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

MATERIALS FOR A REVISION OF THE OCEANIC PENAEIDAE

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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 Eusicyoninae, 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 Eusicyoninae 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 penaeids 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 peneid 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 penoids 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 Benthescymae.

Four features in which the Benthescymae 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 Benthescymae than in Aristeae; the antennal flagellum is sharply inflected at some distance from its base in most Benthescymae; 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 Benthescymae 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 Benthescymae 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 Benthescymae opens posterior to the genital apertures.

The series Benthescymae includes about twenty-five or -six probably valid species, which have been variably divided among the four generic names *Benthescymus* 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 *Benthescymus* 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 *Benthescymus* (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 Benthescymae other than *Benthescymus 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 *Benthescymus* (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	+	+	+	+	+	+	+	+	0
brasiliensis	+	+	+	+	+	+	⊖	⊖	⊖
bartletti investigatoris	+	+	+	+	+	+	+	⊖	+
tanneri	+	+	+	+	+	⊖	+	⊖	+
altus	+	+	+	+	+	0	+	⊖	+
<i>Bentheogennema</i> , n. nom. intermedia	+	+	0	0	+	0	0	⊖	0
<i>Gennadas</i> Bate 11 spp.	0	0	0	0	0	0	0	0	0

EXPLANATION OF CAPTIONS AND SYMBOLS

+ indicates the condition to be as stated under the heading in question; 0 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 *Bentheogenemema* 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.* Telycum 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

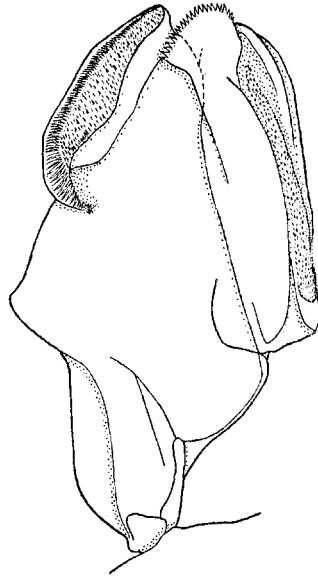
form are doubtfully correct; thus whereas the antennular flagella are described in the text as broken, they are figured as complete. Special mention of the differences from subsequent descriptions seems necessary only for the figure of the dactyl of the third maxillipede, which shows no resemblance to 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. *Benthescymus 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 *Benthescymae*; 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.

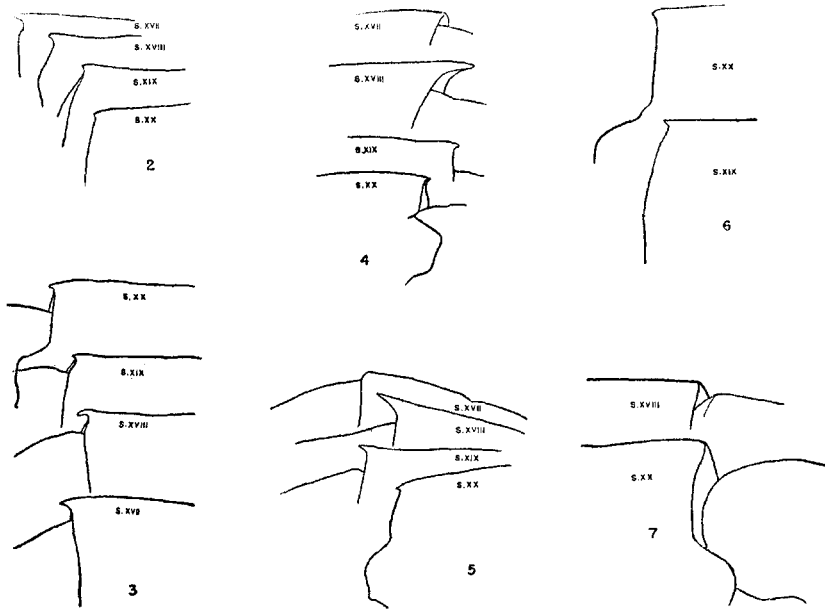
As five specific names are already available for the forms related to *Benthesicymus brasiliensis*, the description of *B. cereus* must be preceded by a revision of the complex. I have been enabled, through the great kindness of Dr. Calman and Dr. Gordon of the British Museum, Dr. Schmitt of the U. S. 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 posteros dorsal armature). 2. *Benthescycymus 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 *Benthescycymus*. 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.)

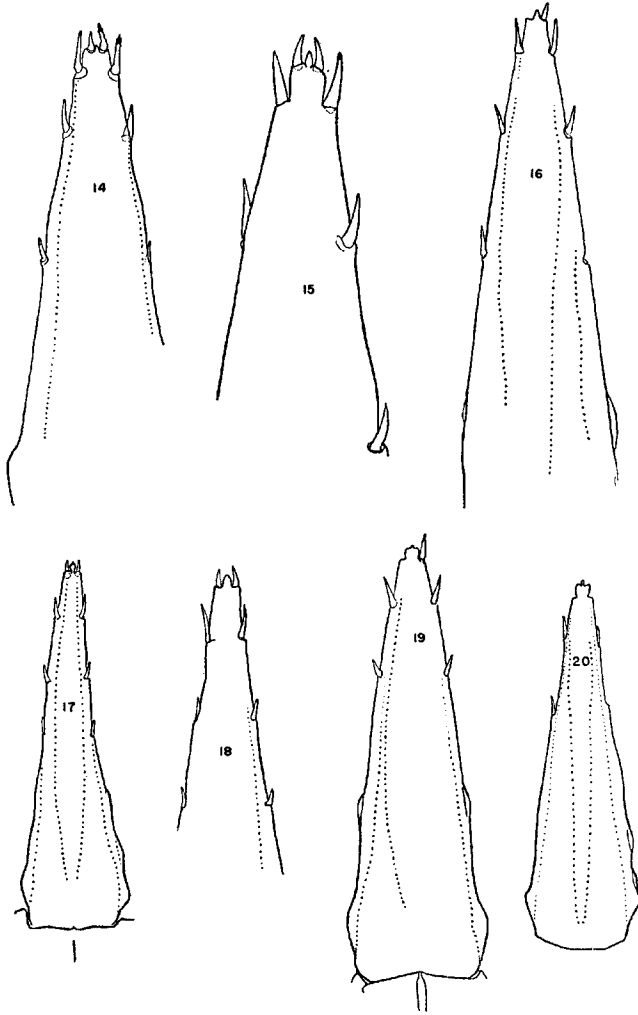
⁷ Shape of the anterior and posterior blades of the appendix masculina. (SYMBOLS: ○ elliptical, Δ triangular, br. broad, (juv.) juvenile, l. long, n. narrow, sh. short, sl. slender, spat. spatulate.)

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.



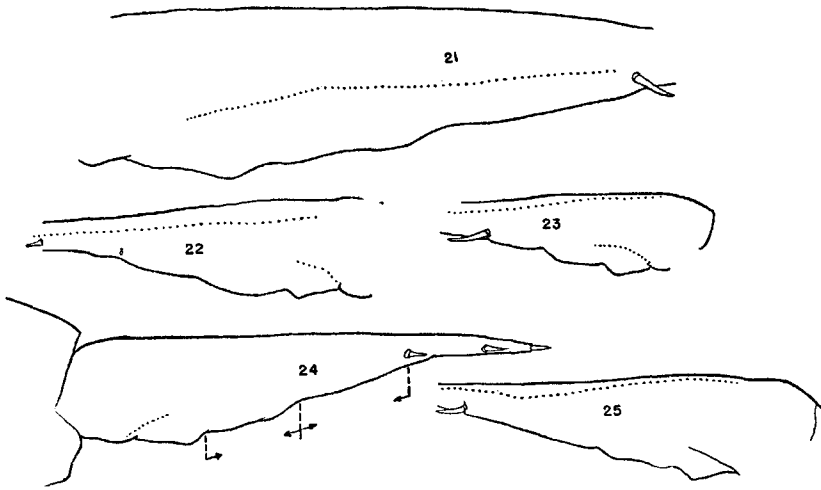
Anterior part of carapace, lateral view. **8.** *Benthescymus urinator*, n. sp. (Specimen No. 8, TYPE), X 3.6. **9.** *B. urinator*, n. sp. (No. 12), X 3.6. **10.** *B. strabus*, n. sp. (No. 18, TYPE), X 3.6. **11.** *B. ceruus*, n. sp. (No. 14, TYPE), X 3.6. **12.** *B. ceruus*, n. sp. (No. 17), X 3.6.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



Telson, dorsal view (showing lateral and terminal spines). 14. *Benthescymus 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