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CRUSTACEA.

PART IX.—DECAPOD LARVAE

BY

ROBERT GURNEY, M.A., F.L.S.,

WITH SEVENTY-EIGHT FIGURES IN THE TEXT.



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CRUSTACEA.

PART IX.—DECAPOD LARVAE.

BY ROBERT GURNEY, M.A., F.L.S.

WITH 78 FIGURES IN THE TEXT.

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I.—INTRODUCTION.

I AM greatly indebted to Dr. W. T. Calman for the opportunity of examining and reporting on the Decapod larvae collected by the "Terra Nova" Expedition, and for much help and encouragement in the carrying out of the work. Many of the larvae had already been sorted out from the plankton samples, and the greater part of this work was done by Miss Webb, to whom I wish to express my thanks. I have, however, myself looked through nearly the whole of the samples, since, even when these had already been examined, it was sometimes necessary to make a special search for additional stages of certain larvae. The result of such a careful and repeated inspection has been the gathering together of an extensive material containing larvae representing nearly all the groups of the Decapoda. Nearly all the samples were taken at or near the surface and consequently advanced larvae of deep-sea forms are very rare.

It seldom happens that in plankton material of this kind a series of stages of the same larva is taken which is sufficiently complete to enable the genus to be determined, and only one such case (*Upogebia*) is recorded below. The remainder must be identified as nearly as possible by reference to published descriptions of

larvae whose parentage is known, and such identification must in many cases be very speculative. It is, however, in my opinion, more profitable to refer such larvae to definite genera or families, even if the reference prove eventually to be wrong, than to describe them under generic and specific names of their own as has so often been done. I have therefore avoided describing any larva unless it can with some probability be systematically placed; but I have, on the other hand, described a number of larvae whose approximate position can with some certainty be given in the hope that, in this way, family and generic characters may be established. My object has been to provide from larval characters new material for a satisfactory classification of the group.

Where such a course has been possible I have given a summary of the characters of families based on previously established information and supplemented by the material available from these collections. I do not, of course, claim that the following report can be regarded as in any sense a "monograph of Decapod larvae," but it is, I think, the first attempt that has been made to systematize the available information. Williamson's work (1915) is a most valuable mine of information on the subject, but he has made no attempt to summarize or to draw any conclusions from the facts, and his system of nomenclature is so eccentric as somewhat to detract from the undeniable value of his work.

II.—DISTRIBUTION.

Ortmann, in his account of the Decapoda of the Plankton Expedition (1893), has shown that there is a very close relation between the numbers of Decapod larvae and the proximity of land, indicating that the larvae of the littoral species are not carried out to the open sea to any large extent. The "Terra Nova" collections, so far as they permit conclusions to be drawn, fully confirm Ortmann's result. In these collections Decapod larvae are seldom abundant, but the greatest numbers of individuals and of species were taken, firstly at stations 40 and 43, the former in Rio de Janeiro harbour and the latter some distance to the north of it, and secondly in the waters surrounding Three Kings Islands and at station 148 in the Bay of Islands, New Zealand. At each of the stations 40, 43, and 148 twelve or more species of larvae were taken, which is a very large number. In nearly all the samples from the waters surrounding Three Kings Islands and from Spirits Bay, New Zealand, the variety of Decapod larvae was comparatively large, ranging from five to nine species. The plankton from the Bay of Islands was remarkable for the very extraordinary abundance of these larvae, for the collection contained practically nothing else. I have examined large numbers of plankton samples taken off the east and south coasts of England and have never seen any collection approaching this one in the preponderance of Decapod larvae.

On the other hand, the collections made south of New Zealand were most

unproductive, while those taken near or within the Antarctic Circle were entirely barren. Many of these collections were extremely rich in Copepods and other forms of plankton, but though they were examined with much care and labour not a single Decapod larva was found. A few Euphausiids only represented the higher Crustacea.

It should be noted that a number of plankton samples taken in the North Atlantic were remarkably unproductive, though taken at a season when larvae should have been present in numbers. The explanation probably is that these samples were taken, for the most part, at "full speed."

It seems probable that the larvae of Decapods and Euphausiids are not so much at the mercy of the currents as might be supposed. It is not very unusual to find swarms of the larvae of one species in different stages of development, which seems to indicate a power of keeping together from hatching onwards, or of collecting in a suitable locality. For example, I have met with such a swarm of Zoeas of *Corystes* at Plymouth, while in these "Terra Nova" samples at station 251 great numbers of larvae of one species were taken (see p. 95, *Petalidium*) and the sample from the Bay of Islands may be regarded as a swarm of this kind. Lastly at station 52 the sample, from which other Crustacea were almost absent, contained a quantity of eggs and early larvae of a species of *Euphausia*.

Some species seem to have decided preferences for certain regions, if one may judge from the behaviour of the British species of *Leander*. Quite early stages of the larvae are taken singly or in small numbers near Plymouth Sound, but later stages are exceedingly rare in in-shore waters, although the adults are abundant. But, as the time for transformation approaches, the larvae seek the shore. Sollaud (1916, p. 69) states that they may be found in numbers in pools left between tide-marks in the case of *L. serratus*, and I have myself found larvae of *L. longirostris* in the last stage in estuarine waters, although earlier larvae have never been taken there. Larvae are no doubt frequently carried by currents out of their normal habitat, and Faxon (1879) has given the examples of *Porcellana macrocheles* and *Calappa marmorata* which are sometimes so carried by the Gulf Stream to the shores of New England, but I believe that this is exceptional, and that the larvae for the most part have power to control their movements.

III.—THE SYSTEMATIC AND PHYLOGENETIC IMPORTANCE OF DECAPOD LARVAE.

Of the many authors who have attempted the classification of the Decapoda few have taken the larval stages into consideration, but Boas made use of them to some extent, and Cano drew far-reaching conclusions from his extensive study of Decapod

development, and constructed phylogenetic trees to illustrate his views. Particular attention should, however, be drawn to P. Mayer's work (1877). Mayer attached the greatest importance to the structure of the embryonic and larval telson, and drew conclusions from its study which may be summarized as follows :

- (1) The primitive telson was forked.
- (2) The Caridea form a group apart from and equivalent to the rest of the Decapoda.
- (3) The Loricata, Nephropsidea, Thalassinidea, and Anomura form equal groups in a division opposed as a whole to the Brachyura.

Mayer's work does not seem to have received the consideration it deserved, and it must be admitted that the evidence drawn from these larvae has not had much influence upon existing systems of classification. This is due in part to the very incomplete state of knowledge, but more to a general scepticism as to the value of such evidence.

So long as the Zoea was regarded, as it was regarded by Dohrn, Fritz Müller, and Balfour, as representing an adult phase incorporated in the ontogeny, its structure gave rise to phylogenetic speculations which have now only an historic interest, and did little to advance the classification of the group. On the other hand, since it has been shown by Claus and others that the Zoea cannot be regarded as recapitulating an adult ancestry, there has been a tendency rather to underestimate its phylogenetic significance and to dismiss developmental stages as irrelevant in discussions of classification. This point of view is well expressed by Ortmann (1901, p. 1311) thus : "Sobald wir indessen uns bemühen den genetischen Beziehungen auch nur der grossen Abtheilungen der Decapoden unter sich nachzuforschen, lässt uns die Entwicklungsgeschichte ganz im Stich, ja, sie führt uns auf Irrwege, so dass faktisch hier die Verhältnisse so liegen, dass die Thatsachen der Embryologie und Entwicklungsgeschichte so lange unverständlich blieben bis sie durch die Resultate der vergleichenden *morphologischen* Untersuchungen in die richtige Beleuchtung gerückt wurden." Bouvier (1896), without going so far as Ortmann, regards such evidence as "au dernier rang," partly from the great uniformity among the larvae of different groups, and partly owing to the small number of species of which the development is known. The force of the last objection must be freely admitted. We do know the development of a considerable number of species representing all the larger groups of Decapods, but the proportion to the whole is infinitely small. At the same time I entirely disagree with Ortmann's opinion, and in part with that of Bouvier, and believe that the ontogeny when known is likely to be of the greatest value in classification and should by no means be neglected.

The adult stage is only one phase in the individual cycle, and it is hardly logical to concede to one phase the importance which is denied to another. It is true that in the majority of species the larval stages are passed in conditions totally

unlike those to which the adult is adapted, and that they may therefore be subject, independently of the adult, to adaptive modifications of their own,* and it is conceivable that similar modifications might arise in larvae of unrelated forms and lead to erroneous conclusions as to relationship. We are familiar with such difficulties in the case of the adult, and it is not improbable that there may be cases of convergence among the larvae. At the same time the precautions in the estimation of systematic value of structural features that are applied in the case of the adult can be used. It is obviously unwise to place too much reliance for example on such adaptational structures as may be supposed to affect the floating power of larvae.

Our knowledge of Decapod larvae, limited though it is, all goes to show that the larvae of related groups do have recognizable common characters which are sometimes very striking—e. g. the Phyllosoma of the Scyllaridea. Similarly the Brachyura (excluding the Dromiacea) have a characteristic type of Zoea which is extraordinarily uniform throughout the whole order. In both groups a common type of larva has been inherited unchanged from a common ancestor. These are two particularly striking examples in which the form of the body alone is distinctive, and yet it would readily be agreed that the possession of a Phyllosoma larva would definitely place the adult among the Scyllaridea even if, like *Sacculina*, it possessed none of the characters of its allies.

When, therefore, a structure which is apparently of trivial importance is found to characterize all the larvae of a group, either large or small (e. g. the reduced second seta of the telson of some Reptantia), it would be unreasonable to refuse to recognize it as important evidence of affinity, even if it were not in accordance with the evidence drawn from the structure of the adult.

It is true that structures of this kind distinguishing the larvae of certain groups are few, but the particular examples given below are very definite and striking, and to my mind of a higher order of significance than some of the adult features on which far-reaching systematic conclusions have been based.

These considerations concern only the systematic importance to be attached to the larval phase in individual life history, but the phylogenetic significance of this phase is also a subject of importance about which there has been much difference of opinion. Although Claus's view that the Zoea is a secondarily modified larval form is undoubtedly essentially correct, it should not be interpreted as disposing altogether of the phylogenetic importance of the larva. The view recently so forcibly expounded by Garstang (1922), that larval and embryonic stages recapitulate equivalent stages of ancestral forms and not those adult ancestral forms themselves, may be unreservedly accepted without at the same time denying to these stages significance in discussions of phylogeny.

* None the less, the greatest difference between adult and larva is to be found where both apparently lead the same sort of life (Penaeidea).

To take, for example, the case of the Hermit Crab, which has been claimed by MacBride as an example of true Recapitulation. If the symmetrical post-larval stage of a Pagurid actually recapitulated an adult symmetrical ancestor such as a Galatheid, it must be a stage added to the ontogenetic cycle of the ancestor, and of such an addition there is no evidence here or elsewhere. Stage for stage the larval phases of the Pagurid and the Galatheid (or of the Thalassinid for that matter) are identical in their grade of development, and if there were such an accretion of adult stages in the ontogeny then the ontogenetic series would necessarily gain in length or be notably modified in the most evolved forms. And yet the longest series of larval stages is found in some of the most primitive forms, and the normal cycle of the higher Decapods commonly contains the same number of essentially similar stages. The symmetrical post-larval stage of the Pagurid is, in fact, no more than the first post-larval stage of the Galatheid or the Thalassinid. At the same time it is definitely a Pagurid in all respects except its symmetry, and it does not seem to me to matter whether we regard it as representing an adult or an adolescent stage in ancestral history. In this particular instance we do not need any evidence from the larval history to enable us to arrive at the conclusion that the asymmetrical Pagurid must at some period have had a symmetrical ancestor, but, if there were not other evidence of the fact, this symmetrical post-larval stage would suffice under any interpretation of it. For as we see the post-larval stages of allied forms giving rise to symmetrical adults, so it must be evident that the existence of a symmetrical stage in the Pagurid implies a symmetrical ancestral adult.

Primitively development must have been a process of gradual growth, without metamorphosis or transformation, as it is in the Branchiopoda now, and the larva would not be greatly different from the adult in the character of the appendages for example. So, though the Nauplius cannot be regarded as representing an adult ancestral type, it probably does indicate that it originally grew into an adult having a cephalic region with three appendages only, and those appendages of the special nauplius form. I cannot believe that the nauplius appendages, so different as they are from those of existing adults, can have been confined to a larval stage. In this sense, then, one may regard the Nauplius as preserving adult ancestral characters without itself "recapitulating" an adult. No existing Crustacea have retained the characters of such an ancestor either with regard to their appendages or their degree of cephalization, and in all at least two more pairs of appendages have been drawn in and modified in the service of the mouth. The head with five appendages is then, in a sense, a "Neocranium," and is found in some Entomostraca, but in Copepoda and in all Malacostraca (except *Bathynella*) one or more additional somites have been drawn into the head.

It is perhaps permissible to postulate three stages of cephalization—the "Nauplius" stage, with three pairs of appendages; the "Entomostracan" stage, in which two

additional pairs are added; and the "Malacostracan" stage, in which a variable number of thoracic appendages are transformed into maxillipedes.

Any modification of the adult in evolution would be accompanied by modification of the larval and adolescent stages, and abrupt transformation and metamorphosis would occur only when the habit of life of the larva is so divergent from that of the adult that the adult type of appendage becomes unsuitable to larval life and the transition must be a sudden one. Preparation for adult life would necessarily be made as far as possible in the larval period, with the result that the larval stages of Decapoda show not only adaptation to their own conditions of existence, but also modifications which belong more properly to the adult phase. Consequently we should not expect these larvae to represent at all exactly either ancestral larval or adult forms. It may, however, be that the "stages" in metamorphosis indicate, in a much disguised condition, landmarks in the evolution of the group. The series of Nauplius and Protozoa stages of the Penaeidea, modified in some directions in anticipation of the "Decapod grade," preserve some of the characters of the "Archiphyllopod" ancestry of the Decapoda—particularly the great biramous second antenna, the pediform maxillae, and the freedom of the thoracic somites. With the transformation to the Mysis stage development enters suddenly the "Decapod grade" at which the remainder of the Decapoda start their life.

But, though the Zoea of the remaining Decapoda resembles the Mysis stage of the Penaeidea, it may perhaps be more correct to say that, at least in its first stage, and perhaps also up to the fourth, it is in fact a much modified Protozoa. Apart from the remarkable transitory structures seen in the embryonic cuticle, there are certain features of the early free larvae which may be regarded as survivals from a Protozoa. These are:

1. Sessile eyes and nauplius eye.
2. Occasional presence of a "frontal organ."
3. Uniramous first antenna.
4. Jointed exopodite of second antenna and presence of long setae on the endopodite, which has not the character of a flagellum.
5. Occasional trace of an exopodite on the first maxilla.
6. In some forms the second maxillae have a somewhat more pediform character than in later stages.

If this view be justified the great discrepancy between the Penaeid and the typical Decapod development to some extent disappears. There remains a great contrast, but no essential difference. In the Penaeidea the "Decapod grade" is foreshadowed in the last protozoal stages, but is attained at a profound metamorphosis leading to an animal corresponding to the Mysis stage of Caridea. In the Caridea and remaining Decapoda the "Decapod grade" is attained very much earlier, and the Protozoa is suppressed—consequently there is not so great a metamorphosis at any stage.

IV.—CLASSIFICATION.

In the arrangement and nomenclature of the groups of the Decapoda used in this report I have not followed the course now generally adopted of making a primary division into Natantia and Reptantia, but have simply dealt with the various groups as sections of equal value.* I should not be justified in entering here upon a general discussion of the relationships of the larger groups, founded as they are upon adult characters, but I should say that, in my opinion, the Penaeidea have so many characters in common with the more primitive Reptantia that so fundamental a distinction as is implied by Boas's classification is entirely unjustified. I have given below reasons for the removal of the Stenopidea from association with the Penaeidea and Caridea to a position among the Reptantia, but the relation of the Penaeidea to the Caridea is a matter upon which it is difficult to form a decided opinion. The relation does not seem to be so close as to justify the grouping of the two into a single division opposed to the whole or to any section of the other Decapoda; rather the Caridea seem to be a separate and divergent branch of the Decapod stem preserving some primitive features, but in other respects highly evolved.

On the other hand, the evidence to be drawn from a study of the larvae tends to emphasize the primitive nature of the Caridea, and to this extent their relation to the Penaeidea.

The type of development preserved in the Penaeidea may be taken as approximating to that of the ancestral Decapod, and survival of characters which can be referred to the Protozoa is some evidence of phylogenetic position. There can be no doubt that the embryonic cuticle which is thrown off at or immediately after hatching provides evidence of the structure of a larval stage corresponding to the Penaeid Protozoa which at one time led a free existence in the ancestors of Caridea and Reptantia (see Conn, 1884). This larval cuticle frequently shows a structure of telson and antennae quite different from that of the later larva, and much importance has been attached to these transitory structures by Faxon, Conn, and Mayer. I only wish here to deal with the evidence from the telson. Mayer and others have shown that the telson of the Brachyura, whatever its ultimate form may be in the Zoea, has in the embryo a form which is comparable to the forked telson of the Penaeid Protozoa. It is true that this has been seen only in a few types, such as *Carcinus maenas*, but in other Brachyura intermediate forms of telson may be found which show that the form with two divergent branches is primitive and must at one time have been general. This primitive telson was armed with seven large ciliated spines on each branch, and Mayer

* At the same time the division is convenient and I have, perhaps inconsistently, used the terms rather freely.

found the number 7 + 7 to be so general that he assumed it to be the primitive number both for Brachyura and for Caridea. It is also the number usually found in Penaeid larvae.

Now, though it is true that 7 + 7 is the number almost invariably present in the telson of the Zoea of Caridea, it is a remarkable fact that the number in the embryonic telson is 6 + 6. Apparently neither Faxon, Conn, nor Mayer examined the embryonic telson of any Caridea, but I have done so in a number of species and find the result in all cases the same. The two innermost setae of the later Zoea are always seen to be enclosed in a single envelope.* In respect of this character, and it is unquestionably a character of importance, the Caridea stand in a class apart from all other Decapoda except possibly the Penaeidea in which a formula of 6 + 6 is found in some Protozoeas. How far it is general in that group it is impossible at present to say.

The Caridean Zoea is, in some respects, more primitive than that of the Reptantia, and the embryonic telson is evidently reminiscent of an early form of Protozoa.

Among the Caridea the Hoplophoridae are agreed to be the most primitive. The presence in the larva of a distinct exopodite on the first maxilla (p. 107) is an additional piece of evidence. This is a survival in the Zoea of a protozoal character which is lost in all other Caridea except the Atyidae, in which a homologous structure has been seen in *Paratya compressa*. The occasional presence of one or more setae in the same position in some other Caridea and Reptantia may probably be regarded as the last vestige of a structure once universal in the protozoal stage.

The presence and number of exopodites on the legs in the adult are characters of doubtful significance, since all Caridea possess them on some of the legs in the larva and they cannot therefore be regarded as wholly lost in any case. They might well be retained or re-acquired in the adult stage in quite unrelated forms, and they are often retained in a reduced condition in early post-larval life. The presence of a rudimentary exopodite in some species of *Pontophilus* (e. g. *P. abyssi*, Smith) is no doubt an example of the retention of a larval character, for the Crangonidae are in other respects perhaps the most highly evolved family of Caridea.

On the other hand, the presence of an exopodite on the fifth leg in the Pasi-phaeidae, Hoplophoridae, some Atyidae and the genus *Discias* cannot be dismissed as insignificant. In all other Caridea this exopodite is lost, even in the larva, and its presence in larva or adult cannot be regarded as other than a primitive character. This would readily be conceded in all cases but that of *Discias*, but this genus presents the difficulty, as Kemp has shown, that it is not in other respects at all primitive. At the same time it cannot be placed in any other family, and it seems most

* Species examined—*Leander* (four species), *Pandalus* (two species), *Hippolyte varians*, *Caridina simoni*, &c.

reasonable to suppose that it has retained its exopodites from the ancestral Caridean stock. But the presence in the larva or retention in the adult of these exopodites, while they may be survivals, are not evidence of relationship to the Penaeidea any more than to the Homaridea or Thalassinidea, in both of which the full number of exopodites may be found.

I have dealt below in the case of the remaining groups with the evidence for systematic relationship to be derived from the larvae, but there is one point with regard to the telson on which something should be said here. Stress has been laid on the reduction of the second seta in the telson of the Thalassinidea and Anomura, but I have not attached importance to a character which might be considered of equal value, namely the presence or absence of a median spine. Such a spine is found in the Euphausiacea, the Homaridea, and in all the Thalassinidea except the Laomediidae and *Upogebia* in its first stage. It is not found in any Caridea, Anomura, Stenopidea, or Brachyura. It is associated with a squarely truncated telson, and it is never found when the telson is in any degree forked, unless the Homarid telson may be regarded as a modification of that type. The fact that such a median spine may be occasionally found among the Penaeidea (see p. 68), in which group a forked telson is apparently characteristic, seems to show that this character may not be of great significance and may be independently acquired.

V.—THE NOMENCLATURE OF LARVAL STAGES.

A number of names, originally founded as generic names for unidentified larvae, have been used to define stages in development, and others have been expressly introduced as general terms for such stages, but the sense in which they have been used has varied so much that they have to a large extent ceased to have any precise meaning. The term *Zoea*, for instance, has long since lost its original generic significance, and has been used by Claus and others to define certain stages intermediate between the "Protozoa" and the "Mysis" stages, while by others it is used simply in a sense synonymous with the word "Larva." There is, I think, no advantage in attempting to restore to it any precise significance, and it is better that it should be used, if used at all, in the general sense. The term "Protozoa" should, on the other hand, be retained, since in its original sense, as first used by Claus, it defined a stage of particular interest and importance. In its definition, or the definition of any stages in Decapod development, insistence on the actual number of appendages present is apt to lead to restricted or ambiguous application, and the important thing for this particular name is that it should define a certain

“grade” of organization which is indicated by general structure. The three chief characters of the Penaeid Protozoa are :

1. Natatory antennae.
2. Biramous, more or less pediform, maxillae.
3. Thoracic somites not fused with the carapace.

These characters are retained in the Penaeids up to the transformation to the “Mysis” stage, and are found in no other free Decapod larvae. Claus attempted to define in the Penaeids an intermediate Zoa stage, but, as Brooks has pointed out, no clear distinction can be made, and I consider that there is distinct advantage in using the word Protozoa to include all post-Naupliar stages up to the Mysis stage of the Penaeidea. It is entirely wrong to apply it, as Meek has done (1918), to the Zoa of the Brachyura, which has none of the essential characters of the Penaeid larva. No doubt the Penaeid type of development is a primitive type, at one time general, and the protozoal stage is now for the most part passed through in the egg. It is probably quite correct to regard the peculiar antennae and telson of the embryo of many Decapods as the last vestiges of protozoal structures, and I have given above certain characters of the free larva which I regard also as surviving traces of the earlier grade.

The term “Mysis stage” is useful, though ill-used. If it is to be retained at all it must certainly not be founded on the presence or number of exopodites, since it is obvious that the last larval stage of a Hoplophorid, for example, is the precise equivalent of the similar stage in either a Crangonid, a Thalassinid, or a Brachyuran. The essential feature they have in common is that all the thoracic appendages have reached their full larval development. As a matter of fact it is impossible really to define a “Mysis stage” in such a way that it can have any precise meaning of general application, and I have, as a rule, avoided its use. The only group in which the term has a really useful meaning is that of the Penaeidea, where there is a profound and sudden transformation from the Protozoa. In the Caridea Protozoa, Zoa, and Mysis so grade into one another that no real distinction is possible, and it is generally better simply to describe development as consisting of certain numbered stages corresponding, as a rule, to as many moults.

Some authors, such as Daday (1907) and Sollaud (1923), have given special names to different stages or phases in development. For instance, Daday calls the first three stages in *Caridina* Euzoa, Mesozoa, and Metazoa and the following stages Protomysis, Mesomysis, and Metamysis. Since the first three stages in the majority of Decapoda are essentially similar no serious objection can be raised to giving them names if desired, but later stages vary so much in number and character that such names can have but little meaning. The terms introduced by Sollaud are only applicable to the Palaemonidae. It seems to me that the introduction of these special terms of restricted meaning serves no useful purpose ; they merely burden the memory and focus attention upon unimportant detail.

VI.—LIST OF STATIONS.

The following list includes only those stations which are actually mentioned in this Report. With the exception of the stations in the Antarctic zone, Decapod larvae were found in the majority of the plankton samples, but it has not been thought necessary to include all these stations in the list.

I. ATLANTIC.

Station 12.	30° 21' N.,	18° 14' W.
„ 17.	26° 17' N.,	20° 54' W.
„ 39.	Six miles off mouth of Rio de Janeiro harbour.	
„ 40.	„	„
„ 43.	22° 6' S.,	39° 40' W.
„ 45.	21° S.,	37° 50' W.
„ 46.	20° 30' S.,	36° 30' W.
„ 49.	18° 51' S.,	33° 40' W.
„ 50.	18° S.,	31° 45' W.
„ 52.	5° S.,	27° 15' W.
„ 61.	2° N.,	24° 45' W.
„ 62.	4° 50' N.,	24° W.
„ 65.	23° 28' N.,	34° 45' W.
„ 66.	25° 35' N.,	34° 10' W.
„ 67.	„	„
„ 311.	35° 29' S.,	50° 26' W.

II. PACIFIC. New Zealand region.

Station 85.	From Cape Maria Van Diemen Light, W.N.W. 24 miles.
„ 86.	Off Three Kings Islands.
„ 92.	From Summit Great King, S. by W. 24 miles.

Station 93.	From Summit Great King, S.E. by S. 13 miles.
„ 97.	Anchorage, North Cape.
„ 106.	From West Island, Three Kings Islands, S.W. 5 miles.
„ 107.	„ „ „
„ 109.	34° 15' S., 172° E.
„ 114.	32° 55' S., 170° 38' E.
„ 120.	34° 26' S., 172° 14' E.
„ 122.	From Cape Maria Van Diemen, S. 80° W. 21 miles.
„ 129.	Off Three Kings Islands.
„ 130.	„ „
„ 131.	„ „
„ 132.	Spirits Bay, near North Cape.
„ 133.	„ „
„ 135.	„ „
„ 136.	„ „
„ 139.	34° 30' S., 171° 53' E.
„ 148.	Bay of Islands, 35° 15' S., 174° 10' E.
„ 161.	Melbourne harbour.

III. SUB-ANTARCTIC ZONE.

Station 232.	55° 51' S., 165° 49' E.
„ 251.	54° 2' S., 177° 0' W.

VII.—DESCRIPTIONS OF LARVAE.

PENAEIDEA.

The larval development of the Penaeidea is well known to be of a very primitive character, the larva leaving the egg either as a Nauplius (Penaeidae and Luciferinae) or in the form of a Protozoa (Sergestinae). The general course of development, so far as concerns the appearance and the character of the appendages, is remarkably uniform and would alone prove the very close relationship of the Sergestidae to the Penaeidae.

The close similarity of the larval series with that of the Euphausiacea has rightly been regarded as important evidence of the relationship of the latter to the Decapoda and their separation from the Mysidacea, but the similarity does not extend to details. In the Euphausiacea, development is quite continuous without any marked metamorphosis, and may for that reason be regarded as more primitive. On the other

hand the appendages themselves, particularly the antennae and maxillae, differ greatly from those of the Penaeidea which seem to have retained a more primitive structure, while the Euphausiacea also are characterized by extreme compression of the thoracic somites and reduction of the pereiopods. The Euphausid telson, which is, so far as is known, of very uniform structure throughout the order, has invariably a square, truncated apex with a median unpaired spine.* A precisely similar telson is found occasionally in the Penaeidea (see p. 68), but it is exceptional, and the usual type is quite different. A median spine is, however, characteristic of some Reptantia, and may be an inheritance from an ancestor related to the Euphausiacea. There is one point in which the genus *Gennadas* strikingly resembles *Euphausia* in its development, and that is in the precocious appearance of the first pair of pleopods. But the great compression of the thoracic region and the reduction of the posterior pairs of pereiopods in the Euphausiacea are strong reasons for regarding them as occupying a less primitive position than that commonly credited to them. They are true Decapods, and they are primitive Decapods, but they cannot be regarded as representing the ancestral form of any higher group.

The Penaeidea differ from the Euphausiacea fundamentally in having a pronounced metamorphosis. This is especially marked in the Sergestidae, where two distinct breaks in the continuity of development, namely those between the Elaphocaris and Acanthosoma stages and between the latter and the Mastigopus, involve great changes in body form. In the Penaeidae the corresponding stages of transformation are at the moults from the Protozoa to the Mysis stage and from the Mysis to the post-larval condition. The first change in the Sergestidae is a change of body form alone, while the second involves also the assumption of the adult form of the appendages; but in the Penaeidae there is also a double transformation of the appendages. This double break in the larval series is a feature peculiar to Penaeid metamorphosis, since in Caridea, and also in Reptantia where a Mysis stage can be recognized, that stage is entirely similar in general form and in the character of the appendages to the stages which precede it, but the transformation from Mysis to post-larval condition is, as a rule, very marked.

I. Penaeidae.

The fact that the majority of the Penaeidae are deep-sea forms, and that the eggs are always set free before hatching, makes the difficulty of connecting the larvae with the adults very great. Thanks to the splendid work of F. Müller and Claus we know with sufficient detail the general course of development from the Nauplius to the Mysis stage, but we do not know with what genera they were dealing, or whether the larval series which they succeeded in tracing is typical for the whole of the family. Later authors have added remarkably little to our knowledge. Brooks (1882) was able to trace a series of larvae up to a stage recognizable as belonging to

* Claus's figures (1876, Taf. I) do not show this median spine, but it is present in all the larvae figured by Sars (1885) and in all those found in the "Terra Nova" collections.

Penaeus, but his description is not illustrated, and is too brief to be of much help to others. Kishinouye (1900) and Lo Bianco and Monticelli alone have actually observed the hatching of the Nauplius, while the latter authors have had the singular good fortune to follow the complete metamorphosis in two species—*Sicyonia sculpta* and *Solenocera siphonocera*—and in part that of *Parapenaeus longirostris* and of a species of *Gennadas*. It is most unfortunate that, with the exception of *Solenocera* and *Aristaeomorpha*, they have published no figures of any of the stages observed, and their written description is often exceedingly difficult to understand or to make use of.

Spence Bate in his "Challenger" report (1888) deals at some length with the larval stages of Penaeids, several of which are figured, but it is not possible to connect these larvae with any definite genera. His figure Pl. XLVI, fig. 1 evidently represents the Mysis stage of a species of *Gennadas*, but those shown on Pl. XLVII, figs. 1, 2, though of the same type and probably belonging to some genus of the Aristaeinae, differ from *Gennadas* in not having the large globular first pleopod which seems to be characteristic of that genus. Pl. XLVII, fig. 3 probably belongs to the Penaeinae and is referred to below (p. 68).

The earlier larvae, of which Suhm's figures are reproduced in the "Challenger" report, represent a larval series distinct from any elsewhere described. They differ from other Penaeid larvae in the early appearance of the rostrum, which attains to a very great length, and in the fact that three pairs of pereopods appear before any trace of the last two pairs is seen. In other forms the whole (Penaeinae) or the first four (Aristaeinae) appear together. Another very unusual feature is the transformation of the jointed exopodite of the second antenna into a scale, setiferous on both margins, in the Zoea stage. The same feature is shown in the larva figured on Pl. LVIII, fig. 2, which clearly belongs to the same series. These larvae evidently do not belong to the Aristaeinae, if the larva of *Gennadas* may be regarded as typical of that family, but the arrangement of the spines on the pleon is consistent with the supposition that they may belong to a genus of the Penaeinae.

The larva shown in fig. 46, p. 240 has some of the features of an Aristaeine, but is unique in the possession of a pair of spines on the posterior margin of the carapace and of long, slender eye stalks. It is impossible to conjecture to what group it may belong.

Stephensen (1923) has described some Penaeid larvae taken by the Danish Oceanographical Expedition, and some of these will be referred to below.

As the result of the work hitherto published the only Penaeid larvae which are recognizable with certainty are those of *Gennadas* and *Solenocera*, the former through Claus's figure (1876, Taf. III, fig. 2) which Lo Bianco and Monticelli refer to as representing that genus.

In these circumstances it is not to be expected that the Penaeid larvae of the "Terra Nova" collections should be referable to definite species or even genera by

comparison with published descriptions. On the other hand, although the naming of the larvae can only be purely tentative and based on most slender grounds, it seems to me advisable to describe those that I have had for examination, since, even if the determinations are proved entirely false, there is some value in showing the variety of larval form which exists within the family. The differences between genera and sub-families, at least in later stages, are very great, and there is reason to believe that it may prove to be possible to recognize the larvae of individual genera even in the early Protozoa stages. I give below some account and figures of two series of larvae belonging, as I believe, to the genera *Penaeus* (or a sub-genus thereof) and to *Gennadas*, which are entirely different the one from the other at all stages, while Lo Bianco and Monticelli found that the Protozoa of *Sicyonia* has also recognizable characters.

I have drawn up a statement of the characters which I believe to separate the larvae of the Penaeinae and the Aristaeinae in the Mysis stage, but I recognize that the statement is not too securely founded.

There are many genera of which we do not know the larvae, and, in particular, neither those of *Cerataspis* nor of *Sicyonia* representing the other two sub-families of the Penaeidae are known. That of *Sicyonia*, it is true, has been seen and, in part, described by Lo Bianco and Monticelli, but I have not been able to form any idea of its appearance from the published description.

PENAEIDAE. CHARACTERS OF THE MYSIS STAGE.

1. ARISTAEINAE.

Rostrum very long, with large basal spine.

Supra-ocular spines present.

Pleon somites with large dorsal spines, that springing from the second somite usually exceedingly large.

Pereiopod 5 developing later than 4.

First pleopod developed early and globular in form.

Telson deeply cleft, the two branches narrow and parallel.

2. PENAEINAE.

Rostrum long, with or without dorsal spine.

Supra-ocular spines very long and slender.

Hepatic spine present.

Pleon somites with, or in later stages without, dorsal spines, but these spines sub-equal.

Pereiopod 5 appearing at the same time as 4.

Pleopoda all appearing together and of same form.

Telson variable, sometimes truncate; sometimes the posterior margin lunate; never with parallel rami.

3. SICYONINAE.

Unknown.

ARISTEINAE.

Gennadas (Syn. *Amalopenaeus*) (figs. 1-4).

Stage I. The earliest larva found is a Protozoëa 0.98 mm. long (fig. 1). This type of Protozoëa occurs in several of the collections from widely separated localities

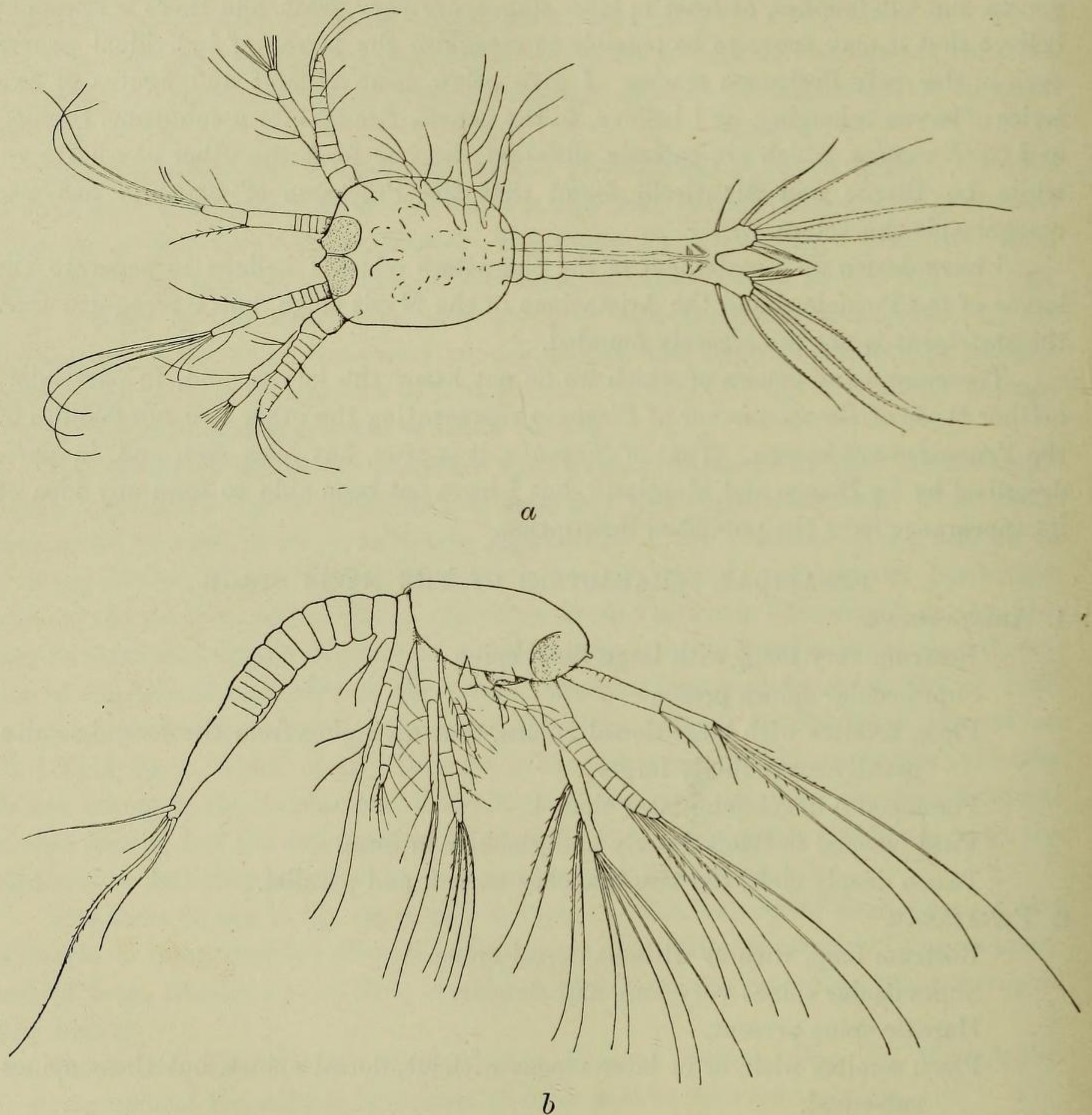


FIG. 1.—*Gennadas*. Protozoëa, stage I. a. dorsal view (station 65). b. side view (station 114).

(stations 17, 66, 67, 114, 120) and it is possible that it is a type common to several Penaeid genera.

The eyes are not yet distinct, and the small frontal organs spring from the ocular region.

The carapace covers only the somite of the first maxillipede, leaving the rest of the thorax bare. All the thoracic somites are distinct, but there is no trace of pereopods. The third maxillipede is a uniramous rudiment with two setae.

The abdomen is not yet fully segmented. The first somite is distinct, but the remaining somites, though distinguishable beneath the cuticle, are not separated until the next moult.

The telson is forked, and bears six setae on each branch.

First antenna (fig. 2, *a*). A simple uniramous appendage, consisting of three segments. The basal segment is subdivided into five sub-joints, while the third, which corresponds to the outer ramus, bears three very long ciliated setae and three short sensory setae or aesthetes. In later Protozoas the secondary segmentation of the first joint is lost, and the appendage then consists of three joints only. In *Sicyonia* (Claus, 1876, Taf. II, fig. 3) there are four, but I do not find more than three in any of my specimens. Since the subdivision of the basal segment in the first stage is evidently nothing more than a wrinkling such as is seen in the second antenna of the Conchostraca, the peduncle primarily consists of two joints only.

Second antenna (fig. 2, *b*). The stem is two-jointed, and no evidence has been seen of the presence of three joints in any specimen examined. The second joint may be indistinctly separated, or not distinct at all from the inner branch, which is then a simple extension of the protopodite. The inner branch is two-jointed, the first joint very long and bearing a pair of long setae on a conspicuous notch about mid-way along its inner side. The short distal joint bears four long natatory setae. The exopodite is very distinctly articulated to the protopodite and is divided into eleven short joints. The fourth and sixth each bear a seta on the outer side, and natatory setae spring from the fourth and each subsequent joint.

The mandible has no trace of a palp, and the edge is armed with short spines. There is a distinction between "pars secans" and "pars molaris," but no cleft between the two.

First maxilla (fig. 2, *c*). The basal part consists of two joints each with a spine-bearing endite or lacinia. The second joint bears a small lobe with four long ciliated setae which corresponds to the exopodite and is found in precisely similar form in the Euphausiacea. One or more setae are occasionally found in this position in the maxilla of other Decapod larvae* (e. g. *Processa*, some Brachyura) and probably represent the last trace of an exopodite. In the adult *Upogebia* there is a bundle of long setae which may perhaps represent the same structure. The large exite, which develops later on the coxopodite in the Euphausiacea and corresponds to the epipodite, is not developed in the Penaeidea, but is conspicuous in *Stenopus*, some Thalassinidea, and Anomura.

The endopodite in the Penaeidea is remarkably large, consisting of three well-defined joints each bearing a pair of setae on the inner face. The terminal joint

* See below, Hoplophoridae, p. 107.

bears three long setae. The endopodite is usually greatly reduced in the Caridea, but is often well developed in the Reptantia. When well developed, e.g. in *Callianassa*, it consists, as in the Penaeidea, of three joints each with a pair of inner setae.



FIG. 2.—Appendages of larvae of *Gennadas*. *a-e*. Protozoa. *f, g*. First Mysis stage. *h-q*. Last Mysis stage. *a*. First antenna. *b*. Second antenna. *c*. First maxilla. *d*. Second maxilla. *e*. First maxillipede. *f*. Mandible. *g*. First maxilla. *h*. First maxilla. *i*. Second maxilla. *k*. First maxillipede. *l*. Second maxillipede. *m*. Third maxillipede. *n*. Leg 1. *o*. Leg 2. *p*. Leg 3. *q*. First pleopod.

Second maxilla (fig. 2, *d*). The stem of this appendage may well be regarded as consisting of three joints. There are four well-marked endites corresponding to the coxopodite and basipodite, but there is also a proximal part which has no

endite and may represent the pre-coxa. This part is better marked in the Sergestidae, where Hansen has seen a suture between it and the coxa. The exopodite is small and bears five ciliated setae. In the Sergestidae four of these setae are lost in the Acanthosoma stage and one or more may be absent in the Protozoa of Penaeidae. The endopodite, which directly continues the line of the stem, consists of four joints.

The maxillipedes (fig. 2, *e*). The two pairs of maxillipedes are very much alike, and consist of a two-jointed stem continued into a five-jointed endopodite and an exopodite which is shorter than the endopodite. The first joint of the endopodite may be partly fused with the basipodite. The exopodite differs from that of the

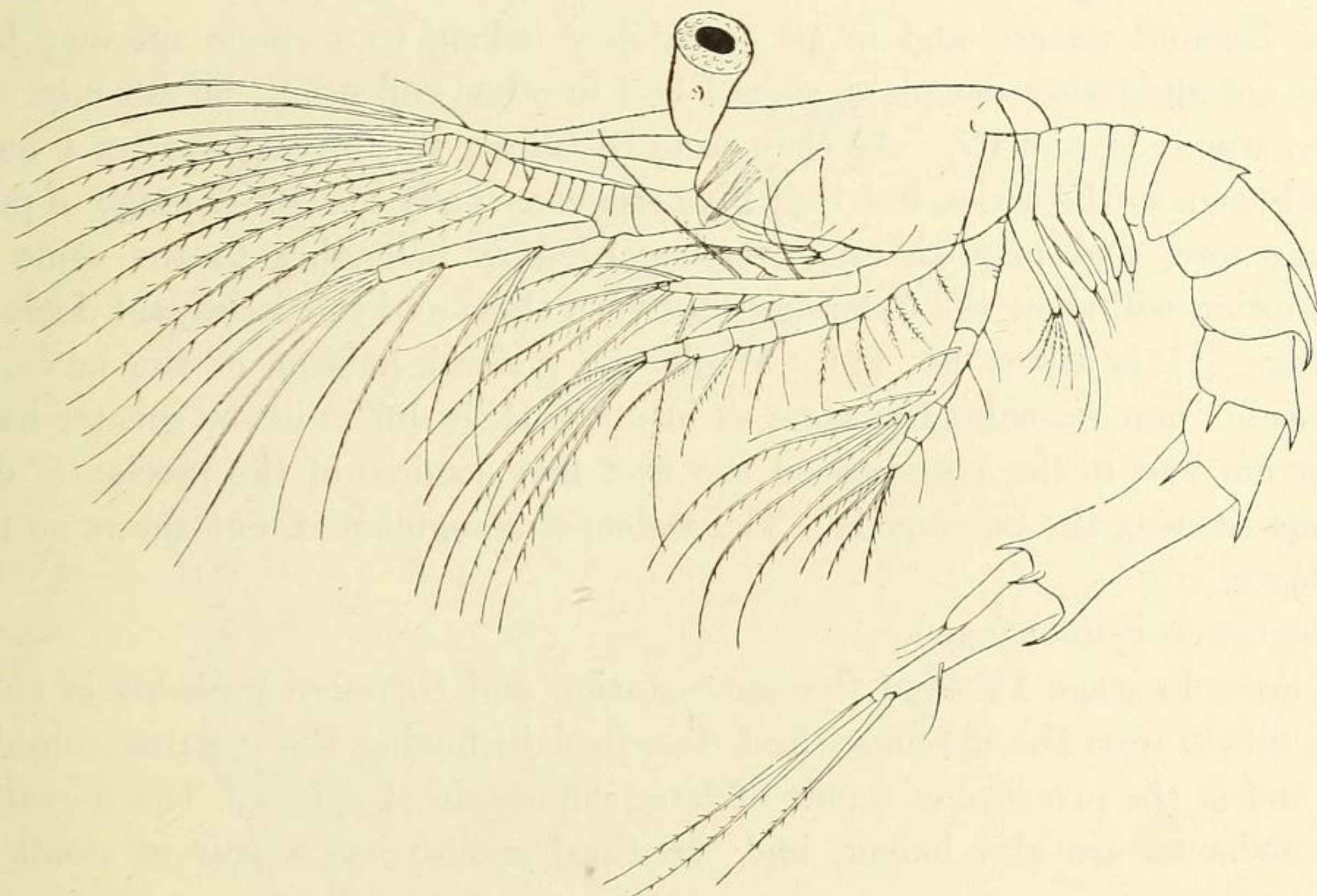


FIG. 3.—Larva of *Gennadas*. Stage IV. Station 114. Side view.

higher Decapods and resembles more the exopodite of the second maxilla in having setae disposed along its outer edge instead of concentrated at the end.

Stage II. The next protozoal stage measures 1.4 mm., but differs little in general form from the first. The eyes are stalked, and the carapace, which now covers the somite of the second maxillipede, is prolonged into a distinct rostrum.

The telson bears seven setae on each branch.

The appendages are unchanged. There are traces of pereiopod buds on somites 1 to 3.

Stage IV (fig. 3). This larva, which measures 3 mm., probably belongs to the fourth and not to the third stage (see below).

The rostrum is longer than the first antenna and the carapace covers the somite of the third maxillipede, though the tergites of this and the preceding somite are still free. Rudiments of the first four pairs of pereiopods are present.

The abdominal somites have developed median dorsal spines, that of the first somite being very small. The spines of somites 3 to 6 are about equal, while that of the second is the longest. Somites 4, 5, and 6 have each a pair of lateral spines, the sixth having also a pair in a ventro-lateral position. The telson is unchanged.

The labrum bears a rather large spine, as it does in stage II.

The anterior appendages are essentially the same as before. The third maxillipede is larger, biramous, and bears setae on each branch.

There is no trace of pleopods except for a small knob on the first somite, but the uropods have appeared, though in a functionless condition.

The three stages above described were taken in a single collection (station 114) in New Zealand waters, and in all probability belong to a single species; but the series is not altogether complete, since I find in other collections larvae intermediate between stages II and IV. As they seem to belong to different species I have not included them in the series, but they give rise eventually to a Mysis stage of precisely the same form and may therefore be regarded as belonging to the same genus. A description will show the differences between them and the series just dealt with.

Stage III (stations 66, 67). While the general habitus of the larva, which measures 2.1 mm., remains the same as in stage II, it differs in the greater length of the rostrum and in the presence on the first four somites of the pereion of distinct buds representing the pereopods. The abdomen is segmented, but shows no trace of appendages.

The telson is unchanged.

A larva in stage IV from the same station and therefore probably of the same species, differs from the specimen first described in having the rostrum considerably longer and in the presence of a pair of large supra-orbital spines. The dorsal spines of the abdomen are also longer, and the third somite has a pair of small lateral spines.

At station 120 a number of larvae were taken in which three stages may be distinguished corresponding to stages III and IV as described above and another somewhat more advanced. Brooks found that there were only three stages in *Penaeus* between the first Protozoa and the Mysis stage, but that the stages which he was able to define did not agree exactly with those described by Claus (1876, Taf. II). Claus's larvae are referred by Lo Bianco and Monticelli to *Sicyonia sculpta*, and it is clear that even in these early stages of development there are generic and specific differences not only in structure but also in the order of the appearance of the appendages.

Stage V. First Mysis stage. Station 114. Length, 3.77 mm., including the rostrum, which is 0.92 mm. long.

The rostrum has a large basal spine, but is otherwise smooth. There is a pair of large supra-ocular spines, but no hepatic spines. There is also a pair of large sub-ocular spines. The spines on the abdominal somites are as before, but there are now

also small median ventral spines on somites 4 and 5. The dorsal spine on the second somite is very long. On somites 1 and 2 there is a pair of lateral projections which overlap the carapace when the abdomen is flexed, and are not easy to see in side view.

The pereopods are all present and biramous, but the fifth is not fully developed. They are inserted in a curving series so that, in side view, the posterior legs are more or less overlapped by the anterior pairs. The first three pairs are not chelate.

The first pleopod is present in the form of a round knob, but the others are not visible. The uropods are fully developed, but the exopodite has no outer spine.

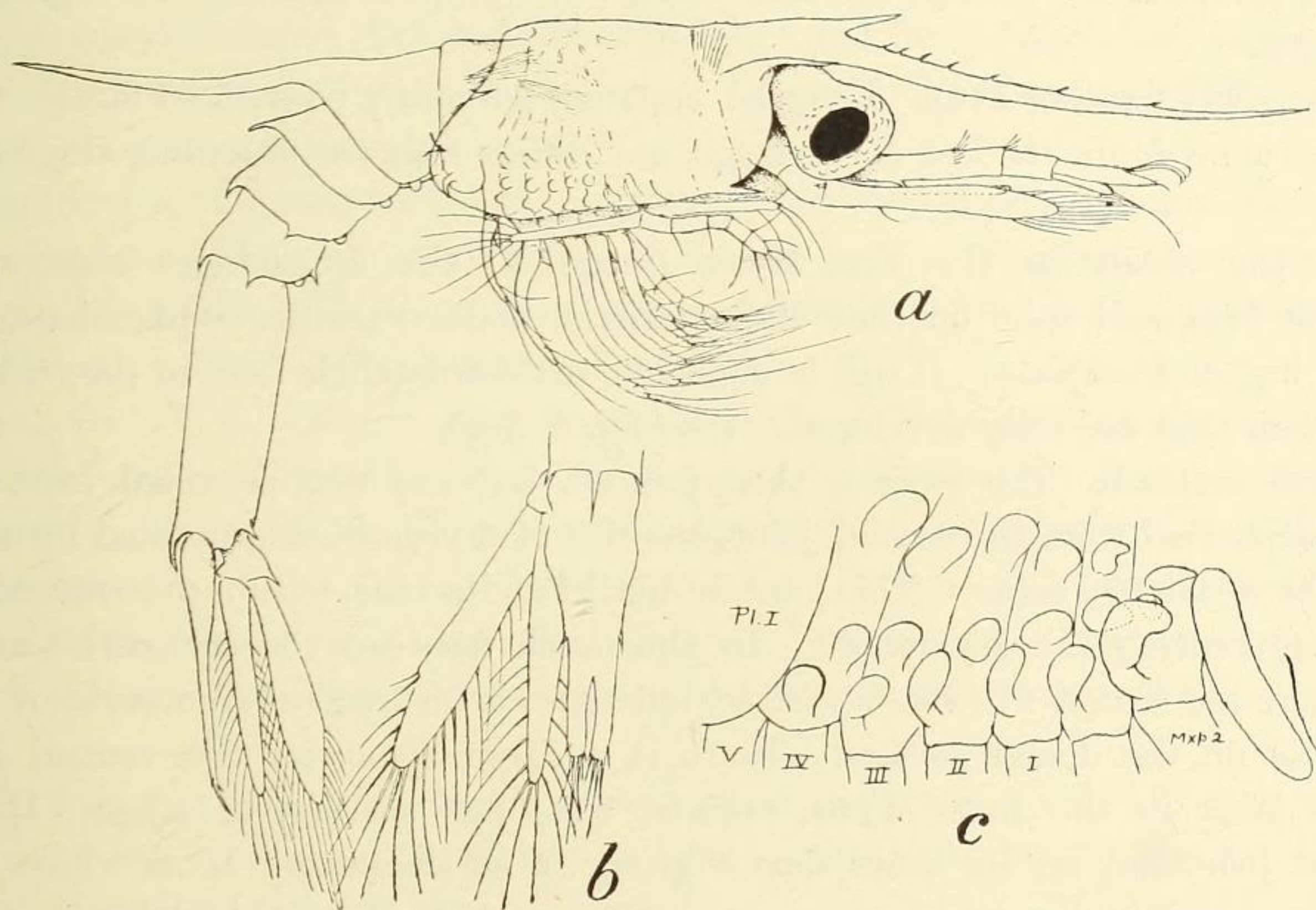


FIG. 4.—Second Mysis of *Gennadas*. Station 133. *b*. Telson. *c*. Gills of specimen from station 114.

The telson is long and deeply cleft, having the appearance of the two branches of the protozoal telson squeezed together and lying parallel and approximated to each other. There is a pair of small lateral spines anterior to the bifurcation, and the two branches each bear six terminal spines. The spine formula is therefore still $7 + 7$.

There is a profound change in the appearance of the antennae and mouth-parts, which now closely resemble in form those found in the larvae of Caridea. They will be described below in a later stage, as the structure remains much the same until the transformation to the post-larval condition. This first Mysis stage seems to correspond to Brooks's stage IV.

Stage VI (fig. 4*). Length, 3.7 mm. without rostrum (which is broken).

The part of the rostrum remaining bears five small teeth beyond the large basal

* A specimen of the same species from station 133 is figured, being better preserved than those from station 114.

spine. The second abdominal somite bears a huge dorsal spine, while the following somites have small dorsal spines, and the fifth and sixth a pair of small lateral spines. There is a median ventral spine on the fifth somite.

All the pereopods are present and biramous, but the first three are not chelate and the fifth is still small. Gills are developed on all the somites except that of the fifth leg. There are six pleurobranchs on the somites of the second and third maxillipedes and legs 1 to 4. Each of these has also an arthrobranch and an epipodite, the epipodite of the second maxillipede rather large. The first maxillipede bears an enormous plate-like epipodite.

The pleopods are present as small buds, while uropods and telson are practically unchanged.

Stage VII (station 114). Length: rostrum, 2.3 mm.; body, 5.55 mm.

This is no doubt the last Mysis stage, and differs from the preceding stage only in detail.

At the moult to the first Mysis (stage V) the appendages change their primitive form and take on that characteristic, under various modifications, of the Zoea of higher Decapods. It will be sufficient to describe their form in the last Mysis stage when they are fully developed. (See fig. 2, *h-q*).

First antenna. The stem is three-jointed, but the long proximal joint is not clearly separated from the second joint, the line of division being marked by a transverse row of sensory setae. This joint is dilated at its base, with a pronounced outer knob representing the stylocerite. In the notch between the stylocerite and the stem there are seated five sensory setae, but there is no trace of an otocyst or of any otic setae on the dorsal surface. There is a large spine on the ventral surface of this joint in the first Mysis, present also, but smaller, in stage VII. The terminal joint has on its inner face a group of small sensory setae which represent the "antennular lobe" (Gurney, 1923, p. 250), but this lobe is scarcely recognizable. In the last Mysis the two terminal branches are nearly as long as the peduncle, the outer branch bearing sensory rods on the first five joints. Both branches consist of one joint only in stage V.

Second antenna. The endopodite is, in stage V, a rod shorter than the scale and without setae, but in stage VII it greatly exceeds the scale in length. It is not distinctly segmented, but two joints are distinct at the base. The scale in stage V has no terminal spine and has one seta on its outer edge, but in stage VII it is a long, narrow lamella with a terminal spine and no outer setae.

The mandible in the last stage has a simple cutting edge with no spinules, and usually has no palp. The presence or absence of a palp seems to be a specific character, since in some specimens a small but distinctly two-jointed palp is present.

First maxilla. The exopodite is entirely lost. The palp may remain large in the first Mysis (fig. 2, *g*), but is reduced to a single joint in later stages.

Second maxilla. The change in the second maxilla is most striking, and the

pediform limb of the Protozoa gives place suddenly to the foliaceous type of appendage. The four inner lobes are well developed, the proximal larger than the second lobe. The endopodite is short and broad, without trace of joints. The setae of its inner edge are borne on small projections which correspond to, but are less developed than, the lobes which are found on the endopodite of some Caridea and Thalassinidea. The exopodite is a huge plate fringed all round with short setae.

First maxillipede. The stem has two large inner laciniae bearing many setae. The endopodite is five-jointed, and the exopodite bears setae along its whole outer margin. There is a large epipodite and a minute knob which may represent the rudiment of the arthrobranch.

Second maxillipede. The endopodite is large and five-jointed, but the exopodite is small and bears eight setae at the end. The epipodite shows a trace of division into mastigobranch and podobranch.

The third maxillipede differs only in the greater length of the endopodite.

Pereiopods. The first three pairs are chelate in the last stage, the endopodite of the first pair considerably longer than the two following pairs. Each of the pereiopods has an exopodite bearing eight terminal setae.

Pleopods. The first pair appears very early, and has a peculiar structure which may be distinctive of the Aristeinae. They are at first simple globular structures with a small inner spiniform process which does not correspond with one of the rami of the appendage. Later the outer ramus grows out from the globular base as a long rod, at the base of which, in stage VII (fig. 2, *q*), can be seen a minute rudiment of the endopodite. The four posterior pairs are simple biramous rudiments without setae.

The telson is long and slender and ends in a pair of pointed processes, each of which has a pair of short spines near its base. Apparently four of the seven spines of the previous larva are lost.

The gills are still rudimentary in the last Mysis, but are distinctly visible and disposed as follows:

	Mxp. 1	Mxp. 2	Mxp. 3	Leg 1	Leg 2	Leg 3	Leg 4	Leg 5
Epipodites	Ep.	Ep + r.	Ep.	Ep.	Ep.	Ep.	Ep.	—
Arthrobranchs	—	?	2	1	1	1	1	—
Pleurobranchs	—	?	1	1	1	1	1	1

Penaeid larvae in the Mysis stage and agreeing almost exactly with those just described are common in the "Terra Nova" collections from a number of stations. The agreement is so close that there can be no doubt that they belong to the same genus, but it is possible to find differences among them which prove that they do not belong to the same species. For example, the rostrum may be smooth, armed with small denticles, or strongly spined as in the form figured. All the larvae from the

Atlantic have smooth or nearly smooth rostra, while those taken in the Pacific have strong spines. I have made no special effort to find minor specific differences such as may probably exist in the form of the telson, relative length of spines, &c.

The identification of this type of larva with the genus *Gennadas* rests upon the authority of Lo Bianco and Monticelli, who (1900) refer to Claus's figure 6, Taf. III (1876) as representing the Mysis stage of *G. elegans*. On the other hand, it is possible to utilize the evidence of the gill formula of the late Mysis to obtain at least an approximate determination, even though the formula is not complete at that stage.

The presence of an epipodite on the fourth leg and of a pleurobranch on legs 4 and 5 excludes the whole of the Penaeinae from consideration.

Of the Aristeinae the absence of hepatic spines excludes *Hepomadus* and *Aristaeomorpha*, while *Aristeus* and *Hemipenaeus* have no epipodite on the fourth leg. There remain *Plesiopenaeus*, *Aristaeopsis*, *Benthesicymus*, and *Gennadas*, none of which have an hepatic spine. Beyond this it is impossible to go on the structure of the larva, but it is permissible to suppose that, as the pleurobranches are so well developed, they would probably give rise to gills of normal size; so that *Benthesicymus* or *Gennadas* is indicated.

Stephensen (1923, p. 20) has discussed the identity of larvae of this type, and has given reasons for believing that more than one species are included in it. It seems probable that this "*Euphema armata*" type, without hepatic spine, is the larva of the genus *Gennadas*, and that the same general form, of which the chief characteristic is the enormous spine on the second somite of the abdomen, may be confined to the Aristeinae.

ARISTEINAE.

2. *Hepomadus*? (fig. 5).

At station 232 a single larva in the Mysis stage was taken in company with others attributed to *Gennadas*, but it differs from them in several important respects. This larva in its general habitus is clearly of the same type as that of *Gennadas*, and no doubt belongs to some genus of Aristeinae.

This larva, which is in the first Mysis stage, is 5.5 mm. long, the rostrum alone being 0.9 mm. from the basal tooth to the end. It differs from *Gennadas* in having a pair of hepatic spines, but lacks the spine at the anterior angle of the carapace (pterygostomial). There is no spine on the second somite of the abdomen, but the following somites each bear a large spine, that of the sixth being the longest. There are short lateral spines on somites 4 to 6.

The telson is long, narrow, and deeply cleft, but the two limbs are not narrowed as in *Gennadas*. Each branch bears a lateral and seven terminal spines.

The fifth pair of legs is not fully developed, but the first pair of pleopods is

represented by large globular structures with a minute inner branch. The remaining pleopods are not visible. The uropods are large, the exopodite expanded distally but with no outer spine.

The general form of the body and rostrum together with the retarded development of the fifth pereopod and the precocious appearance of the first pleopod are characters which I believe distinguish the larvae of the Aristeinae from those of

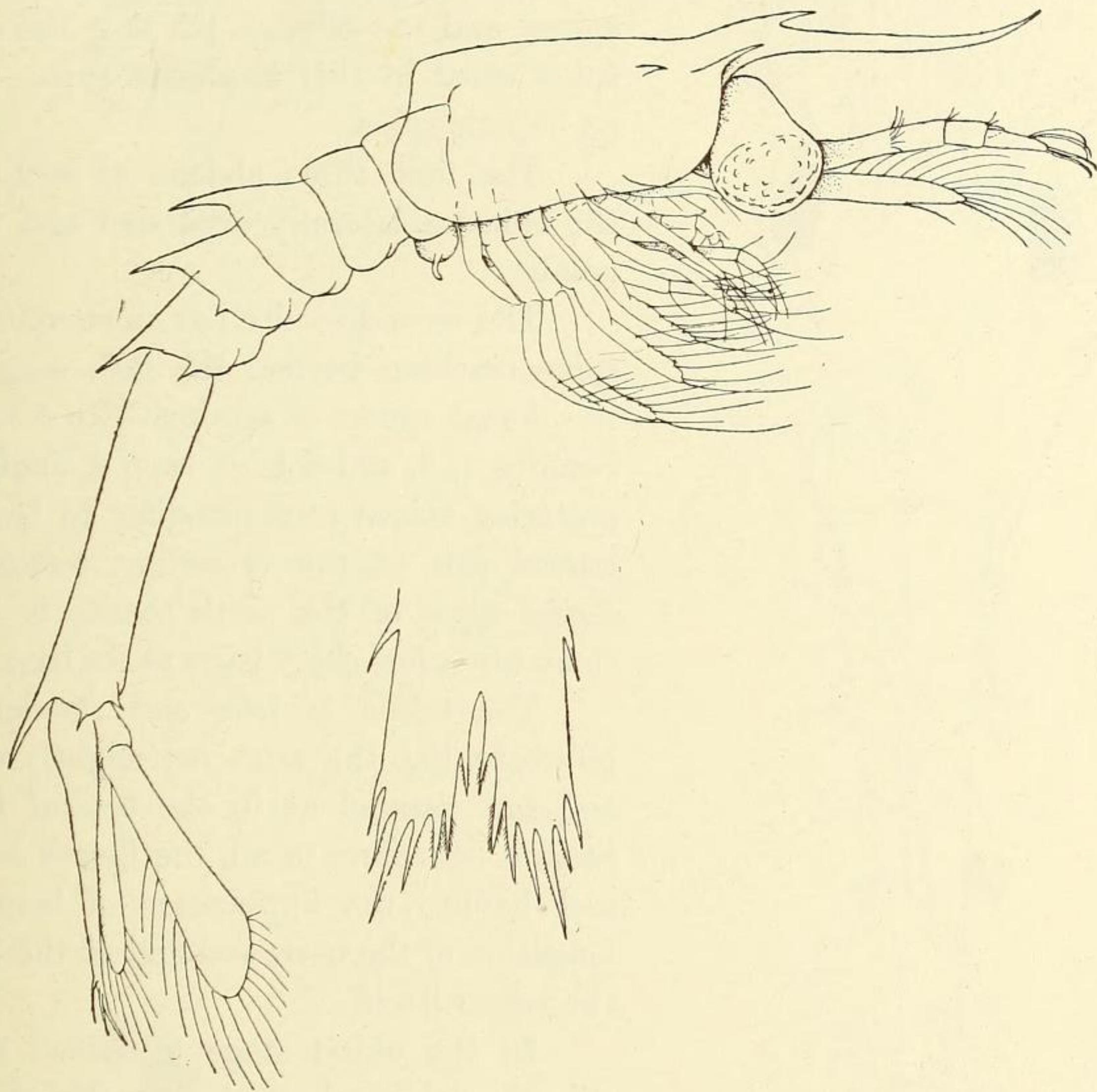


FIG. 5.—Mysis of *Hepomadus*(?) with enlarged view of end of telson. Station 232.

the Penaeinae; but the presence of an hepatic spine, and the absence of a large spine on the second abdominal somite sharply distinguish this form from the larva of *Gennadas*. Among the Aristeinae the hepatic spine is present in some *Benthosicymus*, in *Aristaeomorpha*, and in *Hepomadus*. As the larvae of none of these genera are known,* and the gills are not developed in this young specimen, it is impossible to do more than to assign it to one of these genera.

* Lo Bianco and Monticelli (1902) have described the larva of *Aristaeomorpha foliacea* (*Aristeus antennatus*), but I believe that they were mistaken in their identification (see below, p. 68).

ARISTEINAE.

Larva 3. (*Benthesicymus?*) (fig. 6).

Station 251. Length, 7.75 mm., including rostrum, 1.85 mm.

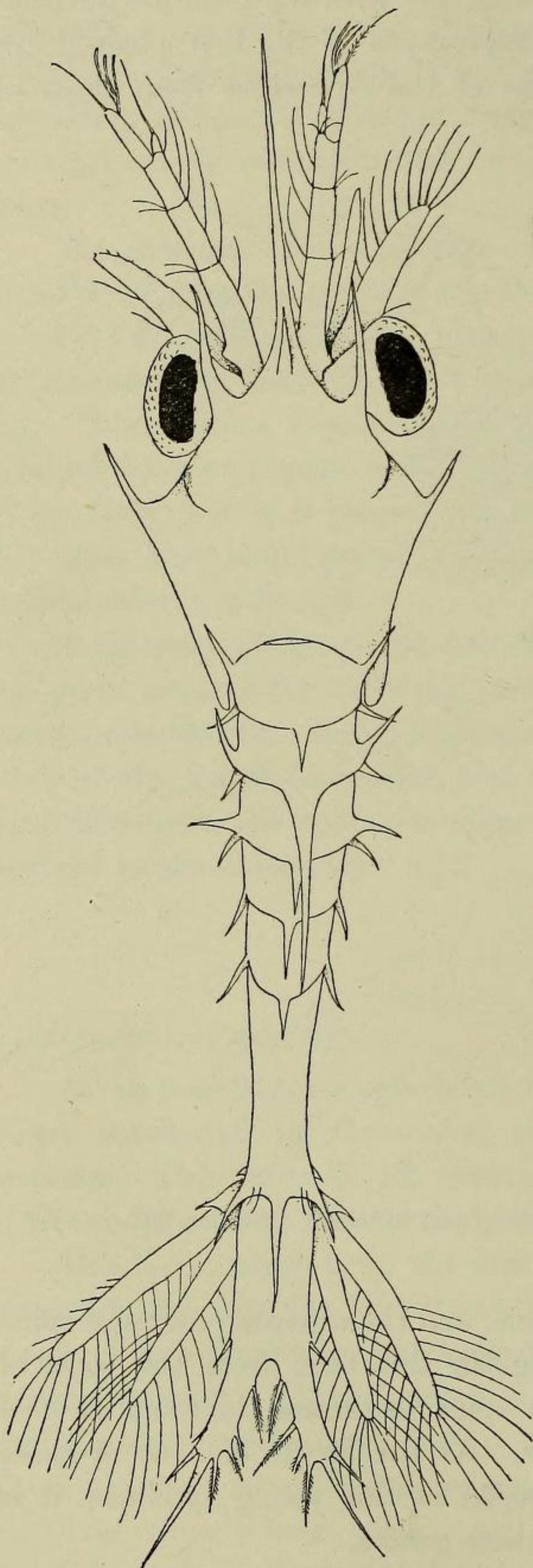


FIG. 6.—Mysis stage of *Benthesicymus?*
Station 251.

This larva is of the same general form as that attributed to *Gennadas*, and differs only in detail, particularly with regard to the armature of the abdominal somites.

There are long supra- and sub-orbital spines, and the rostrum has only the one basal spine usual in this *Euphema* type. There is no hepatic spine.

The first three abdominal somites have the epimera laterally expanded and with two points.

The second somite has an enormous dorsal spine reaching beyond the fifth somite, while the dorsal spines of somites 3 to 5 are small. Somites 4, 5, and 6 have each a single pair of posterior spines corresponding to the ventro-lateral pair of the preceding somites. The dorsal spine of the sixth somite is long and there are a few short hairs at its base.

The telson is long and slender, deeply bifurcate, but the arms are slightly divergent and not parallel as in the typical form. It bears 8 + 8 spines in all, the fourth being long and having the appearance of being a prolongation of the narrowed end of the branch of the telson itself.

In the oldest stage examined there are epipodites on each of the maxillipedes and on legs 1 to 4.

The third maxillipede and first four legs have each an arthrobranch, and pleurobranchs also are present on the second maxillipede and the fifth leg. The first three legs are chelate.

The exopodites of the legs are very long and bear an unusually large number of setae, e. g., twelve on leg 1.

The mandible bears a rather long, narrow palp of two joints.

There is a median ventral spine on the fourth and fifth somites of the abdomen.

This larva differs from that of *Gennadas* in the presence of additional spines on the abdomen, and in the form of the telson, and probably represents a distinct genus.

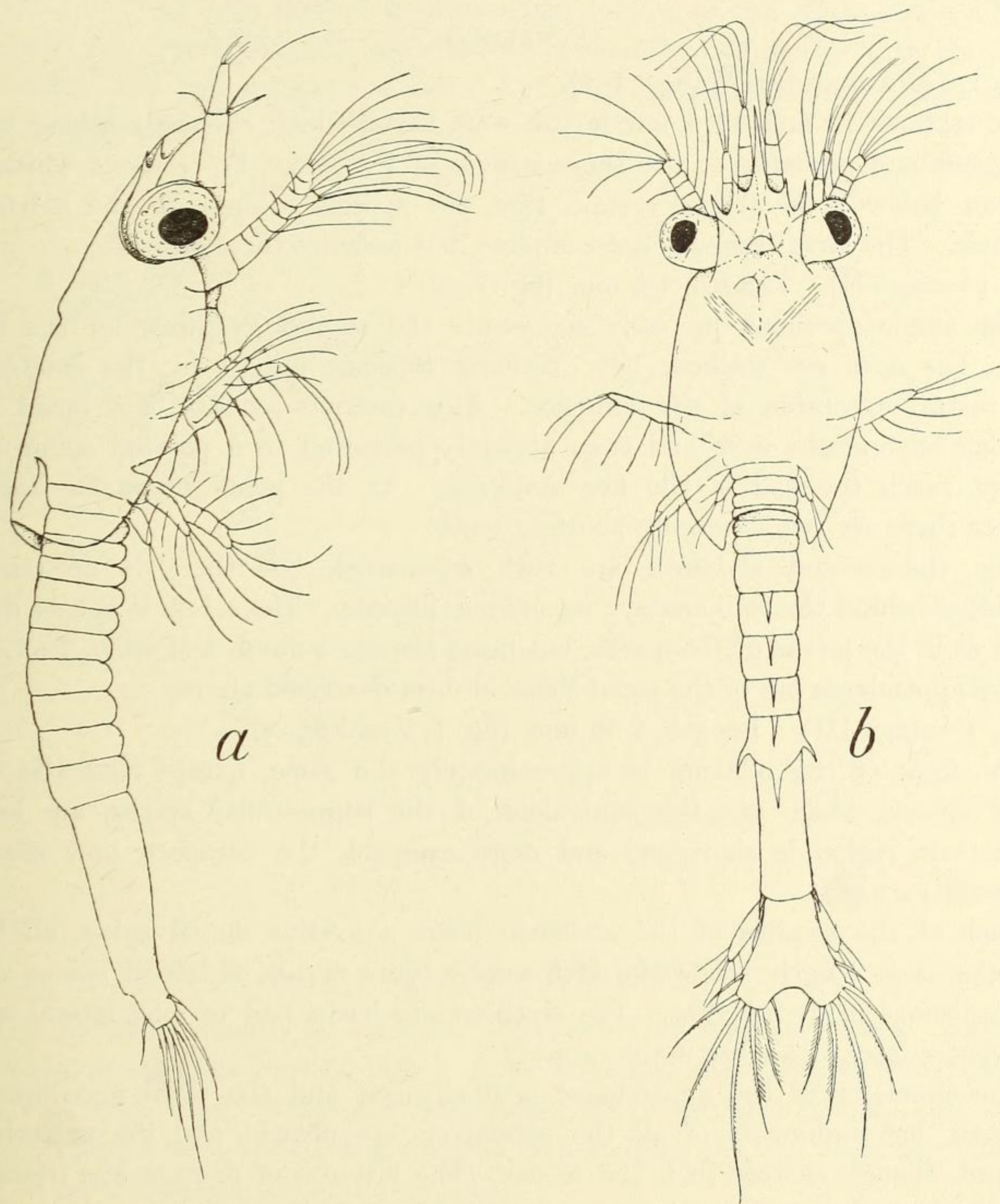


FIG. 7. *Parapenaeus* (?). Station 40. Stages I (a) and II (b).

I assume from the general form that it belongs to some genus allied to *Gennadas*, and therefore a member of the series *Benthesicymae*. It would then belong probably to *Benthesicymus*.

A similar larva has been described by Ortmann (1894, p. 77) under the name of *Euphema polyacantha*, and Stephensen (1923, p. 24) describes another form which

closely resembles both Ortmann's larva and also another described by Bate (1888, p. 241) as possibly belonging to *Aristeus*.

It seems that, as in the case of the *Euphema armata* type, we have in larvae of the type of *E. polyacantha* a generic series.

PENAEINAE.

Species I. (*Parapenaeus?*) (figs. 7-9).

At stations 40 and 43 a few larvae were taken which evidently belong to the same genus and probably to the same species of Penaeid. For reasons which will be given below it is almost certain that the species belongs to the sub-family Penaeinae. The larval series is not complete, but includes three stages.

I. (= stage II). Length, 1.6 mm. (fig. 7, *a*).

The single specimen probably represents the second Protozoa of the whole series. The eyes are stalked, but overhung to some extent by the enormously broad rostral extension of the carapace. This rostrum consists of a broad plate extending beyond the eyes and then abruptly narrowed to a pointed spine which does not reach the end of the first antenna. At the point where the rostrum contracts there are two forwardly pointing teeth.

The thorax and abdomen are both segmented, but there is no trace of appendages behind the rudimentary second maxillipede. The telson is not so deeply divided as in the larvae of *Gennadas*, but bears the same number of setae, 7 + 7.

The appendages are of the usual Penaeid form described above.

II. (= stage III). Length, 2.35 mm. (fig. 7, *b* and fig. 8).

The form of the rostrum is approximately the same, except that the outer pair of spines, which are the equivalent of the supra-ocular spines, are longer. The thoracic region is shortened and more compact, the carapace now covering the greater part of it.

Each of the somites of the abdomen bears a median dorsal spine, all being about the same length, while the fifth somite bears a pair of lateral spines which are conspicuous in dorsal view. The sixth somite has a pair of long lateral spines and a ventro-lateral pair below the uropods.

The character of the appendages is unchanged and the third maxillipede is still small, but rudiments of all the pereopods are present and the uropods are developed, though shorter than the telson. The latter is of more or less triangular form, with a shallow posterior sulcus and a formula of 7 + 7.

III. (= stage V). Length, 5.3 mm. (fig. 9).

This is probably the first Mysis stage.

The rostrum is long and slender, with two very small teeth at its base and a pair of large supra-ocular spines. There is a small hepatic spine, and the anterior ventral margin of the carapace is denticulate. The first two somites bear no spines, but segments 3 to 6 have median spines increasing in size backwards. Somites

5 and 6 have a lateral pair of spines, the sixth having also a ventro-lateral pair. The telson is long, parallel-sided, and the end square with a very small median incision. There are two pairs of short lateral spines and six terminal pairs, a formula of 8+8. The fourth spine is greatly the largest (fig. 9, *b*).

The appendages are now of the form characteristic of the Mysis stage. All the pereopods are developed and have setose exopodites, while the first three pairs are chelate. Pleopods are present and the uropods are well developed, the exopodite with a terminal spine.

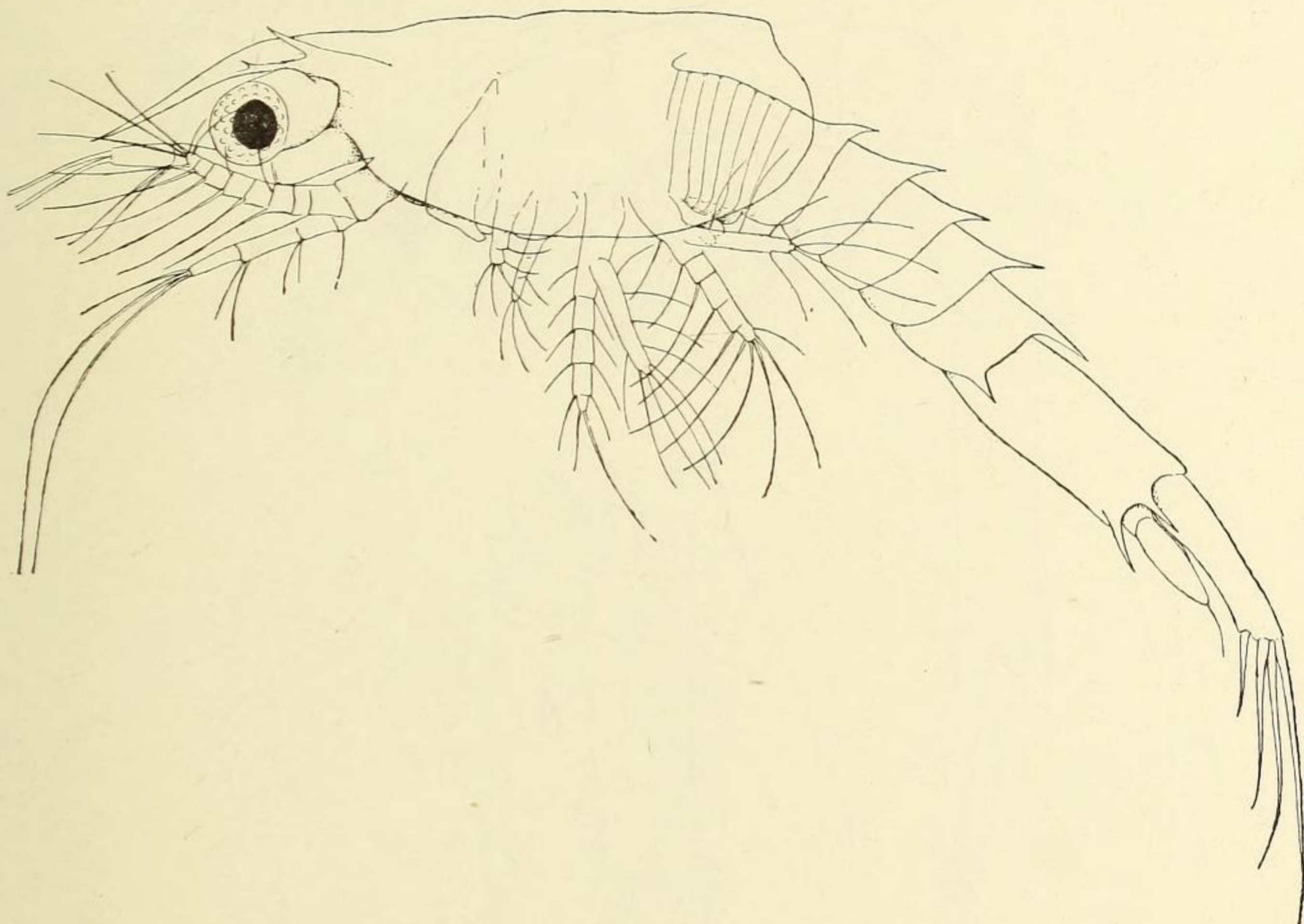


FIG. 8. *Parapenaeus* (?). Stage II, side view. Station 43.

The gills are so small and indistinct that their number is uncertain. Epipodites are visible on the maxillipedes and the first three legs, but there are none on legs 4 and 5. A series of six small gills are visible above the second and third maxillipedes and legs 1 to 4, having the position of pleurobranchs, but they are extremely small. I have not seen any arthrobranchs.

One other larva may be mentioned here as probably belonging to the same genus, but to a different species. This larva was taken at station 43 together with those just described. It is 1.7 mm. long, and differs only from stage III as described above in its smaller size, in the much greater size and length of the first antennae, in the smaller dorsal abdominal spines, and in the absence of a lateral pair on the fifth somite. The rostral region is damaged, and it is uncertain if a rostrum was present at all. The eyes are on longer stalks.

There is very little in published records to assist in assigning the systematic position of these larvae, since I know of no figure of any larva at all resembling them. If Brooks's identification of his larvae as belonging to *Penaeus brasiliensis* is correct then four characters of value for the genus may be found in his description.

1. The fifth pereopod appears simultaneously with the preceding pairs.
2. The pleopods all appear together, the first not preceding the others as in *Gennadas*.

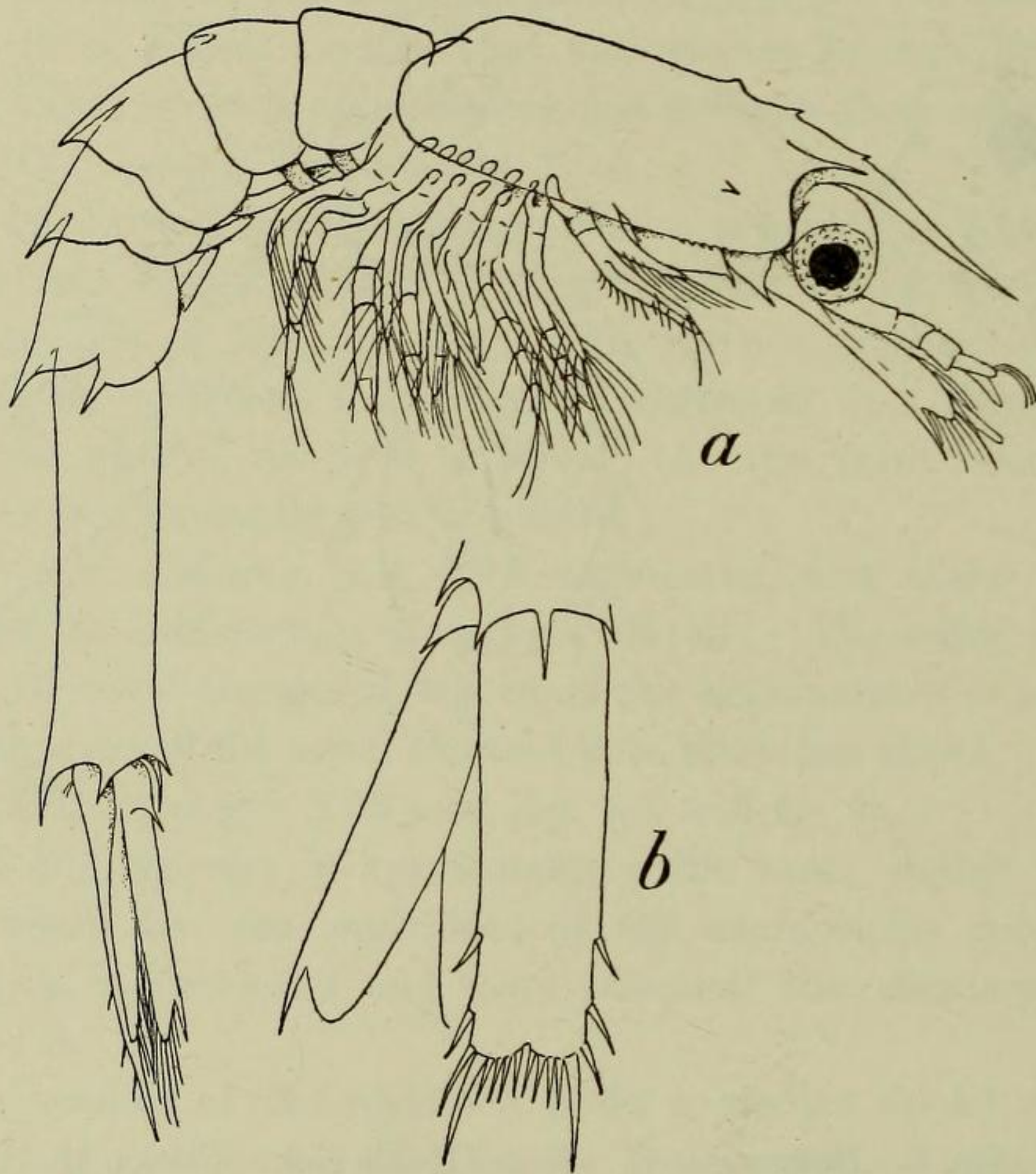


FIG. 9. *Parapenaeus* (?). Station 40. Mysis stage. b. Telson and Uropod.

3. The telson in the Mysis stage is square at the end.
4. There is no large spine on the second somite of the abdomen.

These characters are all found in the larvae in question. Lo Bianco and Monticelli (1901) describe some stages in the development of *Parapenaeus longirostris* (*Penaeus membranaceus*), but their account is not illustrated, and I find the utmost difficulty in understanding it. They refer to Claus's Taf. III, figs. 7, 8 (1876), as representing a larva closely resembling the Mysis stage of *P. longirostris*, and this larva possesses all the characters given except that the telson is deeply incised. It is, however, of the parallel-sided type. Their description of the rostrum of the early larva, if I interpret it correctly, agrees well with the form above mentioned.

The absence of an epipodite from the fourth leg, and of a pleurobranch from

the fifth, points also to the genus *Parapeneus*, although the presence of an epipodite on the third maxillipede is rather against such an identification.

There can, I think, be no doubt that these larvae belong to a species of the sub-family Penaeinae, and I have very little doubt also that they belong to the genus *Parapeneus*.

F. Müller (1863, Taf. II, fig. 9) describes a larva which evidently belongs to a closely allied species, but he does not suggest any identification.

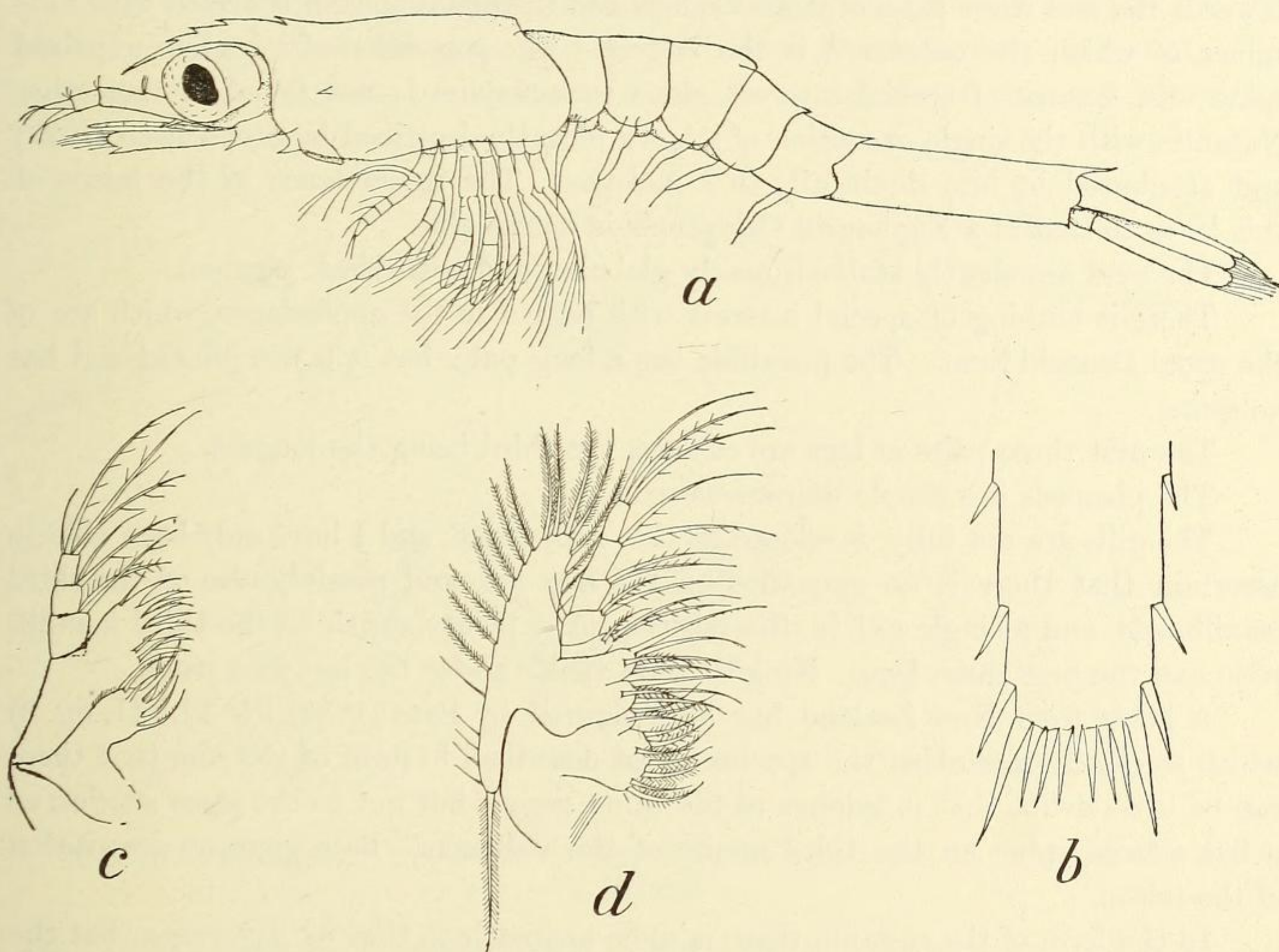


FIG. 10. *Penaeopsis* (?). Station 40. a. Mysis stage. b. Telson. c. First maxilla. d. Second maxilla.

PENAEINAE.

Species II. (*Penaeopsis* or *Artemesia*?) (station 40). Length, 4.5 mm. (fig. 10).

This larva, which is in a late Mysis stage, evidently belongs to the Penaeinae, and possesses certain features of interest which make a description advisable.

The rostrum resembles that of some Hoplophoridae (*Bentheocaris*), being down-curved, sharp-pointed, and with three or four dorsal spines. In addition, one spine springs from the carapace behind the eye leaving a wide gap between it and the first rostral spine. The rostrum is about half the length of the carapace and without spines on its lower border. In one of the two specimens there are a few short hairs on the upper margin between the teeth.

There is no supra-orbital spine, but a small hepatic spine is present, and a spine on the anterior ventral angle of the carapace. The anterior third of the ventral margin is minutely denticulate.

The first three abdominal somites are altogether devoid of spines, but the succeeding somites have each a very short dorsal spine, that of the sixth somite being the longest.

The telson is long, narrow, and parallel-sided, truncated at the end. It bears towards the end three pairs of lateral spines and the distal margin is armed with nine spines of which the outermost is the largest. The possession of a median unpaired spine is a feature of special interest, since such a spine is not found in any other Natantia with the single exception of a larva recently described by Stephensen (1923) and attributed by him doubtfully to *Funchalia*. The resemblance of the telson of this larva to that of a Euphausiid Calyptopsis is remarkable.

The eyes are shortly stalked, nearly globular, and with black pigment.

There is nothing of special interest with regard to the appendages, which are of the usual Penaeid form. The mandible has a long palp, but it is not jointed and has no setae.

The first three pairs of legs are chelate, the third being the longest.

The pleopods are simple uniramous rods.

The gills are not fully developed at this early stage, and I have only been able to ascertain that there is an epipodite on the first two and possibly also on the third maxillipede, and a single gill in the position of a pleurobranch on the third maxillipede and the first three legs. No gills were visible above the last two pairs.

A larva from New Zealand has been figured by Bate (1888, Pl. XLVII, fig. 3) which so closely resembles the specimen just described in form of rostrum that there can be little doubt that it belongs to the same genus, but not to the same species, as it has a large spine on the third somite of the abdomen. Bate gives no description of the telson.

In the form of the rostrum there is some approach to that of *Artemesia*, but the uncertainty with regard to the gill formula makes any real comparison with the adult valueless. The very rudimentary condition of the gills in the Mysis stages seems to be rather characteristic of the Penaeinae as compared with the Aristaeinae (*Gennadas*).

PENAEINAE.

Species III. (*Funchalia*?) (fig. 11).

At station 92 a single specimen of a late Penaeid larva was taken which agrees so closely with a larva described by Stephensen (1923, p. 15) that I cannot doubt that it belongs to the same genus, though not to the same species. Stephensen's larva is the same as that described by Lo Bianco (1903) as belonging to *Aristaeomorpha foliacea* (*Aristeus antennatus*), and Stephensen accepts this identification;

but my own specimen, which is in an older stage, has characters which, as I hope to show, render an identification with the genus *Funchalia* more probable. The larva was first described by Monticelli and Lo Bianco (1902) and attributed to *Aristaeomorpha* by a process of exclusion, since they were, as they supposed, familiar with the larvae of all the remaining species of Penaeids occurring in the western Mediterranean. *Funchalia woodwardi* is now known to occur in the Mediterranean, where it is apparently not uncommon (Stephensen, 1923).

The "Terra Nova" specimen measures 10.3 mm. and is of very slender form, the abdomen nearly three times as long as the thorax (excluding the rostrum). The rostrum is long, slightly down-curved, and without any dorsal spines. There is a

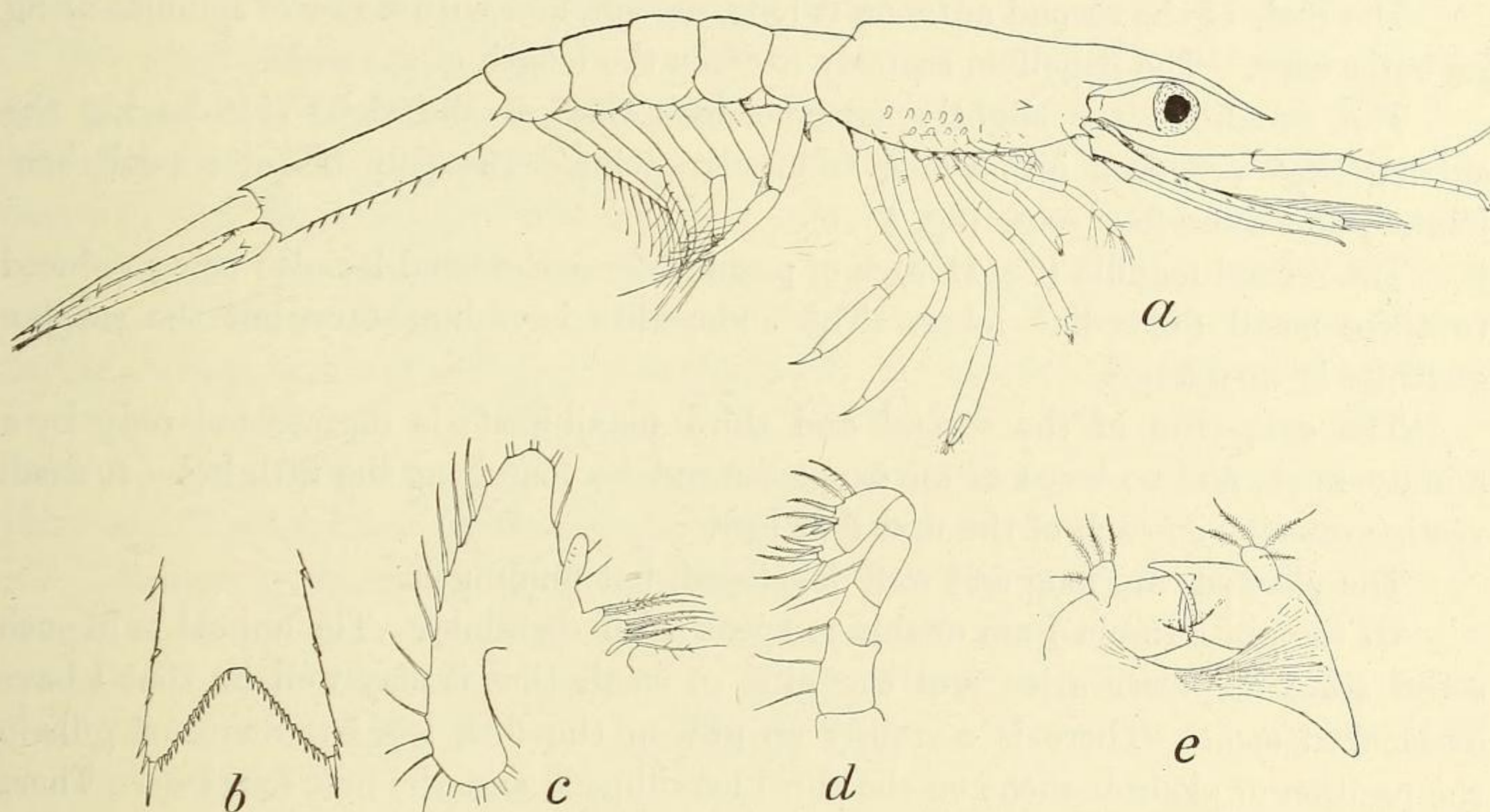


FIG. 11.—*Funchalia* (?). Adolescent. *b.* Telson. *c.* Second maxilla. *d.* Second maxillipede. *e.* Mandibles.

small supra-ocular spine, an hepatic spine, and a spine at the anterior ventral angle of the carapace.

The somites of the abdomen have no dorsal spines except the sixth, which has a slight median ridge which projects backwards as a short spine. The first four somites have each a stout ventral spine which, in the first and second somites, is fairly large and curves slightly forward. In Stephensen's species these somites bear much longer and more slender spines, and these are directed backwards.

The fifth and sixth somites each have a pair of lateral spines. The sixth somite is very long and slender, and armed along its lower edge with a series of small spines—a character which is most unusual and enhances the similarity of this larva with that of Stephensen.

The telson is of great length and size, and in general form resembles that of Stephensen's larva, widening out distally and being deeply hollowed behind (fig. 11, *b*).

But in place of a single pair of marginal spines there are three such pairs, and the large terminal spine is not so long. The differences in the telson are, however, such as would be accounted for by a difference in age, and the agreement is otherwise very close. The uropods also agree in shape so far as can be seen, but they are so damaged that their shape is difficult to be sure of. The outer branch has a row of spinules along its margin which is another striking point of resemblance to Stephensen's larva.

The peduncle of the first antenna is exceedingly long and slender, the first joint longer than the second and third combined, and having a strong spine on its outer terminal angle. The flagella are broken.

The scale of the second antenna is long, narrow, and with a row of spinules along its outer edge. The flagellum scarcely exceeds the length of the scale.

The mandibles are slightly asymmetrical, that of the right side having the cutting edge produced into a long triangular point. The palp is quite small, one-jointed, and bears four setae (fig. 11, e).

The second maxilla (fig. 11, c) is of peculiar form, the basal laciniae being reduced to three small finger-like lobes. The endopodite is rudimentary, but the scaphognathite is very large.

The exopodite of the second and third maxillipede is represented only by a minute knob, and no trace of an exopodite can be found on the fifth leg. A small vestige remains on each of the first four legs.

The pleopods are long and well developed, but uniramous.

Of the gill formula I am unable to speak with certainty. The animal is in such a bad state of preservation and the gills so small that it may well be that I have overlooked some. There is certainly no gill on the fifth leg, but there are gills in the position of pleurobranchs on the third maxillipede and the first four legs. There appears also to be a single arthrobranch on the third maxillipede and on each of the first three legs. I have not seen any epipodites.

The affinities of this adolescent specimen cannot be determined by the gill formula, but there are some characters which are very distinctive and seem to justify the conclusion that it belongs to the genus *Funchalia*.

Bouvier (1908) has given a very full account of *Funchalia woodwardi* and also of its young stage *Grimaldiella*, with which my specimen may be compared.

As regards the mandible it must be admitted that the agreement is not close, but the form of the palp, though one-jointed, is not unlike that of *Grimaldiella* with its enlarged distal joint, and there is undoubtedly an elongation of the blade which might well change to the sickle shape at the next moult. It may be worth mentioning that the right mandible *in situ* had so distinctly a falcate appearance that the possibility of *Funchalia* being the parent at once occurred to me. This impression is not so clear when the appendage is seen from behind, as it is shown in my figure.

The resemblance between the second maxilla of my specimen and that of

Grimaldiella is almost complete. In both of them this appendage is degenerated in respect of the endites, the proximal endite being lost entirely. This loss of the proximal endite is a feature unique, so far as I can find, among the Penaeidae.

As regards the loss of the exopodites of the maxillipedes Bouvier has already commented on the remarkable fact that, whereas in the adult *Funchalia* the second and third maxillipedes have long flagelliform exopodites, in the young Grimaldiella stage these exopodites are reduced to functionless rods without setae, and he supposes that the Mysis stage preceding Grimaldiella possessed, as is the case in other Penaeids, functional exopodites on these appendages.

I consider the absence of these exopodites, which is unknown in any other Penaeid, to be the strongest possible reason for identifying my specimen with *Funchalia*. If this identification is correct, it is evident that this is an additional stage between the Mysis and Grimaldiella stages in which the reduction of the exopodites is even more complete. The phenomenon is comparable to the total loss in the Mastigopus stage of the Sergestidae of the last two pairs of pereopods and their subsequent reappearance. Such loss or degeneration of appendages in larvae and their later regeneration is one of the most unaccountable features of Decapod metamorphosis, and is perhaps less rare than has been supposed. An example of temporary degeneration is given below (p. 99) in the case of the mouth-parts of the larvae attributed to *Petalidium*, and a similar temporary degeneration of the exopodites of the second and third maxillipedes takes place in *Leander* and *Palaemonetes*.*

The same phenomenon of the temporary disappearance of parts is illustrated in the mandible and second antenna of all Decapoda. In the Penaeid Nauplius there is a biramous palp on the mandible, but this is lost in the Protozoa, and in all Decapods the mandible has no palp in early stages. It is often not acquired until post-larval life.

The case of the second antenna is rather different. The endopodite is, in the Protozoa of Penaeids, a well-developed natatory branch with long setae. In the Mysis stage it becomes reduced to a functionless rod which develops later into the flagellum. In the same way in most Decapods it bears setae in the earliest Zoea, and it is transformed at the first or second moult into a simple, unarmed rod. There is no disappearance here, but there is a distinct regression.

In *Funchalia* the exopodites of the pereopods disappear altogether in the Grimaldiella stage, to reappear again in the adult in a rudimentary condition—an even more inexplicable example. These exopodites are, as I have said, rudimentary, though not altogether absent, in the "Terra Nova" specimen. Apparently the same temporary disappearance of the exopodites of the pereopods occurs in some species of *Penaeus*. Brooks (1882) states that the exopodites disappear in stage VI (a post-larval stage) of *Penaeus brasiliensis*; but exopodites are present in the adult of this species.

* See also p. 171, *Upogebia*.

If I am right in supposing that the specimen here described is a stage in the development of a species of *Funchalia* it is certain that it represents an undescribed species, and is of interest in extending the range of the genus to New Zealand waters. Only two species of the genus have been described—*F. woodwardi*, Johnson, and *F. vanhoeffeni*, Lenz and Strunck, both from the Atlantic. Balss has, however, recorded *F. woodwardi* from the Indian Ocean (1914), where it was taken by the "Valdivia" at station 182, 16° 8' S. lat., 97° 14' E. long.

I am greatly indebted to Dr. Stephensen for most kindly sending to me his two *Aristaeomorpha* larvae for examination. A study of these two specimens brings out one or two points of some interest.

The earlier larva is sufficiently described by Dr. Stephensen. At this stage there is no trace of gills, and the mouth-parts have not lost the larval characters. The mandible has no palp, and the second maxilla has four well-developed basal lobes.

The young specimen from station 384 is in the first post-larval stage and agrees with my own in all essentials, though differing in details which may be regarded as specific. The ventral spines which are so striking on the abdominal somites in the preceding stage are now greatly reduced, that of the second somite alone being large and pro-curved.

The telson differs but little from the preceding stage, and has only a single pair of lateral spines.

The scale of the second antenna has a row of five spines along its outer margin, in this respect resembling my specimen very closely.

The mandibles I have not dissected out, but they appear to have the blade rather more produced than in my specimen and to have a rudimentary palp without setae.

The first maxilla consists of a small basal and a very large distal lobe bearing about seven strong spines, while the endopodite is rudimentary.

The second maxilla resembles that of my specimen in the great reduction of the laciniae, but in this case the reduction has gone even further and only two lobes remain.

The labrum still retains a trace of the larval spine.

The exopodites of all the maxillipedes and pereopods are reduced to minute buds.

The pleopods are large, setose, but uniramous.

I was unable to see any trace of gills, but epipodites were seen on the first and second maxillipede, and on legs 2 to 4. From the appearance of the telson I should judge that the next moult would have brought little change, and probably the "Terra Nova" specimen represents a stage slightly older than that just described.

The close similarity between these larvae in every respect leaves no doubt at all that both belong to the same genus, but it must be admitted that there seems to be a radical difference with regard to the epipodites. On the other hand the branchial system is so ill-developed and errors of observation consequently so easy to make that no great importance should be attached to this fact.

Stephensen (1923, p. 26) has described a larva taken in the Mediterranean which he refers doubtfully to *Funchalia*, mainly on the ground of the similarity of the telson to that of Grimaldiella. He gives no account of the mouth parts beyond stating (p. 21) that the mandibles show no sign of elongation. If I am right in identifying his *Aristaeomorpha* larva and the "Terra Nova" specimen with *Funchalia* some other parentage will have to be found for his *Funchalia* larva. May this perhaps be the true *Aristaeomorpha*?

PENAEINAE.

Solenocera.

Monticelli and Lo Bianco have followed the development of *Solenocera siphonocera*, and the latter has fortunately published figures of the larva (1904) which make its recognition easy. The larva is of very remarkable form, strikingly unlike that of any other Penaeid, and has been described by Bate (1888) under the name of *Platysacus crenatus* and by Ortmann (1893) as *Opisthocaris mülleri*. Stephensen (1923) records the capture of numbers of larvae, mostly in the Mysis stages, in the Mediterranean, and also at stations in the Channel and outside Gibraltar. He notes that the larvae were met with at considerable depths (500 to 1,000 m.). Bate's specimen, which he regarded with good reason as belonging to some genus of Sergestidae, was taken off Sierra Leone and Ortmann's from the Florida Stream and off the Brazilian coast. Ortmann pointed out the resemblance of his larva to that described by F. Müller (1863, Taf. II, figs. 18-22)—also from the coast of Brazil—and there can be no doubt that Müller's larva also belonged to a species of *Solenocera*.

In the "Terra Nova" plankton I have found a few specimens of *Solenocera* larvae from station 43, and from three stations in the Pacific north-west of New Zealand. As these specimens differ in some respects from those previously described, and probably represent distinct species, some description may with advantage be given.

Atlantic Species. (Station 43) (figs. 12 and 13).

Stage I. Protozoa. Length, 1.7 mm.

Unfortunately the only specimen of this early stage is moulting and too distorted for its structure to be accurately made out, but it seems to me not to differ much in appearance from the next stage. There are no uropods, and the third maxillipede is present though rudimentary. The telson has seven setae on each side.

While the spines and lappets described below appear to be arranged in a similar way in this larva, it is important to note that there is a pair of large spines on either side between the rostrum and the supra-ocular pair. These spines are branched like those of Sergestids and are lost at the next moult.

Stage II. Length, 2.8 mm. (fig. 12).

The carapace is broad and rather flattened, with a stout rostrum slightly exceeding the length of the first antenna. The rostrum has a row of small spinules, and on

either side of it is a long denticulate supra-ocular spine. The margin of the carapace is drawn out into a series of five lobes or lappets on either side, each of which bears a number of short spines, while a sixth pair projects from the posterior margin. On the dorsal surface of the shell are a number of spines arranged as shown in the figure. A remarkable feature is the very great size of the "dorsal organ," which is a structure rather recalling the end of an elephant's trunk, with four small terminal lobes.

The abdominal somites bear dorsal and lateral spines of great length.

The two branches of the telson diverge so much that it has almost a T-shape, and each lobe bears eight setae.

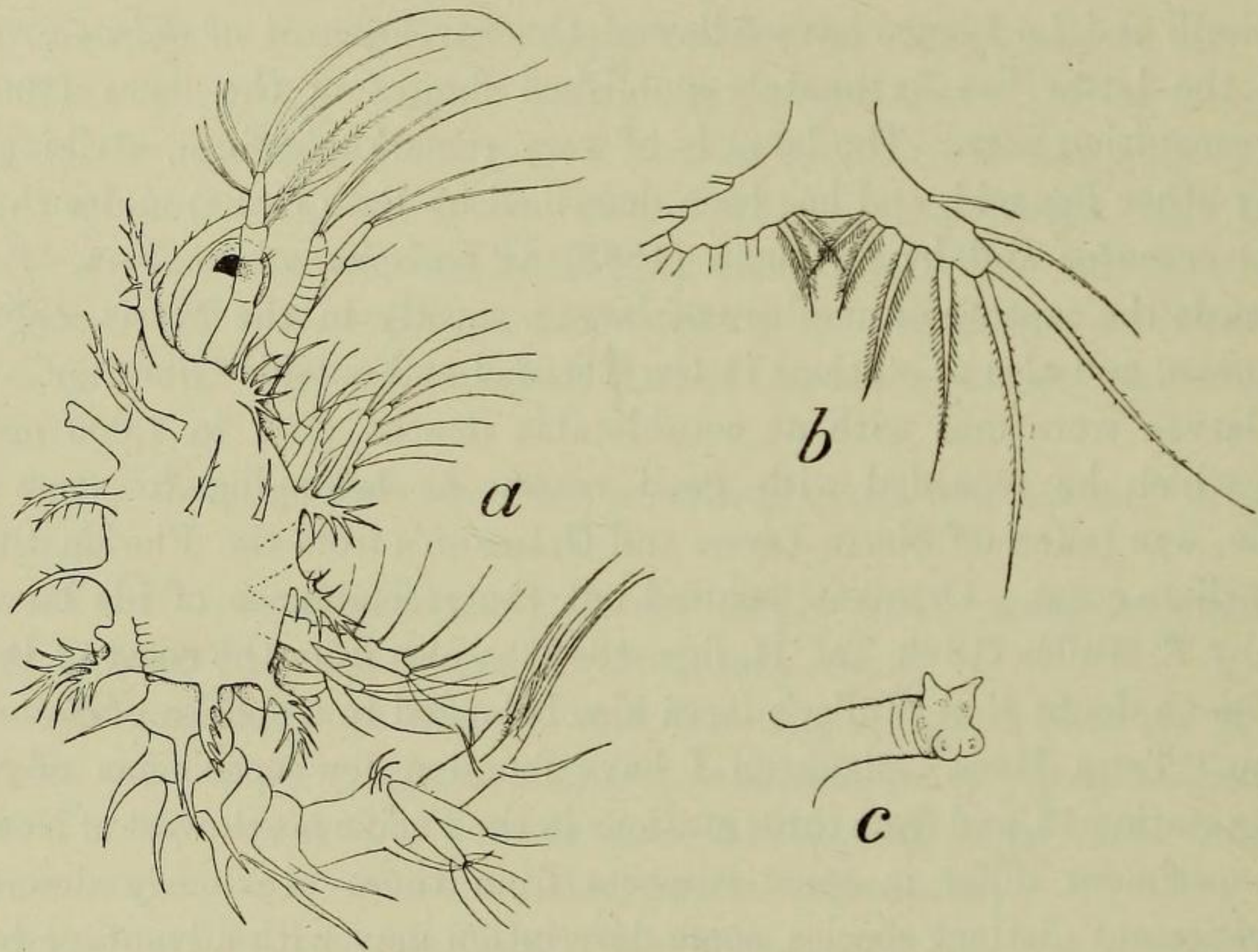


FIG. 12.—*Solenocera*. Station 43. Protozoa. *b*. Telson. *c*. Dorsal organ.

The pereiopods are present in rudimentary form, and the uropods are large and with a few terminal setae, but there are no pleopods.

The spiny carapace, and especially the abdomen, are remarkably like those of Sergestid larvae, and, if it were not for the dark pigmentation of the eyes, the larva at this stage would easily be taken for that of a Sergestid.

Stage III. Length, about 4.3 mm. (fig. 13).

This stage resembles very closely the Mysis stage figured by Lo Bianco, but differs in detail, the surface of the carapace bearing more numerous small spines, and its margin being less spiny. The lateral lappets have disappeared, but there are three pairs of small spiniferous processes on the posterior margin. The dorsal organ is still present, but more reduced.

The shape of the telson and its armature differ a good deal from that of *S. siphonocera*, and the uropods also differ in having a spine on the outer margin

of the exopodite. In this last respect it resembles Müller's larva, but the latter differs in its much longer rostrum and the arrangement of the spines on the carapace.

It is quite clear that this specimen does not belong to the same species as Müller's

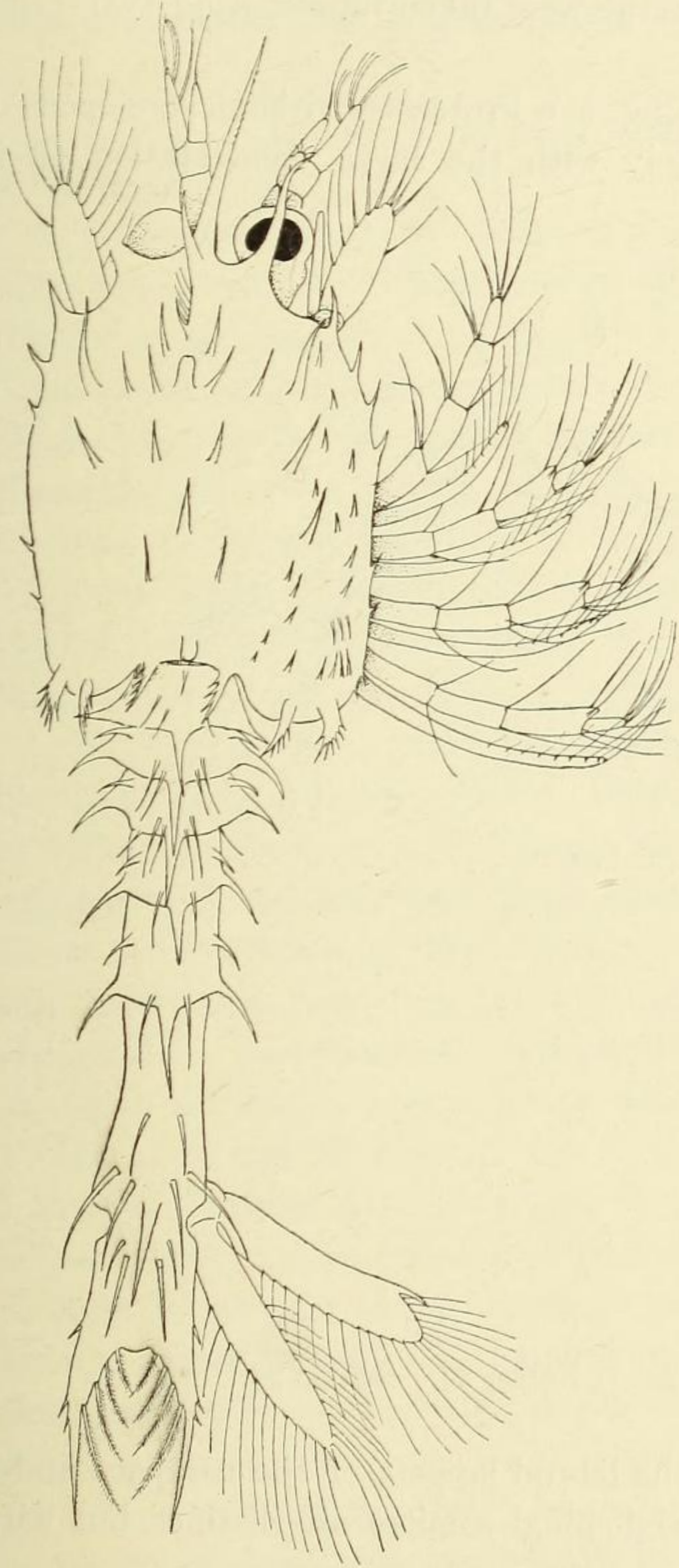


FIG. 13.—*Solenocera*. Stage III. Station 43.

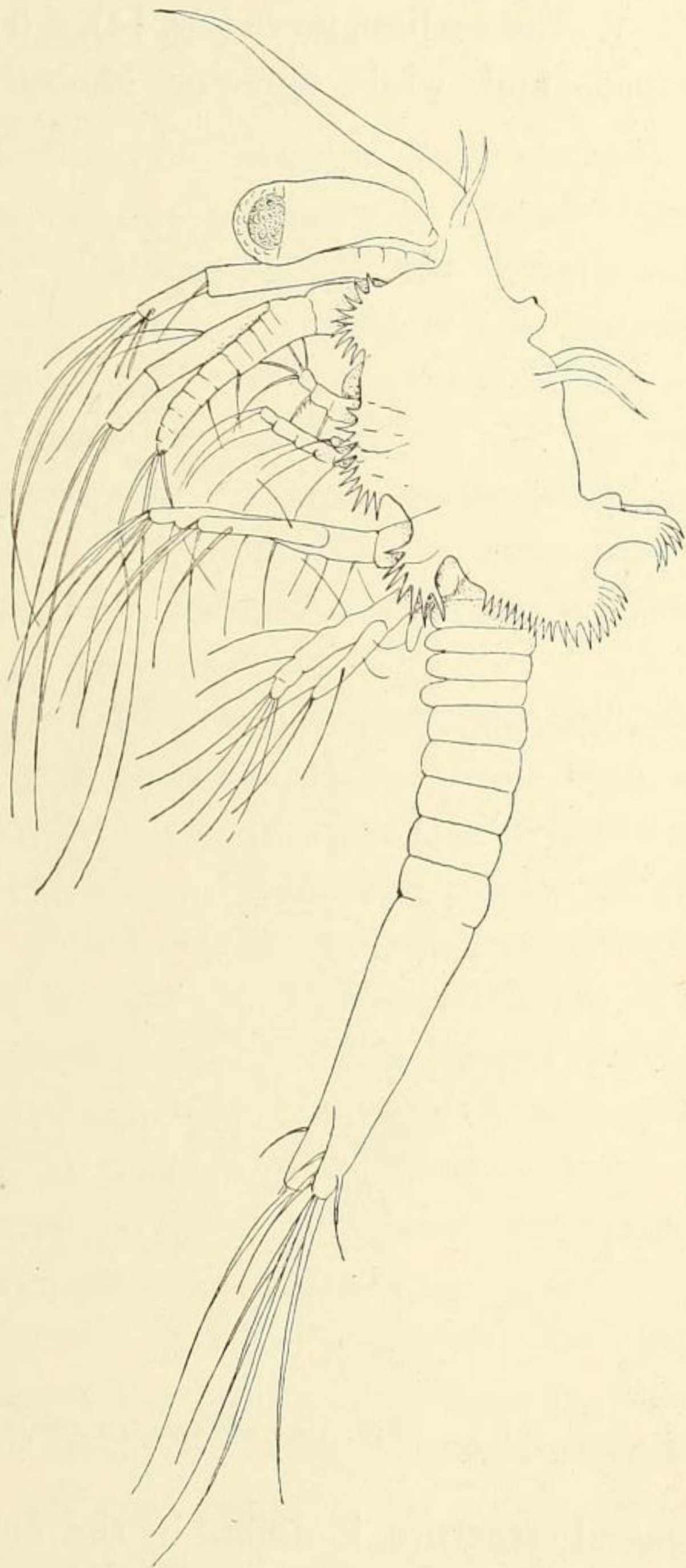


FIG. 14.—*Solenocera novae-zealandiae* (?).
Protozoa. Station 93.

larva, neither is it the same as Ortmann's *Opisthocaris mülleri* if Ortmann's figure is correct. But if this is so we have here larvae of three species of *Solenocera* from a region where no adult species has, so far as I am aware, been recorded. On the other hand two species, *S. africana*, Stebb. and *S. comatus*, Stebb., have been described from the region of the Cape, and there may well be others yet to be discovered.

Pacific Species.

Solenocera novae-zealandiae, Borr. ? (figs. 14 and 15).

At stations 93, 120, and 129, all within the area surrounding Three Kings Islands, north of New Zealand, a few *Solenocera* larvae were taken representing two stages in development.

1. The earliest larva (fig. 14), 2.5 mm. long, is a Protozoa without pereopods or uropods and, while agreeing almost precisely with the larva from station 43 in

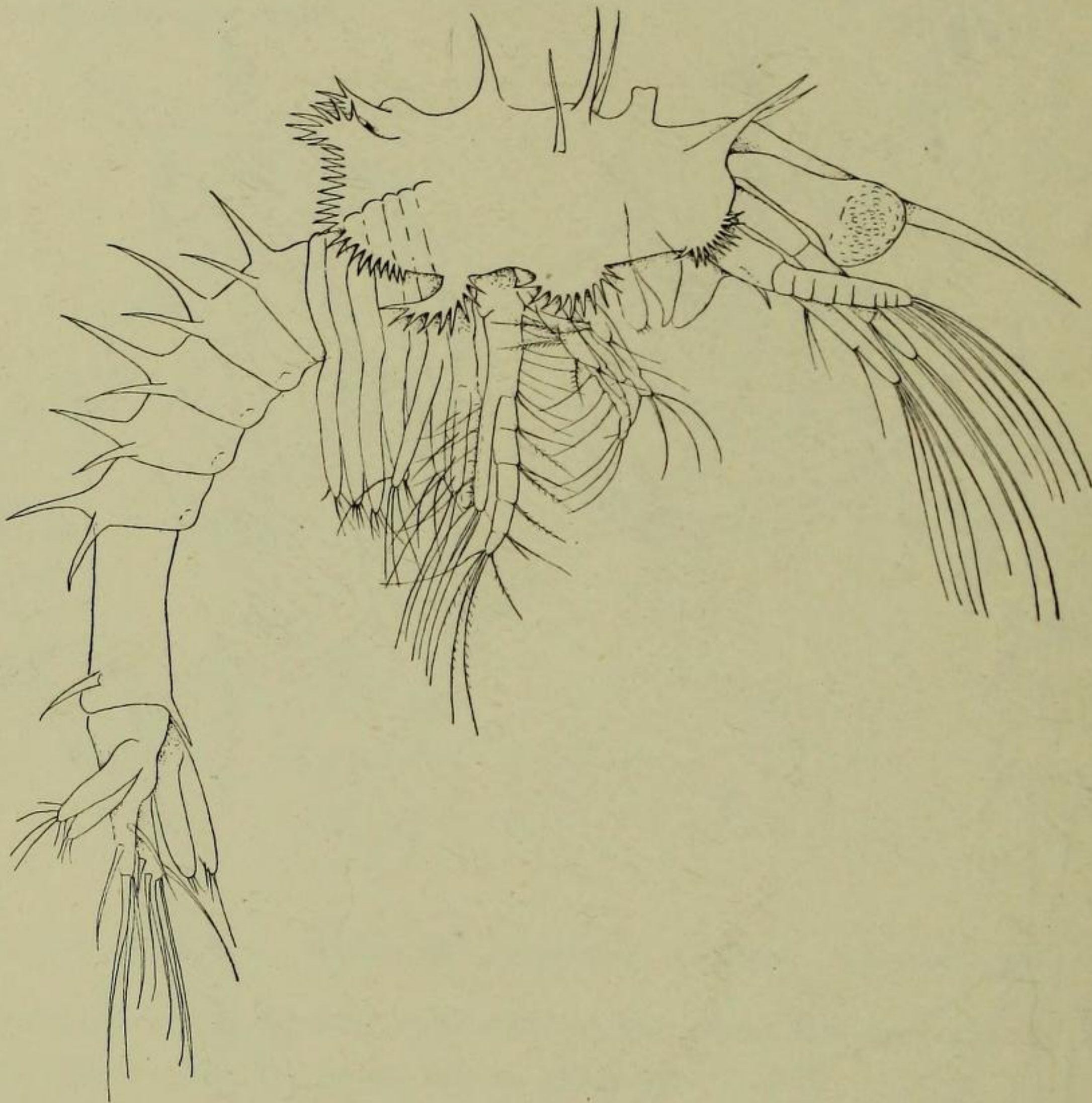


FIG. 15.—*Solenocera novae-zealandiae* (?). Stage II. Station 93.

general structure, it differs in the form of the lateral lappets of the carapace and in the smaller size of the dorsal organ. The abdominal somites are distinct, but without spines.

The eye is very faintly pigmented.

The telson formula is 7 + 7, the two rami not so divergent as in later stages.

2. The older larva (fig. 15), about 4.4 mm. long, possesses rudiments of all pereopods, and the uropods are present, though shorter than the telson and not yet functional. There is no trace of pleopods.

The abdominal somites are each armed with three long spines except the sixth,

which has two pairs, dorsal and ventral. The arms of the telson are widely divergent and bear sixteen setae in all.

Several species of *Solenocera* have been described from the Indo-Pacific region, but it seems most probable that these larvae belong to the species described by Borradaile from the same district as that in which the larvae were taken.

II. Sergestidae.

1. *Sergestes*.

The history of our knowledge of the development of the genus *Sergestes* has been fully summarized by Wasserloos (1908) and it is not necessary to repeat it here. Since the publication of Wasserloos's paper, Nakazawa (1916) has described the development of *Sergestes prehensilis*, but his paper is in Japanese and is not easily obtainable. So far as concerns the later stages of the Acanthosoma and Mastigopus, Hansen's two reports (1919 and 1922) mark an important advance. In his great work on the Sergestidae of the Atlantic he has been able to connect the Mastigopus with the adult in nearly all the species dealt with, and in some cases has also identified the Acanthosoma stage. For the species of the Indian and Pacific Oceans, however, our knowledge of the larval forms is still most scanty.

While the development of the Sergestidae in all its main features was made clear by Claus and Willemoes Suhm, Wasserloos and Nakazawa alone have been able to follow the whole series of changes in a single species (*S. arcticus* and *S. prehensilis* respectively), and their work is therefore of the greatest importance. Although these larvae are so commonly taken in the plankton of tropical waters, it is impossible from such material to piece together with any certainty the whole series of larvae of any one species. The plankton samples of the "Terra Nova" contain numbers of these larvae in all stages, and in many cases several different stages from the earliest Protozoa to the Mastigopus are to be found in a single sample, but in every case I have found these larvae to belong to more than one species. In such circumstances it is a matter of pure guess-work to connect one stage with another, so great are the changes which take place between the Elaphocaris, Acanthosoma, and Mastigopus. Having regard to the bathymetrical distribution of the adult *Sergestes*, it is probable that the larvae in the older stages will only rarely be found in the same stratum as the younger Acanthosoma and Elaphocaris. Hansen (1922, p. 24) goes so far as to say that a study of the early stages found in plankton samples is not likely to lead to results of any value and should be abandoned. This is probably true from the purely systematic standpoint, but it seems to me that results of some interest are to be obtained from a comparison of the various forms of these early larvae, even if it is not possible to connect them with the adults. I have examined all the larvae with some care and, though from the point of view of the systematist the large amount of time spent has been almost entirely wasted, I think it is worth while to give some account of the early larval types which it is possible to distinguish.

The material at my disposal contains a good number of specimens of the early stages of development, but they are taken from widely separated stations, and, as a rule, but few were taken at any one spot. Although it has not been possible, for the reasons already given, to piece together complete series, I have found that the earliest or *Elaphocaris* stages differ strikingly in some respects and may be divided into three groups which, for the purposes of description, I define under the names of *Elaphocaris dohrni*, *E. ortmanni*, and *E. hispida*. I use these names as indicating generic and not specific types, and consider that a description of these types should be of some interest as illustrating the great diversity of larval form within a single and apparently homogeneous genus.

In the larval development of *Sergestes* the following stages may be distinguished.

1. *Elaphocaris*. This corresponds to the Protozoa of the Penaeidae and includes three stages. In the first stage the eyes are not stalked, but consist of a rather ill-defined area of pigment embedded in the head region. The carapace bears an anterior pair of branched spinous processes, a pair of similar lateral processes, and a posterior median process. The first two pairs of maxillipedes are present as biramous swimming organs and the third is a small uniramous rod.

There can, I think, be no doubt that, at least in the majority of species, this is the first stage hatched from the egg. Nakazawa states that there is a Nauplius stage in *S. prehensilis*, but such a stage has not been seen by Wasserloos or any other observer. The body of the larva at this stage is opaque and appears to contain yolk.

In the second stage the eyes are stalked; the anterior pair of processes is lost, while a long rostrum has appeared with a number of lateral and ventral spines.

The third stage differs from the second in several respects. The rostrum is flanked by a pair of large branched supra-orbital processes, the thorax bears the full number of rudimentary legs, and the uropods have appeared in a rudimentary form.

2. *Acanthosoma*. The change of form in transformation to the *Acanthosoma* is very great, but the mouth-parts retain the same structure. In this respect this stage differs from the corresponding Mysis stage of the Penaeidae.

The spines of the carapace are greatly reduced, but are generally traceable. All the thoracic appendages are present and functional, and the pleopods appear. There are two stages of the *Acanthosoma* differing only in small details.

3. The *Mastigopus* differs from the *Acanthosoma* in the functional development of the pleopods, the great reduction or loss of the carapace spines, and the loss of the fourth and fifth pairs of pereopods. There is also a complete change in the character of the mouth-parts, which have taken on the adult form. The *Mastigopus* stage therefore corresponds to the post-larval stage of the Caridea, but persists through a number of moults and is gradually transformed into the adult. (For a full account of those stages, see Hansen, 1922, p. 24.)

I. ELAPHOCARIS.

A. *E. dohrni* (figs. 16-20).

This type of larva was first described by Dohrn (1870), and was later figured by Claus (1876, Taf. VI) and Bate (1888, Pl. LXII).

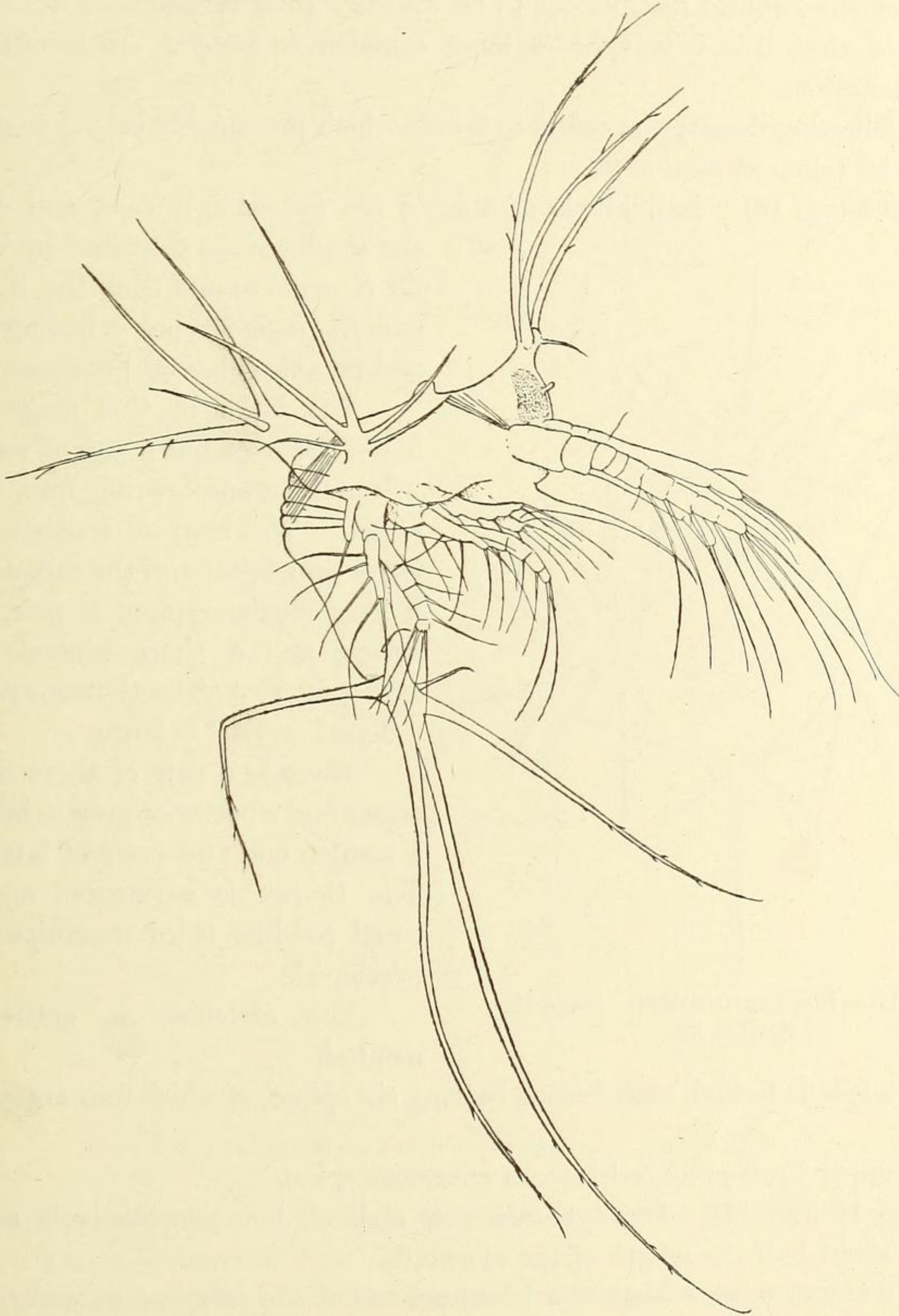


FIG. 16.—*Elaphocaris dohrni*. Stage I. Station 92.

Larvae of this type occur in the "Terra Nova" collections from many stations, specimens from the Pacific differing in no way from others from the Atlantic, and

it is, I think, certain that larvae of this type belong to adults of several species. There are differences to be found between individual larvae in respect of the number of spines on the rostrum and other processes of the carapace, but these spines are easily damaged and the material is not sufficiently extensive or well enough preserved to allow of any definite distinctions to be drawn. It is sufficient to draw attention to the fact that this is a type of larva common to several species from widely separated stations.

The following description refers to larvae which presumably belong to one species and were all taken at station 92.

Stage I (fig. 16). Individuals of stage I are exceedingly rare, and differ from the similar stage described by Wasserloos for *S. arcticus* and from the *E. ortmanni* and *E. hispida* types in having a rostrum and no antero-lateral processes.

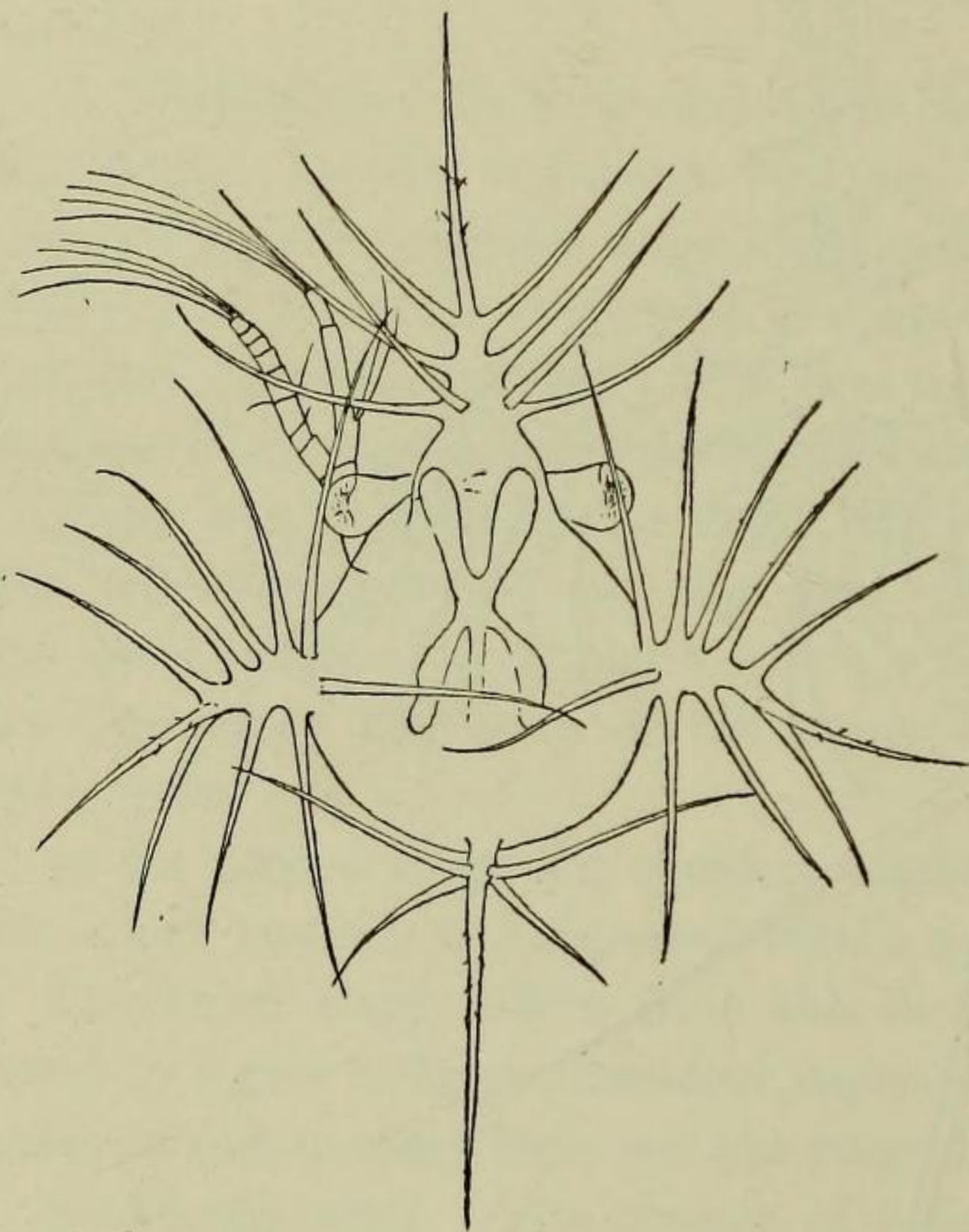


FIG. 17.—*Elaphocaris dohrni*. Stage II.
Station 92.

The larva in this stage has very ill-defined eyes, but a pair of very distinct "frontal organs" spring from the ocular region. The rostrum consists of an anterior prolongation of the carapace bearing a long median spine, a pair of lateral spines, and a short ventral spine, all springing from about the same point. The "dorsal organ" is large.

There is a pair of short lateral processes and a posterior process bearing each a median and two pairs of lateral spines. The thorax is segmented and bears a small rod-like third maxillipede, but no pereiopods.

The abdomen is entirely unsegmented.

The telson is forked, each branch bearing six spines, of which four are exceedingly long.

The upper lip is produced into an enormous spine.

Stage II (fig. 17). The eyes are now stalked, but comparatively small, their diameter about half the length of the eye-stalk.

The rostrum now consists of a broad process of the carapace extending forwards beyond the eyes and bearing three pairs of lateral and one pair of dorsal spines. The median, or rostral, spine is itself nearly as long as the carapace. The lateral processes are long and bear ten long spines. The posterior process bears a long median spine and two pairs of lateral spines near its base.

The appendages are unchanged.

The abdomen is partly segmented.

Other larvae in this stage differ in the much larger eyes and in the comparative length, but not in the number, of the spines. At station 50 some larvae of the

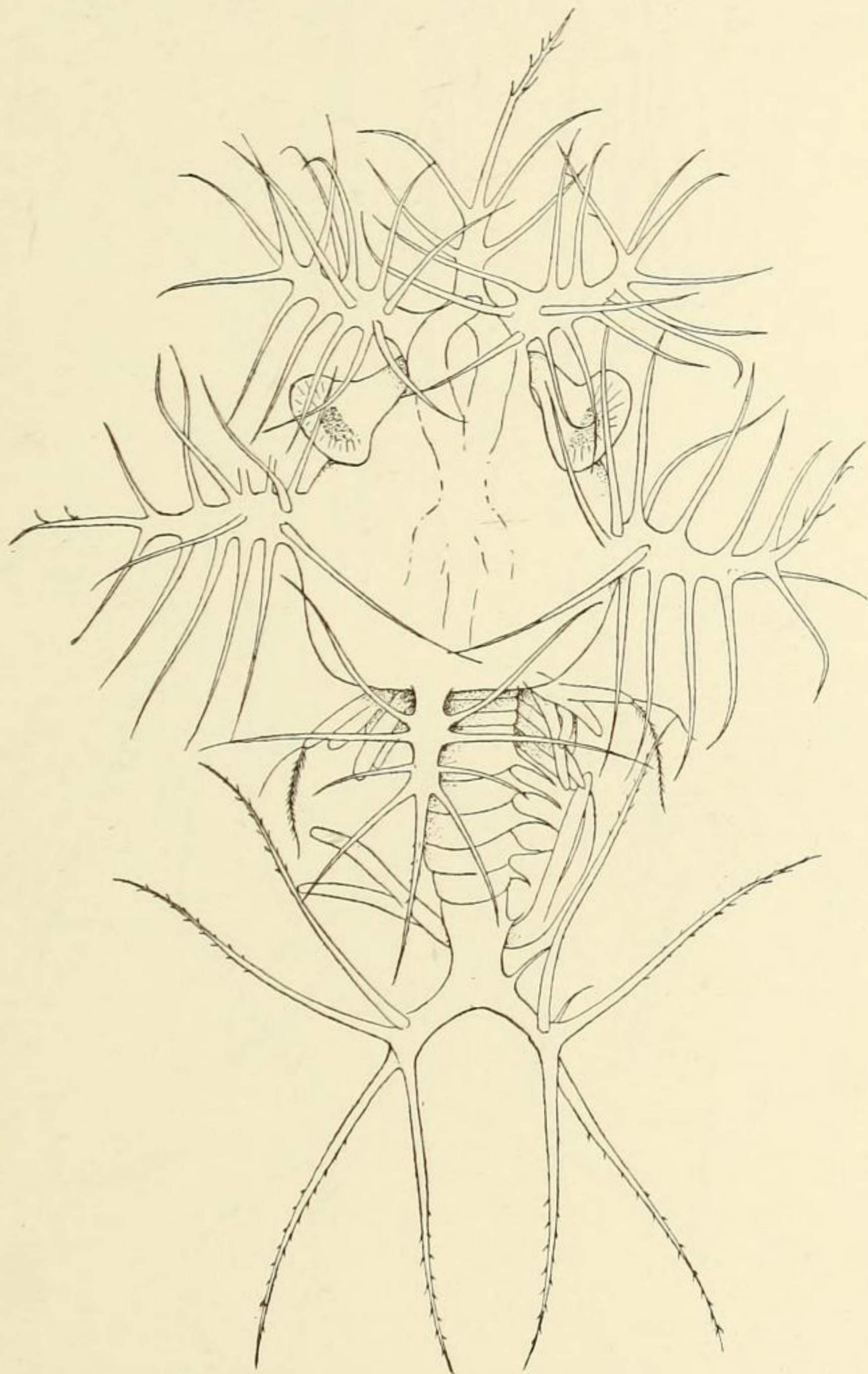


FIG. 18.—*Elaphocaris dohrni*. Stage III. Station 120.

following stage were taken which have no posterior median process, but it is possible that this has been broken off.

Stage III (figs. 18-20). All the larvae of this stage, except one to be mentioned below, agree in having large short-stalked eyes. The rostrum varies in the number of lateral and ventral spines. These spines may be all ventral, or there may be one or two pairs of lateral spines, and it is probable that these differences are specific. In the species with which we are now concerned there are two pairs of lateral spines. On

either side, at the base of the rostrum, there is a large supra-orbital process bearing fifteen spines in most cases. Here again, when the number is less, as in a larva from

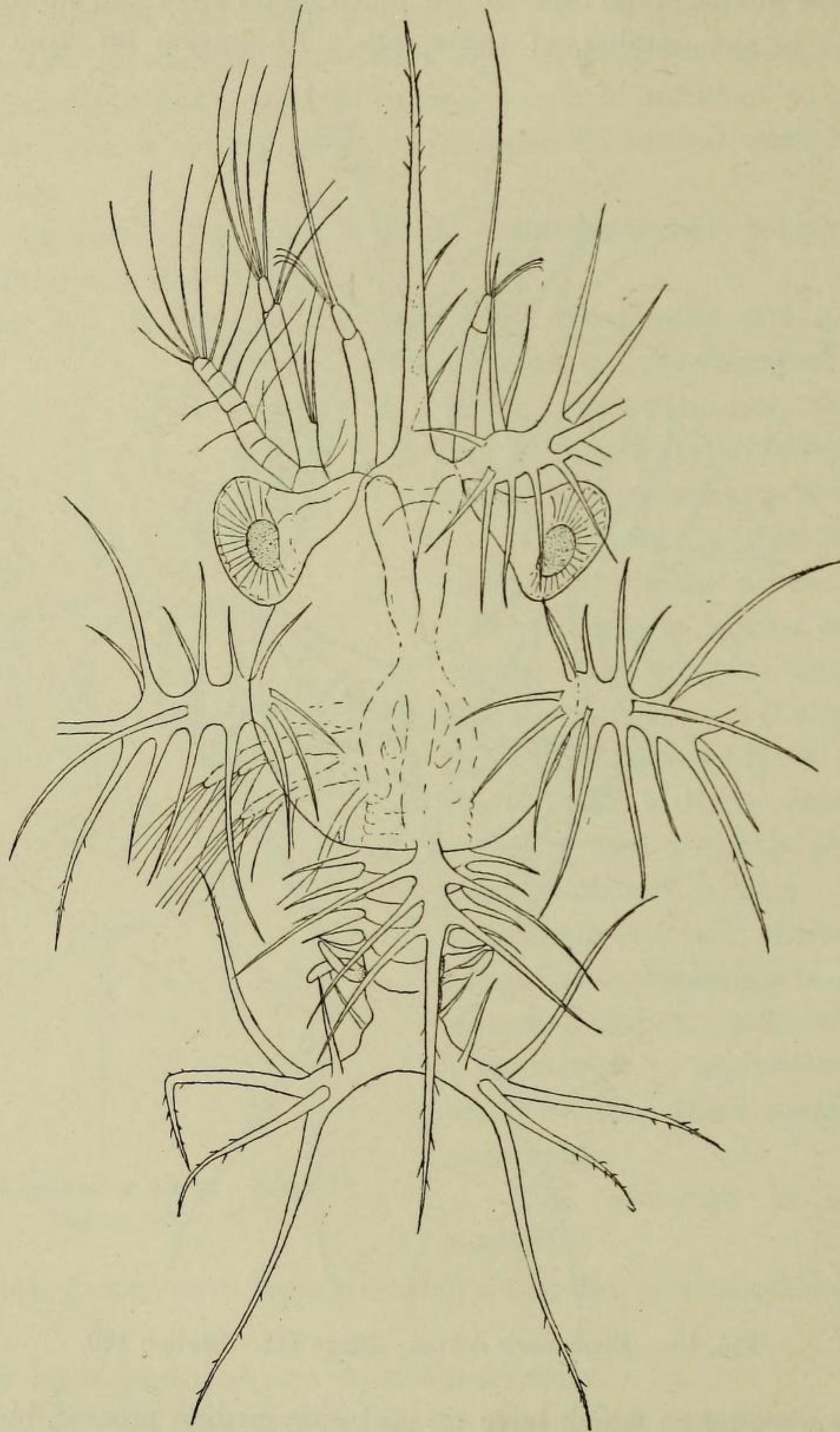


FIG. 19.—*Elaphocaris dohrni*. Stage III. Station 61.

station 61 (fig. 19), the difference is probably a specific one. The lateral processes also bear fifteen spines, of which some are ventral. The posterior process has four pairs of lateral or latero-dorsal spines.

The telson is forked, each arm bearing four long spines and two short ones.

The pereopods are all present as biramous rudiments.

The abdomen is segmented, each somite bearing a lateral spine, while the uropods are developed as long biramous rudiments turned forwards.

A larva in the third stage, which is quite distinct from the type above described, was found in the plankton from station 129 (fig. 20). This larva is very much

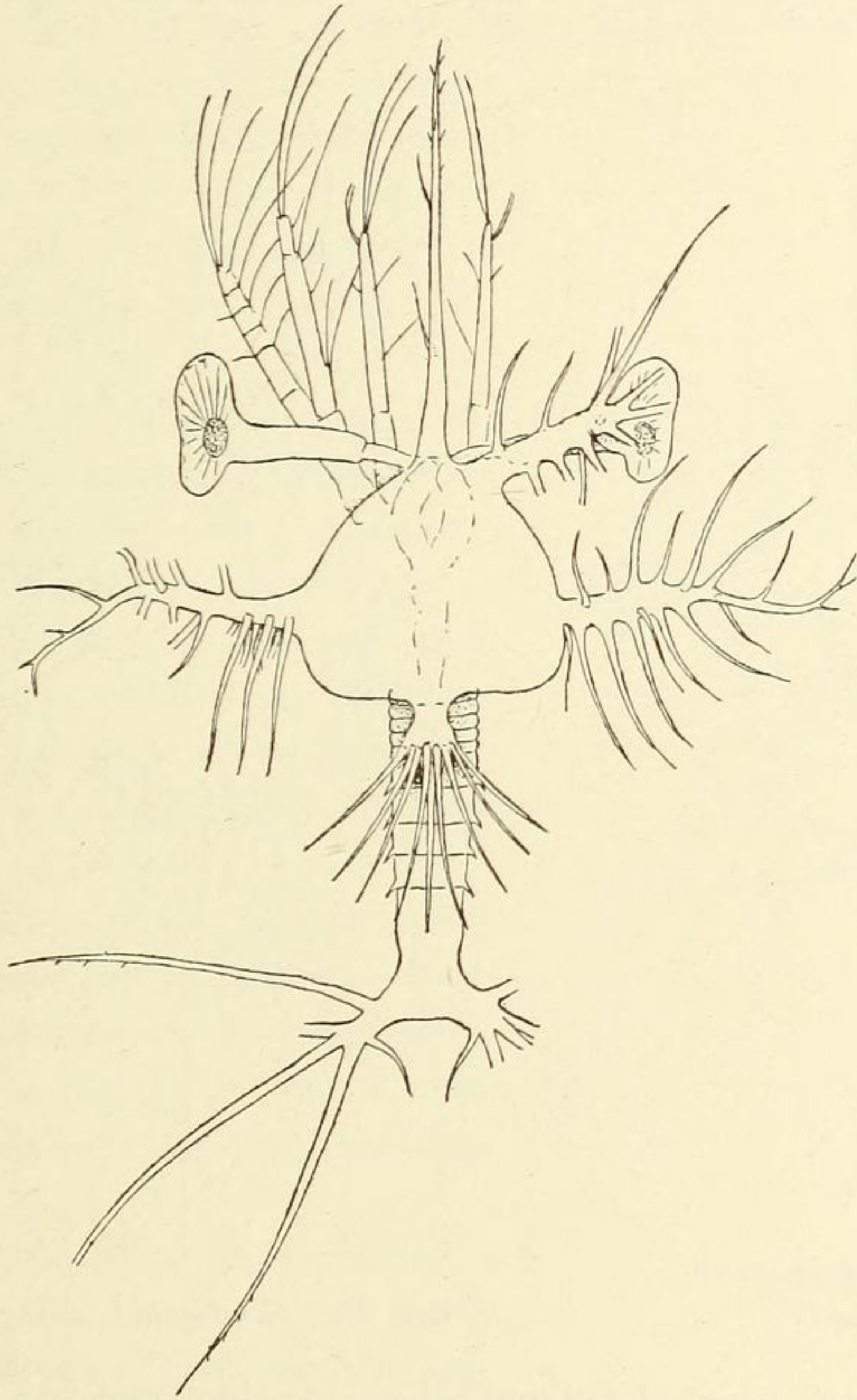


FIG. 20.—*Elaphocaris dohrni*. Stage III. Station 129.

distorted. The eyes are large, on extremely long stalks, and of peculiar shape. The rostrum has neither lateral nor ventral spines. The supra-ocular and lateral processes are not strikingly different, but the posterior process is pear-shaped at its base, where it bears a transverse row of eight spines. In respect of this process it provides a transition to *E. ortmanni*.

The larvae of *S. arcticus* as described by Wasserloos, though differing in detail in several respects from any larvae that I have seen, belong to the *E. dohrni* type.

B. *Elaphocaris ortmanni* (figs. 21-23).

Ortmann (1893, p. 66) briefly described a larva in the second stage which differs from the *Elaphocaris* of Claus and Bate in having all the spines of the rostral, lateral, and posterior processes arranged in a group at the base of the processes. The same type of *Elaphocaris* occurs in several of the "Terra Nova" samples, both from the Atlantic and the Pacific, and I have little doubt that they represent more than one species.

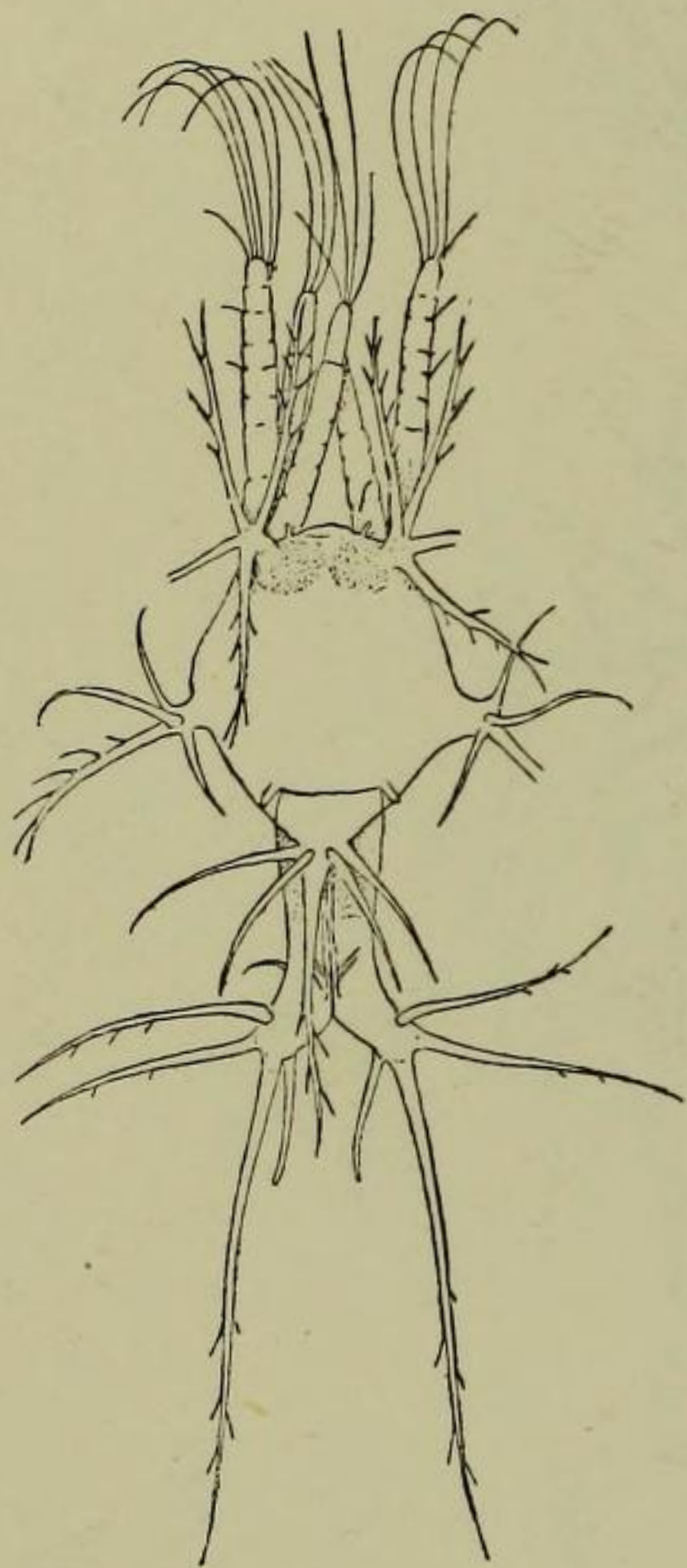


FIG. 21.—*Elaphocaris ortmanni*.
Stage I. Station 17.

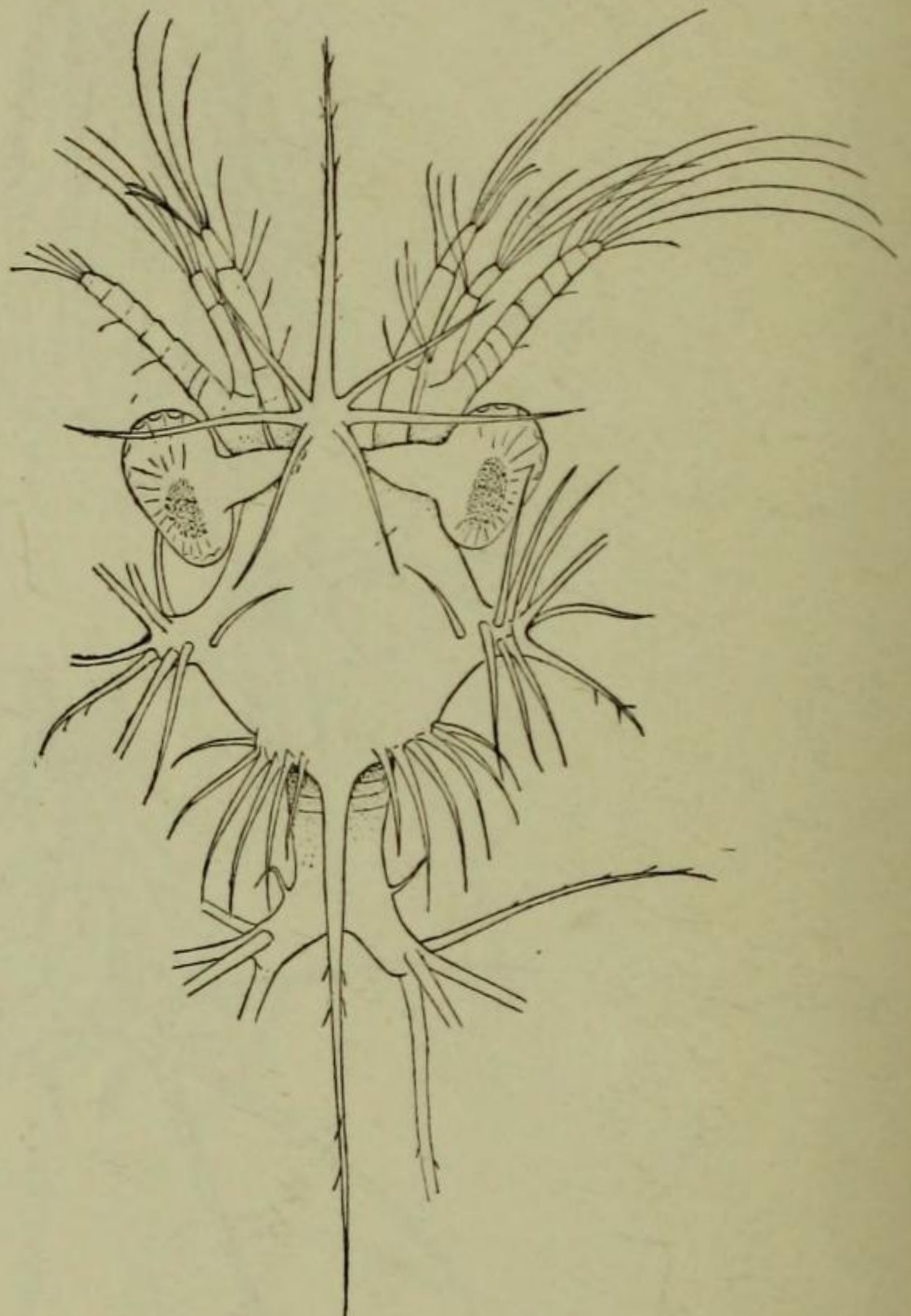


FIG. 22.—*E. ortmanni*. Stage II. Station 17.

Stage I. A larva which I believe belongs to this type was taken at station 17 (fig. 21).

This larva, of which the body measures 0.7 mm., has the usual eye rudiments and frontal organs of this stage. There is no rostrum, but a pair of anterior processes which divide into four long spines. These processes are precisely similar in *S. arcticus*, but there are only three spines in that species. The lateral processes consist of a main spine and three shorter basal spines, while the posterior spine has two pairs of lateral spines at its base.

The telson is of the usual form, forked, and with five spines on each fork.*

* The long spines of the telson of these larvae are usually broken and often lost, so that I give the actual number observed with some reserve.

Stage II. In the second stage (from the same locality), which in the specimen figured (fig. 22) measured 1 mm. in length of body, the eyes are stalked and a rostral spine is present, at the base of which are three pairs of long spines springing from the same level. In place of the lateral spinous process there is now a rounded lateral outgrowth of the carapace upon which a number of almost equal-sized spines are grouped. One of these may in some cases be recognized as the equivalent of the main lateral spine from its bearing denticles, while the others are smooth. The carapace is prolonged posteriorly into a very long spine which projects far beyond the telson, and on either side of it are a number of long spines (six or seven) which form a transverse row across the posterior end of the carapace.

Stage III (fig. 23). In this stage the rostrum is a long unbranched spine, and there are a pair of supra-orbital processes which Ortmann likened to stags' horns. These processes bend at first outwards and then back towards the middle line, and bear a series of spines along their outer margin and a few smaller spines on their inner face at their base.

The lateral processes have now the form of semi-lunar expansions of the carapace armed with a row of spines along their margin. Similarly, there is a posterior spine-bearing expansion at the base of the long posterior spine.

The whole animal is, as it were, a thicket of spines which, in preserved specimens, are often tangled so that the arrangement of them is difficult to make out. This arrangement is, perhaps, best shown in a view from in front (fig. 23).

C. *Elaphocaris hispida* (figs. 24-28).

The larvae which I distinguish under this name are less common than either of the other types, but occur both in the Atlantic and the Pacific, and certainly belong to different species. One species which has a larva of this type is *S. prehensilis*, Bate, a species found in such abundance in Japanese waters that it is fished on a commercial scale in the Bay of Suruga. Nakazawa* (1916) has figured four

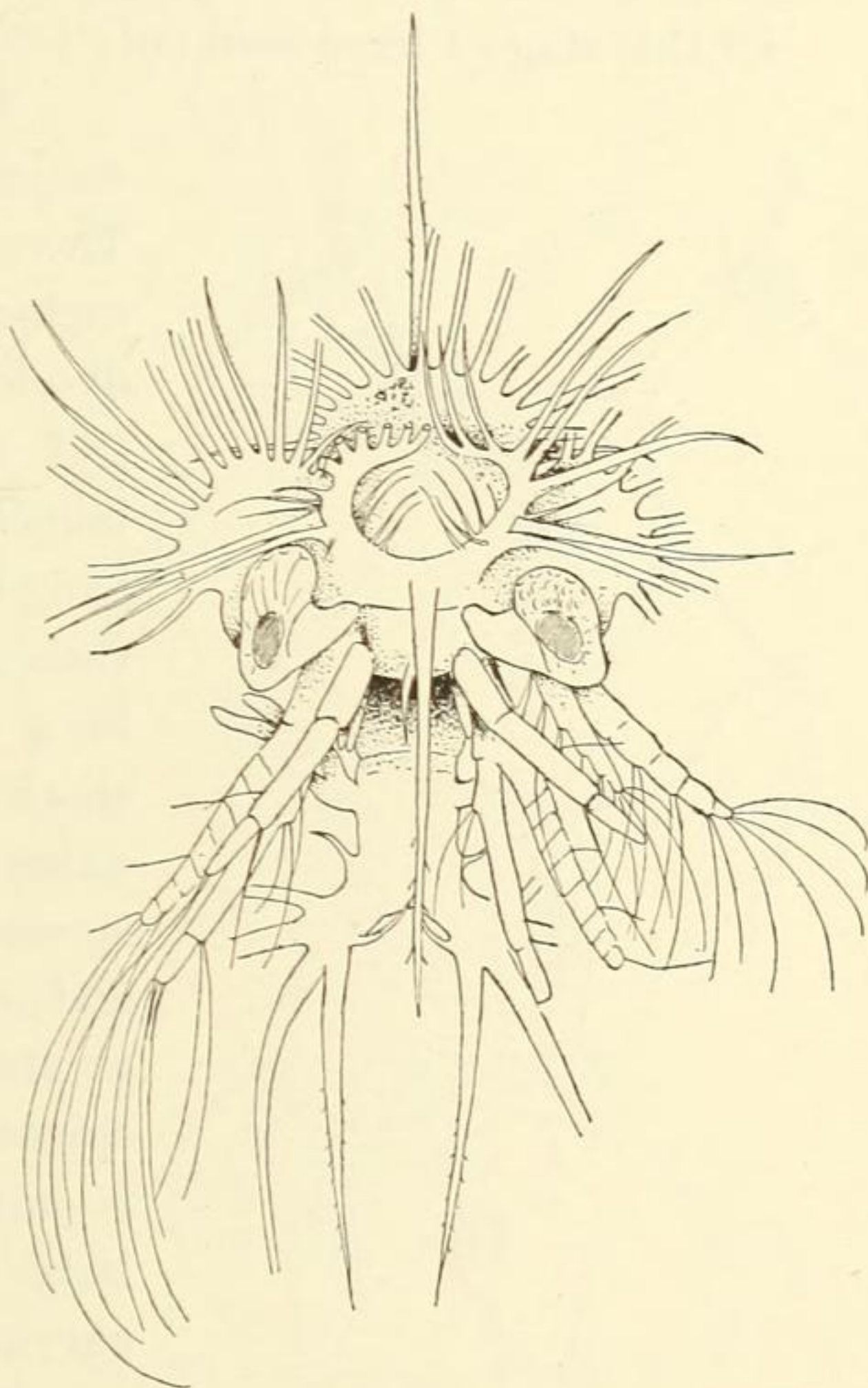


FIG. 23.—*E. ortmanni*. Stage III.
Station 87.

* I am indebted to Dr. Calman for the loan of a copy of this paper, which is in Japanese. To this copy Mr. Nakazawa has added a short MS. abstract in English.

stages in the development, but states that the first larva is a Nauplius. As he does not figure any stage earlier than the first Protozoa described below, and as the available evidence is strongly against the existence of a Nauplius stage in other species, this statement can hardly be accepted without further proof.

I have not been able to follow the metamorphosis through specimens taken at a single station, and the following series must be taken merely as illustrating a generic series.

Stage I. Length of body, 0.73 mm. (fig. 24).

Of this stage I have seen only two specimens, from stations 65 and 66.

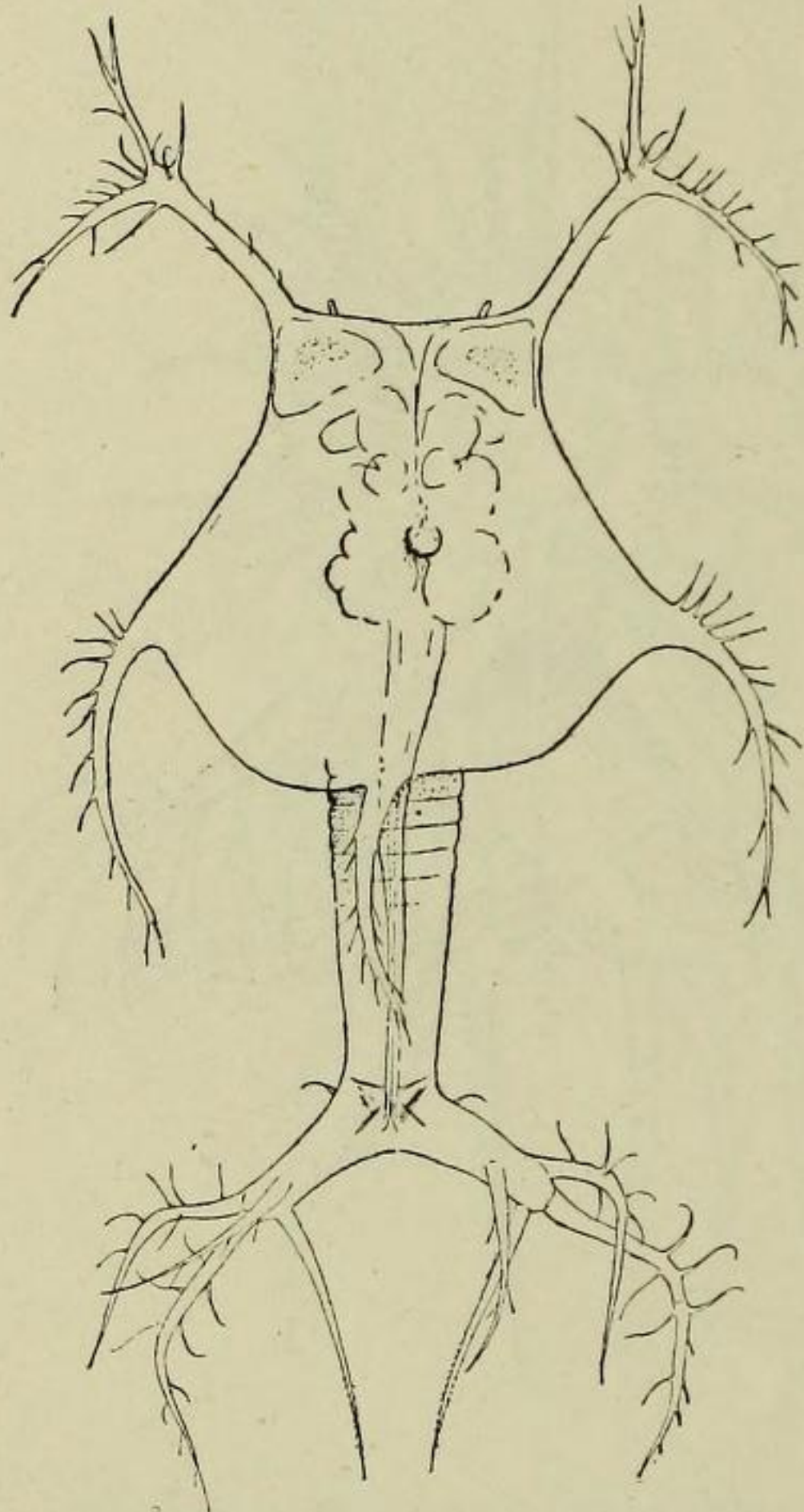


FIG. 24.—*Elaphocaris hispida*.
Stage I. Station 65.

The eyes are, as usual, undifferentiated, with distinct frontal organs. The dorsal organ is present. There is no rostrum, but the carapace is produced at each anterior angle into a long narrow process which divides into two branches, the anterior limb short and the posterior limb long and slender. Each branch bears spinules. The lateral processes are long, backwardly directed spines, with spinules along their margin, those towards the base being close-set in a basal group. The posterior spine is much shorter than the abdomen, and likewise bears spinules. The telson is forked, the two arms of it spreading almost at right angles to the line of the abdomen. There is the usual short hooked spine at the base of each branch and four long terminal spines; of these the fourth is slightly curved and is minutely denticulate, while the others, particularly the third, are armed with strikingly long curving spinules.

Stage II. Of stage II I have specimens of two distinct forms, both from station 120. In both of these the eyes are small, round, and with black pigment.

This black pigment is a remarkable character since, as Hansen has shown, it is characteristic of the genus that the eye-pigment remains pale till the adult condition is nearly reached, and the colour of the eye is generally a certain indication of maturity.

In both forms there is a small process attached to the inner face of the eye-stalk which seems to represent the frontal organ of the earlier stage. I have seen the same organ in the same position in the first larva of *Philocheras fasciatus* (Gurney, 1903, Pl. V, fig. 1).

In one of these larvae (fig. 25), the body of which measures 1.32 mm., the rostrum is long and simple, without any accessory spines. The lateral spines are likewise simple, backwardly directed, and spinulose. The dorsal spine in this

specimen is broken off. The telson has much the same form as in stage I, but the arms of it have elongated, and there are now six spines in all on each branch, none of which is distinguishable by special armature.

The second larva (fig. 26) does not differ from the first in size, but is distinguished by three characters. At the base of the rostrum there are about five spines on either side on a slight elevation of the carapace. In front of the point of origin of the lateral spines there is a knob-like protuberance of the carapace bearing eight closely packed spines. Lastly, the arms of the telson are short and not greatly diverging.

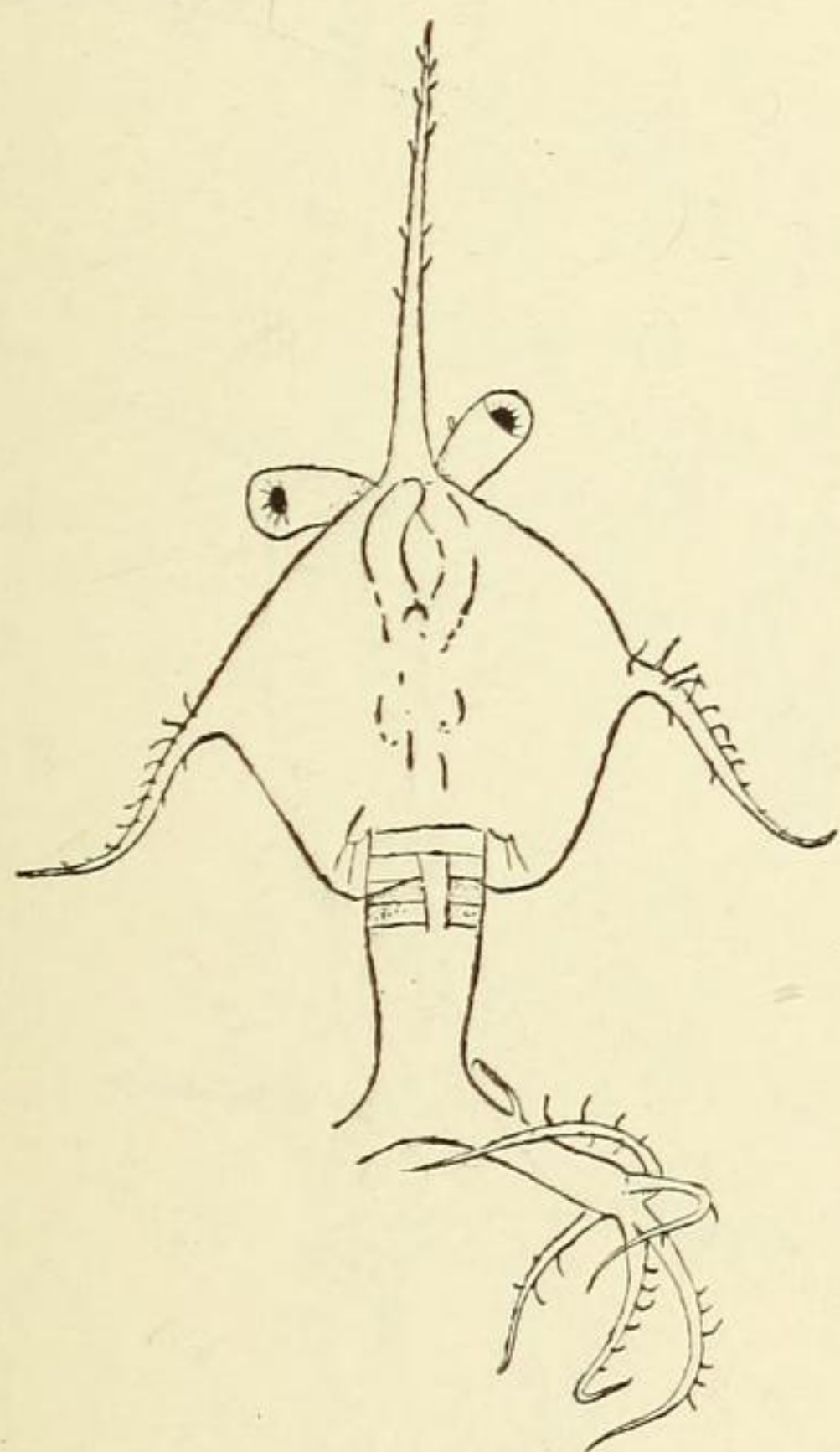


FIG. 25.—*E. hispida*. Stage II.
Station 120. Form A.

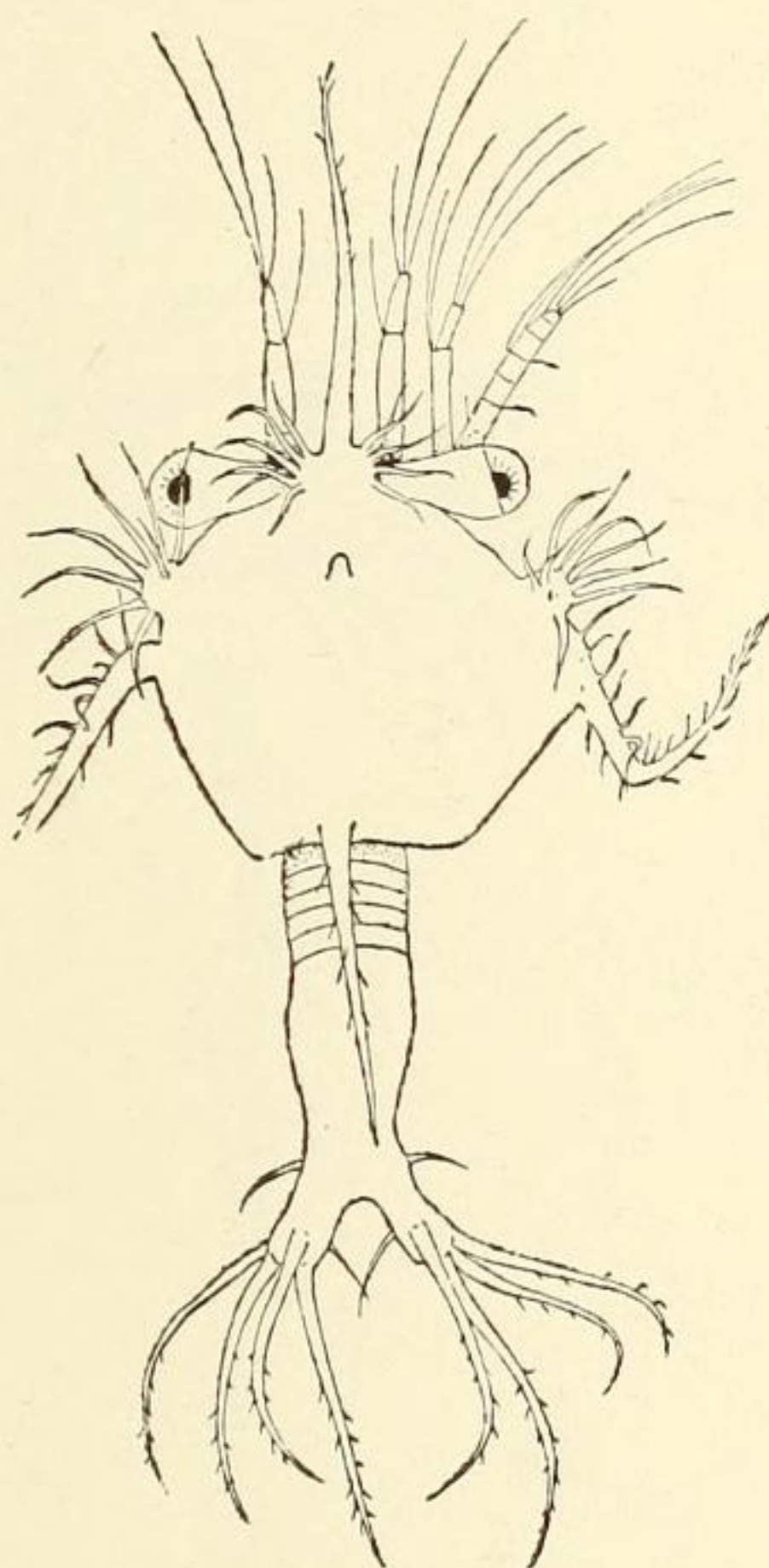


FIG. 26.—*E. hispida*. Stage II.
Station 120. Form B.

The eye-pigment is darker in this form than in the first, both in this and in the next stage.

Stage III. A larva in this stage which can be recognized as belonging to type 1 of stage II is figured (fig. 27). This larva measures nearly 3 mm. excluding the rostrum, and was taken at station 109.

The eye-stalks are very long and slender, and it is characterized by its enormous lateral spines, which are unarmed towards the base. The long rostrum is flanked by a pair of denticulate supra-orbital spines. The arms of the telson are long and divergent, and the spines on them are armed with more or less hooked spinules.

The larva of type 2 unquestionably changes into the form shown in fig. 28. This

larva differs from that above described in the form of the telson, which resembles that of stage II, and chiefly in that of the lateral spines. The lateral protuberance of stage II has become joined to the lateral spine to form a sort of shoulder to it, the spine having the appearance of being fused to the carapace for about one-third of its length, the free part being directed straight backwards.

Both these types of larva differ from *E. dohrni* and *E. ortmanni* in having the uropods much shorter and not curved forwards.

A third form of this larva in the third stage was met with in a sample from

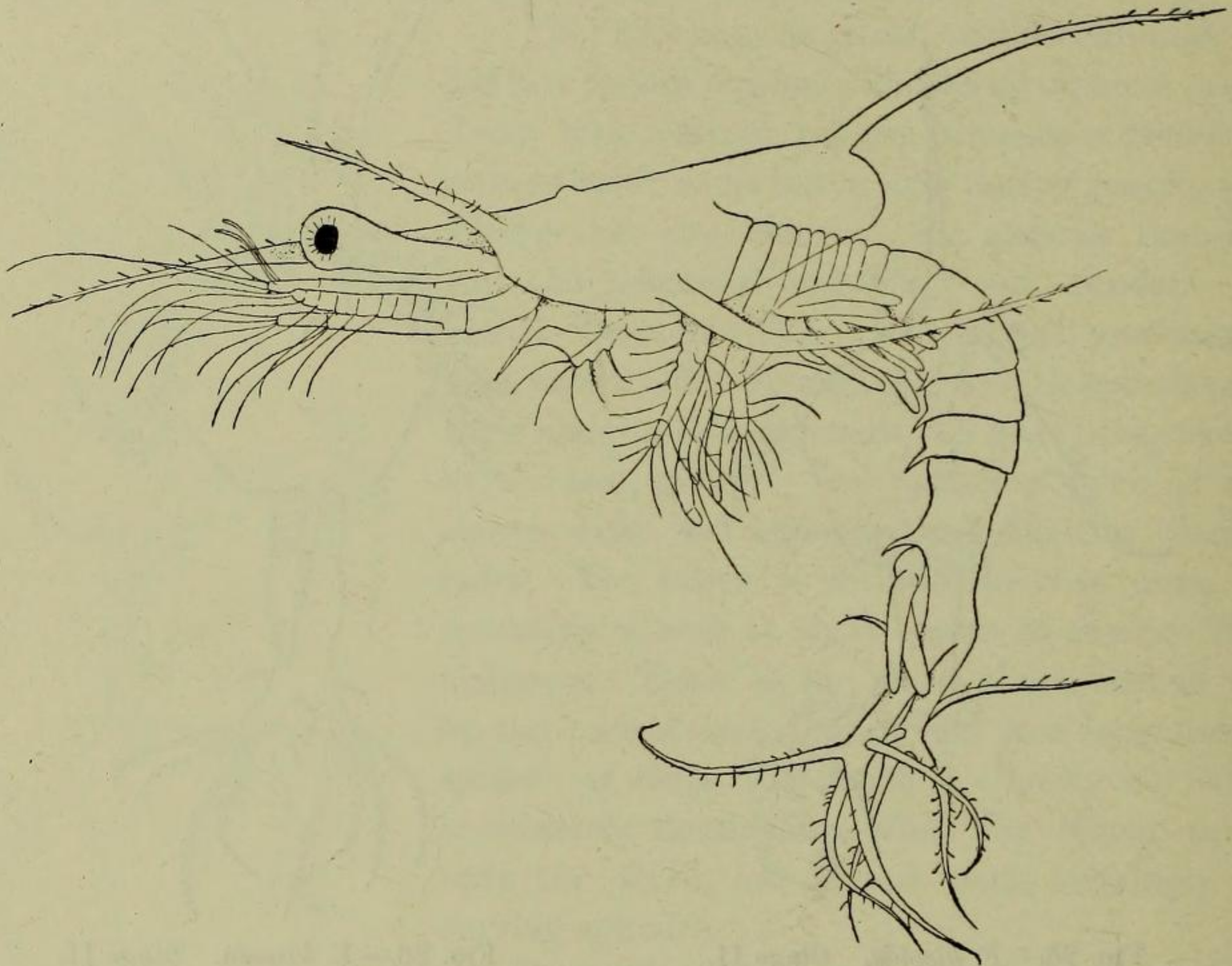


FIG. 27.—*E. hispida*. Stage III. Station 109. Form A.

station 65. In this form the eyes are relatively much larger and the pigment not particularly dark. While the arrangement of the carapace spines is much the same as in type 1, the branches of the telson are excessively elongated and slender.

I have dealt with these early larvae in some detail, since I think it a matter of some importance to establish that within one and the same genus not only are the early larvae of strikingly different types, but also these types represent not species but groups of species. Within the same type—*E. hispida*—the differences between the larvae are as great as, or greater than, those which distinguish genera, or even families within the Caridea (cf. *Processa* and *Pandalus*). It is permissible to suggest that the genus *Sergestes* may be a composite of two or more really distinct genera which have reached a great similarity of form by convergence.

Acanthosoma Stage.

The Acanthosoma stage has been so fully described by Hansen (1922) for a number of the Atlantic species that it is unnecessary to deal with the larvae of this phase in detail. There is great variety among them, but there seems to be but little relation between the type of Elaphocaris and the Acanthosoma into which it is transformed, and it is by no means easy to connect the one with the other.

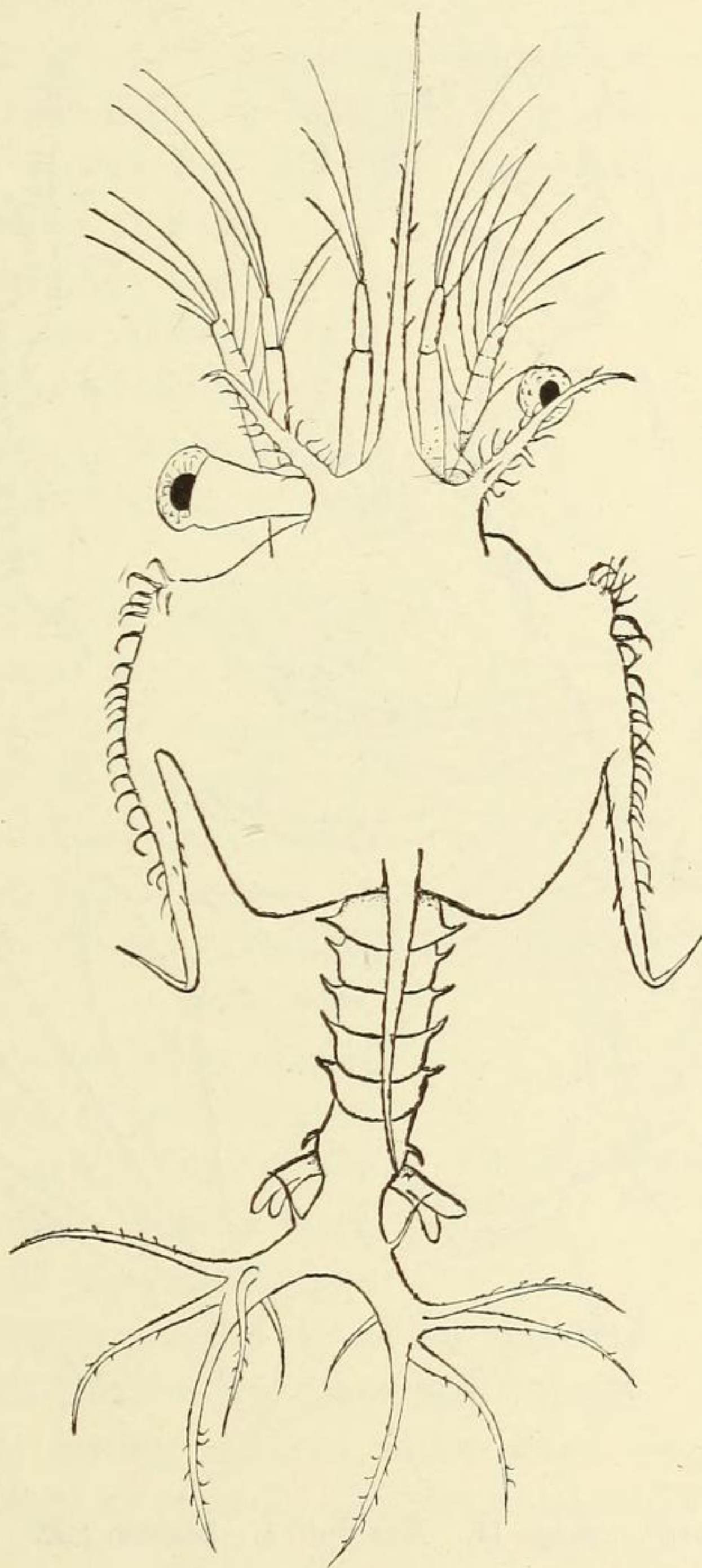


FIG. 28.—*E. hispida*. Stage III. Station 120. Form B.

It is, I think, worth while to describe two types of Acanthosoma belonging respectively to the *hispida* and the *dohrni* type of Elaphocaris for the purpose of showing, firstly, that the very distinct types of Protozoa produce Acanthosomas which are not so distinct, and, secondly, that, although less defined, types may be distinguished at this as in the earlier stage.

I. *Acanthosoma* of *hispid*a type (figs. 29 and 30).

At station 129 a number of Sergestid larvae in later stages were taken, among which several species were represented. Two of these may, with some certainty, be related to the *hispid*a type of Protozoa.

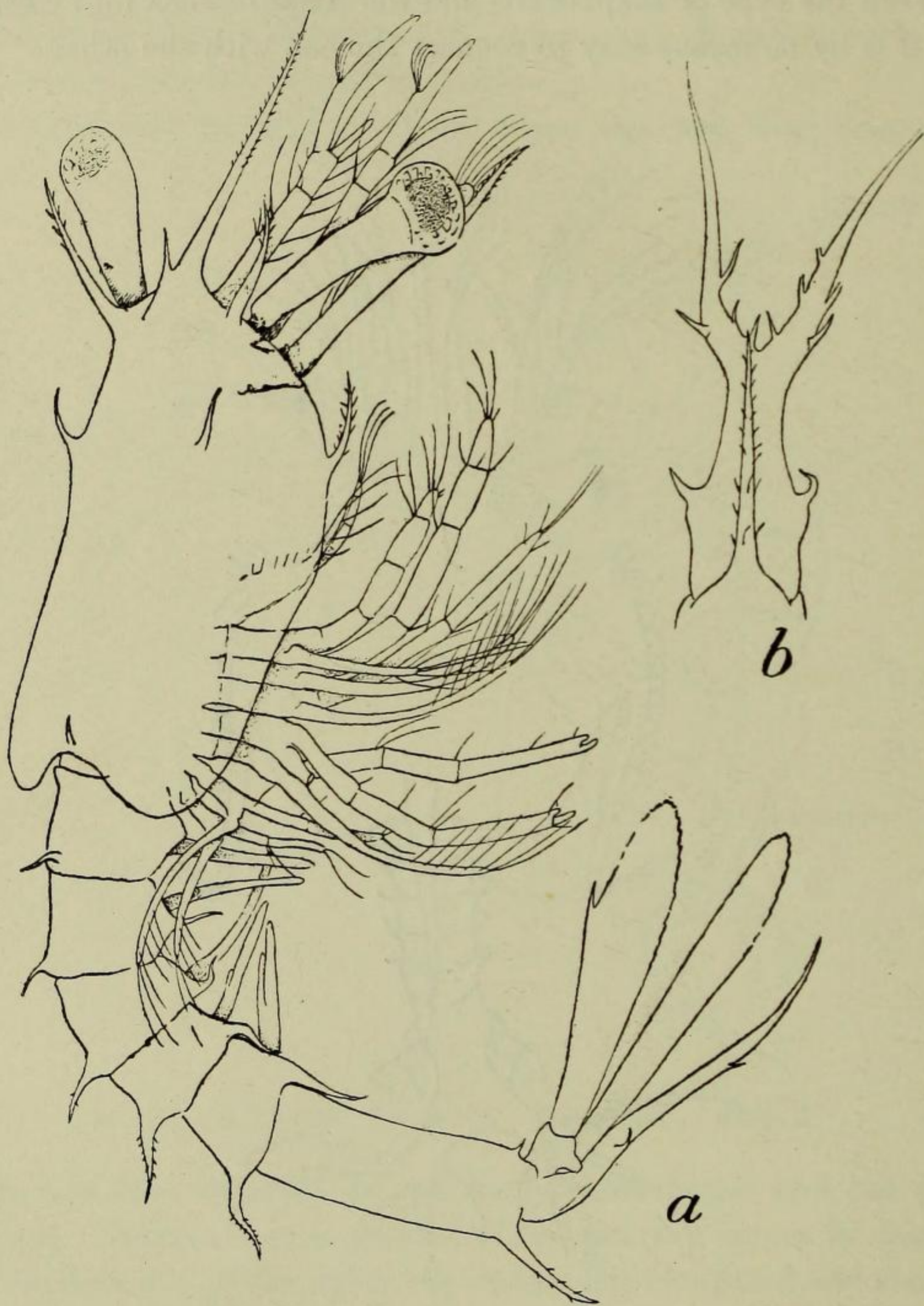


FIG. 29.—*Acanthosoma hispida*. Stage II. Example 1. Station 129. *b*. Telson of previous stage.

Example 1 (fig. 29). This specimen is in the second *Acanthosoma* stage and measures 6.4 mm. from tip of rostrum to end of telson. The rostrum is considerably longer than the peduncle of the first antenna, and is denticulate, with a basal spine. The supra-ocular and lateral spines are present and of some length, and there is a pair of hepatic spines. There is a very small posterior dorsal spine on the carapace.

The abdominal somites have dorsal spines, increasing in size from before back-

wards, and also small ventro-lateral spines. In the previous stage these abdominal spines are very much longer.

The telson is very long and bifurcate, the arms of the fork equalling in length the undivided portion which bears a pair of lateral curved spines.

The eyes are long, round, and with very dark pigment.

The first antennae have the basal joint slightly the longest, and the third joint the shortest.

The second antennae are of the usual form characteristic of the second stage. In the first stage the scale is armed at the end with four stout setae, which differ from the marginal setae and appear less stiff than these (see fig. 30). In the second stage the setae are all alike, and there is a large denticulate spine near the apex of the scale. The endopodite also differs in the two stages. In stage I it is a long unjointed rod with a number of spines at the end, while in the second stage it has become a long jointed flagellum.

The mandible has a small palp. The maxillae are much the same as in the Protozoa, but the exopodite of the second pair loses in the second stage all the setae except the posterior one. The maxillipedes and legs are long, slender appendages with long exopodites which, in the second stage, have the setae confined to the distal end. The third pair of maxillipedes in the species under consideration are not of great length, reaching scarcely as far as the base of the antennae. In species which have a very large third maxillipede in the Mastigopus the appendage is noticeably larger also in the Acanthosoma.

The second and third pairs of legs have small chelae. The pleopods are long, the fourth and fifth only having a short endopodite. There seems to be much difference between different species in the stage at which the pleopods become biramous.

The uropods are of characteristic shape, the exopodite narrow at its base and widening distally, the setiferous part of the outer edge scarcely more than half the length of the basal part.

Example 2. A second species, very similar to that just described, was found in the same sample from station 129.

This larva, which is 7.5 mm. long, is in the first Acanthosoma stage, and is

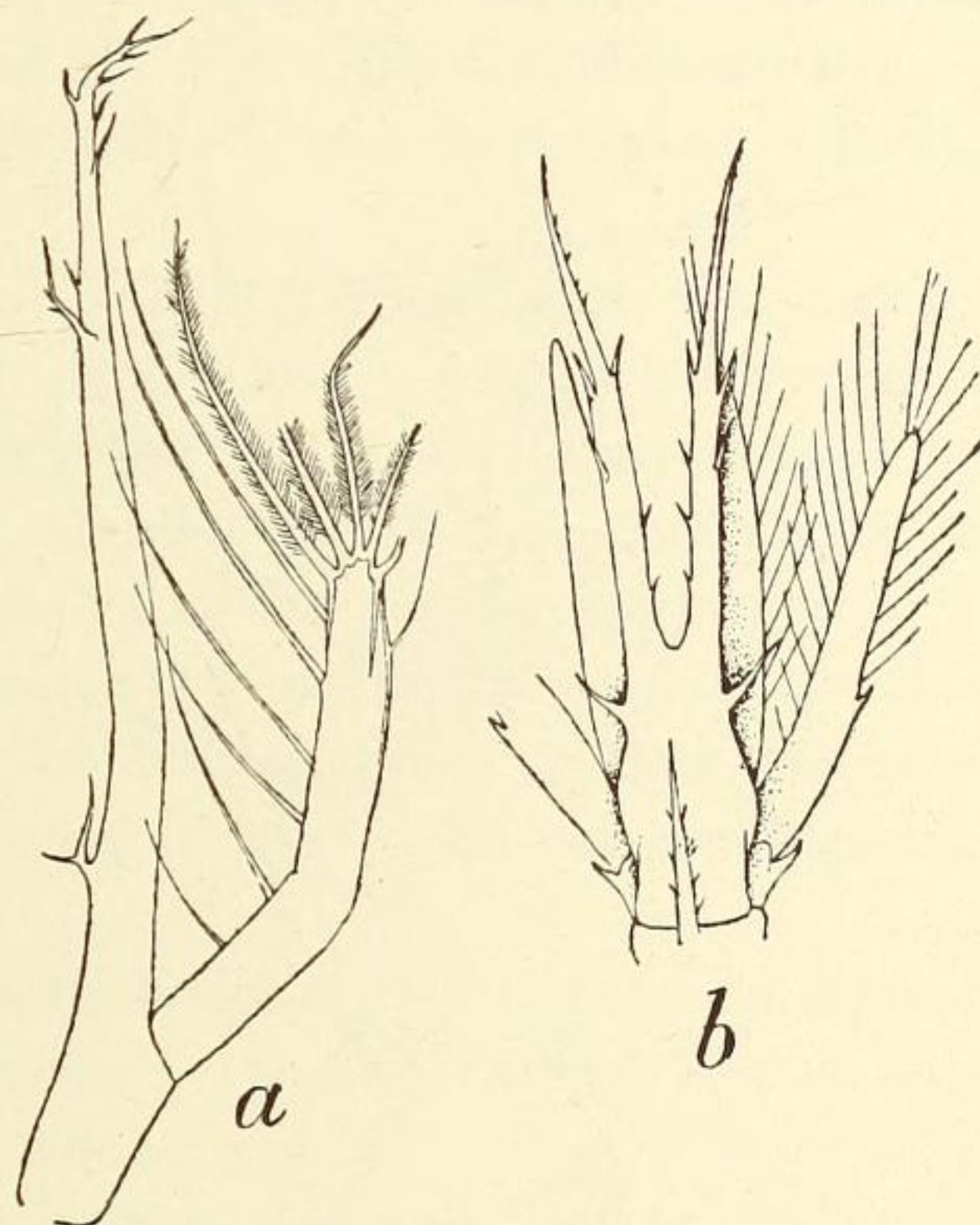


FIG. 30.—*Acanthosoma hispida*. Stage I. Example 2. Station 129. *a*. Second antenna. *b*. Telson.

chiefly distinguished from the first species by the narrow lanceolate form of the exopodite of the uropods, of which the setiferous part is more than half the whole length (fig. 30).

The spines of the carapace have a similar arrangement, and the very much greater development of the lateral spines of the abdomen is no doubt largely a matter of age. The spine on the fifth somite reaches back to the end of the long sixth somite. The telson has much the same form, being very long with a long, slender fork.

Acanthosoma of *dohrni* type (fig. 31).*

In the sample from station 129 a form of *Acanthosoma* was found which I consider belongs to the same species as the *Elaphocaris* in the same collection, which

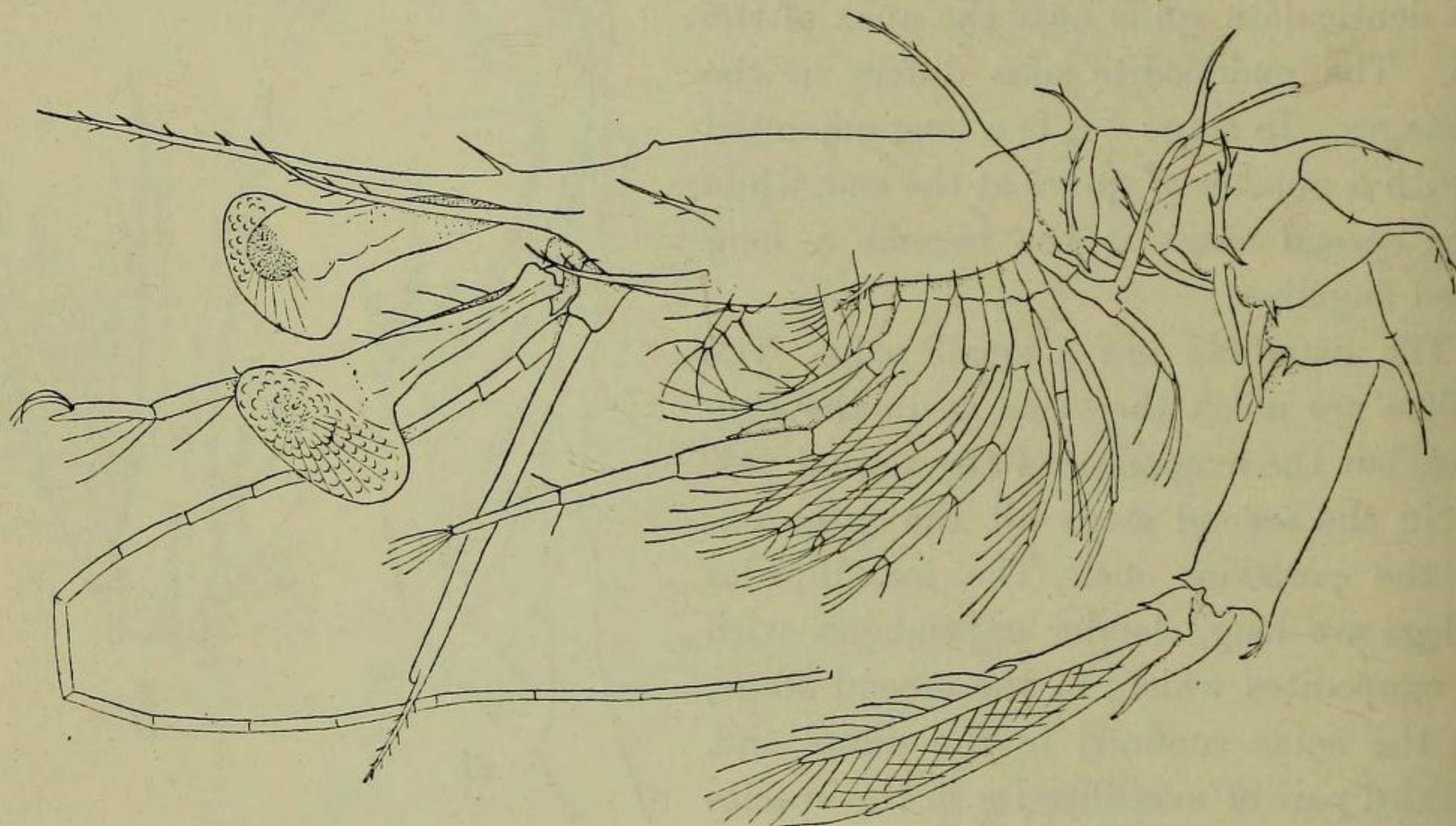


FIG. 31.—*Acanthosoma dohrni*. Station 311.

I have described as a peculiar form of the *dohrni* type (see p. 83). This *Acanthosoma* measures 5.7 mm. including the rostrum, which is 1.4 mm. long, and it is in the second stage.

The rostrum reaches just beyond the peduncles of the first antennae, and has a rather long basal spine. The supra-ocular spines are about two-thirds of the length of the eye-stalks. The sub-ocular spines are long, and there are also hepatic, lateral, and posterior median spines of good size.

The abdominal somites have long dorsal spines and a pair of ventro-lateral spines of which those of the first somite are the longest, while they are reduced to small points on the fifth somite. These lateral spines on somites 1 to 4 are armed with long teeth.

The telson is short, bifurcate, without spines.

* A specimen from station 311 is figured which differs slightly from the description.

The eyes are on long stalks reaching beyond the second segment of the first antenna and are large, oval, with pale pigment. The peduncle of the first antenna is of two joints only, but the position of the line of division between the first and second joints is marked by sensory setae. The first joint slightly exceeds the length of the second, and the second that of the third, all being equally slender.

The third maxillipedes are very large, reaching nearly to the end of the eye-stalks.

The first three pairs of legs show no signs of chelae.

The pleopods are present, all of them except the fifth being uniramous. The fifth bears a minute endopodite.

The exopodite of the uropod is very long and slender, the smooth basal part of the outer margin scarcely more than half the length of the distal setiferous part.

To this *Acanthosoma* undoubtedly belongs a *Mastigopus* in the same collection which measures 5 mm. in total length.

In this *Mastigopus*, which is evidently in the first stage after the *Acanthosoma*, the rostrum is still long and denticulate, but is not so long as the eye-stalks. It has a very small basal dorsal spine. The supra-ocular and hepatic spines are present, but very small, while the two pairs of lateral spines of the *Acanthosoma* are still represented by small points. There is a small posterior median spine.

The dorsal spines of the abdominal somites are present but reduced in size, those of the third and fourth being the longest. The lateral spines are lost except for a very small spine on the fifth somite. The telson is short, with two small terminal points.

The eye-stalks are very long, reaching nearly to the end of the second segment of the first antenna. The joints of the peduncle in the first antenna are of about the same proportional length as in the *Acanthosoma*.

The third maxillipedes are of enormous length, reaching beyond the end of the first antenna, but the last joint is not divided. The arrangement of the setae indicates a later division into three joints.

Legs 4 and 5 are represented by minute buds.

The pleopods are, as in the *Acanthosoma*, all uniramous except the fifth which has a minute endopodite, but all bear setae and are functional.

The exopodite of the uropod has the smooth basal part about half the length of the setiferous part.

An older *Mastigopus* of the same species of 8 mm. length has a little black pigment in the eye, but does not differ materially from that just described. The endopodite has appeared as a bud on the third and fourth pleopods. The ventral marginal spines of the carapace are retained.

It would be possible to multiply descriptions of *Acanthosoma* and early *Mastigopus* stages, of which there is great variety in the collection, but there is little

advantage in doing so unless these stages can be referred to the adult species. This I have, as a rule, found to be impossible from the material at my disposal, largely owing to the fact that the Mastigopus stages are, almost without exception, seriously damaged. In almost every individual the third maxillipede, which is of such great systematic importance, is broken off, and generally all the legs also are missing. A few species however have, with the aid of Hansen's admirable monograph, been identified, either as Acanthosomas or Mastigopus.

Sergestes crassus, Hansen.

A specimen of a Mastigopus 4.35 mm. long was taken at station 50, which certainly belongs to *Sergestes crassus* according to Hansen's description, though it

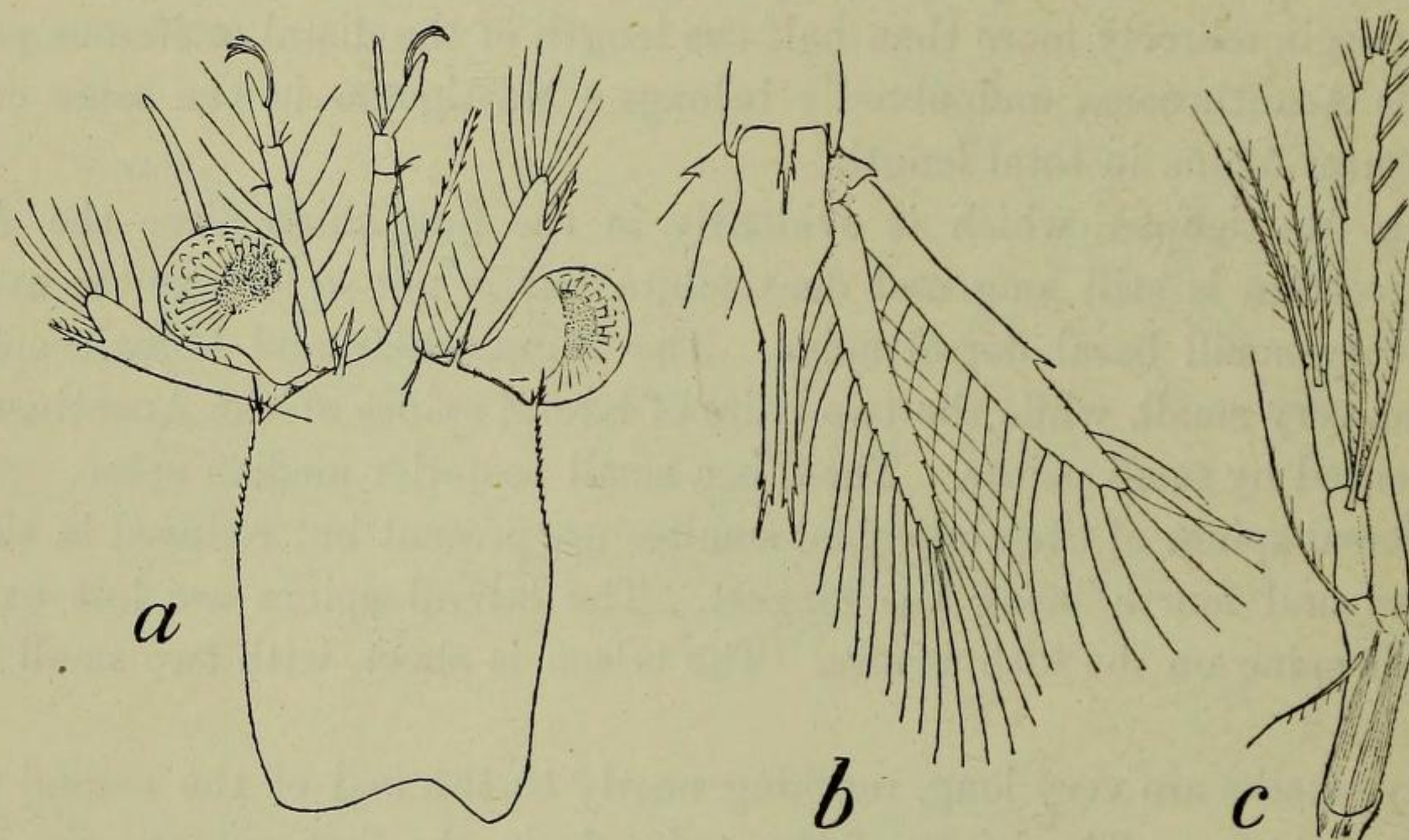


FIG. 32.—*Sergestes crassus*. Acanthosoma, stage II. a. Carapace. b. Telson. c. Leg 5.

represents rather an earlier stage than that figured by him (Pl. VI, fig. 1). In the same sample was an Acanthosoma which, from the structure of the telson and shape of the eyes, I consider to belong to the same species. Unfortunately, the abdomen of the specimen was so damaged that I can only figure the thorax and telson (fig. 32).

The width of the thorax is about two-thirds of the length, the rostrum, which is closely denticulate, being about as long as the antennular peduncle. At its base is a rather long median spine, but the supra-ocular spines are very short.

The ventral edge of the carapace bears anteriorly a series of about ten teeth, and is prolonged at its anterior angle into a short sub-ocular spine. There are no lateral, hepatic, or posterior median spines.

Each of the abdominal somites bears a dorsal and a pair of ventro-lateral spines.

The telson is long and narrow, and deeply cleft into two parallel branches (fig. 32, b).

The eyes are shortly stalked and nearly round, the pigment rather dark.

In the exopodite of the uropod the smooth basal part is about one and a half times as long as the setiferous part, and is separated therefrom by a large tooth.

Sergestes vigilax, Stimpson.

Stations 12 and 65.

S. pectinatus, Sund.

Station 50. Mastigopus.

S. cornutus, Krøyer.

Station 65. An adult male in fragmentary condition, but recognizable from the structure of the petasma.

2. *Petalidium foliaceum*, Bate?

The reasons which have led me to regard the larvae described below as belonging to *Petalidium* will be given later.

A similar type of larva has already been met with more than once, but, as only the first stage was seen, no reference to its systematic position was possible. The first description is that of J. V. Thompson (1828), who figured (Pl. I, fig. 4, *a* and *b*) a peculiar larva taken in $17^{\circ} 30' S.$, $1^{\circ} 30' W.$, which was "discovered by its luminous scintillations in the dark." In 1871 Dohrn described and figured (Pl. XXX, fig. 53) a Zoea of unknown origin and affinity from the Indian Ocean which evidently belongs to the same genus, and a similar larva was again figured by Claus (1876, Taf. IV, fig. 2) as a "Phyllopod-like" Protozoa of unknown origin. Finally, the same form was met with by Lister (1899), who doubtfully referred it to a stage in the development of a Stomatopod. Lister's description of his larva as a Metanauplius was not founded on a detailed examination, since the single specimen had been lost at the time his note was written and he was only able to say, from his notes made thirteen years before, that "rudimentary" appendages to the number of "perhaps three" were situated behind the antennae. The appendages are not easy to make out, and I have no doubt that some were overlooked, and that the larva was not in a Metanauplius stage. It is still more certain that it had no relationship to the Stomatopoda. Lister's figure has been reproduced by MacBride in his *Text-book of Embryology* (1914, p. 217), and its designation as a Metanauplius belonging to the Stomatopoda is accepted. It is for this reason important that it should be made clear, not only that the evidence was originally insufficient, but also that the rediscovery of the same larva definitely proves Lister's conclusions to have been wrong.

Brooks (1882) suggested that Claus's and Dohrn's larvae might represent early stages in the life history of *Acetes*, a guess which was remarkably near the truth.

In the plankton sample taken by the "Terra Nova" at station 251 a large number of larvae were taken in several stages, and a single specimen was also taken at station 129. I am able therefore to give a description of the whole course of development up to an early Mastigopus stage.

Stage I. Length (from end of rostrum round curve of body), 2.7 mm. (fig. 33, *a* and *b*).

The smallest larva found has a very peculiar appearance, the body being usually curled round so that the abdomen is completely covered by the dorsal shield. The latter is very large, with a large rostrum bent downwards at right angles in front of

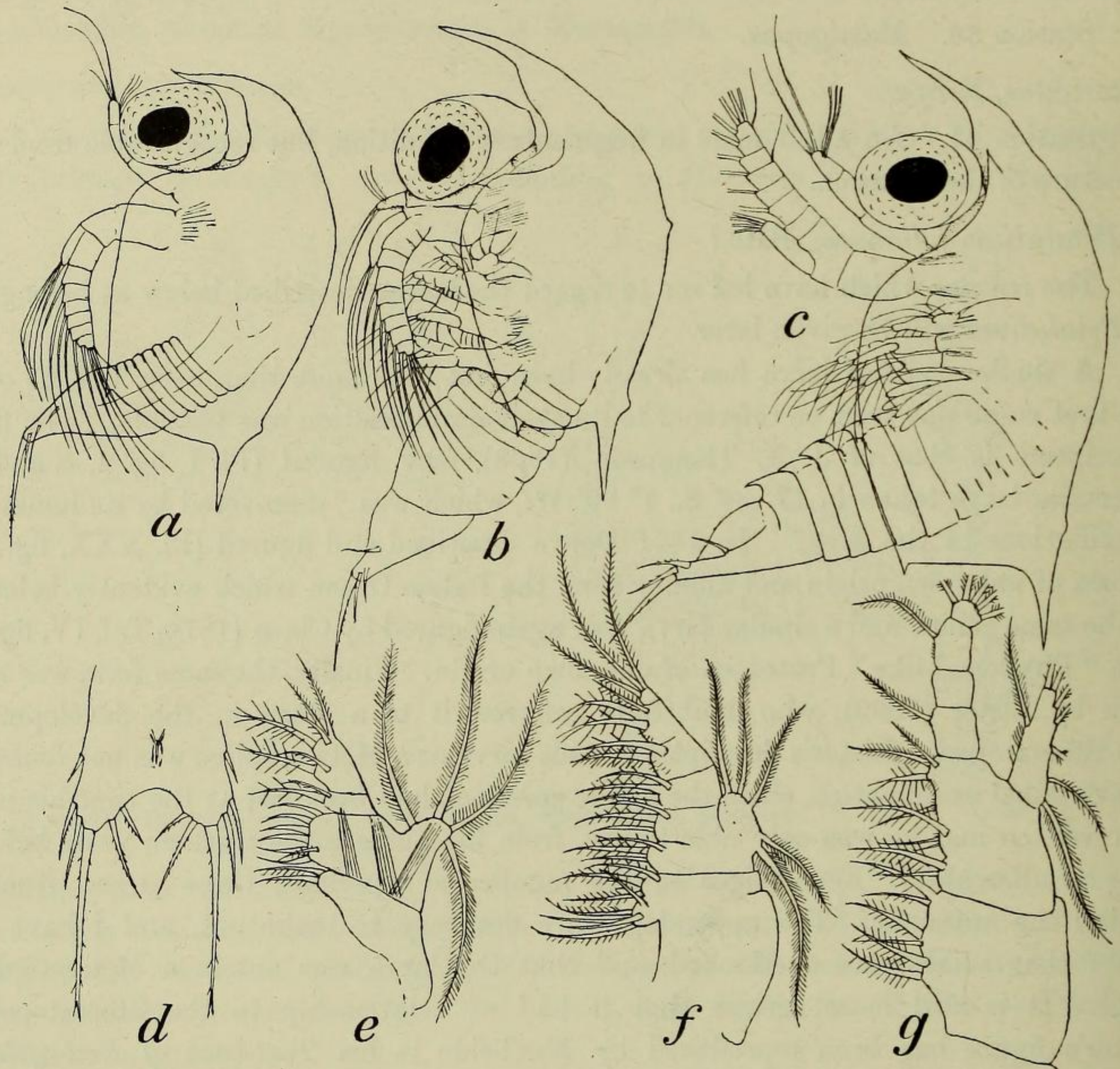


FIG. 33.—*Petalidium*. *a* and *b*. Stage I. *c*. Stage II. *d*. Stage I. Telson. *e*. Stage III. First maxilla. *f*. Stage III. Second maxilla. *g*. Stage III. First maxillipede.

the eye, and produced backwards into a stout posterior spine. The ventral edge is nearly straight, ending behind in a small spine.

The abdomen is short and unsegmented, terminating in a slightly forked telson. The telson bears one large spinous seta and five shorter setae, three on the outer and two on the inner side of it.

The thoracic region shows rings corresponding to the five somites of the pereion and the third maxillipede.

The eyes are very large and stalked.

The appendages have the same form throughout larval life and will be described in detail under stage III. At this first stage the first two pairs of maxillipedes are fully developed, and the third is present as a small simple rod.

Stage II. Length, 3.5 mm. (fig. 33, *c*).

The general form is the same, but a short, stout supra-orbital spine has appeared.

The thorax and abdomen are now fully segmented, and short rudiments of all the pereopods are present, the third pair being the largest.

The abdominal somites have epimera which are produced each into a backwardly turned point. The pleopods are not visible. The telson is of the same form as before and has the same number of spines, but the uropods have now appeared as large functionless appendages, without setae, and almost hidden beneath the telson.

Stage III. Length, 4.4 to 4.56 mm.

The form of the carapace remains the same, but the abdomen is greatly elongated and entirely uncovered by it. Even the last somite of the pereion is uncovered.

On the abdomen the first signs of the pleopods appear as simple ridges. The telson is unchanged, and the uropods are still functionless and without setae.

The first antenna has a three-jointed stem and a small terminal joint which bears two distal setae and four aesthetes in two pairs.

The second antenna is a powerful swimming limb, the exopodite being divided into eight joints of which the six terminal joints each bear a long seta. The endopodite is one-jointed and bears four terminal setae.

The mandible is not cleft, but the chewing edge is distinguished into a toothed anterior part and a small posterior molar part. There is no palp.

The first maxilla (fig. 33, *e*) consists of the usual spine-bearing coxopodite and basipodite, the latter bearing a distinct exopodite with four long ciliated setae. The endopodite is two-jointed and armed with stout spines.

In the second maxilla (fig. 33, *f*) the coxopodite and basipodite are distinct, and each has two inner lobes armed with spines. The exopodite is small and bears five long setae. The endopodite is stout and four-jointed.

First maxillipede (fig. 33, *g*). The two basal joints bear a number of stout spine-like setae. The exopodite is shorter than the endopodite and has eight long swimming setae. The endopodite is four-jointed and well developed.

The second maxillipede has no setae on the basal joint and only three slender setae on the basipodite. The exopodite bears only five setae, and the endopodite is obscurely three-jointed.

The third maxillipede is a biramous rudiment without setae. All the pereopods are present as biramous rods without setae. There are a number of specimens of this stage, and they differ a good deal among themselves in size and degree of development of the pereopods. Possibly there is more than one moult.

Stage IV. Length, 6.8 mm. (fig. 34).

With the moult from stage III the whole appearance of the animal is entirely changed, but that stage III does give rise directly to stage IV is conclusively proved by the examination of two specimens which were found actually in the moult from the one stage to the other. In one of these, measuring 5.8 mm., the carapace, antennae, mouth-parts, and telson were as in stage III, but the cuticle had been stripped off some of the pereopods and the anterior part of the abdomen, revealing setiferous exopodites on the former and long pleopods on the latter.

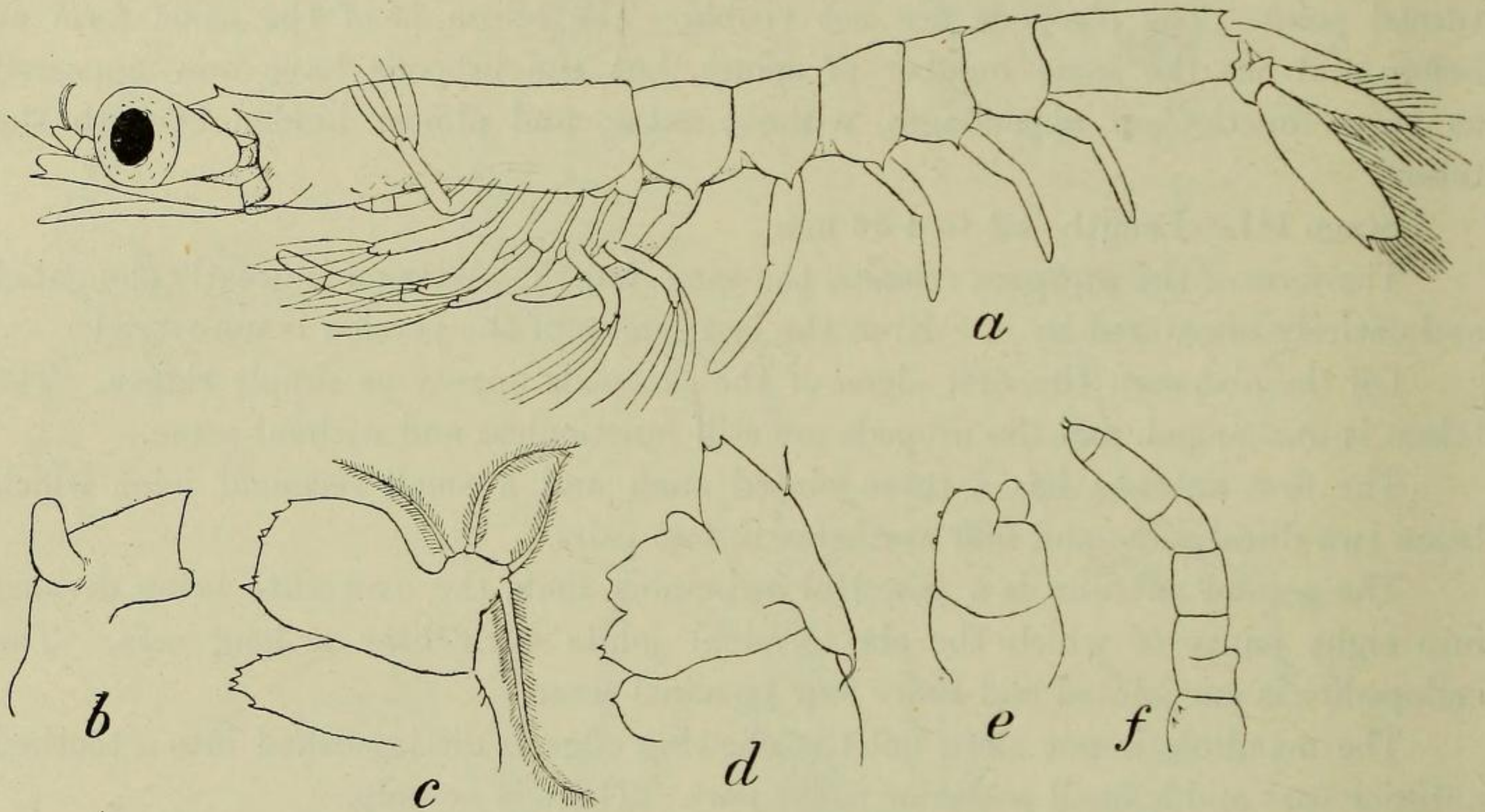


FIG. 34.—*Petalidium*. Stage IV. *b*. Mandible. *c*. First maxilla. *d*. Second maxilla. *e*. First maxillipede. *f*. Second maxillipede.

In stage IV the larva has taken on the general appearance of a Sergestid Mastigopus, with long slender thorax and abdomen.

The rostrum is short with a large basal tooth; the supra-ocular spine is retained, but two new spines have appeared, namely, an hepatic, and a sub-ocular at the anterior angle of the carapace.

The epimera of the abdominal somites are pointed, and somites 4, 5, and 6 have very short dorsal median spines. The telson is considerably shorter than the uropods, and bifurcate. It has somewhat the form of a *Sergestes* telson, with sinuate outer edge and a small lateral spine about half-way along its edge.

The first antennae have a stout three-jointed stem, but the line of division of the first and second joint is not clear and may only be marked by a row of sensory setae. The inner branch is represented by a minute bud.

The second antenna has completely changed its appearance, the scale now having

the ordinary "Caridean" form, somewhat widening distally and with a strong terminal spine. The inner branch is a simple rod, shorter than the scale.

The mandibles (fig. 34, *b*) have a smooth cutting edge and have developed a rudiment of the palp.

The remaining mouth-parts have suffered a very remarkable degradation and appear to be quite functionless.

The first maxilla (fig. 34, *c*) consists as before of two large lobes with an exopodite bearing four long setae, but the lobes have neither setae nor spines, and the endopodite has disappeared.

The second maxilla (fig. 34, *d*) likewise has lost all setae and spines from its inner lobes, and the endopodite is reduced to a minute papilla. The basal joint of the appendage bears a single inner lacinia, and the basipodite bears two inconspicuous lobes. The exopodite is large, but has lost its setae. In the appendage drawn two very short setae remain.

The first maxillipede (fig. 34, *e*) is reduced to its two basal joints which lack all setae. The exopodite is entirely gone, but the endopodite is still represented by a small papilla.

The second maxillipede (fig. 34, *f*) has also lost setae and the exopodite, but the endopodite consists of a five-jointed appendage without setae.

The third maxillipede is functional and bears a large exopodite with five terminal setae and a five-jointed endopodite with a terminal spine.

Each of the five pairs of pereopods has an exopodite with five setae, the endopodites of the first two pairs resembling the third maxillipede but being four-jointed. The endopodite, however, of the third leg is of enormous size, reaching forwards beyond the mouth and consisting of four joints. The terminal joint is long and bluntly pointed, without claw or setae. The endopodites of the fourth and fifth legs are small papillae, each with a single seta.

I have seen no trace of gills.

The pleopods are all present and are large, decreasing in size from before backwards. They bear no setae and the endopodite is absent. The uropods are large and setiferous, the exopodite broad and with an outer terminal spine.

This stage seems to correspond to the *Acanthosoma* stage of *Sergestes*, but the complete reduction of the mouth-parts is a character which is quite exceptional.

Stage V. Length, 7.8 mm. (figs. 35 and 36).

The general form is unchanged, but the mouth-parts have more or less recovered their function.

The eyes are longer and more slender. The two pairs of antennae differ little from the preceding stage except that the inner branch of each is a little longer.

The mandible (fig. 36, *a*) has a large one-jointed palp with five setae.

The first maxilla (fig. 36, *d*) has lost the exopodite which is now represented only by a small knob, but the two inner lobes bear setae and spines and are evidently functional.

The second maxilla (fig. 36, *c*) is not altogether easy to interpret. It appears that the two lobes which are retained belong to the basipodite and that the lobes of the coxopodite are lost altogether. The endopodite is reduced to a small knob. The exopodite is large and bears six setae.

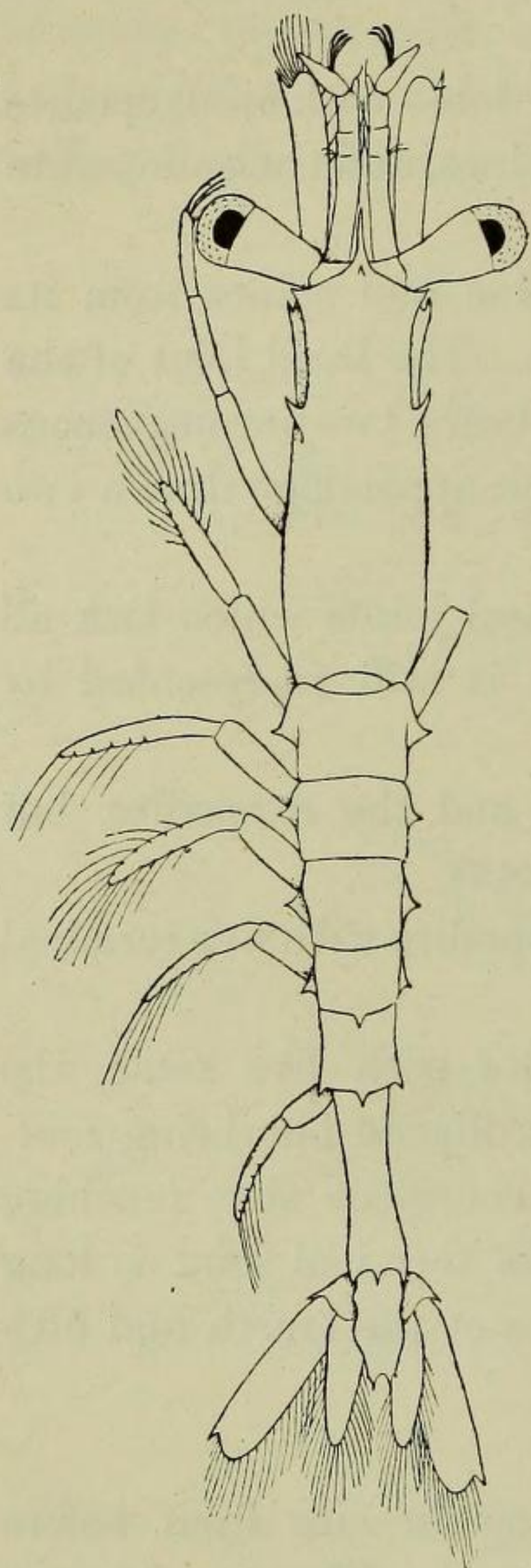


FIG. 35.

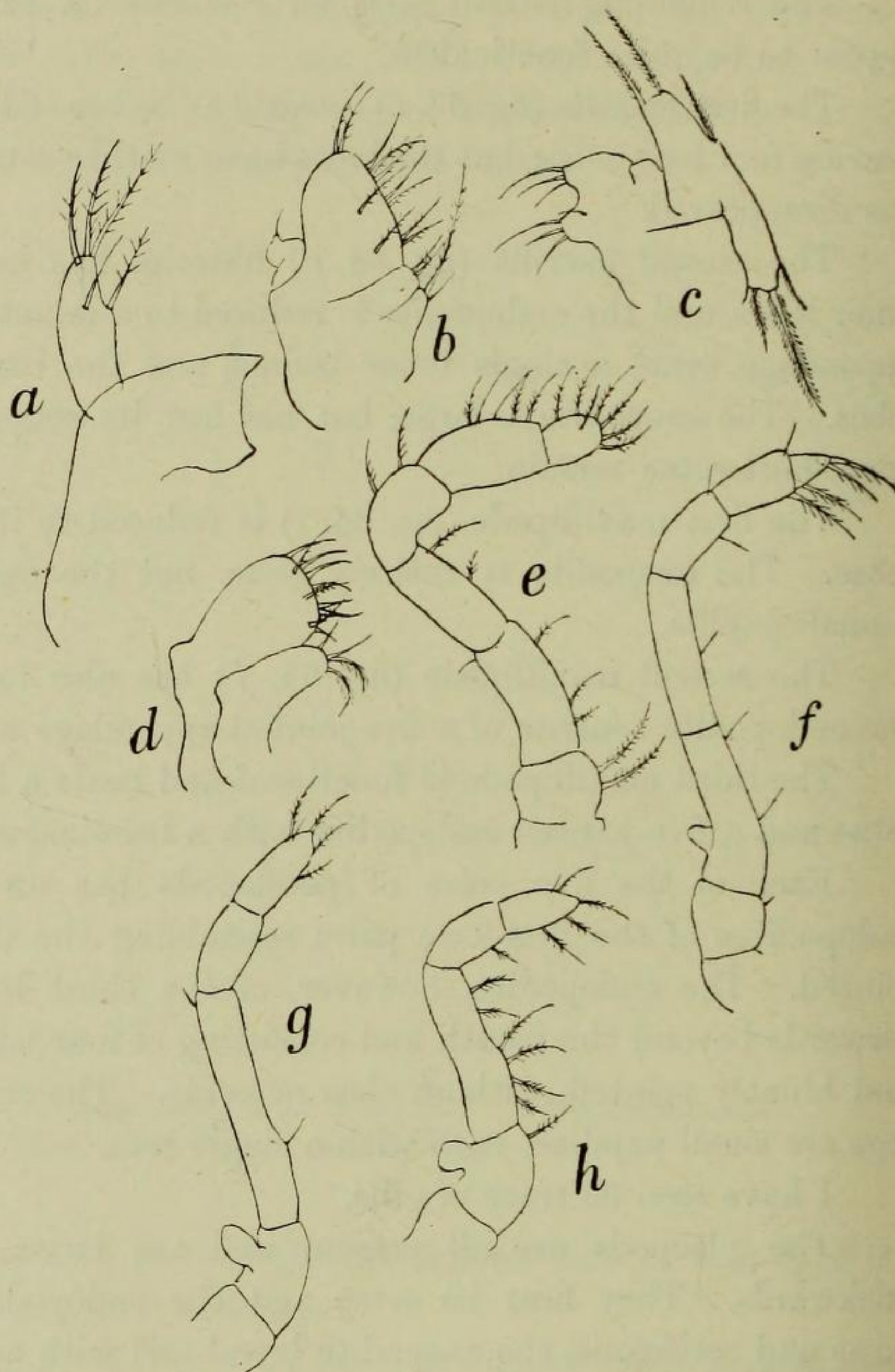


FIG. 36.

FIG. 35.—*Petalidium*. Stage V.

FIG. 36.—*Petalidium*. Stage V. *a*. Mandible. *b*. First maxillipede. *c*. Second maxilla. *d*. First maxilla. *e*. Second maxillipede. *f*. Third maxillipede. *g*. Second leg. *h*. First leg.

The first maxillipede (fig. 36, *b*) has redeveloped setae on its inner lobes, but the exopodite has disappeared and the endopodite is reduced to a peculiarly bent papilla.

The second maxillipede (fig. 36, *e*) likewise has no trace of an exopodite, but the endopodite is a large five-jointed appendage fully provided with setae.

The third maxillipede (fig. 36, *f*) has a trace of the exopodite, and the endopodite is very long and five-jointed.

The pereopods have all lost their exopodites except for a small papilla on the basipodite. The endopodites are four- or three-jointed, the first and second joints not being clearly separated (fig. 36, *g, h*). The third leg is an enormous appendage reaching forward nearly as far as the end of the eye. It is of six joints, and the terminal joint bears several stiff curved setae. The fourth and fifth legs have disappeared.

The pleopods are still uniramous, but are clothed with setae.

The gills are scarcely developed, but there appears to be a single gill in the position of a pleurobranch on the somites of the third maxillipede and first three legs.

This stage evidently corresponds to the early Mastigopus of *Sergestes*, and the extraordinary hypertrophy of the third leg recalls the large third maxillipede of Hansen's group II.

Not only in general form of body, but also to some extent in the course of its development, the larva described above differs greatly from any hitherto known. It is unfortunate that the series of stages, complete and consecutive as they are through a number of moults, should stop short before the appearance of distinctive generic and specific characters. That it is the larva of a Sergestid is certain, but it cannot be referred without some doubt to any known genus.

Stages I to III correspond in the number of appendages to the Elaphocaris of *Sergestes*, and the agreement in structure is almost exact, with the exception that the appendages are less slender. Stage IV cannot, however, be exactly compared with any stage in the development of *Sergestes*. In the development of all the pereopods with natatory exopodites it agrees with the Acanthosoma stage, but in other respects it may more properly be compared with the Mastigopus. The Acanthosoma stage has, in fact, been dropped out of the series, and has been replaced by a larva of unique character intermediate between the Acanthosoma and the Mastigopus. The second maxilla and the first maxillipede are reduced in a remarkable way, but still their structure is recognizably similar to the shape of the corresponding appendages in the Mastigopus, having lost entirely the primitive protozoal form and approximating to that of the adult.

Stage V, on the other hand, reveals itself as distinctly a Mastigopus of *Sergestes* or an allied genus. Not only is the general facies the same, but the appendages, which have now recovered their setae, are obviously those of a Sergestid, though details might be pointed out in which they differ from those of any known *Sergestes*. How far such differences are likely to be carried on to the adult and whether they are to be regarded as generic or not it is impossible to say. We know the Mastigopus stages of many species of *Sergestes* and the earlier stages of some, and these are so uniform in general character that it is unlikely that any species of *Sergestes* could depart so much from the normal type as the larvae above described. There remain the genera *Sicyonella*, *Petalidium*, and *Acetes* as possibilities.

Of the development of *Sicyonella* we know nothing, but Brooks (1882, p. 101) * has described stages in the development of *Acetes* and Hansen the Mastigopus of *Petalidium*.

The larva of *Acetes*, as figured by Brooks, has a certain resemblance to that of *Lucifer* and agrees with the "Terra Nova" form in having a carapace with median, dorsal, and posterior lateral spines. On the other hand, it differs in its greater slenderness, absence of the pronounced ventral flexure of the body, and in various details of the appendages and telsons. But the later course of the development as described by Brooks makes it perfectly clear that the larva in question does not belong to *Acetes*, since the stage corresponding to the Acanthosoma in *Acetes* differs in almost every respect from stage II of my series. It is not necessary to enter into details, but I may refer to Brooks's Pl. II, fig. 84. Brooks himself claimed Dohrn's and Claus's larvae as Sergestids and suggested that they might represent earlier stages of *Acetes*, but there can be no doubt at all that they belong to some other genus of the family.

The description of the early Mastigopus of *Petalidium obesum* by Hansen (1922, p. 195) is taken from an older stage than my own latest larva, as shown by the condition of the first antennae, but it is smaller (5.5 mm.). Hansen does not figure either the whole animal or the mouth-parts, but his description tallies so nearly with the "Terra Nova" species that I am convinced that the latter can with reasonable probability be referred to the genus *Petalidium*. Whether it may belong to *P. foliaceum* or to an undescribed species it is of course impossible to say, but I have attributed it provisionally to the former.

The characters upon which the generic determination may be made are as follows:

1. Antenna. Stem short and stout as compared with *Sergestes*, the basal joint longer than the two distal joints combined.
2. Antennal scale rather broad, parallel-sided, with large terminal spine.
3. Eyes short, pear-shaped.
4. Supra-orbital, sub-orbital, and hepatic spines well developed.
5. Third maxillipede little longer than second.
6. The first leg shorter than the third maxillipede, but the third leg enormously prolonged, six-jointed, the two terminal joints long and slender. The last joint without chela, and bearing a tuft of stout spines.
7. Exopodite of the uropods broad, setiferous only along inner and terminal margins. Outer margin terminating in a spine.

3. *Lucifer*.

Early larvae of *Lucifer* are very rare in the "Terra Nova" collections, but occur singly at stations both in the Atlantic and Pacific. The material is not sufficient to

* Brooks does not claim his larva definitely as that of *Acetes*, but the probability of his identification being correct is very great, and it may be accepted.

permit of any comparison being made between the larvae of different species or to add anything to our knowledge of the development of the genus of which such an excellent account has been given by Brooks (1882).

CARIDEA.

Throughout the large group of the Caridea the larvae are not only extraordinarily alike in general structure, but pass through an almost precisely similar series of stages, and it is exceedingly difficult to find characters by which those of the different families may be distinguished. It is true that many of the larvae possess striking and distinctive features, but these as a rule are due to characters of minor importance, and are generic or specific and seldom available for the characterization of larger groups. In some cases, as for example among the Crangonidae,* the larvae of different species are even more unlike than the adults, while in other cases, as in the genus *Leander*, it is almost impossible to distinguish species, whereas the generic characters are well defined. The relationship of the families of the Caridea to one another is most obscure, and at the present moment but little light can be shed upon the subject by their ontogeny.

In all the Caridea with a complete larval series of which the whole course of development is known, the first three stages are so precisely alike in respect of certain characters that it is difficult to avoid feeling that there must be some phylogenetic significance in the fact. Invariably the first larva has sessile eyes and no spines on the carapace, whereas the second larva has the eyes stalked, and spines, when present at all, make their appearance. The uropods always appear first in the third stage, and at this stage always have the endopodite more or less undeveloped. I do not know of any exception to this rule, except in the case of those species, such as certain Palaemonidae and Crangonidae, in which an excess of yolk leads to an abbreviation of larval life. When development is so abbreviated the larva hatches with all the appendages present, the only exception being the uropods, which in such cases are always delayed. A retardation in the appearance of the uropods seems to be in some way correlated with abbreviated metamorphosis, and is not peculiar to the Caridea (cf. *Axius stirhynchus*, *Calocaris macandreae*, *Homarus*, *Nephrops norvegicus*), but it may perhaps be regarded not so much as an abnormality as rather a reversion to the primitive order of the appearance of appendages, since these appendages do not appear till after the pleopods in some cases where development is not abbreviated in this way—*Porcellana*, *Brachyura*.

The larvae of the Caridea, while readily recognizable as such, are not easily defined when compared on the one hand with the Mysis stage of the Penaeidea, and on the other with those of the Thalassinidea. The possession of only six pairs of setae

* It is necessary to note that *Crangon* and Crangonidae are here used in their older and more usual sense. Miss Rathbun's transference of these names to the Alpheidae should be ignored.

on the telson of the larval cuticle has been already mentioned as an important distinction. The chief characteristic of all is that they invariably possess three pairs of biramous maxillipedes on hatching (except when larval life is abbreviated). The pereopods appear and become functional in succession and not simultaneously; two or more pereopods bear exopodites; the rostrum is never horizontally flattened; the second maxilla has usually only three inner lobes; the antennal scale is usually jointed; the third abdominal somite is usually larger than the rest; the abdominal somites usually lack dorsal spines.

Of the sixteen families of Caridea nothing at all is known of the development of seven, while of the remainder our knowledge is, for the most part, scanty, generally only one genus or even species being known in each. It is true that in most cases the larval characters of a family may be satisfactorily illustrated by any given species within it, but this is not always so.

For example, the development of *Hippolyte varians* is certainly not typical for the great family of Hippolytidae, differing as it does greatly from that of *Spirontocaris*, and even more from *Lysmata seticaudata*.

Many Caridean larvae have been described by Bate, Ortmann, and others under generic and specific names, and, as the descriptions are often incomplete, it is generally impossible to assign them with any certainty to their appropriate families. Coutière (1907) has attempted to group some of them under families, and with his determinations I am in general agreement.

The "Terra Nova" collections naturally contain a number of Caridean larvae, but a large proportion of them are in early stages which are indeterminable and may be ignored. Some which would otherwise be of interest are so damaged as to be useless, but there remain a few which seem worthy of notice.

I. Amphionidae.

Amphion.

The systematic position of *Amphion* is still a matter of complete uncertainty. The most recent discussion of the question is that of Koepfel (1902), who gives a summary of the literature, and concludes that *Amphion* attains maturity without further transformation and should be placed among the Sergestidae. For neither of these conclusions is the evidence given at all satisfactory, and it does not seem that Koepfel's work advances our knowledge materially. His statement that he found traces of "brood lamellae" on the appendages is not confirmed by his figures, and is not consistent with the inclusion of the genus in the Decapoda. There can be no doubt that none of the specimens of *Amphion* so far described can be regarded as adult, but whether any great transformation occurs or is to be expected is a matter for speculation.

The general similarity to a Phyllosoma is very obvious, and Boas's view that *Amphion* represents the larva of *Polycheles* is not to be dismissed lightly. Sund

(1915) has claimed *Eryonicus* as the larva of *Polycheles*, but this is not accepted by Selbie (1914) or Bouvier (1917). Bouvier's argument against Sund's view is convincing, and there still remains therefore the possibility that *Polycheles* has a free larva which might resemble *Amphion*. On the other hand, Selbie has described (1914, p. 40) an immature stage of *Eryonicus* which is of great importance in this connexion. This specimen has practically the adult form, but has a long rostrum, much reduced antennae, and two pairs of pereopods only, both of which have exopodites, but are otherwise fully developed. Now, having regard to the near relationship of *Eryonicus* and *Polycheles*, it is to be expected that both would have at least approximately the same course of larval development; but, if that is so, a form like *Amphion* can have no place in it. *Amphion* differs totally from this early stage of *Eryonicus* in almost every respect, and particularly in having, in its oldest stage, all the pereopods present and yet none of them fully differentiated. Although I admit that the assumption that *Eryonicus* and *Polycheles* should have much the same larval development is no very secure foundation for an opinion, it seems to be justifiable, and its acceptance involves the conclusion that *Amphion* is not the larva of *Polycheles* or of any other known Reptantia.*

It cannot be included within the Penaeidea. The youngest known *Amphion* has three pairs of maxillipedes only and no trace of pereopods, while at the same time the appendages have none of the characters of those of the Penaeidea at an equivalent stage.

The only remaining group to which *Amphion* may belong is the Caridea, and it seems to me that it is with some confidence to be there placed. This position has already been assigned to it by Korschelt and Heider (1892, vol. ii, p. 46), chiefly on the ground of its possession of phyllobranchs in the oldest observed stage. The only serious difficulty in the way of such a conclusion is the dendritic form of the liver diverticula which so closely resembles those of Phyllosoma, and the absence (according to Koepfel) of pleopods from the first abdominal somite. The latter may probably be dismissed, as Bate and Claus both show an appendage on this somite in late stages, though Bate mentions its absence in a specimen of 15 mm. Apart from these two characters, on neither of which much stress can be laid, there is nothing to exclude *Amphion* from the Caridea, and it has a considerable degree of similarity to the "Eretmocarid" larva, which probably belongs to the Latreutidae. The great length of the coxopodite of the maxillipedes and pereopods is, it is true, a feature not found in other Caridea, but it is probably a special adaptation. The structure of the mouth-parts fully resembles that of Caridea, and the presence of only three inner lobes on the second maxilla is, in this connexion, a character of much importance. (See Claus, 1876, Taf. VIII, figs. 9, 10.)

Whether *Amphion* is to be regarded as a larval form of any known Caridean is another matter. Koepfel states that the rudiment of the fifth pereopod is biramous,

* *Willemoesia* has an abbreviated development according to Doflein (1904).

and, if this is really so, it could only belong to the Hoplophoridae or Pasiphaeidae, to neither of which does it otherwise bear any resemblance. The oldest known stage is so near maturity that the most reasonable conclusion is that the genus *Amphion* includes larval and adolescent stages of a Caridean, the adult of which is at present unknown and which is probably not referable to any existing family.

Three specimens of this peculiar form were taken by the "Terra Nova" at stations 62, 65, and 66 (Atlantic), in each case at the surface and between 1.30 and 2.30 a.m.

They are all young individuals about 5 mm. in length, and represent stages intermediate between the two figured by Bate (1888, Pl. CXLVI, figs. 1 and 4), having three pairs of maxillipedes only developed, but the uropods already present. In one of them the first pereopod is represented by a small bud. The telson still has the rounded form of the earlier stage.

In Bate's account of the genus no less than ten different stages may be separated, while the "Terra Nova" specimens represent an additional stage not taken by the "Challenger." These specimens, however, do not throw light on the systematic position of the genus, and any further description is unnecessary.

II. Hoplophoridae.

In *Acanthephyra* (*Systellaspis*) *debilis* (Coutière, 1906) and *Hymenodora glacialis* the eggs are of very large size and the development is abbreviated, but *A. purpurea* hatches as a normal Zoea and passes through a series of stages similar to those of other Caridea (Kemp, 1907). The larva described by Coutière (1907) under the name of *Hoplocaricyphus similis* has been ascribed to *A. multispina*, and this is perhaps correct since it is evidently an *Acanthephyra*, but is distinct from the larvae described by Kemp and ascribed by him to *A. purpurea*. Stephensen (1923) suggests that Kemp may have been dealing with *A. multispina*, but the distinctness of Coutière's larva is against this supposition.

Coutière has drawn attention to the fact that the larvae of Hoplophoridae develop the mandible palp at an early stage, and the presence of this palp in conjunction with the possession of exopodites on all the legs is a first-rate character for distinguishing these larvae. This palp, however, though appearing earlier than in any other Caridea, is not present in the first four stages of the larva, and can therefore only be used as a distinguishing character in late stages. The peculiar form of the abdomen is not distinctive, since it is shared with larvae belonging to other families (see *Caricyphus*, sp. Kemp, 1907, and below, p. 113).

Larvae which, in reliance on Kemp's and Coutière's work, I attribute to Hoplophoridae, were taken by the "Terra Nova" at the surface at several stations. As the larvae of this primitive family are of rather special interest some description of these should be given.

These larvae are all in rather early stages, as was to be expected, since it is known

that larvae exceeding 5 mm. are practically confined to deep water (Murray and Hjort, 1912, p. 623).

Acanthephyra, sp.

Stations 120 and 122.

Stage I. Length, 2.9 mm.

The rostrum extends to the end of the antennal scale and has no dorsal spine. Immediately behind it is a small knob representing the dorsal organ. The carapace has no pterygostomial spine and its posterior margin is not denticulate.

The abdomen is very long, without spines, and the third somite is large and somewhat protuberant. The telson is triangular, deeply hollowed, and bears fourteen spines.

Second antenna. The basipodite has a large inner spine. The exopodite has two outer setae and five distinct joints. The endopodite is slender, continued without suture into a long spiniform seta. A short slender seta springs from the point at which the suture between endopodite and spine should be present. Mandible without palp.

The first maxilla is of special interest as having on the basipodite a round plate bearing three long ciliated setae (fig. 37, c). This obviously corresponds to the exopodite of the Euphausiacea and Penaeidea.* The endopodite is large and two-jointed. The exopodite is not present in the earliest known stage of *A. purpurea* (Kemp, 1907).

Second maxilla. There are four distinct basal lobes, a suture running across between the first and second pair, but the endopodite was not, in the specimen examined, distinctly marked off by a joint. On the other hand, there is a distinct joint between the basal lobe of the endopodite and the second lobe, giving the appearance of the existence of five lobes on the protopodite and a two-jointed endopodite. Actually, the endopodite appears, from a comparison with later stages, to be three-jointed. The exopodite is a small plate with five setae. The whole limb is distinctly more pediform than is usual in Caridea.

There are three pairs of maxillipedes and no trace of pereopods. The maxillipedes have the endopodite four-jointed, and the exopodite of the first pair has four setae arranged asymmetrically, i. e. two apical and one sub-apical strong setae, and a short slender seta on the inner side at some distance from the end.

Stage II. Length, 3.55 mm. (fig. 37).

This stage differs but little from the first. There is a small dorsal knob at the posterior end of the carapace, and a large pterygostomial spine has appeared. The eyes are moveable, and a single pereopod rudiment is present. The telson has a formula of 8 + 8. The mouth-parts are unchanged, the first maxilla having still an exopodite.

* In *Paratya compressa* Ishikawa (1885) figures a pair of ciliated setae on a papilla on the first maxilla. This is also a vestigial exopodite.

A larva of 6 mm. from station 106 (fig. 38) represents a slightly further advance on that mentioned above, since it has an additional pair of leg rudiments, but it no doubt belongs to a different species although it is practically identical in other respects. In this larva and also in those from stations 120 and 122 the first three abdominal somites do not appear to be movable on one another, and I have been unable to see any distinct suture between them.

Stage III. Of this stage there are no specimens in collections from stations 120 and 122, but I believe that a specimen from station 109 (fig. 39) belongs to the same species. This specimen measures about 5.15 mm. The general form is very slender.

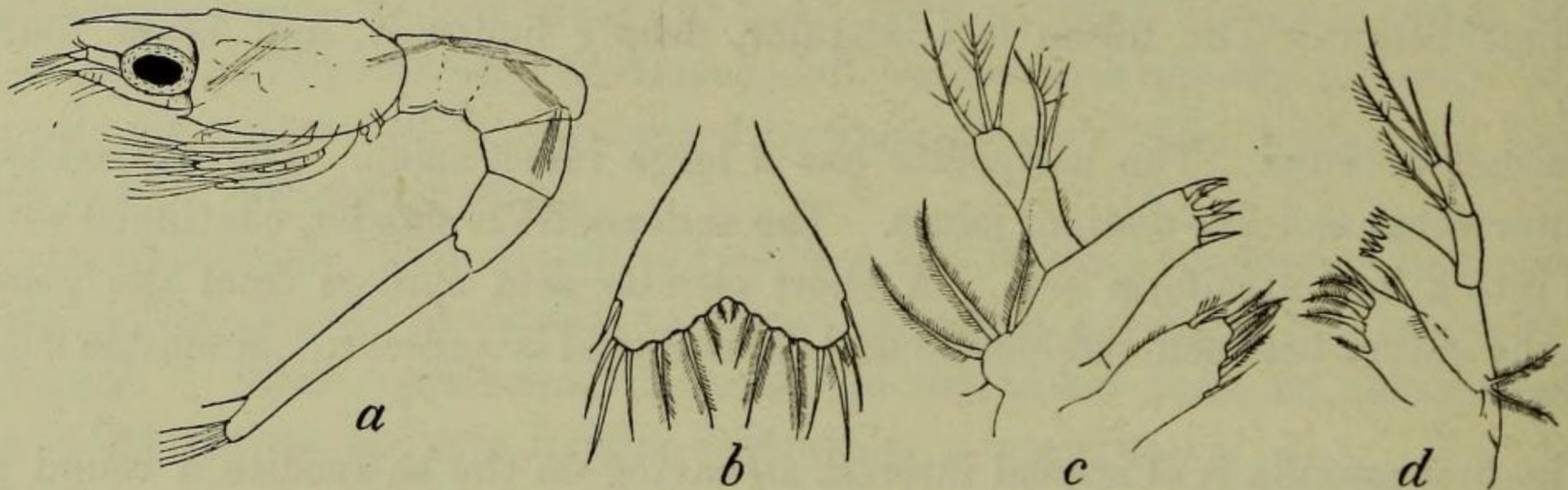


FIG. 37.—*Acantheephyra* (?), sp. Station 120. a. Stage II. b. Stage II. Telson. c. Stage I. First maxilla. d. Stage IV. First maxilla.

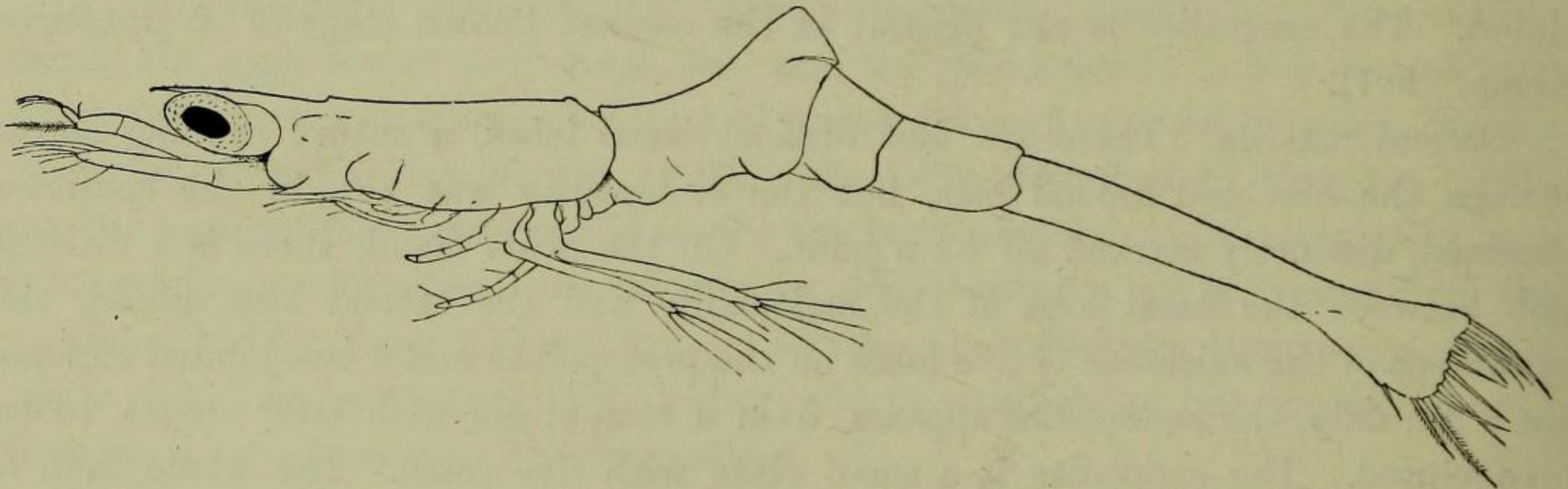


FIG. 38.—*Acantheephyra* (?), sp. Station 106. Stage II.

The third abdominal somite has grown out into a kind of hood over the fourth somite. The eyes are rather small, and are on very long stalks extending beyond the rostrum, which is relatively shorter than before. The first antenna has rudimentary exopodite and endopodite and a three-jointed stem. The antennal scale is still jointed, but the endopodite is reduced to a pointed rod. The maxillipedes have five-jointed endopodites, and there are two pairs of pereopod rudiments. There is no sign of pleopods, but the uropods have appeared, the exopodite with six setae, but the endopodite quite rudimentary. The telson is narrow but deeply cleft and bears 8 + 8 setae.

A specimen from station 65 of 3.1 mm. is evidently the larva of a Hoplophorid in stage III. It has two pairs of rudimentary pereopods, but no trace of pleopods; the uropods are present, shorter than the telson, and the endopodite has two setae.

I give a figure of the extremity of the first antenna of this specimen (fig. 40, *b*) since it shows very well the great development of the "antennular lobe." This

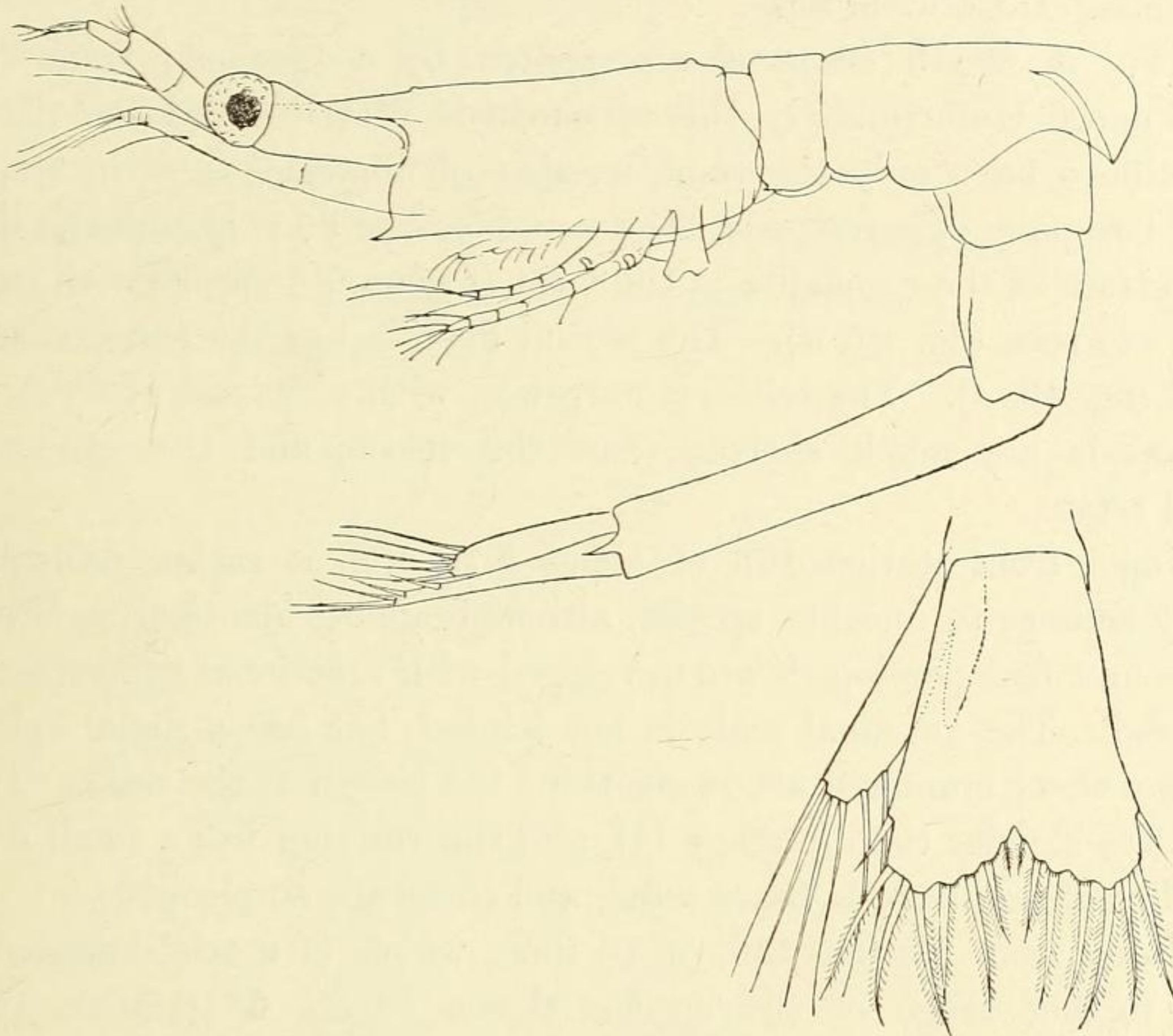


FIG. 39.—*AcanthePHYRA* (?), sp. Station 109. Stage III.

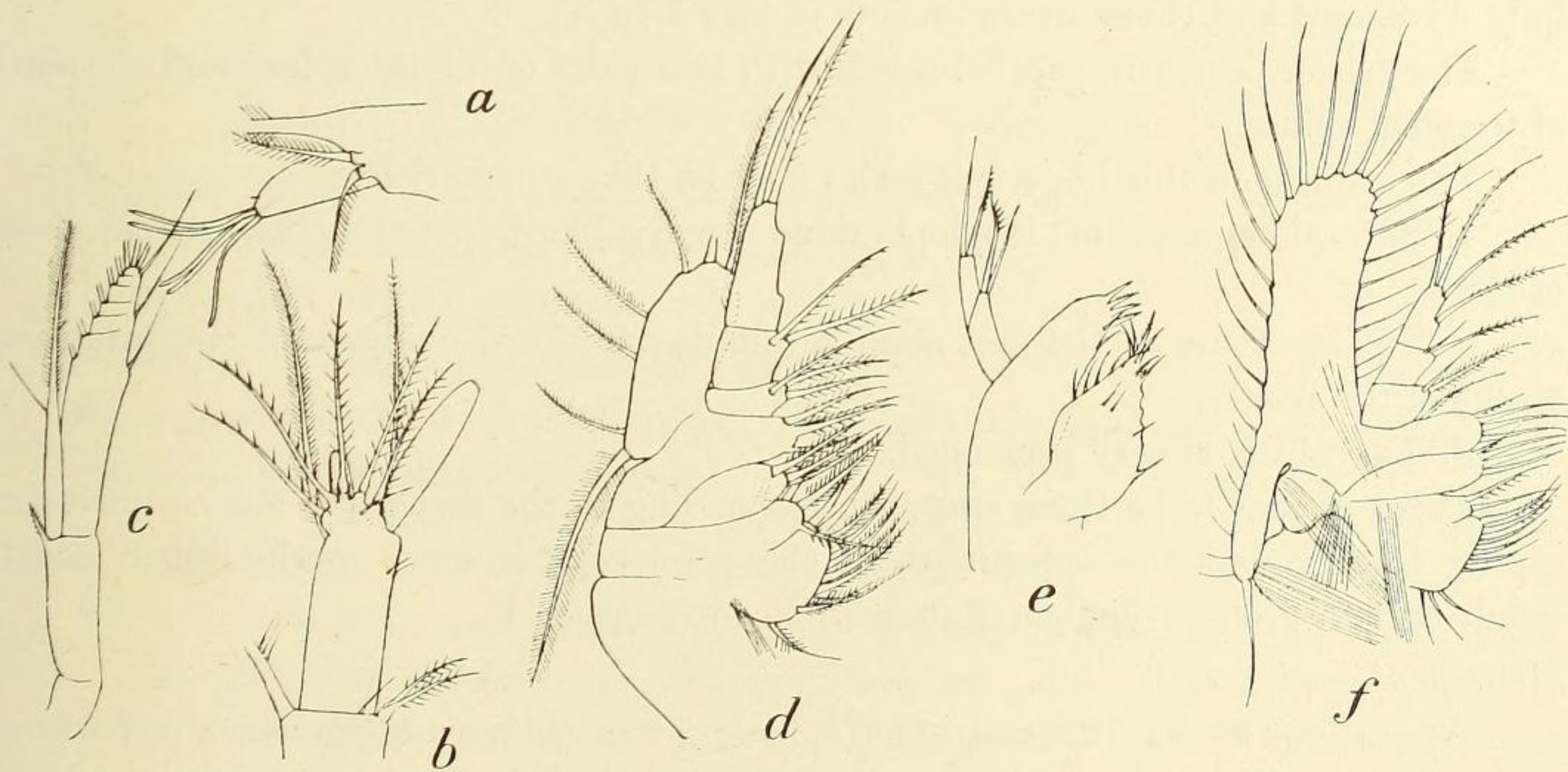


FIG. 40.—*AcanthePHYRA*. *a*. First antenna. Stage III. Station 106. *b*. First antenna. Stage III. Station 65. *c*. Second antenna. Stage III. Station 106. *d*. Second maxilla. Stage IV. Station 120. *e*. First maxilla. Station 129. *f*. Second maxilla. Station 129.

structure is particularly well developed in all the larvae examined, but in the earlier stage bears only two sensory setae (fig. 40, *a*) instead of five as shown here. This

lobe, which is traceable in almost all Caridea and in some other Decapods, is found also in Euphausiacea and Mysidacea and is evidently an inheritance from a primitive ancestral Caridoid form.

Stage IV. A fourth stage is represented by a specimen from station 120 of about 7.6 mm. Unfortunately this specimen is very decayed and damaged, but it appears still to have only the same number of appendages as in stage III, i. e. rudiments of two pairs of pereopods. The mandible has no palp, and the first maxilla still retains a trace of the exopodite in the form of a minute papilla with two long and one very minute seta (fig. 37, *d*). The second maxilla has the endopodite distinctly three-jointed (fig. 40, *d*). The telson is narrower, with a formula of 8 + 8.

The uropods are much shorter than the telson, and the endopodite bears two terminal setae.

A specimen from station 109 of about 5.75 mm. is rather difficult to place, and probably belongs to another species, although almost identical in form. In this specimen the first four pereopods are developed with functional exopodites, and leg 5 is a minute rod. The antennal scale is not jointed, but has a distal spine, and the endopodite is a short blunt rod about one-third the length of the scale. The eyes are shorter and less slender than in stage III, and the rostrum has a small dorsal spine. The endopodite of the uropods bears setae, and there are no pleopods.

A specimen from station 130, of 10 mm., which is much damaged, seems to represent a further stage of the species shown in fig. 38 (station 106). It is characterized by its very short eyes. There are no pleopods, but legs 1 and 2 are fully developed and there are rudiments of legs 3 to 5.

The telson is nearly parallel-sided, with two pairs of lateral spines and six pairs of terminal spines.

The interest of this imperfect series may be thus summarized :

1. Several species of Hoplophoridae have almost precisely the same form of larva.

2. The structure of the first maxilla affords additional evidence of the primitive status of the family.

3. Larval life is very prolonged.

There appear to be three stages corresponding to the first three stages universal among Caridea, but the appearance of the pereopods is more gradual than usual, resulting in a greater number of stages following stage III.

Acanthephyra (?), sp.

At stations 86, 92, 129, and 131 Hoplophorid larvae were taken which differ from the series described above in having the posterior ventral margin of the carapace and the epimera of the first abdominal segment denticulate. According to Kemp the older stages of *A. purpurea* have the carapace denticulate, while in younger stages it is smooth, and it is therefore possible that these specimens really belong to the same series as those above described.

Specimen 1. Station 131. Length, about 8 mm. (fig. 41).

Eyes very long and slender. No mandible palp.

Legs 1 to 4 developed, leg 5 rudimentary.

Pleopods small. Uropods fully setose.

Telson narrow, parallel-sided, formula 8 + 8.

Specimen 2. Station 129. Length, 15.5 mm.

Eyes long, slender. All legs developed, with exopodites.

Endopodite of second antenna about half length of scale.

Rostrum short, with dorsal spine.

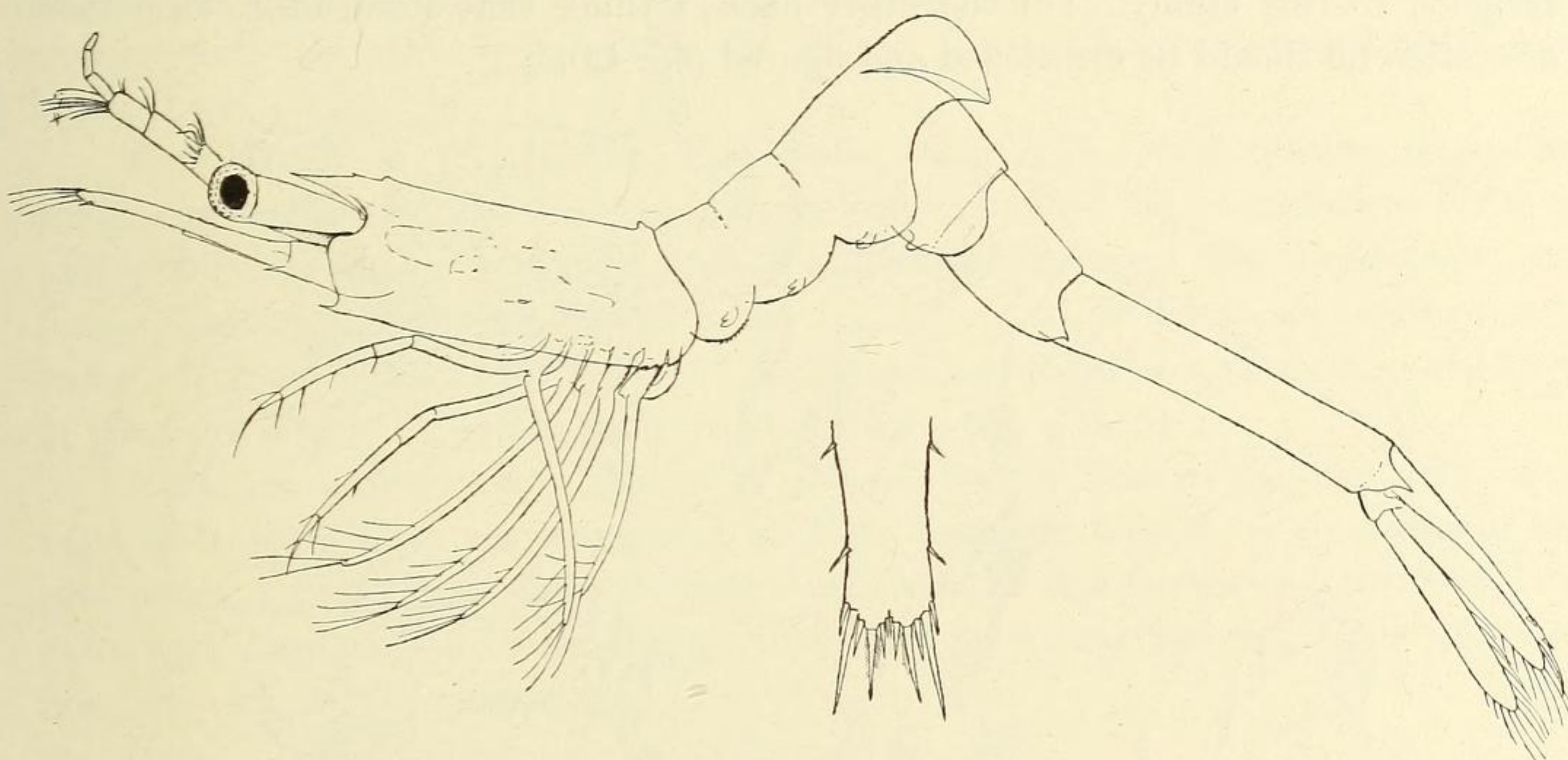


FIG. 41.—*Acantheephyra* (?), sp. Station 131.

Pleopods present, the first and fifth the smallest.

Mandible with minute rudiment of palp.

First maxilla without exopodite (fig. 40, e).

Specimen 3. Station 86. Length, 12 mm.

All legs developed, with exopodites. Rostrum with three small teeth.

Mandible with rudiment of palp.

III. Pasiphaeidae.

Very little is known of the development of the Pasiphaeidae. In some cases, as in *Parapasiphaë sulcatifrons*, the eggs are of great size and development consequently abbreviated, which is rather an exceptional feature for a pelagic or bathy-pelagic species. The larva of *P. sulcatifrons*, which has been described by Kemp (1910), hatches in a very advanced condition and, as is usual in such cases, the uropods appear later than the pleopods. In *Pasiphaea tarda* also (Björck, 1911) the eggs are large and the young hatch with all the appendages except the uropods. How far such a shortened development is general it is impossible to say, since it

is unusual for the size of the egg to be given by those who describe species, but in some cases the eggs are small and numerous (*Leptochela robusta*, DeMan, 1920) and larvae which may reasonably be attributed to Pasiphaeidae have been described. Coutière (1907) has attributed to this family larvae of the type described by Ortmann under the name of *Anisocaris*. These larvae are generally characterized by the smooth, straight rostrum, the possession of an exopodite of the fifth leg, and strongly flexed abdomen without spines but with a large protuberance on the third somite. There is no mandible palp.

I have not found in the "Terra Nova" collections any early larvae which can be assigned to this family. On the other hand, I think that a sub-adult form taken at station 93 should be mentioned and figured (fig. 42).

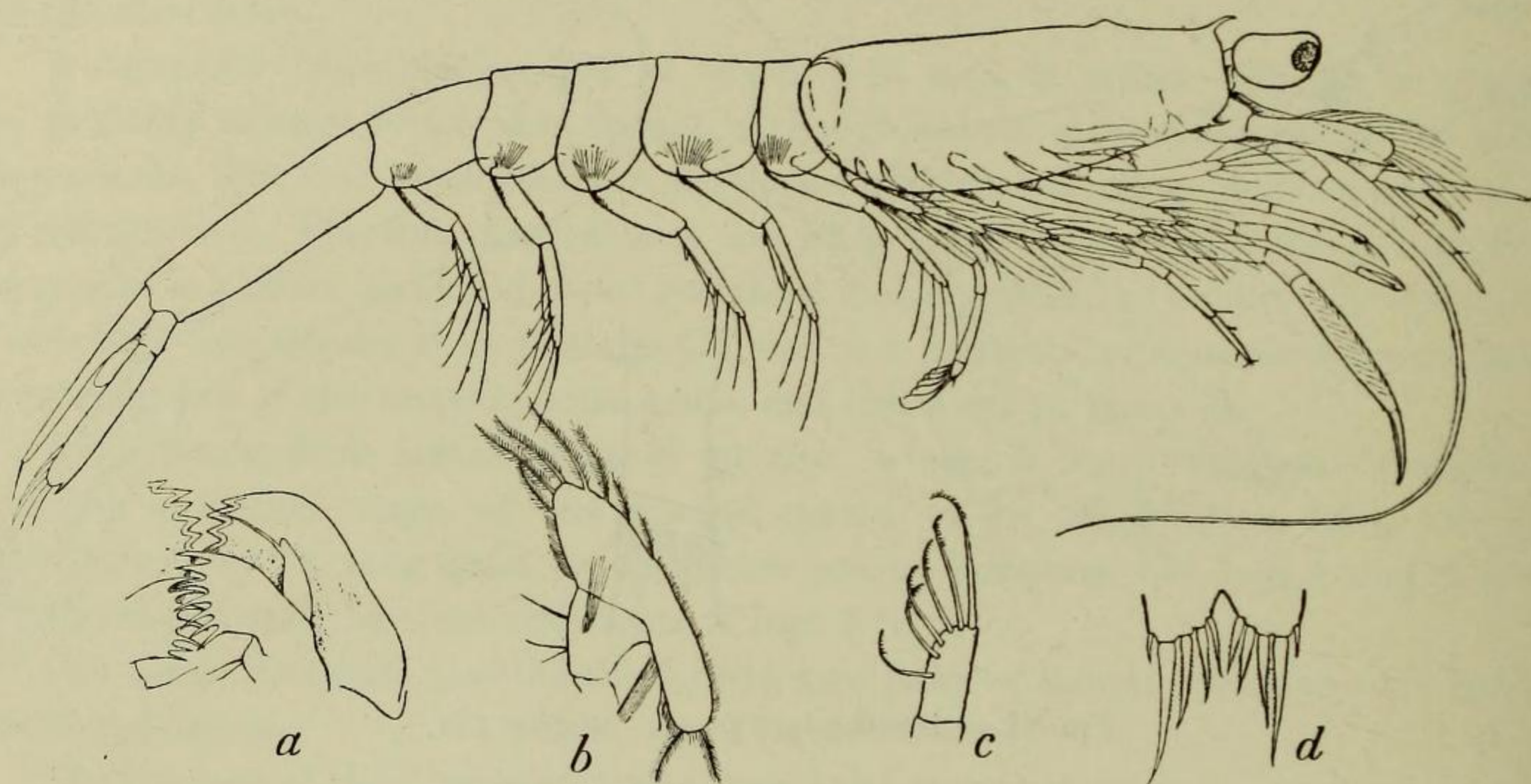


FIG. 42.—*Pasiphaea* (?), sp. Station 93. *a*. Mandibles and first maxilla. *b*. Second maxilla. *c*. Endopodite of fifth leg. *d*. Telson.

In this collection two specimens, each of about 6 mm., were taken which, although no doubt immature, have all the appendages of adult form. A detailed description is superfluous, but the following points should be mentioned.

1. The mandible has no palp. Having regard to the degree of development of the other appendages I do not think the absence of the palp is due solely to immaturity.

2. The second maxilla has no trace of enditic lobes.

3. The endopodite of the first maxillipede is absent.

4. The exopodite of the second maxilla is reduced, and without setae.

5. The fourth leg is scarcely longer than its exopodite and considerably shorter than the fifth.

These characters taken together undoubtedly place this animal within the genus *Pasiphaea*, but I am unable to find any species with which it agrees. In one respect

it seems to be unique, namely in the very peculiar form of the eyes. These are of fair size, but they have no retinal pigment, and the ommatidia are arranged apparently in a small flat disk at the end of the eye-stalk.

IV. Pandalidae.

The development of the European species of *Pandalus* and *Pandalina* has been fully described by Sars (1899), but it is by no means certain that these species can be taken as typical of the whole of this large family. Coutière (1907, p. 20) has attributed to the Pandalidae the larvae described under the names of *Icotopus*, *Kyptocaris*, and *Oligocaris*, and has himself described an additional genus, *Pandacaryphus*.* He also suggests that the genera *Eretmocaris* and *Atlantocaris* may belong here.

The larvae of Pandalidae, Processidae, and some Hippolytidae (*Spirontocaris*) are very much alike, and the information available is quite insufficient for their satisfactory separation. Confusion is also possible between the Pandalidae and Hoplophoridae in early stages before the last pereopod is developed, since in some cases which seem to be referable to the Pandalidae there is a distinct prominence of the third abdominal somite as in *Acanthephyra* (see p. 115).

I am not aware of any species of Pandalidae (or Thalassocaridae) with large eggs and abbreviated metamorphosis, so that the larvae should be abundant in the plankton. I have found larvae which I attribute to this family in collections from seventeen stations, but in most cases they have no special interest. The following are, however, worth noticing.

Pandalidae, species 1 (fig. 43). Stations 132, 133, 136.

Though quite a large number of specimens of this species have been found, they nearly all belong to the first stage, and there are no specimens sufficiently advanced to give a clue to the adult characters. The species is remarkable for having the ventral margin of the carapace armed with a row of teeth, and the third, fourth, and fifth abdominal somites have also a fringe of teeth, which give a striking appearance to the larva.

The rostrum is very long, and armed with spines at the end. The telson is very large and triangular, rather resembling that of a Palaemonid. The third maxilliped has the endopodite of unusual length and size, reaching forwards beyond the eyes. The second antenna has a jointed scale, and the endopodite is slender and continued into a long spiniform seta with a short seta at the origin of it.

The first maxilla is quite normal without trace of exopodite or outer setae, and with a one-jointed endopodite.

The second maxilla has four inner lobes and a broad one-jointed endopodite. The exopodite bears five setae and has no proximal prolongation.

* Coutière's *P. pandaliformis* has an exopodite on the fifth leg. It seems more likely that it belongs really to the Hoplophoridae.

The first stage measures about 4 mm. The second stage, which is about 5.3 mm., differs from the first in the following respects :

1. There is a pair of supra-orbital spines, a knob behind the rostrum, and another at the posterior end of the carapace.

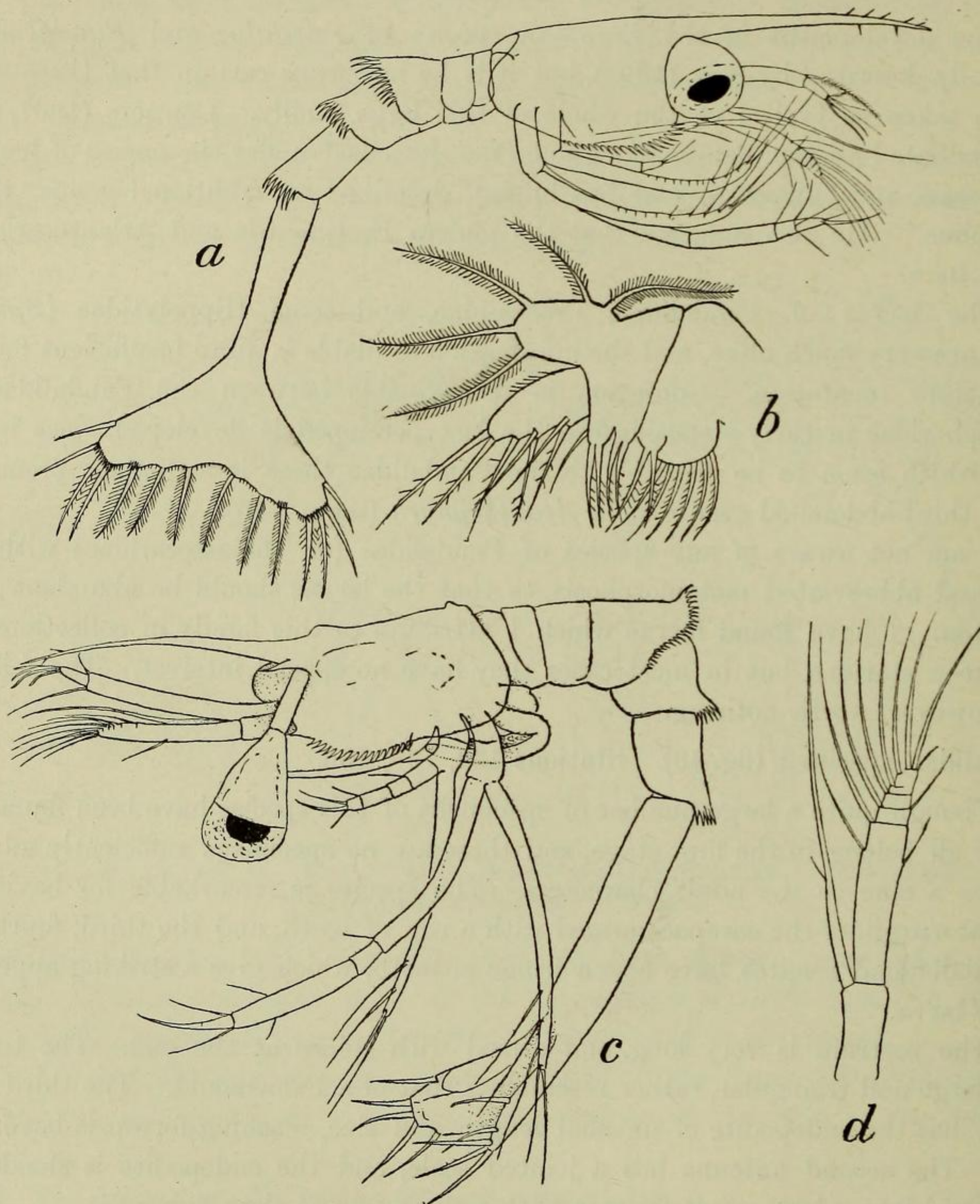


FIG. 43.—Pandalidae. Species 1. *a.* Stage I. *b.* Second maxilla. Stage I. *c.* Stage II. *d.* Second antenna. Stage I.

2. The eyes are seated on long slender stalks (fig. 43, *c*).
3. There are rudiments of two pairs of legs.
4. The uropods are visible beneath the skin.

This larva seems to provide a means of transition between the normal Pandalid

type and the "Eretmocarid" type of larva with its enormously elongated ocular peduncles; in fact it is possible that it is actually itself an early stage of an "Eretmocarid." At the same time, as I shall show below, some "Eretmocarid" larvae do not belong to the Pandalidae.

Pandalidae, species 2 (fig. 44).

A rich plankton collection from Melbourne harbour contained several specimens

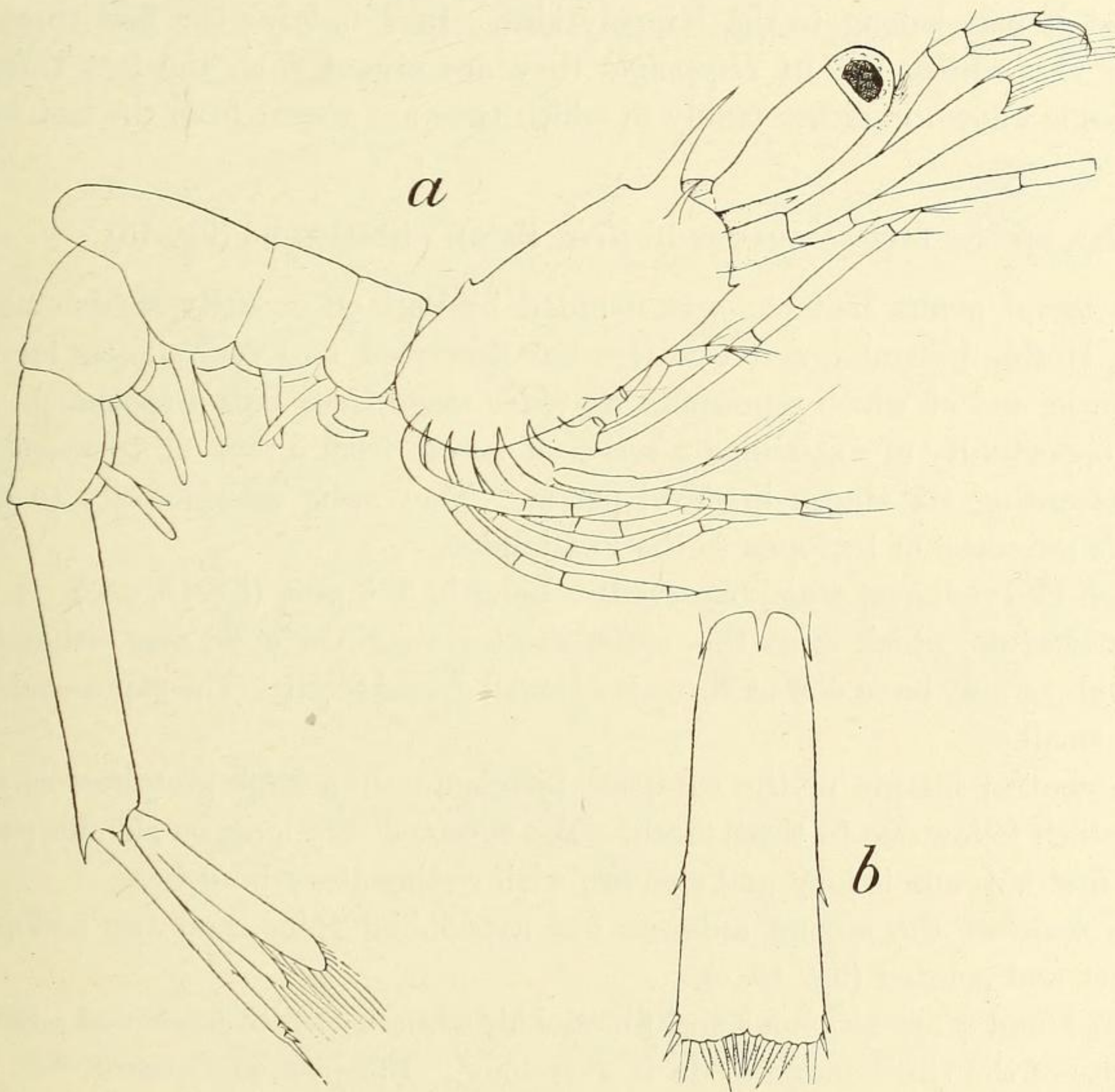


FIG. 44.—Pandalidae. Species 2. *b.* Telson.

of a larva which I attribute with some doubt to a genus of Pandalidae. Four stages are represented, the youngest measuring 4.25 mm. and having only one pair of legs developed, the remainder being visible as small buds. The pleopods are just traceable, but the uropods are present. It is therefore in stage III.

The next stage differs but little, having still only one pair of biramous legs, but this stage is marked by the prolongation of the third abdominal somite into a distinct posterior hump and the appearance of the pleopods.

The oldest larva (5.5 mm.) is shown in fig. 44, and has all the legs developed, the second pair having a rudimentary chela. It will be seen that this larva has

a marked resemblance to that of a Hoplophorid, but it differs in having no trace of mandible palp, in the one-jointed endopodite of the first maxilla, and especially in having no exopodites on the last four legs. In the form of eye, the long slender first antenna, the large supra-orbital spine, and the order of appearance of the legs this larva agrees best with the Pandalidae (*Pandalus*), but the small toothless rostrum, the humped third abdominal somite, and the absence of exopodites from the last four legs are characters which weigh against such an identification and suggest the possibility that it may belong to the Hippolytidae. In *Pandalus* the first three or four legs bear exopodites, but in *Hippolyte* they are absent from the last three pairs. No species is known in either family in which they are absent from the last four.

Pandalidae, species 3 (*Icotopus arcurostris*, Bate). Station 93 (fig. 45).

The larval genus *Icotopus* was founded by Bate on an early Mysis stage taken off Cape Howe, Australia, and Coutière has described two very similar larvae from the Atlantic, one of which represents an older stage than Bate's specimen. I have had the opportunity of examining a series of larvae from 5 mm. up to about 20 mm. and representing six stages in development. They seem satisfactorily to establish Coutière's reference of *Icotopus* to the Pandalidae.

Stage IV (youngest stage observed). Length, 5-6 mm. (fig. 45, a-c).

The rostrum, which is at this stage shorter than the eyes, may either have no teeth at all, or may have one to three very small dorsal teeth. The supra-ocular spines are very small.

The ventral margin of the carapace terminates in a large pterygostomial spine, behind which follow one to three teeth. The eyes are very long, on slender peduncles, and the first antenna is long and slender, with rudimentary branches.

The scale of the second antenna has a terminal spine, and the endopodite is very short and pointed (fig. 45, c).

Legs 1 and 2 are biramous and functional, while legs 3 to 5 are rudiments. The endopodite of the third maxilliped is very long. Pleopods are absent, but uropods are developed, with setae on the endopodite. The telson scarcely widens distally, is deeply hollowed, with a formula of 8 + 8 (fig. 45, b).

Stage V. Length, 8 mm.

There are now seven dorsal spines in front of the "dorsal organ," four of which are post-orbital. The rostrum extends beyond the eyes.

Legs 1 to 4 are fully developed, but the fifth is still a small rudiment. There are no pleopods.

Stage VI. Length, 10 mm.

Rostral teeth, 11/5. Eyes rather shorter than before.

All legs fully developed.

Pleopods as small buds.

Stage VII. Length, 11–13 mm. Mysis stage I.

Rostral teeth, 10–12/5–6.

About six spines on ventral edge of carapace.

All legs fully developed, with exopodites on legs 1 to 4. Pleopods large.

Stage VIII. Length, 14 mm. Mysis stage II.

(Rostrum broken.)

This stage differs from the preceding only in the great narrowing of the telson, which has three pairs of lateral and six terminal spines, and in the structure of the second leg, which is sub-chelate.

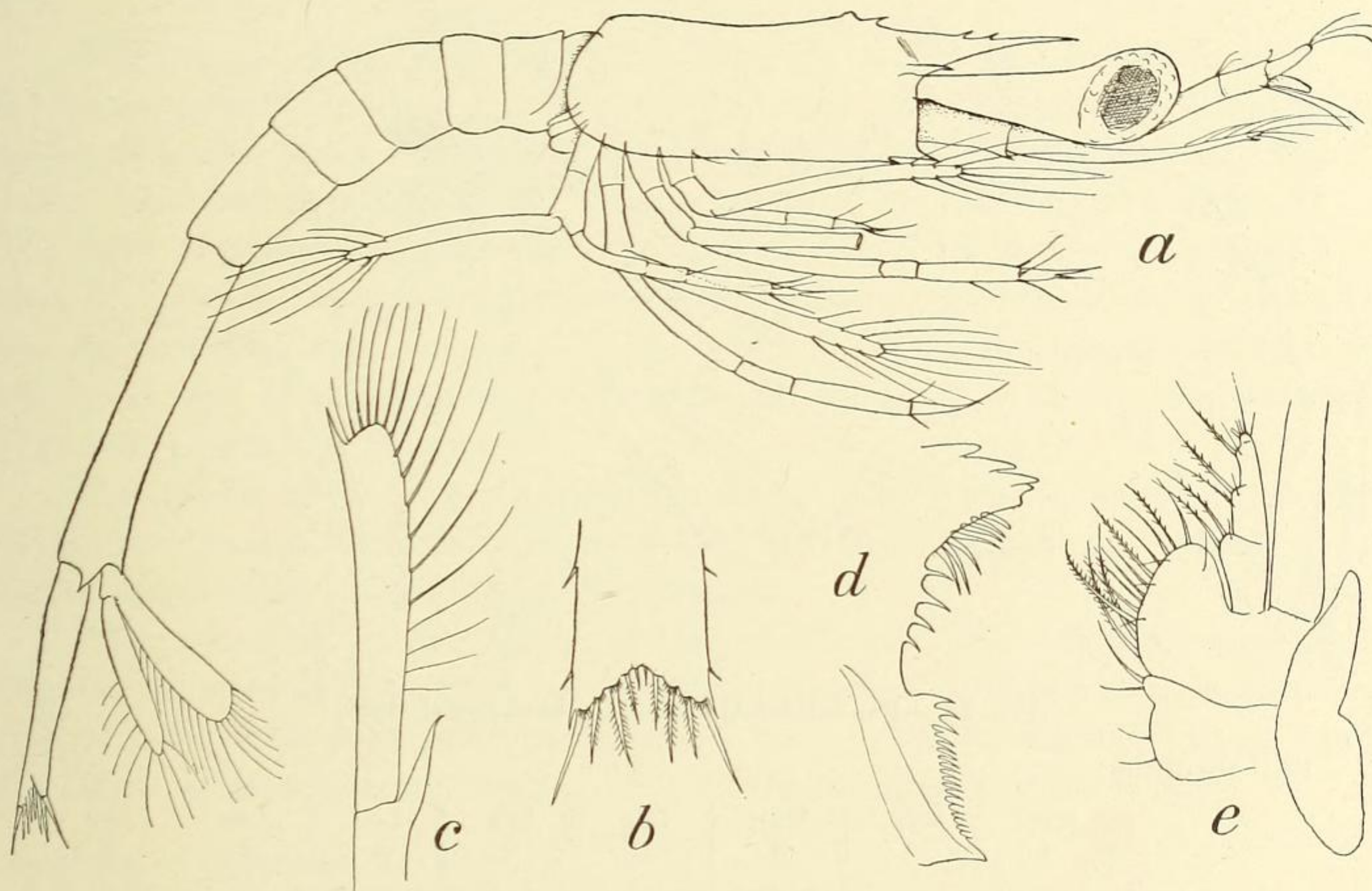


FIG. 45.—Pandalidae (*Icotopus*). Station 93. *a*. Stage IV. *b*. Telson. Stage IV. *c*. Second antenna. Stage IV. *d*. Mandible of last larva. *e*. First maxillipede of last larva.

Stage IX. Length, 20 mm. Mysis stage III (figs. 45, *d*, *e*, 46).

This is evidently the last larval stage. The eyes are very much shortened, and the rostrum of great length. In the specimen figured the rostrum is down-curved, but this is probably accidental.

The antennae approximate to the adult form, the flagellum of the second pair being very long and slender.

The mandible has no palp and is not cleft (fig. 45, *d*).

First maxilla of usual form, with one-jointed palp.

Second maxilla with four inner lobes, the endopodite one-jointed.

First maxillipede with the coxopodite lobe small, basipodite lobe very large and produced distally. Endopodite four-jointed (fig. 45, *e*).

Second maxillipede five-jointed, the terminal joint not modified. There is a large bi-lobed epipodite.

Third maxillipede of four joints, the ischium and merus fused. Carpus short, propodus long.

Leg 1 shows no trace of a chela.

Leg 2 is chelate, but the chela imperfectly formed.

Pleopods large, biramous, with appendix interna but no setae.

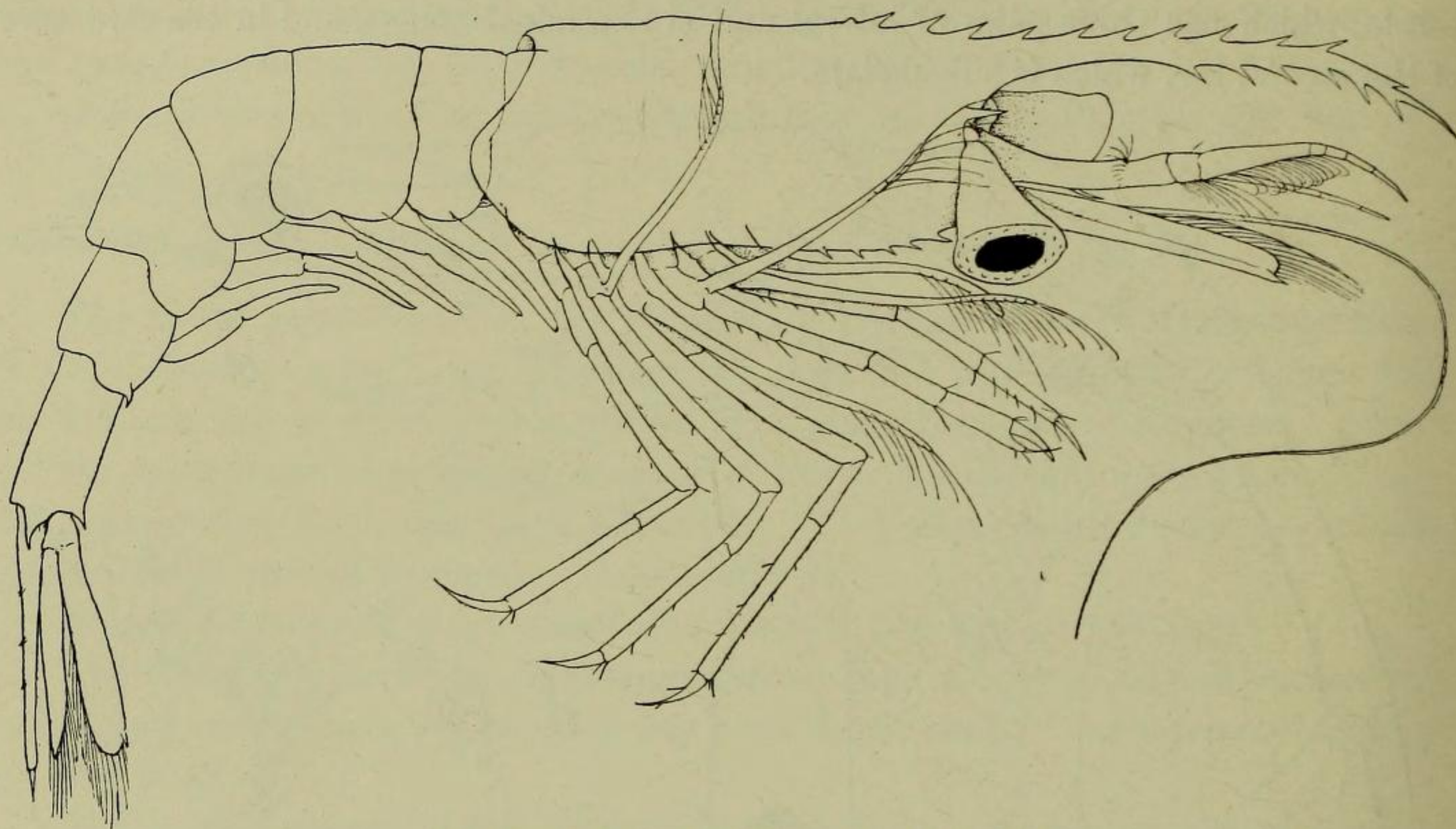


FIG. 46.—Pandalidae (Icotopus). Last larval stage.

Gill formula :

	Mxp. 1	Mxp. 2	Mxp. 3	Leg 1	Leg 2	Leg 3	Leg 4	Leg 5
Podobranchs	Ep.	1 + Ep.	Ep.	Ep.	Ep.	Ep.	Ep.	—
Arthrobranchs	—	—	2	1	1	1	1	—
Pleurobranchs	—	—	—	1	1	1	1	1

V. Alpheidae.

The development of the Alpheidae has been fully described by Brooks and Herrick (1891) for *Alpheus*, and by Sars (1906) for *Athanas*, while unidentified larvae have been figured by Bate and others under the generic names of *Anebocharis* and *Diaphoropus*. It appears to be characteristic of the family that the larvae have a small, untoothed rostrum, and that the fifth leg develops precociously into an enormously long styliform appendage.

Alpheid larvae are very common in the "Terra Nova" collections from a number of stations, but none can be identified, and they add nothing to our knowledge. A larva probably belonging to the genus *Athanas* is figured on p. 127 (fig. 51, *h*) for comparison with the larvae of *Pontoniinae*.

At station 46 a single specimen was taken of the remarkable Alpheid larva described by Coutière (1907) under the name of *Anebocaris ancylifer*. I have nothing to add to his description.

VI. Hippolytidae.

The only species of which the development is known with certainty are *Hippolyte varians* (Sars, 1912) and *Lysmata seticaudata* (Caroli, 1918), but there is no reason to doubt the correctness of Stephensen's reference of certain larvae to the genus *Spirontocaris* (1912, 1916). Kemp has also identified the larva of *Tozeuma* (1916).

Whereas in every other family of Decapods, so far as information goes, the larvae are of one type and generally show no great dissimilarity, the Hippolytidae stand altogether apart, for each of the larvae mentioned differs so much from the other three that it is difficult to believe that they are members of a single family. The larva of *Spirontocaris* is scarcely distinguishable from that of *Pandalus*, while that of *Lysmata* has the long, slender endopodites of *Spirontocaris* but resembles the Palaemonidae and Alpheidae in the order of the appearance of the legs and the great size of the fifth pair. *Tozeuma*, so far as it is known, is not unlike *Hippolyte* in essential features.

The species known are obviously too few in proportion to the whole to allow of any systematic deductions to be made, but the necessity for extending our knowledge of these larvae seems to be emphasized.

I have met with a few larvae in the collections which may with some doubt be referred to the Hippolytidae, but there is too much uncertainty in their identification to make their description profitable. I have, however, referred to this family the larvae of Bate's genus "*Eretmocarid*," which should be mentioned here.

Lysmata? (*Eretmocarid*, Bate.)

Larvae of the larval genus *Eretmocarid* were taken only at stations 40 and 43, and these are in early stages and badly damaged.

One of these larvae (length, 4.7 mm.) is in stage IV, having well-developed uropods but no trace of pleopods, and has certain features of interest.

1. It is usual at this stage in Caridea for the flagella of the antennae to be rudimentary, but in this specimen the first antenna, the peduncle of which is very long and extends beyond the long-stalked eyes, bears two branches, each of three slender joints, of which the inner is about two-thirds of the length of the peduncle.

The flagellum of the second antenna is broken off, but the broken stem indicates a greater length than is usual.

2. All the functional legs are broken off, but while legs 1, 2, and 5 were evidently fully developed, legs 3 and 4 are still quite rudimentary.

So far as I know, the only description of "Eretmocarid" is that of Bate, whose specimens were all in the Mysis stage and were much damaged, and it seems to me that the "Terra Nova" larva provides the evidence necessary to refer the genus to its adult family.

The only larva approaching Eretmocarid in form is that described by Chun (1888) as *Miersia clavigera** and finally identified by Caroli (1918) as the larva of *Lysmata seticaudata*. This larva has the peculiarity that leg 5 is developed precociously in stage II, and is of enormous size when legs 3 and 4 are still rudimentary. Exactly the same thing is found in the larva now in question, which is undoubtedly an "Eretmocarid," whereas such an order of appearance is quite unknown among the Pandalidae to which larvae of this type have been referred.

For this reason I consider "Eretmocarid" to be the larval stage of *Lysmata* or of an allied genus.

The great paddle-shaped enlargement of the propodite of the fifth leg in *Miersia clavigera* recalls the similar enlargement in legs 1 and 2 of *Pandalus borealis*, but does not indicate any relationship.

VII. Palaemonidae.

The most complete account of the development of a Palaemonid is that of Mortensen (1897) for *Leander fabricii*, but Sollaud has quite recently (1923) given a very full description of the larvae of *L. serratus*, *Palaemonetes varians*, and a number of other species in which the development is more or less abbreviated. In addition, larvae evidently belonging to the family but which could not be referred to adults have been described by Bate and Ortmann under the larval genera Retrocaris and Mesocarid.† The larva to which Bate (1888, p. 665, footnote) gave the name *Odontolophus serratus*, was certainly that of a species of *Leander*.

Unfortunately, nothing is known about the development of any species of Pontoniinae.‡

Within the genus *Leander*, the larvae of the four European species of which the development is known are so alike that they are difficult, or even impossible, to separate, while that of *Palaemonetes varians microgenitor* (*P. occidentalis*, Sollaud) is built on precisely the same plan.

Quite similar larvae were taken by the "Terra Nova" in Melbourne harbour, and these may be referred without doubt to *Leander* or *Palaemonetes*, but the identity of the remaining larvae, which fall within the genera Retrocaris or Mesocarid, is doubtful.

* Excellent figures of this larva are given by Brooks and Herrick (1891), Pls. IX, X, as the larva of *Stenopus hispidus*.

† *Coronocarid*, Ortmann probably does not belong to the Palaemonidae although so referred by Coutière.

‡ Gourret (1884) described the first larva of *Pontonia* in a very unsatisfactory way.

It is well known that, within the Palaemoninae, the species inhabiting fresh or slightly brackish water tend to have development more or less abbreviated, and Sollaud has given a number of instances showing progressive stages in this abbreviation in the genus *Palaemon*. But, although this genus is characteristic of fresh water, there is no doubt that some of the species have a complete metamorphosis which is probably carried out in the sea. This is certainly the case in *P. jamaicensis*, in which the eggs measure about 0.65 by 0.5 mm.* and the young on hatching have the characters of a normal Zoea. Similarly *P. olfersi*, according to Aurivillius (1898), hatches as a normal Zoea, and it is noteworthy that both these species occur on both sides of the Atlantic and may owe their wide distribution to having preserved a complete metamorphosis. On the other hand it is difficult to believe it possible for the whole width of the Atlantic to be crossed within the period of metamorphosis, especially having regard to the present direction of surface currents.

There is no doubt then that the larvae of the genus *Palaemon*, in addition to those of the marine genera of Palaemoninae and Pontoniinae, are to be looked for in the sea, and I suggest that the large forms of *Retrocaris* may belong to *Palaemon*. Sollaud has suggested that all these problematical larvae may belong to the Pontoniinae, but all the Pontoniinae are comparatively small, most of them very small, and it is hardly possible that these larvae could reach the sizes attained by *Retrocaris*.

For these reasons I have assigned the Palaemonid larvae met with provisionally to *Leander*, *Palaemon*, and Pontoniinae.

PALAEEMONINAE.

1. *Leander* (figs. 47 and 48).

A considerable number of specimens of *Leander* larvae belonging to two species were taken in Melbourne harbour. The two species are quite easily distinguished, but in both the resemblance to the larvae of European species such as *L. serratus* is most striking. The earliest stages are not represented, but there are examples of stages III, IV, and V which agree precisely with those of *L. serratus*.

Species I.

Stage III. Length, 3.7 mm.

This larva exactly resembles the corresponding stage of *L. serratus* with the exception that there is only a single median dorsal spine on the carapace.

Legs 1 and 2 are functional, but without trace of chelae.

Legs 3 to 5 are rudimentary, leg 5 being the largest.

Four pairs of pleurobranchs present.

The telson is of the usual form with a formula of 8 + 8, and the uropods have the inner branch without setae.

* From specimens in the British Museum.

Stage IV. Length, 4.35-4.55 mm.

An additional toothed dorsal spine has appeared.

All the pereopods are developed with the exception of the fourth which is still a biramous rudiment, while the fifth pair is exceedingly long. Legs 1 and 2 are sub-chelate.

Five pairs of pleurobranchs present.

The pleopods appear as small buds, and the endopodite of the uropods bears setae.

The telson is parallel-sided, with two pairs of lateral and five pairs of terminal spines.

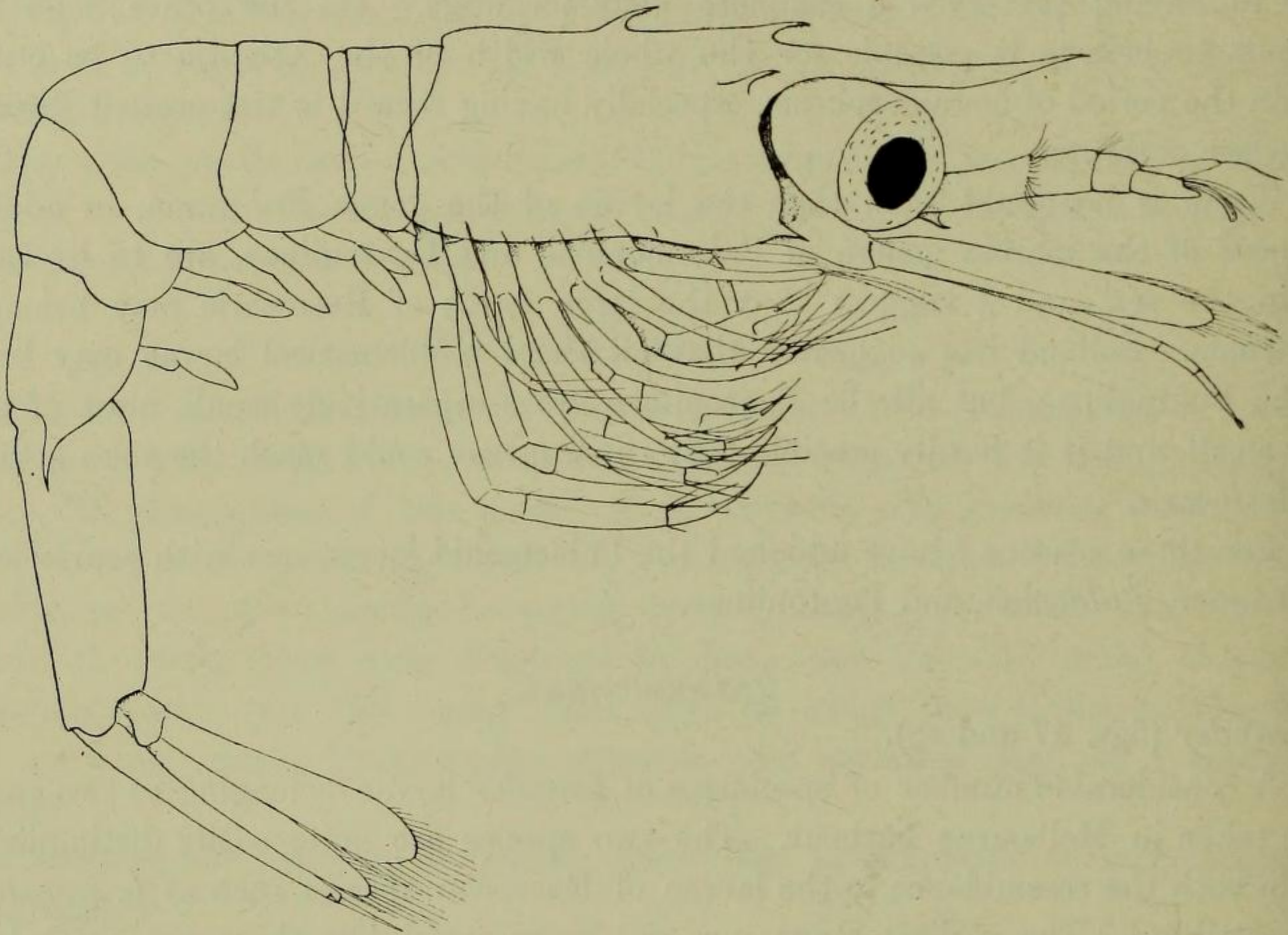


FIG. 47.—*Leander*. Species I. Stage V. Melbourne Harbour.

Just as is the case in *P. varians* (Gurney, 1924) there is some variation in this stage with regard to the degree of development of the pleopods and chelae, but there do not seem to be more than two definite stages, IV and V, corresponding to two moults.

Stage V. Length, 6-6.9 mm. (fig. 47).

This stage differs from the preceding in the large size of the pleopods, which have traces of the appendix interna, the development of the fourth legs, and the enlargement of the chelae of legs 1 and 2. The flagellum of the second antenna is also longer than the scale, and partly jointed. The telson is long and narrow, but with spines as before.

Species II (fig. 48).

This species is distinguished from the first in the fourth and fifth stages, which alone are present, by having three dorsal spines instead of two. In other respects there is no difference, and it would be exceedingly difficult to separate them from the larvae of any European species. Larvae in stage IV measure about 5.75 mm., but there are two individuals both referable to stage V of 6.6 mm. and 11 mm. respectively. I have no reason to doubt that they both belong to the same species, but if so it is clear that the last stage may persist for some time and include a number of moults as is apparently the case in *Retrocaris*.

The specimen of 11 mm. is approaching the moult to the post-larval condition, and it is possible to recognize under the cuticle of the rostrum four dorsal and two ventral spines (fig. 48). It is clear, also, that the three dorsal spines of the larva

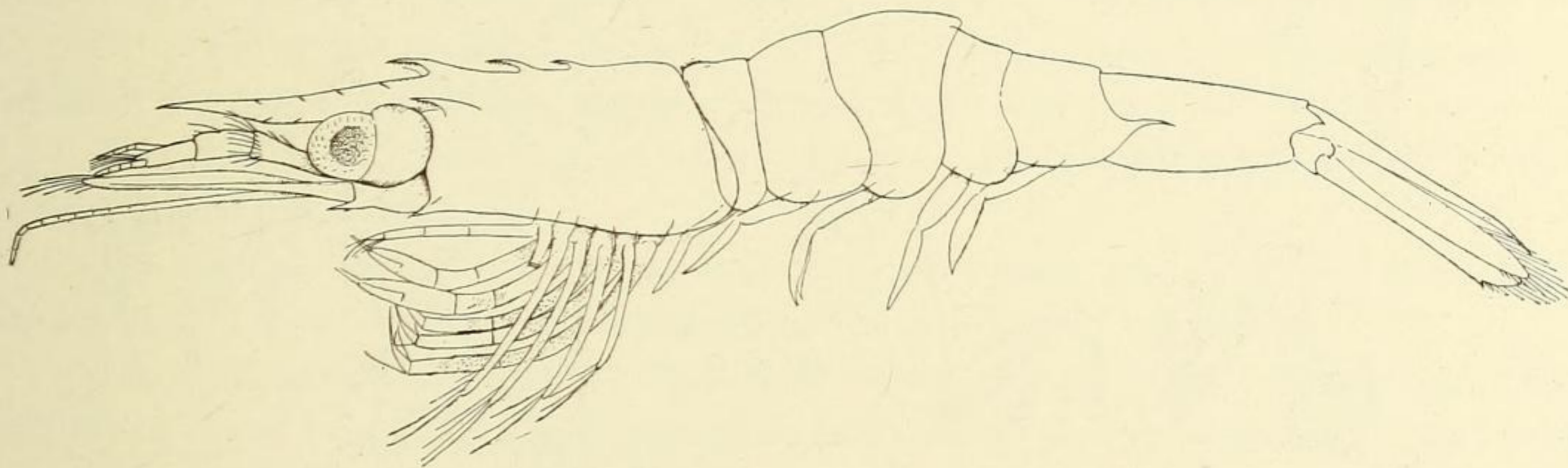


FIG. 48.—*Leander*. Stage V. Melbourne Harbour. The exopodites of this specimen were broken off. They have been drawn in rather too long.

would be preserved in the post-larval stage. In *P. varians* two of the three spines are lost at the moult, but in *L. serratus*, according to Sollaud (1923, p. 598), all three are lost.

Palaemon, sp.? (*Retrocaris*) (fig. 49).

At stations 46 and 49 six specimens of a remarkable Palaemonid larva were taken which closely resemble *Retrocaris contraria*, Ortmann. One of these specimens measures 9.5 mm., but the remainder are from 13.5 to 19 mm. in length, the largest therefore considerably exceeding Ortmann's type (16 mm.). They are not only exceptional in size, but remarkable in structure. I have not dissected the smallest specimen, but, so far as can be seen, it differs so little from the others that the same description applies to all.

They are stout, heavily built animals with strong integument. The rostrum is long, sloping slightly upwards, with five to seven dorsal and three ventral teeth, only the hindmost of which is serrated. In addition there are two serrated spines on the carapace and a small blunt knob (dorsal organ?) immediately behind them. There is a long, straight supra-orbital, a pterygostomial, and a large hepatic spine, all smooth. A deep groove runs across the carapace behind the posterior spine and forwards on

either side to the supra-orbital, and there may be another transverse groove in front of the first post-orbital spine.

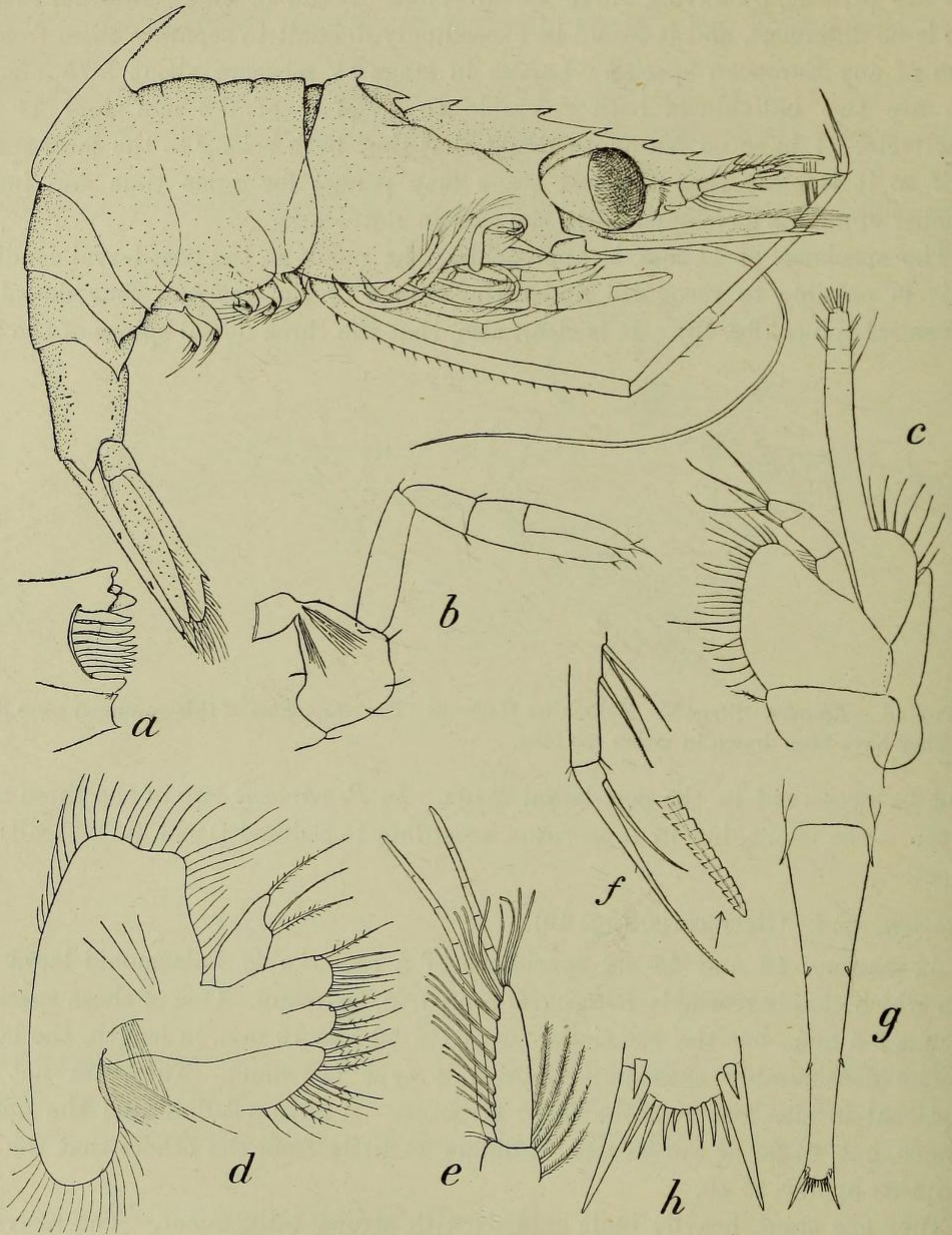


FIG. 49.—*Palaemon* (?) (*Retrocaris*). Station 46. *a*. Edge of mandible. *b*. First leg. *c*. First maxillipede. *d*. Second maxilla. *e*. End of first antenna. *f*. End of fifth leg. *g*. Telson. *h*. End of telson.

The abdominal pleura are very large. The first has a small median point, and the second a smaller one near its posterior edge, while those of somites 4 and 5 are

produced backwards into sharp points. The third somite is keeled, with a large, forwardly directed spine toothed on its lower edge.

The telson is long and exceedingly narrow towards the end, with two pairs of lateral and six pairs of terminal spines of which the second is greatly the largest (fig. 49, *g, h*).

The first antenna approaches the adult form. The otocyst is not formed but is represented by an open pit, the stylocerite being a simple pointed process without membranous overlap. The dorsal side of the first joint is hollowed, but does not widen out distally. There is a strong spine at the outer distal angle. The outer branch consists of a thick unjointed basal part bearing many aesthetes, and a slender terminal part, but no accessory branch (fig. 49, *e*). In the largest specimen there are traces of joints in the proximal part and an incipient accessory flagellum. This appendage is therefore much more advanced than it is in the last larva in *Leander*.

The scale of the second antenna has a large terminal spine, and the flagellum is slender, jointed, and of great length. In *Leander* it does not much exceed the scale.

The mouth-parts are of the usual larval form. The mandible has no palp, and is undivided (fig. 49, *a*).

The second maxilla has three well-developed lobes and a small one-jointed endopodite. The exopodite is very large and broad distally (fig. 49, *d*).

The first maxillipede has the basal lobe scarcely distinct and with one seta only, while the distal lobe is very large and produced distally. The endopodite has three joints, and the exopodite is expanded at its base and bears a number of setae. The epipodite is bi-lobed (fig. 49, *c*).

The second maxillipede is of larval form, with a large epipodite and a minute lobe which may represent the podobranch.

The third maxillipede has two very small papillae at its base which possibly are the rudimentary arthro- and pleurobranch.

Legs 1 to 4 have short exopodites. Legs 1 and 2 have large chelae and are of nearly the same size. Whereas legs 1 to 4 are relatively small, inconspicuous appendages leg 5 is enormous, flexed at the mero-carpal joint, and reaching forwards beyond the eyes. The dactylus has a stiff seta at its base and is prolonged into a peculiar spine with transverse ridges (fig. 49, *f*). The pleopods are almost hidden by the large epimera, but are fringed with setae and apparently functional.

Coutière has discussed at some length the problem of larvae such as this which attain sizes quite unusual as compared with the species of which we know the development, and concludes that they are abnormal and not destined to be transformed into normal adults (1907, p. 60). Bouvier arrived at the same conclusion with regard to *Glaucothoë* (see p. 185). It is indeed difficult to account for some of the extreme forms such as Ortmann's *Atlantocaris gigas*, which reaches 53 mm., but in view of the prolonged larval and "semi-larval" development of some Hoplophoridae and Penaeidae (*Funchalia*), it seems to me that we are not justified, on the

information available, in postulating abnormality as an explanation and formulating hypotheses to account for it. Our knowledge of Decapod development is wholly inadequate, and of the deep-water forms we know practically nothing. Still, such knowledge as we have does not support Coutière's view, for instances are known of larvae of established parentage which reach sizes as great as those he discusses. For example :

<i>Pontophilus spinosus</i>	16 mm.
<i>Stenopus spinosus</i>	30 mm. (Cano)
<i>Tozeuma armatum</i> *	31 mm. (Kemp, 1916, p. 400).

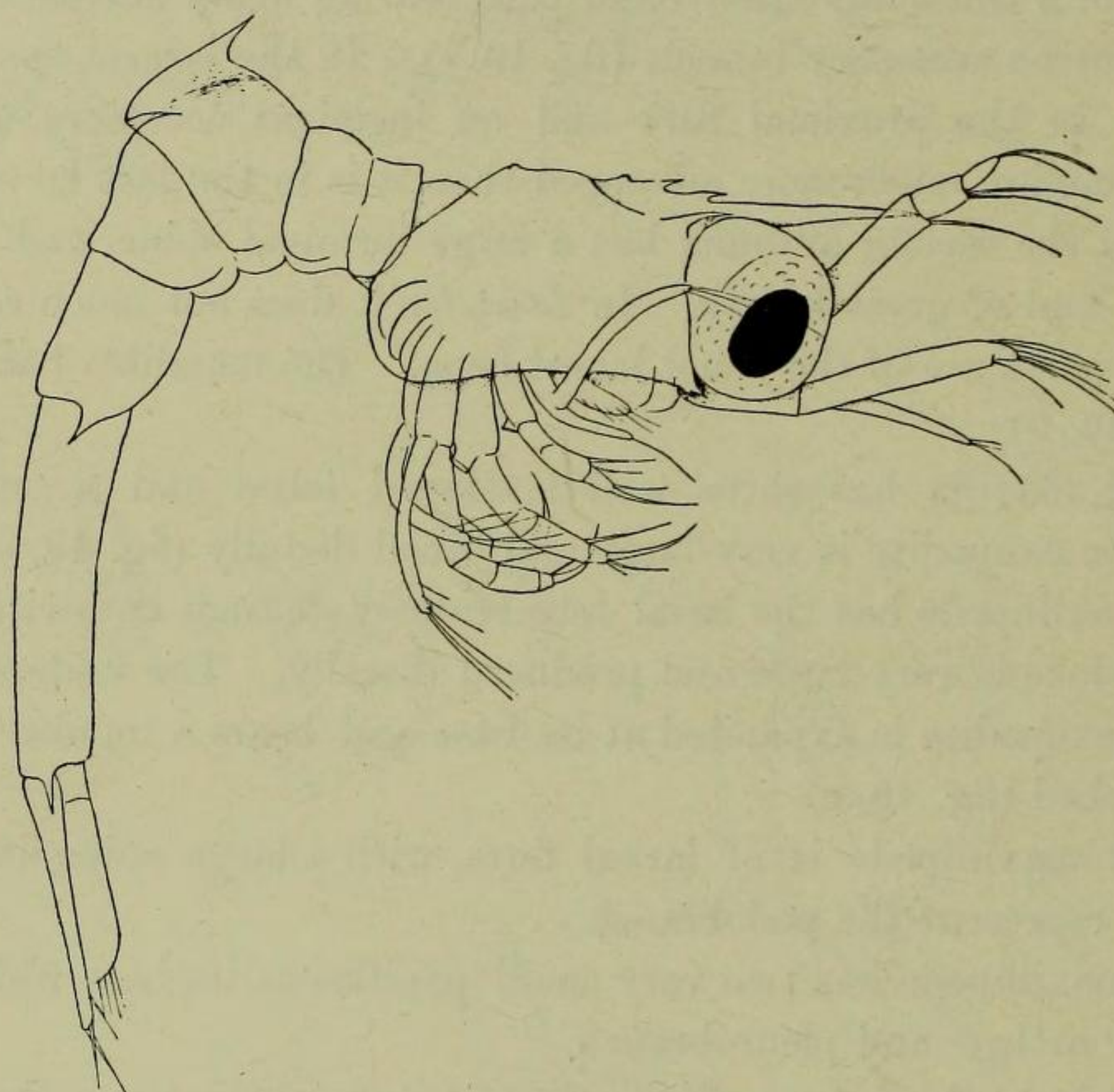


FIG. 50.—*Palaemon* (?) (*Retrocaris*). Stage III. Station 43.

In the particular case before us we have specimens of similar structure, taken in the same haul, of 10 mm.—which is quite a normal size for a *Leander* larva—and of 19 mm., and I see no reason why the latter should be assumed to be in any way abnormal. It does not fit in exactly with our knowledge of *Leander* development, but it is not for that reason to be considered abnormal. At the same time a larva of 19 mm. must develop into an adult of some size, and the whole of the Pontoniinae seem to be excluded for this reason alone. Also I have described below certain larvae which I believe do belong to Pontoniids and these are of quite different structure. On the other hand we know that some species of *Palaemon* have free larvae, and some of the adults are of very large size (e.g. *P. carcinus*), and it seems extremely likely that the larvae of the genus *Retrocaris* may belong to *Palaemon*.

* Coutière's *Caricyphus acutus* (19 mm.) is probably also a *Tozeuma* (1905, p. 21).

Three very small specimens of *Retrocaris* larvae were taken at station 43 (fig. 50). These measure about 2.8 mm. and are all in stage III, having legs 1 and 2 developed and 3 to 5 rudimentary, while the endopodite of the uropods has no setae.

The close resemblance to the large forms just described is very striking. Dorsally the carapace bears two median spines followed by a small blunt knob at the hind end. There is also a transverse furrow running from behind the anterior knob to the supra-ocular spine. The two dorsal spines are serrated, but the supra-ocular is smooth. There is a pterygostomial but no hepatic spine. In the arrangement of the

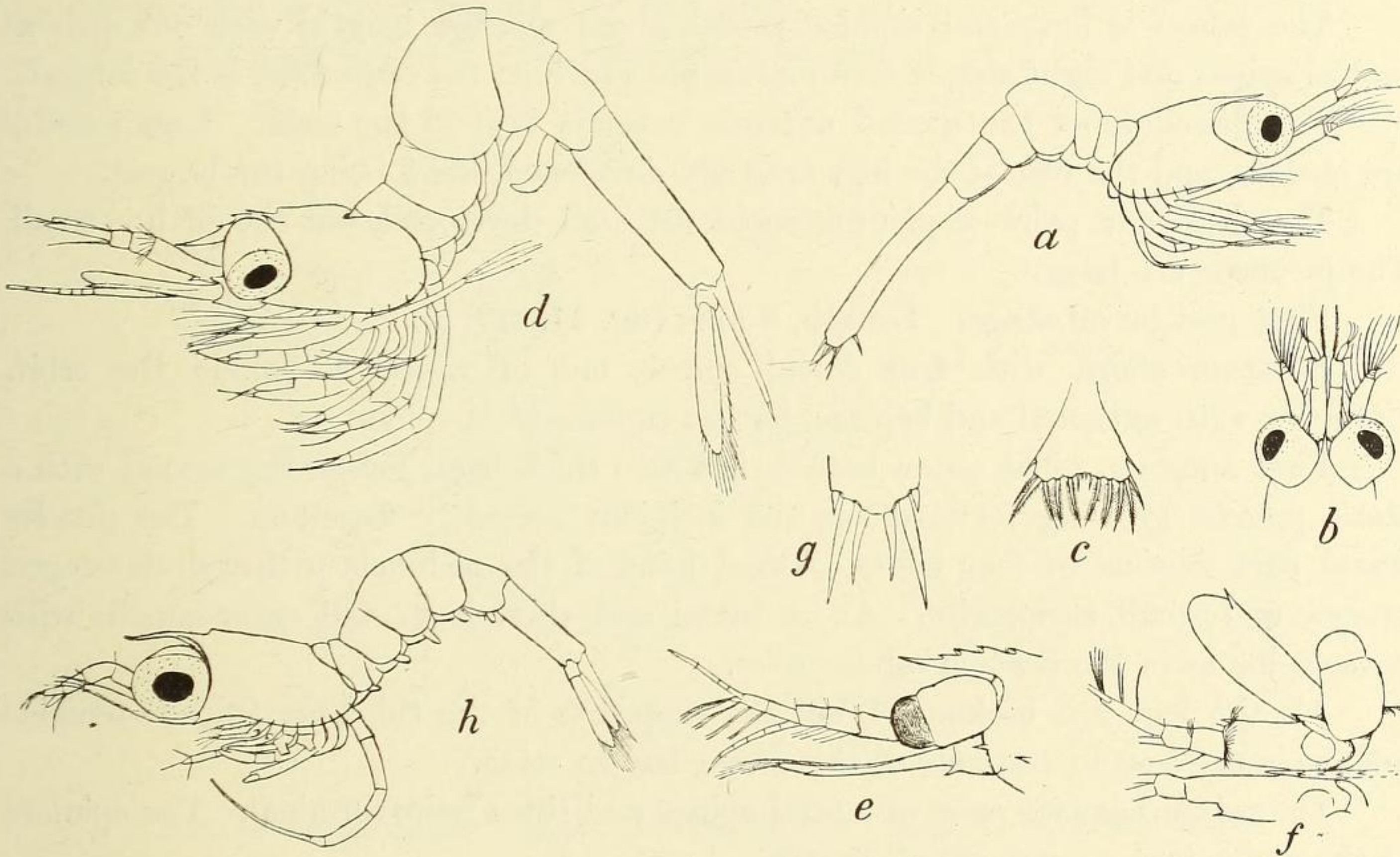


FIG. 51.—Pontoniinae. Species I. Station 40. *a*. Stage II. *b*. Stage II. Dorsal view of head. *c*. Stage II. Telson. *d*. Stage V. *e*, *f*. First post-larval stage. *g*. First post-larval telson. *h*. *Athanas*(?), Alpheidae. Stage IV. Station 40.

dorsal spines the agreement is exact, but I do not think this larva actually belongs to the same species as the large form, not only by reason of its small size, but also from its having a pair of lateral spines on the fifth abdominal somite. At all events it represents a closely allied species, and is not unlike Coutière's *R. antarcticus* which measures 5–6 mm. in its last stage.

PONTONIINAE. Species I (fig. 51).

Station 40.

At this station a series of larvae were taken together with one post-larval specimen which almost certainly belongs to the same species and enables the larvae to be referred to the Pontoniinae with some confidence.

Stage II. Length, 2.14 mm. (fig. 51, *a*, *b*, *c*).

The body of the larva is much bent at the third somite, which is very large.

The rostrum is small, pointed, without spines, but with a small knob at its base ("dorsal organ"). The carapace is entirely without spines. The first two pairs of legs are developed, the third pair rudimentary. No trace of pleopods or uropods. Telson triangular, with eight pairs of spines.

Stage V. Length, 5.2 mm. (fig. 51, *d*).

The rostrum has now three dorsal teeth, and there is a pair of supra-orbital spines. The third abdominal somite is greatly enlarged and the abdomen sharply bent at this point.

The telson is long and slender (width about quarter length) with one pair of lateral spines and eight simple terminal spines of which the outermost is the largest.

The flagellum of the second antenna extends beyond the scale. Legs 1 and 2 are chelate, and the rest of the legs are fully developed, leg 5 being the largest.

The first four pairs of pleurobranchs are well developed, but the fifth is small. The pleopods are large.

First post-larval stage. Length, 6 mm. (fig. 51, *e, f, g*).

Rostrum short, with four dorsal spines, one of which is behind the orbit. Carapace with antennal and hepatic, but no supra-orbital spines.

First antenna. The outer branch has two thick basal joints, the second with a short process growing forwards as the incipient accessory flagellum. The slender distal part consists of four joints. Basal joint of the peduncle with well-developed otocyst and small stylocerite. At its distal end there is a small outer lamella with outer spine as in the post-larval *Leander*.

All the legs are broken off, but the exopodite of the third maxillipede remains and, as is the case in *Leander* at this stage, has no setae.

The telson has two pairs of lateral spines and three pairs terminal. The epimera of the abdominal somites are all round.

It is impossible to identify such a specimen in the first post-larval stage with any precision, especially as at this stage the mandible palp and the gills of the third maxillipede may not be developed, but there can be little doubt, from the presence of an hepatic spine and the six spines of the telson, that it is a member of the Pontoniinae, and possibly of the genus *Periclimenes*.

Coutière has described (1905 and 1907, p. 59) a post-larval Palaemonid of 21 mm. which he refers to *Periclimenes*.

The presence of vestigial exopodites indicates an animal in the first post-larval stage, and Coutière is not therefore justified in attaching importance to the absence of a mandible palp. Except for this one character there is nothing in the description to support the reference of the specimen to *Periclimenes* rather than to *Palaemon*. The large size seems strongly to suggest that it was in fact a post-larval form of some species of *Palaemon*. It should be pointed out that the preceding larval stage might well have been as large as any *Retrocaris* larva known!

PONTONIINAE. Species II (fig. 52).

In the Bay of Islands, New Zealand (station 148), a complete series of larvae from stage II to the first post-larval was taken which I do not doubt belong to one species. The general resemblance of these larvae to the form just described is so close that they no doubt belong to allied genera though probably not to the same genus.

Stage I. Length, 1.75 mm.

Scale of second antenna jointed, the endopodite with one seta.

Legs 1 and 2 developed, leg 3 rudimentary.

Telson triangular, 8 + 8. No pleopods or uropods.

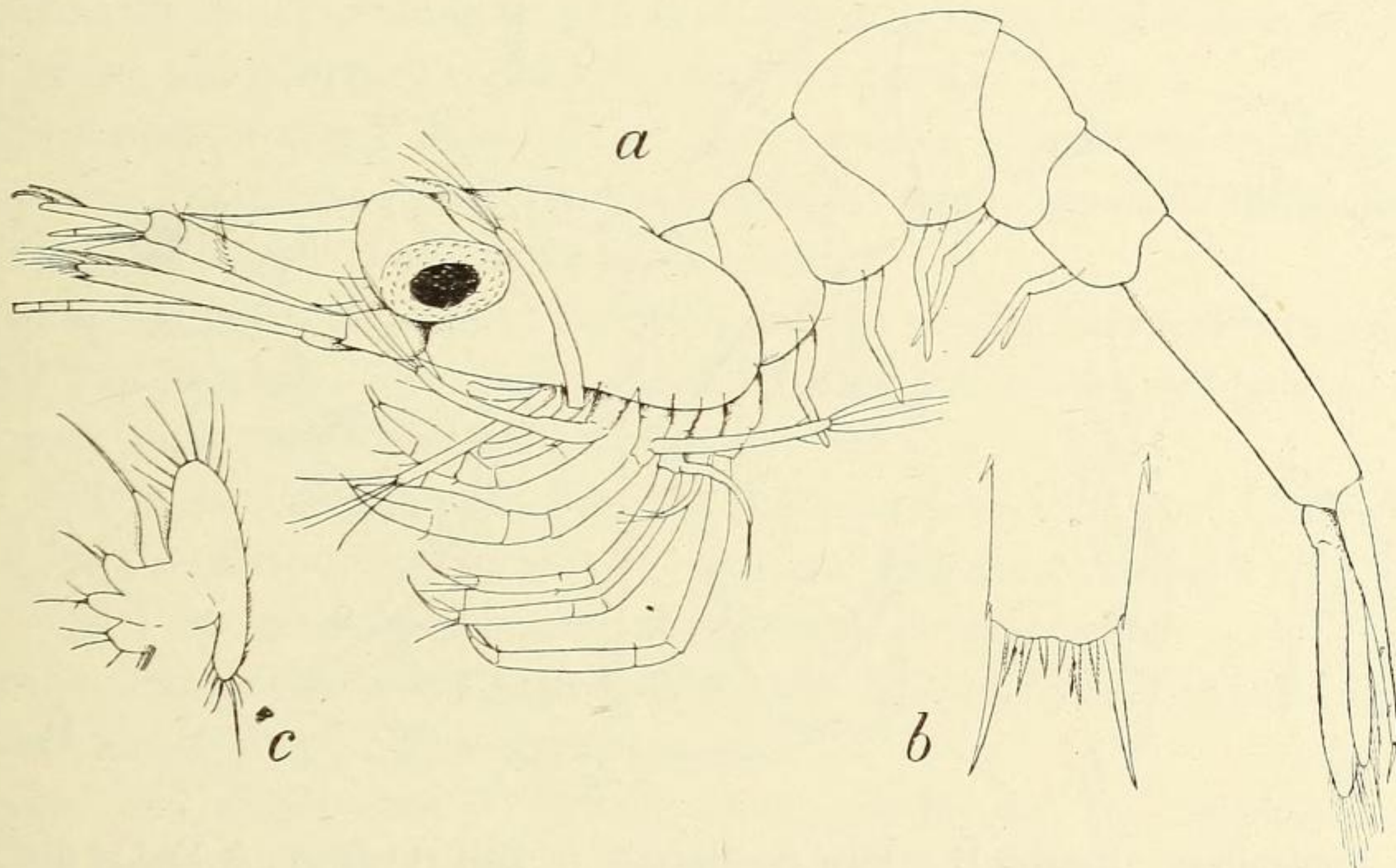


FIG. 52.—Pontoniinae. Species II. Station 148. Stage V. *b*. End of telson.
c. Second maxilla.

Stage III. Length, 2.7 mm.

Ventral angle of carapace with two small spines.

Second antenna. Endopodite a rod shorter than scale. Scale not jointed.

Legs 1 and 2 developed, legs 3 to 5 rudimentary.

Traces of gills on legs 1 and 2.

Telson narrower. Uropods present, the endopodite without setae.

Stage IV. Length, 3.85–4 mm.

Flagellum as long as scale, the latter with terminal tooth.

Legs 1, 2, 3, and 5 developed, leg 4 rudimentary.

Uropods with endopodite bearing setae.

Telson narrow, formula 6 + 6.

Pleopods visible as small buds.

Stage V A. Length, 4.45–5.6 mm.

Flagellum longer than scale.

All legs developed. Legs 1 and 2 chelate.

Pleopods of varying size.

Stage V B (fig. 52). Length, about 7 mm.; last larval stage.

The rostrum is long, and without dorsal spines. The supra-orbital spines are large and serrated.

Abdomen greatly flexed at the large third somite.

None of the somites have spines.

First antenna. Both branches developing. Basal joint of peduncle curved, with large stylocerite, but no otocyst. The mouth-parts are of the usual Palaemonid form, the mandible having no palp and the second maxilla with only three lobes (fig. 52, c).

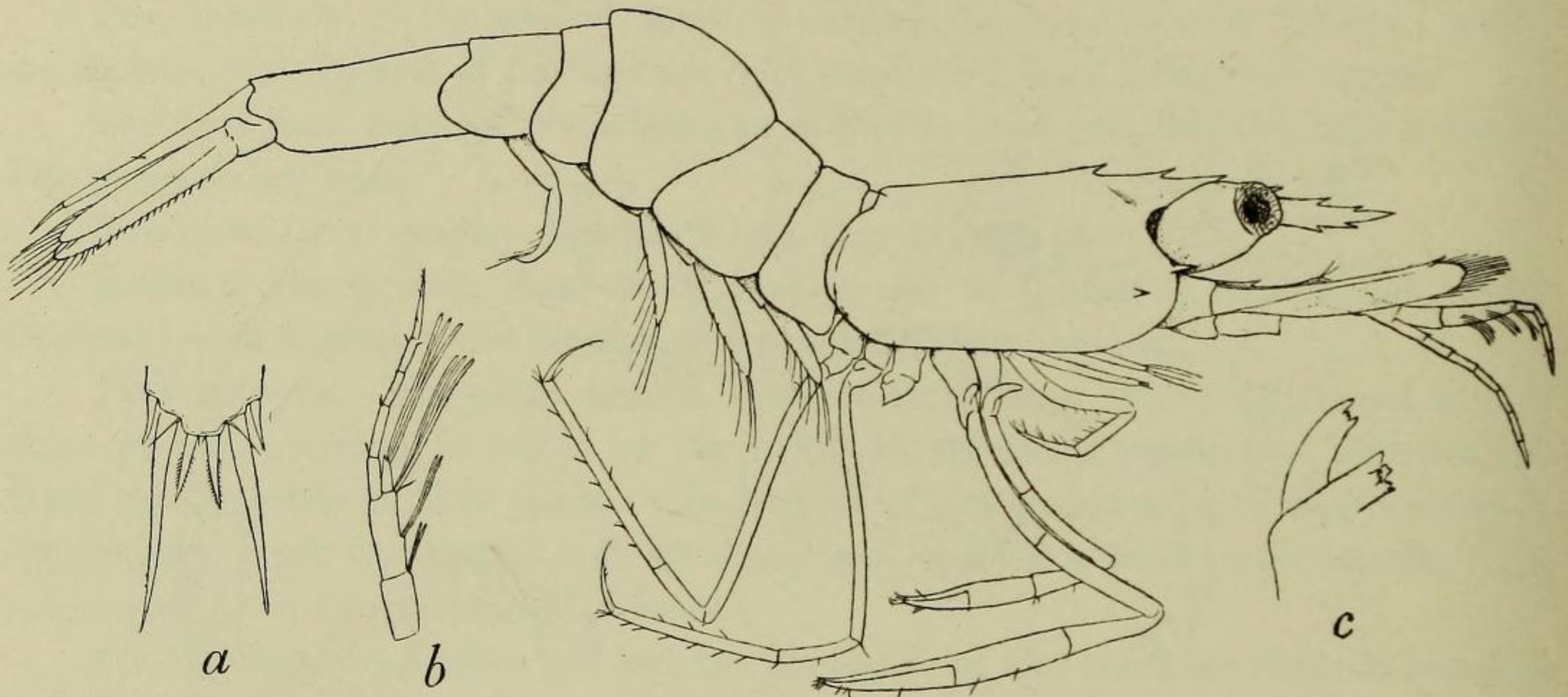


FIG. 53.—Pontoniinae. Species II. First post-larval. a. End of telson. b. End of first antenna. c. Mandible.

First maxillipede. Coxa and basis are fully developed, but the division between them is not marked by the slightest indentation.

Legs 1 to 4 have exopodites. Legs 1 and 2 have large chelae, the second being the larger. Leg 5 is larger than legs 3 and 4, but not markedly so.

Pleopods long, biramous, but without setae.

This larva differs from that above described in the absence of teeth from the rostrum.

Another larva was taken at station 85 which differs only in having a single toothed spine on the rostrum.

A single post-larval Prawn, no doubt belonging to the same series, was taken in the same collection (station 148). This specimen (fig. 53) measures 6.25 mm., or smaller than the oldest larva, but this is no reason for not accepting its identity since in *Leander* and *Palaemonetes* there is much variation in size of the last larva, and also the post-larval stage may moult from either stage V A or V B.

The armature of the telson places this species among the Pontoniinae, and it

appears to belong to the genus *Periclimenes*. The simple dactyli of the last legs would then restrict it to the subgenus *Ancylocaris* as defined by Kemp.

There are five pleurobranchs decreasing in size from before backwards and no trace of gills on the third maxillipede. In the first maxillipede the division between coxa and basis is scarcely indicated, and the epipodite is small and so deeply divided as to have the shape of a V with two equal curved branches.

Another post-larval Prawn was taken at station 129. This specimen has no supra-orbital or hepatic spine, and has small and slender chelae. The dactyli of the last legs are biunguiculate.

I should like here to call attention to certain facts regarding the relationship of the Palaemonidae to other families. If I am right in the identification of the larvae described above, the following conclusions may be drawn :

1. The larvae of the Palaemoninae have common characters which distinguish them from the Pontoniinae, but those of *Leander* and *Palaemon* differ from each other to a greater degree than would be expected.

2. The larvae of Palaemoninae and Pontoniinae possess characters in common by which they may as a whole be distinguished from all other Decapod larvae.

The most important characters are three :

- (a) Absence of the basal lobe of the second maxilla.
- (b) Retarded development of leg 4 and sometimes of leg 3.
- (c) Precocious development of leg 5 and its great size.

Now these three characters are combined also in the *Alpheidae* and in *Lysmata*, but none are found in any other larvae known.

Coutière has emphasized the very close affinity of the *Alpheidae* to the *Hippolytidae* and the difficulty in defining the limits of the families, but he does not recognize any close resemblance to the *Palaemonidae*.

So far as concerns the larvae only it seems to me that this agreement in respect of these three characters demands explanation and implies some relationship, unless we are to follow Ortmann and dismiss all larval characters as irrelevant.

The question of the relation of *Lysmata* to the *Alpheidae* is more difficult since we are not dealing here with characters applicable to a whole family but only to a single genus.

The close resemblance between the *Alpheid* and *Palaemonid* larva is illustrated by the specimen shown in fig. 51, *h*, which probably belongs to *Athanas*. In general form it differs little from the *Pontoniid* shown in the same figure, and the long fifth leg and rudimentary legs 3 and 4 are exactly paralleled in *Palaemonetes varians*.

VIII. Processidae.

I have myself followed the development of *Processa canaliculata* (Gurney, 1923), and Coutière (1907) has attributed Bate's larval genus *Hectarthropus* to the *Processidae*, describing also a new species, *H. nikiiformis*, which is remarkable for

the pronounced furrows on the carapace. Bate's species are not sufficiently described to be discussed, but Coutière's species, unlike though it is to *Processa*, must apparently be included in the family. As it cannot belong to *Processa* it may possibly belong to *Nikoides*.

No larvae of Processidae were recognized in the "Terra Nova" collections, but a single post-larval specimen of *Processa* was taken at station 135.

IX. Crangonidae.

Larvae of Crangonidae were taken at five stations, sometimes with post-larval stages, but they cannot be identified with certainty and add nothing to our knowledge of the family, which is already fairly complete.

PALINURA.

Of the development of the Eryonidea little is known (see p. 105), except that *Willemoesia* has an abbreviated development (Doflein, 1904). Of the Scyllaridea the metamorphosis is now completely established, although the whole series of changes has only been followed in *Palinurus vulgaris* and in *Scyllarus arctus*. The most complete and recent accounts of the development of these two genera are those of Bouvier (1914) and Stephensen (1923, p. 71). A Phyllosoma has been proved to exist in *Jasus*, *Panulirus*, *Ibacus*, and *Thenus*, and is probably universal. It is remarkable that, in spite of the fact that the Palinura hatch with the first three pairs of pereiopods developed, yet as many as nine or ten stages can be distinguished, and very large sizes may be attained by the larva. There is evidently a very prolonged larval period which should lead to very wide dispersal of the adults. *Jasus lalandi* is an example of such wide distribution, being found off the coasts of S. Africa, Chile, New Zealand, and Australia, besides Tristan da Cunha and St. Paul's Rocks in the Atlantic. The Phyllosoma of *Jasus* is exceptional in hatching with a large biramous natatory second antenna, and it has been given the name of Naupliosoma by Gilchrist (1913, 1916). Precisely the same larva has been found by Archey (1916) to hatch from the eggs of the New Zealand form of the species. The Naupliosoma stage lasts from four to six hours, and evidently corresponds to the transitory free stage sometimes found in the Brachyura (e.g. *Eurynome*), in which the embryonic cuticle is not yet thrown off and the antennae and telson are provided with large ciliated setae. There is no corresponding stage in *Palinurus vulgaris*, neither is there any trace of antennal setae in the larva before hatching.

It is difficult to make any comparison between the Phyllosoma and any other Decapod larvae. It cannot be said that it gives the slightest indication of the relationship of the Palinura, and, apart from the fact that some of the pereiopods are functional on hatching, there is no resemblance between it and the larva of the Nephropsidea. Claus (1876, p. 50) has already pointed out that the Phyllo-

soma unites in itself certain characters of the Protozoa and of the Mysis stage, and the presence of a biramous antenna in *Jasus* adds to the force of the contrast. The Phyllosoma is, in fact, a Protozoa in which structures properly belonging to later stages appear precociously.

Phyllosoma larvae, generally in the first stage, are not uncommon in the "Terra Nova" collections, but add nothing to our knowledge and need not be described. It should be noted, however, that some of these specimens show that the order of the appearance of the appendages does not always follow exactly that established for *Palinurus* and *Scyllarus*.

ASTACURA.

No larvae belonging to this section were taken by the "Terra Nova."

STENOPIDEA.

Stenopus hispidus.

The larva of this interesting species was first described by Brooks and Herrick (1891), the latter having observed the hatching of the young from the egg and therefore placed the identity of the first larva beyond doubt. Their detailed description of the segmentation of the egg and of the first Zoea is most valuable, but unfortunately the three subsequent stages described as belonging to *Stenopus* are undoubtedly referable to three other and very distinct genera. Thus the larva described as resulting from the first moult of the *Stenopus* Zoea certainly belongs to a species of *Callinassa*, while the two later stages (Pl. IX and XII) represent respectively the Mysis stage of *Lysmata*, or an allied genus, and a Mastigopus stage of *Sergestes* (probably that of *S. vigilax*).

Ortmann (1893) has already pointed out the error with regard to the last two stages, but he did not realize that even the second stage, stated to be derived by actual moult from the first in the laboratory, belonged also to quite a different genus of Decapod.

Curiously enough, Cano was engaged at about the same time in a study of the metamorphosis of *S. spinosus*, and his account was published on January 15, 1892. Cano described three stages of the larva and two post-larval stages, and his first stage agrees in all essentials with the first stage of the American species, though it differs in some details and agrees more closely with the second stage of the latter, to be described below. Cano does not state that he hatched the larva from the egg.

A few specimens belonging to four stages in the development of *Stenopus* were taken at stations 43 and 45 off the Brazilian coast, and as the genus possesses exceptional systematic interest some account of these larvae should be of interest, even though it may to some extent merely confirm that already given by Cano.

Stage I. Length, including rostrum, 3.1 mm. (fig. 54, *a*). Length of rostrum, 0.8 mm.

Brooks and Herrick give a length of 4 mm., of which 1.5 mm. was taken up by the rostrum, which was therefore much longer than in my specimens.

Carapace deeply indented dorsally above the sessile eyes, leaving uncovered the whole of the enormous mandibles. Rostrum at this stage smooth and slightly up-turned towards the end. Posteriorly the ventral edge of the carapace is minutely denticulate and terminates in a sharp tooth.

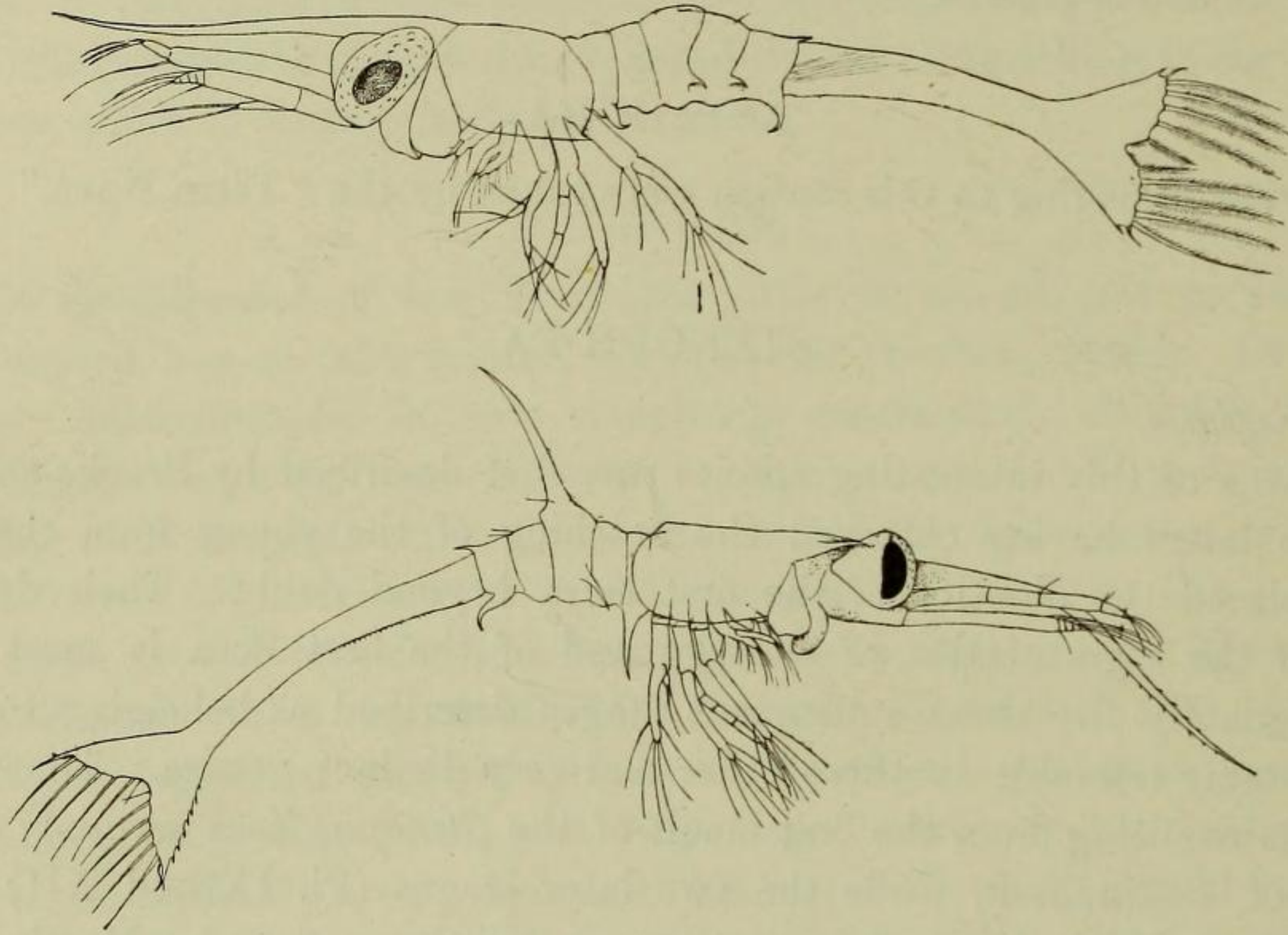


FIG. 54.—*Stenopus*, sp. Station 43. *a*. Stage I. *b*. Stage III.

First, third, and fourth pleon segments have each a pair of lateral spines, while the fifth has a strong ventral procurved spine and a small dorsal spinule. The third somite has no dorsal spine at this stage. In this respect it differs most strikingly from the first stage figured by Cano, and to a less extent from that of *S. hispidus* in which there is a short spinous prolongation of the segment. The sixth segment, which is not separated from the telson, is of great length, greatly exceeding that of the first five segments combined.

The telson is triangular, not very deeply incised, and therefore of the form characteristic of most Caridea. At each outer angle is a small spine, and it bears on the posterior margin twelve setae, of which the outermost is very small and is not ciliated. The second seta (the third of the whole series) is very long and ciliated along its inner side only.

The first antennae are very long, consisting of a single-jointed peduncle bearing a short outer branch. The inner ramus is represented by a seta mounted on a bulbous base.

The second antennae consist of a stem bearing a narrow scale with four terminal joints and an inner branch bearing two long setae.

There is a very large upper lip, and an enormous mandible without a palp.

The first maxillae have the usual pair of inner lobes or laciniae, but are remarkable for the total absence of a palp. In Cano's figure of this appendage in his first stage a very small protuberance is shown which may indicate the rudiment of a palp.

The second maxillae have four well-defined basal lobes, an inner ramus which shows indications of two joints, and a very small exopodite (scaphognathite) bearing five setae, of which the proximal one is very large. Brooks and Herrick figure this appendage from a larva before the first moult, and show apparently no trace of an exopodite. On the other hand, Cano's figure shows a large scaphognathite with numerous setae, which tends to confirm my opinion that his first stage is really the second.

The first maxillipede consists of a stem with two distinct joints, an obscurely three-jointed endopodite, and a short exopodite bearing four setae.

The second and third maxillipedes have long endopodites of four joints, the fourth and fifth not being separated. The exopodite bears in each case six setae.

The first pair of pereopods are present as biramous appendages, the endopodite consisting of a single short joint. There is no trace of any other appendages.

Stage II. Length, 4.35 mm. Rostrum, 1.52 mm.

This stage is precisely the same as the preceding stage with regard to the appendages, but differs in the following respects:

1. The rostrum is now armed with numbers of small spinules towards the end.
2. The ventro-lateral pair of spines on the first somite of the pleon are greatly enlarged, and the third somite bears a huge dorsal spine as figured by Cano.

Both dorsal and lateral spines of somite 5 are larger, and the sixth somite has small spinules on its ventral surface. The fourth somite has lost its pair of lateral spines, and the form and armature of the telson have changed considerably. In place of the broad triangular form the telson now has two narrow divergent arms and bears a series of short spines along its outer margin. Each arm terminates in a strong smooth spine, and, as before, there are six pairs of posterior setae of which the outermost is minute and is now ciliated. The outer terminal spine obviously corresponds to a seta, and the armature is therefore 7 + 7 setae. The reduction of the second seta to a minute hair is a character of great importance to which I shall return later.

Stage III. Length, 5.45 mm. (fig. 54, *b*). Rostrum, 2.05 mm.

This stage differs in no essentials from the preceding stage with the exception that a minute knob represents the second pereopod, and there is an additional seta on the telson. Further, the inner branch of the first antenna appears and a large supra-ocular spine is developed.

Stage IV. Of this stage I have no specimens, but the larva figured by Cano (fig. 1, *b*) measuring 8 mm. evidently succeeds the stage just described. In this stage, according to Cano, there are still no additional functional legs, but the four posterior pairs are present as rudiments, of which the first two are biramous. The uropods are developed, the internal branch having no setae.

The next stage in the series is represented by a larva of 14.8 mm. taken by the "Terra Nova" at station 45. Having regard to the great increase in size, I think

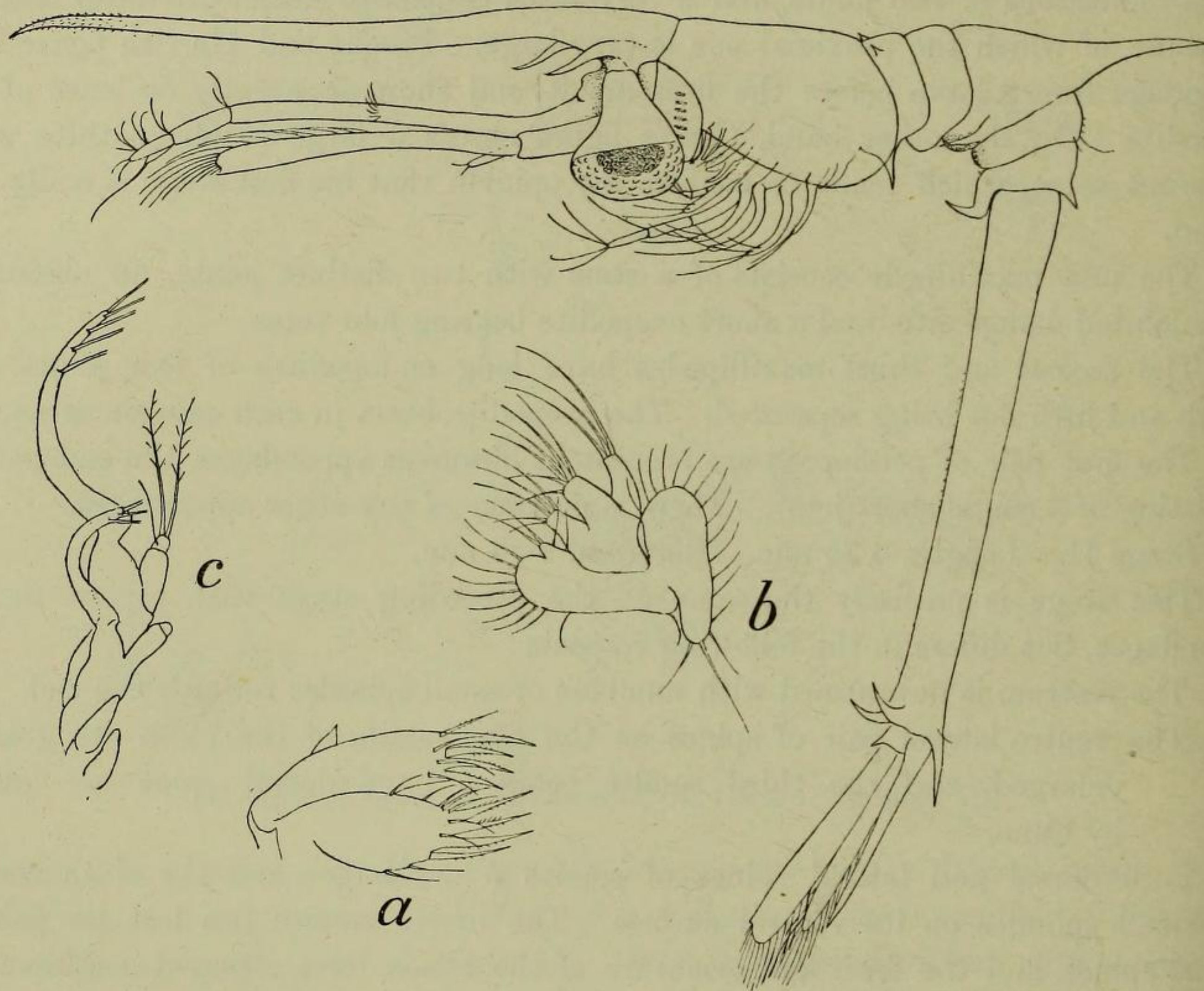


FIG. 55.—*Stenopus*, sp. Station 45. Stage VI. *a*. First maxilla. *b*. Second maxilla. *c*. Legs 2 to 5.

it probable that it represents a sixth stage rather than the fifth which remains unknown.

Stage VI. Length, 14.8 mm. Rostrum, 4 mm.

This larva is of some special interest as it is at once recognizable as being a slightly earlier stage of the form described by Ortmann (1893, p. 85) as *Embryocaris stylicauda*. Ortmann's specimen was taken off the Brazilian coast in much the same region as the "Terra Nova" specimens, and no doubt belongs to the same species—probably *S. hispidus*. The differences between this larva and stage III are, with the exception of the changes in the telson and uropods, rather of degree than of the appearance of new characters.

The supra-ocular spines are larger. The first somite of the pleon bears a pair of small dorsal spines in addition to the pair of ventro-lateral spines. The median ventral spine of the fifth somite is bent forwards at right angles to form a peculiar hook.

The telson is separated from the sixth somite and is now a narrow linear plate, forked at its extremity, and with four small hairs within the depression of the fork. All the setae of the early stages seem to have been lost and the form has entirely changed. The sixth somite terminates in a large dorsal spine and a pair of ventral spines curving forwards.

The stem of the first antenna is three-jointed, and the inner branch nearly equals the outer in length.

The inner branch of the second antenna is a very short rod, with two delicate setae.

The mandible still has no palp.

The first maxilla now has a trace of a palp as a small triangular excrescence without setae (fig. 55, *a*).

The second maxilla is a distinctly four-jointed appendage, the second joint bearing a bi-lobed lacinia, and the third two deeply separated lobes. The exopodite is a large setiferous plate (fig. 55, *b*).

The maxillipedes are as before, and I have not seen any trace of an epipodite on the first pair.

The first three pairs of pereopods are developed, with setiferous exopodites, but the endopodites are very small, two-jointed, those of legs 1 and 2 with three setae on the terminal joint. That of the third leg has no setae. These three endopodites are borne, not at the end of the basipodite, but about half-way down it, in this respect resembling *Jaxea* and certain other Anomura.

Legs 4 and 5 are present as minute uniramous rudiments.

There is no trace of pleopods.

Gills are not yet developed, though a small papilla above the first and second leg may represent the first pleurobranch.

Stage VII. Of this and later stages I have no specimens, but both Ortmann and Cano described a stage which is evidently the last larval stage. Ortmann's specimen measured 19 mm., while Cano's had the enormous size of 30 mm. In this larva the general form is the same as before, but all the pereopods are developed and the endopodites of the first three are chelate, though functionless and indistinctly jointed. The last two pairs are uniramous.

As regards the pleopods Cano and Ortmann differ. The former states that there are five pairs, of which the first pair is uniramous, while Ortmann says that the first somite bears no pleopods and that the four pairs present are uniramous. On the other hand Cano's figure shows the first somite without pleopods, so that I accept Ortmann's statement as applying to both forms. It is unfortunate that any doubt should attach to a question of so much importance.

Stage VIII. This is the first post-larval form described and figured by Cano (fig. 1, *d*). The adult characters are to a large extent assumed, but the abdomen is shown as flexed at right angles at the third somite, which shows a pronounced Caridean hump. Cano's figure shows no pleopod on the first somite. According to Cano the gills are present in their full number with the exception of the arthrobranch on the first maxillipede.

The development of *Stenopus* as here described is remarkable in several respects and seems to me to throw some light on the systematic position of the genus.

1. The larva is unique among Decapods in having when hatched four pairs of natatory limbs. In the Caridea there are three only, and in Reptantia there are, as a rule, only two. Further, it is a general if not universal rule, in Caridea and also in Reptantia, where the larval series is complete, that the uropods appear at the second moult. In *Stenopus* apparently they are first developed in stage IV.

The pereiopods also do not develop in the same way as in the Caridea, since the posterior pairs are delayed till the sixth stage, whereas they appear much earlier as a rule both in Caridea and in Reptantia.

2. The general appearance of the larva is quite distinctive, but resembles most closely the Mysis stage of the Penaeidea, particularly with regard to the great size of the rostrum and supra-orbital spines, and the median dorsal spines of the third, fifth, and sixth pleon-somites. But whereas the huge spine is borne by the third somite in *Stenopus*, it is on the second in the Penaeidae and the resemblance does not extend to the appendages.

3. In some characters *Stenopus* resembles in a remarkable way certain of the Reptantia.

(*a*) The telson. The reduction of the second pair of marginal spines to a small hair is a character confined to *Stenopus*, the Thalassinidea, and the Anomura. Such an apparently trivial modification can hardly be conceived of as independently acquired. The exact resemblance in form of the telson in the later stages to that of *Jaxea*, together with the great development of the dorsal and lateral spines on the end of the sixth pleon-somite is very striking. Even the serration of the outer margin of the telson, which is not found in any other Decapod larva, is the same in the two genera.

The great development of spines on the pleon-somites is also a character found more commonly among Penaeidae and Reptantia than in Caridea.

In fact the general facies of the larva in the "Embryocaris" stage is such that, at first sight, it would undoubtedly be referred to the Thalassinidea.

(*b*) The absence of a pleopod from the first somite of the pleon is entirely unknown among the Natantia, either larval or adult, and it is absent only in the adults of some Reptantia. It is absent from the larvae of all Thalassinidea whether present in the adults or not.

(*c*) The reduction of the endopodites of the third maxillipede and the first three

pereiopods, and their place of origin far from the distal end of the basipodite, is a feature which is found elsewhere only in the larvae of some Thalassinidea and Anomura, e. g. *Upogebia*, *Jaxea*, *Galathea*, and *Eupagurus*.

Of the development of the remaining genera of the Stenopidea—*Spongicola*, *Engystenopus*, and *Richardina*—practically nothing is known.

Spence Bate (1888, p. 216) reproduces a drawing by Willemoes Suhm of the first-hatched larva of *Spongicola*, of which Suhm says that it is "a Zoea in which, however, some appendages are to be seen which, as a rule, come out only in a later stage." His figure shows a very remarkable animal with sessile eyes, but with five pairs of thoracic appendages of which the third and fourth only are biramous. These appendages must be the three pairs of maxillipedes and two pairs of pereiopods. The body behind the carapace is shown with six distinct somites and a long unsegmented posterior portion. If this figure is correct, which it is difficult to believe, the larva of *Spongicola* is even more strange than that of *Stenopus*. On the other hand, Bate himself figures a larva taken from the egg having only the first two maxillipedes developed and the abdomen unsegmented. Both agree in representing the carapace as very short and leaving part of the thorax uncovered, a feature recalling the Penaeid Zoea, and in the form of the telson, which closely resembles that of *Stenopus*. As is the case in *Stenopus* the telson has an outer spine and five setae on either side, but it is probable that the minute second seta was also present in *Spongicola* but was overlooked.

In *Richardina* the eggs are very large (2 mm. in long diameter in *R. spinicineta* and in *S. fredericii*) and development consequently abbreviated. Kemp (1910, p. 169) has examined larvae taken from the eggs of *R. spinicineta* and finds that "all the pereiopods and pleopods are present, though the uropods are not yet free." The telson is deeply bifurcate as in *Spongicola venusta*.

The position of the Stenopidea in Decapod classification has long remained a matter of uncertainty.

De Haan (1850) included *Stenopus* with the Caridea, but Huxley in 1883, dividing the Decapods on the basis of gill structure, placed it in his group of Trichobranchiata, wherein were contained the Thalassinidea, Homaridea, and Penaeidea. Spence Bate (1888) followed Huxley in laying stress on the structure of the gills, but separated the Penaeidea in a new group, the Dendrobranchiata, leaving *Stenopus* with the Astacidea.

Boas (1880), on the other hand, definitely included the Stenopidae as a family of the Penaeidea. Ortmann (1896), while retaining them among the Natantia, separated them from the Penaeidea as a division Stenopidea equivalent to the Penaeidea and Eucyphidea. Alcock (1901), though he did not adopt Boas's primary division, included the Stenopidea in his Macrura Caridides. Finally Calman (1909), while expressing some doubt as to their affinities, leaves the Stenopidea in the same position as Ortmann, namely, among the Natantia.

The prevailing opinion therefore has been that the Stenopidea hold a position intermediate between the Caridea and the Penaeidea, with, on the whole, a greater relationship to the latter.

It seems to me that this view is not altogether in accordance with the structure of the adult, and is certainly not supported by the larval history.

So far as concerns the adult, *Stenopus* seems to have practically no relationship with the Caridea. The only structural points of agreement of any importance are the possession of a well-developed antennal scale and the relatively large size of the first abdominal somite. Neither of these characters can be regarded as of great significance, while there are many serious points of difference.

With the Penaeidea the relationship is very much closer; but, on the other hand, it is very striking that *Stenopus* resembles the Penaeidae mainly in just those characters in which the latter resemble the Reptantia. Ortmann (1890) has given a statement of the resemblances to the Penaeidea as follows:

1. The first three pairs of pereopods are chelate.
2. The endopodite of the third maxillipede is seven-jointed.
3. The exopodite of the first maxillipede has not the basal enlargement characteristic of the Caridea.
4. The inner lobe of the first maxilla is rounded.
5. The mandible is undivided.
6. The pleopods have no appendix interna.

All these characters are shared with the Reptantia.

The Stenopidea differ from the Penaeidea in the following points:

1. The gills are trichobranchs.
2. The chela of the third pereopod is the strongest.
3. The epimera of the first abdominal somite slightly overlap those of the second.

With regard to the first point the Stenopidea resemble some Reptantia. The second is hardly a point of serious difference from the Penaeidae, in which the third pereopod is usually the longest, while the third character is peculiar to the Stenopidea.

A character which is not mentioned by Ortmann, but which seems to me to be of some importance, is the possession of a distinct exitic lobe on the first maxilla of *Stenopus*. This lobe, which is so striking a feature of the first maxilla of Euphausids, is found in a number of Reptantia (e. g. *Upogebia*) but very rarely in Caridea. The only instance known to me is that of *Atyaephyra desmarestii*, but it is not present in the nearly allied genus *Caridina*. It is true that this exite is a primitive structure present in the ancestral Decapod and therefore it may be expected to be retained in some Caridea, but it has been almost entirely lost in that group and is not infrequently found in Reptantia.

With regard to its gill formula *Stenopus* differs radically from the Caridea, and agrees perhaps better with the Penaeidea than with the Reptantia (Homaridea).

I have, through the kindness of Dr. Calman, been able to examine a specimen of *Stenopus* from Penang and find that it has a pleurobranch also on the second maxillipede and a rudiment of a podobranch on the third maxillipede, the total number of gills therefore being $21 + 7ep.$ instead of $19 + 7ep.$ as usually given. In total number, therefore, the formula is one of the most complete known and is evidence of the primitive position of the genus.

It seems to me that, on the evidence of the adult structure, *Stenopus* holds a position between the Penaeidea and the Homaridea.

If we now consider the evidence to be drawn from the structure of the larva, the first conclusion, namely that *Stenopus* has no relation to the Caridea, is fully borne out. The differences are pointed out above (p. 138) and need not be further discussed here.

On the other hand, it is by no means easy to decide to what relationship the facts actually do point. The larva has certain quite distinctive characters of its own, but in general form it presents somewhat of a combination of Penaeid and Thalassinid characters. The huge spiny rostrum and large supra-orbital spines recall the Penaeids, but the arrangement of the dorsal spines on the abdomen agrees more closely with that of the Reptantia such as *Nephrops* or some Thalassinidea. The large supra-orbital spines, however, are the only feature which can fairly be said to be shared with the Penaeidea, such spines being absent from the Reptantia as a rule. They are, however, present in *Nephrops*.

But it is to the detailed structure of appendages and telson that we must turn rather than to the general body-form in seeking for real evidence of relationship, and here we have certain well-defined characters which must be regarded as of phylogenetic significance. These are the form and armature of the telson, and the form of the third maxillipede and first two pairs of pereopods. As has been noted above, the telson almost exactly resembles that of *Jaxea*, while the reduction of the endopodite of the third maxillipede and its point of origin near the base of the basipodite are characters otherwise confined to *Jaxea*, *Naushonia*, and *Upogebia* among Thalassinidea, and to the Anomura. The reduction of the second seta of the telson implies close relationship with the Thalassinidea and Anomura rather than to the Homaridea. In the same way the peculiarly twisted and rudimentary pereopods in the last larva sharply distinguish *Stenopus* from the whole of the Natantia and also from the Homaridea, but rather closely resemble those of the Anomura.

The absence of the first pair of pleopods from the last larva is a character of some importance. The appendage is invariably developed in the Penaeidea and Caridea but is absent from the larva of the majority of the Reptantia.

So far, then, as the development goes, *Stenopus* must certainly be placed among the Reptantia, and within that group it finds its nearest kin in the Laomediidae and the higher Anomura.

THALASSINIDEA.

Thanks to the work of Sars, Cano, Thompson, and Miss Webb, we are acquainted with the larvae of representative species of each family of the Thalassinidea except the Thalassinidae, while some larvae of this tribe have been described by Bate and Ortmann under the names of Oodeopus, Anomalocaris, and Sestertius.

As these larvae are not uncommon in the plankton and possess very distinctive features, I think it may be useful to summarize the information regarding each family before proceeding to describe the larvae from the "Terra Nova" collections belonging to that family.

I. Axiidae.

Species of which the development is known :

Axius stirhynchus, Leach. Miss Webb (1921) has described the larva and has shown that the larvae described under this name by Cano (1891) belonged to *Callianassa*.

Calocaris macandreae, Bell. Sars (1889). Björck (1913).

Characters of these species :

Rostrum broad, serrated in *Axius*.

Abdomen with or without dorsal spines. These spines when present are small (*Axius*).

Telson with median spine and numerous setae, the second seta reduced to a hair.

Mandible palp developing early.

Exopodites present on all pereopods, but rudimentary on the last pair.

Endopodites normally placed and not reduced.

Pleopods absent from first somite.

Uropods not developed in larva (*Axius*), or developed but not functional (*Calocaris*).

It is probably a general rule in the family that development is abbreviated, the eggs being usually of great size. In *Axius stirhynchus* they measure 2.5×1.2 mm. and the larva possesses all its appendages except the uropods on hatching. In *Calocaris* also there are apparently only two larval stages.* In all the species of *Eiconaxius* and of *Iconaxiopsis*, so far as I can find, the eggs are large—e.g. *E. kermadecensis* 1.7×1.3 mm.

In the case of *E. parvus* Bate extracted the embryo, and his figure shows (1888, Pl. V, fig. 5) that the animal leaves the egg in practically the adult form.

On the other hand, within the genus *Axius* there are certainly species with eggs of normal size and an extended metamorphosis. For instance, the eggs of a species of *Axius* from the West Indies in the collection of the British Museum

* The earlier stages attributed to *Calocaris* by Sars belong to *Callianassa*. Only that represented on Table 2 belongs to *Calocaris*.

measure 0.55×0.4 mm. The young extracted from them have three pairs of biramous appendages only, though I am unable to say if there are rudiments of the succeeding limbs.

The presence of a rudiment of the exopodite on the fifth pair of pereopods is a character of great importance which may be distinctive of the larvae of the Axiidae as compared with other Thalassinidea. Among the Reptantia it is only the Homaridea, to which the Axiidae are in other respects also closely related, that have an exopodite on this leg. It must be regarded as a most primitive character found elsewhere only in the Penaeidea and the Hoplophoridae among Caridea.

Miss Webb states (1921, p. 407) that the last two pairs of legs are uniramous in the larvae of *A. stirhynchus*, but I have had the opportunity of studying specimens from Plymouth and find the rudiment of the exopodite to be quite distinct on each of these appendages.

In the "Terra Nova" collections there are larvae of the "Oodeopus" form with exopodites on the last leg, and these I refer with some confidence to the Axiidae. On the other hand, the same general form is undoubtedly characteristic of the Callianassinae, to which the majority of the Oodeopus larvae belong, and it may be that only those forms which combine the two characters of an exopodite on the fifth leg and of an indefinite number of setae on the telson should be included in the Axiidae.

In *Calocaris* there are no spines on the abdominal somites, while in *Axius* the dorsal spines are small and equal. It is probable that absence or reduction of these spines is an additional character that can be used to distinguish Axiid larvae from those of Callianassinae.

Axiidae. Species I (fig. 56).

Station 93. Length, 7.4 mm. to end of rostrum.

This larva is of some interest as presenting a transition from that of *Axius stirhynchus* to the Oodeopus form characteristic of the Callianassinae.

The rostrum is as long as the whole carapace and is flattened horizontally, with a row of denticles along each margin. The carapace has a sub-ocular spine, but its ventral margin is smooth. The second and third somites of the abdomen bear each a dorsal spine, that of the second being the longer, but the somite has no dorsal ridge as in *Callianassa*, and there are no lateral spines. The telson, which is not separated from the sixth somite, is triangular, with convex margin and a large median spine which is a prolongation of the telson plate itself. On either side there are ten relatively short spines, the second being reduced to a small hair.

The eyes are large, on short stalks, and without pigment.

The mandibles have a small papilla representing a rudimentary palp.

The three pairs of maxillipedes bear exopodites with 5, 5, 6 setae respectively, and their endopodites are fully developed, springing from the apex of the basipodite.

All the pereopods are large, the first pair having a chela and the second being sub-chelate, while each bears an exopodite, these exopodites, however, having no setae. There are four pairs of rudimentary pleopods, but the uropods are absent. The first two maxillipedes bear epipodites, but I am not certain if there are

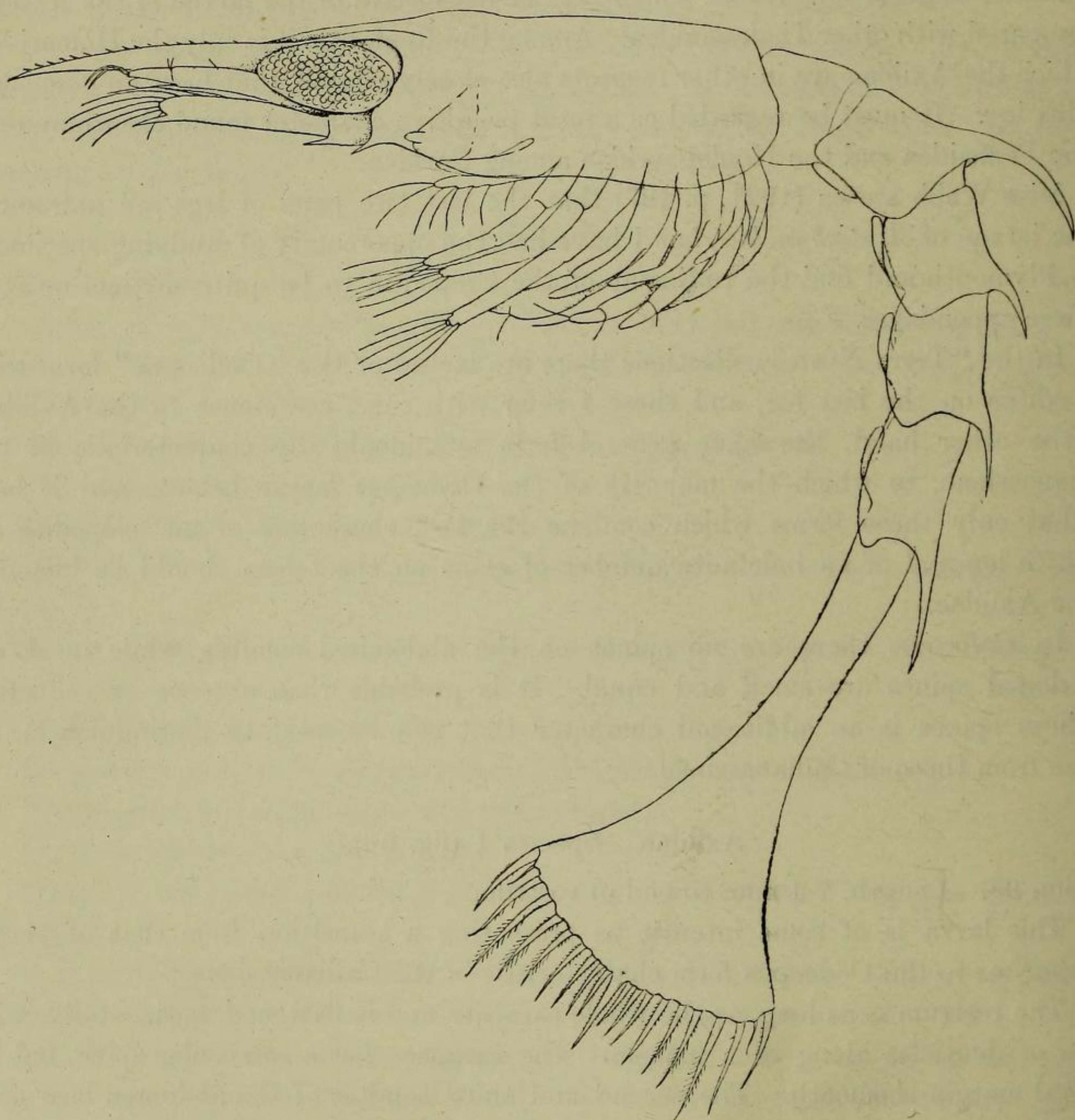


FIG. 56.—Axiidae. Species I. Station 93.

epipodites on the remaining appendages. I think I can detect a minute trace of an epipodite on each appendage except the fifth leg, but there are no gills.

This larva seems to correspond to the first stage of *Axius stirhynchus*, which in many respects it closely resembles. In *A. stirhynchus* in its first stage all the pereopods are present, though the fourth and fifth are small, and the first three pairs bear exopodites without setae. In the last stage the exopodites of these three pairs have setae, while the fourth and fifth pairs have rudimentary exopodites.

The telson, though differing in its posterior contour and in the smaller number of spines, is distinctly of the same type. *A. stirhynchus* also has the second spine reduced to a hair, an important point which is not mentioned by Miss Webb. The complete suppression of the uropods in larval life is a curious feature which seems to be in some way connected in Caridea with abbreviated metamorphosis (e.g. *Palaeomonetes varians macrogenitor*). Among the Thalassinidea it may be a characteristic of the genus *Axius*, but apparently not of the family, since uropods are developed (in a rudimentary form) in *Calocaris* and are present in some of the Oodeopus larvae described by Bate which, on other grounds, seem to be referable to the Axiidae. It is perhaps unsafe to place too much reliance on Bate's figures, particularly with regard to characters to which he would probably not have attached importance; but I am inclined to refer to some genus of the Axiidae his *Oodeopus geminidentatus* (Pl. CXLII, fig. 1) and *O. intermedius* (Pl. CXLIII, fig. 1). Ortmann's *Anomalocaris macrotelsonis* (1893, p. 87), although the form of the telson has a distinct resemblance to that of *Axius*, is probably rightly referred by him to the Callianassinae.

The identification of the larva just described with the genus *Axius* seems to me to be beyond question, but there remain a series of larvae which in some respects so closely resemble that of *Callianassa* that any positive identification seems to be impossible. This close resemblance is in itself of interest and importance, and for this reason I think it worth while to figure and describe some of these larvae even though they cannot be referred to their genera.

I accept provisionally the presence of a rudimentary exopodite on the fifth pereopod, and of a pleopod on the second abdominal somite as characters distinctive of the Axiidae, although I am aware that this pleopod is developed in some Callianassidae (*Upogebia* and *Callianassa subterranea*) and the exopodite is figured by Bate in larvae which are probably referable to the Callianassinae.

Axiidae. Species II and III. (*Iconaxiopsis?*) (figs. 57, 58).

At stations 131 and 148 larvae were taken of two species so closely resembling each other that they certainly belong to the same genus and may be dealt with together.

Stage I. Length, 4.85 mm. Station 148 (fig. 57, a).

Rostrum long, not flattened, and with a few small teeth at the distal end. Carapace with a very long sub-ocular spine, and smooth (species II, station 148) or with a few small denticles (species II, station 131) on its ventral margin.

The abdominal somites are without spines, except the fifth, which has a median dorsal spine.

The telson is triangular, with a deep median cleft and a median spine. Spine formula 7 + 1 + 7, the second being reduced.

The second antenna has the endopodite as a short rod bearing three setae of

about equal length. The scale has no setae on its outer margin and no terminal spine.

The endopodites of the maxillipedes are well developed, and the exopodites bear 4, 4, 4 setae respectively. The pereiopods are traceable as five rudiments beneath the skin.

Species III appears to hatch in a rather more advanced condition, since the earliest

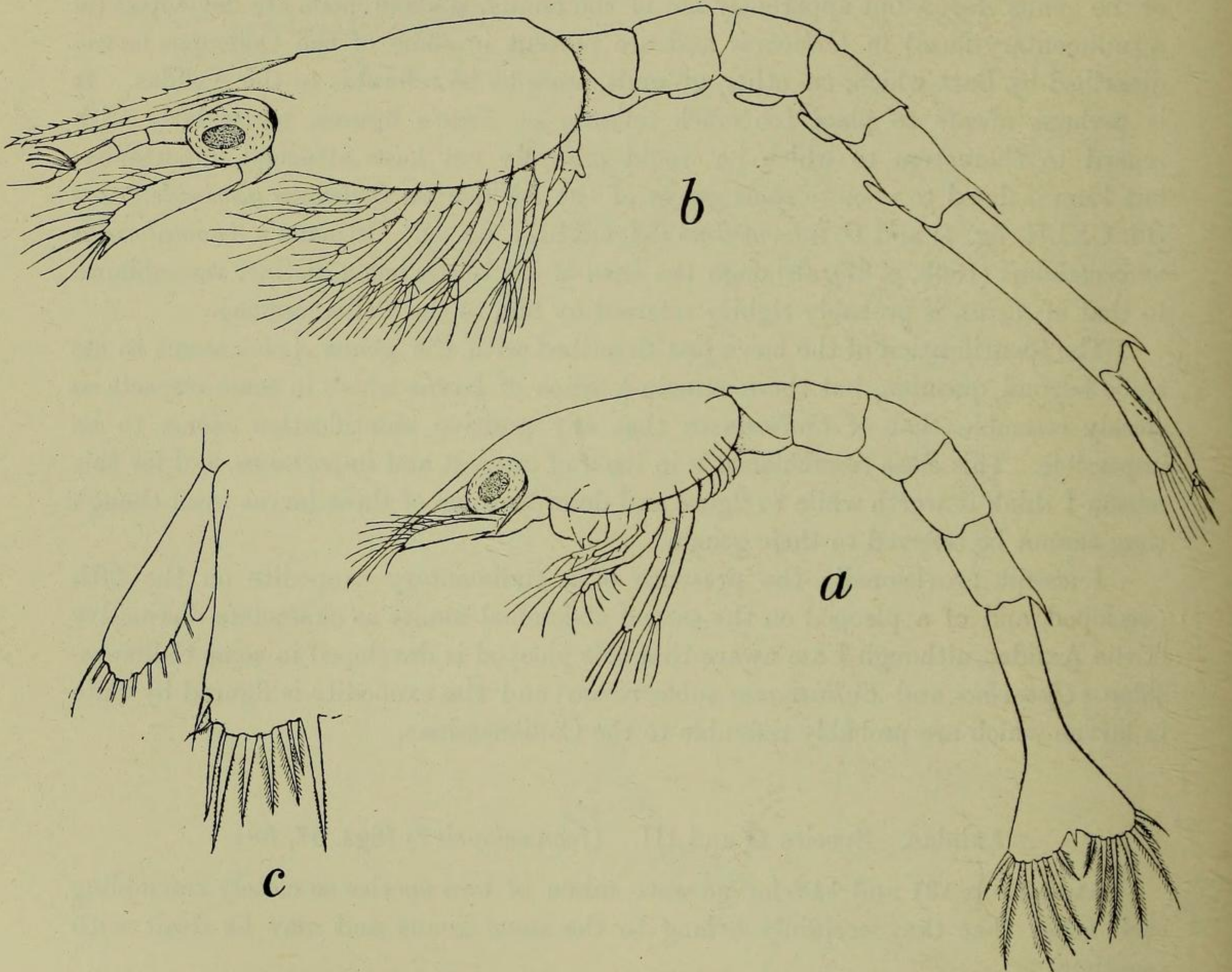


FIG. 57.—Axiidae. Species II. Station 148. *a.* Stage I. *b.* Stage III. *c.* Stage III. Telson.

larva found measures 5 mm. and the pereiopods are more developed. In most cases they are still beneath the skin, but in some specimens they are separated and are biramous.

Stage II. Length (species III), 6.45 mm.

The rostrum is broad, serrate, and constricted at the end, the carapace and abdomen as before.

The telson is of the same shape, but its formula is now $8 + 1 + 8$ and the median spine is longer. The second seta is even more reduced.

The first antenna has the rudiments of both branches.

The scale of the second antenna has a terminal spine, but the endopodite has lost its setae and is a simple rod about two-thirds of the length of the scale.

With regard to the pereopods there are differences between the two species. In both, these rudiments are all equally large and biramous, but whereas in species III the exopodites are all without setae, in species II those of legs 1 and 2 bear one or two setae.

Pleopods are absent, but are just traceable in some specimens of species III.

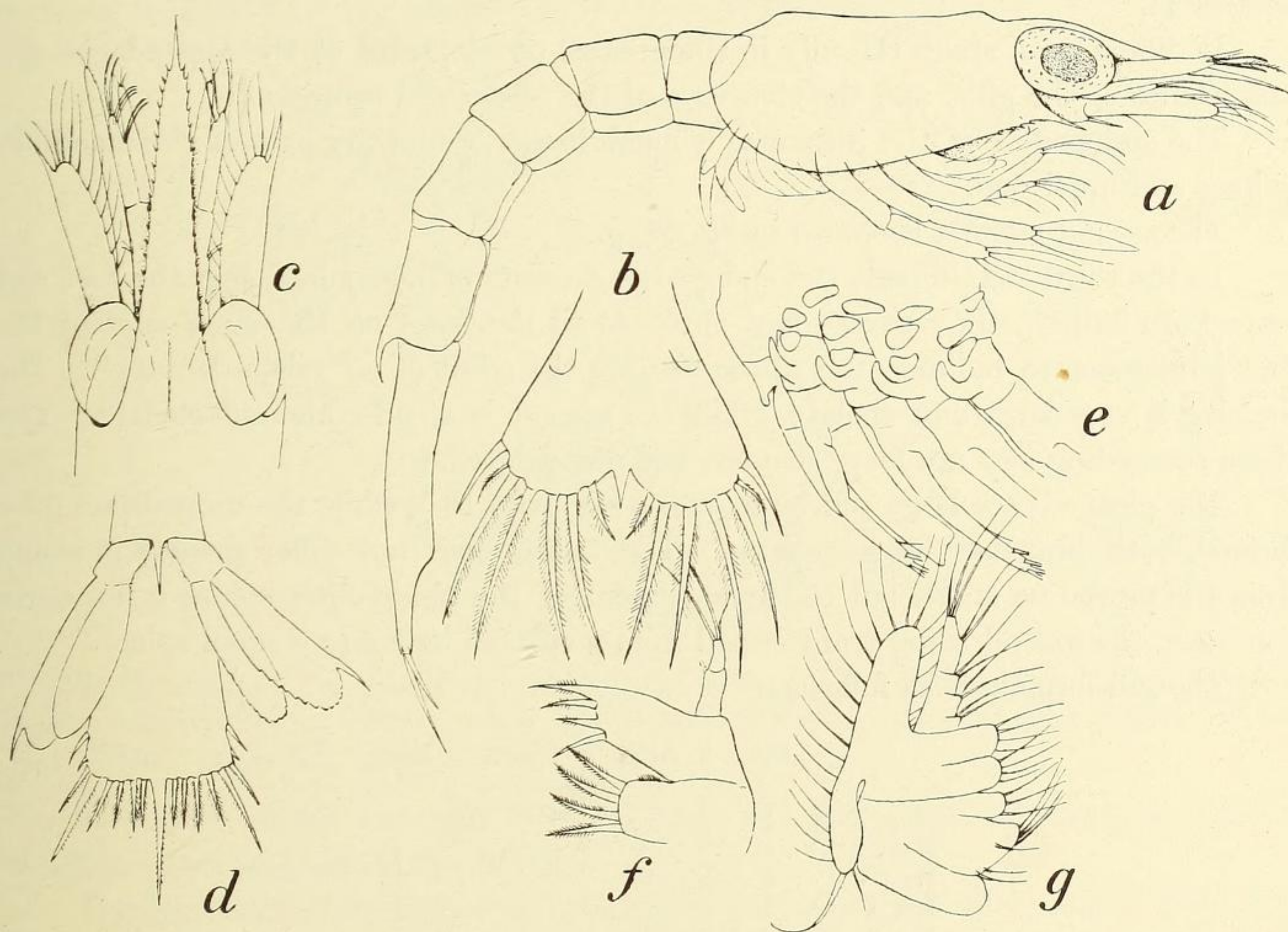


FIG. 58.—Axiidae. Species III. Station 131. *a.* Stage I. *b.* Stage I. Telson. *c.* Stage IV. Head. *d.* Stage IV. Telson. *e.* Stage IV. Gills. *f.* Stage IV. First maxilla. *g.* Stage IV. Second maxilla.

Stage III. Length (species II), 6.6 mm. (fig. 57, *b*).

In general form this stage does not differ from the preceding except that the telson is separated from the sixth somite, which has dorsal, lateral, and ventral spines, and the uropods have appeared.

The telson is longer and narrower, and the arrangement of the spines is changed. The median spine is very long, and there are eight spines on either side; but they are shorter and stouter than in stage II (fig. 57, *c*). The small reduced second seta remains the same.

All the pereopods are well developed, the first two pairs beginning to become

sub-chelate. On the first four pairs the exopodite is functional, bearing 6, 5, 5, 5 setae, while that of the fifth pair is reduced to a small papilla.

Small pleopods are present on somites 2 to 5.

Gills are not yet developed, but there are traces of epipodites on each of the maxillipedes and on the first four pereopods. The epipodite of the second maxillipede is exceedingly small.

Stage IV. Length (species III), 8 mm. (fig. 58, c-f).

This stage, which is the last before metamorphosis, is not represented in species II.

It differs from stage III only in the greater development of the appendages, the appearance of the gills, and the structure of the telson and uropods.

The endopodite of the antennae is much longer, while the palp of the mandible is long and unjointed.

The second maxilla is shown in fig. 58, g.

In the third maxillipede the endopodite consists of five joints, but the first and second are indistinctly separate and three small denticles on the inner edge of the first joint seem to indicate the appearance in the adult of a "crista dentata." The first leg is very large and chelate, while the second is slender and sub-chelate. The three succeeding legs are long, slender, and four-jointed.

The pleopods are large and biramous on somites 2 to 5, while the uropods are fully formed, both branches bearing setae. The telson does not differ greatly in shape from the preceding stage, but the arrangement of the three outer spines is not quite the same, the second being transformed from a ciliated hair into a small spine.

The gill formula is as follows :

	Ep.	Arth.	Pleur.	Exop.
Mxp. 1	1	—	—	1
Mxp. 2	1	—	—	1
Mxp. 3	1	2	—	1
Leg 1	1	2	—	1
Leg 2	2	1	1	1
Leg 3	1	2	1	1
Leg 4	1	2	1	1
Leg 5	—	—	—	rud.

The presence of pleurobranchs alone suffices to place this larva within the Axiidae, since all the other Thalassinidea have lost these gills. Even within the Axiidae the genera *Axiopsis*, *Calocaris*, and *Calocarides* may be excluded since they have no pleurobranchs; while within the genus *Axius* itself the sub-genera *Neaxius* and *Paraxius* have none. The sub-genus *Axius* may also be excluded since the larva is known and differs in many respects from that just described, so that only *Iconaxiopsis* and *Eiconaxius* remain. There are, it is true, other genera of the Axiidae described since the publication of Borradaile's revision of 1903, but I am not aware of the gill formulas of these genera.

Of *Eiconaxius* the three species hitherto described have direct development and are therefore excluded. There remains only the genus *Iconaxiopsis*, and it is therefore to this genus that I provisionally refer these two larvae. I am well aware of the slenderness of the grounds for doing so, but there is some advantage in attaching a name to the larva even if it may later prove to be incorrect.

Axiidae. Species IV (fig. 59, *a, b*).

At station 43 a larva was taken which I place with some doubt among the Axiidae by reason of the absence of a large dorsal spine on the second abdominal somite.

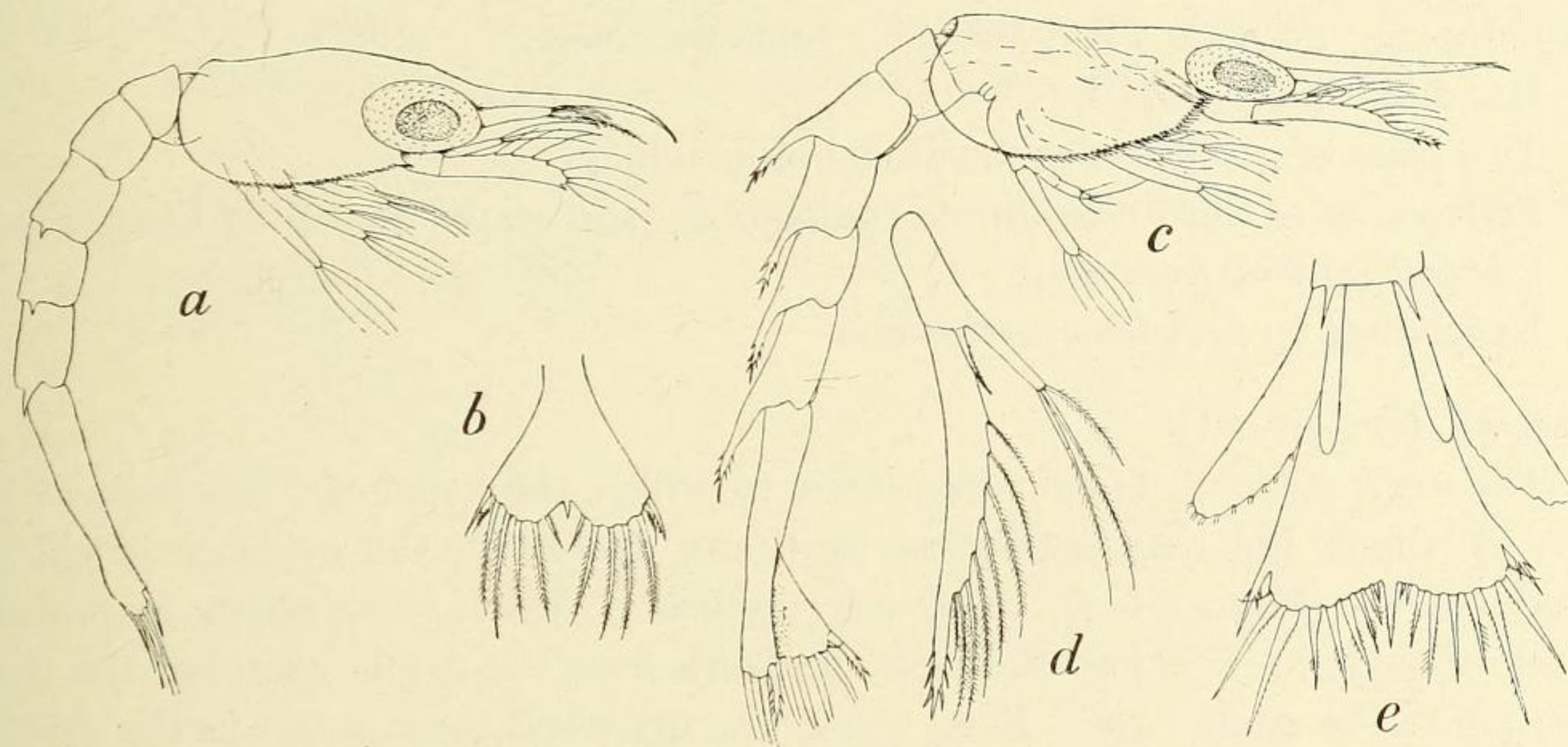


FIG. 59.—Axiidae. *a*. Species IV. Station 43. *b*. Species IV. Station 43. Telson. *c*. Allied species. Station 133. *d*. Allied species. Station 133. Second antenna. *e*. Allied species. Station 133. Telson. Stage III.

This larva, which measures 2.8 mm., is in the first stage, and therefore has not the distinctive features of the family.

The rostrum is very long, and has only one or two teeth at the distal end. The carapace is denticulate along the whole of its ventral margin.

The abdominal somites have no dorsal spines, but somites 3, 4, and 5 have each a pair of small lateral spines.

The telson is triangular, with a formula of 7 + 1 + 7, the second seta reduced.

The endopodite of the second antenna has three long setae.

The three pairs of maxillipedes are fully developed, their exopodites having four setae in each case.

There is no trace of pereopods.

A very similar form (fig. 59, *c*) was taken in some number at stations 122, 131, 133, and 135. This species is distinguished by having long spines on pleon-somites 2 to 5, each of which bears a series of denticles. The antennal scale also has a long denticulate spine.

II. Laomediidae.

The larvae of *Jaxea* (Cano, 1891, &c.) and of *Naushonia* (M. Thompson, 1903) have been described, and it is interesting to find that, strange as is the form assumed by the former, there are characters common to it and to *Naushonia* in respect of which both differ from other Thalassinidea. In fact the larvae provide the strongest evidence for the inclusion of *Naushonia* in the Laomediidae.

The characters of the two forms may be combined as follows:

Rostrum small.

Abdomen without dorsal spines, but with ventro-lateral procurved spines.

Telson deeply hollowed, the angles produced, without median spine. Second seta reduced. Formula 7 + 7, becoming numerous later.

Mandible sickle-shaped.

Two pairs of maxillipedes functional on hatching.

Endopodite of third maxillipede rudimentary and seated at base of basipodite.

Pleopods absent from somite 1.

Exopodites on first four pereopods.

Jaxea, sp. (figs. 60, 61).

The very striking *Lucifer*-like larva to which the name of "Trachelifer" was given by Brook has been attributed by Claus, mainly on the evidence of the gill formula of the Mysis stage, to *Jaxea nocturna*. This identification is probably correct, though no one has obtained the larva from the egg or observed the transformation to the adult form. Even Cano, who described three stages in the development, was unable to obtain any post-larval stages. The larvae are but rarely taken on the British coasts, so that the opportunity seldom occurs of keeping living specimens in the last Mysis stage till their transformation.

In one plankton sample from the Bay of Islands (station 148) several specimens were taken of a larva which agrees in almost every detail with the European *Trachelifer* and must therefore be attributed to a species of *Jaxea*, though, on account of certain minor differences, it certainly does not belong to *J. nocturna*. So far as I am aware, the only species of the genus which has been described is *J. nocturna*, which has been taken in the adult state on rare occasions in the Mediterranean and round the British coasts. The larvae which I have to describe prove that a second species occurs in New Zealand waters, and probably in abundance.

The larvae represent five stages in the development, and form an almost complete series to the last Mysis stage.

Stage I. Length, 4.5 mm. (fig. 60).

This larva agrees in almost all respects with the first larva of *J. nocturna* figured by Cano (1891, Taf. IV, fig. 1, a), but it is not certain that this is the first stage hatched from the egg, since Claus has figured one which appears to be younger (1884, p. 32, Taf. VIII, fig. 48).

The mouth-parts are in all respects the same, the left mandible and the left paragnath being modified as slender sickle-shaped organs.

The first two pairs of maxillipedes are developed as biramous appendages, of which the endopodite is four-jointed, and the exopodite bears four terminal setae only.

The third maxillipede is represented by a uniramous rod, and there are two pairs of small papillae which are the rudiments of the first two pairs of pereiopods.

Each of the five abdominal segments bears a pair of lateral hooks curving forwards. In *J. nocturna* according to Cano the first somite has no spine, but I am doubtful if this is a real specific difference, since this spine is certainly present in a larva in a later stage (stage IV) taken on the Eddystone ground near Plymouth. This spine is, however, omitted from Bouvier's drawing (1914, fig. 1).

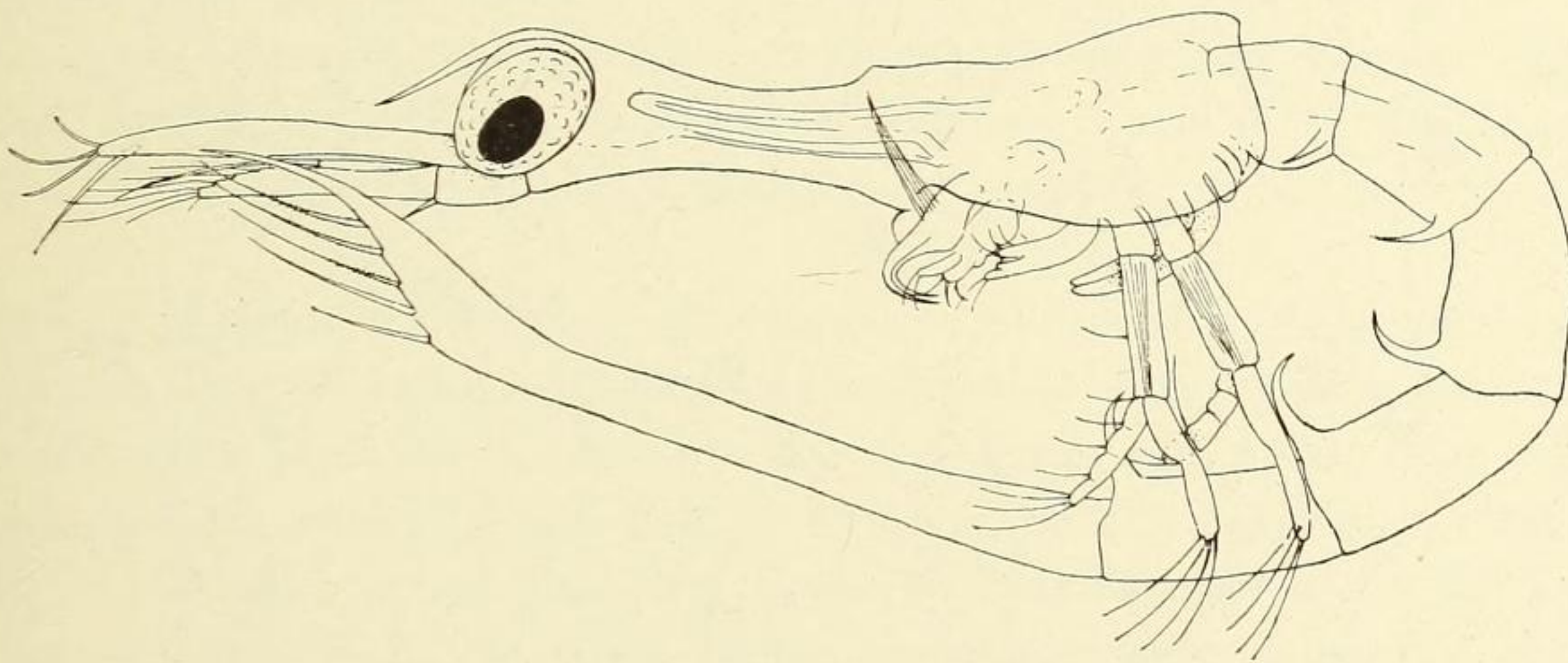


FIG. 60.—*Jaxea*, sp. Station 148. Stage I.

The telson is deeply cleft, with two narrow arms each produced into a slender spine, and there are five pairs of long spinous setae on the posterior margin. At the base of the outermost seta, and somewhat on the ventral side of it, there springs a very small hair. This hair, which is easily overlooked, is not shown by Cano, neither does Thompson show it in his figures of the nearly allied species *Naushonia crangonoides*. This and the stout terminal spine represent modified setae, the formula being the usual 7 + 7 setae. The specimen is approaching the moult, and the appearance of three more setae at the next stage is indicated beneath the cuticle.

Stage II. Length, about 6 mm. (fig. 61).

Of this stage there are three specimens. It differs from the first in the development of the third maxillipede which has an exopodite with five setae. The endopodite, however, is represented only by a small papilla half-way down the inner face of the basipodite.

The first pereiopod is a long biramous rod without setae, turned forwards and lying between the bases of the maxillipedes. The remaining legs are small papillae, the first of which is bi-lobed.

The telson is of the same shape as before, but with eight well-developed setae

on either side (the formula is therefore 10+10). It is not separated from the sixth somite, and the uropods are not developed.

The second maxilla is of somewhat unusual form (fig. 61, *e*). Bouvier's figure of this appendage at a later stage (1914, fig. 3) shows only the distal part of it, but it is correctly figured by Claus 1891 (fig. 4, *b*). It is actually a distinctly three-jointed appendage, the second and third joints bearing each a pair of endites or laciniae. The endopodite is a small papilla not separated from the distal endite, while the exopodite

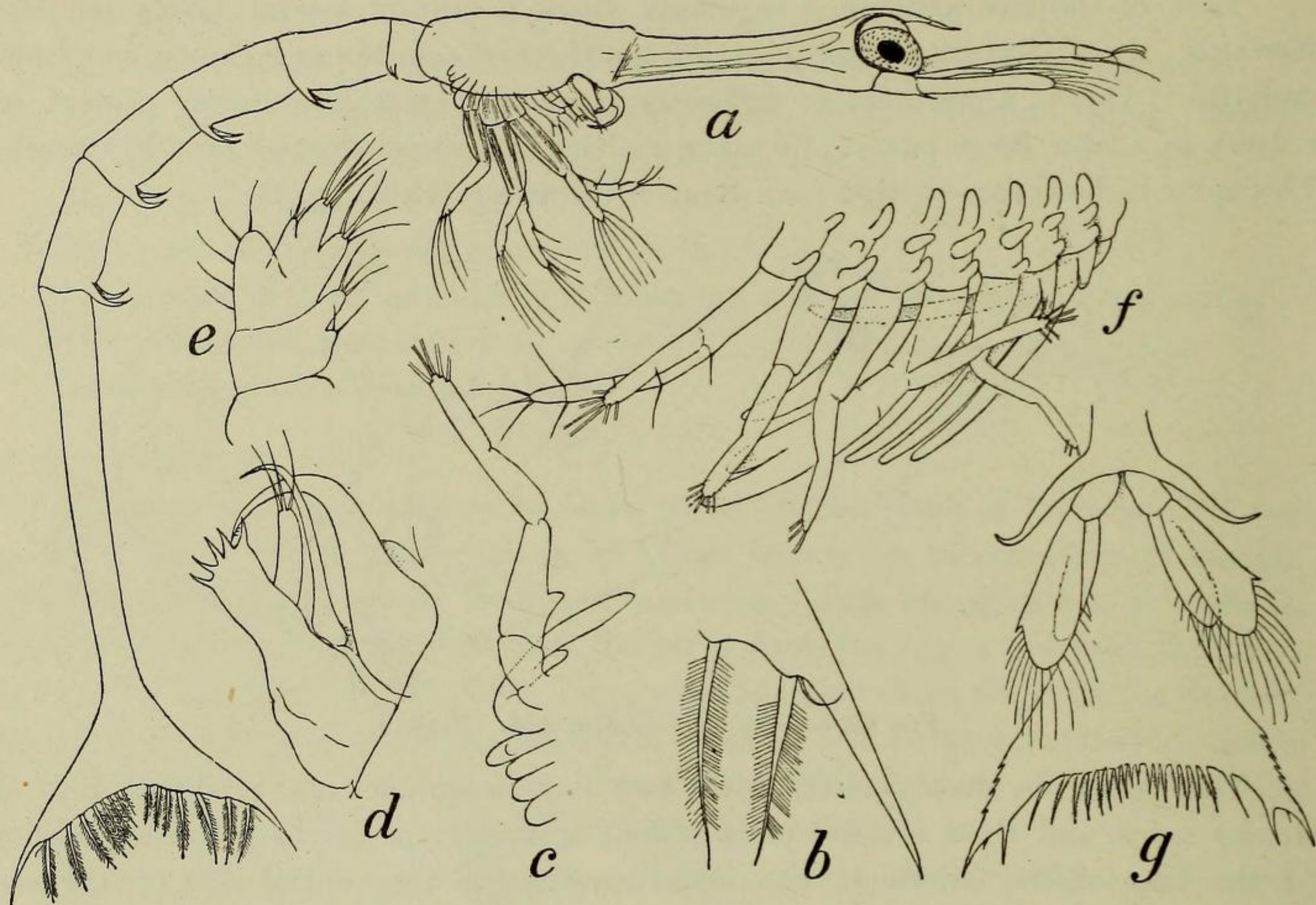


FIG. 61.—*Jaxea*, sp. *a*. Stage II. *b*. Stage II. Part of telson. *c*. Stage II. Third maxillipede and pereopods. *d*. Stage II. Mandible and first maxilla of left side. Inner lacinia of maxilla hidden. *e*. Stage II. Second maxilla. *f*. Stage V. Pereopods. *g*. Stage III. Telson.

is a small plate bearing five setae and entirely lacking the proximal prolongation so characteristic of this part in most Decapods. The endites are provided with relatively few spines.

The peduncle of the first antenna is still of one joint, but there is a small rudiment of the endopodite.

Stage III. Length, 10.7 mm.

Three specimens. This stage differs from the preceding in the following characters:

1. The endopodite of the first antenna exceeds the length of the exopodite, and the peduncle is two-jointed.

2. The endopodite of the second antenna exceeds the length of the scale. The basipodite bears in this and also in the preceding stages two spines on the ventral margin.
3. The first two pairs of pereopods have natatory exopodites, though the endopodite is rudimentary. The third and fourth pairs have traces of exopodites.
4. The telson (fig. 61, *g*) is separated from the sixth somite, and has changed its form to a large, broadly triangular plate with a hollowed posterior margin bearing about twenty short spines. The outer margin is serrated in its distal third. The sixth somite bears two large spines.
5. The uropods have appeared, both branches being setiferous. The exopodite has a tooth on its outer margin. This tooth is not found in *J. nocturna*.
6. The pleopods are just visible.

This stage seems to correspond to the larva described by Bouvier as "*Mysis imparfaite*," but I should point out that his figures 5 and 11 (1914) have been transposed, fig. 11 referring to his larva of 9 mm. and fig. 5 to the form shown in fig. 9.

I cannot agree with Bouvier's interpretation of the thoracic appendages. He states that in the first two maxillipedes the endopodite is fused with the exopodite, while in the third pair and in the first two pereopods it is free. If he were right then the epipodites would, in this species, be borne on the basipodite, which would be unique. The real fact is that the first two maxillipedes show the condition normal for all Decapod larvae, while in the succeeding appendages the endopodite has been shifted down the basipodite so that it arises from near its base. This shifting of the endopodite is a feature characteristic of the Anomura, and is found also in *Upogebia* and in *Stenopus*.

Stage IV. Length, 13.65 mm.

The changes which have taken place are as follows:

1. The endopodite of the second antenna is as long as the peduncle of the first pair.
2. The first leg has now a large endopodite ending in a distinct chela.
3. Legs 3 and 4 have long, simple, rod-like endopodites and rudimentary exopodites. In this respect the New Zealand form differs from *J. nocturna*, since the latter has a setiferous exopodite on the third leg.
4. The pleopods have appeared as biramous rudiments on somites 2 to 5.
5. There is an epipodite on the first maxillipede, but I have seen no trace of gills.

This stage seems to correspond to Bouvier's first *Mysis* of 10-11 mm. and to Cano's 1, *b*.

Stage V. Length, 16.6 mm.

This corresponds to Bouvier's "Mysis à chélipèdes," fig. 9, and shows little change as compared with stage IV.

1. The endopodite of the second antenna extends to the end of the first pair.
2. The mouth-parts are apparently unchanged, except that the exopodite of the second maxilla has a proximal prolongation and has now the usual form of the scaphognathite.
3. The pereopods are as before, except that the endopodites have increased in size and the chela of the first leg is much larger. The fifth leg is a long rod turned forwards and reaching to the base of the second maxillipede. The exopodites of the third and fourth legs remain rudimentary (fig. 6, *f*).
4. The gills and epipodites have appeared to the full number of the adult, except that the podobranchs are not separated from the epipodites.
5. The pleopods are somewhat longer.
6. The telson has practically the same form and armature, with eleven or twelve spines on each side of the posterior margin. But the outermost spine, which in stage IV approached the outer apex and was not articulated to the telson, has now moved even farther, in such a way that the apex appears bifurcate, with a minute spinule (corresponding to the outer hair of stage I) between the forks.

There is a radical difference between the telson of the New Zealand form and that of *J. nocturna* as figured by Cano (it is not described by Bouvier). Cano states that it is "trapezoidal" and armed in its median part with 6 + 6 spines, and it is figured with convex margin and rectangular corners. But Scott's figures and my own experience of the larva of *J. nocturna* taken at Plymouth, lead me to suppose that Cano's specimen was either abnormal or wrongly described.

Bouvier (1914) has endeavoured to summarize the available information with regard to the metamorphosis of *Jaxea*, and to complete it, but it is a little difficult entirely to reconcile his account with others, and he has not included the stages described by Cano. Brook's description is very brief, and only one stage is actually described and can be recognized, while neither Claus nor Cano attempt to separate a complete series of moults. I cannot altogether agree with Bouvier in his interpretation of the stages described by Brook and Claus, and the following seems more correctly to summarize the changes at the successive moults.

Stage I. Claus, 1884, p. 32, Taf. VIII, fig. 48.

Length, 3.5 mm. Two maxillipedes only developed. Small rudiments of succeeding appendages. No uropods.

Stage II. Claus, 1884, Taf. VIII, fig. 49.

Cano, 1891, Taf. IV, fig 1, *a*.

"Terra Nova" stage I. Length, 4.5 mm.

Two maxillipedes only. Large rudiments of maxillipede 3 and leg 1. No uropods.

Bouvier includes here Brook's larva, fig. 1, but describes it as having maxillipede 3 a simple rod, whereas Brook states that it is biramous.

Stage III. Brook, 1889, p. 42, fig. 1.

"Terra Nova" stage II. Length, 6 mm.

Three pairs of biramous maxillipedes. No uropods. Claus (1884, p. 32) alludes to a larva of 4.5 mm. with three maxillipedes, but states that on the abdomen "sind bereits Fächergliedmassen gesondert." It seems there must be some error here.

Bouvier's stage III is the larva of 7.5 mm. described by Claus, but he states that it has only the three pairs of maxillipedes, whereas Claus distinctly says that the first pereopod is developed in that larva.

Stage IV. Claus, 1884, p. 32. Length, 7.5 mm. (not figured).

Brook, 1889, p. 422, fig. 2.

First pereopods with functional exopodites. Uropods present. This stage is not represented in my series.

Stage V. Bouvier, 1914, p. 196, figs. 1 and 2. "Mysis imparfaite."

"Terra Nova" stage III. Length, 10.7 mm.

Pereopods 1 and 2 with functional exopodites.

Brook does not attempt to give any detailed account of this or later stages.

Stage VI. Bouvier, 1914, p. 200, fig. 8. Length, 10-11 mm.

Cano, 1891, Taf. III, fig. 1, b.

"Terra Nova" stage IV. Length, 13.65 mm.

Pereopod 3 with functional exopodite in *J. nocturna*.

Endopodite of this and following appendages long. Endopodite of leg 1 begins to be chelate. Pleopods appear.

Stage VII. Bouvier, 1914, p. 200, figs. 5 and 9.

Cano, Taf. III, fig. 1, c.

"Terra Nova" stage V. Length, 16.6 mm.

Leg 1 chelate, pleopods present.

Stage VIII. Claus, 1885, p. 63, Taf. V, fig. 45. Length, 15-16 mm.

This stage, which has only been seen by Claus, differs only in the greater development of the appendages and of the gills.

I give this summary of stages with some diffidence, since it is by no means certain that in all cases the whole series of stages will be passed through by any one larva, and the descriptions of the various authors are not always clear. But it is evident that *Jaxea* does have a much longer series of moults than is usual among the Reptantia, and it is therefore of some interest to place the facts on record.

Laomediidae, species (?) (fig. 62).

A single specimen of a larva in stage III from station 129 deserves notice for the reason that it has certain characters which enable it to be referred with some probability to the family Laomediidae. It is unfortunate that the specimen is too young to show the characters of the pereopods or any trace of gills.

The rostrum is large, with a median ridge, and is not flattened or toothed as it is in the Axiidae and Callianassinae.

The eyes are large and almost devoid of pigment.

The second and third somites of the abdomen have a pair of large postero-ventral spines directed backwards.

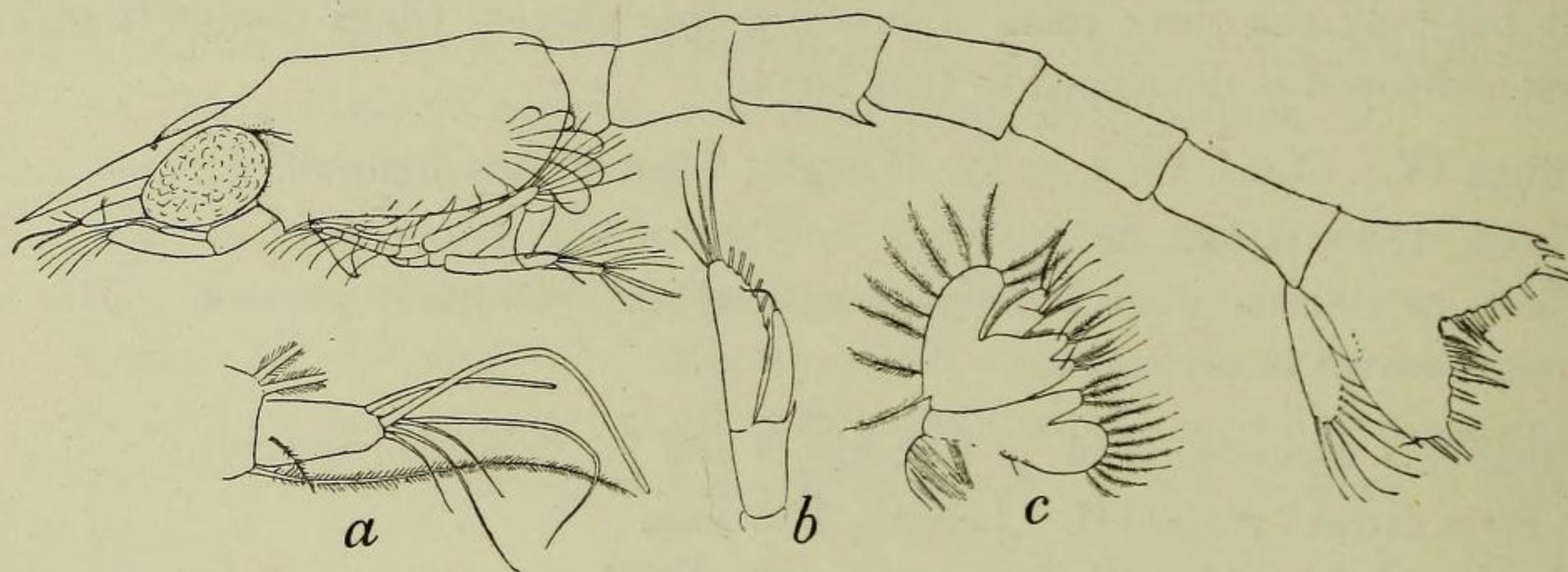


FIG. 62.—Laomediidae, sp. (?). Station 129. Stage III. *a.* First antenna. *b.* Second antenna. *c.* Second maxilla.

The telson is deeply cleft, with a tooth at its outer angle representing the first spine. The second is reduced to a hair, and the formula is $10 + 10$, there being no median spine.

The mandibles are large, the outer angle somewhat produced, but not sickle-shaped as in *Jaxea*. The cutting edge is armed with a series of small points, but the exact form of the appendage cannot be illustrated owing to the distortion caused by the approach of the moult.

The third maxillipede has the endopodite reduced to a simple rod inserted near the base of the basipodite and scarcely reaching to the end of that segment.

In respect of the last character, of the form of the abdomen and of the telson, this larva agrees with *Jaxea* and *Naushonia*, and differs from all other Thalassinidea. Since the only other known genus of the family is *Laomedia*, it is possible that it belongs to that genus.

III. Callianassidae.

The larvae of the Upogebiinae are so distinct from those of the Callianassinae that they cannot be included in the same definition, and must be dealt with separately.

III A. CALLIANASSINAE.

The larval development of *Callianassa* has been described very fully by Sars, Cano, and Miss Webb, while Claus also has given figures of certain stages. Some uncertainty still prevails as to the species (and consequently the sub-genera) with which the different writers have dealt, but it seems clear that three species have been studied, so that probably the characters drawn from these descriptions may be regarded as valid for the whole genus.

If we were concerned only with the larvae of *Axius* and of *Callianassa* it would be easy to show strong differences between them and to lay down definite family characters; but, if I am right in attributing to the Axiidae the larvae described above, and to the Callianassinae those that follow, it is found that the differences practically disappear, and it is hardly possible to draw up any definition which will separate the two families. Both are characterized by the long, broad rostrum toothed along the sides which is so striking a feature of the genus *Oodeopus*, Bate, but some minor differences may be detected, as follows:

1. The Callianassinae seem always to have a very large spine on the second abdominal somite, while the succeeding segments are carinated and sometimes, as in *C. subterranea*, this carina is toothed; whereas in the Axiidae the segments are never carinated, are sometimes without dorsal spines, and when such spines are present those of somites 3 to 5 are not greatly smaller than that of the second.

2. Whereas it seems to be a rule that the Axiidae have exopodites on all the pereopods, in the Callianassinae, as a rule at least, the last leg is uniramous.* But there are, I believe, exceptions to this rule, since there is a distinct exopodite on the fifth leg of the post-larval *Callianassa* described below.

3. In the Axiidae a pleopod is developed on the second abdominal somite, but in the Callianassinae pleopods seem to be generally absent from the first two somites. The only exception to this rule at present known is the larva described by Sars (under the name of *Calocaris macandreae*), in which four pairs of pleopods are figured.

4. The telson of the Axiidae is typically (*Axius*) very broad and bears more than eight spines on either side, whereas in the Callianassinae it is, in later stages, narrowed, more or less rectangular, and bears only 8+1+8 spines. On the other hand, the larva described above as possibly belonging to *Iconaxiopsis* has a telson indistinguishable from that of a Callianassid.

From this it appears that the characters usually holding good for the Callianassinae are as follows:

1. Rostrum broad, flat, toothed along edges.
2. Eyes oval.
3. Pleon somite 2 with a very large dorsal spine which is hollowed below.

* In one of the species of *Callianassa* described by Cano only legs 1 and 2 bear exopodites.

4. Pleon somites 3 to 5 with median carina and small spines.
5. Telson with median spine, broad and triangular in stage 1 and elongated, rectangular in last stages, with a formula $8 + 1 + 8$.
6. Fifth pereopod without exopodite.
7. Pleopods absent from somites 1 and 2.

CALLIANASSINAE.

Callianassa, sp.

At station 43 (fig. 63) a single and rather badly damaged specimen of a post-larval Callianassid was taken which, though it cannot be connected with any larva, deserves some description by reason of the extreme rarity of such specimens.

The specimen measures about 3.85 mm., of which the abdomen alone measures 2.5 mm., or more than twice the length of the cephalothorax.

The carapace is apparently without any grooves, and is prolonged into a rostrum of broad triangular shape which bends downwards over the eyes. The last somite of the thorax is quite distinct and not covered by the carapace. The abdominal somites have fairly well developed epimera which, except the sixth, are without setae.

The telson is rectangular, slightly longer than broad, with a median spine and a number of short setae and spinules. There is a group of setae on the dorsal surface near the base. The eyes are darkly pigmented.

The first antenna has a long peduncle with an otocyst and two flagella.

The second antenna has a vestigial scale without setae. The flagellum is broken off.

The mandible has a simple rounded molar surface and a small unjointed palp curving inwards towards it.

In the first maxilla the basal joint has a small papilla on its outer end which may represent the exite of certain Decapods, e. g. *Upogebia*. The endopodite or palp is rather large and two-jointed.

The second maxilla has four distinct inner lobes. The endopodite is rather large, indistinctly jointed, and with setae. The exopodite is very large.

The first maxillipede has the basal joint almost devoid of setae, but bearing on its outer face a large Y-shaped epipodite. A minute projection from the epipodite may represent the podobranch. The second joint has an enormously long lacinia which projects greatly beyond the minute endopodite. The exopodite is a large plate of irregular form without a terminal flagellum and with scattered setae.

The second maxillipede has the coxopodite and basipodite distinctly separated, but the two basal joints of the endopodite are fused. The exopodite is not longer than the two fused joints, rather broad, and without a flagellum.

The third maxillipede is a very large and conspicuous appendage. The exopodite is reduced to a minute papilla. Ischium and merus are fused. The propodite is

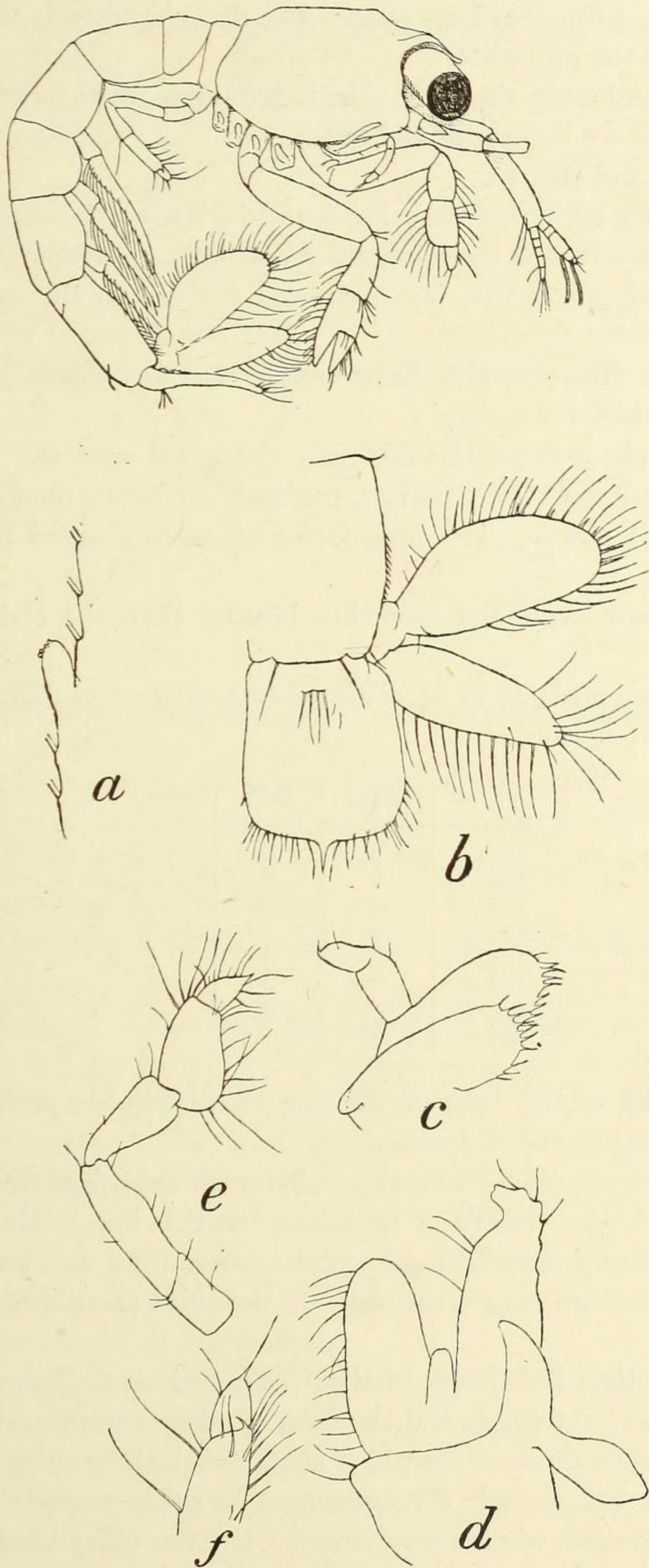


FIG. 63.—*Callianassa*, sp., post-larval. Station 43. *a*. Edge of pleopod showing retinaculum. *b*. Telson and uropods. *c*. First maxilla *d*. First maxillipede. *e*. Third (?) leg. *f*. End of fifth leg.

expanded and bears a fringe of long setae. The dactylopodite is small and seated on the anterior part of the propodite.

All the legs, including the fifth pair, bear minute vestiges of exopodites. The first and fourth legs are broken off and lost.

Leg 2 is large and chelate.

Leg 3 is broken off, but a loose leg found in the bottle is probably one of the missing appendages. In this leg the ischium and merus are separate. The propodite is greatly expanded proximally, but narrowed distally to the same width as the dactylus.

Leg 5 is small. The propodite has a minute claw at its distal end, and a number of long setae; the dactylus is simple.

There are no pleopods on the first two abdominal somites. On the remaining somites they are very long, with narrow, profusely setiferous rami of which the inner is shorter than the outer. The endopodite of each pleopod bears an appendix interna.

The uropods are large, the exopodite broader than the endopodite, and both without sutures.

The gills are so small as to be distinguished with great difficulty, but I believe the formula below to be correct.

	Ep.	Arth.	Pleur.
Mxp. 1	1	—	
Mxp. 2	1	?	
Mxp. 3	—	2	
Leg 1	—	2	
Leg 2	—	2	
Leg 3	—	2	
Leg 4	—	2	
Leg 5	—	—	

A small papilla at the base of the second maxillipede probably represents an arthrobranch, but is somewhat doubtful.

That this specimen belongs to the Callianassinae is clear from its general form, its gill formula, and other details of structure, but it is impossible to identify it with any certainty with any described genus. It differs from any known genus in the absence of the *linea thalassinica*, the shape of the third maxillipede, and in the shape of the eye.

If we assume that it belongs to the Callianassinae *Callianidea* and *Glypturus* are excluded by the gill formula and the form of telson and uropods.

Within the genus *Callianassa* which alone remains, the sub-genus *Scallasis* only has rounded eyes, but, though the agreement in other respects is fairly close, the form of the third maxillipede is very distinct. On the other hand it agrees still less with the remaining sub-genera both with regard to the form of the eyes and of the third maxillipedes. It is naturally impossible to say whether either of these

structures would change materially with later growth, but I do not think it at all probable that they would.

I must therefore leave the identification uncertain, but place the animal provisionally in the genus *Callianassa* in its wider sense.

Callianassa, species II (fig. 64).

This larva, taken at station 40, measures 5.1 mm. and closely resembles *C. subterranea*.

The rostrum is of great size, and toothed along both margins, and there is a minute rudiment of the dorsal organ behind it. The carapace has a pair of sub-orbital

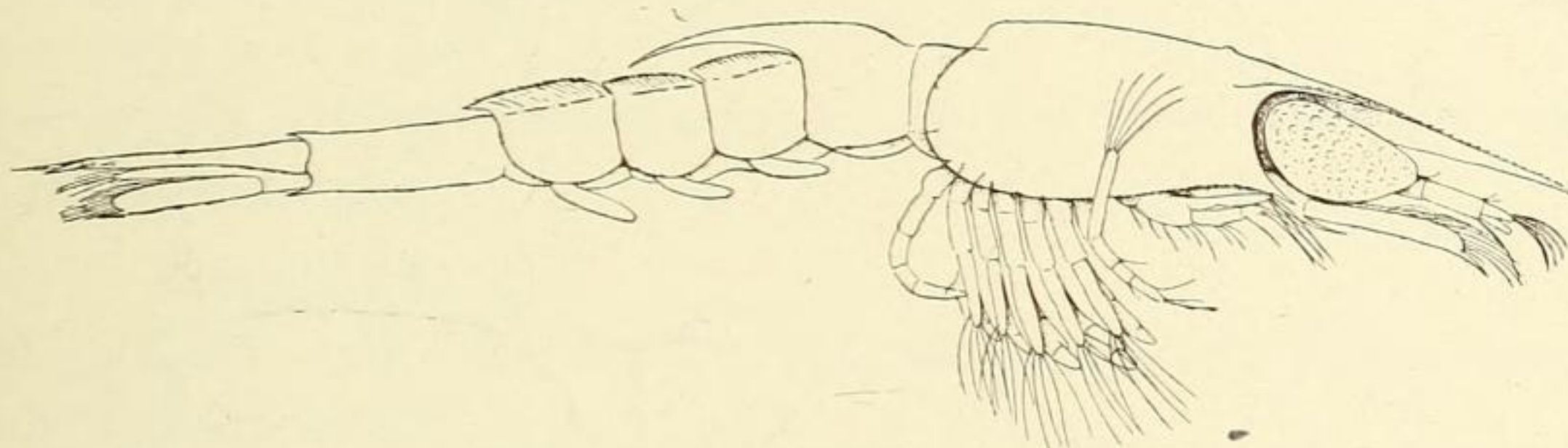


FIG. 64.—*Callianassa*, species II. Last larval stage. Station 40.

spines and is denticulate along the anterior part of its ventral margin. The second abdominal somite bears a very large spine which reaches nearly to the end of the fourth somite. Somites 3 and 5 have each a pronounced dorsal carina which has a "fluted" appearance and is serrated along its margin.

The sixth somite has a small dorsal, a pair of ventro-lateral, and a median ventral spine.

The telson is longer than the uropods and rather narrow, its greatest width scarcely more than half its length. The median spine is very small, and there are eight spines on either side, the outermost three being very small and two of them seated on the outer margin. The fourth spine is greatly the largest.

The antennal scale has a long outer terminal spine and there is a strong spine on the basipodite.

The first four pairs of pereiopods bear exopodites, each with five setae. The endopodites of the first two pairs are sub-chelate.

Leg 5 is well developed and uniramous.

There are three pairs of rudimentary biramous pleopods on somites 3, 4, and 5.

The uropods are fully developed, each branch bearing setae, and there is a long terminal spine on the exopodite.

The eye is large, of a peculiar oval shape, but apparently without any black pigment.

The gills are scarcely developed, and there appears to be only a single gill in the position of an arthrobranch on the first four pereiopods.

This larva closely resembles *Oodeopus serratus*, Bate (1888, p. 877, Pl. CXLII, figs. 2, 3), from the New Hebrides, but differs in the structure of the telson and absence of an exopodite on the fifth leg. The similarity to the larva of *Callianassa subterranea*

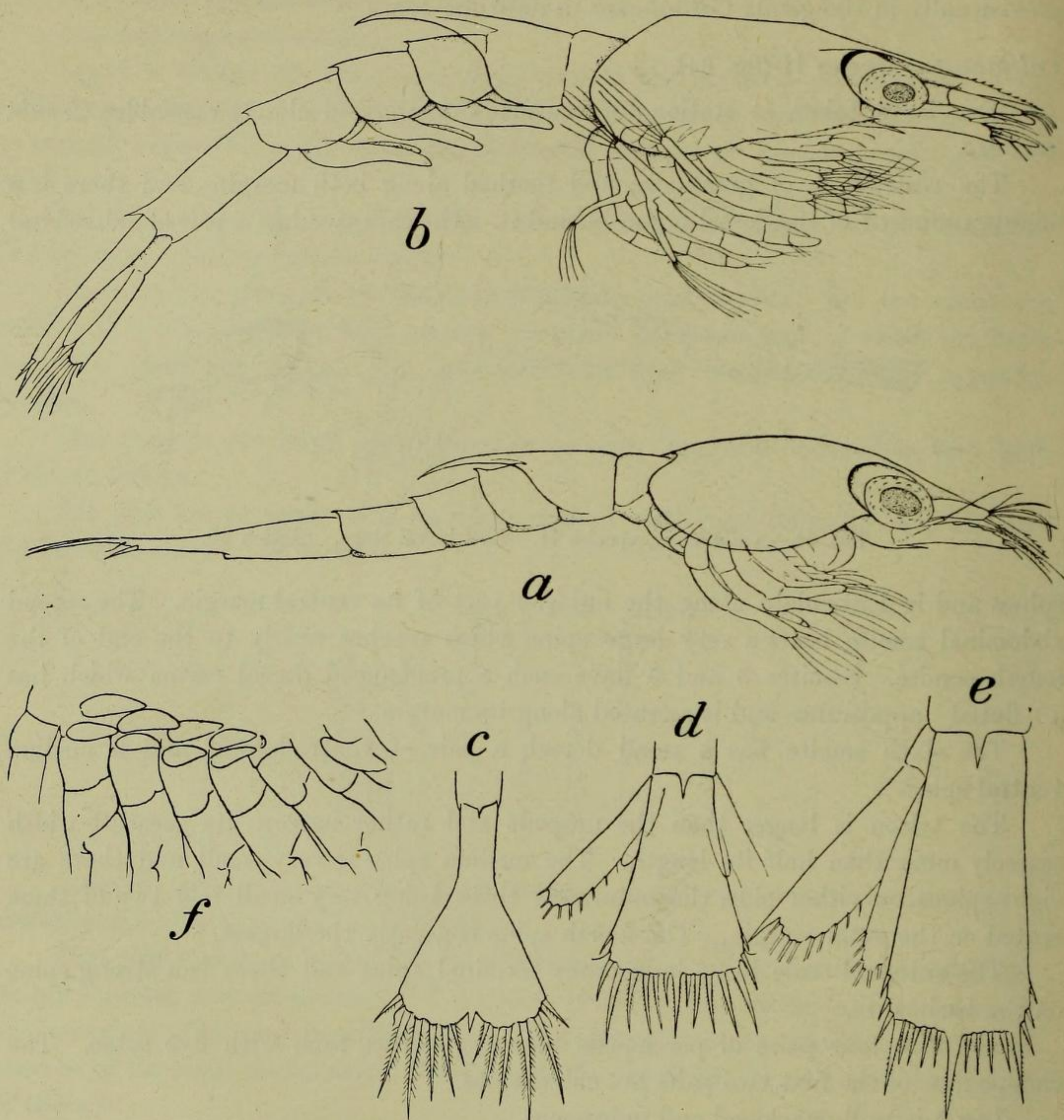


FIG. 65.—*Callianassa*, species III. Station 148. a. Stage I. b. Stage V. c. Stage I. Telson. d. Stage III. Telson. e. Stage IV. Telson. f. Stage V. Pereiopods.

is also very striking, and there can be no doubt that it belongs to a species of that genus.

Callianassa, species III (fig. 65).

Of this species, which was taken at station 148 there are larvae representing five stages.

Stage I. Length, 1.64 mm. (fig. 65, *a*).

The rostrum is very long, slightly down-bent, and not flattened, but bears a few small denticles near the end.

The ventral margin of the carapace is smooth and there are neither supra- nor sub-orbital spines. A sub-orbital spine appears in stage III.

The second abdominal somite bears a long hollowed spine reaching to the end of the fourth somite, while somites 3, 4, and 5 have very small dorsal spines.

The telson is broad and triangular, with a spine-formula of $7+1+7$ (see fig. 65, *c*).

The endopodite of the second antenna bears a single long seta.

The three pairs of maxillipedes are developed with exopodites bearing 1, 4, and 5 setae respectively.

The pereopods are not developed, though the first two pairs may be distinguished through the skin.

Stage II. Length, 3.67 mm.

This stage differs only from the first in that the first two pairs of pereopods are present as free rudiments.

The telson is unchanged except for the presence of an additional spine.

Stage III. Length, 4.45 mm.

The endopodite of the second antenna is now a short rod without a seta, and the endopodite of the first antenna has appeared.

There are two pairs of biramous legs, and very small rudiments of the succeeding pairs.

There are no pleopods, but the uropods are present, the endopodite about half as long as the exopodite and with one terminal seta. The telson has changed its form, being much narrower in proportion to its width (fig. 65, *d*). The median spine has increased in length, and the proportional length of the spines has changed. The second seta is still represented by a minute hair.

Stage IV. Length, 4.9 mm.

This stage differs from the next (stage V) only in the smaller size of the pereopods and pleopods, and the proportion of width to length in the telson—the width being more than half the length.

Stage V. Length, 6 mm. (fig. 65, *b*).

This is evidently the last stage before metamorphosis. The endopodite and exopodite of the first antenna are still very small and one-jointed, but the endopodite of the second antenna exceeds the length of the scale and shows joints beneath the skin.

All the pereopods are fully developed, each, except the last, having setose exopodites. The first leg is much the largest, and is chelate, as is also the second leg.

There is a median ventral spine at the end of the sixth abdominal somite.

The pleopods on somites 3, 4, and 5 are large and biramous.

The telson is narrow, the width being about equal to half the length. The median spine is very long.

The fourth spine is the largest, and the outer three are small, sub-equal, and placed on the outer margin.

The uropods are shorter than the telson, both branches setose, and the exopodite with a terminal spine (fig. 65, e).

Gills are present at this stage. There is a large epipodite on the first maxillipede and a pair of arthrobranchs on legs 1 to 4, but none on leg 5 or on the third maxillipede (fig. 65, f).

IIIB. UPOGEBIINAE.

The metamorphosis of the allied genera *Gebiopsis* and *Upogebia* is completely known, though there remains a little uncertainty as to the exact species dealt with by the authors who have described the larvae. Sars (1884) described the development of a species named by him *Gebia littoralis* Risso, but certainly belonging to the genus *Gebiopsis* and therefore not to *Upogebia littoralis*. Cano in 1891 followed the metamorphosis of *Upogebia littoralis*, while Miss Webb (1919) has given a very full account of the larvae of both *Gebiopsis deltaura* and *Upogebia stellata*, together with a comparison of these larvae with the description previously given by Sars. There can be no doubt, on comparing Sars's and Cano's descriptions, that the former's species was not *Upogebia littoralis*, and Miss Webb's conclusion is that the larvae may have belonged to a Norwegian species hitherto undescribed. On the other hand, Sars's figures show quite clearly that he was dealing with a species of *Gebiopsis*, and the differences between his description and that of Miss Webb of the larval and post-larval stages of *Gebiopsis deltaura* seem to be so small that I have no doubt that the Norwegian larvae belonged to *G. deltaura*, which is known to occur on the coast of Denmark if not of Norway.*

The following characters may be regarded as distinguishing the larvae of the Upogebiinae :

1. Rostrum very small, not flattened horizontally.
2. Abdominal somites without dorsal or lateral spines.
3. Telson with reduced second seta, and, in later stages, with small median spine.
Fourth spine the largest in later stages.
4. Mandible without palp.
5. Two pairs of biramous maxillipedes present on hatching. Legs 1 to 3 develop exopodites.
6. Pleopods absent from abdominal somite 1 only.
7. Endopodite of third maxillipede rudimentary and springing from base of basipodite.

* Stephensen (1910) has given Sars's *G. littoralis* as a synonym of *Upogebia stellata*. With this I do not agree.

Upogebia danai, Miers (figs. 66 and 67).

A number of larvae, apparently belonging to the same species of *Upogebia*, were taken by the "Terra Nova" at stations 130, 133, 135, and 148. The material contains larvae in every stage and fortunately includes a single specimen in the first post-larval form, so that it is possible to identify them with certainty as belonging to the genus *Upogebia*, and with reasonable probability to the species *U. danai*.

Miss Webb's account of the development of *G. deltaura* is so complete that it is unnecessary to describe the structure of the New Zealand form in detail, but it is of some interest to show that the course of development is almost precisely the same in the two cases.

Four larval stages may be distinguished as follows :

Stage I. Length, 3.15–3.2 mm.

Of this stage, which I believe to be the first-hatched larva, there are several specimens, and they differ from the European form only in size. The first and second maxillipedes bear setose exopodites, and the remaining thoracic appendages are present as rather large rudiments. Minute knobs on the ventral surface of the abdominal somites represent the pleopods. The telson is precisely the same as that of *G. deltaura*. I should point out that Miss Webb has omitted from her figure (Pl. III, fig. 9) the very small hair which represents the second seta of the telson. This reduced seta is of great systematic importance and is undoubtedly present in *G. deltaura*, *U. stellata*, and *U. littoralis*, as it is also in *U. danai*. It is, however, exceedingly small and inserted on the ventral surface, so that it is often invisible from above. It has been figured, and its importance appreciated, by P. Mayer (1877), but it was not observed by G. O. Sars.

Stage II. Length, 3.7–4.15 mm.

Miss Webb found a certain variation in respect of the exopodites among the individuals of this and later stages, such that she was able to divide them into two series, Class A and Class B, but I do not find any such differences among the specimens at my disposal. These specimens do vary to some extent in the degree of development of the pereopods and pleopods, but it is probable that these differences are due to growth of the soft functionless appendages between the moults. The endopodite of the second antenna is now nearly as long as the scale and usually bears only two setae, but in some cases the third is also retained, while in others all are lost. The three pairs of maxillipedes and the first three pairs of legs each bear a setiferous exopodite, the numbers of setae on them being 6, 7, 7, 7, 6, 6.

The endopodites of the five pairs of pereopods are large, curving forwards, but they are not as a rule packed tight under the sternum as is the case in *G. deltaura*. In the latter only the exopodite of the first pair of legs is developed and functional.

The pleopods are now present, and may be so large as to overlap each other.

The telson is of the same shape as before, but has a median unpaired spine and

an additional pair of setae, the formula being $8 + 1 + 8$. The outer hair is so small that it can only be seen with difficulty (fig. 66, *f*).

In two specimens which were ready to moult to stage III the pereopods and pleopods are considerably larger, and the uropods can be distinctly seen beneath the cuticle.

The endopodite of the rudimentary uropods is small and bent forwards, instead of lying parallel with the exopodite.

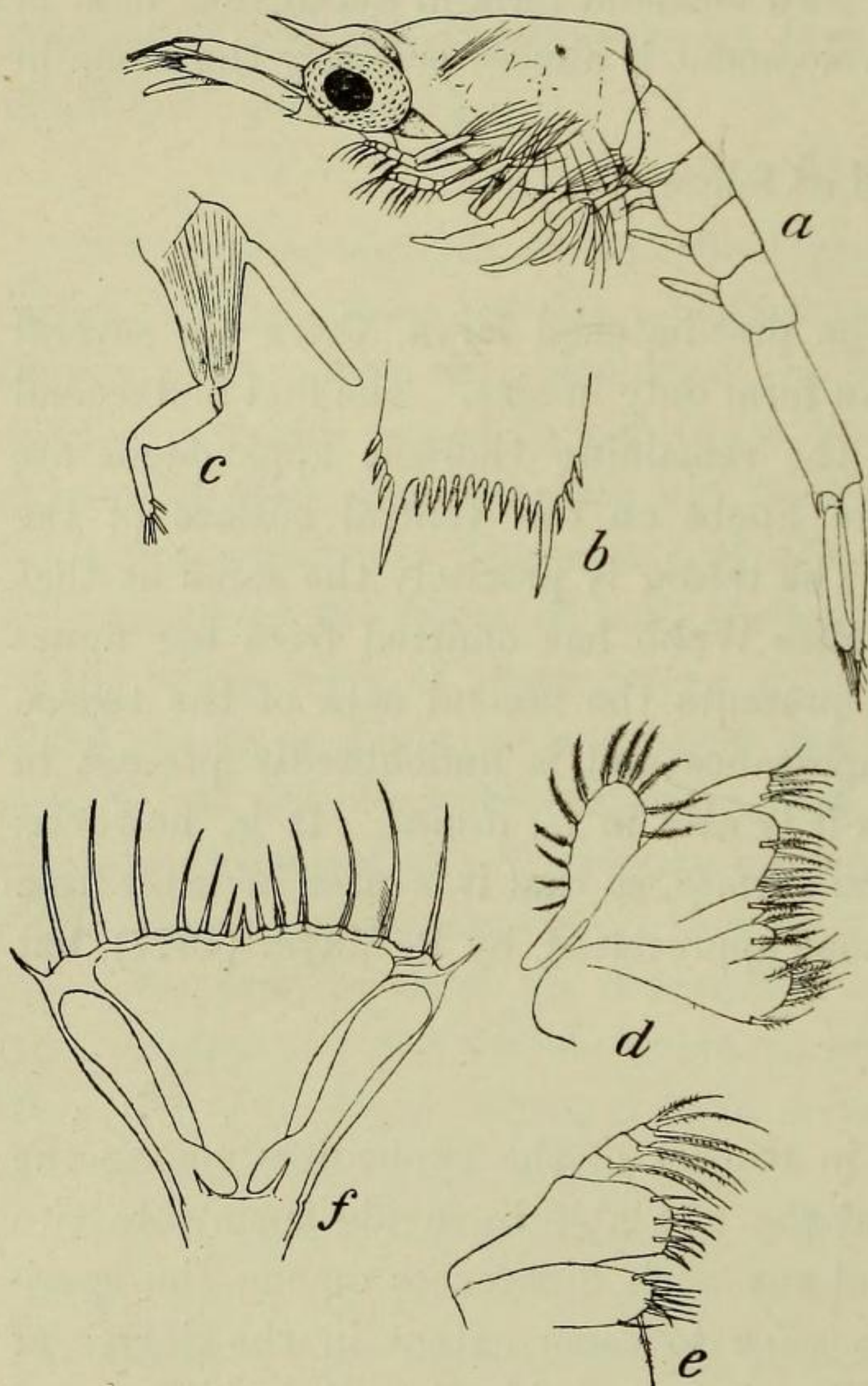


FIG. 66.—*Upogebia danai*. Station 133. *a*. Stage IV. *b*. Telson. *c*. Third maxillipede. *d*. Second maxilla. *e*. First maxilla. *f*. Stage II. Telson.

Stage III. Length, 4.55–4.6 mm.

I have had eleven specimens of this stage for examination, and find among them little or no variation in the degree of development of the appendages.

The endopodite of the second antenna is longer than the scale, and without setae.

The pereopods are very large, the first two legs reaching forwards beyond the mouth. The first pair shows no trace of a chela.

The pleopods are but little larger than in stage II, and are uniramous.

The telson and uropods are as figured for *G. deltaura* by Miss Webb (Pl. IV, fig. 10), the inner ramus being small and without setae, and the telson narrower than in the preceding stage and with shorter setae but the same seta-formula.

The gills are not yet developed, but may be faintly detected under the skin; each of the maxillipedes, however, bears a minute rudiment of an epipodite.

As Miss Webb has shown to be the case in *G. deltaura*, this stage may, and apparently usually does, moult directly to

the post-larval form. This is quite definitely proved by two specimens which are about to moult, and show distinctly that at the moult the antenna would develop a long segmented flagellum, while the scale would be reduced to a small vestige.

Stage IV. Length, 4.85 mm. (fig. 66, *a-e*).

One specimen only of this stage was taken. This specimen differs only from stage III in the narrower form of the telson and the greater development of the uropods, the inner branch of which now bears a number of setae, but I propose to

describe this stage in some detail for the purpose of comparison with the European species, and also with the larvae of other Decapods here dealt with.

In general form it does not differ in any way from *G. deltaura* of corresponding age, but there are certain small differences in the appendages which should be mentioned.

The antennae and mandibles have no special features.

The first maxilla differs from that of *G. deltaura* in the form of the two basal segments, which unite to form a conspicuous hump at their outer edge (fig. 66, *e*). The endopodite is more slender than in *G. deltaura* as figured by Miss Webb, but agrees exactly with Sars's figure. The second maxilla (fig. 66, *d*) is remarkable for the complete absence of setae from the proximal part of the exopodite, a feature specially characteristic of the Paguridae, while the total number of setae borne by the distal part is only twelve. Both Sars and Miss Webb show setae covering the whole margin of the exopodite except the proximal inner margin. The number of setae apparently differs in *G. deltaura* and *U. stellata* (eighteen and fourteen according to Miss Webb), while Sars figures twenty-one. There is, therefore, in the European species a tendency to the loss of setae on the proximal part which is complete in *U. danai*. I am not aware of any Decapods, except *Upogebia*, *Gebiopsis*, and the Paguridae, in which the second maxilla has this proximal lobe bare or nearly so.

The first maxillipede of *U. danai* agrees with that of *G. deltaura*, having a four-jointed endopodite, of which the second joint bears a long ciliated seta on its outer margin, and an exopodite shorter than the endopodite and bearing six terminal setae. These setae are not arranged symmetrically. Four of them are placed in pairs at the end, but the other two are both on the anterior margin. This asymmetrical disposition of these setae in this and the other thoracic appendages is frequently found among the Anomura and Thalassinidea, but never, so far as I know, among the Natantia.*

The second maxillipede has a four-jointed endopodite, and its exopodite bears seven setae. The endopodite springs from a point not quite at the end of the basipodite, so that the exopodite appears as if elevated on an extension of the basipodite.

The third maxillipede has the endopodite in the form of a long slender unjointed rod, springing from quite near the base of the basipodite, and is considerably more slender than in *G. deltaura*. This peculiar position of the endopodite, which is repeated in the succeeding limbs, is found also in *Jaxea*, most Anomura, and in *Stenopus* (see p. 139).

In *U. stellata* and *G. deltaura* the endopodite of leg 1 is very large and thick, and shows a distinct incipient chela, but in *U. danai* it is much more slender and has no trace of a chela.

* There is sometimes a certain amount of asymmetry in the exopodite of the first maxillipede in Caridea.

Legs 2 and 3 do not differ noticeably from *G. deltaura*, but the exopodites bear eight and six setae respectively, instead of seven in each as given by Miss Webb.

The last two pairs of legs are uniramous and unjointed rods which hang nearly straight downwards instead of being curved forwards as in the European species.

There are four pairs of pleopods, the first somite of the abdomen having no trace of appendages.

Stage V. (Fig. 67.)

A specimen evidently in the first post-larval stage was taken in the plankton at

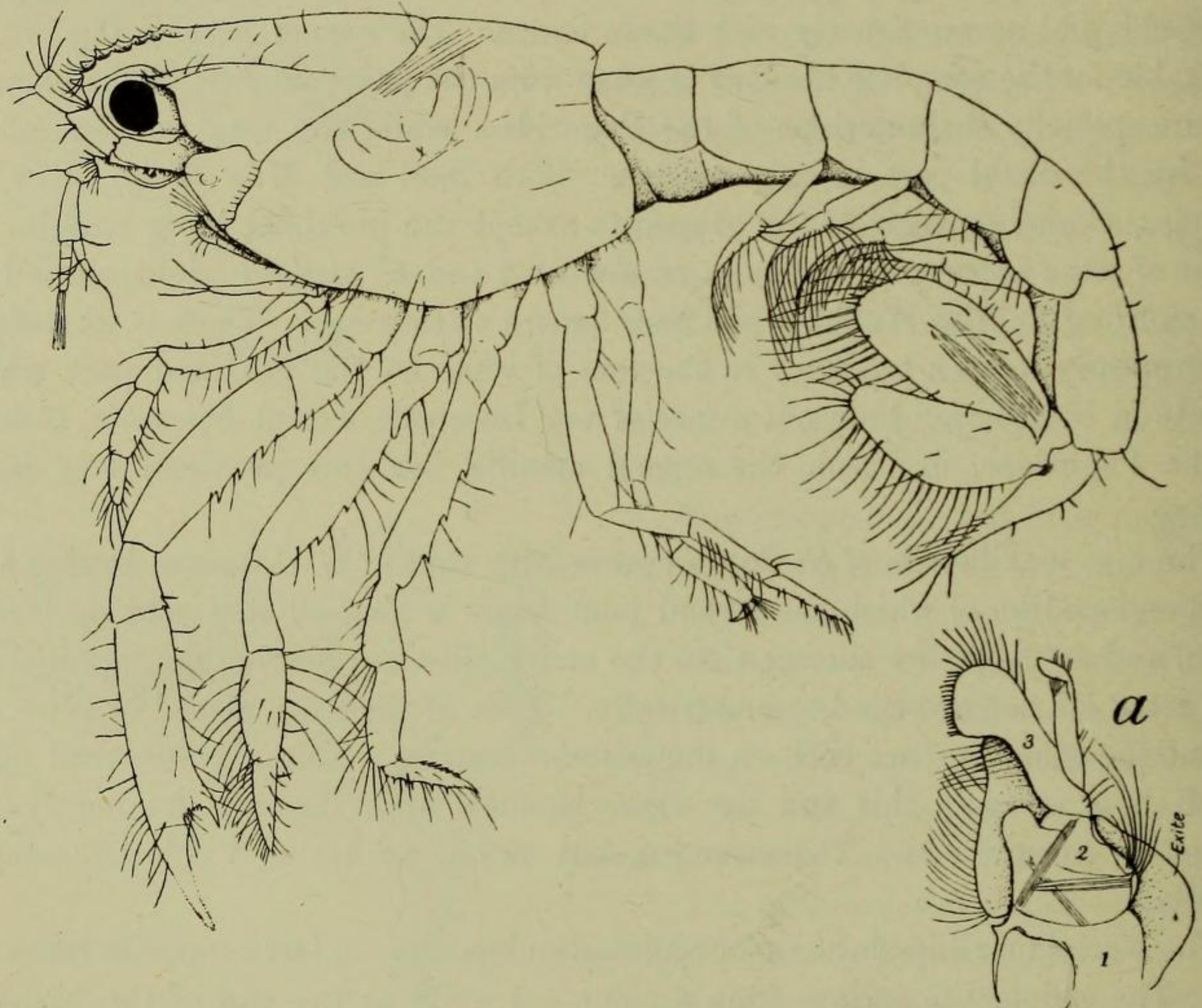


FIG. 67.—*Upogebia danai*. Post-larval. Station 135. *a*. First maxilla. *Upogebia stellata* adult.

station 135. This specimen measures 4.5 mm., or slightly less than the larva just described, but the difference in size is quite compatible with specific identity of the two individuals. Not only is there considerable individual variation in size among Decapod larvae, but also a certain amount of shortening of the body seems commonly to take place at the last larval moult. Miss Webb gives the size of the larva in Stage IV as "just over 4 mm.," while the first post-larval stage moulted therefrom was only 3.9 mm. Sars gives the size of the last larva and first post-larval form as identical (5 mm.), while in *Naushonia* Thompson (1903) found a reduction of length from 10 to 6 mm.

The animal has now all the characters of the genus *Upogebia* as distinct from *Gebiopsis*.

The rostrum, which projects considerably beyond the eyes, is a concave, down-turned extension of the carapace with six large teeth along each margin.

On either side of the rostrum is a conspicuous supra-orbital tooth overhanging the eye and continued backwards as a ridge bearing a few hairs. The carapace is soft, and I have not detected any trace of a "Linea thalassinica" such as is present in the adult *Upogebia*, though there is a distinct transverse cephalic groove which runs forwards and joins a line running back from the incision in the shell below the eye. It is continued downwards to the margin of the carapace, bearing here a line of short hairs and cutting off a triangular area between it and the above-mentioned incision.

The first antenna has a conspicuous auditory sac in the basal joint, and the second joint of the peduncle is very short. There are two short flagella, each of three joints only.

In the second antenna the second joint of the peduncle bears a vestige of the scale in the form of a thin plate with an apical tooth, which projects very slightly beyond the end of the joint and is very faintly jointed off from it. The degree to which the scale is retained in the adult seems to vary a good deal with the species. It is conspicuous in *U. stellata*, and also in *U. littoralis*, but it is altogether absent from a specimen of *G. deltaura* examined by me.

The mandibles and maxillae have the form of the adult.

The first maxilla (fig. 67, *a*) is of very remarkable form in this genus, and is distinctly three-jointed. Viewed from behind it appears two-jointed, the basal joint having a very large outer plate or exite (see Boas, 1880, Pl. III, fig. 106) corresponding to the similar plate in Euphausiids. Viewed from in front (fig. 68, *a*) it is seen to be very distinctly three-jointed, and it is a little uncertain whether this exite springs from the first or second joint. I assume that it belongs to the first, and that the second joint is here unusually well developed and bears on its outer side a tuft of long hairs.

The second maxilla has a distinctly two-jointed stem, each joint bearing two well-developed endites. The endopodite is a long slender rod hidden by the distal endite. The scaphognathite bears setae along its whole margin except upon the proximal inner face.

The first maxillipede differs in detail from that of *U. littoralis* as figured by Boas, the distal lacinia being rather pear-shaped and the exopodite bearing very few setae; but the latter is probably a character of immaturity. The endopodite is well-developed but not segmented. There was no trace of an epipodite.

The second maxillipede likewise bears no epipodite. The endopodite is distinctly five-jointed, and the exopodite long and fringed with short stiff setae along its outer margin.

The third maxillipede bears one arthrobranch in place of the pair that is usual

in the adult, and a rudiment of the epipodite. The endopodite is distinctly five-jointed, but the exopodite is very small and bears only three terminal setae. The first joint of the endopodite is expanded on its inner face into a thin, strongly toothed plate.

The first pair of legs are very long, and scarcely sub-chelate, the propodus being produced into a spine which barely reaches beyond the base of the dactylus. There are three or four small teeth on the inner edge of the propodal process. The merus has three teeth on its inner face instead of five or six as described by Chilton in the adult. The merus of the second and third legs each bears three teeth. The dactylus of the third leg has a row of small teeth on the anterior face and a serrated posterior margin.

The pleopods, of which there are only four pairs, have the endopodite very small, but bearing numerous long setae. The posterior margin of the telson is simply rounded and profusely setiferous.

The gill formula is as follows :

	Ep.	Arth.
Mxp. 3 *	rud.	1
Leg 1	—	2
Leg 2	—	2
Leg 3	—	2
Leg 4	—	2
Leg 5	—	—

thus agreeing with the formula as given (e.g. by Huxley) for the genus, with the exception of the presence of one rudimentary epipodite and only one arthrobranch on the third maxillipede. Probably a second arthrobranch would develop later, since Sars found only one gill on this limb in the post-larval stage of *G. deltaura*. He shows, however, an additional rudimentary epipodite on the second maxillipede.

Borradaile (1903, p. 543) draws special attention to the presence of an arthrobranch on the fifth leg of *U. capensis* described by Stebbing, with the observation that the extra gill may make it necessary to found a new sub-genus to include species having this character. I have dissected a specimen of *U. stellata* and find a rudimentary epipodite on the third maxillipede and also a well-developed gill on the fifth leg, whereas neither are present on a specimen of *G. deltaura*. Huxley does not state which species he examined, while the formula given by Claus is for *U. littoralis*. I am not aware of any other independent observations on the gill formula of *Upogebia*, but it seems likely that a gill may be found on the fifth leg more frequently than has been supposed. Its presence or absence would hardly justify the foundation of a separate sub-genus.

There are a few differences between the post-larval stage as above described and the first post-larval stage of *G. deltaura* as described by Miss Webb and Sars which

* The presence of rudimentary epipodites on maxillipedes 1 and 2 in the larva has already been mentioned. Probably they are present also in the post-larval stage, but could not be seen.

are worth mentioning. In *G. deltaura* the endopodite of the first maxillipede and the exopodite of the second and third maxillipedes are altogether without setae, whereas in *U. danai* both are fairly well developed and setiferous. Further, the terminal joint of the second maxillipede and the end of the exopodite of the first maxillipede are likewise without setae in *G. deltaura*, but are provided with them in *U. danai*. This temporary loss of setae in appendages or parts of appendages is referred to above, p. 71.

It is hardly to be expected that all the specific characters of the adult should be developed in the first post-larval stage, but I have compared my specimen with the description of *U. danai* given by Chilton (1907), and the agreement seems to be remarkably exact. The only serious discrepancy is in the length of the carpus of the first leg which, according to Chilton, should be about half as long as the merus. In this specimen it is almost exactly one-third of it. The propodus also lacks the small teeth mentioned by Chilton. The shortness of the carpus is probably a juvenile character, since it is particularly this joint which elongates greatly in post-larval life in Palaemonidae, and it may be so in other Decapods. At present we know practically nothing about post-larval growth and changes in any species.

Thalassinidea, incertae sedis (fig. 68).

At stations 40 and 43 some larvae were taken which it is impossible to refer to any family, since they combine a general resemblance to the Thalassinidea with certain characters of the Anomura.

Specimens have been seen in two stages, but later stages which would have given better indications of affinity are absent.

The earliest stage measures 2.23 mm. (fig. 68).

The rostrum is long, pointed, but widening out at its base to cover the eyes.

The carapace is produced into a small sub-ocular spine, and has two or three spines on its anterior ventral margin and a pair of spines at its posterior ventral angle.

The abdominal somites have no dorsal spines, but the fifth somite has a lateral pair.

The telson, which is not separated from the sixth somite, is narrow, widening but slightly towards its end. There is no median spine, and the spine formula is 7+7. The second spine is the smallest, but it is not reduced so much as is usual in the Thalassinidea and Anomura.

The first antenna consists of an unjointed stem bearing a terminal seta and a small exopodite.

In the second antenna the peduncle bears a very large spine and a long tapering spinous endopodite. In the Thalassinidea the endopodite in the first stage always bears two or three setae. The scale is large and broad, with a large terminal spine.

The first maxilla is of the usual form, the endopodite of two joints.

The second maxilla has four distinct lobes, a short thick endopodite with two lobes, and an exopodite with four setae.

There are three pairs of biramous maxillipedes. The setae, of which there are five on each exopodite, are arranged in a rather peculiar manner (see fig. 68, *d*).

The terminal joint of the second and third maxillipedes bears a spine and two (mxp. 2) or three (mxp. 3) setae.

The second stage observed differs little from the first. One pair of legs is developed with setiferous exopodite and a small endopodite, while leg 2 is represented by a small hump.

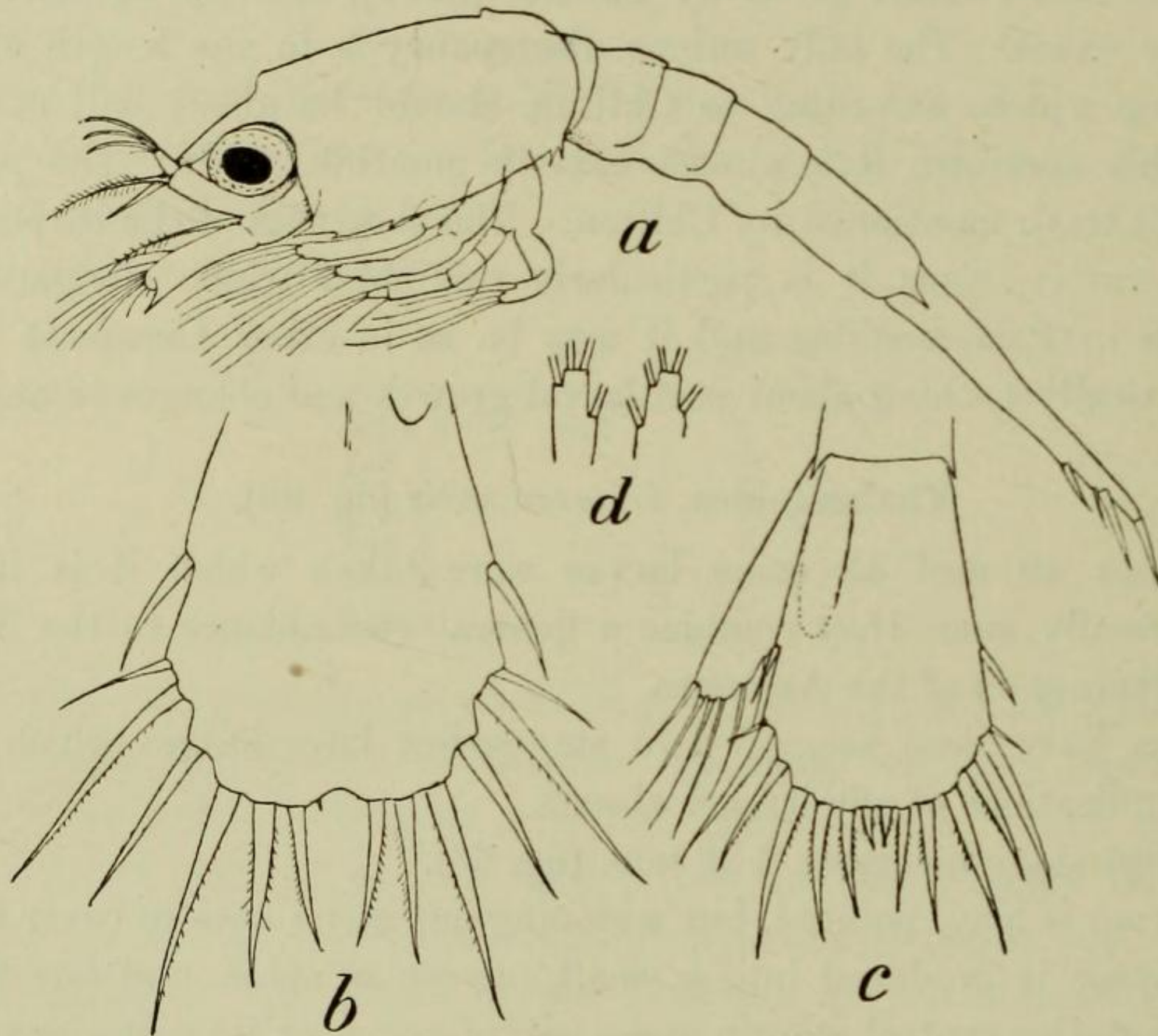


FIG. 68.—*Thalassinidea*, incertae sedis. *a*. Stage I. *b*. Stage I. Telson. *c*. Stage III. Telson. *d*. Arrangement of setae on exopodite of maxillipedes.

There are no pleopods, but the uropods are present, the endopodite without setae (fig. 68, *c*).

The telson is of the same shape, but with eight setae on either side.

THE SYSTEMATIC POSITION OF THE THALASSINIDEA.

The Thalassinidea have been recognized as holding a position somewhat intermediate between the Homaridea and the Anomura, but have generally been regarded as more nearly related to the former. Ortmann (1890–1) considered them to be specialized Homaridea, though Borradaile, followed by Calman (1909), included the Thalassinidea as a section of the Anomura. Bouvier (1917) has reverted to the older view that they belong more naturally to the "Macrura Reptantia," pointing out the very

close resemblance of the Axiidae to the Homaridea, and particularly to such forms as *Thaumastocheles*.

The evidence as to the relationships of this puzzling group supplied by the larvae is rather conflicting. It is not easy to find in the unspecialized larvae of Decapods many well-defined characters which can be used as evidence of affinity, and the development of the Palinura and Homaridea is either so abbreviated or so peculiar that comparison is difficult.

Such evidence as there is may be stated in this way :

Homarine characters of Thalassinid larvae.

1. Presence of exopodites on three or more legs.
2. Median spine in the telson of all but Laomediidae.
3. Presence usually of dorsal spines on the abdomen.

Anomuran characters.

1. Reduced second seta in the telson. The fourth spine the largest.
2. Rudimentary endopodite on the third maxillipede seated at the base of the basipodite in *Jaxea*, *Naushonia*, and *Upogebia*.
3. Undifferentiated endopodites of the pereopods.
4. Epimera usually reduced.

The early appearance of the mandible palp is a character of the Reptantia in general as distinguished from the Caridea (with the exception of the Hoplophoridae).

It seems that, on the whole, the balance of resemblance is in favour of the Anomura, since they have the greater number of characters in common. If the Laomediidae and *Upogebia* are removed the position is a good deal changed, and the only Anomuran character of real significance remaining is the reduction of the second seta in the telson, and the preponderance of the fourth spine. But the Homarine telson is armed with an "indefinite" number of small spines, among which the reduction of one would hardly be noticeable, neither is it to be expected in these more primitive forms.

The Laomediidae, on the other hand, by the form of their telson and the peculiar position of the endopodite of the third maxillipede and biramous legs, are most strikingly Anomuran, and are also very distinct in other respects from the larvae of the other Thalassinidea. As has already been pointed out, the larva of *Stenopus* closely resembles that of the Laomediidae in just these characters, which cannot be disregarded as of small significance.

It is tempting to suggest that the Thalassinidea should be divided into a Homarine series including the Axiidae and Callianassinae, and an Anomurous section embracing the Laomediidae.* If this is done a difficulty arises in connexion with the Upogebiinae, since the larvae which are known have little or

* Since no larva is known of any species belonging to the Thalassinidae this family cannot be considered.

no resemblance to those of the Callianassinae but show such strong affinity to those of *Jaxea* and *Naushonia* that they would have to be included in the Anomurous section.

Such a splitting of the family Callianassidae may be entirely unwarranted by adult structure, and I am not in a position to defend it by a study of the whole group. At the same time it does not seem to me that the family is necessarily a natural one. The only important character uniting the two sub-families and separating them from the remaining Thalassinidea is the reduction of the gills.

Boas (1880, p. 187) has already pointed out certain characters in which *Callianassa* agrees with the Axiidae and is distinct from *Gebia* and *Thalassinia*. Perhaps one of the most important characters in this connexion is the *appendix interna*, which is present only in the Axiidae and Callianassinae. It is true that it is also absent from the Homaridea, but a statement that the Axiidae and Callianassinae form together a Homarine series does not necessarily imply direct descent from existing Homarids.

Another character which may be mentioned here is the exite on the coxopodite of the first maxilla. This exite is very large in *Upogebia* and is also developed in *Jaxea*, but is not present in *Callianassa* or in *Axius*.

I am aware that I am trespassing beyond my province in attempting to deal with adult anatomy, but it seems to me that if the larval characters alone are considered it is certainly necessary to draw the conclusion that the Thalassinidea are not a homogeneous group. This conclusion may be stated thus:

1. The Thalassinidea larvae fall into two series—
 - (a) A Homarine series including the Axiidae and the Callianassinae.
 - (b) An Anomuran series including the Laomediidae and Upogebiinae.
2. The Stenopidea are Reptantia allied to the Anomuran section of the Thalassinidea.

With regard to the second proposition it may be objected that the Stenopidea with a well-developed antennal scale cannot be descended from ancestors which have none or only a vestige of it, but there is not, I think, a great deal of force in this objection. The adult is only the last phase in the individual cycle, and the scale is as large in the larvae of the Thalassinidea and Anomura as it is in any other Decapods. The organ is therefore not wholly lost, and there is no reason why it should not either have persisted throughout in certain lines or be re-acquired in the adult by persistence of a larval character.

ANOMURA.

Galatheidea.

Large eggs, with an abbreviated or suppressed larval life, are commonly found among the Galatheidae of the deep sea such as *Diptychus* and *Galathodes*, but

Milne Edwards and Bouvier point out (1893, p. 234) that there is no definite relation between the depth of the habitat and the size of the egg. For instance, some species of *Munida* live at the same depth as *Galathodes* and *Diptychus* and yet have small eggs. But a large proportion of the Galatheidae, and apparently all the Porcellanidae, are littoral species and have free larvae, so that it is to be expected that these larvae should be taken in considerable number and variety in the plankton. This is indeed the case, and the "Terra Nova" collections contain larvae of Galatheidae and Porcellanidae in abundance.

Larvae of the Galatheidae and of the Porcellanidae have been repeatedly described, but the most comprehensive account is that of Sars (1889), who described fully the development of species of *Galathea*, *Munida*, *Galathodes*, and *Porcellana*, while Faxon has dealt in some detail with *Porcellana (Polyonyx) macrocheles* (1879).

As is to be expected in the case of two such closely related families as the Galatheidae and the Porcellanidae the essential characters of the larvae are practically identical, and it is difficult to frame any definition which will distinguish them. If it were a case of comparing those of *Galathea* or *Munida* with *Porcellana* a distinction would be easy, but a series of larvae taken in Melbourne harbour and described below so completely bridges the gap between the two families that a real distinction becomes out of the question. The following summary of the chief characters of the Galatheid larva must therefore be taken as applying to the tribe as a whole. It will be seen later that it is almost equally difficult to find characters for the separation of the larvae of Galatheidea from those of the Paguridea.

Characters of the Galatheidae.

1. Rostrum long, broad at base, dentate along margin in *Galathodes*.
2. No supra-orbital spine.
3. Posterior margin of shell usually (always ?) dentate and produced into a short spine on either side.
4. Abdomen without median dorsal spines on somites 1 to 4. Lateral spines usually present, especially on somite 5.
5. Telson with second seta reduced. The fourth seta becomes a large spine in later stages. No median spine.
6. Antennal scale with terminal spine large or very large. Scale sometimes acicular (*Munida*). Inner branch usually with one seta, rarely with two in stage I.
7. Exopodites on all three maxillipedes. Endopodite of third pair rudimentary and basally placed.
8. Exopodite of second maxilla bears setae on its proximal lobe. Four inner lobes, of which the basal lobe is the largest.
9. Fifth pair of legs placed inside and hidden by legs 3 and 4.
10. Pleopods absent from first abdominal somite, and also from the fifth in *Diptychus* (Bouvier, 1892).

The Porcellanidae, if the species described below is properly referred to that family, share all these characters with only two important exceptions, namely:

1. The rostrum and posterior spines of the carapace are enormously long.
2. There are no teeth on the posterior edge of the carapace.

The genus *Porcellana* itself has some peculiar features—*

- (a) The antennal scale is reduced to a spine.
- (b) Peculiar form of the telson which may, in some species, have a median spine.
- (c) In some species (e. g., *P. longicornis*) the fifth pair of pleopods are absent, as in *Diptychus*.

I. Galatheidae.

The characteristic larva of the Galatheidae has been so fully described by Sars and others that it is unnecessary for me to deal with the representatives of the genus from the "Terra Nova" collections, especially as it is out of the question to refer them to any adult species. The accompanying figure (fig. 69) of the larva of a species of *Munida* (from station 106) will give a good idea of the Galatheid type of larva, and shows that the rostral and posterior spines which attain to such extreme dimensions in the Porcellanidae may be of great length in the Galatheidae.

The great length of the spine of the basipodite of the second antenna, which is rather a feature of the Anomura in general, is particularly noticeable in *Munida* where this spine exceeds the endopodite in length. In the Brachyura it is always of great size. This larva also shows the peculiar form of the antennal scale which characterizes the genus. The larva illustrated is in the first stage, and the telson has a form quite unlike that found in the later stages (Sars, 1889, pl. 6). The great development of the first seta into a spinous prolongation of the telson is a feature peculiar to *Munida* as compared with *Galathea*, but, in the last stages it is reduced to a small tooth, and the fourth spine of the series becomes greatly the largest and, like the first spine in stage I, it is fused and not jointed to the telson.

The animal described by Bate under the name of *Zoontocaris* is a larva of *Galathea*, and a precisely similar larva was taken at station 139. Bate's specimen was taken off Cape Howe, Australia.

II. Porcellanidae.

The larva of *Porcellana* has been described or referred to perhaps more often than that of any other Decapod, but it is rather remarkable that no complete account of its transformation has ever been given except that of Faxon (1879), who dealt with *Polyonyx macrocheles*, and that the larvae only of this species

* Miss Webb states (1921, p. 413) that the last larva of *Porcellana* has no exopodite on the third maxillipede. This is not in agreement with the descriptions of Sars and Faxon, or with my own observation. I find a setiferous exopodite in the larva of *P. platycheles* and in all the larvae of this stage in the "Terra Nova" collections.

and of *P. longicornis* and *P. platycheles* have been identified. All the larvae described agree in their general form and in the structure of the appendages, but,

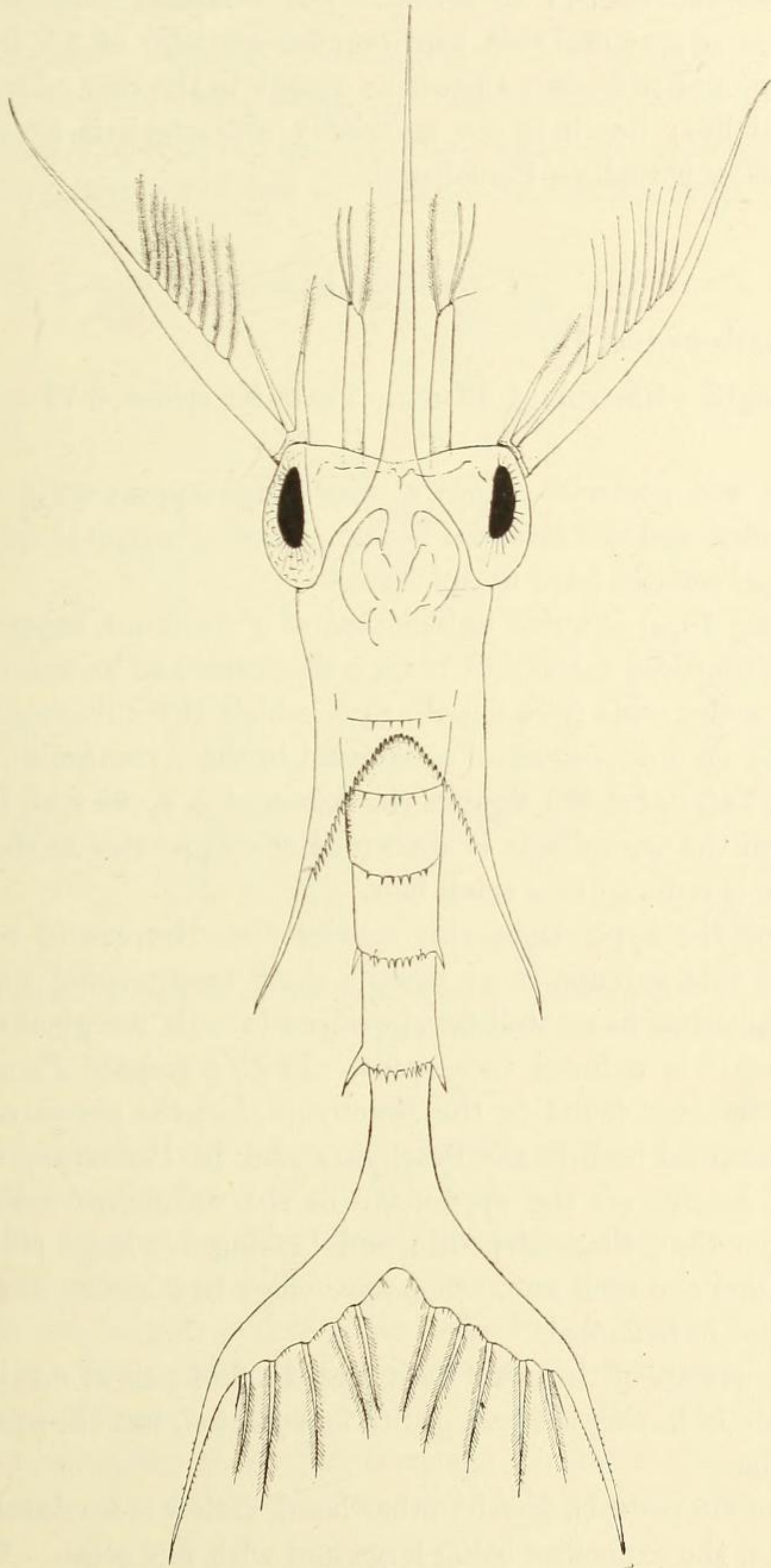


FIG. 69.—*Munida*, sp. Station 106.

whereas the telson of these three species has a formula of 7+7, the larvae of unnamed species have been figured by Claus and Cano in which there is a large

median spine in addition. There is also a lack of agreement as to the number of pleopods developed, since there appear to be only three pairs in *P. longicornis* and *P. platycheles* and four in all others. The complete suppression of the uropods in larval life is a remarkable feature characteristic of all Porcellanid larvae hitherto described, and unknown elsewhere except in the case of some Caridea with abbreviated larval life; but it is not invariably characteristic for the family if the larva described below is really a Porcellanid.

Porcellanid larva.

Melbourne harbour (fig. 70).

Stage I. Length—Rostrum, 4.35 mm. Posterior spines, 3.75 mm. Total length, 9.75 mm.

The rostrum and posterior spines at this stage appear quite smooth, but have very minute spinules, and the carapace has no spines or marginal spinules.

The abdominal somites have no spines.

The telson (fig. 70, e) is quite unlike that of *Porcellana*, being more or less triangular with a rather deep sulcus. It bears a short spine at its outer angle and seven ciliated setae on either side (formula 8 + 8) of which the outermost is the shortest. But this seta is by no means so small as is usual in the Anomura and Thalassinidea.

Cano (1893, Taf. 2, fig. 82) figures the telson of a species of *Porcellana* in the last stage in which the second seta is almost of the same size as the others, whereas in other species it is reduced to a small hair.

In respect of the appendages this species also diverges to some extent from *Porcellana*. The first antenna is as usual a short unsegmented rod with aesthetes, but the second antenna has a well-developed scale with marginal setae, whereas in *Porcellana* the scale is reduced to a spine. In this respect *Porcellana* shows an advance to the condition found in the Brachyura, but the primitive form of a scale-bearing setae is retained both in the Brachyura and in *Porcellana* up to the time of hatching. In *P. longicornis* the appendage in the unhatched embryo has a scale considerably longer than the endopodite and bearing five large ciliated setae, while the endopodite bears one such seta. The appendage has, in fact, at this stage a close resemblance to that of *Galathea*.

The mouth-parts are of the usual form, and the first pair of maxillipedes resemble those of *Porcellana* in having the endopodite four-jointed, but the exopodite bears five setae instead of four.

The third maxillipede is, on the other hand, rather more developed than is the case in *Porcellana*, the exopodite being large and with five setae. The endopodite is rudimentary and springs from the base of the basipodite.

Small rudiments of all the five pairs of pereopods are present, that of the fifth being placed inside and hidden by the third and fourth pairs. Each of the first four

pairs has a small forwardly turned papilla at its base which represents a rudimentary gill.

There is no trace of pleopods.

Stage II. Length—Rostrum, 7 mm. (fig. 70, *b*). Posterior spine, 4.65 mm. Total length, 13.85 mm. (A second specimen measured 12 mm.)

The enormously long rostrum has now a few small spines along its ventral side, while the posterior spines have three strong spinules near the base. There is a small

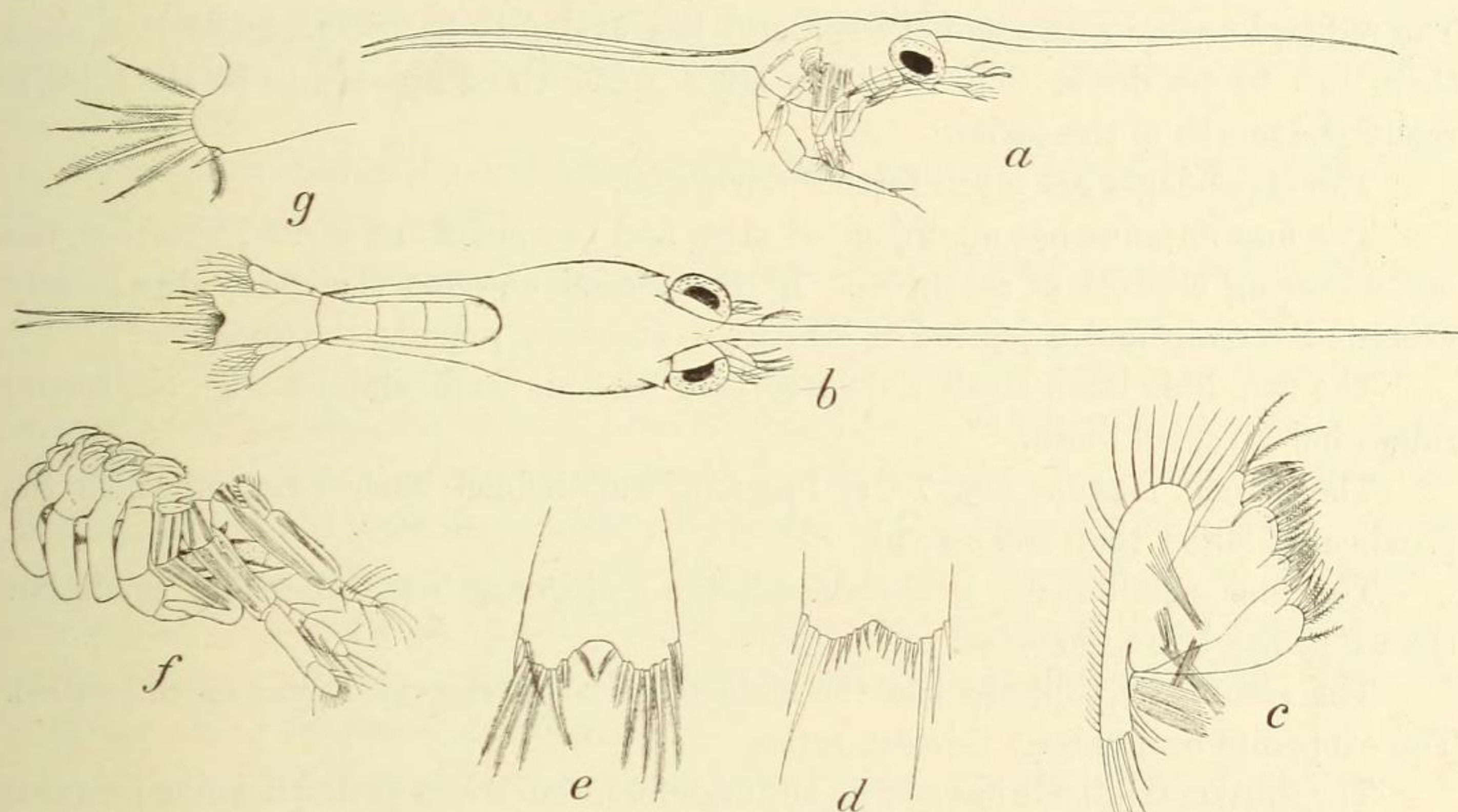


FIG. 70.—*Porcellanid*. Melbourne harbour. *a*. Stage I. *b*. Stage II. *c*. Second maxilla. Stage III. *d*. Stage III. Telson. *e*. Stage I. Telson. *f*. Stage III. Pereiopods. *g*. Telson of youngest stage. Station 136.

spine on each side at the level of the eye corresponding to supra-orbital spines—a most exceptional feature in Anomura.

The abdominal somites have no dorsal spines, but there are very small ventro-lateral spines on somites 4 and 5. The telson is more or less rectangular, the width about half the length, and slightly hollowed posteriorly. The formula is, as before, 8+8, but the number is not invariably the same and I have seen two specimens in which it was 10+8 and 9+8 respectively. The second seta is now much smaller and, springing as it does from the ventral surface, it is not easy to see. The fourth spine is greatly the largest, and this and the two outer spines are smooth.

The first two pairs of maxillipedes remain the same, but the endopodite of the third pair has grown into a large rod, but is unjointed and without setae. Its exopodite bears eight setae, while that of the first two pairs have ten.

The pereopods have greatly increased in size, but there is no sign of pleopods. The uropods are developed and both branches bear setae.

Stage III. Length—Rostrum, 5.8 mm (end broken). Posterior spine, 4.4 mm.

The rostrum bears very minute spinules, but the posterior spines are bare except for about four strong spinules near the base on the ventral side.

The abdominal somites have no spines, except a very minute lateral pair on the fourth somite and a larger pair on the fifth. The telson scarcely differs from that of stage II, and, in the single specimen available, has a formula of 9 + 8 (fig. 70, *d*). The reduced second seta was not seen, and has evidently been completely lost, since there can be no doubt that the very large spine which appears to be the third is really the fourth of the series.

The appendages are much further developed.

The first antenna has an unjointed stem and two short one-jointed branches, the outer bearing clusters of aesthetes. In the second antenna the endopodite greatly exceeds the scale, and is jointed at its base. The scale remains the same.

The mandible has a small unjointed palp without setae, and its edge has strong ridges but no small teeth.

The second maxilla (fig. 70, *c*) has four well-defined inner lobes of which the proximal is larger than the second.

The first maxillipede is unchanged, the endopodite remaining very small, but the exopodite bears ten setae.

The second maxillipede has the endopodite large, the third joint much swollen. The exopodite bears about thirteen setae.

The third maxillipede has a large but undifferentiated endopodite bending forwards under the preceding appendages.

The pereopods (fig. 70, *f*) are very large, the first pair with rudimentary chelae, and the fifth hidden beneath the fourth pair. The third and fourth pair have the appearance of enclosing either a chela or two apposed spines at their ends under the cuticle, while the fifth pair is distinctly bi-lobed at the end.

The gills are well developed, as follows:—

	Mxp. 3	Leg 1	2	3	4	5
Arth.	2	2	2	2	2	—
Pleur.	—	—	1	1	1	1

There is no sign of epipodites.

Although this must be the last larval stage there is no trace of pleopods. This is the only example known of a Decapod in which the pleopods are entirely suppressed in larval life.

At station 136 a single specimen of a Porcellanid larva was taken which either belongs to the same species as that above described or at all events to one closely allied to it. It is apparently in the first stage after hatching and is younger than the larva described above as stage I.

The rostrum is broken, but the posterior spine measures 2.85 mm. and the body 1.15 mm. The rostrum is very spiny and the posterior spine, in addition to the large spinules at the base, has a number of smaller spinules scattered along its whole length.

Somites 3 and 4 of the abdomen have very small ventro-lateral spines.

The telson is triangular, with a deep sinus (fig. 70, *g*), and bears a short spine at each angle and six feathered setae. The first of these (no. 2 in the series) is much larger than is usual in the Anomura.

The antennal scale is as in the larva just described, having a long terminal spine and five setae. The endopodite is a small knob, and there is a short stout spine on the basipodite.

The endopodite of the first two maxillipedes is very small and four-jointed, while the exopodite has four setae.

The third maxillipede is a short uniramous rod without setae, and there is no trace of pereopods.

The larvae just described emphasize most forcibly the extremely close relationship between the Galatheidae and the Porcellanidae. Between them and the larvae of the Galatheidae there is no distinction possible except as regards the enormous development of the rostrum and posterior spines and the absence of serration on the carapace. These characters give the animal so close a resemblance to the larva of *Porcellana* that there can be little doubt that we are dealing with a Porcellanid, but in the presence of uropods and of an antennal scale, and in the form of the telson the contrast with *Porcellana* is profound.

In respect of these characters this larva is more primitive than *Porcellana*, but in the total loss of the pleopods in larval life it is more specialized. There is a tendency to loss of pleopods in *Porcellana* since some species have none on the fifth somite. This peculiar character is found also in *Diptychus* (Bouvier, 1892) but is unknown in any other Decapod.

Paguridea.

The development of a number of Paguridea is known, the best accounts being those of Sars (1889), Thompson (1903), and Issel (1910). So far as is known all species have free larvae, but in the case of *Lithodes* and of *Paguristes oculatus* larval life is to some extent abbreviated. There are generally four Zoea stages followed by transformation to a symmetrical post-larval or Glaucothoë stage. The Glaucothoë is a free-swimming stage during which transformation of the internal organs occurs, so that at the next moult the adult structure and torsion of the abdomen is obtained. A full account of this transformation is given by Thompson, who devoted special attention to this phase and to the question of the relation between the torsion of the abdomen and the choosing of a shell.

So far as concerns the larval stages the Paguridea very closely resemble the

Galatheidea, and the summary of the characters of the latter given on p. 175 applies also to the Paguridea with the following exceptions.

1. The rostrum is usually shorter, but may be very long, e.g. *Eupagurus bernhardus*.

2. The carapace is never serrated posteriorly and is never produced into a long spine. It may be simply rounded behind (*Paguristes oculatus*) or it may be pointed, but it is commonly produced into a more or less down-curved hook.

3. The scaphognathite of the second maxilla lacks setae on its proximal part. It is not quite clear whether this is so in *E. longicarpus* (Thompson, Pl. V, fig. 11), but I have found it to be so in such larvae as I have examined, and Sars figures the proximal lobe as bare in the species dealt with by him.

4. The distal lobe of the first maxilla has only two large spines in early stages.

5. The telson is never so deeply incised as it is in the Galatheidae, and often has a convex posterior margin. The arrangement of the spines is the same. The second seta is always reduced to a very small hair which may be so small that it can only be seen with great difficulty in ventral view. The fourth spine is, as in Galatheidae, in late stages a prolongation of the telson and not jointed off from it, but it is variable in size in different species and may be reduced to a mere point.

6. The fourth leg, though still as a rule visible in side view, tends to move inwards below the other legs. The fifth pair is always completely hidden as in the Galatheidae.

Although I have had numbers of Pagurid larvae for examination, none of these can be referred to their adults, and for the most part they do not possess any structural features sufficiently striking to require description. One larva only may be mentioned which very closely resembles that of *Spiropagurus chiroacanthus*, and it is necessary to describe one post-larval stage and to enter into the question of the significance of the genus *Glaucothoë*.

Spiropagurus (?), sp. (fig 71.)

The larva here figured was taken at station 109. It is apparently in the first stage and measures 3.65 mm.

A detailed description is unnecessary, since it agrees very closely with the description given by Sars (1889) of *Spiropagurus chiroacanthus*. The following points may however be mentioned.

1. First maxilla. The distal lobe is armed only with two very large spines, with one small one between. This seems to be a feature characteristic of the Paguridea, at all events in the first stage, since it is found in each of the species figured by Sars. There is a tendency to a reduction of the spines in the Galatheidae, but it is not so pronounced as it is in the Paguridea.

2. The mandible is of remarkable size, the anterior part being produced into a long pointed process. There is no palp at this stage.

3. The third maxillipede is present and uniramous, but this branch represents the exopodite, as it has, at its base, a very minute papilla which is the rudimentary endopodite. The Paguridea may in fact be regarded as hatching with three pairs of biramous maxillipedes of which the third is rudimentary.

4. The posterior margin of the telson is convex, with a formula of 8+8, the second seta being a small hair and the fourth a rather large spine. In the next stage the telson is precisely the same.

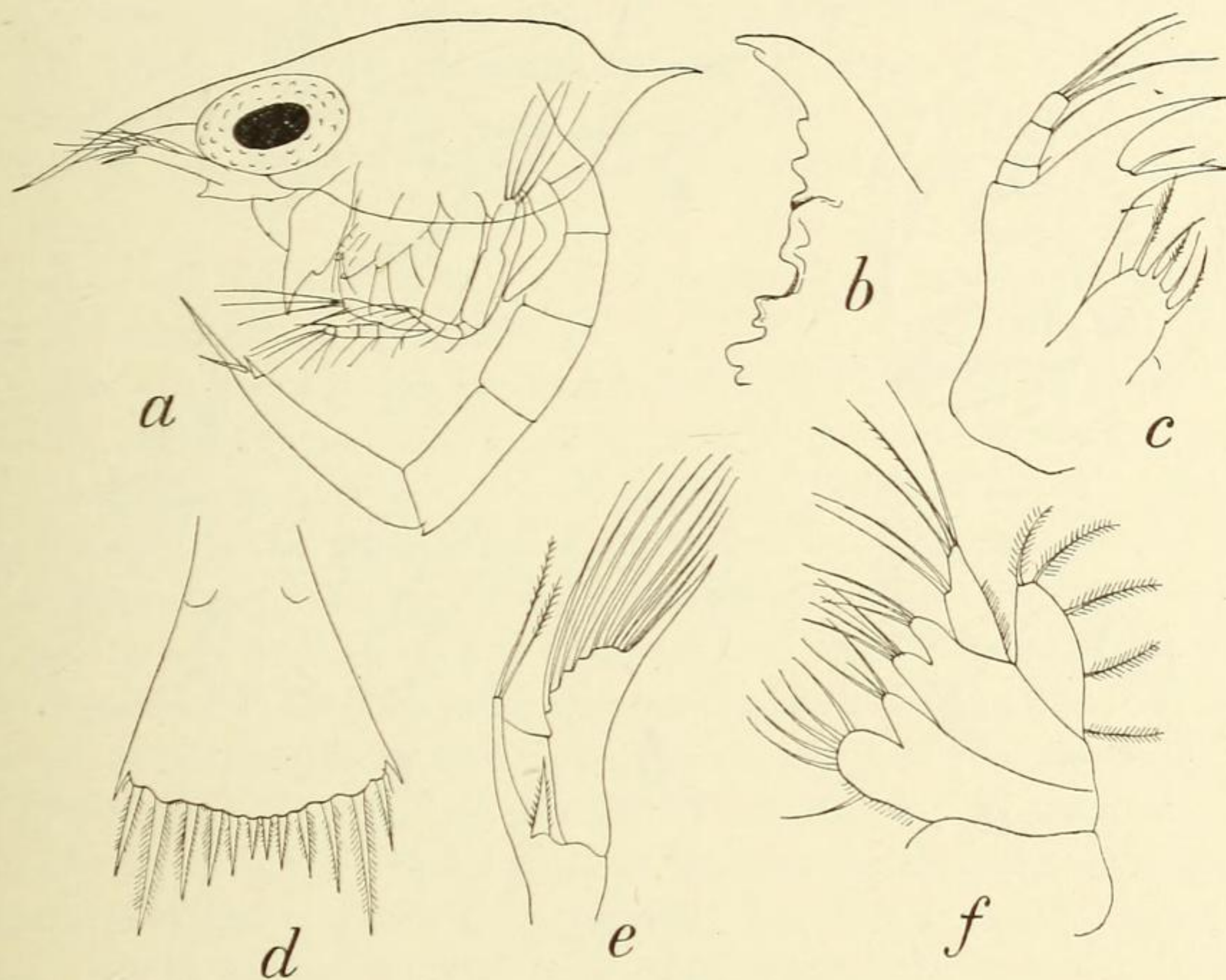


FIG. 71.—*Spiropagurus* (?), sp. Station 109. *b*. Mandible. *c*. First maxilla. *d*. Telson. *e*. Second antenna. *f*. Second maxilla.

Glaucothoë peronii, M. Edw. (fig. 72), and the Glaucothoë stage.

The Glaucothoë or free-swimming first post-larval stage is very commonly taken in plankton, and a fair number were found in the "Terra Nova" samples at stations 130, 132, and 232, but in every specimen the chelipeds, and in most of them the remaining legs, were lost, so that it is impossible to identify and useless to describe them. One specimen, however, which was taken at station 107 deserves some description, since it is identical with *Glaucothoë peronii*, M. Edw., and differs absolutely from the Glaucothoë stages of those species of which we know the development.

This Glaucothoë stage corresponds to the Megalopa of Brachyura and is a transition from larva to adult. It has lost most of the characters of the larva both in body form and in form of the appendages, but it has not wholly acquired the adult

characters of either. On the other hand, these forms are all quite recognizably Pagurids, and in all cases the eyes are reduced to the shape and small size of the adult, and ophthalmic scales are present.

In the specimen now in question (fig. 72) although the appendages have all changed to the form characteristic of adult Pagurids, the eyes remain of large elongated-oval shape with large facets and resemble most closely the eyes of larval Thalassinidea.

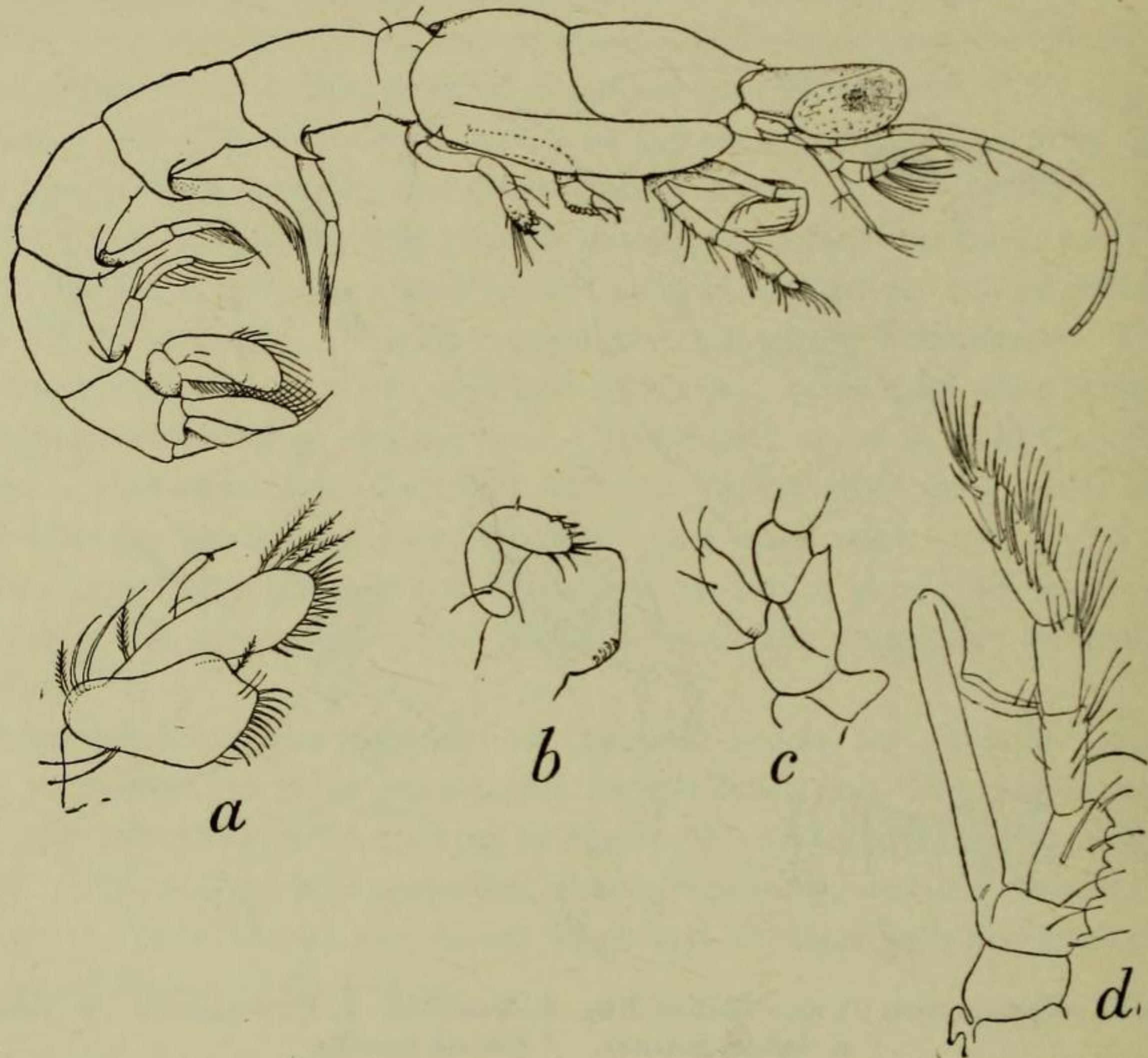


FIG. 72.—*Glaucothoë peronii*. Station 107. *a*. First maxilla. *b*. Mandible. *c*. Stem of second antenna showing vestigial scale. *d*. Third maxillipede.

These eyes are scarcely pigmented, such dark pigment as there is being confined to the ommatidia of the anterior part.

The abdomen is very much larger than is usual in the *Glaucothoë* stage of normal Pagurids and is only slightly down-curved, while the epimera of somites 2 to 5 are produced downwards into procurved hooks recalling those of the larvae of *Jaxea* and *Naushonia*. In fact, the shape of the eyes and of the abdomen give the animal a striking resemblance to a Thalassinid.

On the other hand, the appendages are unmistakably those of a Pagurid, as is also the gill formula. There are at this stage only six fully developed phyllobranchs on each side, but traces of others are visible as follows :

	Mxp. 1	2	3	Leg 1	2	3	4	5
Epip.	—	—	1	—	—	—	—	—
Arth.	—	—	rud. ?	2 r.	1+r.	2	2	—
Pleur.	—	—	—	—	—	—	1	—

The animal unfortunately lacks all legs except the fourth and fifth. Two of the walking legs were found loose in the collection, but the chelipeds were altogether lost.

The resemblance of this specimen to *Glaucothoë peronii* in respect of the two characters wherein they both differ from all other Pagurids, namely the size of the eye and the epimera of the abdominal somites, is obvious and complete. There cannot, in fact, be any doubt that both belong at least to the same genus, but it is remarkable that, whereas *G. peronii* measures about 15 mm., my specimen is only 7.75 mm. long.*

I am indebted to Dr. Calman for the opportunity of examining some specimens of *Glaucothoë* from South Africa (35° 55' S., 17° 6' E., depth 1014 fathoms), among which are four specimens which are undoubtedly identical with *G. peronii*, M. Edw. They measure about 14 mm., and the eyes, though very large, are not quite so large in proportion to the body as in the small specimen described above. The structure of the appendages is the same in all essentials, and the epimera of the abdominal somites have the same procurved hooks. *Glaucothoë* of this form are therefore to be found varying in size from about 7 to about 15 mm., and in the Pacific and the north and south Atlantic. Milne Edwards's type was believed to come from "Asiatic Seas," and Bouvier has recorded its occurrence on four occasions off the coast of N.W. Africa between 20° 38' and 31° 44' N. Lat. and 19° 37' and 42° 31' W. Long.

G. hendersoni, Bouvier, which was taken between the Maldives and Cape Comorin (Henderson, 1896), has not been fully described, but it is evidently closely allied to *G. peronii*. Alcock says of it (1905, p. 23) that it has "the same enormous squilla-like eyes" as *G. peronii*.

Here is the old *Glaucothoë* problem revived! The facts are these: from time to time there have been found, generally in deep water, rare examples of free-swimming symmetrical Pagurids measuring from 14 to 20 mm. to which specific names have been given on the assumption that they are adult or semi-adult forms. There can be no doubt that they are not adult forms, but, in that case, of what kind of Pagurid can they be the larvae? Three points are of the greatest importance—they are of large size, they are very rare, and they have all the mouth-parts fully developed and of the adult form. In all these points they differ totally from the so-called *Glaucothoë* stage of the European littoral Paguridea. Bouvier has dealt in great detail with the significance of these remarkable forms (1891, 1905), and came to the conclusion that each of the known species of *Glaucothoë* could be referred, mainly on the evidence of the gills, to some known genus of Pagurid of which it was an early

* Bouvier (1905) records specimens of *G. peronii* of 12 mm. and of 7 mm.

post-larval stage. Thus *G. peronii*, which has the gill formula of *Eupagurus*, he refers to *Sympagurus*.

Bouvier's conclusion as to the nature of these curious animals is that they are larval forms arrested in development either by reason of failing to obtain shells, or of being carried away by currents outside their natural habitat. In ordinary circumstances the Glaucothoë stage lasts but four or five days (Thompson, 1903, p. 202), and the moult to a symmetrical form takes place whether a shell is found or not; but in the case of the true Glaucothoë the asymmetrical form is not assumed and growth continues. A similar explanation has been given for the exceptionally large Caridean larvae which have occasionally been taken.

No final answer to this difficult problem is possible without keeping the animals under observation, but I find Bouvier's explanation difficult to accept for the following reasons:

1. While the Glaucothoës have the appendages of the adult form, or more developed than in the "Glaucothoë stage," they are less advanced than this stage in their lack of ophthalmic scales and in the form of the tail plate. In respect of these characters they represent a stage which is not found at all in the ontogeny of any species of which the development is known. It is not, therefore, a case of further development of a known form, but of an entirely different organization. The Glaucothoë stage always has these ophthalmic scales and a tail plate with more or less asymmetrical uropods.

2. Of the true Glaucothoës there are only five "species" known, and some have been repeatedly seen, while Bouvier has found examples of *G. peronii* and of *G. rostrata* of very small size—4 mm. in the case of the latter.

From these facts one is justified in concluding that there exist certain species of Paguridea whose first post-larval state differs from those hitherto known in having, for example, no ophthalmic scales, and which have also a more prolonged post-larval life than is usual. Since there are recognizable "species" the course of development is in each case definite and specific, and in all probability it leads in the end to transformation to an asymmetrical adult. One would be inclined to suggest that they belong to the large species of *Coenobita* or to *Birgus*, but the gill formula seems to exclude such a possibility.

If Bouvier's theory were correct there seems to be no reason why Glaucothoë stages of the normal form (with ophthalmic scale) should not sometimes grow into the large Glaucothoë form. It might be answered that, for some reason, this scale is always lost when such an abnormal development supervenes, and that the uropods also become transformed. But the peculiar *G. peronii* stands in the way of such a supposition, since it is hardly permissible to postulate that the eyes themselves should revert to the larval condition, and that the epimera should take on the very special form characteristic of that species.

Well-founded knowledge of Pagurid development is far too scanty to permit of

any definite conclusion on this question, and the very incompleteness of our information is a strong reason for refusing at present to accept abnormality as an explanation.

That the Glaucotohœs are immature there can be no reasonable doubt, and they should be accepted provisionally as normal stages in development. Probably the adults to which they belong live at great depths, and an extended post-larval life may be connected with this habitat. The Sergestidae and some Penaeidae (e. g. *Funchalia*) have a long series of post-larval stages, and it may be found that this is characteristic of deep-sea forms.

Hippidea.

The larvae of *Hippa* and of *Albunea* have been described and figured by various authors, but only that of *Hippa* has, so far as I can ascertain, been definitely identified by hatching from the egg (Faxon, 1879). At the same time there is no reason to doubt the identification of the larvae of *Albunea* by Claus (1876), Boas (1880), and Cano (1893). Cano (1893) has also described the Zoea of *Remipes*, so that the characters of the group are sufficiently established. The following characters are common to the three genera:

1. Carapace, at least in later stages, with large postero-lateral or lateral spines.

2. Telson more or less quadrangular, with entire posterior margin armed with numbers of small denticles. No median spine or reduced second seta.

3. Second maxilla with inner lobes reduced or absent.

4. Pereiopods without exopodites. Exopodite present on third maxillipede in *Albunea*, but absent in *Remipes* and *Hippa* (?). In *Albunea* the endopodite is basally placed.

5. Antennal scale well developed in *Albunea* and *Remipes*, but absent in *Hippa*.

In their general characters these larvae are typically Anomuran. Their chief distinguishing feature is the large spade-shaped telson with its small denticles.

Albunea (fig. 73).

At station 39 some larvae were taken which entirely agree with the description of the Zoea of *Albunea* as given by Claus (1876, p. 59). The larva has, at first sight, somewhat the appearance of a Brachyuran, but the telson and appendages are quite of Anomuran form. *Albunea* differs from *Hippa* and *Remipes* in having the uropods uniramous,

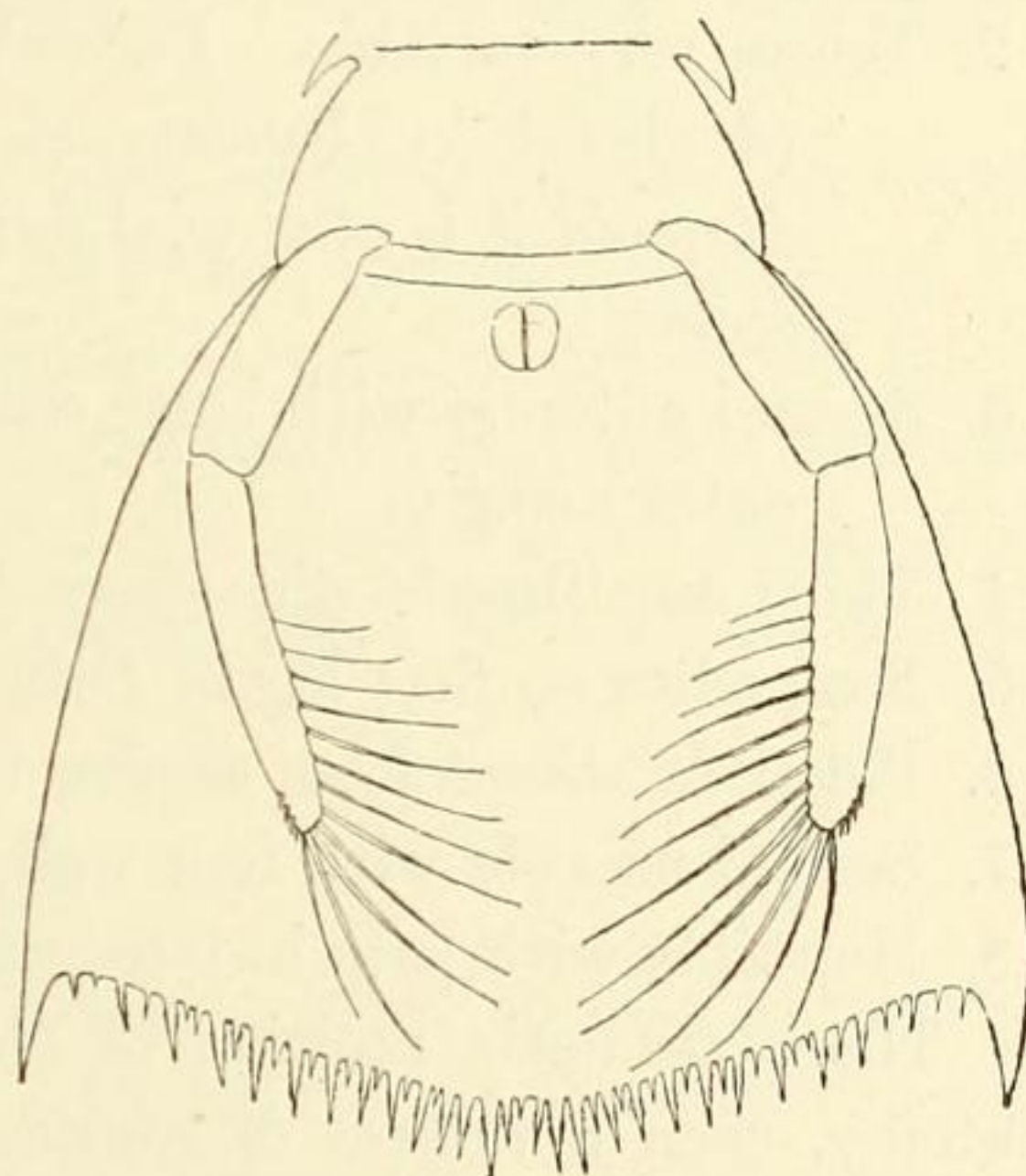


FIG. 73.—*Albunea*, sp. Telson and uropods. Station 39.

DROMIACEA.

The information available with regard to the Dromiacea is by no means complete. The Zoea of *Dromia* has been traced from the egg (Gourret, 1884; Cano, 1893), while Boas has also described a late stage of the same genus. Cano has figured some stages in the development of *Dynomene*, *Latreillia*, and *Homola*, but his identification of them is not beyond question and the information given is scanty. Boas has also identified the larva of *Homola*, and his figures both of *Dromia* and of *Homola* are excellent.

Assuming these larvae to have been correctly identified their characters may be combined as follows:

1. Rostrum long; carapace without supra-orbital spines, either rounded behind or with a short posterior spinous projection similar to that of Paguridea.
2. Telson very variable. Formula 7 + 7 in *Dromia* and 7 + 1 + 7 in *Latreillia* (doubtful in *Dynomene*). In both cases with reduced second seta. In *Homola* it is of special form, with very numerous spines and a small median spine.
3. Second antenna with large scale, sometimes (*Dromia*, *Homola*) with setae along outer margin.
4. Third maxillipede with exopodite, the endopodite rudimentary and basal.
5. Exopodite on first leg in *Dromia* only.
6. Pleopods absent from somite 1.
7. Second maxilla with four well-defined lobes.
8. Mandible with palp in later stages.

The systematic position of the Dromiacea has, on the evidence of the adult anatomy, been a subject of considerable difference of opinion, and they have been associated on the one hand with the Anomura and on the other with the Brachyura. Boas, who appreciated the importance of the larval characters, and gave a long list of adult features wherein the Dromiacea resemble the Anomura, concluded by grouping them within the Brachyura, but derived them from an ancestral form more primitive than the Anomura. Bouvier (1896), after discussing all the evidence both from the adult and from the larvae, concluded that they are Brachyura and stand in the line of descent of the Brachyura, not from the Anomura or the Thalassinidea, but from the Homaridea. Calman (1909) accepts the Dromiacea as a tribe of Brachyura equivalent to the tribes Oxystomata and Brachygnatha.

Bouvier seems to have felt the difficulty which the development of *Dromia* placed in the way of his argument and treats the evidence, as it seems to me, in rather summary fashion.

Arguments derived from or sustained by the general facies of a larva and not supported by other structural features are likely to prove unreliable, and Bouvier is quite justified in dismissing Cano's derivation of *Latreillia* from the Paguridae and

its separation from the remaining Dromiids, which Cano considered to be descended from the Thalassinidea. But he is certainly not justified in concluding that it is equally easy to derive the larva of *Dromia* from that of a Homarid as from that of a Thalassinid. The Homarid larva is of very primitive type in which *all* the pereopods have exopodites, all the endopodites are normal and functional, and the telson has a median spine and numerous sub-equal marginal spines. I have attempted to show that the Thalassinidea fall into two groups, a Homariform and an Anomuriform series, and the latter is characterized by two features which are of the highest systematic importance and are repeated without exception throughout the Anomura, namely the rudimentary condition of the endopodite of the third maxillipede and its position at the base of the basipodite, and the reduction of the second spine of the telson to a small hair (the latter is also shared by the Homarine series). These characters are also found in the Dromiacea, and the only possible conclusion seems to be that they have sprung from an ancestor related to the Anomuriform Thalassinids and resembling *Upogebia* in its larval characters.

The Dromiacea should, in my opinion, not be included at all in the Brachyura, but should form a group independent of both the Anomura and the Brachyura, and it does not seem even to be certain that the Dromiacea stand in the direct line of descent of the Brachyura. The tendency of the whole evidence from larval characters seems to be rather in the direction of the abolition of the larger sub-divisions of the Decapods, and a substitution of a series of smaller groups which do not form a linear series.

Dromiacea species ?

At stations 43, 106, and 129 larvae of two closely related species were taken whose systematic position is extremely doubtful. Unfortunately the specimens are in early stages, and therefore no information can be obtained from their pereopods or gills. They have the appearance of holding a position intermediate between the Anomura and Brachyura, though belonging to neither. On the other hand, there is a distinct general resemblance to the Zoea of *Homola* as figured by Cano (1893, Taf. 2, fig. 50), and there is the same type of telson. For this reason I refer these larvae to some genus of Dromiacea without attempting any more precise identification.*

Species I. Station 43 (fig. 74).

There are two specimens of this form, both apparently in the first stage. The animal measures about 1.6 mm. from the end of the rostrum round the curve of the abdomen which is curled round under the body.

There is a long rostrum, somewhat turned up at the end, and there is a small

* It is not unlikely that these two larvae may really belong to the Raninidae (Gymnopleura), see p. 194.

stout dorsal spine on the carapace with a short median knob behind it (fig. 74, *a*). The posterior edges of the carapace are fringed with teeth, and there is a large wing-like expansion on either side also bearing marginal teeth and produced into a large, lateral, forwardly directed spine.

The abdominal somites have short median spines and a pair of lateral spines in addition to a dorsal pair of hairs. The telson is of a T-shape, the two arms forming a straight line at right angles to the abdomen. Each arm has a very small terminal spine and six setae, of which the first is not ciliated. This seta corresponds to the

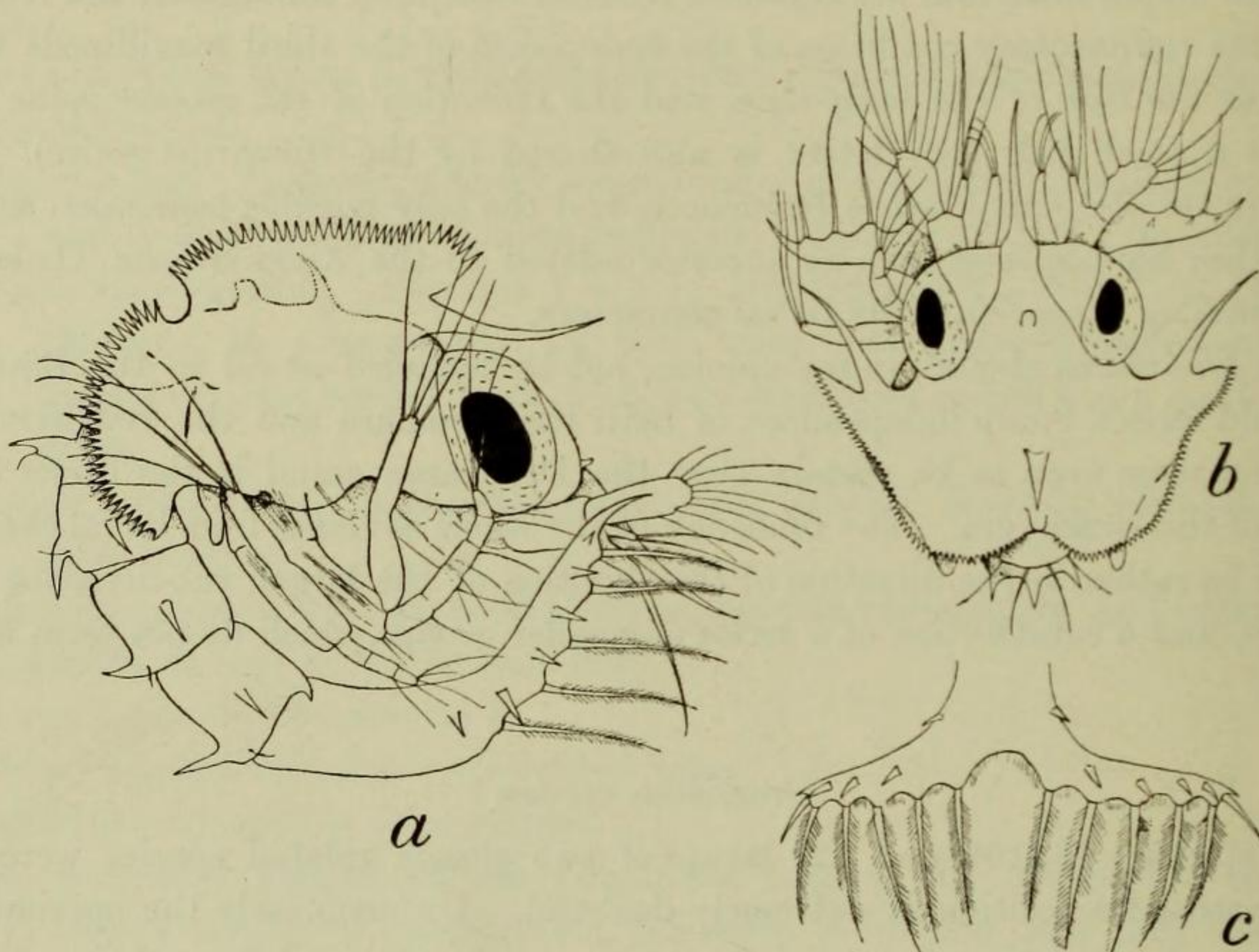


FIG. 74.—*Dromiacea*. Species I. Station 43. *a*. Lateral view. *b*. Dorsal view. Another specimen. *c*. Telson.

reduced seta of *Anomura*. On the dorsal surface of the telson is a row of three or four strong spines, and there is also another pair at the base of it.

The eyes, the pigment of which is brown, are not mobile, and a small "frontal organ" may be seen on the anterior edge of each.

The first antenna is a short unjointed rod.

The second antenna has a relatively large scale with nine setae, and a short endopodite with two setae, while an enormous spine springs from the basipodite and extends beyond the rostrum.

The exopodites of the first two pairs of maxillipedes bear four setae. The third pair is represented only by a short uniramous rudiment, and there is no trace of pereopods.

Species II. Stations 106 and 129 (fig. 75).

The species from station 106 differs from that above described in the lack of a dorsal spine on the carapace and of the great lateral toothed wings. There is, however, a pair of simple lateral spines.

The abdominal somites also have no dorsal spines, and lateral spines are present only on the fourth and fifth somites.

The telson is rather triangular in shape, the arms not being long and narrow as in the first species. Each arm has a strong terminal spine and five ciliated setae.

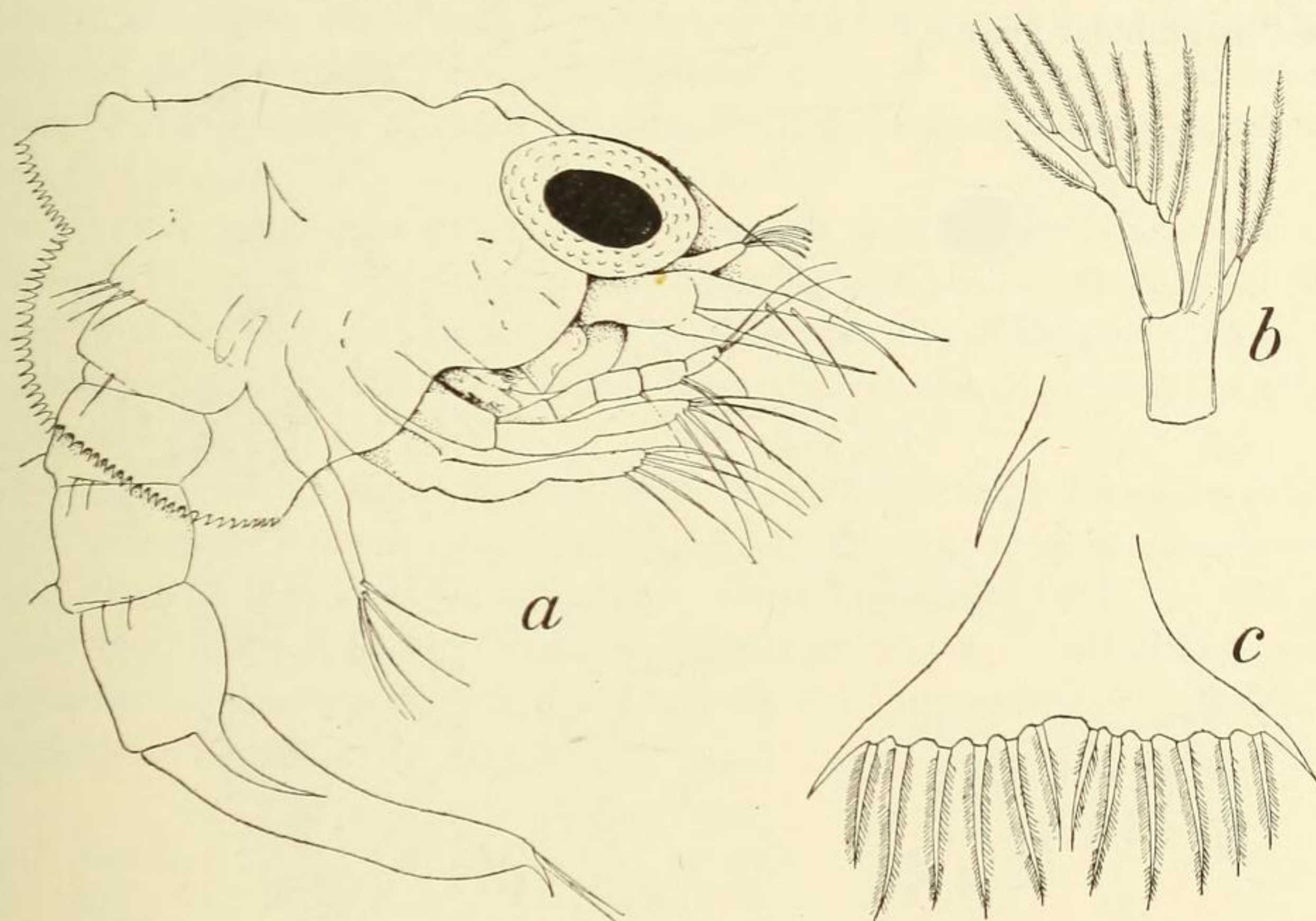


FIG. 75.—*Dromiacea*. Species II. Stations 106, 129. *a*. Larva from station 129. *b*. Second antenna. Station 106. *c*. Telson. Station 129.

There are only six setae (including the spine) on either side, and I have no doubt that the second seta has been entirely lost.

A specimen from station 129 which is in a slightly older stage, has a formula of 7+7 which rather confirms this view, since it is usual for an additional seta to be present in the second stage.

The appendages are essentially the same as in the first species, the second antenna having the same huge spine. In the older specimen the third maxillipede is developed, having an exopodite with four setae. The endopodite is very small, at the base of the appendage, and with one seta at the end of it.

Dromiidae.

Species I. Station 43 (fig. 76).

The larva here described so closely resembles that of *Dromia* in the form of the second antenna and of the telson, and in the presence of an exopodite on the first leg

that I have no hesitation in referring it to the Dromiidae, even though it probably does not belong to the genus *Dromia* itself. Three stages are represented, of which the second may be described.

Stage II. Length, 3.6 mm. (fig. 76, *a*).

The carapace extends over the eyes as a broad rostral process with two lateral and a median spine. There are neither dorsal nor posterior spines, but the posterior edge is simply rounded and denticulate. The surface of the shell posteriorly has distinct concentric striae. A deep transverse groove anteriorly seems to correspond to the "mandibular groove."

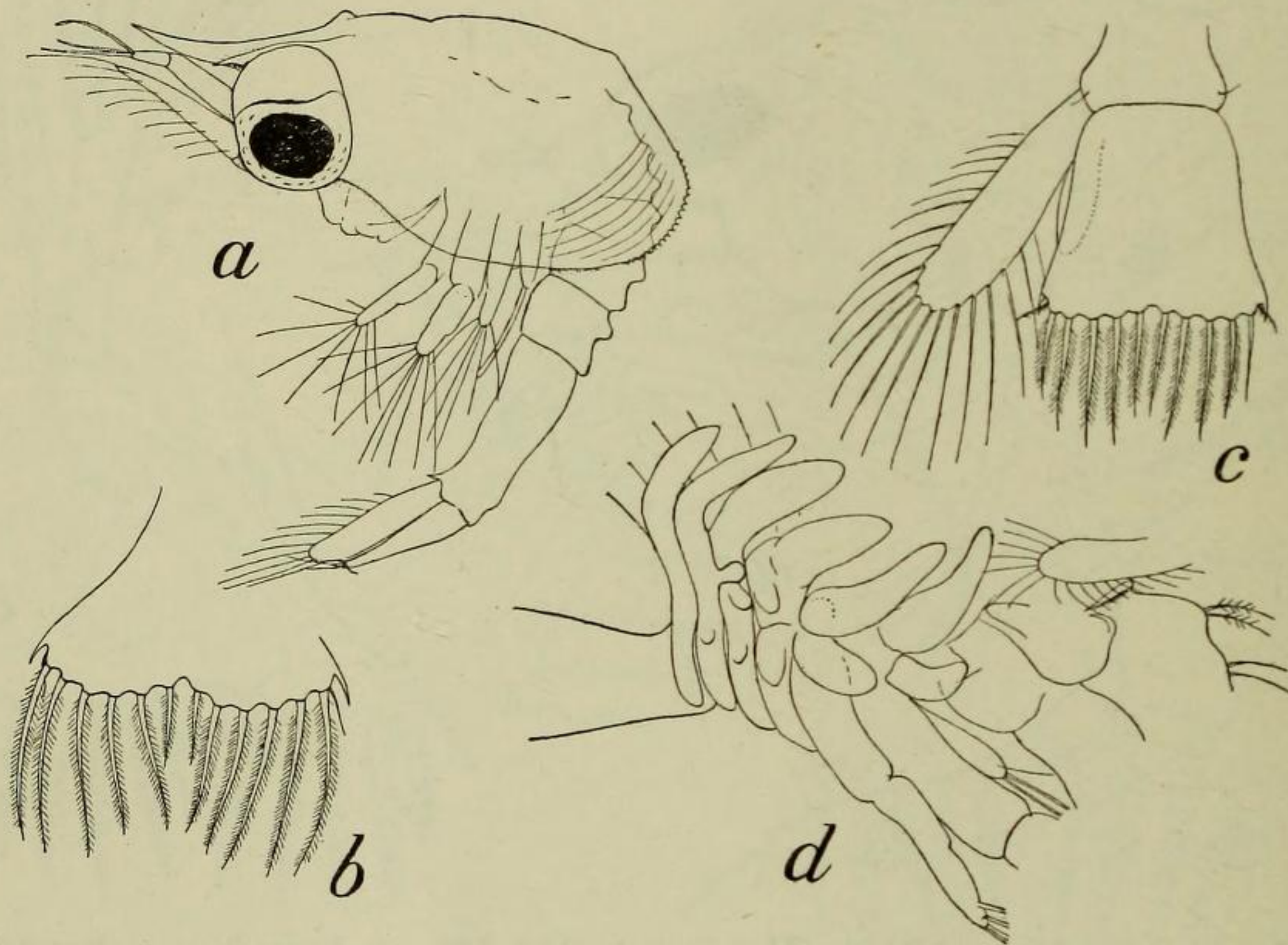


FIG. 76.—*Dromiidae* species. Station 43. *a*. Larva, 3.6 mm. Stage II. *b*. Telson. Stage I. *c*. Telson. Stage II. *d*. Gills. Oldest stage.

The somites of the abdomen have no spines, but each has two pairs of small papillae, which give them a ridged appearance in side view. The telson (fig. 76, *c*) is almost rectangular, little broader at the end than the base, and with no median sinus. There is a small spine at each angle and six setae (formula 7 + 7), of which the outer one is very small.

The uropods are present, but the endopodite has no setae and is much shorter than the exopodite, which has no terminal spine.

The first antenna has a one-jointed stout stem, and there is a trace of the endopodite as a minute papilla bearing a seta.

The second antenna has a very large scale bearing setae along the whole of the outer as well as of the inner margin. The endopodite is a short rod without setae.

The mandible has no palp.

The three pairs of maxillipedes are developed and biramous, the endopodite of the third being rudimentary and seated at the base of the appendage.

The first leg has also a seta-bearing exopodite and a rudimentary endopodite, and the rudiments of the succeeding four pairs are visible.

The gills are visible, but not in their full number. There appear to be two rudiments on the third maxillipede and the first leg, and one on each of the following limbs.

The general appearance of the larva differs little by reason of age, but in the first stage the telson (fig. 76, *b*) is triangular and very closely resembles that of *Upogebia* in its first stage, though the formula is 8 + 8. A further resemblance to *Upogebia* is the presence of three setae on the endopodite of the second antenna at this stage.

In the last stage seen (which is not the last larval stage) the mandible has a rudiment of a palp. The first leg has the endopodite rudimentary, in the form of a small bud at the base of the basipodite. On the following three pairs of legs, which show no sign of joints, there are minute lobes which seem to represent vestiges of exopodites.

It is much to be regretted that there is no older stage which would make this point clear, but it must be admitted that in this young stage the interpretation of these lobes and of the gills is uncertain. There appears to be a line of division across the base of the second leg which would seem to make the distal lobe certainly an exopodite, but the succeeding legs are entirely undifferentiated. I regard the gills at this stage as follows :

	Mxp. 1	2	3	Leg 1	2	3	4	5
Epip.	1	1	—	—	—	—	—	—
Arth.	—	—	2	2	1	1	1	—
Pleur.	—	—	—	—	1	1	1	1

BRACHYURA.

If the Dromiacea be excluded the remainder of the Brachyura (Oxystomata and Brachygnatha) have a characteristic larval type from which few species depart to any great extent. This is so far true that it is as a rule quite impossible to define the Zoeas of separate families or even to distinguish between those of the different tribes and sub-tribes. Here and there a distinguishable type appears to characterize a family, as is the case in the Dorippidae, and here and there a single genus may have a readily recognizable larva, as in *Pinnotheres*, but this is exceptional.

The position of the Raninidae, however, is peculiar. Bourne (1922) has made an exhaustive study of the group and has come to the conclusion that the Raninidae, "though by definition they must still be included among the Crabs, are not derived from a Dromiid ancestor, but have been evolved as an independent group from the Astacura" (p. 28). To this group he gives the name "Gymnopleura." Unfortunately we do not know the larva of any Raninid with certainty, but Cano (1892, p. 21) has

claimed a peculiar larva described by Claus under the name of *Acanthocaris* as a Raninid,* and, by reason of its "Anomuran" character, has himself concluded that the Raninidae should be excluded from the Brachyura. The reasons for the identification are not conclusive, but if they are accepted the conclusion that the Raninidae should form a separate tribe independently evolved along much the same lines as the Dromiacea cannot be avoided. It is possible that the larvae described above as Dromiacea (p. 189) should really be referred to the Gymnopleura.

The *Acanthocaris* larva and the two larvae in question provide to some extent a transition to the Brachyurous form, since they show the origin of the dorsal and lateral carapace spines which are so characteristic of the latter.

The peculiar Brachyuran telson is easily derived from the Galatheid type. The embryonic cuticle shows a telson having seven pairs of large spines, of which the fourth is not ciliated and is smaller than the rest. In the Zoea this spine has become a large spinous continuation of the telson, and the other spines are reduced, one or more of them being sometimes absent. The three inner spines are always retained. Throughout the Anomura (and also in some Thalassinidea) the fourth spine is greatly the largest, and in *Munida* the form is almost precisely the same as in the Brachyura.

In the Brachyura the antennal scale is vestigial, but it is well developed in the Protozoea stage, and the great predominance of the basipoditic spine is foreshadowed in the Anomura and still more in the Raninid Zoea.

The larva hatches with two pairs of maxillipedes only, but the third, though rudimentary, is biramous. There are never exopodites on the legs. In these respects there is also agreement with the Anomura.

For these reasons it seems reasonable to derive the Brachyura from a stem common to the Galatheidea and Dromiacea.

In the "Terra Nova" collections Brachyuran Zoeas and Megalopas are common, but it is for the most part quite impossible to refer them to their proper systematic position. Some of the Megalopas, which possibly belong to the Oxyrhyncha, are of striking form, but are of no special interest otherwise. The following alone can be approximately identified with known genera.

Dorippe (?) (fig. 77).

At station 39 several specimens were taken of a remarkable Zoea resembling that of *Cymopolia* or *Dorippe* (Cano, 1891), but differing in the great size of the lateral spines, and to some extent in the structure of the telson.

The gill formula differs from that of *Dorippe* only in the absence of epipodites and of gills from the second maxillipede. Cano found in *Dorippe* and *Cymopolia* no epipodite or gill on the second maxillipede, and only a single gill and epipodite on the third pair in the Zoea. It is impossible in my specimens to distinguish between arthrobranchs and pleurobranchs.

* Claus (1885) also attributed this larva to the Raninidae.

Ebalia (?), sp.

A single specimen of a larva taken at station 40 resembles in form of telson the Zoea ascribed by Cano (1893) and Williamson (1915) to *Ebalia*, but not identified by them with certainty.

The "Terra Nova" specimen differs from Williamson's larva in having short dorsal and rostral spines and also very small lateral spines, but the telson is so much the same and differs so much from the normal Brachyuran form that the two larvae must at least be closely related.

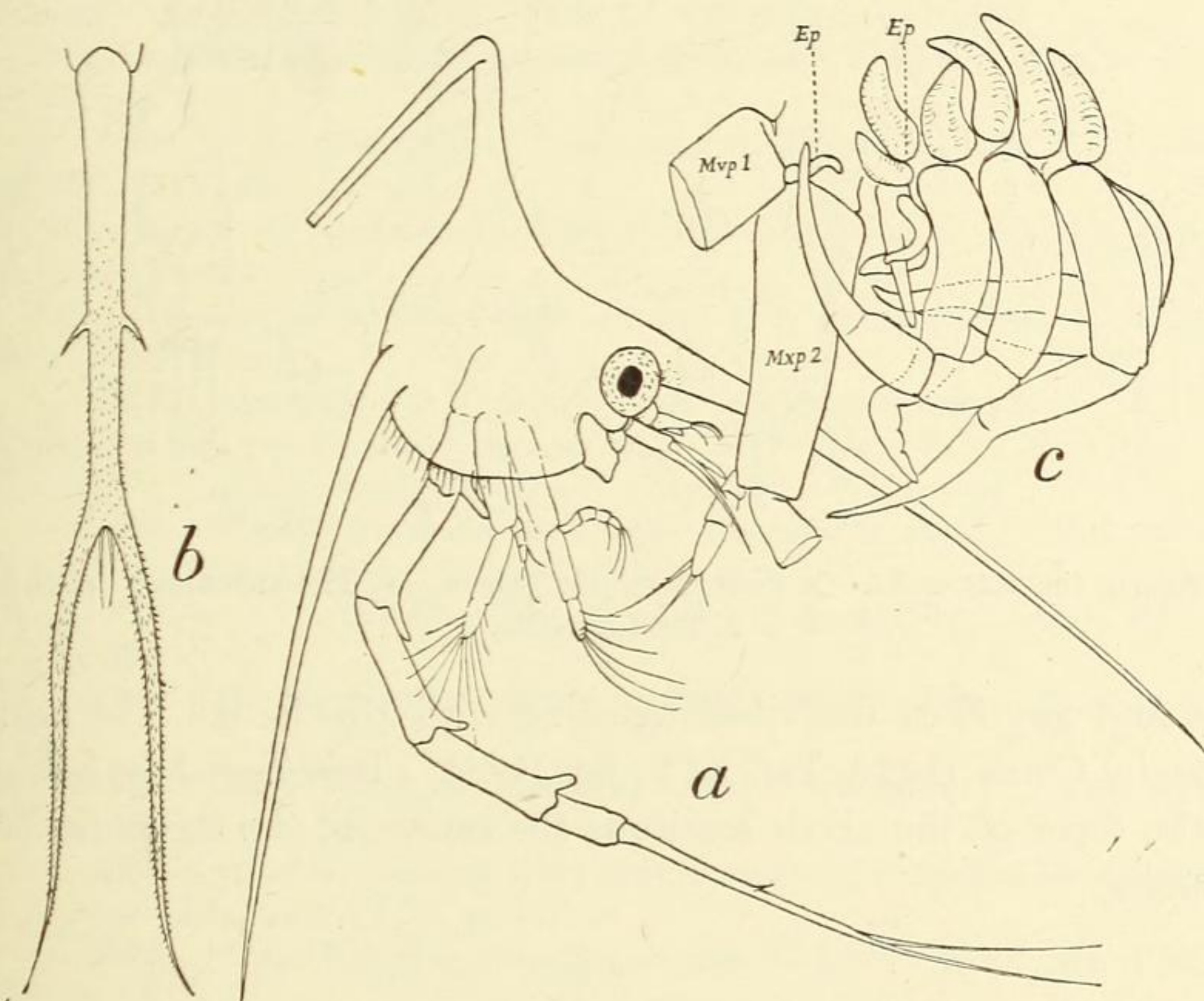


FIG. 77.—*Dorippe* (?), sp. Station 39. *b*. Telson. *c*. Pereiopods and gills.

Pinnotheres pisum.

The characteristic Zoea of *Pinnotheres* was taken at stations 97, 148, and 161. As Borradaile records *P. pisum* from two New Zealand stations no doubt these larvae belonged to this species.

Brachyura, *incertae sedis* (fig. 78).

At stations 133 and 135 a peculiar Brachyuran Zoea was taken in some numbers, which is of interest although it is impossible even approximately to identify it.

The body is almost entirely enclosed within the carapace, which measures about 1.2 by 1.35 mm. The rostrum is of fair size, but there is no trace of dorsal or lateral spines.

The second antenna is reduced to a simple unjointed conical structure without setae, and there is no basipoditic spine such as is usual in Brachyura.

In the oldest larvae seen there were no rudiments of pleopods.

The fifth and sixth somites of the abdomen are dilated, the latter expanding into thin lateral plates which extend back and overlap the telson. The latter is of unusual form, but is evidently derived from the normal type, all the outer spines being lost, but the three inner pairs of setae retained.

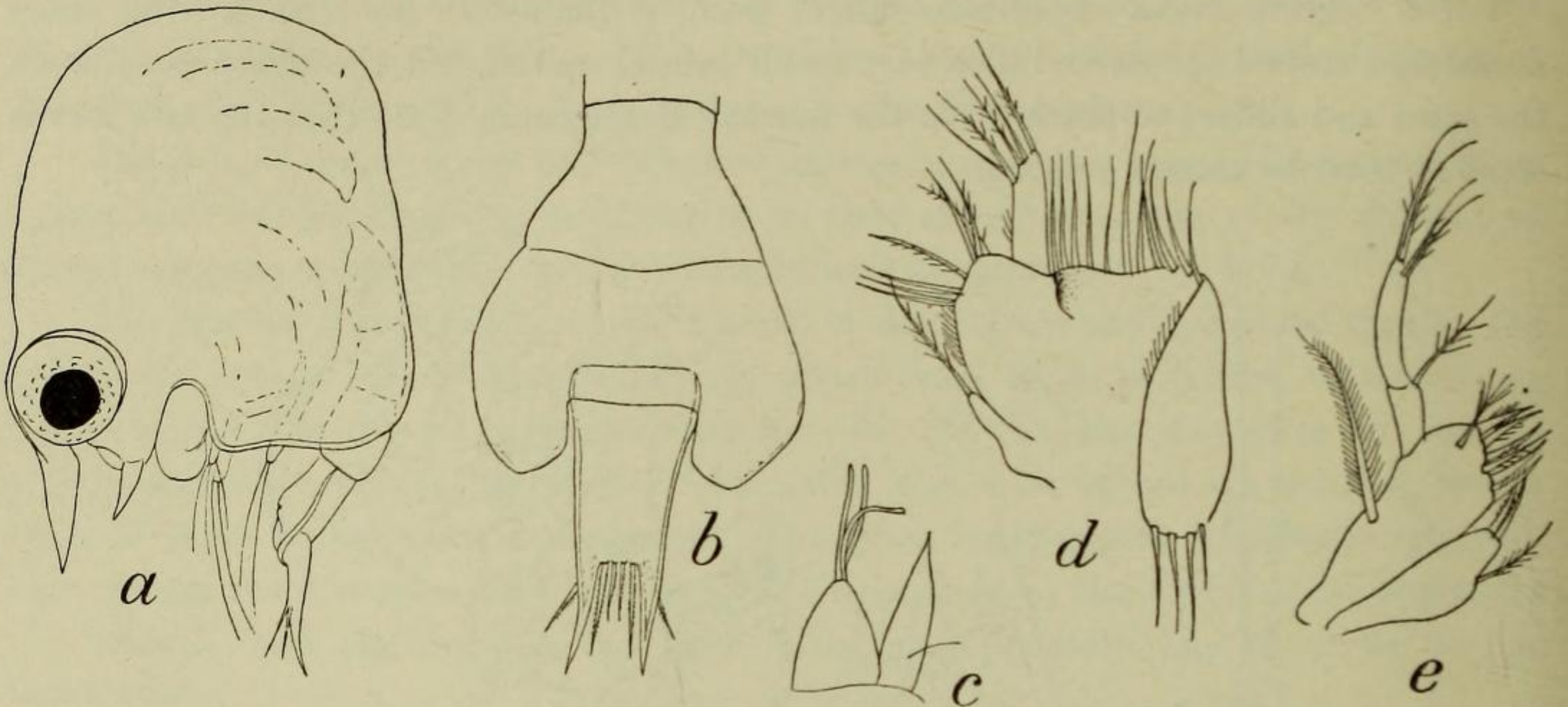


FIG. 78.—*Brachyura*, incertae sedis. a. Side view. b. Telson. c. The antennae. d. Second maxilla. e. First maxilla.

I cannot find any Zoea described agreeing with this form. The nearest to it is one described by Claus (1876, Taf. XIV, figs. 1-4). This Zoea has, however, lateral spines, but the form of the sixth somite is the same and the structure of the telson somewhat similar.

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