. urinator*, n. sp. (No. 12), $\times 4.8$. 34. *B. strabus*, n. sp. (No. 18, TYPE), $\times 11$. 35. ? *B. cereus*, n. sp. (No. 15), $\times 11$. 36. *B. iridescens* Bate (No. 20), $\times 11$. 37. *B. iridescens* Bate (No. 19, TYPE), $\times 4.8$.

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

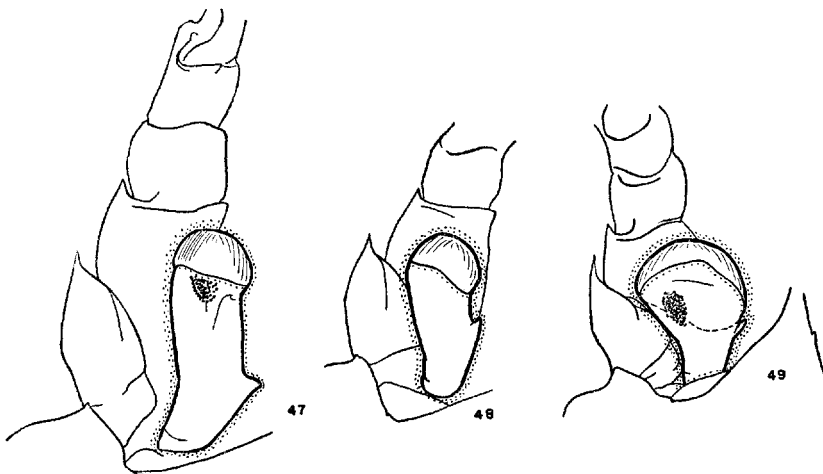
Specimen No. 18, here designated as *B. strabus* n. sp., is distinct in so many features not only from the other specimens with a single armed pleonic tergite, but from all the other material available, that I have been forced to conclude that specific differentiation exists in the *B. brasiliensis* complex even beyond the limits set by the possible variations in pleonic formula. As is shown by table and by illustrations, this specimen resembles *B. cereus* 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 *B. urinator*. The proximal spine (the only remaining) is, however, relatively very much



Second maxillipede, posterior view (showing degree of expansion of merus). 45. *Benthescymus 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 measurable 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 *Benthescymus*, 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. *Benthescymus 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 penaeids, 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.¹

¹ 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 species "Le telson est loin d'atteindre la longueur du segment abdominal précédent"; 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 endopod of the first maxillipede of *B. longipes* 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

- I. Posterior margin of the fourth pleonic tergite armed with a tooth.
Posterior rostral tooth usually behind the level of the orbital margin.
- IA. 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, p. 40; 38, p. 41.
- 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 one-half 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.
- II. 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 pereopodal meri, which in this species is no greater than in *Benthescymus 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 pereopods 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 distomedian 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 petasmas 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

***Benthescymus bartletti* Smith**

Benthescymus 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.

Benthescymus pleocanthus, Bate, 1888; DeMan, 1911.

? *Benthescymus 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 pereopods 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,

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. *Benthescymus 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:

Benthescymus 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-faceted 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 endopod 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 nächsten 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 well-enclosed cavity is thus formed, in which it seems possible that the sperm-mass 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 Benthescyidae 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 pterygostomial 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.¹ Kemp, 1925, suggests an analogous cyclical dimorph-

¹ 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 *Leptocheila*, 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 wholesale 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 *Benthescymus tanneri* FAXON

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

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 *Benthescymus 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 *Benthescymus*. 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 adequate¹ 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 pereopodal 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.

¹Since 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

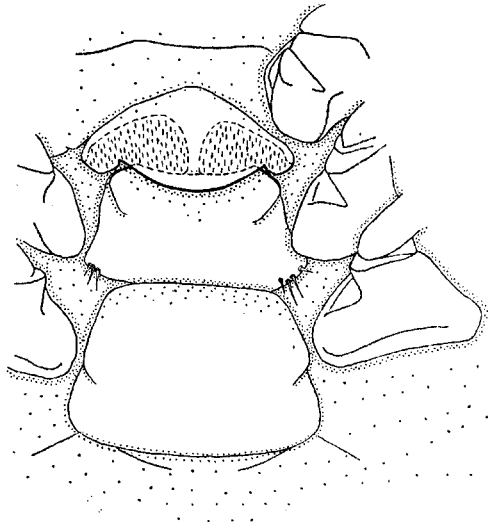
2 subadult females and three fragments. *B.O.C.* 226. Atlantis St. 2427; April 10, 1935. Wire 3164 meters.

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 post-rostral carina; in its possession of a strong pterygostomial 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 disto-ventral projection (proximal 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' indeterminate 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-



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

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 synonymizing 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 pterygostomial 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 post-cervical 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 kempfi* 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 kempfi* 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 super-specific 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

¹ 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 maxilliped; 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. bartiletti* 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 DISTOLATERAL,¹ and the DISTOVENTRAL. These lobes are often subdivided. 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

¹ 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 FLAP. As the distoventral flap (proximolateral to the notch) is in *Gennadas* not much produced, the more conspicuous part of 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 Benthescymae that the sperm receptacles of *Gennadas* (and of *Bentheogennema* and the *B. bartletti* group of *Benthescymus*) 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 Euscicyoninae, 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-Euscicyoninae 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. This 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 encapsulated 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, Benthescymine, end of the series Solenocerinae-Aristeae is completely parallel to that found at the Peneaeine end, although probably independent in origin. Like certain of the series Peneae of Penaeinae, some species of Benthescymae 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 Benthescyinae 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.¹ In the first instance, the openings are usually closed by papilliform

¹ 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* BATE¹

- 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 A-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. kempfi* 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.

¹ 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. Distomedian 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 XIII.
- IIA 1.** MALE. Lobules of the distolateral lobe curved toward one another and acuminate.
 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. bowieri* Kemp, 1909, ♀; Balss, 1927, ♂ (sub *G. alcocki*).
- IIA 2.** MALE. Lobules of the distolateral lobe not hooked and acuminate.
 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, ♂ [♀, 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 acuminate.

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 tip.

FEMALE. No free projection from XIV.

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

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. *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.

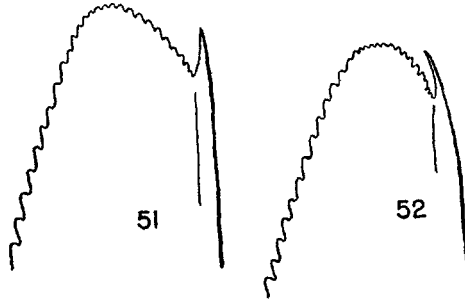
GULF OF MEXICO

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. kempfi* 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. kempfi* 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 ♀, × 35. 52. *G. kempfi* Stebbing (D. T. E. St. 89), × 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. kempfi* being symmetrically placed in the center of the distal margin, rather than near the lateral edge as in Calman's species.

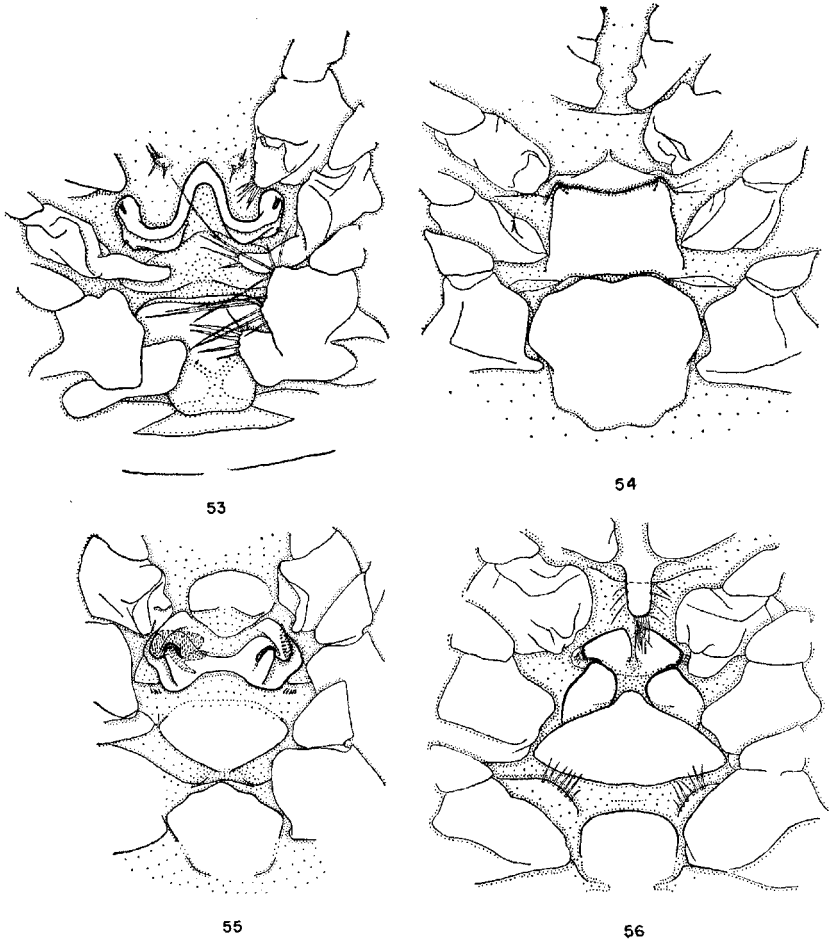
The resemblance of the petasma of *G. capensis* and *G. kempi* to that of *Bentheogennema intermedia*, which has been noted by previous workers, does not extend to details; since an accessory lobe is not developed in the latter form. The "complete correspondence" of the thelycum of *G. kempi* with that 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 ♀, × 11. 54. *G. kempi* Stebbing (D. T. E. St. 89), × 11. 55. *G. elegans* (Smith), Bahaman ♀, × 11. 56. *G. tinayrei* Bouvier, Bahaman ♀, × 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 distomedian 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 eastern 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. bowieri*, and one of *G. capensis*; and the "Atlantis" took two specimens of *G. elegans* to none of *G. valens*, one of *G. bowieri*, 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. bowieri*, 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 Museum, have been available. 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

2 males. *B.O.C.* 192. Pawnee St. 58; April 20, 1927. Wire 10,000 feet.

1 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 laterad 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. bouvieri*, the spermatozoa of *G. tinayrei* are aggregated as small egg-shaped 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.

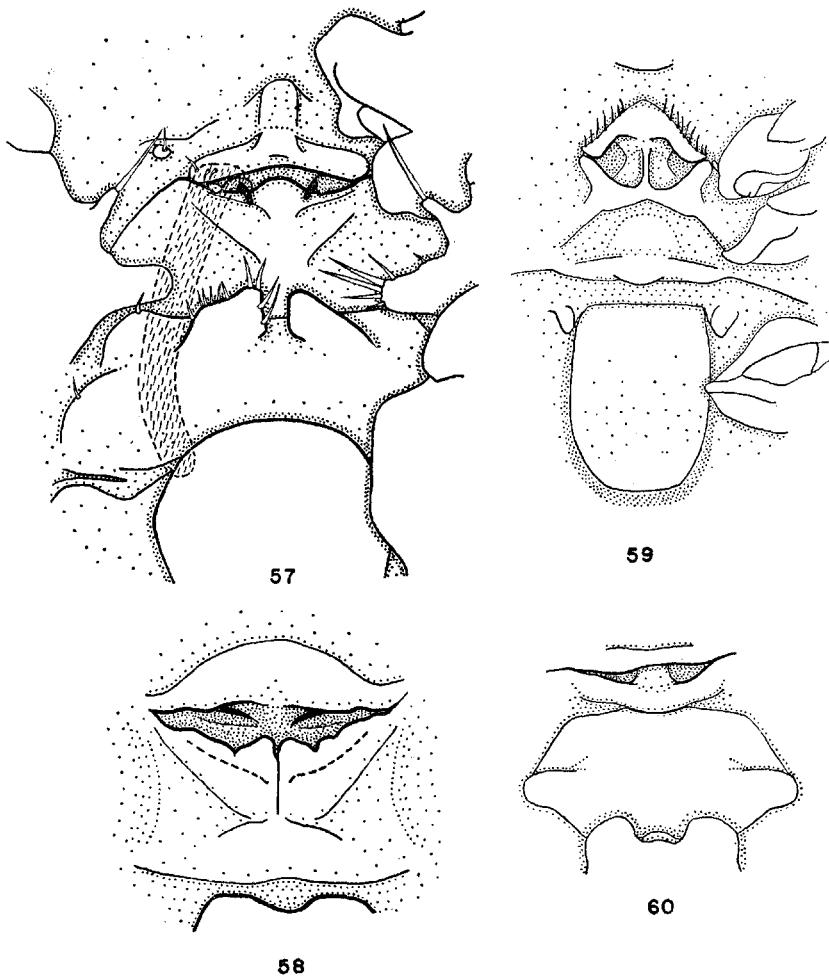
The type of *G. valens*, taken at 37° N, 74° W off the Middle Atlantic coast of the United States, represents the most southwesterly capture heretofore known. The record of "*Amalopenaeus elegans*" from "Albatross" station 2201, 39° N, 71° W, by Smith, 1887, also refers to *A. valens*, as determined 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. bowieri* 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 endopod 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 line, Figure 57. Produced lamella of XIV in *G. scutatus* turned back to expose XIII and XII, Figure 59). 57. *Gennadas valens* (Smith), Bermudan ♀, × 30. 58. *G. gilchristi* Calman (D. T. E. St. 91), × 30. 59. *G. scutatus* Bouvier, Caribbean ♀, × 20. 60. *G. talismani* Bouvier (D. T. E. St. 67), × 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 two-thirds of their length in the divergent shallow invaginations forming the receptacles proper.

Gennadas bouvieri Kemp

Gennadas bouvieri, Kemp, 1909 and 1910b.

Amalopenaenus bouvieri, Balss, 1927.

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

Amalopenaenus 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. bowieri* 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. bowieri* 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. bowieri*. It may be noted that the female incorrectly paired with the male by Kemp is evidently attributable to *G. propinquus* Rathbun (*G. clavicornis* 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. bowieri*.

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 medially; 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 distomedian 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 \wedge -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. bowieri* Kemp and two of *G. sordidus* Kemp.

The spermatophore of *G. scutatus*, as freed from the accessory 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 thelycum (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 Cerataspinæ, 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

¹ 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 posteroinferior 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 *Benthescymus 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 diomedea* (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 reexamination 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*.¹ 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*

¹ It may be observed in this place that contrary to Faxon's statements, pleurobranchs of *Aristaeus occidentalis* posterior to IX bear a number of simple pinnulae.

is as clearly distinguished from *Hemipenaeus* as are any other of the super-specific groups of the series from one another. Unfortunately, however, *Hemipenaeus* (assuming the branchial structure here observed to be representative) 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 cardiobranchial 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. trilon* 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 sulci 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, that of XIII 5 mm. There seems to be more variation in development of 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 pterygostomial 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 pterygostomial 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.

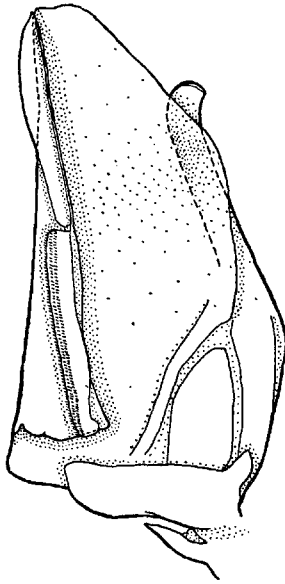
There is a high shield-shaped scute, anteriorly pointed, on the thirteenth sternite, a low elevation with a sharp slender tooth near its anterior end on the twelfth, and a low pyramidal projection on the fourteenth sternite.

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 ♂. $\times 4.4$.

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.

SOLENO CERINAE 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,¹ 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-*

¹ 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 disto-medial 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 pterygostomial 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. The

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 PARAPENEID 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*.¹

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.

¹ 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 pterygostomial 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 pterygostomial 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 pterygostomial 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* Ortman)]. Branchiostegal but no pterygostomial 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. diomedea* (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). *H. ...*

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

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 externo-distal 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. diomedea* is not correct. *H. robustus* differs from *H. diomedea* in all the features mentioned in the preceding paragraph (with reference to *H. taprobanensis*) as characteristic of Group III. The petasma of *H. diomedea* 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 disto-median 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. diomedea*, *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, Aristaenae 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 peridinium 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 pterygostomial 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 pterygostomial is certainly absent. *H. equalis* (Bate) and *H. neptunus* (Bate) are described and figured by their author as lacking pterygostomial, and DeMan, 1911, concurs for *H. aequalis*; but Wood Mason and Alcock, 1891b, mention the presence of pterygostomial 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 pterygostomial is present) save in a few characters among which are not included differences in occurrence of pterygostomial. 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 pterygostomial is absent. *H. neptunus* is not noted by DeMan to differ from *H. aequalis* by possession of a pterygostomial. 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

endopod, 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. androgynus* 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. A low carina runs from the branchiostegal to the pterygostomial 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 dorsal the hepatic spine. From this notch a ridge runs downward and backward to near the point where the cardiacobranchialis 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 *Haliporus curvirostris*. It is possible that the posteriormost dorsal carapacic tooth of the *Eusicyoninae*, the only other penaeid 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 Aristaeninae 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 penaeids, 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 head-rope 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.

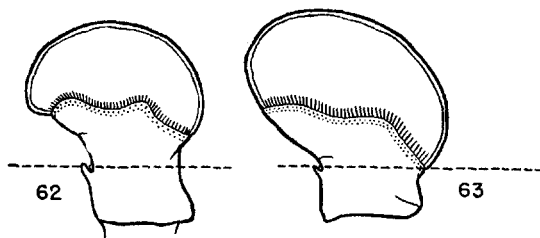
Type, carapace 18 mm, total length about 60 mm. Paratype, carapace 15

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.

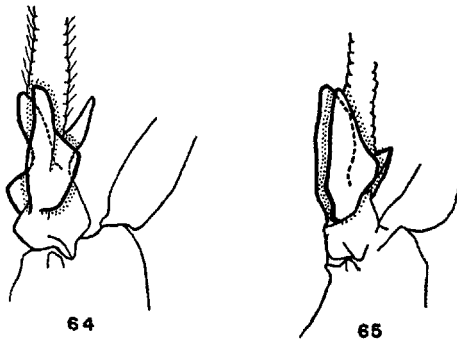
The depth of the carapace of the three specimens of *H. aphoticus*, measured with ocular micrometer vertically from the dorsal crossing of the cervical groove to the branchiostegal carina, varies with reference to carapace length (rostrum excluded) from 42 to 48.5%, average, 46%. In the six specimens 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 ♂ of carapace length 16 mm, $\times 12$. 63. *Hymenopenaeus debilis* Smith, Honduran ♀ 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.



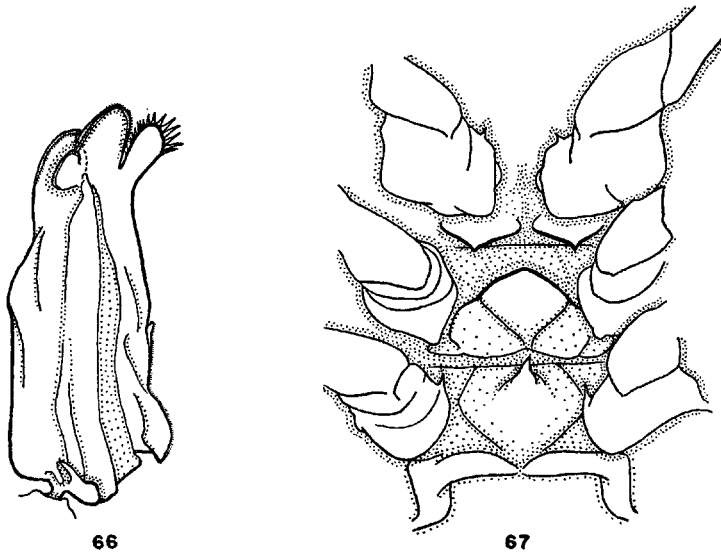
Appendix masculina of right pleopod, antero-lateral view. 64. *Hymenopenaeus debilis* Smith, Honduran ♂, × 17. 65. *H. aphoticus*, n. sp., TYPE, × 17.

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, $\times 17$. Thelycum. 67. *H. aphoticus*, n. sp., COTYPE, $\times 17$.

In both *H. debilis* and *H. aphoticus* the first legs bear a long and slender ischial spine in addition to the basal 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^{er}, 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 pterygostomial 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)¹ 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.

¹ 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 :

John
...

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. aequalis*, *H. propinquus*, *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 pterygostomial spine, *H. laevis*, *H. doris*, and *H. nereus*), in that they lack a pair of posteriorly-directed 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. propinquus*, 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. propinquus*; 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 basal 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 blue-green 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. diomedea* (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 Solenocerinae, 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 setiferous 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 setiferous 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.

The genus stands in the closest possible relationship to *Hymenopenaeus*, and parallels it in a curious manner in certain diversities of structure; thus, as in *Hymenopenaeus*, the orbital angle is in some species of *Solenocera* imperceptible, in others strong and dentiform; a notch in the cervical carina above the hepatic spine is in some species present or even dentiform, in others absent; either pterygostomial or branchiostegal spine may be present, or both may be absent.

A number of characters occurring in some species of *Hymenopenaeus* seem never to appear in *Solenocera*; thus branchiostegal and pterygostomial spine are never simultaneously present in the latter; there are no post-cervical mid-dorsal teeth on the carapace; and except in the doubtful form *S. maldivensis* described by Borradaile, 1910, there are no ventral rostral teeth; the branchiostegal carina is always marginal, the portion of the carapace ventral to it forming a membranous branchiostegite; the tooth of the externodistal margin of the uropodal exopod, when present, is terminal rather than lateral.

The channel-like nature of the antennular flagella of *Solenocera* is the only certainly diagnostic character upon which the generic separation is based. The additional differences between *Hymenopenaeus* and *Solenocera* noted by Smith, 1885, and Bouvier, 1908, that in the latter the terminal segment of the mandibular palp is broader than the basal one, is not universally applicable, the distal segment being reported to be narrower than the basal in *Solenocera comatus* Stebbing. In most species of *Solenocera*, contrary to the usual condition in *Hymenopenaeus*, the exopod of the uropod completely lacks a tooth on its external distal margin, but a terminal tooth is figured for *Solenocera melanitho* DeMan. A difference which will probably prove not to be of diagnostic value has been observed in available material, where the seventh somite bears a gill much more minute and weakly branched than that of *Hymenopenaeus*.

The genus has been briefly reviewed by Burkenroad, 1934a, who, in the lack of sufficient material, was unable to determine whether the presence or absence of branchiostegal and pterygostomial spines indicated the boundaries of natural subdivisions within the genus. As a contribution to the clarification of synonymies undertaken in the preceding paper, it may be mentioned that Bate's confusion of *Hymenopenaeus aequalis* with *Solenocera crassicornis* H. Milne Edwards, in 1881, seems good indication that the latter possessed a pterygostomial rather than a branchiostegal spine; but that the type of *S. crassicornis*, which, on enquiry, can not be located at the Paris Museum, was evidently destroyed subsequent to Bate's visit, in the course of morphological investigations by Mocquard, 1883.

In a freshly-caught specimen of *Solenocera vioscai*, the antennular flagella were observed to be prolonged beyond the abrupt constriction previously thought to terminate them, by a slender, segmented filament about one-eighth as long as the main part of the flagellum in the case of the superior ramus; shorter in the inferior. Search among the types of *Solenocera agassizii* Faxon revealed a

similar termination in an unmutilated specimen. These filaments are evidently equivalent to those described by Wood Mason and Alcock for *Solenocera* ("Parasolenocera") *annectens*. The figures of the tips of the antennulae of *S. jaxoni* by DeMan, 1911, seem to indicate that a similar filament has been broken off in the figured specimen. It seems possible that such terminal appendages may occur in all species of *Solenocera*; and the opinion expressed in a preceding paper (1934a), that the filamentous termination of the antennular flagella (upon which the separation of *Parasolenocera* Wood Mason and Alcock from *Solenocera* was chiefly based) represents a character of no generic significance, seems to stand confirmed by the present observation.

***Solenocera vioscai* Burkenroad**

Solenocera vioscai, Burkenroad, 1934a.

Solenocera siphonocera, Smith, 1886, part.

1 female, juvenile. Carapace length, 8.8 mm, rostrum 3 mm. *B.O.C.* 225. N. 29° 16', W. 87° 54' ("Atlantis" St. 2377), March 24, 1935. Trawl, 125 fathoms.

For comparison with the above, the smaller of the two cotypes (*B.O.C.* 130) has been obtained by exchange, through the great kindness of the American Museum of Natural History.

The previous records of the species are from considerably less than the present depth.

Like the Venezuelan juvenile mentioned in the description of *S. vioscai*, the present juvenile has only six instead of nine dorsal carapacic teeth, of which the anteriormost is far posterior to the tip of the rostrum. Also unlike the types, the posteriormost (epigastric) tooth is nearly half as far from the dorsal crossing of the cervical groove as from the orbital margin; and the second tooth is less than one-fifth the distance between cervical and orbit, instead of one-fourth. The orbital angle, although sharp, is not dentiform as in the adult. The carina posteriorly margining the anterior (ventral) part of the cervical groove extends farther ventrally, to the level of the pterygostomial spine, before turning forward. The pterygostomial is relatively longer than in the adult. The dorsal carina of the carapace is hardly perceptible behind the level of the cervical sulcus; likewise, the third pleonic tergum is uncarinated. The telson falls much shorter of the tip of the uropodal endopod; and its lateral teeth are relatively much longer than in the adult. The antennular flagella are slightly shorter and broader than in the types; the inferior flagellum is .6 mm in breadth, the superior .4 mm. The antennal scale is very much longer than in the adult, extending nearly one-sixth of its own length past the tip of the antennular peduncle. The breadth of the distal segment of the mandibular palp is nearly as great as the length of the basal segment, instead of considerably less as in the available cotype. The coxae of the fifth legs bear a strong spine

at their inner anterior margin (as in many species of *Hymenopenaeus*) which has disappeared in the adult.

The thelycum of the present juvenile very closely resembles that of the much larger types.

A comparison of *S. vioscai* with the types of the Pacific American *S. agassizi* reveals three diagnostic features not previously noted. These are:

(1) The epipodites of *S. vioscai* are at most mitten-shaped (like those of the Mediterranean *S. membranacea*), whereas the middle three epipods of *S. agassizi* are deeply furcate.

(2) The prolongation of the inner surface of the coxa of the fourth leg of *S. vioscai*, which abuts proximally against a sternal "stop," does not extend medially nearly to the midline, whereas that of *S. agassizi* is so produced as to overlap its fellow of the opposite side.

(3) The high longitudinal ridge of the thirteenth sternite of *S. vioscai*, which ends anteriorly in a strongly projecting tooth overlapping the posterior margin of the twelfth sternite (omitted from the previous description and figure) is unrepresented in *S. agassizi*, where this sternite completely lacks carination.

It may be noted that in adult females of both *S. membranacea* and *S. agassizi* the coxa of the fifth leg bears a tooth like that which is present in the juvenile of *S. vioscai*, but absent in the adult.

The coloration of the freshly captured, but dead, juvenile of *S. vioscai* was as follows: An unpatterned translucent pale orange-red over-all, chiefly produced by small chromatophores. Eyes deep reddish-brown with greenish reflections. Gastric gland brownish-grey with light yellow-green flecks; gut red (as seen through the overlying tissues).

Solenocera species

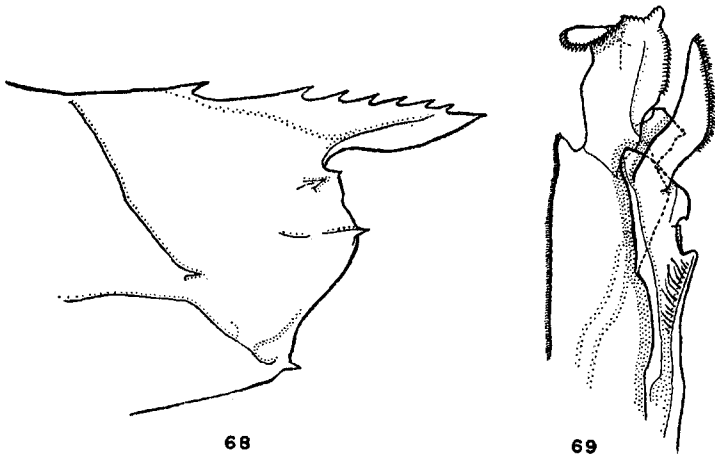
Figures 68 and 69, p. 124

? *Solenocera agassizi*, Faxon, 1893 and 1895.

1 male. Carapace 13 mm, rostrum 3.8 mm, total length 49 mm. *B.O.C. 132*, Pearl Islands, Gulf of Panama (8° 29' 40" N., 78° 52' 30" W.); March 31, 1926; trawl 19-24 fathoms.

The present specimen has been compared with the types of *S. agassizi*, from "Albatross" Station 3389 in the Gulf of Panama, which were made available through the great kindness of the Museum of Comparative Zoology. These specimens are of much larger size than is that of the Bingham Collection, the two males measuring 29 mm in carapace length, the females ranging from 23 to 40 mm. Since the present individual, despite its small size, is fully adult in sexual characters (joined petasomal endopods; well developed deferent apertures) and presents numerous differences from the types, it was at first

intended to describe it as a new species under the name *S. florea*, which is suggested for it in case further material indicates that two species of *Solenocera* actually do occur in Pacific America. However, the discovery that the juvenile female of *S. vioscai* considered in preceding paragraphs presents to a considerable degree the external characters of maturity (well developed oviduct apertures and sternal sculpture), and differs from the adults somewhat as does the present specimen from *S. agassizii*, has determined me to await further material before creating a new name.

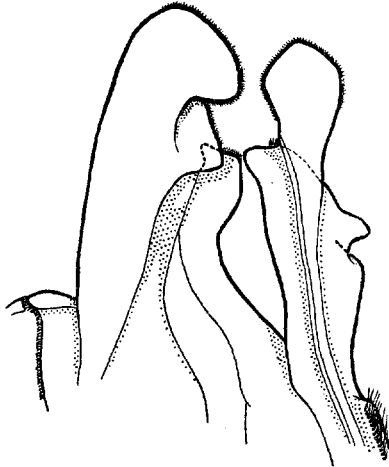


Carapace, anterior part, lateral view. 68. *Solenocera* species, $\times 5.5$. Petasma, left half, distal portion of posterior face. 69. *Solenocera* species, $\times 7.5$.

B.O.C. 132 compares with Faxon's material as follows: The rostrum of the Bingham male is relatively short and deep, the distal part of its ventral margin strongly convex; whereas in the types of *S. agassizii* the rostrum is narrow, with a straight, or even concave, ventrodiscal margin. There are only six dorsal carapacic teeth, a smaller number than usually occurs in *S. agassizii*; the epigastric tooth is placed less than one and one-quarter times as far from the orbital margin as from the dorsal end of the cervical sulcus, rather than twice as far as in the types; and the interval between the first and second teeth of the rostral series is less than one-fifth the distance between the first tooth and the dorsal end of the cervical sulcus, as compared with more than one-third in the types. The postrostral carina, which, although low, reaches nearly to the posterior margin of the carapace in *S. agassizii*, disappears behind the level of the cervical sulcus in *B.O.C. 132*; and the sharp carina of the third pleonic somite of the type is represented only by a faint ridge in the Bingham specimen. The dorsal margin of the pterygostomian spine forms a right angle with the

anterior margin of the carapace, instead of curving gently into it as in *S. agassizii*. It seems possible, as indicated by the comparison between juvenile and adult of *S. vioscai*, that the above differences between *B.O.C. 132* and the types of *S. agassizii* are those between juvenile and adult.

In two characters, the Bingham male differs from the types in a manner the reverse of that in which the juvenile female of *S. vioscai* differs from the adult: Its antennular flagella are longer (nearly two and one-third times their peduncle) and more slender than those of *S. agassizii*; and the antennal scale barely reaches to the end of the antennular peduncle, instead far beyond it. The significance of these differences is doubtful.



Petasma, left half, distal portion of posterior face. 70. *Solenocera agassizii* Faxon, COPYE (Albatross St. 3389), $\times 5$.

Finally, *B.O.C. 132* differs strikingly from the male of *S. agassizii* in petasma (figure 70, p. 125). It seems possible that the copulatory organs of the two available specimens of the latter are worn or broken, but the fact that the two types are identical in petasma is against this possibility. It is difficult to believe that the petasmal characters of the Bingham male are those of juvenility, because in no other peneid has gross change in the copulatory appendage been observed to occur after the coupling of the two rami has taken place. I believe it to be a fact that individual variations at all approaching in strength those described below have not been found in any species of peneid. The lateral part of the petasma is heavily chitinized. The distal part of its external margin is corrugated by three projections, the proximal of which (marked by the row of setae) is placed at about the third quarter of the external margin in the Bingham male, close to the two more distal projections, the distalmost of which

is much larger than the middle one. In *S. agassizii* the proximal projection of the external margin is placed far from the distal ones, at about the middle of the margin; and the middle projection is larger than the distalmost. Surmounting the lateral part of the petasma in *B.O.C. 132* is a long, slender, acuminate distoventral projection only one margin of which is edged with strong denticles; in *S. agassizii* this lobe is a short, oval lamella minutely denticulate on both lateral and median edges. The distal end of the lateral part of the petasma (distoventral flap), behind the base of the distoventral projection, is unarmed in *B.O.C. 132*; in *S. agassizii* this area bears a row of large spinules. The distolateral lobe of the petasma of the Bingham male bears a pair of rigid lamellar projections on its dorsolateral face; its distal part is a large subrectangular structure with a heavily armed and crenellated distal margin conspicuously projecting at its median end. The distolateral lobe of *S. agassizii* is small; its lateral edge is deeply notched, and its distal margin rounded and not projecting medially.

In other features than the above, *B.O.C. 132* closely resembles the types of *S. agassizii*. Its precise identity must remain in doubt until further specimens have become available.

PENAEINAE Burkenroad

Series *PENAEAE* (*Penaeus series*, Burkenroad, 1934a)

FUNCHALIA Johnson

Funchalia, Johnson, 1867; Bouvier, 1908; Lenz and Strunck, 1914; Calman, 1925; Burkenroad, 1934a.

Aristeus, part, Bate, 1888.

Penaeus, part, Faxon, 1895; Lenz and Strunck, 1914, part; Schmitt, 1935, part.

Hemipenaeopsis, Bouvier, 1905a.

Grimaldiella, Bouvier, 1905a.

? *Penaeus*, part, Hanström, 1933.

The genus as here defined includes a species regarded by previous workers as pertaining to *Penaeus*, but separated from that genus and placed with *Funchalia*, in the subgenus *Pelagopenaeus*, by Burkenroad, 1934a.

The relations of *Funchalia* s. s. to other Penaeinae have been discussed in some detail by Bouvier, 1908, who regards the genus as the most primitive of the subfamily, and as forming, with *Penaeopsis* and *Parapenaeus*, a group not very directly related to *Penaeus*. This arrangement is accepted by Balss, 1925. In the preceding paper, it has been briefly indicated that *Funchalia* forms, with *Penaeus*, a very compact series well distinguished from the other three maniples of *Penaeinae*, the *Parapeneae*, *Trachypeneae* and *Macropetasmae*. Bouvier is correct in assigning to *Funchalia* a position very close to the *Solenocerinae*, but he is quite wrong to separate it from *Penaeus*.

The Peneae are distinguished from all other Penaeinae by the presence of a pleurobranch on the fourteenth somite, and of an epipodite on the third maxilliped; the occurrence of ventral rostral teeth and of an unenclosed sperm receptacle in some or all of the species of both the included genera; and the presence of a relatively simple open petasma (which also occurs in a single group of the Parapeneae). These are all characters indicative of a near approach to the Solenocerinae. The maxillary palp has a much elongated distal lobe, and all the epipodites are strongly forked. It may be noted that the branchial formula of *Funchalia* is identical with that of *Penaeus*; in addition to the erroneous attribution by Bouvier of three gills to the eighth somite, the branchial lamella of the seventh is filamentose and not, as implied by Bouvier, naked.

Funchalia differs from *Penaeus* in a number of characters. The carapace of the former lacks any trace of orbital angle, a structure which appears late in development in *Penaeus*. The carapace of *Funchalia* has a produced dentiform anteroinferior angle, but in agreement with *Penaeus*, where such a projection is lacking, this is not a true pterygostomial spine, since the pterygostomial which is reported present in larvae disappears in postmysis stages. The sulci of the carapace of *Funchalia* are obsolescent, while the various carinae chiefly represent ridges ill-marked or absent in *Penaeus*, as will be described in detail in a further paragraph. The lateral carina of the sixth pleonic segment of *Funchalia* is, like that of most other peneids, continuous, rather than interrupted as in *Penaeus*.¹ The telson of *Penaeus*, when armed, bears three pairs of mobile lateral spines. The telson of *Funchalia* is armed with three pairs of fixed spines, homologous with the mobiles found in Group II of *Penaeus*; but proximal to this true armature there occurs an extensive series of adventitious spinules not distinguished by appearance in the adult stages from the original, persistent, larval series. The carapace and pleon of *Funchalia*, like the telson, are covered

¹In two available specimens of the Jurassic *Antrimpos speciosus* Münster, the carina of the twentieth somite seems to be continuous, although it does not, as in *Funchalia*, extend to the anterior and posterior margins of the somite. In other features, *Antrimpos* seems identical with the living species of *Penaeus*, to which genus (sensu stricto) it is referred by Balss, 1923. In the disappearance of the adrostral sulci at the level of the epigastric tooth, and the lack of telson armature, the Jurassic form agrees with Group I (Burkenroad, 1934a) of the living genus; in the presence of only a single ventral rostral tooth, with Group II. The posteroventral margin of the sixth pleonic somite, behind the tooth which terminates the inferior margin, is somewhat more convex than in any living species of *Penaeus*, and is rather more as in *Funchalia*. It seems very probable that *Antrimpos* is in the direct line of ancestry of the modern species of *Penaeus*, which have diverged from it slightly by modification of the more primitive continuous lateral carina of the twentieth somite.

The above observations are derived from a study of material from Solenhofen in the collection of the Department of Invertebrate Paleontology of Peabody Museum, for the opportunity to examine which I am deeply indebted to Dr. C. O. Dunbar.

with a peculiar dense pubescence. The superior antennular flagellum of *Funchalia* is longer than the carapace. The molar process of the mandible is obsolete; the incisor process much elongated. There are only three endites on the second maxilla, as in the postmysis of all Penaeinae, but as in the adults of Eusicyoninae alone; it may be noted that the proximal endite is in *Penaeus* reacquired very late in post-larval development. The basis and ischium of both first and second legs are armed. There is a well-developed tooth on the external margin of the uropodal exopods, far proximad the tip. The petasma (in the subgenus *Pelagopenaeus*, that of *Funchalia* s. s. adult being unknown) differs from that of *Penaeus* in bearing a distoventral projection like that of the Parapeneae, some Solenocerinae, and the Eusicyoninae.

Funchalia is a pelagic genus, *Penaeus* a benthonic, littoral or sublittoral one. A number of the differences between the two genera are very probably connected with this difference in habit, and have little significance as indicators of phylogeny. Thus *Penaeus*, a considerable portion of the food of which is composed of heavily-shelled molluscs and other tough or rigid objects, might be expected to have a vigorously-developed molar process. The peculiarities of the exoskeletal sculpture of *Funchalia* are similar to those of many of the oceanic forms, but the fact that the absence of hepatic spine in *F. villosa* is demonstrably secondary, whereas it is primary in Aristaeinae, suggests that the resemblances may be the results of convergence. In both subgenera of *Funchalia*, the mass of bottom-debris utilized as lithocyst concretion by *Penaeus* is replaced by a large pellet of clear gelatinous material (more elongate in *Funchalia* s. s. than in *Pelagopenaeus*), although the lithocyst chamber retains an opening to the exterior. This statolith is presumably composed of cuticular material secreted by tegumental glands, such as Lang and Yonge, 1935, have shown to be employed in cementing the sand-grains of the homarid statolith. A similar condition has been noted in *Sergestes* by Hanström, 1933, and in the Aristaeine "*Amalopenaeus*" by Hanström, 1934, who suggests that an autogenous statolith will be found to characterize other pelagic shrimp.

Subgenus FUNCHALIA s. s.

Species of the subgenus have been recorded from the Mediterranean (Stephensen, 1923), the temperate North Atlantic (Johnson, 1878; Bouvier, 1908 and 1922; Lenz and Strunck, 1914; Sund, 1920; Stephensen, 1923), and the temperate South Atlantic (Lenz and Strunck, 1914; Calman, 1925), as well as from the Indian Ocean (Balss, 1925). The present records extend the range of the subgenus to the Caribbean. Unfortunately, the specific determination of much of the previously recorded material is uncertain, as will be shown below. The bathymetric range of members of the subgenus is not certainly determined, but the majority of the catches are from slight depths.

Two species attributable to the subgenus have in the past been named,

Funchalia woodwardi Johnson and *F. vanhoeffeni* Lenz and Strunck. The latter, known from two specimens taken in the South Atlantic near Tristan de Cunha, actually represents the male of material reported as *F. woodwardi* by Lenz and Strunck. For reasons detailed below, it appears that material attributed to *F. woodwardi* by previous investigators comprises two species. Since the name *Hemipenaeopsis villosa* (later retracted in favor of *Funchalia woodwardi*) was applied by Bouvier to material which apparently consisted of both forms, the name *villosa* is available for the undescribed component.

***Funchalia villosa* (Bouvier)**

Hemipenaeopsis villosus, part, Bouvier, 1905a.

Grimaldiella richardi, part, Bouvier, 1905a.

Funchalia woodwardi, Bouvier, part, 1907 and 1908; Lenz and Strunck, 1914.

Funchalia vanhoeffeni, Lenz and Strunck, 1914.

(*Funchalia* ?), Gurney, 1924.

1 female, impregnated. *B.O.C. 143*. Atlantis St. 1939; February 3, 1934. N. 16° 10', W. 76° 28'. Depth between 50 and 200 m.

1 female, impregnated. *B.O.C. 141*. Pawnee St. 18; March 10, 1927. N. 23° 39' 25'', W. 76° 41'. 7000 feet wire.

1 female, unimpregnated. *B.O.C. 142*. Pawnee St. 48; April 6, 1927. N. 21° 44', W. 72° 43' 25''. 7000 feet wire.

B.O.C. 143, carapace 17 mm, rostrum 6 mm, total 71 mm. *B.O.C. 141*, carapace 16 mm, rostral tip broken, total about 70 mm. *B.O.C. 142*, carapace 14 mm, rostrum 5 mm, total about 65 mm. In addition to the above, a juvenile female of carapace 9.8, rostrum 4.0, total 46 mm (Atlantis St. 1034, Aug. 8, 1931, tub 1) has been loaned for examination by Dr. J. G. F. Wheeler of the Bermuda Biological Station for Research. Seven juvenile males and four juvenile females of carapace length 5.4 to 8.0 mm, 50 to 1000 fathoms, June, July, August and September; and an adult female, impregnated, carapace 16, rostrum 5, total 67 mm, 1000 fathoms, July, from pelagic collections of the Bermuda Oceanographic Expeditions of the New York Zoological Society have been placed at my disposal by Dr. William Beebe.

The rostrum of *Funchalia villosa* is broad at base, very slender distally; the tip is horizontal or depressed, and reaches little beyond the eyes, not to the end of the first segment of the antennular peduncle. The rostrum is armed, in the

three Bingham specimens, with $\frac{6+1}{0}$, $\frac{5+1}{0}$, $\frac{5+r+1}{0}$ teeth, of which the

epigastric is separated from the posterior rostral by an interval equal to that between the first (posterior) and the third to fourth rostral teeth. The posterior tooth of the rostral series lies behind the orbital margin. The lateral ridge of the rostrum is very poorly marked. The postrostral carina is distinct to about the posterior one-ninth of the carapace. The hepatic spine is completely absent.

The antennal angle terminates in a small spine. The anteroventral angle of the carapace is strongly produced as a dentiform projection slightly dorsad the turning point of the margin. There is an extremely faint trace of dorsal cervical sulcus, the upper portion of which turns posteriorly. From the unarmed hepatic buttress, which is faintly outlined by very shallow sulci, a slight trace of ventral cervical sulcus runs obliquely downward to reach the anterior margin above the anteroinferior angle; dorsally this sulcus is continued backward beneath the obtuse ridge of the hepatic buttress. From the posterior end of the hepatic ridge, a low obliquely vertical carina runs to posteroventral, while from the same point a well-marked cardiaco-branchial ridge takes rise and, sloping sharply upward, then turning posteriorly, reaches the hinder margin of the carapace. From the anterior end of the dorsal limb of the cardiocbranchialis, a very faint ridge and sulcus run anterodorsally. From the anteroventral angle of the carapace a well-marked longitudinal carina runs posteriorly to less than halfway between the anterior margin and the vertical ridge. The antennal carina is well marked; the sulcus dorsal to it turns dorsally at the level of the hepatic buttress as a very shallow groove paralleling and anterior to the faint cervical sulcus. On the posterodorsal lateral surface of the carapace is a short obtuse carina sloping anterodorsally from its posterior end. There is a sharp, unisulcate middorsal carina on the fourth, fifth, and sixth pleonic somites, that of the sixth ending in a rather long tooth. On the dorsal midline of the second somite, just behind a deep transverse depression, is a very faint oval elevation, and a still fainter one exists in a similar position on the third somite. There is a midlateral longitudinal unsulcated carina on the sixth, fifth, and fourth pleonic somites, that of the fourth running obliquely to dorsal. There is a vertical ridge on the first to fourth pleonic pleura. The telson is more than three-quarters the length of the sixth pleonic somite. Its basolateral shoulder is conspicuously cut into three lobes. The lateral margins of the telson bear a considerable series of fixed spines, largest distally, the three distal pairs of which represent spines present in the mysis stage (at which time the anterior two are mobile, the distal fixed), while the remainder are modified setae such as clothe the telson dorsally, and are not homologous to the true lateral armature of other peneids. It is possible that the fourth larval pair also persists, at about the middle of the telson, but it cannot be distinguished in adults from the adventitious series.

There is a strong vestige of a tubercle on the median distal surface of the ocular peduncle. The superior antennular flagellum is as long as the carapace plus the rostrum; the inferior about three-fifths of the superior. The second segment of the antennal peduncle bears a well-developed ancecerite. There is no trace of a parapaneid spine in the adult. The antennal flagellum is about two and one-half times as long as the animal; on the distal three-fifths of it each segment bears a pair of plumose setae arched over toward one another

and producing by their repetition a sort of hollow cylinder of considerably greater diameter than the flagellum, somewhat as in certain Sergestidae. The mandibular palps are one-fifth longer than the distance from the outer base of the palp to the tip of the incisor process; the tip of the second joint of the palp is obliquely deeply concave, and the inner margin is considerably produced. The palp seems subject to asymmetrical development or frequent loss and regeneration, the right one in No. 142 having, by contrast with the left, the inner margin of the tip scarcely produced, while in No. 141 the left palp is quite small, with an oval distal segment. The dactyl of the third maxillipedes is subcylindrical, tapering from slightly swollen base to tip. The finger of the third chela is nearly three-quarters of the palm. The dactyls of the fourth and fifth legs are more than two-thirds as long as the propodi. The endopod of the uropod extends from one-third to one-fourth of its length beyond the telson, and falls considerably short of the tooth on the external margin of the exopods.

The median plate of the thelycum is a high narrow Λ -shaped ridge forming the anterior wall of a deep depression. Posteriorly, on the fourteenth somite, this depression is bounded by the rim of the transverse groove, which is rather low posteromedially, but is produced anteriorly into somewhat overhanging lateral hoods which meet the posterior ends of the median plate, and form the lateral margins of the depression. The depression of the thelycum thus has the shape of a U somewhat narrowed at its open end, capped, by a $\Lambda = \hat{\Lambda}$. The depression runs posteriorly more than half-way between the fourth and fifth leg bases, and the part enclosed between the lateral hoods is considerably longer than wide. The oblique anterolateral margin of either lateral hood is only slightly concave. From the inner anterior end of each lateral hood a ridge which in its anterior part forms the free median edge of the hood runs back to the posterior margin of the fifth legs. Slightly behind the level of the posterior margin of the depression, this ridge curves conspicuously to lateral. There is no longitudinal ridge on the floor of the depression. In the three available impregnated specimens, the depression of the thelycum is completely filled by a white spermatophoric mass.

The four adult females and the twelve juveniles of *Funchalia* available to me appear to be conspecific with the two immature females of 45 mm and less total length partially described by Bouvier, 1908 as "*F. woodwardi*" and evidently included in his "*Hemipenaeopsis villosus*"; as well as with the seven females and two males of from 72 to 85 mm total length described by Lenz and Strunck under the names "*Funchalia woodwardi*" and "*F. vanhöffeni*"; and with the 66 mm female of Station 3028, the 25 mm male of Station 3030, the 24 mm female of Station 3033, and the 25.5 mm male of Station 3036 briefly characterized by Bouvier, 1922, under the name "*F. woodwardi*."

Of the true *F. woodwardi*, here considered to be distinct from *F. villosa*, information is available as to the type, a female of 157 mm (Johnson, 1867,

Miers, 1878, and Calman, 1925); an immature male of 56 mm described by Bouvier, 1908; three females of from 130 to 149 mm described by Calman, 1925; and a male of 100 mm from Station 3028, briefly characterized by Bouvier, 1922. The differences between descriptions of this latter group of specimens and of those referred above to *F. villosa*, which have led me to regard them as representing distinct species, are as follows:

In all material 60 mm or more in length which is described in the present paper or by previous investigators as lacking the hepatic spine (comprising 12 females ranging in length from 65 to 85 mm and two males of between 72 and 85 mm), the rostrum and postrostral carina are armed with from 5 to 7, usually 5, teeth. In material described as with an hepatic spine (it may be noted that although Johnson describes the surface of the carapace as unarmed, Calman has observed a small hepatic spine in the type), comprising four females ranging in length from 130 to 157 mm and two males of 56 and 100 mm, there are 11 to 13, usually 11, teeth on the rostral carina. There is thus a range of variation in each group in number of rostral teeth of 2, an interval between the maximum of one group and the minimum of the other of 4, and an interval between the modes of 6 teeth.

Turning now to available descriptions and specimens of less than 60 mm, it is found that Bouvier has described an early postlarva of 17 mm, as with hepatic spine and only six rostral teeth; and has described two males of 25 and 25.5 mm and two females of 24 and 45 mm as without hepatic and with 5 or 6 rostrals. In the twelve small specimens available to me, ranging from 23.3 to 46 mm, the rostral teeth are 6 or 7 in number (of which, however, the distalmost is so minute as to escape observation at magnifications of less than 30 diameters) and there is no evidence of multiplication with increase in size of the individual. In all of the available specimens an hepatic spine is present. In the smallest it is .19 mm, in the largest .09 mm, in length, the rate of reduction with increase in size being fairly regular. In the small specimens, in which the carapacic tomentum is just beginning to appear, the spine is rather conspicuous; but in larger specimens the hepatic is scarcely larger than the surrounding setae, and may be found only by determined search. It is therefore suggested that an inconspicuous hepatic spine was probably present in juvenile specimens which Bouvier believed to lack it; but it may definitely be stated that in juveniles up to 46 mm with only 5 to 7 rostral teeth, the hepatic spine decreases in length with increase in size of the individual to the point of disappearance at 46 mm; while in specimens of more than 60 mm with similar rostral formula it is completely absent.

There are two records of specimens of *Funchalia* less than 60 mm in total length and with more than seven rostral teeth: Lenz and Strunck describe a juvenile of 24 mm as with 9 rostrals and a very distinct hepatic; and Bouvier describes a male of 56 mm as with 13 rostrals and a conspicuous hepatic.

To summarize the foregoing, it seems fairly evident that known material of *Funchalia*, far from displaying haphazard irregularities in development and number of hepatic and rostral teeth, may be divided into two groups: one with a reported maximum size of 85 mm, fewer than eight rostral teeth in postmysis stages, and an hepatic spine dwindling to disappearance with the progress of maturation; the other with a maximum of 157 mm, more than eight rostral teeth in postmysis stages, and an hepatic present at all sizes. It seems fairly clear, although the evidence presented is not conclusive, that a simple explanation of this bimodality on the grounds of appearance of hepatic and increase in rostral count with increase in size of the individual is impossible. A search for further distinctions between these groups may therefore be made. As a first item, it may be observed that the smallest impregnated female of *Funchalia* is 65 mm total length. The largest known female of the genus is 157 mm in total length. If this latter specimen is conspecific with the smallest impregnated one, females of *Funchalia* must attain a length more than double that of sexual maturity. An increase of this order of magnitude is known in Eusicyoninae (Burkenroad, 1934b) but not among other Penaeidae.

There are certain points of resemblance between Bouvier's description of an immature male of 56 mm and Calman's of very large females, both with hepatic spine; which are not shared by the females of the present collection, or those described by Bouvier and by Lenz and Strunck, all without hepatic spine. Thus, in the former specimens, the rostrum is shown as reaching beyond the first segment of the antennular peduncle; in the latter group, not to the end. In the former the mandibular palp is indicated to be not much longer than the blade (measured from the outer margin of the palp); in the latter it is considerably longer. In the former, the produced inner distal end of the terminal segment of the mandibular palp is shown as sloping broadly out from the concave anterior margin; in the latter, though variable, it is narrow and is rather sharply inflected to meet the anterior margin. In the former, the dactyl of the fourth and fifth legs is less than half as long as the propodus; in specimens of the latter over 65 mm in length it is two-thirds or more of the propodus. This last difference between the two groups requires critical examination, however, since it is discovered that juveniles of *F. villosa* have fifth dactyls relatively much shorter than in the individuals of *F. woodwardi* described by Calman and Bouvier. Briefly, in *F. villosa* of total length 23.3 mm, the propodus is 5.7 times as long as the dactyl; by 46 mm the dactyl has increased to more than two-fifths, while at 67 mm it is almost two-thirds the penultimate joint. We have here, therefore, a heterogonous growth series into which, however, Bouvier's, and especially Calman's specimens cannot be fitted.

The above agreements between the descriptions of two specimens with hepatic spine and numerous rostrals, one individual being smaller, one much larger than specimens lacking hepatic, are emphasized in order to demonstrate

that the differences described in the next paragraph between adult females of *F. woodwardi* and of *F. villosa*, the former twice the length of the latter, are indicative of specific distinctions and are not merely referable to individual variation or to difference in size.

Through the very great kindness of Dr. W. T. Calman and Dr. I. Gordon of the British Museum, I have been enabled to examine one of the South African females of *F. woodwardi*, compared with the Madeiran type and described by Calman, 1925. The specimen is an impregnated female of carapace 37, rostral length 11 mm. It differs from *F. villosa* as follows: The rostrum is relatively longer, reaching to the end of the first segment of the antennular peduncle; and is armed dorsally with a larger number of teeth (11), of which the third from the rear is behind rather than in front of the level of the orbital margin. The rostrum has a strong lateral ridge, (as in *Pelagopenaeus*), which is only vaguely indicated in *F. villosa*. The antennal angle is not unarmed as indicated by Calman's figure, but bears a small tooth like that of *F. villosa*. The longitudinal carina running posteriorly from the hepatic prominence is strong (as in *Pelagopenaeus*) rather than very weak as in *F. villosa*. An hepatic tooth (as in *Pelagopenaeus*) is present. The oblique ridge from the anterior end of the dorsal limb of the sigmoid cardiacobranchial carina is much stronger than in *F. villosa*. There is a strong longitudinal carina ventral to the midlateral one, on the posterior part of the lateral surface of the sixth pleonic somite (also present in *Pelagopenaeus*) which is not perceptible in *F. villosa*. The telson extends to the level of the distolateral tooth of the uropodal exopod, instead of falling far short of this point. The oblique distal margin of the mandibular palp is only very slightly concave, whereas in *F. villosa* it is strongly so. The mandibular palp is not so long as the blade, instead of being considerably longer. The dactyl of the third maxillipede is shorter, broader, and more flattened than the narrow, almost styliform segment found in females of *F. villosa*, but is not so lanceolate as that of the male of the latter species, according to figures by Lenz and Strunck. The chelae are much shorter and stouter than are those of *F. villosa*, the palm and finger of the third pair measuring, respectively, 2.7 and 2.8 mm in length as compared to 2.2 and 1.6 mm for the much smaller adults of *F. villosa*. The dactyls of the fourth and fifth legs are (as in *Pelagopenaeus*) conspicuously shorter than in *F. villosa*, the dactyl of the fourth in *F. woodwardi* being only slightly more than one-half the propodus, as compared to nearly two-thirds in the latter. The thelycum in the available female is obscured by a sperm-mass which is not, as in *F. villosa*, an ellipsoid neatly fitted within the receptacle, but an irregular body covering the median plate and extending back over the posterior lip of the depression. The following conspicuous differences from the thelycum of *F. villosa* may be made out: The ridge of the lateral hoods is straight, not inflected; the anterolateral margin of the hoods is deeply emarginate rather than only slightly concave, and the part

of the receptacle enclosed between the hoods is evidently wider than long, instead of longer than wide.

In presence of hepatic spine and in shortness of the dactyls of the posterior legs, *F. woodwardi* is evidently equivalent to juvenile instars of *F. villosa*. In other features, *F. woodwardi* is completely independent of the newly distinguished form.

Brief comment on described larvae of *Funchalia* may be given here. The early postmysis of *Funchalia*, described by Gurney, 1924, from New Zealand, seems referable to *F. villosa*, since a postmysis of 13.34 mm from the Bermuda collections of the Department of Tropical Research of the New York Zoological Society, clearly attributable to the juvenile series of *F. villosa* described in preceding paragraphs, appears to be a slightly older stage of the same species as Gurney's larva. The Mediterranean larvae described by Monticelli and Lobbiano, 1902, as referable to *Aristaeus antennatus*, and by Stephensen, 1923, as *Aristaeomorpha foliacea*, seem, especially because of the earlier appearance of rostral teeth, ascribable to *F. woodwardi*. The juvenile of 24 mm from St. Helena, described as *Funchalia* sp. by Lenz and Strunck, 1914, is probably ascribable to *F. woodwardi*; in addition to characters of rostral and hepatic teeth, the double carina of the sixth pleonic pleura is strongly suggestive of the condition of adult *F. woodwardi*.

I have referred to *F. villosa* the specimens taken in company with females of their "*F. woodwardi*," which are described by Lenz and Strunck as females of a new species (*F. vanhoeffeni*) distinguishable by the expanded dactyls of their third maxillipedes and their peculiar "thelycum." The suspicion of the identity of these specimens was based on the fact that the figure of the "thelycum" of *F. vanhoeffeni* is strongly reminiscent of the genital sternites of males of *Pelagopenaeus*, in which males, also, the dactyls of the third maxillipedes are lanceolate in comparison with the styliiform dactyls of the available females. In response to an inquiry, Dr. A. Schellenberg of the Zoologisches Museum der Universität, Berlin, has been so kind as to examine the types, and to offer the following information: "Beides [exemplare von *F. vanhoeffeni*] sind ♂ mit wohl ausgebildeten Petasma." The supposed differences between *F. "vanhoeffeni"* and *F. "woodwardi"* can therefore be stated to represent sexual dimorphism within *F. villosa*.

The distribution of the two species of *Funchalia* s. s. as far as the records permit differentiation, is as follows: Adults of *F. villosa* are known from the eastern and western North Atlantic, the south central South Atlantic, and the Caribbean; adults of *F. woodwardi* from the eastern North Atlantic and the southeastern South Atlantic. Larvae probably of *F. villosa* are known from the western North Atlantic and the South Pacific; larvae probably of *F. woodwardi* from the Mediterranean and the central South Atlantic.

Subgenus PELAGOPENAEUS Burkenroad

Pelagopenaeus is distinguished from *Funchalis* s.s. by the presence of a ventral armature on its rostrum; the elongation of the branchiostegal carina of its carapace; and the occurrence of a prominent dorsal longitudinal carina of which no complete equivalent exists in *Funchalia* s. s. or in *Penaeus*; its unarmed antennal angle; the shorter incisor process of its mandibles; and the median extension, as free flaps, of the lateral hoods of the fourteenth sternite of the female. No other differences of importance between the two subgenera have been found.

The ventral rostral armature which occurs in some Penaeinae has been invested with considerable significance by certain systematists, but serial arrangements founded on this character in the past are clearly artificial. Within such homogeneous genera as *Eusicyonia* and *Hymenopenaeus*, a ventral armature may be either present or absent. Therefore, since *Funchalia* and *Pelagopenaeus* are clearly very closely related, and possess very numerous characters in common which are not shared by *Penaeus* and *Heteropenaeus*, the other group of the series, it seems better not to set up *Pelagopenaeus* as an independent genus.

Nine specimens have heretofore been taken. One female, described as *Penaeus balboae* by Faxon, 1893 and 1895, was captured off Cocos Island in the American Pacific, at a depth between surface and 770 fathoms; another female, described without recognizance of Faxon's work as *Penaeus meridionalis* Lenz and Strunck, 1914, was taken in the middle of the temperate South Atlantic, at a depth of ten meters, during the night; while four females and three males are recorded as *Penaeus balboae*, without detailed description, by Schmitt, 1935, from the American Pacific, at the surface. Whether "*Penaeus* sp." noted from east of Madeira at 3800 meters by Hanström, 1933, is referable to *Pelagopenaeus* is not known. Of the three individuals of *Pelagopenaeus* in the Bingham Collection, all males, two were taken in the North and Southwestern Caribbean at the surface, by night, and one off Bermuda, at a depth of less than 2000 meters.

The above specimens seem to represent a single uncommon but widely distributed species which, like *Funchalia*, chiefly inhabits the upper water-layers of the open sea.

***Funchalia* (*Pelagopenaeus*) *balboae* (Faxon)**

Figure 71, p. 139

Penaeus balboae, Faxon, 1893 and 1895; Alcock, 1906; Schmitt, 1935.*Penaeus meridionalis*, Lenz and Strunck, 1914.*Funchalia* (*Pelagopenaeus*) *balboae*, Burkenroad, 1934a.*Funchalia* (*Pelagopenaeus*) *meridionalis*, Burkenroad, 1934a.

1 male, adult. B.O.C. 130. Pawnee Station 59; N. 32° 19' 18", W. 64° 32' 30"; April 21, 1927. 8000 feet wire.

1 male, adult. *B.O.C. 131*. Sargassum Haul 111; N. 21° 04', W. 84° 11'; February 28, 1934, night. Surface.

1 male, badly damaged. *B.O.C. 132*. Sargassum Haul 77; N. 10° 20', W. 79° 15'; February 6, 1934, night. Surface.

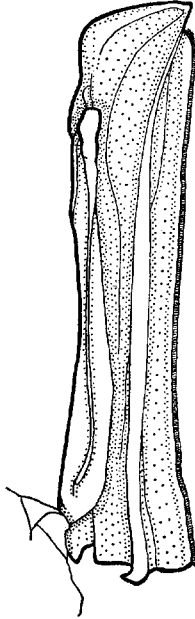
B.O.C. 130, carapace 31 mm, rostrum 14.2 mm, total 135 mm. *B.O.C. 131* and *B.O.C. 132*, respective carapace lengths 30 and 28 mm.

The rostrum of the largest specimen reaches about to middle of second segment of the antennular peduncle and is armed with $\frac{13+1}{4}$ teeth. Two teeth in addition to the epigastric lie behind the orbital margin. The epigastric is nearly as far distant from the posterior tooth of the rostral series as is this from the third tooth of the rostral series. The ultimate tooth is as far from the rostral tip as from the antepenultimate tooth. The ultimate tooth of the ventral margin lies beneath the ultimate of the dorsal margin; it is succeeded by three well-spaced teeth, the posterior of which lies just anterior to the sixth dorsal tooth from the tip, well posterior to the distal end of the first antennular segment. The rostrum is horizontal, with a slightly upturned tip. Its lateral carina is well marked and extends from somewhat in advance of the epigastric tooth nearly to the rostral tip. The rostra of both of the smaller specimens are broken short; the remaining portions are in agreement with the above. The postrostral carina runs to within about one-seventh of the posterior margin of the carapace, at which point it terminates abruptly. There is a short, faint, transverse ridge just behind the end of the postrostral carina. There is no trace of an orbital angle. The antennal angle is broadly rounded and unarmed; its inferior margin has a sigmoid curve. The anteroventral angle of the carapace is produced and dentiform. There is a small hepatic spine placed just in advance of the level of the epigastric tooth, somewhat closer to the vertical carina than to the end of the antennal angle. The faint sulci which occur in *Funchalia* (ventral and dorsal parts of the anterior cervical and the groove parallel and anterior to the ascending limb of the dorsal cervical) are perceptible, but the horizontal limb of the dorsal cervical of *Funchalia* is absent. The sigmoid cardiacobranchial carina is like that of *Funchalia*, and reaches the posterior margin of the carapace. At a point slightly in advance of the middle of the carapace an obliquely vertical ridge slopes downward and backward from the base of the ascending part of the sigmoid curve of the cardiao-branchial ridge, to meet the elongated branchiostegal carina. This latter reaches to within one-sixth of its length of the posterior margin of the carapace. A well-marked, longitudinal carina, dorsal to the cardiao-branchial ridge, with a shallow sigmoid curvature in its midsection, extends from somewhat anterior to the level of the epigastric tooth as far posterior as the end of the postrostral carina. At its ill-marked posterior end, it recurves upon itself, reappearing as a short ridge extending anterodorsally. This oblique ridge occurs in *Funchalia*, where the

main, longitudinal carina is absent. From the apex of the ascending part of the sigmoid curve of the cardiaco-branchial carina a very broad, faint, transverse crest anteriorly margined by a shallow sulcus runs dorsally to meet the dorsolateral longitudinal carina. This crest is present in *Funchalia* though the dorsolateral carina is not. The pleon is nearly identical with the same part in *Funchalia* save that the dorsal (but not the lateral) carinae of the fourth, fifth, and sixth somites are sulcate; and that the carina of the fifth somite ends in a slight projection, the sixth being toothed in both subgenera. The tip of the telson is missing in all the specimens, but it appears to have reached beyond the externodistal tooth of the uropodal exopods.

The superior antennular flagella are somewhat stouter than the inferior and extend well beyond them. In the largest specimen the complete inferior ramus measures 28.5 mm, less than the carapace without the rostrum. In No. 131, the incomplete superior ramus measures 72 mm; the complete inferior ramus measures 26 mm. The antennular peduncle is like that of *Funchalia*; a very short external scale occurs on the basal segment. The upturned outer rim of the distal part of the basal segment, as in *Funchalia*, lacks any longitudinal carina. The inner distal margin of this joint supports a large projection. The external border of the antennal scale terminates in a large tooth which extends well beyond the end of the antennular peduncle. The distal segment of the mandibular palp is little more than twice the length of the basal segment, and tapers to a narrow tip. The mandible resembles that of *Funchalia*, but the incisor process has a relatively more slender tip and is much less produced, the length of the anterior margin measured from the external base of the palp being less than three-fifths of the palp. The cutting edge of the mandible is concave, the blade being shaped like the end of a scimitar. The exopodites of the second and third maxillipedes reach beyond the middle of the antennal peduncle. The endopod of the third maxillipede reaches a dactyl beyond the peduncle. The dactyl is laterally flattened, lanceolate, more than one and one-half times as long as the propodus. Dactyl and propodus together exceed the carpus in length. As in *Funchalia*, the exopods of the pereopods have a conspicuous joint in the middle; those of the first legs reach nearly to the end of the ischium, being rather larger than those of the succeeding legs. In No. 131, the exopodites of the fifth legs are completely absent, whereas in the largest specimen these rami are as large as those of the preceding legs. It may be noted in this connection that the fifth exopod is delayed in reappearance longer than are the others, in postmysis stages of *Funchalia*. The third legs extend to the middle of the antennal peduncle. As in the chelae of the preceding legs, both fingers bear teeth, and the inner margins of both as well as the median margin of the fixed finger and part of the palm are finely denticulated. The fourth legs are subequal in length to the third; the fifth are even shorter. The dactyls of these two pereopods are less than half the length of the propodus, and form slender,

sharp, curved grappling hooks. The diaeresis of the uropodal exopods is well marked, and there is a strong, projecting tooth about one-fourth the external margin proximad the tip. The uropodal endopodite extends well beyond this tooth.



Petasma, right half, posterior face. 71. *Funchalia (Pelagopenaeus) balboae* Faxon, North Atlantic ♂, $\times 6.2$.

There is a conspicuous lameliform tooth-like projection in the midline of both thirteenth and fourteenth pereonic sternites. The male genital orifices are subcoxal, and, as in certain species of *Penaeus*, the anterior margin of the swollen area bearing the gaping, transverse orifice is produced as a fleshy finger armed with long setae. The petasma is simple and open, bearing a close superficial resemblance to that of *Penaeopsis megalops* (Smith), Burkenroad, 1934b. It is, however, unique among Penaeinae with open petasma in that the ventrolateral margin gives rise to a free *distoventral projection*, as in many Solenocerinae. The free edge of distolateral lobe is weakly denticulate, as in the Solenocerine *Hymenopenaeus robustus* Smith or *Solenocera agassizii* Faxon.

The color in fresh (though dead) specimens was whitish (translucent in life?) stippled with red chromatophores.

The present material differs from the description of *Funchalia meridionalis*

(Lenz and Strunck) 1914, in a number of points, but these differences seem referable in the main to errors on the part of the German investigators. Doctor A. Schellenberg of the Zoologisches Museum der Universität, Berlin, has had the great and deeply appreciated kindness to compare the type of *F. meridionalis* with drawings of the Bingham specimens. According to the information supplied by Doctor Schellenberg, the exopod of the uropod of *F. meridionalis*, described and figured as lacking a tooth on the external margin, and figured as lacking the normal sculpture, actually possesses the latter as well as the damaged remnants of the former. The anterolateral corner of the basal segment of the antennular peduncle, figured as unarmed, bears a spine. The shape of the mandible, of which the cutting edge is figured as strongly convex instead of strongly concave, and as separated from the lateral portion by a deep notch, instead of by a projecting corner, is actually similar to that of present material. The antennal angle is rounded, rather than acute as figured, and its ventral margin is sigmoid, not convex. The anteroinferior angle is tooth-like rather than merely sharp-cornered. Other differences between the description and figures by Lenz and Strunck and the present material, which probably lack real basis, are as follows: The cardiaco-branchial carina is shown as not reaching the posterior margin of the carapace. The recurved portion of the dorsolateral carina of the carapace is not indicated in the figures, nor is the lateral carina of the rostrum. The blunt projection figured as on one side only at the distal end of the telson, is probably the result of injury-repair. The upturned lateral margin of the basal segment of the antennular peduncle is figured as less deep and as less rounded anteriorly than it is in our material. The midlateral carina of this margin, figured and described by Lenz and Strunck, perhaps represents the ventral margin of the peduncle, the supposed ventral margin of the investigators probably being formed by the distal ends of a thickly set row of setae. The antepenultimate segment of the second maxillipede is figured as triangular, without a distomedian corner overlapping the penultimate segment. The immovable fingers of the chelae are described and figured as lacking teeth (although these structures are correctly noted by the same authors as present on both fingers in *F. "woodwardi"*). The rostrum is described as with a tooth less both above and below; and the ventral teeth are figured as more crowded, than in the undamaged specimen of the Bingham Collection.

The present material has been directly compared with the female holotype of *Penaeus balboae*, in the collection of the Museum of Comparative Zoology at Harvard. Faxon, by a slip of the pen, has stated that the specimen is a male. The rostrum of the type is broken, but according to Schmitt, 1935, in the seven Pacific specimens which he has examined the formula is $16/4$ or 5 , and the tip of the rostrum does not reach the end of the second segment of the antennular peduncle. A number of differences between Faxon's description and the present material are without actual foundation, the type and the Bingham

specimens being identical in these features, which are briefly listed herewith: The ventral margin of the antennal angle of the type is figured as with a distinct subsidiary angle instead of a merely sinuous outline; and the antennal and cardiaco-branchial carinae as reaching neither the anterior nor the posterior margins, respectively; while the recurved portion of the dorsolateral carina of the carapace has not been indicated. The hepatic tooth is figured as placed much closer to the tip of the antennal angle than to the transverse carina, well in front of the epigastric tooth. The stylocerite is described and figured as absent. The antennal scale is figured as with the tooth of the external margin very short and not extending beyond the antennular peduncle. It may be noted that Faxon's figures 1 and 1c are at variance as to the length of the pereopodal exopods which are stated in the text to be very short.

Such differences as are perceptible on direct comparison between the North Atlantic males and the Pacific American female appear to be of the nature of sexual dimorphism. The third maxillipedes are a little longer in the Atlantic males, and have a slightly longer dactyl which is flattened, expanded, and lanceolate, rather than subcylindrical and styliform as in the type of *F. balboae*. The third maxillipedes of the Atlantic female examined by Lenz and Strunck were unfortunately missing. One or another form of sexual dimorphism is known to involve the dactyl of the third maxillipedes in many Penaeidae, including some species of *Penaeus*, and there is evidence for an identical sexual difference in *Funchalia villosa*.

The thelycum of the type, which is partially obscured by an enclosed sperm mass, seems to resemble that figured by Lenz and Strunck for their South Atlantic female. It differs from that found in *Funchalia* s. s. somewhat as the thelycum of most species of *Penaeus* differs from that of certain species of the first division of the genus (Burkenroad, 1934a); in that the lateral hoods of sternite XIV are produced as free flaps, which, however, do not as in *Penaeus* completely cover the spermatophores.

Subsequent to completion of the foregoing paragraphs I have been enabled, through the very great kindness of Doctor W. L. Schmitt, to examine a Pacific male and female of *F. balboae* from the collections of the U. S. National Museum, of the lot recorded by Dr. Schmitt (1935) in his recent study of *Penaeus*. The carapace of the male measures 23.5, the rostrum 12, of the female 26 and 13 mm; the male especially being thus considerably smaller than the Atlantic specimens compared with it. The male rostral formula is $\frac{15 + 1}{5}$, the female $\frac{13 + r + 1}{4}$. The relations of ventral to dorsal teeth are, counting from the distal

end, identical with the Atlantic specimen; the proximal ventral tooth is, however, anterior to the distal end of the first antennular segment. The antennal angle is sharper than in Atlantic specimens; there is a sharp denticle rather

than a rounded protuberance at the posterior end of the postrostral carina, and a faint trace of the larval anterior dorsal organ remains. The prosartema is slightly shorter than in Atlantic specimens. The superior flagellum of the antennule is in the male only 33.5 mm long (the inferior being 19 mm), and is thus relatively much shorter than in the Atlantic males; in the female the superior flagellum is still shorter and slenderer, being only a fourth longer than the inferior. The exopods of the walking legs are shorter, and those of the fifth pair, which are present in the largest Atlantic specimen, are here absent (as in the smaller Atlantic male). The third maxillipede of the male is slightly shorter than in Atlantic specimens, and its dactyl, although narrowly lanceolate as compared with the styliform finger of the female, is much less expanded than in Atlantic males. The petasma differs by its somewhat shorter distoventral projection. The thelycum of the young Pacific female is unimpregnated and certain details not visible in the type are therefore visible. The floor of the receptacle is not depressed below the level of its slightly raised posterior rim; and is setose. The flaps which partly enclose the receptacle are expansions of the ridges found on the lateral hoods of *Funchalia* s. s. Otherwise the thelycum closely resembles that of *F. villosa*. The differences of these from other specimens of *F. balboae*, where not referable to individual variation (as in rostral formula), seem attributable to the more juvenile condition of the Pacific specimens; and it is probable that the stocks of *F. balboae* in the two oceans are to be regarded as specifically identical.

SUMMARY

TAXONOMY

ARISTAEINAE.

BENTHESICYMAE. Material examined, *Benthescycymus bartletti*, *tanneri*, *altus*, *investigatoris*, *carinatus*, *laciniatus*,* *brasiliensis*,* *urinator** n. sp., *cereus** n. sp., *strabus*, n. sp. *iridescens*.* *Bentheogennema intermedia*.* *Gennadas capensis*,* *kempi*,* *elegans*,* *brevirostris*, *tinayrei*,* *parvus*, *valens*,* *gilchristi*,* *bouvieri*, *talismani*,* *scutatus*.*

1. The distinctions between the maniple Benthescycymae and the maniple Aristaeae are reviewed. It is found that there is only a single completely diagnostic difference.
2. The species of Benthescycymae are divisible into four genera, *Benthonectes* Smith, *Benthescycymus* Bate, *Bentheogennema* n. nom., and *Gennadas* Bate, the diagnostic characters of which are discussed in detail. *Amalopenaeus* Smith is a synonym of *Gennadas* Bate.
3. *Benthescycymus* is composed of two superspecific groups, centering about *B. crenatus* Bate and *B. bartletti* Smith, for the species of which diagnostic keys are presented.

* Figured. Illustrations from camera lucida drawings by the author.

4. *Benthescycymus hjorti* Sund and *Gennadas pectinatus* Schmitt appear to be synonymous with *Benthescycymus laciniatus* Rathbun, which may be identical with *B. crenatus* Bate. *B. pleocanthus* Bate is synonymous with *B. bartletti* Smith. *Benthescycymus moratus* Smith is synonymous with *B. brasiliensis* Bate. *B. mollis* Bate, *B. armatus* MacGilchrist, and *B. longipes* Bouvier are synonymous with *B. iridescens* Bate. Bate's material of *B. brasiliensis* includes the three new species *B. urinator*, *B. strabus* and *B. cereus*, with the former of which *B. moratus* Rathbun (*not* Smith) is identical.
5. *Bentheogennema calmani* (Kemp) is distinct from *B. intermedia* (Bate) but synonymous with *B. borealis* (Rathbun). *Gennadas* sp. Rathbun represents *Bentheogennema intermedia* (Bate).
6. The species of *Gennadas* are divisible into two groups on the basis of differences in genital structure.
7. From consideration of the demonstrable correlations in form between male and female copulatory organs, it is suggested that *Gennadas gardineri* (Balss) may be the female of *G. incertus* (Balss). The female of *G. capensis* Calman, previously unknown, is described; the species is distinct from *G. kemp* Stebbing. *G. alcocki* Kemp, part, is the male of *G. bowieri* Kemp. *G. scutatus indicus* Kemp, *G. alcocki* Kemp and *G. clavicarpus* DeMan are synonyms of *G. propinquus* Rathbun. *G. similis* Stephensen seems to be a synonym of *G. brevirostris* Bouvier (*G. elegans* A. Milne-Edwards and Bouvier). A diagnostic key to the species of the genus is presented.

ARISTEAE. Material examined, *Hepomadus tener*. *Plesiopenaeus armatus*, *coruscans*.* *Hemipenaeus carpenteri*, *spinidorsalis*. *Aristaeus occidentalis*.

8. The distinctness of *Hepomadus tener* Smith from *H. glacialis* Bate is observed to be not entirely certain.
9. *Plesiopenaeus* and *Aristaeopsis*, as used by recent authors, refer each to the other's original genotype. Since the two groups are structurally not clearly distinguished, the latter is synonymized with the former thus avoiding confusion.
10. The distinctness of *Plesiopenaeus armatus tridens* (Smith) from *P. armatus* (Bate) is observed to be doubtful.
11. An Atlantic form apparently identical with *Plesiopenaeus coruscans* (Wood-Mason), heretofore known only from the Indo-Pacific, is described.
12. The diagnoses of the genera *Hemipenaeus*, *Aristaeus*, and *Plesiopenaeus* are modified in recognition of the occurrence of a podobranch on XII and an epipodite on XIII in species of *Hemipenaeus*.
13. It is indicated that the Atlantic form indistinguishable from the Pacific-American *Hemipenaeus triton* Faxon is probably identical with *H. carpenteri* Wood Mason.

SOLENO CERINAE. Material examined: *Haliporus thetis*. *Hymenopenaeus*

laevis, nereus, doris, debilis, aphoticus* n. sp., diomedea, robustus, modestus, mülleri. Solenocera agassizii,* sp. indet.* vioscai, membranacea.*

14. The presence of two appendices on the second pleopod of males of this subfamily and of the Aristaeinae is pointed out, and a previous suggestion that the Solenocerinae are more closely related to Aristaeinae than to Penaeinae, based on larval structure, is thereby strengthened.
15. It is pointed out that the Jurassic *Aeger* displays more features in common with the modern Solenocerinae than with the Aristaeinae to which it has been referred.
16. *Haliporus* Bate is restricted to two peculiar species very closely approaching the aristaeine mode, *H. curvirostris* Bate and *H. thetis* Faxon, the latter of which is redescribed.
17. *Hymenopenaeus* Smith is re-established for most of the species of *Haliporus* auct., which are divisible into four superspecific groups. The genus is reviewed.
18. *Hymenopenaeus androgynus* (Bouvier), *H. sp.* (Lenz and Strunck) and *H. microps* Smith, are synonymous with *Hymenopenaeus laevis* (Bate).
19. *H. robustus* Smith is shown to stand in near relationship not to *H. diomedea* (Faxon) but rather to *H. modestus* Smith and *H. lucasii* (Bate).
20. *Hymenopenaeus aphoticus*, a new Atlantic species rather closely related to *H. debilis*, is described.
21. Further distinctions between *Solenocera vioscai* Burkenroad and *S. agassizii* Faxon are made known. Juvenile or variant forms of both are described.

PENAEINAE. Material examined: *Funchalia villosa, woodwardi, balboae.**

22. The members of the series Peneae are compared. It is shown that in at least one character the Jurassic *Penaeus (Antrimpos) speciosus* resembles *Funchalia* rather than the living species of *Penaeus*.
23. It is shown that two species have heretofore been confused under the name *F. woodwardi* Johnson. The name *F. villosa* (Bouvier) is available for the component distinct from the type. It is pointed out that the supposedly female types of *F. vanhoeffeni* Lenz and Strunck represent males of *F. villosa*.
24. *F. (Pelagopenaeus) balboae* (Faxon) is a bioceanic species with which *Penaeus meridionalis* Lenz and Strunck is identical.

MORPHOLOGY

1. It is shown that in *Gennadas, Bentheogennema*, and certain of the species of *Benthesicymus* the thelycum differs from that of other Penaeidae in that the enclosed or invaginated sperm receptacles are placed between the twelfth and thirteenth sternites rather than the thirteenth and fourteenth sternites as in Penaeinae with enclosed receptacles [p. 50]. In certain species of *Benthesicymus*, the Aristeae, the Solenocerinae, and certain

- species of Penaeinae, there are no enclosed receptacles; this open thelycum seems to represent the basic form from which the enclosed receptacles of Benthescyminae and Penaeinae-Eusicyoninae have been independently derived [p. 62].
2. The major portion of the spermatophore as found in males of *Bentheogennema* and *Gennadas*, composed of the sperm-free accessory portions homologous with those which function for anchorage and protection of the exposed spermatophore of peneids without enclosed receptacles, seems to be discarded during sperm transfer, and the sperm mass which it surrounds alone to be inserted into the female receptacle [p. 62]. This mode of adaptation of spermatophore to the mechanical limitations of enclosed storage is contrasted with that found in the Penaeinae, where the accessory material is diminished in bulk and is transferred to the female, instead of being elaborated and cast off. A possible correlation between type of spermatophore reduction and of male copulatory organ is pointed out [p. 63].
 3. It is pointed out that there is no evidence available in support of the view that gross reversible changes in secondary sexual characters (such as, it is shown, may probably occur in certain Astacidae) actually take place in Penaeidae [p. 53, 61].
 4. Additions are made to the descriptions of the ocular pigment-fleck of Benthescyminae [p. 20]. The peculiar reverse-reniform eye of *Benthescymus investigatoris*, in which the proximal part of the layer of crystalline cones appears to have degenerated, is described [p. 49].
 5. The occurrence of intraspecific variation in presence or degree of development of the gills among Aristeae is confirmed [p. 86, 93].
 6. The parapeneid spine of the antennular peduncle is shown to occur, as in Penaeinae, in juveniles of Aristeae which lack the structure as adults. The spine, otherwise known in adults only within the series Parapeneae of Penaeinae, is present in mature individuals of *Benthescymus crenatus* Bate and *Haliporus thetis* Faxon [p. 29, 102].
 7. The occurrence of compound photophores in a species of the family, *Hymenopenaeus debilis*, is made known. The distribution of "open" and of "closed" systems of luminescence among crustacea is considered with reference to *Plesiopenaeus coruscans* [p. 112, 99].

DISTRIBUTION

1. The Aristaeninae and Solenocerinae are chiefly oceanic, the Penaeinae and Eusicyoninae chiefly littoral in habit. It is pointed out that so far as present knowledge goes, the oceanic forms, which are usually, though by no means always, cosmopolitan, seem often to be irregularly distributed within their great range [p. 1].
2. The presence of an Indo-Pacific and extreme southeastern Atlantic com-

- ponent in the oceanic fauna of the Bahaman region, not represented in the eastern basin of the North Atlantic, is made known [p. 3].
3. It is shown that, whereas the littoral peneid faunas of the Atlantic and Pacific American coasts are more nearly related to one another than to the faunas of other regions of the world, the reverse seems to be true of the deep-water peneids. This contrast is indicated to have a possible cause in the shallow depth of post-Cretaceous Middle American intercommunications between the Atlantic and Pacific, which while placing the littoral populations in contiguity, left the deep-water forms effectively at opposite ends of the world. It is therefore suggested that deep-water species common to Atlantic and Pacific America will be found to have maintained their identity by circumferential continuity [p. 6].
 4. Revision of the *Benthesicymus brasiliensis* complex permits a new statement of the distributions of the component species. *B. brasiliensis* Bate seems to be limited to the Atlantic; and *B. urinator* n. sp., to the Indo-Pacific; while *B. iridescens* Bate and *B. cereus* n. sp. are found in both oceans [p. 29].
 5. Although Balss' Indo-Pacific records must be considered as ambiguous, it is shown that *Bentheogennema intermedia* (Bate) does occur in the region [p. 57].
 6. The known Atlantic range of *Gennadas capensis* Calman and *G. bowieri* Kemp is considerably extended. *G. parvus* Bate is recorded from the Atlantic for the first time. The peculiar distribution of *G. elegans* (Smith) is discussed, and its absence from the southwestern North Atlantic is pointed out. Its replacement in this region by *G. capensis* Calman is compared with the similar phenomenon off the Cape of Good Hope [p. 71, 72, 74, 81].
 7. The known range of *Plesiopenaeus coruscans* (Wood Mason and Alcock) and of *Hemipenaeus carpenteri* Wood Mason is extended to the Atlantic [p. 96, 91].
 8. Pelagic captures of *Hymenopenaeus laevis* (Bate) and of *H. aphoticus* n. sp. are recorded. An analysis of the gut and statocyst contents indicates these specimens to have frequented the bottom, and leads to the suggestion that, as possibly also in certain species of *Benthesicymus* with statolith of benthonic derivation, these Solenocerinae may be quasipelagic [p. 105].
 9. The known range of *Hymenopenaeus mülleri* (Bate) is extended north to Rio de Janeiro [p. 120].
 10. The known range of *Funchalia (Pelagopenaeus) balboae* Faxon is extended to the Atlantic [p. 136].

LITERATURE CITED

- AGASSIZ, A.:
1888. Three Cruises of the Blake. II. *Cambridge*.
- ALCOCK, A.:
1901. A Descriptive Catalogue of the Indian Deep-Sea Crustacea Decapoda Macrura and Anomala in the Indian Museum. . . *Calcutta*.
1906. Catalogue of the Indian Decapod Crustacea in the Collection of the Indian Museum. Part III. Macrura. Fasciculus I. The Prawns of the Penacus Group. *Calcutta*.
- BALSS, H.:
1923. Studien an fossilen Decapoden. *Palaeont. Zts., V. Berlin*.
1925. Macrura der Deutschen Tiefsee-Expedition. 2. Natantia, Teil A. *Wiss. Ergeb. D. T-E., XX, 5 (1926)*.
1927. Macrura der Deutschen Tiefsee-Expedition. 3. Natantia, Teil B. *Wiss. Ergeb. D. T-E., XXIII, 6*.
- BATE, C. S.:
1881. On the Penaeidea. *Ann. Nat. Hist. (5) VIII*.
1888. Report on the Crustacea Macrura. . . *Rept. Sci. Res. Voy. H. M. S. "Challenger," Zool., XXIV*.
- BEEBE, W.:
1934. A Half Mile Down. *Nat. Geogr. Mag., LXVI, 6. Washington*.
- BERG, C.:
1898. Sobre el Langostin y el Camarón, dos Crustáceos Macruros de aguas Argentinas y Uruguayas. *Comm. Mus. Nac. Buenos Aires, I*.
- BERKELEY, A. A.:
1930. The Post-Embryonic Development of the Common Pandalids of British Columbia. *Contr. Canadian Biol. Fish. (N. S.), VI, 6*.
- BOONE, P. L.:
1927. Crustacea from Tropical East American Seas. *Bull. Bingham Oc. Coll., I, 2*.
1930. Crustacea: Anomura, Macrura. . . *Bull. Vanderbilt Marine Mus., III. Huntington, N. Y.*
- BOUVIER, E. L.:
1905a. Sur les Pénéides et les Sténopides recueillis par les expéditions françaises et monegasques dans l'Atlantique oriental. *C. R. Acad. Sci. Paris, CXL*.
1905b. Sur les Macroures nageurs (abstraction fait des Carides) recueillis par les expéditions américaines du Blake et du Hassler. *C. R. Acad. Sci. Paris, CXXI*.
1906a. Sur les *Gennadas* ou Pénéides bathypelagique. *Bull. Mus. Oc. Monaco, LXXX*.
1906b. Observations sur les Pénéides du genre *Haliporus* Sp. Bate. *Bull. Mus. Oc. Monaco, LXXXI*.
1907. Sur la position, les affinités et le développement des Pénéides du genre *Funchalia* Johnson. *C. R. Acad. Sci. Paris, CXLIV*.
1908. Crustacés décapodes (Pénéides) provenant des campagnes de l'Hirondelle et de la Princesse-Alice (1886-1907). *Res. Camp. Sci. Monaco, XXXIII*.

1922. Observations complémentaires sur les Crustacés décapodes (abstraction faite des Carides) provenant des Campagnes de S. A. S. le Prince de Monaco. *Res. Camp. Sci. Monaco, LXII.*
- BURKENROAD, M. D.:
- 1934a. The Penaeidea of Louisiana, with a Discussion of their World Relationships. *Bull. American Mus. Nat. Hist., LXVIII, 2.*
- 1934b. Littoral Penaeidea chiefly from the Bingham Oceanographic Collection. *Bull. Bingham Oc. Coll., IV, 7.*
- CALMAN, W. T.:
1925. On Macrurous Decapod Crustacea Collected in South African Waters by the S. S. "Pickle." *Rept. Fish. & Mar. Biol. Survey, IV, Special Rept. 3. Capetown.*
- CREASER, E. P.:
1933. Seasonal Changes in the Male Population of *Faxonius propinquus* (Girard). *Occ. Pap. Mus. Zool. Un. Michigan, XI, 253.*
- EDMONDSON, C. H.:
1929. Hawaiian Atyidae. *Bull. B. P. Bishop Mus., LXVI. Honolulu.*
- FAXON, W.:
1884. On the so-called Dimorphism in the Genus *Cambarus*. *American Journ. Sci. (3), XXVII, 57, 8.*
1893. Reports on the Dredging Operations . . . by the U. S. F. C. S. "Albatross." VI. Preliminary Descriptions of New Species of Crustacea. *Bull. Mus. Comp. Zool. Harvard, XXIV, 7.*
1895. Reports on an Exploration off the West Coasts of Mexico, Central and South America, and off the Galapagos Islands . . . by the . . . "Albatross," . . . XV. The Stalk-Eyed Crustacea. *Mem. Mus. Comp. Zool. Harvard. XVIII.*
1896. Reports on the Results of Dredging . . . by the U. S. C. S. S. "Blake." XXVII. Supplementary Notes on the Crustacea. *Bull. Mus. Comp. Zool. Harvard, XXX, 3.*
- GURNEY, R.:
1924. Crustacea. Part IX. Decapod Larvae. *British Antarctic ("Terra Nova") Exped., Nat. Hist. Rept., Zool., VIII, 2.*
- HANSEN, H. J.:
1908. Crustacea Malacostraca (I). *Danish Ingolf-Exped., III, 2. Copenhagen.*
- HANSTRÖM, B.:
1933. Neue Untersuchungen über Sinnesorgane und Nervensystem der Crustaceen. II. *Zool. Jahrb., Abt. f. Anat. u. Ont., LVI, 3/4.*
1934. Neue Untersuchungen über Sinnesorgane und Nervensystem der Crustaceen. III. *Zool. Jahrb., Abt. f. Anat. u. Ont., LVIII, 1.*
- JOHNSON, J. Y.:
1867. Descriptions of a New Genus and a New Species of Macrurous Decapod Crustaceans belonging to the Penaeidae, discovered at Madeira. *Proc. Zool. Soc. London, 1867.*
- KEMP, S. W.:
1906. Macrura from the West Coast of Ireland. *Fish. Ireland Sci. Invest. 1905, 5.*

1909. The Decapods of the Genus *Gennadas* collected by H. M. S. "Challenger." *Proc. Zool. Soc. London*, 1909.
- 1910a. The Decapoda Natantia of the Coasts of Ireland. *Fish. Ireland Sci. Invest.*, 1908, 1.
- 1910b. Notes on Decapoda in the Indian Museum. I. The Species of *Gennadas*. *Rec. Indian Mus.*, V, 17.
- 1910c. Notes on the Photophores of Decapod Crustacea. *Proc. Zool. Soc. London*, 1910.
1913. The Percy Sladen Trust Expedition to the Indian Ocean . . . Vol. V, No. V. Pelagic Crustacea Decapoda . . . *Trans. Linn. Soc. London* (2) *Zool.*, XVI, 1.
1925. Notes on Crustacea Decapoda in the Indian Museum. XVII. On Various Caridea. *Rec. Indian Mus.*, XXVII, 4.
- KEMP, S. W. AND SEWELL, R. B. S.:
1912. Notes on Decapoda in the Indian Mus. III. The Species obtained by R. I. M. S. S. "Investigator" . . . *Rec. Indian Mus.*, VII, 2.
- LANG, D. AND YONGE, C. M.:
1935. The Function of the Tegumental Glands in the Statocyst of *Homarus vulgaris*. *Journ. Marine Biol. Assoc. (n. s.)*, XX, 2.
- LENZ, H. AND STRUNCK, K.:
1914. Die Dekapoden der Deutschen Südpolar-Expedition 1901-1903. I. Brachyuren und Macruren mit Ausschluss der Sergestiden. *D. Sp.-Exped.*, XV (*Zool. VII*), 3 (6).
- LUCAS, H.:
1850. Observation sur un nouveau genre de l'ordre des Décapodes macroures appartenant a la tribu des Pécécens. *Ann. Soc. Ent. France* (2), VIII.
- MAN, J. G. DE:
1907. Diagnoses of New Species of Macrurous Decapod Crustacea from the Siboga-Expedition, II. *Notes Leyden Mus.*, XXIX.
1911. The Decapoda of the Siboga Expedition. Part I. Family Penaeidae. *Uitk. o. Zool., Bot., Oc. e. Geol. Geb. (Siboga-Exped.)*, XXXIX a [and Plates, 1913, suppl. XXXIX a].
- MACGILCHRIST, A. C.:
1905. Natural History Notes from R. I. M. S. "Investigator" . . . Series III, No. 6. An Account of the new and some of the rarer Decapod Crustacea obtained during the Surveying Seasons 1901-1904. *Ann. Mag. Nat. Hist. (?)*, XV, 87 (27).
- MIERS, E. J.:
1878. Notes on the Penaeidae in the Collection of the British Museum, with Descriptions of some New Species. *Proc. Zool. Soc. London*, 1878.
- MILNE EDWARDS, A. AND BOUVIER, E. L.
1909. Reports on the Results of Dredging . . . by the U. S. C. S. S. "Blake." XLIV. Les Pénéides et Sténopides. *Mem. Mus. Comp. Zool. Harvard*, XXVII, 3.
- MOCQUARD, F.:
1883. Recherches Anatomiques sur L'Estomac des Crustacés Podophtalmaires. *Ann. Sci. Nat. (6)*, XVI.

MONTICELLI, F. S. AND LOBIANCO, S.:

1902. Su la probabile larva di *Aristeus antennatus*. *Mon. Zool. Italiano*, XIII, Suppl.

ORTMANN, A. E.:

1901. Crustacea, zweite Hälfte: Malacostraca. In Bronn, "Klassen u. Ordnungen des Tier-Reich," V, 2. Leipzig.

PARR, A. E.:

1928. Deepsea Fishes of the Order Iniomi from the Waters around the Bahama and Bermuda Islands. *Bull. Bingham Oc. Coll.* III, 3.
1934. Report on Experimental Use of a Triangular Trawl for Bathypelagic Collecting. *Bull. Bingham Oc. Coll.*, IV, 6.

RATHBUN, M. J.:

1902. Descriptions of new Decapod Crustacea from the West Coast of North America. *Proc. U. S. Nat. Mus.*, XXIV, 1272.
1906. The Brachyura and Macrura of the Hawaiian Islands. *Bull. U. S. Fish Comm.* (1903), XXIII, 3.
1910. Decapod Crustaceans of the Northwest Coast of North America. *Harri-man Alaska Ser., Smithsonian Inst.*, X.

SCHMITT, W. L.:

1921. The Marine Decapod Crustacea of California. *Univ. California Publ. Zool.*, XXIII.
1935. The West American Species of Shrimps of the Genus *Penaeus*. *Proc. Biol. Soc. Washington*, XLVIII.

SCHUCHERT, C.:

1935. Historical Geology of the Antillean-Caribbean Region. *New York*.

SMITH, S. I.:

1882. Reports on the Results of Dredging . . . on the East Coast of the United States . . . XVII. Report on the Crustacea. Part I, Decapoda. *Bull. Mus. Comp. Zool. Harvard*, X, 1.
1884. Report on the Decapod Crustacea of the Albatross Dredgings off the East Coast of the United States in 1883. *Rept. Comm. U. S. Comm. Fish & Fisheries for 1882*, X (2), C 15.
1885. On Some New or Little Known Decapod Crustacea, from recent Fish Commission Dredgings off the East Coast of the United States. *Proc. U. S. Nat. Mus.*, VII (1884).
1886. On some Genera and Species of Penaeidae, mostly from recent Dredgings of the United States Fish Commission. *Proc. U. S. Nat. Mus.*, VIII (1885).
1887. Report on the Decapod Crustacea of the Albatross Dredgings off the East Coast of the United States during . . . 1884. *Rept. Comm. U. S. Commission Fish & Fisheries for 1885*, XIII (2), D21.

STEBBING, T. R. R.:

- 1914a. Stalk-eyed Crustacea Malacostraca of the Scottish National Antarctic Expedition. *Trans. Roy. Soc. Edinburgh*, L (1916), pt. 2.
- 1914b. South African Crustacea (Part VII). *Ann. South African Mus.*, XV, 1.

STEPHENSEN, K.:

1923. Decapoda-Macrura excluding Sergestidae . . . *Rept. Danish Oc. Expeds., 1908-10 to the Mediterranean and Adjacent Seas.* II, Biol., D3.

1935. The Godthaab Expedition 1928. Crustacea Decapoda. *Meddel. o. Grønland, LXXX, 1. Copenhagen.*
- SUND, O.:
1920. Peneides and Stenopides. *Rept. Sci. Res. "Michael Sars" N. Atlantic Deep-Sea Exped., III, 2 (republished 1932).*
- VAN STRAELEN, V.:
1925. Contribution a L'Etude des Crustacés Décapodes de la Période Jurassique. *Mem. Acad. Roy. Belgique, Sci., (2), VII, 1.*
- WOOD MASON, J. AND ALCOCK, A.:
- 1891a. Natural History Notes from H. M. I. M. S. S. "Investigator"
No. 21. Note on the Results of the last Season's Deep-Sea Dredging.
Ann. Mag. Nat. Hist. (6), VII, 38.
- 1891b. Natural History Notes from H. M. I. M. S. S. "Investigator"
Series II, No. 1. On the Results of Deep-sea Dredging during the Season
1890-91. *Ann. Mag. Nat. Hist. (6), VIII, 32.*
- YOKOYA, Y.:
1933. On the Distribution of Decapod Crustaceans inhabiting the Continental Shelf around Japan . . . *Journ. Coll. Agric. Tokyo Imp. Univ., XII, 1.*