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TO MY WIFE

LARVAE OF DECAPOD CRUSTACEA

BY

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

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PREFACE

I AM already indebted to the Ray Society for undertaking the publication of my Bibliography, and it is a great satisfaction to me that the Committee has now accepted the remainder of the work on Decapod Larvae which I had not dared to hope would ever be published. The general part is as I originally planned it, but the descriptive part has been much curtailed. I have tried to give all the essential information, with figures of typical species in each family, in most of the groups. Where a family contains such diverse types as are found in Hippolytidae, for example, such treatment is not very satisfactory, but the examples given will probably be found adequate. While I have aimed at describing larvae of each family this has not been done in the Brachyura, since there are so many families and the differences between them are, for the most part, very small. When possible a summary of family characters has been given; but such summaries may be unreliable, or inadequate, owing to the many reservations which have to be made.

I make no apology for the fact that no exactly uniform system has been followed. The variety in treatment arises partly from the nature of the material, partly from the differences in systematic interest attaching to the groups, and partly from personal caprice.

The illustrations are, with very few exceptions, original, since I have made a point of first-hand acquaintance with the facts.

To each family is appended reference to one or more works dealing with it, generally the most recent; but further references will in most cases be found in the bibliography previously published.

The list of publications includes omissions from the Bibliography, papers which have appeared since, and others, not necessarily directly concerned with Decapod larvae, which are referred to in the present volume. I am indebted to a reviewer, to Miss Gordon and to Miss Lebour for drawing my attention to some omissions, but I have little doubt there are others still to find.

For instance, I have not been at pains to include all references to translations or abstracts, and in some cases these contain original notes which should be recorded. I confess that I did not spend much time in searching for references to development in ancient literature, and my attention has been drawn to the omission of Leeuwenhoek's description of the Prezoea of *Crangon* in 1686. I have not been able to see the original publication, but presume that the translation to which reference is given is correct, and the figure exactly copied. The observation unfortunately does no credit to Leeuwenhoek's reputation, and might better have been forgotten. He evidently had no suspicion that the shrimp has a larval phase.

I am more concerned to realize that I have omitted some recent papers of undoubted value. When such papers have not been included in the Zoological Record or reprints have not been received, they have, not unnaturally, escaped my notice.

I would like to express my gratitude to Dr. Crossland and Dr. Wheeler, directors of the Ghardaqa and the Bermuda Biological Stations respectively, and still more to Dr. Allen during his long directorship at Plymouth. It is now nearly forty years since I first paid attention to these larvae at Plymouth, and I treasure the memory of many visits and much kindness from all the staff. To Miss Lebour I owe a great debt for her ungrudged assistance at every point, whether in gift of specimens or advice, and particularly for her encouragement in going on with this work, and for reading and improving it as it proceeded.

ROBERT GURNEY.

Boars Hill,
Oxford ;
Jan., 1941.

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PART I.—GENERAL

LARVAE OF DECAPOD CRUSTACEA

HISTORICAL.

The first Decapod larva described is *Cancer germanus* Linnaeus (1767). This was, no doubt, a Megalopa, and Williamson (1915, p. 566) suggests that it may have been the same as *Megalopa armata*, Leach. In 1775 Slabber described a Zoea, which may well have been that of *Carcinus maenas*, under the name of *Monoculus taurus*, and a summary of his observations is given by Williamson (1915, p. 319), with reproductions of his figures. Slabber claimed to have seen the transformation of his *M. taurus* into a completely different form which can be recognized as the larva of *Callianassa*. He also gave a figure of a Megalopa, and it may be supposed that he did actually witness the moult of the Zoea to the post-larval Crab, and mixed up his drawings. Williamson however points out that the Zoea figured is in too early a stage for such an explanation to be possible.

The name *Zoea* was given by Bosc in 1802 to the early larva of a crab, and *Megalopa* by Leach to 1813 to the post-larval stage, various species being described as belonging to these supposedly adult genera. Another such larval genus is *Monolepis*, Say (1817); but this probalby belonged to the Hippidea.

It is worth noting that, in 1778,* De Geer had actually witnessed the hatching of the Nauplius of

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* Leeuwenhoek, in a letter dated Oct. 16, 1690, described a series of observations on the hatching of the eggs of *Cyclops*. He noted that the "animalcules" hatched from the eggs differed entirely from the parent, so that it might be claimed that he was the first to record metamorphosis in Crustacea. His observations on the unhatched larva of *Crangon* were illustrated by two very crude figures, and showed no appreciation of the difference between larva and adult.

Cyclops, and had commented upon the remarkable dissimilarity between young and adult. His figure of the Nauplius is excellent, and much better than those given by Müller in 1785 for his genera *Nauplius* and *Amymone*.

The systematic position of these larval genera was naturally a matter of peculiar difficulty. The different views taken were summarized by H. Milne-Edwards (1837, II, p. 431), who himself placed *Zoea* in an appendix as "Décapodes douteux." Desmarest (1825) had treated the species as Branchiopods, as Bosc had done, while Lamarck, although dealing with them as Branchiopods, suggested that they might belong to the Schizopods. Leach placed them among the Podophthalmata, but Milne-Edwards observed that his reasons for doing so were not clear, and had not convinced other zoologists.

In 1787 Cavolini had published a figure (pl. ii, fig. 9) showing quite clearly the general form of the Brachyuran Zoea at the moment before hatching, but to Vaughan Thompson (1828, etc.) belongs the credit for the definite proof that most Decapoda leave the egg in a form totally different from that of the adult. His first announcement that *Cancer pagurus* hatches as a Zoea, with his claim that all Zoeas are larval Brachyura, and that metamorphosis is the rule among Decapoda, were not made in a form that carried conviction, and it must be admitted that he did not present his case as well as he might have done. Westwood (1835, 1836) strongly contested the validity of Thompson's conclusions, relying upon the indisputable fact that the Crayfish and also some Crabs do actually hatch in a form closely resembling the adult.* Westwood based his observations upon the examination of the abdomen of a "West Indian Land Crab" to which newly-hatched

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* The level of argument on the subject may be judged from two quotations. Thompson (1831, p. 383) says that, if one case of metamorphosis is proved, "we may safely infer from analogy, as far as regards the particular tribe alluded to, that it is general." And Westwood (1835, p. 318) replies that, if the Crayfish has no metamorphosis, "I think we are fully warranted from analogy in considering that the other Decapods do not undergo metamorphosis."

young were attached. He did not specify the genus. Bell (1853, p. xliv) referred the detached abdomen carrying young which had presumably been seen by Westwood to *Gecarcinus*. As has been pointed out by Calman (1911, p. 192) this identification is most uncertain and unlikely, and it is more probable that Westwood was dealing with a Crab of the family Potamonidae.

The great authority of Rathke (1838) was also cast against Thompson,* though he eventually satisfied himself of the existence of metamorphosis and handsomely acknowledged his error (1842).

To Milne-Edwards the question was still an open one, although he himself leaned to the view that *Zoea* and *Megalopa* were not adult genera; but he felt some suspicion as to the reliability of Thompson as an observer.

By a strange chance Milne-Edwards (1835) observed direct development in *Naxia* (*Paranaxia*) *serpulifera*, the only marine crab outside the Dromiacea which is known not to have a free larva. His prejudice against Thompson's discovery must have been thereby greatly strengthened.

In 1840 the Société Hollandaise des Sciences de Haarlem offered a prize for researches on the development of Crabs, with a view to determine whether metamorphosis existed or not (Joly, 1842, p. 38); but the prize was apparently not claimed. Joly took up the question with the only species available to him, *Atyaëphyra desmarestii*, and gave excellent figures of the developing eggs and first larva. He discussed the controversy between Thompson and Westwood and concluded that, as there certainly was metamorphosis in *Atyaëphyra*, and also in *Palaemonetes* and *Crangon* as described by Du Cane (1839), Thompson's conclusions were sound.

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* Rathke, 1838, p. 120: "Il n'est donc vrai que, comme l'a prétendu Thompson, les Décapodes sortent de l'oeuf dans un état fort imparfait, et les changements qui se passent encore pendant l'accroissement ne méritent point le nom de métamorphose."

Couch (1844, 1845) set himself to test the validity of Thompson's discovery, and proved its truth by hatching the larvae of several species of Crabs and Macrura. He noted the migration of West Indian land crabs to the sea, apparently for the purpose of hatching their eggs, and figured the prezoea of *Porcellana* and other genera.

Even in 1846 Lucas did not regard it as proved that *Zoea* was the larval form of Crabs, and would only concede that it was " more than probable " that *Megalopa* was a genus of young animals.

Dalyell (1851) hatched out the larvae of a number of Decapods, but, by that time, the controversy on the subject had ended, and his small figures added nothing to our knowledge of structure.

Looking back, at this distance of time, it is not easy to understand why zoologists of authority such as Westwood and Milne-Edwards should have failed to realize the confirmatory importance of Cavolini's observation, and why the question was not immediately settled by experiment. There were, however, no marine laboratories where such experiments could easily be made, and those who wished to disprove Thompson's discovery turned first to their museum shelves for evidence, and were able to convince themselves that such evidence was conclusive. Thompson's later work, and the observations of Du Cane, Rathke, Goodsir and Couch left no room for further argument. The discoveries of Thompson and Couch add credit to that army of amateur field naturalists who have done so much for British Zoology.*

The problem of the Decapod development was therefore solved in its general outlines by about 1840; but there remained the special problems of the relation of the various larval forms to the adults, and particularly of such strange and striking creatures as *Phyllosoma* and the Sergestid larvae. The first to observe the

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* Thompson may be claimed as the first real student of plankton. He also suggested the use of sea-water pumps on board ship for collecting floating organisms in stormy weather or when the ship was sailing too fast for a net to be towed (1828, p. 3).

hatching of the egg of *Palinurus* was Couch (1843), but he gave an erroneous description of the larva, and it was not until 1858 that he suggested that it might "be placed in *Phyllosoma* of Milne-Edwards, as belonging to the Stomapodes." The real position of *Phyllosoma* was not finally settled until Dohrn (1870*a*) described stages in the development of *Scyllarus*, and Richters (1873) compared a large collection of specimens and showed that they could be referred to different genera of Palinura.

The most important of the early contributions to knowledge in this second period was the discovery by F. Müller (1863) of the development of *Penaeus* through Nauplius and Protozoea stages. His observations, necessarily founded upon larvae taken in plankton, were not entirely convincing to Spence Bate and others, but the discovery by Metschnikoff (1869) of the Nauplius of *Euphausia*, and by Brooks (1880) of the Nauplius of *Lucifer*, went far to establish the correctness of Müller's identification. The final proof that the Penaeid egg gives rise to a Nauplius was only given by Monticelli and Lo Bianco in 1900.

Claus, in a series of papers from 1861 onwards, and particularly in his great work of 1876, advanced our knowledge of Decapod development to a point at which all that was of serious value to comparative zoology was made known. He and Dohrn, whose work, published in 1870–71, is overshadowed by the magnificence of Claus, both had the wide outlook of the comparative anatomist inspired by Darwin to phylogenetic speculation. This speculation was allowed by Dohrn to run far too freely, but was controlled by Claus within the limits of the facts then available.

With Claus and Dohrn may be said to have ended the period of speculation and grand discovery, and effort has been directed to the tracing of the life histories of individual species and genera. Faxon's description (1879*b*) of the whole series of larval stages of *Palaemonetes vulgaris* is the first full account of this kind if those of Smith (1873*b*) and Sars (1875) of the shorter series in *Homarus* are excepted. Sars' series of papers in 1884–1890 laid a foundation of accurate knowledge of larval stages for a number of genera representing most of the groups of Decapoda, and he published also valuable papers on *Pandalus* (1900), *Athanas* (1906) and *Hippolyte* (1912). The beauty and accuracy of Sars' drawings are unrivalled, and his work in this and other fields is of undying value.

Cano (1891–1893) contributed greatly to knowledge of the development of Mediterranean species, while Monticelli and Lo Bianco (1900–02) did excellent work on Penaeids at Naples. Unfortunately this work was never adequately described, so that we have had to wait nearly forty years for the development of the Mediterranean Penaeids to be satisfactorily dealt with by Mme. Heldt (1938).

Others who have done specially valuable work in recent years are Williamson (1900–15), Caroli (1918–27), Sollaud (1912–24) and Miss Lebour (1925). To Miss Lebour belongs the credit for having established systematic differences among Brachyuran larvae, and she has also studied and described the larvae of most of the British Caridea. Her discovery that the larva ascribed by Sars to *Pandalus bonnieri* is really that of a new species of *Caridion* (1930) is a very satisfactory illustration of the importance of the detailed study of these larvae, and she has followed up this achievement by proving the existence of a new species of *Spirontocaris*, and also that there are two species of *Processa* with perfectly distinct larval and adult characters. The larvae of an unknown species of *Porcellana* and of *Lysiosquilla eusebia* have also been taken at Plymouth, but the adults have not yet been discovered there.

If accurate study of the larvae in an area so thoroughly worked as western Europe can reveal unsuspected species of adult Decapods, how much more is it to be expected that research in other regions will enlarge our knowledge of the group ? Since the larvae are easily taken in plankton, whereas the adults may live in places where they cannot be reached by trawl or dredge, it is not surprising that we already know many larval forms which belong to genera as yet undiscovered. This is probably true of Phyllosoma, and certainly true of Stenopidea and Thalassinidea (Gurney, 1936, 1938). The larva of *Jaxea nocturna* has been seen often in plankton at Plymouth, but it is only quite recently that the adult has been taken there by new methods of capture.

Knowledge of the identity of larvae, together with the duration of larval life, should eventually contribute something to the study of oceanic currents. Conversely knowledge of currents may be essential to the understanding of the life cycle of a species, as in the case of *Euphausia superba* (Fraser, 1936).

Deep-sea expeditions bring back plankton containing strange larval forms which have in some cases been described under special generic names (*e.g.* Bate, 1888 ; Ortmann, 1893) ; it will be the task of the future gradually to eliminate these genera by connecting them with their adult forms. This has already been done to some extent. We know now that *Eryoneicus*, for example, is the larva or natant stage of *Polycheles*, but much remains to be done. It is now known that one species of the larval genus *Retrocaris* develops into *Brachycarpus biunguiculatus*, and this supports, though it does not prove, the suggestion that *Palaemon* also has a larva of this type. We do not know with certainty the ultimate fate of *Amphion*, though it is probable that *Amphionides* is its adult (Gurney, 1936*c*), and the large Pagurid larvae known as *Glaucothoë* present a problem as yet unsolved.

Some approach has been made towards connecting Penaeid larvae with their adult genera, but the true relationship of *Cerataspis* and *Cerataspides* is not known.*

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* Burkenroad (1936) claims that *C. monstruosus* and *C. petiti* may be the larvae of the genus *Aristaeomorpha*, and *C. gubernata* and *C. longiremis* of *Plesiopenaeus*, but the evidence has not been published.

In this particular case the extreme rarity of the larvae is a point which requires explanation.*

The problem of exceedingly large larvae is by no means solved (see below, p. 71). The difficulties in the way of attacking the problems presented by these deep-sea larvae are very great, and perhaps insuperable, since it is necessary to keep them alive until they moult into the adult form. This cannot easily be done on board ship; but the Bermuda Biological Station offers great opportunities, since oceanic plankton can be obtained within a few miles of the station, and experience shows that it is possible to bring material back alive, and sometimes to keep the larvae alive in the laboratory for several days. I have myself kept such delicate creatures as *Amphion* and *Eretmocaris dolichops* alive for a week or more. During a year spent at this laboratory Miss Lebour has got valuable results from study of Sergestid and other deep-sea larvae.

CLASSIFICATION.

The old division into Macrura, Anomura and Brachyura fell to the attack of Boas in 1880, and his system with a primary division into Natantia and Reptantia obtained for a time wide acceptance. It is used by Balss in Kükenthal's Handbook (1927). Claus (1885, p. 64) was led to abandon the group Anomura largely by study of the larvae of *Hippa* and *Albunea*. Alcock did not accept Boas' classification, and there has been of recent years a return to a somewhat modified version of the old system.

Hansen (1908) stated that, while the suborders Brachyura, Anomura and Macrura might be retained as a matter of convenience, they could not really be justified. Alcock, Bouvier and Borradaile divided the Macrura into Macrura Caridides or Macrura Natantia and Macrura Astacides or Macrura Reptantia, the

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* Another example of unexplained rarity is that of the Copepod *Pseudochirella notacantha*. No adult female has yet been seen, though the male and certain Copepodid stages are known (Jespersen, 1934, p. 66).

latter including the Thalassinidea. The Penaeidea have always been included in the same group as the Caridea.

Beurlen (1930) has offered a new system which takes account of fossil forms and, to some extent, of the larvae. He divides the Decapoda into four suborders:

Trichelida (Penaeidea, Stenopidea, Nephropsidea).
Anomocarida (Caridea, Thalassinidea, Paguridea).
Palinura (Eryonidea, Loricata).
Heterura (Galatheidea, Hippidea, Brachyura).

While the association of the Penaeidea with the Nephropsidea and the isolation of the Palinura are points which are in accord with the evidence from development, the position assigned to the Stenopidea, Thalassinidea and Paguridea cannot be accepted.

The main difficulties in framing a satisfactory system for the Decapoda appear to be these:

(1) Relation of the Euphausiacea to the Decapoda.
(2) Relation of the Penaeidea to the Caridea.
(3) Position of the Stenopidea and Thalassinidea.
(4) Relation of the Dromiacea to the Brachyura.

(1) The position of the Euphausiacea is dealt with below (p. 157).

(2) The Penaeidea have, it would seem, only a remote relationship to the Caridea, and are more closely allied to the Nephropsidea. It is only necessary to mention the form of legs 1–3, the gill formula, and form of the abdomen, in respect of which they differ so greatly from the Caridea. So far as the larval development is concerned there is little evidence, since the Nephropsidea all have a more or less reduced metamorphosis; but they have the exopod on leg 5 which is lost in most Caridea. The primitive larval history which characterizes all Penaeidea distinguishes the group sharply from all others.

(3) The Stenopidea are, as adults, in some respects intermediate between the Penaeidea and the Nephropsidea. Their larvae, of which several types are known, are very peculiar, but suggest some relationship to the

Anomura and Thalassinidea. A remarkable Stenopid larva recently described by Miss Lebour (Gurney and Lebour, 1941*b*) has the very primitive character of an exopod on the maxillule.

The Thalassinidea, which Borradaile and Calman include in the Anomura, do not seem to form a natural group. The larvae point to intimate association of the Callianassidae with the Axiidae, which are themselves scarcely separable from the Nephropsidea, while the Upogebiidae and Laomediidae are nearly related to the Anomura (Gurney, 1938*c*).

(4) The larva of *Dromia* is so definitely Anomuran that it is impossible to include this genus in the true Brachyura. The larvae of *Homola* and *Latreillia* (Aikawa, 1937), while differing greatly from the normal Brachyuran Zoea, have some features in common with it, and, if they alone were known, a separation could not be justified. Our knowledge of the development of the Dromiacea is not sufficiently full to be conclusive. Nothing is certainly known of the development of the Gymnopleura. So far as the evidence goes it would seem that a sharp division between Anomura and Brachyura is not practicable.

THE BEARING OF THE LARVAL PHASE UPON CLASSIFICATION.

Systematists concerned with the classification of Decapoda have rarely attempted to draw evidence from the larval phase, and indeed Ortmann (1896, p. 412) goes so far as to say, " das Studium der Decapoden-Larven für das System der Decapoden absolut keine Resultate ergeben hat."

It is perfectly true that until our knowledge of these larvae is very much more complete than it is now the evidence to be drawn from them is weak or disputable; but it should hardly need to be argued that the larval phase must ultimately be taken into account if a system is to be soundly based, unless the position is taken that systems of classification are no more than artificial methods for conveniently grouping the adults alone. It will probably not be maintained that it would be justifiable to draw up one system for the larvae and another for the adults.*

The importance of the larva in separating closely allied species has been amply proved by Miss Lebour's admirable work, since she has been led, by her studies of the larvae, to the discovery of the existence of previously unsuspected species of *Caridion*, *Spirontocaris* and *Processa*. With regard to genera Hansen (1895, p. 74) has noted great differences between the larvae of species of Stomatopoda (*Lysiosquilla*) and says, " Hiernach wäre anzunehmen dass die Gattung in Untergattungen getheilt werden müsste, man kennt jedoch allzu wenige von den entwickelten Formen, um hieruber urtheilen zu können."

When the larvae of two species are found to differ more than the adults it is at least arguable that the adults are less closely related than has been supposed. In the genus *Sergestes*, for instance, the adults are often difficult to separate, while the larvae may be very distinct. Certain species, of which *S. robustus* and *S. crassus* are examples, have a Protozoea (Elaphocaris) of such distinct form that subgeneric separation of this group would seem to be justified. Similarly, within Hansen's Group II, his second tribe containing *S. vigilax* and others has a very characteristic Acanthosoma stage. This group might also become a subgenus, while the species of Hansen's Tribe I (*S. sargassi* and *S. pectinatus*) seem, to judge from their larvae, to be more nearly related to *S. corniculum*, which holds a rather isolated position in Group I (see Gurney and Lebour, 1940*b*).

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* Brooks, 1886, p. 15 : " If, then, comparative anatomy enables us to trace from the study of the adults of an order, a family, or a genus their natural or genealogical classification, it must of course be possible to do the same thing with the larvae, and if the classification which is established is natural, there must be a discoverable relation between the one derived from the larvae and the one derived from the adults."

FIG. 1.

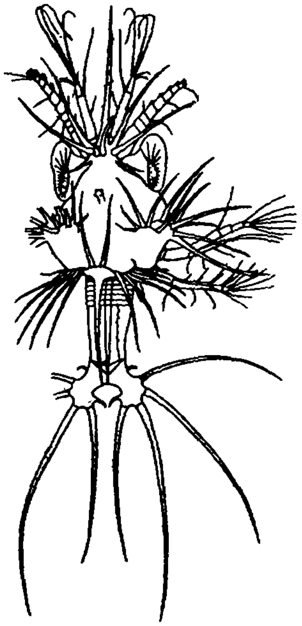

FIG. 2.

FIG. 1.—*Sergestes crassus.* Elaphocaris stage 2.
FIG. 2.—*Sergestes corniculum.* Elaphocaris stage 2.

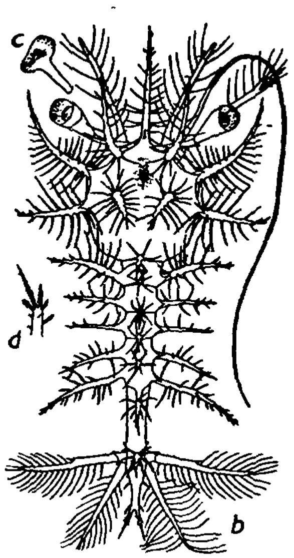

FIG. 3.

FIG. 4.

FIG. 3.—*Sergestes cornutus.* Acanthosoma stage 2. *c.* Eye in side view. *d.* End of antennal scale, stage 1.
FIG. 4. —*Sergestes armatus.* Acanthosoma stage 1.

Among the Caridea I think it would be generally admitted that the existing system is not very secure. Most of the genera of the Hippolytidae are separated by easily defined and generally striking characters, whereas the genera of Palaemonidae and Alpheidae are often distinguishable with difficulty. The larvae of the Hippolytidae are even more distinct than the adults, that of *Lysmata*, for example, being so different from *Hippolyte* that it is difficult to believe that they belong to the same family. So far as is known the larvae of the Alpheidae, when they are not modified by abbreviated development, are extremely uniform; but there are, among the Palaemonidae, larval forms of strikingly different types. Even within the genus *Periclimenes* two very distinct types of larva are found (Gurney and Lebour, 1941). Unfortunately the genera to which some of the most striking Palaemonid larvae belong are not known.

The systematic position of *Rhynchocinetes* has been very uncertain, but the discovery of the larva proves that it is related to the Hoplophoridae (Gurney and Lebour, 1941). Similarly the position of *Discias* has been made more clear by the discovery of its larva by Miss Lebour (Gurney and Lebour, 1941). The two genera *Campylonotus* and *Gnathophyllum* will never be securely placed until their larvae are identified. In such cases the adult anatomy is already fully known, and the larva alone can provide new evidence of relationship.

One good example of the kind of evidence which can be obtained in this way is provided by the genus *Naushonia*, which was at one time supposed to be related to the Crangonidae. The structure of the larva proves that it is related to *Jaxea*, and a member of the family Laomediidae. Other unidentified forms of larvae having the same characteristic form of asymmetrical mandible have been discovered (Gurney, 1938*c*), and show that new genera of Laomediidae remain to be found.

When one finds in a series of larvae the same character, for instance the reduced second seta on the telson in Thalassinidea and Anomura, or the peculiar modification of the endopods of the legs in those groups, it must be obvious that such features are evidence of common descent. These facts have been used as evidence for the division of the Callianassidae into two distinct families (Gurney, 1938*c*).

We know the larvae of so many genera of Brachyura that we are justified in defining a very characteristic larva for the whole group. When a larva departs completely from this type, as that of *Dromia* does, it is impossible to dismiss the fact as irrelevant (Lebour, 1934*b*).

It seems probable that a revision of the Brachyura will be much helped by knowledge of the larvae. The evidence already available seems to show that the group Oxystomata is a heterogeneous assemblage of crabs independently modified in the same direction (see p. 283) and that the Pinnotheridae and Hymenosomidae should be brought into relation with one another.

It must be confessed that the evidence from development so far accumulated has not produced any very serious contribution to the systematics of the group. Indeed extension of knowledge from the littoral fauna of Europe to the deep sea and the richer littoral fauna of tropical waters rather tends at the moment to obscure than to clarify ideas on classification. For example, we now know larvae representing a reasonable number of genera of Hippolytidae, and they do not seem to give any help in grouping related genera. The evidence they do provide only suffices to show that the accepted grouping of the "Latreutid" genera is not a natural one (Gurney, 1937*b*). Again, while in some genera such as *Hippolyte* there is very close resemblance between the larvae of different species, in *Processa*, for example, there may be great differences.

There are larvae which seem to belong to Anomura, Gymnopleura or Dromiacea, but which cannot be referred with confidence to either, and it can hardly be doubted that this knowledge, when it comes, will be most valuable in determining the relationship of these groups.

LARVAE.

The larva is a free-swimming phase in the cycle of the individual which differs in form and habit from the adult, and is commonly transformed into it by a sudden and radical change which constitutes metamorphosis. Where there is no metamorphosis, and transformation is gradual, the two phases may merge into one another; but there may be a more or less abrupt change of habit if not of form.

It may be assumed that development in Crustacea was primitively a continuous process of growth and addition of somites and limbs, as we find it to be in some Branchiopods, and that abrupt changes between successive moults leading to the origin of definable phases are secondary responses to changes in the habit of life of larva or adult. For example, when the larva leads a pelagic life, and the adult walks on the bottom or hides in holes, no gradual transition is possible between larva and adult, and metamorphosis must occur. Where larva and adult lead much the same sort of life transition may be expected to be gradual. None the less metamorphosis is very striking even when the environment of young and adult appears to be approximately the same, as in Euphausiacea and some Penaeidea. On the other hand, we know very little about the environment, and it is certainly true that in many cases young and adult live at very different depths. Bogorov (1932) has found that the larvae of *Calanus finmarchicus* inhabit different strata at different stages of larval life.

In the Branchiopoda Anostraca there is no clearly marked metamorphosis. There is a long series of moults, each of which introduces additions of somites and limbs, and the latter develop directly into the form

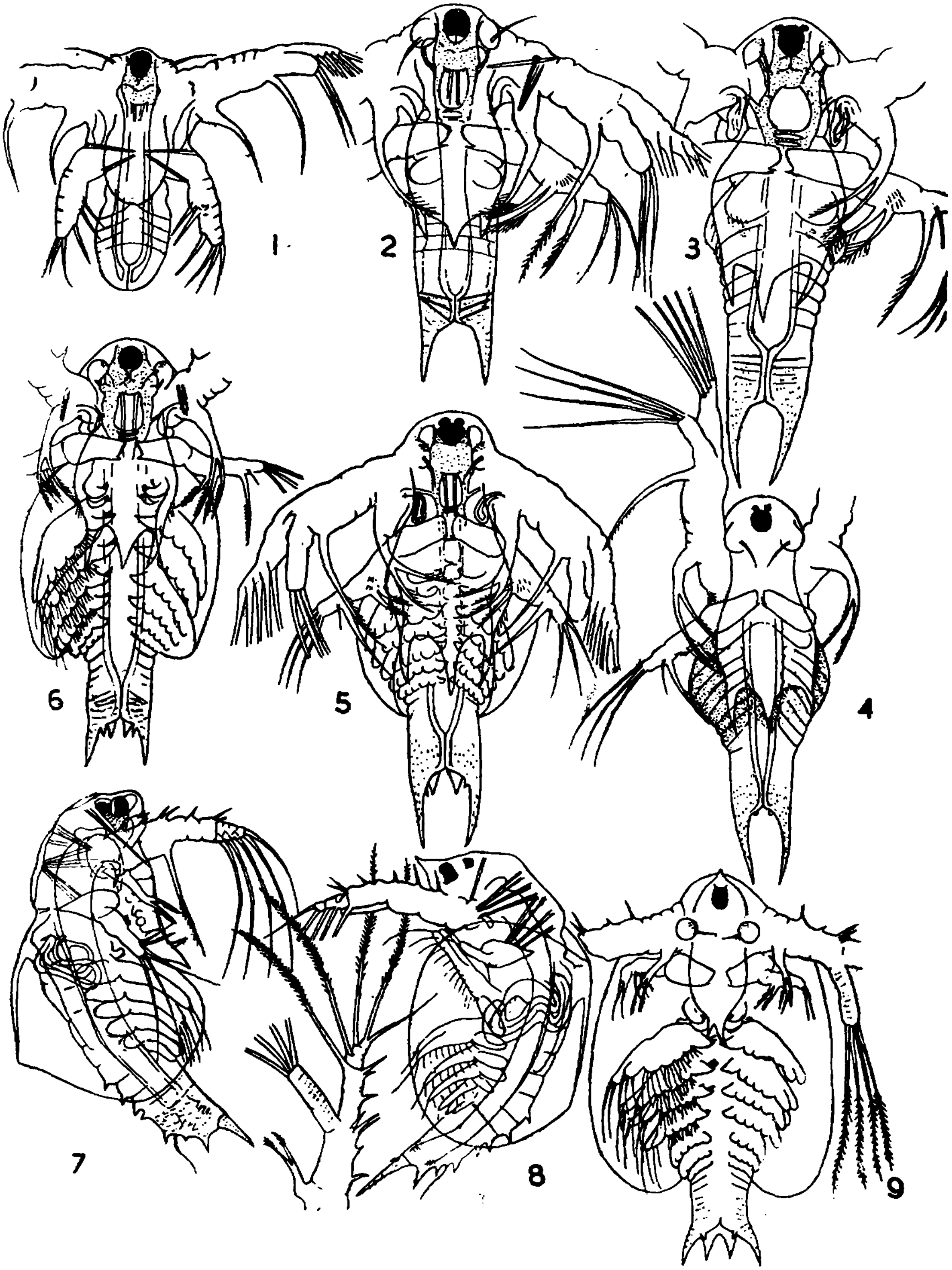

FIG. 5.—Development of *Estheria syriaca*. The scale of magnification is not the same in all cases.

characterizing the adult, without assuming a temporary form distinctive of the larva. Larva and adult have about the same habit, and there is no need for any large change on the approach of maturity. In no Branchiopod is there any marked metamorphosis. The accompanying figure of the larvae of *Estheria syriaca* shows the gradual assumption of the adult form.

In the Copepoda, Ostracoda, Cirripedia and Decapoda, that is to say all other Crustacea in which there is, or may be, a free larva, there is metamorphosis, and it may well be that this distinction corresponds to a fundamental cleavage in the Order.*

The most complete example of metamorphosis is shown by the Copepoda. Here, in the Calanoida for instance, there is a series of six Nauplius stages, with three functional pairs of appendages only, the last stage differing from the first only in small changes in these limbs, and the appearance of rudiments of five additional pairs. The sixth moult produces the first Copepodid stage, in which the limbs have assumed more or less the adult form, and the regions of the adult body are made clear Throughout the whole group of Copepoda, in spite of the infinite variety of form and habit, this first Copepodid stage is precisely the same in number of somites and appendages. Without any known exception there are two pairs of swimming legs, the branches of which are unsegmented, and the hind-body is an unsegmented region within which the remaining somites of the thorax and abdomen will later appear. Where development is most complete there are five Copepodid stages, neither more nor less ; but many of the parasitic forms do not develop further than stage I, a fact which is to some extent responsible for the difficulty which has been found in framing a satisfactory classification for the Copepoda.

In typical Copepods, therefore, there is a striking metamorphosis at one point in development, followed by a definite number of larval stages which lead up,

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* See Garstang and Gurney, 1938, p. 277.

without abrupt transition, to the adult. The Copepodid cannot really be regarded as a larva, since in general form and in structure of the appendages it resembles the adult. From the moult of the last Nauplius development may be said to be direct. The fifth Copepodid can always be distinguished from the adult, but the differences are relatively small, and one cannot regard the final moult as an example of metamorphosis. The changes concern almost entirely the secondary sexual characters. With the assumption of these characters in their fully developed form sexual maturity is attained and reproduction usually, but not invariably, begins. From this moment, so far as is certainly known, there are no further moults.*

It appears that, in Copepoda, bodily development ceases with the ripening of the gonads, and this fact fully accounts for the anomalous form of many of the parasitic genera. In the Branchiura, Branchiopoda and Decapoda periodic moulting continues throughout life.

In the Decapoda metamorphosis is well marked, but ontogeny has been so profoundly modified by "anachronism," or the appearance at one stage of structures properly belonging to a later one, that the unity of sequence so well seen throughout the Copepoda is obscured. There is so strong a tendency to shortening of larval development in all Decapoda in which the eggs are carried and protected by the parent that it is only in the Euphausiacea and Penaeidea that development retains much of what we may suppose to have been its primitive features.

The fundamental fact which determines the organization of the larva is the mode of locomotion.† In the Nauplius the main organ of locomotion is the antenna, as in the primitive Branchiopod, and in the Protozoea of the Euphausiacea and Penaeidea it still has that functional importance. In most existing adult Branchiopods, and in all adult Decapoda, the locomotor function

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* See Gurney, 1928, p. 196, for possible moults.

† See Foxon, 1934, p. 844.

has been transferred to the thorax or, in the latter, to the abdomen, and it is this change-over of function that has led to much of the modification of the larva. In the Copepoda antennal locomotion is retained throughout life, the thoracic appendages becoming, as it were, accessory to it; whereas in Decapoda thoracic locomotion entirely replaces it in larvae later than the Nauplius and Protozoea. The final change, to abdominal propulsion, is acquired only at the moult to post-larval. In most *Decapoda there is a* very *well*-marked change at this point, affecting the functional development not only of the pleopods, but also of the mouth parts, and this phase, though it merges gradually into the adult, is almost as distinct a period in ontogeny as the preceding larval phases.

Decapod development may, therefore, be regarded as made up of four phases of phylogenetic significance:

Nauplius . . .	Antennal propulsion.
Protozoea .	
Zoea	Thoracic propulsion.
Post-larval . . .	Abdominal propulsion.

It has commonly been held that the larval forms of to-day represent, in a modified form, ancestral adult stages. For instance, it has been supposed that the so-called Mysis stage of the Decapoda represents an adult ancestor in which the exopods of the legs were present and functional, and that the symmetrical post-larval stage of the Paguridea recapitulates an adult stage in the phylogeny which has been thrust back into ontogeny. Foxon (1936) has pointed out the weakness of the resemblance in structure and function of the limbs of Decapod larvae to those of Mysidacea and *Euphausiacea, concluding,* "*Thus the larvae of the* Decapoda do not in their ontogeny pass through either a typical Euphausid or Mysid stage, and neither their structure nor their function is recapitulated."

A more easily tested example of such recapitulation is that of the Copepod *Achtheres*. Here MacBride (1914, p. 205) claims that the Copepodid stage represents an adult ancestral form; but it is actually nothing more than the first Copepodid stage which is universal throughout the Copepoda, and represents merely an ancestral larval stage. In this genus, and in all other Lernaeopodidae, the larva attaches itself to the host at this stage, and develops into the adult form without passing through any further stages. These genera are, in fact, paedomorphic.

The larval stages of to-day provide evidence for phylogeny, but indirectly, since the most that can be said is that an animal in its ontogeny recapitulates the ontogeny of its ancestors.*

This difference in point of view does not seem to be of very great practical importance. The Protozoea of the Penaeidea recalls in a general way a creature such as we may assume the nomomeristic ancestors of the Phyllocarida to have been, the most marked characters of which were the natatory antenna and the cephalic shield; but it by no means follows that it recapitulates an adult ancestor. None the less, if it can be said to recapitulate any phase in the life cycle, larval or adult, it offers evidence of affinity.

Something should be said here of a possible relation between the Decapoda and the Copepoda. It has been said that, throughout the Copepoda, there is a stage in which three pairs of thoracic appendages are present and the abdomen is unsegmented. It may be no more than a coincidence, but it seems reasonable to assume that it is a fact of phylogenetic significance, that the first Protozoea of Decapoda corresponds precisely with this grade of development. Apart from the exact correspondence in number of somites and appendages there are other points of agreement in detail which may be significant.

In the first place there is in the Protozoea a caudal fork as in the Copepoda, and this fork bears, in both cases, six setae. It is true that seven is the usual number found in Decapods on either side of the telson in the

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* See De Beer, 1930, 1940.

first Zoea; but six are found in some Protozoeas, and the fact that there are six in the embryonic cuticle of the Caridea shows that this is really the primitive number.*

The antenna of the Penaeid Protozoea bears a remarkable resemblance to that of the Copepoda. The endopod is, as in Copepoda, of two segments; but the arrangement of the setae suggests that it was primitively of three segments, as it is in the Cirripede Nauplius (Fig. 7c). In the exopod eleven segments can be found, but the basal segmentation is uncertain. From the fourth segment each bears an inner seta, with three on the terminal segment—ten in all. In other Decapoda the segmentation is much reduced, but ten setae remains as a rule, and it is clear that there is correspondence with the antenna of the Protozoea.

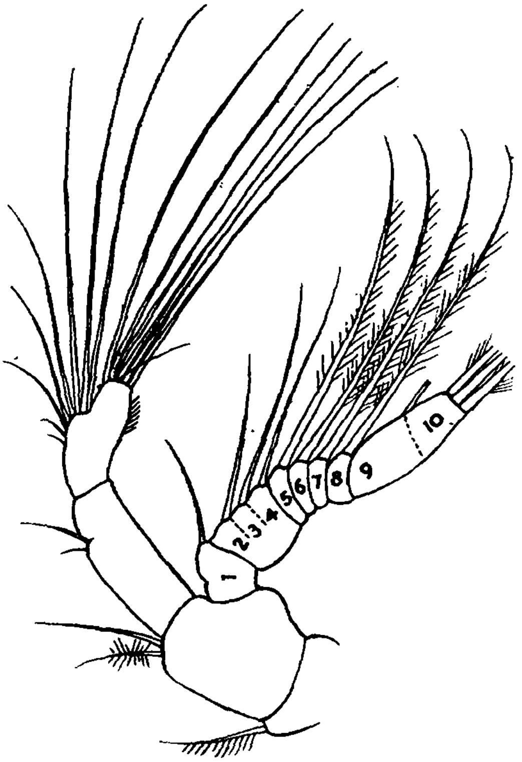

FIG. 6.—*Centropages hamatus.* Antenna.

It may seem that undue importance is attached to

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* See also p. 116.

coincidences in arrangement and number of setae; but they do show a very remarkable consistency which

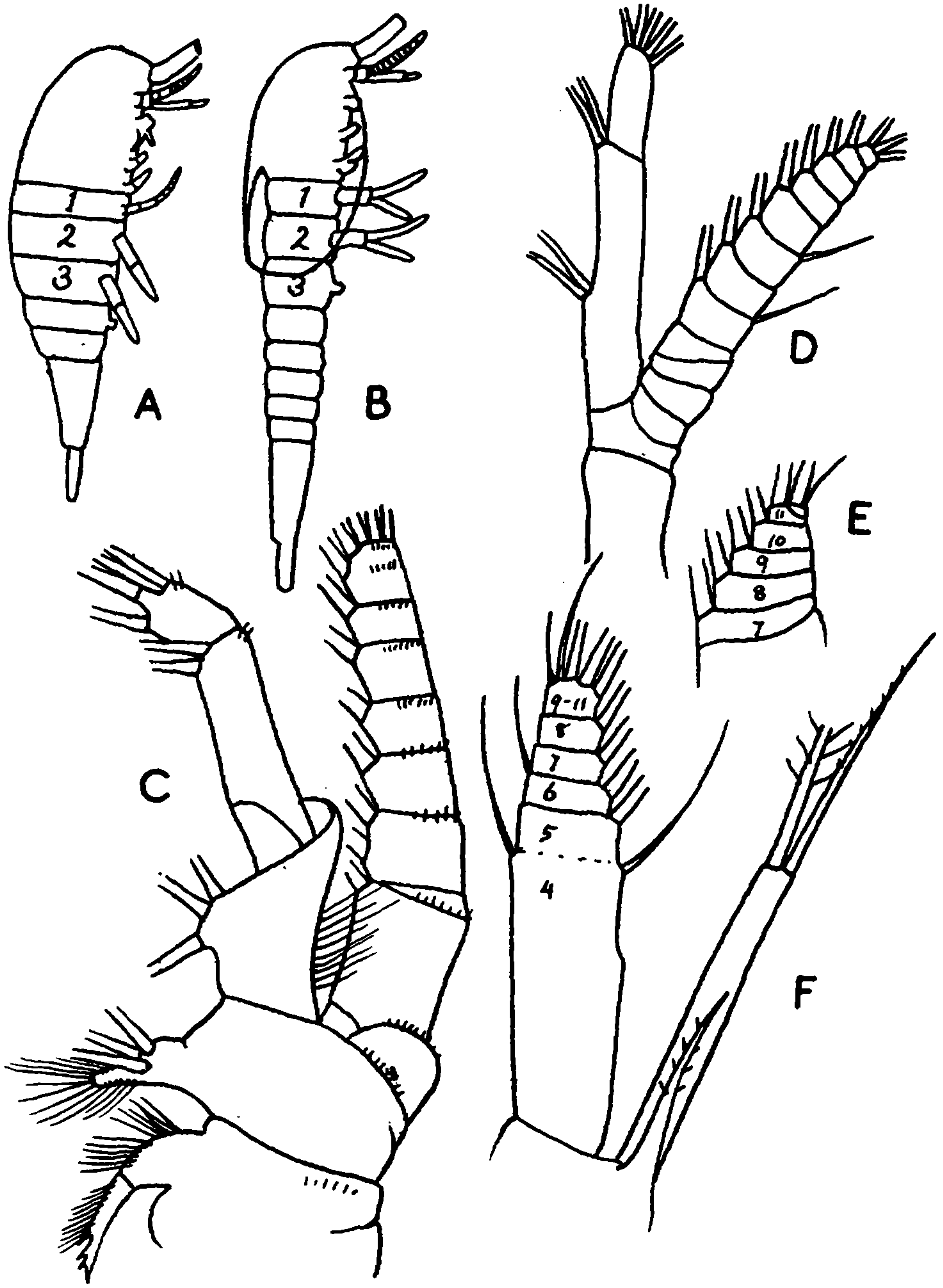

FIG. 7.—A. Diagram of Copepodid stage. B. Diagram of Protozoea. C. Cirripede antenna. D. Antenna of Penaeid Protozoea. E. Part of exopod of antenna of Euphausid larva. F. Antenna of *Pandalina brevirostris*, Zoea.

cannot be without significance. A very striking example is given by Scourfield (1940, p. 295, figs. 5–7), who shows that the mandibular palp of the larva of *Lepidocaris* is identical with that of present-day *Chirocephalus diaphanus* not only in the number of setae, but even in their detailed structure. In each case one only of the setae, on the second segment, has a bulbous swelling at the base, and the three distal setae are smooth, while all the rest are plumose.

In the Calanoida, and also in the Nauplius of most Copepoda and some Cirripedia, the exopod consists of seven distinct segments, but ten can be distinguished in the Nauplius of *Longipedia*. In adult Calanoida there is a maximum of twelve setae, but the number may be reduced to seven, always by loss of those of the proximal segments, or of the proximal seta of the last segment. Having regard to the fact that lost segments are commonly indicated by the retention of the setae borne by them (Gurney, 1931, p. 68), it is almost certain that the exopod was primarily of ten, or possibly more, segments.

Although the swimming legs of the Copepoda are entirely different from those of the Decapoda at any stage of their development, there is evidence that they have been derived, by suppression of segmentation, or arrested development, from a more primitive form of limb with nine segments, such as there is in Decapoda. All nine segments can still be seen in the maxillipedes of some Copepods (Gurney, 1931, p. 63).

In the Protozoea the third thoracic appendage is rudimentary, whereas it is a functional biramous limb in the Copepodid, and in the Euphausiacea only one maxillipede is developed in the corresponding stage. In the latter the compression of the thoracic somites, with general shortening of the body, is evidently a secondary modification which has led also to suppression of maxillipedes 2 and 3, and it seems probable that a larva with three pairs of functional maxillipedes is more primitive than one with fewer. Three pairs are always present in the first larva of Caridea which, as will be shown below, corresponds to the Protozoea. The universality of this stage, modified though it may become, gives good reason to believe that it is a deep-rooted ancestral stage, and it is suggested that it actually corresponds to the first Copepodid stage of Copepoda.

While it must be admitted that evidence of this kind is not very substantial, it does justify putting forward the speculation that the Copepoda have arisen by arrested development from a larval form having the general characters of the Decapod Protozoea. A somewhat similar view has been expressed by Beurlen (1930, p. 477)—"die Copepoden sind gewissermassen auf Jugendstadien stehen gebliebene, degenerative—neoteinische—Pygocephalomorphen. Ein Vergleich der Copepoden mit Jugendstadien der Schizopoden illustriert dies sehr schön."*

It is of interest to note to what extent structures which have been lost in the adult may be preserved in the larva, or may be present in one larva and preserved in a functionless condition in another.

(1) Exopods on the legs: There cannot be any doubt that the ancestral Decapod possessed functional exopods on all the legs, and indeed they are found still in some cases (some Penaeidae; Hoplophoridae; some Atyidae; *Discias*). But they have generally been lost entirely in the adult, and it is only in a few groups that the full number is retained even in the larva.†

In some cases exopods are retained even when incapable, owing to absence of setae, of serving any swimming function. Particularly interesting cases are those of *Axius stirhynchus* and *Calocaris macandreae*, in which small rudiments of exopods appear on leg 5 in the larva, and are even traceable in the former in the first post-larval stage. It is usual for the first post-larval stage to retain vestiges of the exopods which have been functional in the larva, but it is remarkable that this should happen when they are functionless rudiments only in the larva. In *Rhynchocinetes rigens* also a

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* See also Claus, 1871, p. 49, 1876, p. 77.

† Some of them are lost even in the Atyid genera *Caridina* and *Atyaëphyra*.

rudimentary exopod appears on leg 5 in the larva. In *Atyaëphyra desmaresti* rudimentary exopods are present on legs 4 and 5 in the larva, but are lost in the adult.

Another interesting example of the persistence of exopods is found in *Upogebia savignyi* (Gurney, 1937*a*). Here the young hatch in the adult form; but a zoeal stage is passed through in the egg, in which large exopods, without setae, are developed on the first three pairs of legs.

(2) In *Lucifer* the last two pairs of legs are absent in the adult; but a vestige of leg 4 is present in the larval and first post-larval stages (Gurney, 1927, p. 250). In *Sergestes* legs 4 and 5 are fully developed in the larva, but disappear in the first post-larval stage (Mastigopus) to reappear again in the adult. The temporary disappearance of certain structures is not confined to the Sergestidae, and is unexplained (see p. 106).

(3) Pleopods which are absent in the adult may be present in the larva of some Anomura and Brachyura (see p. 153).

It is surprising that so few instances can be found of the survival of lost structures, and it is much more common to find the adult characters appearing directly. For example, when pleopod 1 is absent in the adult it never appears in the larva. In *Leptochela* this appendage, which is present in the adult, is actually absent in the larva and the first post-larval stage, though the four succeeding pairs develop normally (Gurney, 1936). In certain Stenopid larvae pleopod 1 is very much delayed in appearance (Gurney and Lebour, 1941).

When the gill formula of the adult is reduced there is no trace of the lost gills in the larva; but to this rule there are certain exceptions. Bouvier (1908) states that in the young (*Grimaldiella*) stage of the Penaeid *Funchalia* there are two arthrobranchs on leg 4, and only one in the adult. I am indebted to Mr. Burkenroad for the assurance that this is an error, the young form having, like the adult, only one arthrobranch on this leg.

Another recorded case is that of *Albunea symnista*. In this species Menon (1937, p. 14) finds 13 gills on each side in the larva in stage 5, whereas there are only 11 in the adult (Claus, 1885, p. 70). If I understand Menon's account aright there must at this stage be one (and not two as in the adult) arthrobranch on maxillipede 3, two arthrobranchs on each of legs 1–4, and four pleurobranchs (instead of one as in the adult) on the last four legs. Claus himself observed rudimentary pleurobranchs on the last four thoracic somites in a larva attributed to *Albunea*, although he could only find one in the adult (of *A. symnista*). Boas (1880, p. 162), on the other hand, found three pleurobranchs in *A. paretii.*

I have found some difficulty in counting the gills of the larva with certainty; but two specimens agree in having 12 gills, of which two are pleurobranchs.

It must be admitted that there is some evidence that gills do appear in the larva of *Albunea* which are lost in the adult; but the evidence is very weak. In the first place no *Albunea* larva has been definitely identified. Menon gives the name *A. symnista* to his larvae, but only because this is the only species known from the Madras coast. In the second place there may well be differences in the gill formula of different species. Claus and Menon do not give the same number of gills for *A. symnista*, and Boas found two rudimentary pleurobranchs which Claus could not find in *A. symnista.*

In *Upogebia* rudiments of epipods may appear on the maxillipedes which are absent in the adult (Gurney, 1924*c*) but, before this can be accepted as an example of recapitulation, the gill formula of the adult should be re-examined. It does not follow that all species of a genus have exactly the same formula, or that small epipods may not have been overlooked.

It has been stated by Coutière (1919) that the preischium is shown by Williamson in the larva of *Crangon*; but the figure in question (Williamson, 1901, p. 111, fig. 134) is of the first post-larval stage. There is no

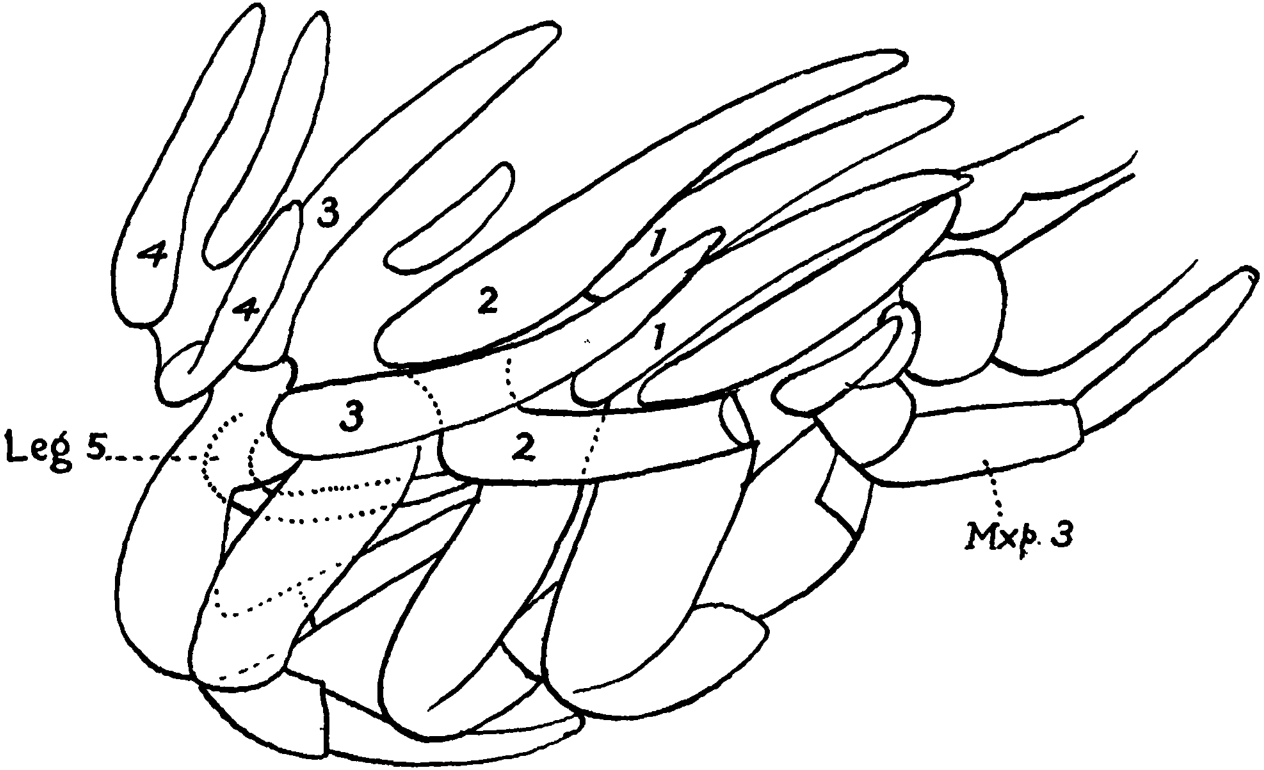

FIG. 7*a*.—Legs and gills of *Albunea* sp. last larva (" Discovery " Station 1587). The arthrobranchs are numbered according to the legs to which they belong.

trace of it in the larva, and I have not seen it in any other species. On the contrary, the distinction between ischium and merus may be absent in the larva when these segments are separated in the adult. In fact the larva offers no evidence whatever for the postulated primitive segmentation of the limb.

Attempts to draw phylogenetic conclusions from larval stages must always take into account the great caenogenetic modifications to which they have been subject. The larva is a stage in the ontogeny of which the end is the production of an adult, and the appearance of adult characters can be advanced to any extent compatible with the main purpose served by the larva, namely, dispersal; or new characters special to the larva itself may arise and obscure to some extent the primitive form. Among the Copepoda even the Nauplius has become greatly modified, so that characters distinctive of the different groups and even of species can be defined.

Among the Decapoda " ontogenetic anachronism " is particularly well marked. For instance, the muscular system of the Zoea is fundamentally the same as that of the adult, and where it is reduced in the adult (Brachyura) it is also reduced in the larva (Daniel, 1930, 1931). When we find, as is commonly the case, that generic and even specific differences may be traced in the earliest larvae,* it is clear that the whole course of ontogeny has been modified, and ancestral characters common to large groups are likely to be lost. For this reason it is most difficult to recognize generalized larval types characteristic of large groups, and it is not easy to find larval characters which are of real use in framing a system for the adults.

LARVAL STAGES.

When definable phases in development can be distinguished it is desirable to be able to give names to

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* Even the Prezoea may have characters distinctive of its particular group of Brachyura (Lebour, 1928*b*).

them; but there is some difficulty in arriving at a satisfactory terminology. While the names Nauplius, Protozoea and Mysis stage have the sanction of long usage, that usage has not always been the same, and other terms have been introduced to define intermediate stages in special cases. Daday (1907), in describing the development of *Caridina*, used the terms Eu-, Meso- and Meta-Zoea; Proto-, Meso-, Meta- and Post-Mysis, some of these stages apparently being supposed to cover more than one moult. Sollaud (1925*b*), while adopting a numbered series of stages in Palaemonid development, also defined certain "phases"—Epizoea, Zoea, Promysis—each of which might include more than one stage. Gauthier (1924) adopted the same system.

In my opinion not more than three really distinct phases can be recognized, namely, Nauplius, Protozoea and Zoea-Mysis, and any multiplication of names beyond these can only lead to a false idea of diversity. These phases are dealt with further below.

I hope to show that the first three stages of the Caridean larva (and consequently of all other Decapods) correspond to the three Protozoeal stages of Penaeidea, but there are objections to using the term Protozoea for them. It is preferable not to distinguish them from subsequent stages, but to number each stage, or moult, consecutively. It is also a convenience to use the term Zoea to include all post-protozoeal stages in Penaeidea and all stages in other Decapods. Although Zoea is actually a generic name for a Brachyuran larva, it has long since lost its restricted application. There is no fundamental difference between the larva of the Brachyura and that of any other Decapod, and it is only misleading to give it a special name.

The term "Mysis Stage" can be dropped with advantage.* It is an unfortunate term, implying a false relationship, and it is not easily definable. Referring as it does to a stage with biramous legs, it cannot

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* Calman (1911, p. 394) has proposed "Schizopod stage" in place of "Mysis stage"; but the objection to the latter is not thereby met.

legitimately be applied to a stage with no exopods, although that stage is precisely equivalent to a Mysis stage in other forms. Furthermore, if the term is really used, as it has been, to imply a phylogenetic meaning, it should be applied to a stage in which the thoracic terga are free from the carapace, since this is a much more fundamental feature of the Mysidacea than the possession of exopods.

When larval life is continued for a considerable time after the acquisition of all thoracic appendages, as it is in so many large deep-sea larvae, and there is no means of knowing how many moults have been passed through, it might be a convenience to allude to these large larvae as Mysis stages for want of a better term, but it must be recognized that there is no real difference between Zoea and Mysis.

The number of stages in larval life in any species is probably a fixed one in most cases; but it is not easy to ascertain with certainty. Artificial rearing of larvae may give misleading results, for, although stages 1–3 are passed through without variation, the natural course of development is apt to be disturbed after that point, and additional stages may be intercalated which are not found normally in nature. Such abnormal stages have been noted in *Homarus* (Williamson, Templeman); *Leander serratus* (Sollaud); *Palaemonetes varians* (Sollaud, Gurney); *Atyaëphyra desmarestii* (Gauthier).

When larvae taken in plankton are sorted into stages by differences in structure or size there is no certainty that every individual passes through all these stages. In Euphausids morphological comparison led to the separation of a large number of Furcilia and Cyrtopia stages (Lebour); but statistical analysis showed that these fell into relatively few dominant stages, each with variants more or less rare (Macdonald, Fraser, John). Fraser and John agree in making no distinction between Furcilia and Cyrtopia, and the latter found in five species of *Euphausia* either six or seven real, or dominant, stages. Adding the three Calyptopis stages (corresponding to the Protozoea of Penaeidea) there are therefore nine or ten post-naupliar stages in all.

The following table gives the number of stages ascertained or presumed in certain Caridea, and it will be seen that the maximum number is nine, a very close correspondence with the Euphausiacea. This number may, perhaps, be much exceeded in some of the oceanic larvae of uncertain parentage, and some Phyllosomas (Gurney, 1936). On the other hand, the tendency

Number of Stages Observed in Some Caridea.

Species.	Author.	Number of stages (not including post-larval).
Pasiphaea tarda	Bjorck	4 ?
Parapasiphaë sulcatifrons	Stephensen	5
Leptochela bermudensis	Gurney	5
Hymenodora glacialis	Stephensen	5
Acanthephyra purpurea	Lebour	more than 7
Systellaspis debilis	Gurney	3
Hoplophorus grimaldii ?	,,	5
Atyaëphyra desmaresti	Gauthier	7
Paratya compressa	Yokoya	8
Pandalus danae	Berkeley	5
,, *borealis*	,,	5
,, *platyceros*	,,	5
Pandalina brevirostris	Lebour	9
Caridion gordoni	,,	9
Chlorotocella sp.	Gurney	6
Spirontocaris cranchii	Lebour	9
Hippolyte varians	,,	9
,, *proteus*	Gurney	4
Athanas nitescens	Lebour	9
Alpheus ruber	,,	9
Leander serratus	Sollaud	8
,, *longirostris*	Gurney	5
Brachycarpus biunguiculatus	,,	11 ?
Processa canaliculata	,,	9
Crangon vulgaris	Williamson	5

throughout the Decapoda is to shorten development, and this tendency may even appear in forms with the longest series of stages. In such cases stages 8 and 9 are not very different, and stage 8 may moult directly to post-larval (*e.g. Processa*).

While stages 1–3 seem to be universal and obligatory* more evidence is needed as to the fixity of the number of the succeeding stages. The only satisfactory method of determining to what extent this number is fixed or variable is to keep larvae taken in plankton alive through one moult. During so short a time there is not likely to be any disturbance of normal development, and each step can so be checked.

Fraser (1936, p. 40) has discussed the significance of stages in development and concludes—"the series of moults may, in fact, be regarded as a kind of 'grid' superposed on a course of actually continuous development. In the more primitive cases this 'grid' may still shift slightly backwards and forwards ; in the more specialized cases the 'grid' has become fixed and all individuals show the same changes at each moult."

As Fraser himself points out, there is, strictly speaking, no such thing as continuous development in those Crustacea which have a free larva, since development is always by a succession of moults, at each of which some fresh structure is acquired ; but in the Anostraca and Notostraca the changes at successive moults are so small that the development may reasonably be called continuous as opposed to metamorphic. The Cirripedes and Ostracods are so specialized that they may be left out of consideration, but in the Copepoda and Eucarida development shows two early phases, Nauplius and Copepodid or Protozoea, in which perfectly definite stages are fixed and practically universal. In the Copepoda development goes no further and, so far as they are concerned, there is no question of a shifting grid. In the Eucarida the same is true for the period

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* There are apparent exceptions to this rule in *Athanas* and *Alpheus* (Lebour, 1932).

ending with the last Calyptopis or Protozoea stage or, in the higher Decapoda, with stage 3 of the so-called Zoea. It is only after this point that irregularity can be found.

In the Euphausiacea inconstancy in development, or shifting of the grid, is found only in certain species which there is no reason to suppose are more primitive than others in which such variability is absent. The variability is, in fact, exceptional, and a specific character for which no explanation can be given. The conception of a shifting grid can therefore only be applied to post-protozoeal stages and to exceptional species.

As I understand it, a shifting grid implies a series of fixed compartments, through which portions of a continuous background can be seen, and these compartments must be fixed in area and represent fixed "units of development." A shifting of such a grid would only cause different parts of the background to be picked out in each compartment, and could not effect any rearrangement of the sequence of the elements of the background.

The development of *Euphausia superba* seems to fulfil the postulated conditions. Without the remarkably thorough study of a large material which Fraser has made it would have been difficult to delimit definite stages, since, as his figures show, every possible gradation in development of the appendages can be found, and it is only by giving weight to certain points, such as number of spines on the telson and number of setose pleopods, and establishing the frequency of combinations of certain characters, that a grouping can be made. All the appendages, of head, thorax and abdomen, "keep step" in development, and it could be said with reason that the conception of a grid with six compartments shifting slightly to and fro across a continuous background would agree with the facts.

For the Decapoda we have no such exhaustive study as that of Fraser for *Euphausia superba*, but there is no doubt that the stages are, for the most part, remarkably constant and limited in number. Where there is a long series of stages and these are not easily separated, as in *Amphion* and Phyllosoma, there is not, I think, the same continuity of background, and two individuals may differ in degree of development of different parts of the body.

Post-larval.

In Euphausiacea and Penaeidea there may be no very clear distinction between larva and post-larva, and the latter may merge into the adult without definable stages. In Caridea the first post-larval stage is commonly different from all subsequent stages by reason of the fact that it generally retains vestiges of exopods on the legs, and there may also be some degeneration of certain of the mouth parts. In *Palinurus* the first post-larval stage is so distinct that it has received a generic name—*Puerulus*—and it is commonly known as the Natant stage (see p. 235). Similarly in Paguridea and Brachyura this stage is very distinct, and has received special names—*Glaucothoë* and *Megalopa*. There is only one Glaucothoë stage in all species of which the development is known, though it is probable that the large Glaucothoës of unknown parentage retain their characters through many moults. In Brachyura Miss Lebour has found only one Megalopa in all species studied, but Aikawa (1937) has recorded two in *Charybdis bimaculata* and *Plagusia dentipes*. It seems that one stage is the rule, but there may be rare exceptions. There is, therefore, some justification for supposing that normal development includes a post-larval stage distinct from both larval and adolescent and ending, as a rule, at the first post-larval moult.

NAMES USED FOR LARVAL STAGES.

Glaucothoë : First post-larval stage of Paguridea.

Megalopa : First post-larval stage of Brachyura.

Metazoea : Used for the late stages of the Zoea of Brachyura, and also in Anomura for those larvae in which five pairs of legs appear together as uniramous rudiments behind the functional maxillipedes.

Mysis : Larva of Penaeidea and Macrura in which some or all of the legs have functional exopods.

Parva : First post-larval phase of Caridea (Sollaud, 1923, p. 576). The term *parva* was used by Kemp (1907) for the first post-larval *Acanthephyra purpurea*, since this stage had been described by Coutière as *A. parva*, n. sp. Sollaud described special stages in some Palaemonidae as " praeparva " and " subparva."

Prezoea : For the larva when first hatched, and still covered by the embryonic cuticle.

Protozoea : For the post-nauplius stages of Penaeidea, and last embryonic stage of some other Decapoda. Sometimes applied to any larva in which maxillipedes 1 and 2 only are present.

Pseudozoea (Czerniawsky, 1884, p. 247) : For a " Stadium transitans inter zoëas et megalopideas." *Zoea gigas*, Westwood, is given as a synonym. Fortunately the name has never been used again, so that no confusion is caused by use of the name for a Stomatopod larva.

Zoea : Properly belonging only to Brachyura, but in general use for the last Protozoea of Penaeidea and for stages preceding the " Mysis " in other Decapoda. Subdivisions of the Zoea phase have been made—Euzoea, Mesozoea, Metazoea (Daday, 1907), Epizoea, Zoea, Promysis (Sollaud).

List of Larval Genera of Decapoda with their Probable Identification.*

Acanthocaris, Claus, 1876	Raninidae ?
Acanthosoma, Claus, 1863	*Sergestes.*
Acanthotribola, Czerniavsky, 1878	Brachyura.
Amphion, M. Edwards, 1832	*Amphionides*, Zimmer ?
Anebocaris, Bate, 1888	Alpheidae.
Anisocaris, Ortmann, 1893	*Discias.*
Anomalocaris, Ortmann, 1893	Callianassidae.

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* I am informed that *Carcinoxiphias* and *Styluroxiphias*, Costa, 1864 ('Rend. Accad. Napoli,' iii, fasc. 4, p. 89, 255) are larval Decapoda, but I have been unable to see this work.

Atlantocaris, Ortmann, 1893	*Heterocarpus.*
Bentheocaris, Bate, 1888	*Acanthephyra.*
Boreocaris, Ortmann, 1893	*Pandalus ?*
Camptocaris, Ortmann, 1893	?
Caricyphus, Bate, 1888	Hoplophoridae (part).
Cerataspis, Gray, 1828	Penaeidae.
Copiocaris, Thiele, 1905	Pandalidae.
Cryptopus, Latreille, 1834	Penaeidae.
Cyllene, Dana, 1852	Portunidae ?
Cyllenula, Czerniavsky, 1878	Brachyura.
Desmarestia, Dana, 1852	,,
Diaphoropus, Bate, 1888	Alpheidae.
Dohrnia, Czerniavsky, 1878	*Xantho* ?
Dymas, Kröyer, 1861	*Pandalus borealis ?*
Elaphocaris, Dohrn, 1870	*Sergestes.*
Embryocaris, Ortmann, 1893	*Stenopus.*
Eretmocaris, Bate, 1888	*Lysmata* (in part).
Erichthina, Dana, 1852	*Lucifer ?*
Eryoneicus, Bate, 1888	*Polycheles.*
Euacanthus, Philippi, 1857	*Porcellana.*
Euphema, M.-Edwards, 1837	*Gennadas.*
Falcicaris, Ortmann, 1893	Pasiphaeidae ?
Fissocaris, Claus, 1876	Brachyura.
Glaucothoë, M.-Edwards, 1830	Paguridae.
Grimothea, Fabricius, 1793	*Munida.*
Hectarthropus, Bate, 1888	Processidae.
Hemisphaerium, Czerniavsky, 1878	Brachyura.
Hippocaricyphus, Coutière, 1907	Hippolytidae.
Hoplites, Philippi, 1857	*Gennadas.*
Hoplocaricyphus, Coutière, 1907	Hoplophoridae.
Hyadella, Czerniavsky, 1878	Brachyura.
Icotopus, Bate, 1888	Pandalidae.
Kyptocaris, Bate, 1888	Pandalidae ?
Lonchophorus, Eschscholtz, 1825	Brachyura, Dorippidae?
Loxopis, Dana, 1852	Penaeidae.
Macropa, Latreille, 1834	Brachyura.
Marestia, Dana, 1852	,,
Mastigopus, Leuckart, 1853	*Sergestes.*
Megalopa, Leach, 1815	Brachyura.
Mesocaris, Ortmann, 1893	Palaemonidae.
Miersia, Chun, 1887	*Lysmata.*
Monolepis, Say, 1817	*Ocypoda.*
Myto, Kröyer, 1842	*Sabinea.*
Odontolophus, Bate, 1888	*Leander.*
Oligocaris, Ortmann, 1893	?
Oodeopus, Bate, 1888	Axiidae and Callianassidae.

Opisthocaris, Ortmann, 1893	*Solenocera.*
Pandacaricyphus, Coutière, 1907	Pandalidae.
Paradesmarestia, Czerniavsky, 1878	Brachyura.
Paramonolepis, Czerniavsky, 1878	,,
Parathanas, Bate, 1888	Alpheidae.
Peteinura, Bate, 1888	*Cerataspides.*
Phyllamphion, Reinhardt, 1850	Palinuridae.
Phyllosoma, Leach, 1817	,,
Platysacus, Bate, 1888	*Solenocera.*
Pluteocaris, Claus, 1876	Dorippidae ?
Podopsis, Thompson, 1829	*Sergestes.*
Problemacaris, Stebbing, 1921	Raninidae ?
Procletes, Bate, 1888	*Heterocarpus.*
Prophylax, Latreille, 1830	Paguridae.
Protomonolepis, Czerniavsky, 1878	Brachyura.
Pseudodesmarestia, Czerniavsky, 1878	,,
Pseudomonolepis, Czerniavsky, 1878	,,
Pterocaris, Claus, 1876	,,
Quadribola, Czerniavsky, 1878	,,
Rachitia, Dana, 1852	Penaeidae.
Retrocaris, Ortmann, 1893	*Brachycarpus* (in part).
Rhomaleocaris, Bate, 1888	*Latreutes ?*
Sceletina, Dana, 1852	*Lucifer.*
Sciacaris, Bate, 1888	Sergestidae.
Spinaria, Czerniavsky, 1878	Brachyura.
Thalassocaris stimpsoni, Bate, 1888	Pandalidae.
Tribola, Dana, 1852	Brachyura.
Tricuspidella, Czerniavsky, 1878	,,
Urozoea, Ortmann, 1893	Thalassinidea ?
Xylaphocaris, Bate, 1888	*Sergestes.*
Zoea, Bosc, 1802	Brachyura.
Zoeaboops, Adams, 1848	Nomen nudum.
Zoeides, Guérin Ménéville, 1856	*Hippa ?*
Zoontocaris, Bate, 1888	Galatheidae.

NAUPLIUS.

It is well known that *Lucifer* and certain Penaeids leave the egg as a Nauplius, and it is claimed by Nakazawa* (1916, 1926) that this is also the case in some species of *Sergestes*.

A well marked Nauplius stage is passed through in the egg by all Decapoda which hatch at a later stage, and

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* Since Nakazawa's paper is in Japanese the only evidence for his statement is from his figures; but these might equally well represent Copepod Nauplii.

embryonic life may be divided into stages, with pauses between, and even moults. Sollaud (1923, p. 205) found, in *Leander serratus*, that there is a pause of about a week after the formation of the embryo with Nauplius appendages. Although these facts seem to show clearly that a free Nauplius was at one time universal among Decapods, the structure of the egg-nauplius shows also how fundamentally development has been modified, for this Nauplius can only be claimed as such in very general terms. It already has the rudiments of compound eyes, which were certainly not present in the free larva, and the body may show marked segmentation, which is not the case in any free Nauplius known.

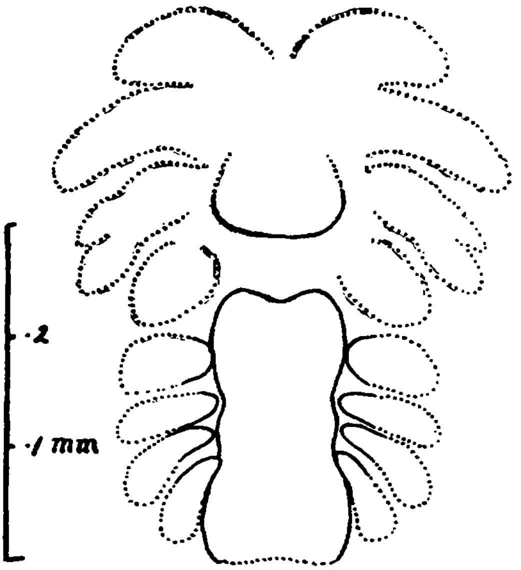

Fig. 8.—Embryo of *Willemoesia challengeri* showing rudiments of compound eyes, nauplius appendages and hind body.

When a larva has a free life, each succeeding stage must obviously be viable, and new structures can only appear in their turn as it were ; but, when any stage is retained and passed through in the egg, there is no longer any need for the preservation of a time-schedule, and structures peculiar to much later stages may appear quite early in ontogeny.

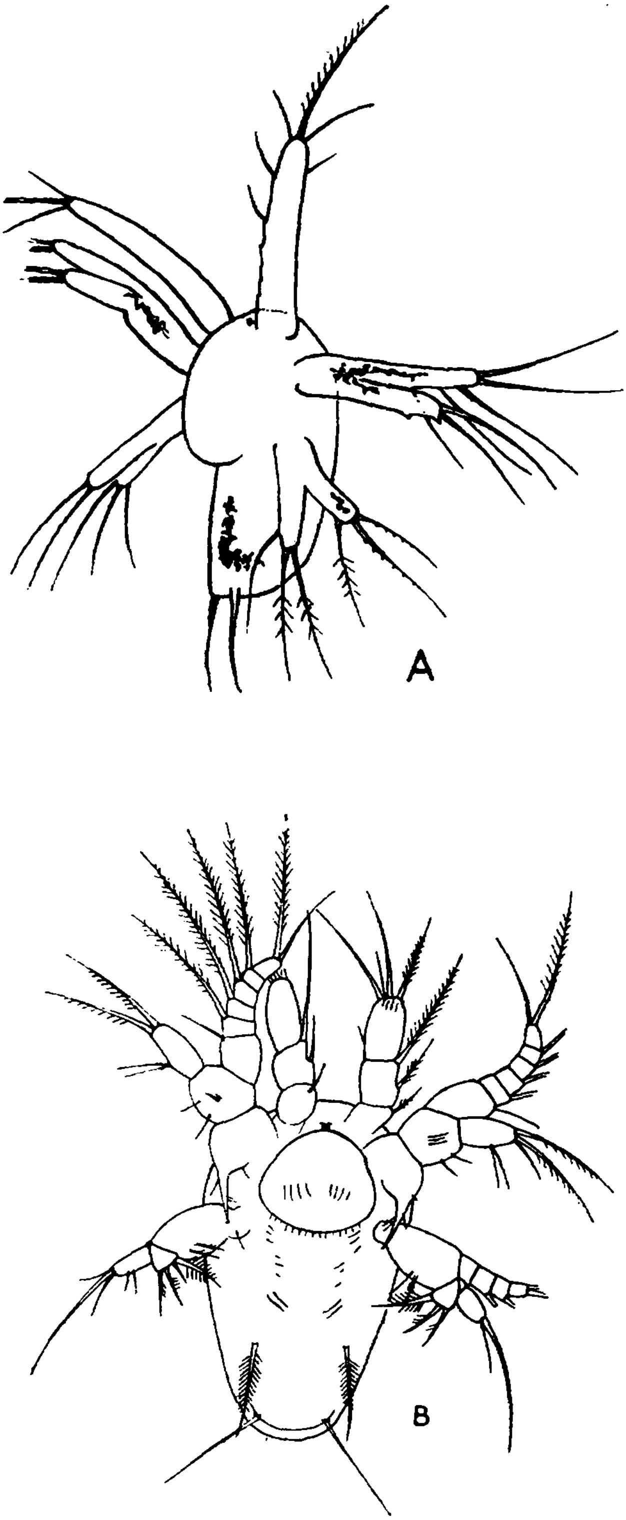

Fig. 9.—a, Nauplius of Penaeid (*Sicyonia*). b, Nauplius of Copepod (*Cyclops americanus*).

The free-swimming Nauplius of Decapoda and Euphausiacea, unlike those of the "Entomostraca," has no spines nor processes on the antennae or mandibles for feeding purposes, and in some, if not all, cases is dependent upon internal yolk, the mouth being closed until the end of the Nauplius phase. There is no trace in early stages of segmentation or of post-mandibular appendages. In Copepoda, for example, the Nauplius is much more highly organized, and the maxillule may sometimes (*Longipedia*) be traced even in the first stage. It is clear that the Nauplius is a larva in which segmentation has been suppressed, and it is most probable that it is directly derived from the Protaspis larva of Trilobites, in which the segments corresponding to the two pairs of maxillae were distinct (Garstang and Gurney, 1938).

Sollaud also (1923, p. 212) has made the suggestion that the Nauplius is a larva secondarily modified from one which possessed four pairs of appendages behind the prostomium, and corresponded to the Protaspis of Trilobites.

The number of Nauplius stages is somewhat uncertain. In *Nyctiphanes couchi* the first two stages are passed through in the egg-pouch, and there are two free stages which are not exactly comparable with the three found in *Meganyctiphanes norvegica* (Lebour, 1924). In *Lucifer* the first stage is passed in the egg during the first 24 hours after egg-laying, and there are only two free stages (Brooks, 1882). In both these cases there is shortening of development associated with the carrying of the eggs by the parent. In some Euphausids (*Nematoscelis*, *Stylocheiron*) the eggs are comparatively large, and it is supposed that there is no free Nauplius.

Mme. Heldt (1938) finds that there are eight Nauplius stages, separated by exceedingly small differences in size and structure, in *Penaeus trisulcatus*, *Parapenaeus longirostris* and *Sicyonia carinata*. I have myself found only three stages in *Metapenaeus stebbingi* and *Sicyonia wheeleri*.

PROTOZOEA.

In the Penaeidea the Nauplius passes without an abrupt transition into the Protozoea, in the sense that the limbs of the Protozoea are present as rudiments in the Nauplius, the body is already considerably elongated, the carapace is partly developed, and the telson has become more or less forked. The Protozoea does, however, represent a perfectly distinct phase of peculiarly interesting structure. Its main characters, in stage 1, are the absence of functional compound eyes, the complete segmentation of the thorax, the freedom of the carapace from these somites, and the forked telson. The antennae have fully natatory exopods, and the mouth parts are of very primitive form as compared with those of the zoeal stages. Of the thoracic appendages only maxillipedes 1 and 2 are functional biramous limbs, while maxillipede 3 may be present as a rudiment.

The protozoeal phase has three stages in Penaeidea, and in the last of them the remaining legs are present as large rudiments, the abdomen is fully segmented, and the uropods are present. The eyes are stalked, and the carapace may have a rostral spine. Claus drew a distinction between the first and the last of these stages, calling the latter a Zoea, but this distinction is misleading. The so-called Zoea in Penaeidea still has some of the characters which are the essential features of the Protozoea, namely, the natatory antenna and the freedom of the thoracic terga from the carapace. The protozoeal type is so markedly different from that of the adult Decapod, lacking as it does the "caridoid facies," that it is hardly possible to avoid the conclusion that it preserves a memory of a pre-Decapod ancestry. Claus (1876) regarded it as an extreme modification of an ancestral "Urphyllopod," but a definitely Phyllopod ancestry for the Decapoda can no longer be upheld. If we accept the Trilobites as ancestors of the Crustacea, it is also necessary to suppose that the Decapods have

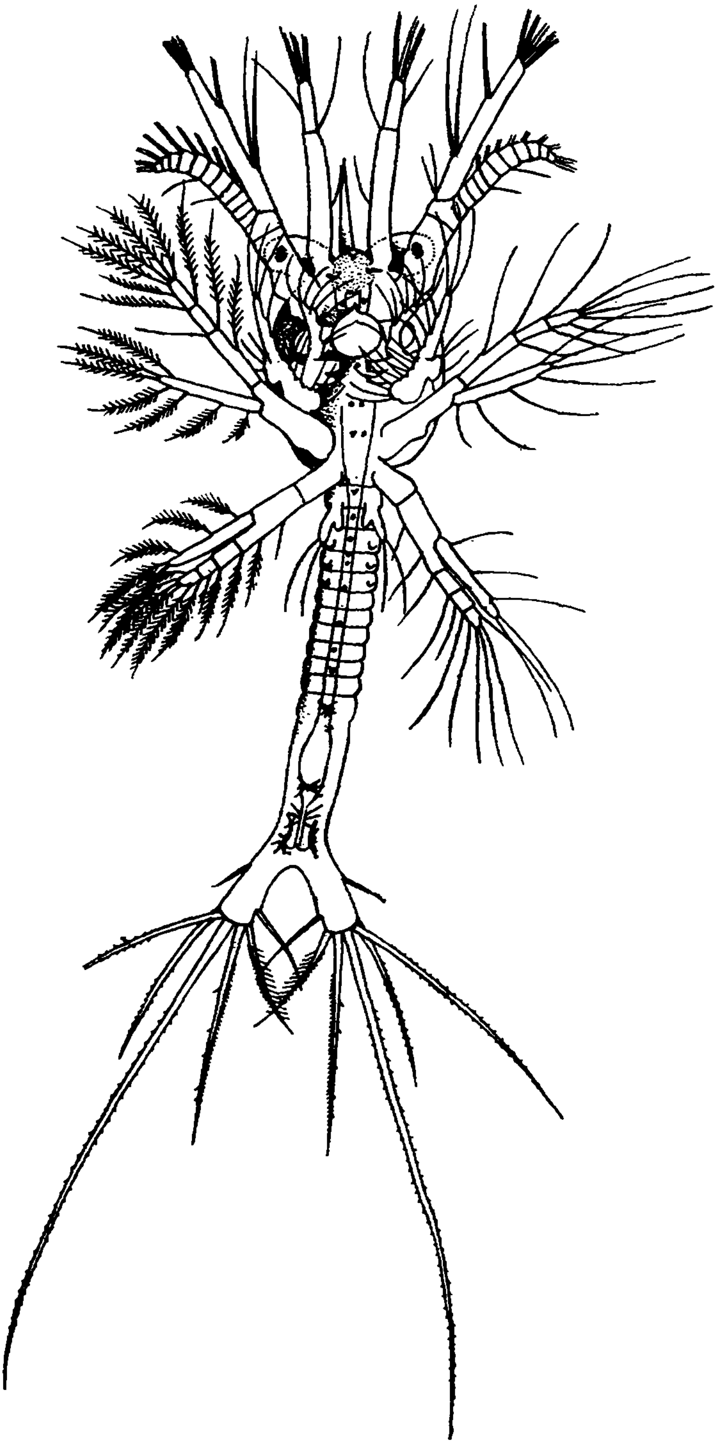

FIG. 10.—Protozoea of Penaeid (*Gennadas*).

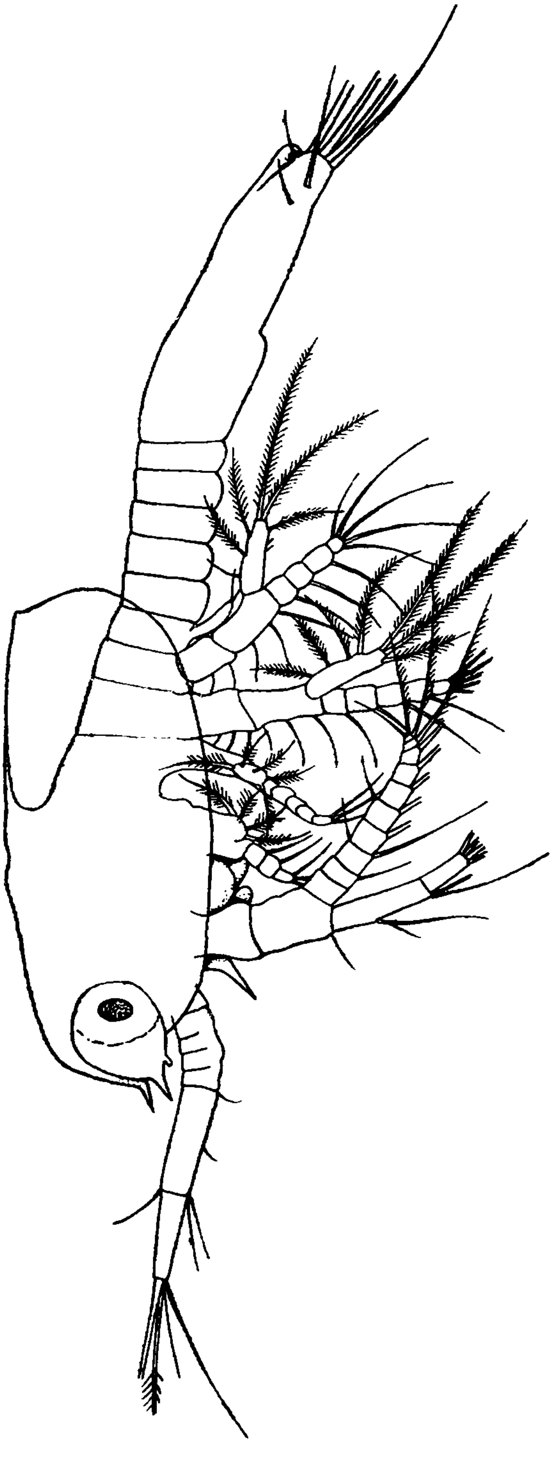

Fig. 11.—Protozoea of Penaeid (*Penæopsis*).

arisen from a branch distinct from that which gave rise to the Branchiopoda (Garstang and Gurney, 1938).*

If we can accept the Protozoea as representing the larva of the ancestral Decapod, we must face the difficulty that it may have either one, two or three maxillipedes. There can be little doubt that the compression of the thoracic somites seen in all Decapoda except the Penaeidea is secondary, and the Penaeid Protozoea has a more primitive form than that of the Euphausiacea. It is possible to believe that the compression of the somites has led to a loss of appendages in Euphausiacea, though it has not done so in the Caridea. It would seem probable, indeed, that the Caridea have retained a primitive number of three maxillipedes, and that the Penaeidea are on the way to loss of the last of them.

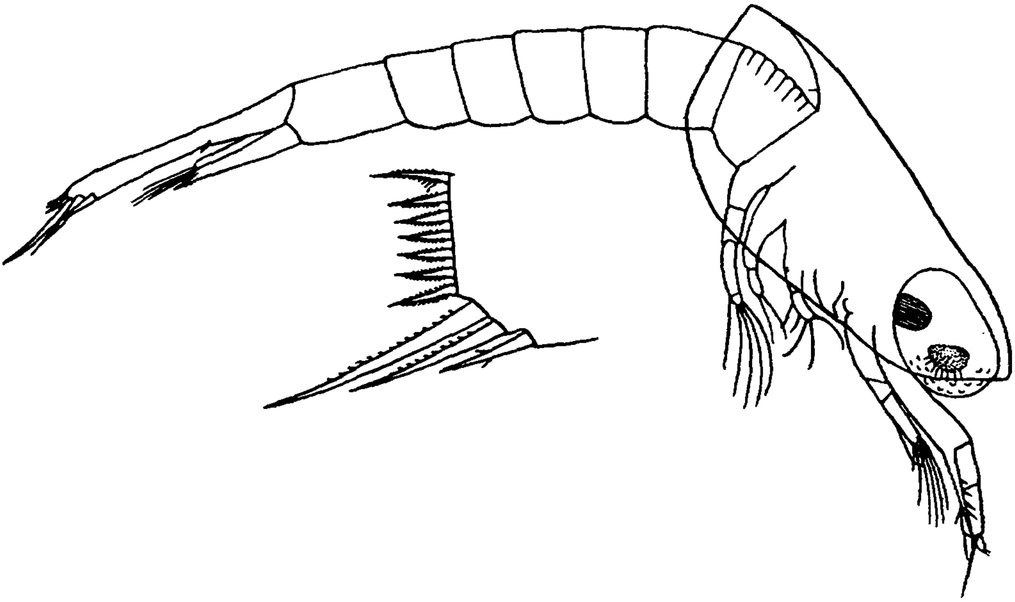

FIG. 12.—Protozoea of an Euphausid.

The Antizoea of some Stomatopoda may fairly be regarded as the equivalent of the Protozoea; but in

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* Størmer's researches on Trilobite limbs which led him to regard the Crustacean affinities of Trilobita as remote have been criticized by Garstang (1940). I see no reason to modify the views expressed in the paper referred to.

this case there are five pairs of thoracic limbs of larval character in the earliest larva. It is possible that the Antizoea is a larva in which two additional pairs have been acquired; but in view of the simple and uniform structure of the limbs, and the contrast between them and the three posterior pairs which appear later, this seems unlikely.

It seems quite probable that the Antizoea, so far as concerns the number of thoracic appendages, has preserved the character of the primary Protozoea. In the Pseudozoea of other Stomatopoda these limbs have been reduced to two, and they have lost their larval character entirely. On this view the Euphausid Protozoea has gone even further and has lost all but one appendage; but this one is of larval form.

In those Decapoda which hatch at a Zoea stage an embryonic cuticle is formed which may bear setae different in number and position from those borne by the free larva. This cuticle is commonly moulted in the act of hatching, and can then only be studied in embryos removed from the egg; but, in many cases, especially among Brachyura, it is retained for a short time after hatching, and the larvae may swim actively. A particularly good example is seen in *Jasus lalandii*, in which the Phyllosoma when first hatched has a biramous antenna which is used in swimming (Gilchrist, 1913, called this stage Naupliosoma). In other cases (*Porcellana*, many Brachyura) both pairs of antennae bear large feathered setae which are not functional, and are lost at the moult which ensues very soon after hatching. The telson may bear large feathered setae which are fewer in number than in the succeeding larva (Caridea), or quite different in size and arrangement (Brachyura). None of these transitory setae are found on the mandible or the succeeding limbs.

It has been suggested by Conn (1883) and others that this "embryonic cuticle" represents the protozoeal stage which has been relegated to embryonic life.

I have suggested (Gurney, 1926) that it is at least possible that it actually represents the Nauplius stage, for the following reasons. If the first Zoea of a Caridean be examined it will be found that it has certain characters which recall those of the Protozoea, and are modified or lost at the first or second moult. These are :

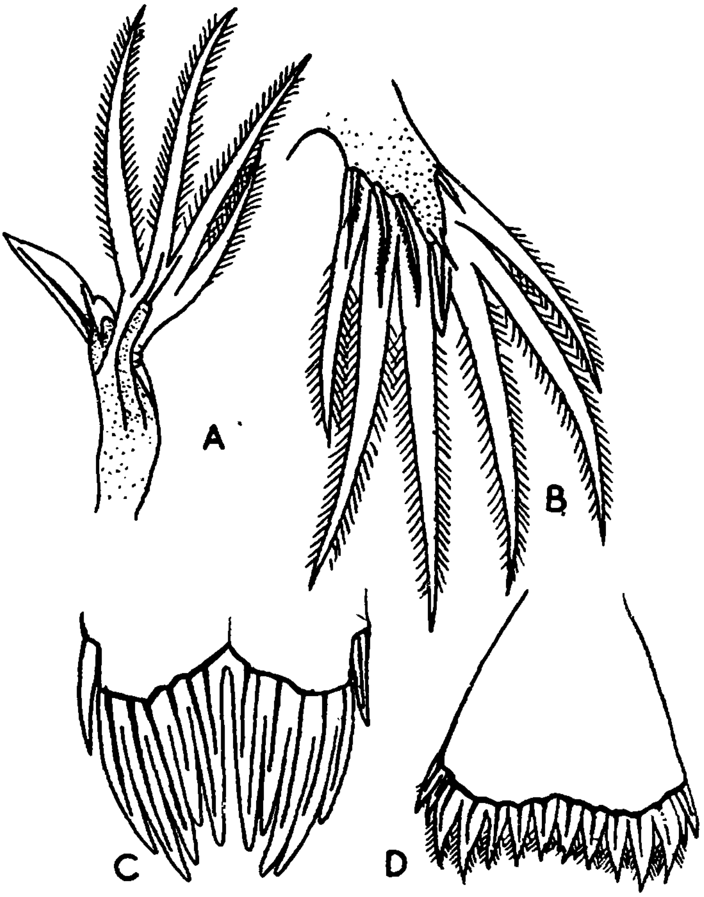

FIG. 13.—Embryonic cuticle. A. *Eurynome aspera*, antenna. B. *E. aspera*, telson. C. *Hippolyte varians*, telson. D. *Eupagurus prideauxi*, telson.

(1) The eyes are not stalked, and the Nauplius eye is present.

(2) Frontal organs may, rarely, be present.

(3) Spines on carapace or abdomen are absent except, very rarely, on somite 5.

(4) The peduncle of the antennule is unsegmented.

(5) The rostrum is usually absent or very small.

(6) A minute labral spine has been seen in larvae of some Hoplophoridae (Gurney and Lebour, 1941).

(7) The endopod of the antenna is a rod bearing one or more plumose setae ; the exopod is more or less segmented, with commonly two outer setae in the same position as in Penaeids.

(8) The maxillule may bear an exopod (*Caridina*, *Rhynchocinetes*) as in Penaeids.

(9) The exopod of the maxilla has no proximal extension, and the whole limb is more of a biramous type than it is later.

(10) The telson is often deeply incised, much more so than it is later.

I attach great importance to the segmentation of the exopod of the antenna. In some Penaeid Protozoeas this branch has as many as 11 segments, segments 4 and 6 each bearing an outer seta. In *Lucifer* there are 9 segments, without outer setae, while in Euphausiacea the segmentation is still further reduced.

Now, in most Caridea a distinct segmentation of the exopod can be seen in stages 1 and 2. In *Pandalina* (Fig. 7*f*), for instance, there are 5 segments, and there are also two outer setae, as in Penaeidea. The last segment bears five setae. In Penaeidea the last segment bears three, and may represent two fused segments, so that the last segment in Caridea may include four. It is a remarkable fact that the outer setae in Caridea, as in Penaeidea, are not borne by consecutive segments, but there is always an intermediate segment without setae. If the first seta is assumed to be borne upon segment 4, opposite to the first inner seta, the second is on segment 6, and the whole branch will represent 11 segments, as it does in Penaeidea. So close a correspondence cannot be fortuitous.

It is suggested that stages 1–3 of the normal Caridean development represent the three protozoeal stages of Penaeids, very much modified by the early appearance of characters which belong properly to the next phase. This would explain the fact that it is always at stage 3 that the uropods appear,* and the antennules and antennae are markedly changed.

Even in such extreme cases of condensed development as that of *Astacus fluviatilis*, where larval life is entirely suppressed, the uropods do not appear till the second moult (stage 3).

In the Palaemonidae, when the young hatch in the form of the adult, there is still a zoeal stage in the egg marked by a prolonged pause in development, and the formation of an embryonic cuticle which moulds the maxillipedes but not the posterior appendages (Sollaud, 1923).

If this argument is accepted, it follows that the stage passed through in the egg, and sometimes surviving into free life, in the form of the embryonic cuticle, must represent the Nauplius and not the Protozoea. The fact that the embryo at that stage has no obvious resemblance to a Nauplius, having in some cases even all the thoracic appendages present as rudiments, need not be regarded as a difficulty. We are dealing with a development profoundly modified at all stages by anachronism, and this would be simply an extension of the process of anticipation seen even in the Penaeidea, where most of the features of the Protozoea are visible in the Nauplius. If the stage represented by the embryonic cuticle actually corresponds to the Protozoea we should expect to find setae on the maxillae and maxillipedes. There is nothing of the kind, and setae are only retained on the limbs which were functional in the last Nauplius of the Penaeidea, and on the telson.

This argument is necessarily based on a comparison of Penaeidae with Caridea, since the larvae of the Macrura Reptantia and the Brachyura are in some respects more evolved, and have lost the segmentation of the antenna and other primitive features. If, however, it holds good for Caridea, it must also be extended to all Decapoda, since it is quite clear that the stages are comparable throughout.

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* See note, p. 34.

EMBRYONIC CUTICLE.

The significance of the embryonic cuticle has been discussed above, but some further reference to it is necessary. Although the stage represented by this cuticle is, as I believe, properly to be regarded as a modified Nauplius, it is convenient to adopt for it the term " Prezoea " which has been used by Miss Lebour and others,* since it implies nothing more than its position in ontogeny.

Cavolini (1792) figured the Prezoea of *Carcinus maenas*, but Du Cane (1839) was the first to draw attention to the difference between the Prezoea and the first Zoea, in *Carcinus*. Couch observed the same thing, but considered this form of the larva as abnormal. Joly (1843, fig. 64) showed clearly the embryonic cuticle covering the limbs and telson of the unhatched larva of *Atyaëphyra*.

Some of the peculiar features of the Prezoea were noted by Bate in 1858, while F. Müller in 1864 pointed out the resemblance of the Brachyuran Prezoea to that of the Caridêa. Mayer (1880) followed up this point, and drew valuable conclusions from study of the telson. His results were these :

(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 other Anomura form equal groups in a division opposed as a whole to the Brachyura. In these conclusions Mayer to some extent anticipated the work of Boas and others, but it must be admitted that they were based upon too narrow a foundation.

Faxon (1880) gave special attention to this stage in *Carcinus* and *Panopaeus*, while Conn (1884) summarized previous references and discussed the significance of it. Since that time there have been many further references to this larval cuticle, and Miss Lebour (1928*b*) has given

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* This stage was called " Sub-zoea " by Packard (1881, p. 788).

an excellent account of the Prezoea of many Brachyura, and has pointed out that even at this stage differences may be found which characterize the three groups Brachyrhyncha, Oxyrhyncha and Oxystomata, while smaller difference exist between certain families.

In the Brachyura the cuticle does not follow the indentations of the abdominal somites, indicating an unsegmented abdomen (Faxon, 1880). The telson is always widely forked, as in the Penaeid Protozoea, and this fork bears seven large seta-like outgrowths on each arm, three on the outer and three on the inner side, the seventh being a short process at the end of the fork, which is later replaced by the long spinous process of the Zoea. This short process is not plumose like the other processes, and it is possible that it may not really be the equivalent of a normal spine, in which case the prezoeal telson would have a formula of 6 + 6, as in Caridea. Such an interpretation does not, however, seem to be tenable, since the long spinous process of the Zoea is certainly homologous with the similar process in *Eupagurus*, for example, and this with spine 4 of the normal telson. Of the six spines the inner three are always preserved in the Zoea, though much reduced, but one or more of the outer three may be lost.

The antennule is unsegmented and bears either one or two large apical feathered setae. The antenna is biramous, the endopod a short stump, but the exopod bearing three or four setae, and a simple sheath over the rudiment of the spinous process. In some cases, *e.g.* Grapsoidea (Conn, 1884) there are no setal outgrowths on the antenna. In *Pinnotheres* it is interesting to note that the antenna, which is entirely absent in the Zoea, is represented in the Prezoea by an empty sac in the prezoeal skin. This is another case of the temporary loss or reduction of appendages in larval life.

In the Caridea the prezoeal skin simply covers the appendages without having any of the setae found in the Brachyura, though the telson has six pairs of large feathered setae. Generally the cuticle is shed at, or immediately before, hatching, and no case is known in which the Prezoea has the power of swimming before the moult.

In some Anomura the prezoeal stage is well marked, *e.g. Lithodes* (Sars), *Porcellana* (Gurney, 1926). In a Samoan species of the latter the scale of the antenna is remarkably developed, with seven large setae, though it is reduced and without setae in the free Zoea. In this case, as the specimens were taken in the plankton, it is clear that the Prezoea has the power of swimming as it has in *Jasus* and some Brachyura.

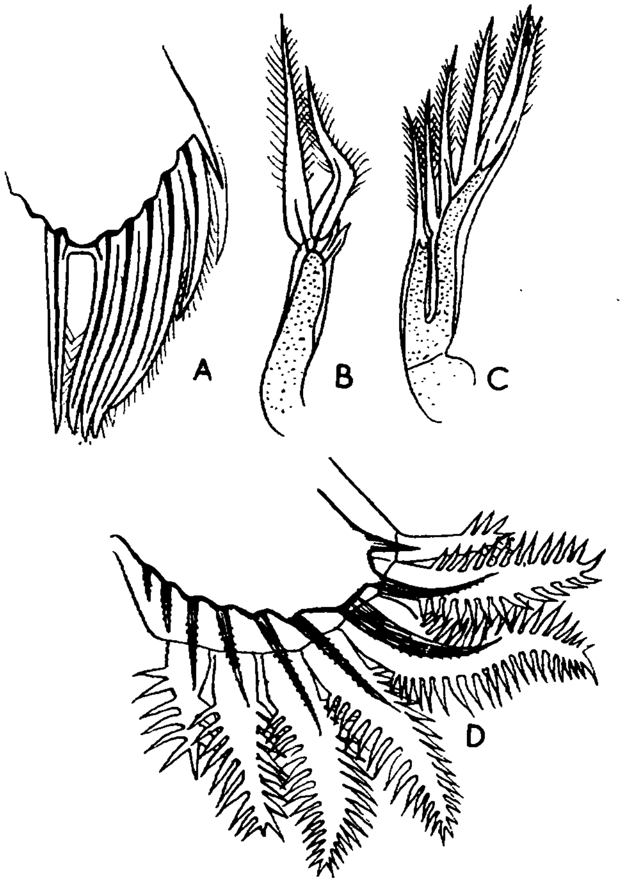

Fig. 14.—Embryonic cuticle. A. *Porcellana longicornis*, telson. B. *P. longicornis*, antennule. C. *P. longicornis*, antenna. D. *Lithodes maia*, telson.

I am informed by Miss Lebour that the Prezoea of both the British species of *Porcellana* swims actively.

ABBREVIATED DEVELOPMENT.

It may be said that whenever eggs are carried in a brood chamber, part of larval development has been compressed within the embryonic phase, since the Nauplius stage is invariably passed through in the egg. The amount of yolk stored in the egg has naturally a great influence on the course of development, since the greater the amount of yolk the more free larval life is curtailed. The size of the egg in proportion to the size of the adult gives therefore some indication of the degree of such shortening. Where larval development pursues its normal course the eggs are up to about one hundredth of the parent's length, but, with increase of yolk, they may reach one seventeenth (*Pasiphaea tarda*) or even one ninth (*Eiconaxius kermadeci*).

In the following table the size of the eggs and the size in comparison with the length of the parent are given for a number of species. In some cases the proportion of egg to parent may be only approximately correct, as the size of the actual egg-bearer is not always given, and I have had to make use of published measurements, which may be greater or less than they should be. Where my own initials are placed against the measurements the actual bearer of the eggs was measured. A further error is introduced by including the rostrum in those species in which it is very long: but the table, none the less, serves to show that a mere statement of the size of the egg is apt to be misleading.

It becomes clear also that, although such measurements do give a useful hint as to the probability of development being curtailed, they cannot be taken as conclusive. For instance, the egg of *Chlorotocella* is relatively but little smaller than that of *Synalpheus laevimanus*; but the latter has its development greatly abbreviated, whereas there is a complete series of larvae in a Red Sea species of *Chlorotocella* (Gurney, 1937*c*). On the other hand, the differences between species of

	Size of egg in mm.	Ratio of egg to length of adult (approximate).	Author.
Acanthephyra purpurea	·82×·64	82*	R.G.
Acanthephyra armata	·8	211	De Man
Systellaspis debilis	3·65×2·45	15*	R.G.
Hoplophorus grimaldii	3·2×1·9	12*	,,
Pasiphaea tarda	3·4–3·9×3	17	Kemp
Pasiphaea princeps	5×4	26	,,
Parapasiphaë sulcatifrons	3·7×3	17	,,
Atyaëphyra desmaresti	·6×·4	66	Gauthier
Paratya compressa	·8×·5	37	Yokoya
Caridina simoni	·94×·8	36	R.G.
Troglocaris schmidti	1·25×·9	14·8	Fage
Pandalus borealis	1·15×·95	78*	R.G.
Pandalina brevirostris	·4×·37	85	,,
Chlorotocella gracilis	·6×·5	25	,,
Hippolyte varians	·56×·44	48	,,
Spirontocaris rectirostris	·6×·4	54	De Man
Chorismus antarcticus	1·7×1·3	31	R.G.
Hippolysmata vittata	·6×·4	55	,,
Thor paschalis	·47×·4	27	,,
Palaemon sundaicus	·55×·47	127	,,
,, *lar*	·7×·55	157	,,
,, *jamaicensis*	·58–·64 ×·47–·49	171	,,
,, *cavernicola*	2·0×1·5	22·5	,,
,, *pilimanus*	1·49–1·6 ×1·04–1·2	19·4	,,
,, *quelchi*	2·46–2·68 ×1·8–2·0	16·8	,,
Palaemonetes exilipes	1·45×1·1	25	,,
,, *punicus*	1·7×1·2	19	,,
,, *varians* (Norfolk)	·9×·8	36	,,
,, *varians lacustris*	1·35×1·06	32	,,
Periclimenes americanus	·6×·45	33	,,
Alpheus ventrosus	·95×·7	36	,,
,, *villosus*	3·0	13	Coutière
Synalpheus laevimanus	·75	23	,,
Crangon agassizi	2·1×1·6	..	R.G.
,, *antarcticus*	1·4×1·4	44	,,
Philocheras fasciatus	·56×·46	37	,,
Pontophilus incisus	·45–·49×·4	29	,,
Richardina spinicincta	2·0×1·34	10·7	,,
Axius stirhynchus	2·3×1·2	15	,,
Eiconaxius acutifrons	1·3×1·0	16	,,
,, *parvus*	1·46×·95	8	,,
,, *kermadeci*	1·7×1·3	9	,,
Upogebia simsoni	·57×·51	61	,,
,, *pseudochelata*	·68×·6	18	,,
,, *savignyi*	1·0	35	,,
Callianassa stebbingi	·9×·67	55	,,
Callianidea typa	·75×·5	51	,,
Calocarides coronatus	1·5	31	Trybom

Measurements marked * are without rostrum.

Crangonidae and Palaemonidae in respect of the degree of development at hatching comes out clearly.

Such large eggs, with correspondingly abbreviated larval life, are found in most groups of Decapoda, but there is no clear connection between habitat and duration of larval life, nor does systematic relationship necessarily imply similarity of development. In the genus *Acanthephyra* the eggs are small, and the first larva of a simple type, whereas in *Systellaspis*, a genus at one time thought to be synonymous with *Acanthephyra*, the eggs are very large and the larva hatches with its body full of yolk, and with most of its appendages present. The same is true of the nearly allied genus *Hoplophorus*, and yet all three genera live under more or less the same bathypelagic conditions. Larvae of *Acanthephyra* may be found at, or very near to, the surface, whereas those of *Systellaspis* and *Hoplophorus* are only to be taken at depths of more than 200 metres.

There is a striking difference between the larvae of *Palaemonetes varians* and those of *P. varians lacustris* (Boas, Sollaud), and, within the genera *Alpheus* and *Synalpheus*, there is every gradation from nine stages in *A. ruber* (Lebour) to complete suppression of the larva in some species of *Synalpheus*. In the genus *Upogebia* there are normally four stages, but, in *U. savignyi*, the young are almost of adult form when hatched (Gurney, 1937*a*). In this case the habitat is peculiar, inasmuch as the species lives in passages in a sponge, but all species of *Upogebia* live in burrows of some kind, and so great a difference in development cannot be attributed to such a difference in habitat.

Abbreviation in development is, perhaps, more common among arctic and antarctic or deep-sea Decapoda. Among the Hippolytidae free larval life is entirely suppressed in the northern genera *Bythocaris* and *Cryptocheles* (Sars), and it is greatly shortened in *Spirontocaris polaris* and *Chorismus antarcticus*. In other Hippolytidae, even within the genus *Spirontocaris*, larval life extends through as many as nine stages

(Lebour). In the Crangonidae there are five stages in normal development, but in *Sabinea* there are only three and in *Sclerocrangon* the young hatch in the adult form (Sars, Wollebaek).

The tendency to suppression of the free larva is very marked in other arctic invertebrates. Thorson (1936) found that, out of about 200 species of Polychaets, Echinoderms, Molluscs and Crustacea of north-east Greenland 95 per cent. had large yolky eggs and no pelagic larval stages. Thorson pointed out that the period of production of phytoplankton in arctic regions is very short, so that a restriction of larval life is necessary. If all had free larvae in this short period competition would be too fierce.

The Brachyura of the arctic regions are not influenced in the same way as the Caridea (Doflein, 1904), and the same seems to be true to a less extent of the abyssal regions. Among the Brachyura development without metamorphosis is extremely rare. It appears to be the rule among the fresh-water family Potamonidae, but in *Cardisoma* (Gecarcinidae), which is a land crab which can be kept and fattened in cages, and in the Robber Crab (*Birgus*), the parent goes down to the sea to hatch the eggs. The only marine Brachyuran which is known to hatch in adult form is *Paranaxia serpulifer* (Oxyrhyncha) (Rathbun, 1914) ; but among the Dromiacea such direct development is known in three genera—*Petalomera*, *Cryptodromia* and *Platydromia* (Hale, 1925, 1927).

In the Caridea of fresh water abbreviation is common ; but here again no general rule holds good. For example, among the Atyidae there are species with a long series of larvae, such as *Atyaëphyra desmaresti* and *Caridella*, and others in which development is shortened. Even within the same species, *Caridina nilotica*, different races have the eggs of different sizes, and consequently hatch in a more or less advanced condition (Gurney, 1927, p. 252). The larva is never, so far as is known, entirely suppressed, but it appears that in *Ortmannia* *edwardsi* there is only one free stage (Bouvier). In the Palaemonidae development seems never to extend over more than seven stages (except perhaps in the larval genus *Retrocaris*), and every gradation from such a series can be found among the species from brackish and fresh water (Sollaud, 1923). Even in the genus *Palaemon*, in which the eggs are commonly large, there are species (*e. g. P. jamaicensis*) in which they are quite small, and presumably there is then a normal series of free larvae. This is now known to be the case in *P. rudis* and *P. carcinus* (Menon, 1938). Two species of Alpheidae are known from fresh water, *Alpheopsis haugi* and *A. monodi*, and both of these have small eggs (Sollaud, 1932*a*). Other species of the genus are marine and live at a considerable depth.

Doflein (1904) has paid particular attention to the size of the eggs of deep-sea species, and has noted that those with reduced eyes have large eggs and hatch in an advanced condition, while those with normal eyes have small eggs and normal larvae : " Wenn wir nun die Formen mit grossen Eiern denjenigen mit kleinen Eiern, oder mit anderen Worten, die Formen ohne Metamorphose den Formen mit Metamorphose gegenüberstellen, so erkennen wir, dass die beiden Gruppen sich je aus denselben Formen zusammensetzen, die wir bisher zu einer ganzen Reihe von Eigenschaften vereinigt fanden ; die Formen mit Metamorphose sind die beweglichen Arten mit gut Gesichts- und Gleichgewichts-sinnesorganen, ohne Schutzanpassungen besonderer Art und ohne hoch entwickeltes Geruchsorgan ; die Formen mit direkter Entwicklung dagegen haben rückgebildete Augen, mässig entwickeltes Gleichgewichts-sinnesorgan, viele Tasthaare, lange Antennen, hoch ausgebildetes Geruchsorgan, es sind wenig bewegliche Formen mit Schutzanpassung oder Maskierung " (p. 259). An example of the species with small eggs is *Geryon affinis*, a crab of very deep water. Doflein's rule is not without exceptions outside the Brachyura, since species of *Polycheles*, a typical deep-sea genus with reduced eyes, may have very numerous small eggs ; but nothing is known about its larva when first hatched.

Cuénot (1911, p. 306) considered that the special characters possessed by fresh-water species which are regarded as adaptive—euryhalinity, absence of pelagic larva, etc.—were already manifested in their marine ancestors : " Parmi les innombrables formes maritimes en voie d'extension, seules sont entrées dans l'eau douce, dans les temps passés comme de nos jours, celles qui réunissaient par hasard les préadaptations indispensables ; c'est l'eau des estuaires qui a effectué la sélection en arrêtant comme un filtre les espèces non aptes a la pénétration." The truth of such a postulate is to some extent self-evident, since it is obvious that a species could not take the first step into fresh water without being euryhaline already ; but there is no need to suppose that the invasion could not be effected without preadaptation with regard to the eggs. Species such as *Leander longirostris* are able to penetrate long distances up rivers and to live in perfectly fresh water although their eggs cannot hatch or their larvae survive in fresh water. In such cases the final step to complete adaptation, if it were ever taken, would be long after the original entry. A similar case is that of *Eriocheir sinensis*, a crab which is itself able to live in fresh water and has penetrated of recent years into the heart of Europe ; but it has to return to the sea to liberate its larvae. The common crab, *Carcinus maenas*, is able to tolerate most exacting conditions of temperature and salinity, but cannot bear, even as adult, anything approaching fresh water.*

Among the Macrura Reptantia and Anomura the larval stages are usually few, and there is marked abbreviation among the Axiidae ; but complete suppression of the larva is only known in *Upogebia savignyi*. Hale (1927) states that the young of *Axius plectorhynchus* hatch in adult form, and cling to the pleopods of

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* For a discussion of the salinity limiting development in *Carcinus* see Broekhuysen, 1936, p. 100.

the parent; but the observation requires confirmation (Gurney, 1938*c*, p. 303)

Abbreviated development presents certain features of special interest. In free larval life the struggle for existence has full play, and may result in the loss or modification of structures, whereas if a stage once free is relegated to the embryonic phase structures now useless may still be developed in simplified form. Thus certain characters of the Nauplius are still retained in the embryonic cuticle, though they are generally lost (see p. 50).

The primitive course of development through Nauplius, Protozoea and Zoea has imprinted itself so deeply that it is hardly ever completely obliterated, and it is exceedingly rare for the young to hatch actually in the adult form. In the case of *Astacus*, although the appendages are, for the most part, built on the adult plan, and the young remain attached to the parent until fully formed, the uropods do not appear until the second moult, and it is quite clear that the first three stages correspond to the three first stages of the normal free larva. However much larval life is suppressed the young almost always hatches without uropods and with the telson in larval form, and passes through two moults before reaching the final post-larval form. When the young hatch with all the appendages of the adult except the uropods, as in some Palaemonidae, they have still some of the characters of the normal first stage, such as sessile eyes and unsegmented antennule, while no appendages behind the maxillipedes are functional, and the maxillipedes are of larval form. In *Chorismus antarcticus*, where there are only three free stages, the first larva retains traces of segmentation in the antennal scale, and even the arrangement of setae on the exopods is that of the normal free larva.

Coutière (1907*c*, p. 62) suggests that the occasional cases of condensed development may be examples of the reappearance of a mode of development normal in Mysidae and Lophogastridae; but it is fairly obvious that it cannot be accounted for by any relationship to these groups.

It appears that increase of yolk in the egg, leading to extension of embryonic life, may occur quite sporadically, for reasons beyond our speculation. All that can be said is that abbreviation of larval life is more usual among land and fresh water species, and, to a less extent, among those of the arctic and antarctic regions and of the deep sea.

REPRODUCTION OF DECAPODA OF LAND AND FRESH WATER.

Allusion has already been made to the strong tendency among fresh-water species to abbreviation of development, which may lead to total suppression of the free larva, but such abbreviation is by no means general.

The family Atyidae is a primitive one, now confined to fresh water, but none the less some species (*Atyaëphyra desmaresti, Caridina nilotica*) have a normal series of free larvae. Among the Palaemonidae of fresh water many have large eggs and shortened development; but others have small eggs and normal larvae. Whether any of these can develop in fresh water is not certainly known. Kemp (1915, p. 272) considered that *Palaemon rudis* migrated to Chilka Lake from the flooded rice fields during the period of fresh water in the lake in autumn, for the purpose of hatching the eggs, with the inference that development took place in the lake itself. That this conclusion was justified is not certain. Egg-bearing females were also taken in the outer channel near the sea, and in March the young were abundant in the channel in water as salt as the Bay of Bengal. The possibility that the adults migrate further and hatch their eggs in the sea is not excluded. Menon (1938) has described normal Zoeas in *Palaemon rudis* and *P. carcinus*, but here again there is the possibility that development normally takes place in the sea. He states that the egg-bearing females were taken in "backwaters" near Ernakulam on the coast of Travancore, and that the larvae were hatched in brackish water. It is certain that the river prawn *Leander longirostris* in this country migrates to the sea in the breeding season (Gurney, 1923*a*, p. 113).

Some species of *Penaeus* and *Metapenaeus* inhabit estuarine waters or lagoons connected with the sea, but return to the sea to breed. The young pelagic form of *P. carinatus* is carried up the Ganges by the tide and "settles down in weedy pools and backwaters many miles from the sea" (Kemp, 1915, p. 319). On the coast of New South Wales *P. plebejus* is caught in large numbers in estuaries and lagoons, but it breeds only in the sea (Dakin, 1938).

It is most probable that *P. canaliculatus* and *P. monoceros* which abound in Lake Menzaleh in Egypt migrate to the sea to spawn as certain fish from the lake do. On the other hand *Metapenaeus stebbingi* breeds in the Bitter Lakes of the Suez Canal, where the water is more saline than that of the sea (Gurney, 1927).

It is interesting to note that the Grey Mullet (*Mugil capito*) introduced into Lake Qarun in Egypt has apparently begun to breed there in water of a salinity of 17–22 parts per 1000. Possibly *Penaeus* introduced there might also establish itself (Wimpenny and Faouzi, 'Nature,' 1935).

The Robber Crab (*Birgus latro*) is known to go down to the sea at the breeding season and to have a normal marine larva (Harms, 1937).

Some land crabs have a normal Zoea, and their migrations to the sea have long been known (see Couch, 1845, p. 23; Stebbing, 1893, p. 80; Calman, 1911, p. 190). In 1750 Hughes, in his 'Natural History of Barbados,' described the migration to the sea of the "Red Land Crab" thus: "These crabs, after a heavy shower of rain in the months of March, April, and May, are to be seen in great numbers, loaden with spawn, going down to the seaside to deposit it in the sand, near the wash of the water, and soon afterwards to return into the country."

The genera *Gecarcinus*, *Gecarcoidea* and *Cardisoma* are known to have normal Zoeas.

Probably all genera of the Potamonidae, on the other hand, have direct development, the young being hatched in the form of the parent and carried for a time under the abdomen. So far as is known the young have no special modification of the limbs for clinging to the parent. I have myself seen newly hatched young of a West African Potamonid, and could find no such modification. The chelae, however, are so fully developed that they would be quite adequate for the purpose of attachment.

In the fresh-water crayfish (*Astacus*) the young, when first hatched, remain for a short time attached to the parent by a filament. This filament is the moulted embryonic cuticle which remains adherent to the telson on the one hand, and to the empty egg-case on the other. When this cord breaks the young animal clings to the pleopod of the parent by means of the chelae of leg 1, which are hooked at the end for this special purpose. This double means of attachment seems to be general in the northern Astacidae; but in the crayfishes of Australia and South America (Parastacidae) the claws of legs 4 and 5 are modified, and the animal attaches itself by these legs instead of by leg 1. In *Cheraps preissii* (from Australia) I have seen a filament of attachment between telson and egg-case in some specimens; but it appears to be ineffective and perhaps only momentary. Legs 4 and 5 seize the hairs of the pleopods immediately after hatching. In the South American *Parastacus pilimanus* there is a similar attachment by legs 4 and 5, but leg 1 is also used, and has incurved spines on the chela for the purpose. There seems to be a fundamental distinction between the two families of crayfish in their method of attachment, which suggests that they have become independently adapted to fresh water (Gurney, 1935).

In the arctic Caridean *Sclerocrangon ferox* the young hatch in the same condition as in *Astacus*, and legs 4 and 5 are very strong and armed with claws at their ends for clinging to the parent (Wollebaek, 1906, see p. 222).

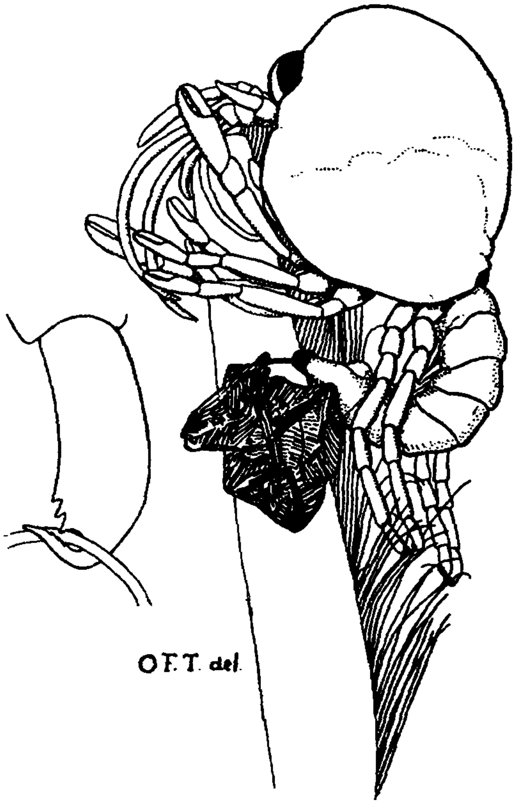

FIG. 15.—*Cheraps preissii.* Young attached to parent, and claw of leg 4 enlarged.

POECILOGONY.

Boas (1889) first drew attention to the fact that *Palaemonetes varians* has a different mode of development according to its habitat, the form which lives in brackish water in northern Europe having small eggs and a normal larva, while that which inhabits fresh water in the Mediterranean region has very large eggs, from which hatches a larva with all the appendages of the adult, and also with fewer exopods. Boas stated, and it was for a long time accepted as a fact, that there was no specific difference between the *Palaemonetes* of brackish water and fresh water, and it was generally held that this was an excellent example of poecilogony, perhaps directly due to the influence of the conditions of life.

Sollaud (1912*c*) has made known a new form from Tunisia which he described as *P. varians mesogenitor*, and a fourth was found by Pesta in Mesopotamia. In the Tunisian form all the appendages are present on hatching, and the legs have no exopods (Sollaud, 1923*b*, p. 590). Closer examination of the adults (Sollaud, 1924) shows that each form is distinguished by quite definite, if small, characters, the Tunisian form indeed being so distinct as to be rightly separated as a species, *P. punicus*, Sollaud. (See also Gurney, 1923, p. 131.) Sollaud therefore treated these forms as systematically distinct, thus:

P. varians occidentalis, Sollaud = *P. v. microgenitor*, Boas. Brackish water in northern Europe.

P. varians lacustris, v. Martens = *P. v. macrogenitor*, Boas. Fresh water in south Europe.

P. varians mesopotamicus, Pesta.

P. punicus, Sollaud = *P. v. mesogenitor*, Sollaud.

Poecilogony, in the sense of a different mode of development among individuals which are not systematically distinguishable, does not, therefore, really exist, and there is no reason to suppose that acclimatization and maintenance of the northern form in fresh water would lead, within any practicable period, to any change in the mode of reproduction.

Much the same may be said of the supposed poecilogony in Alpheidae. Brooks and Herrick (1892) claimed that the same species, *Alpheus saulcyi*, in different localities produced eggs of different sizes, and larvae correspondingly more or less advanced. Coutière (1899), while showing that Brooks and Herrick were actually dealing with distinct species, himself claimed that poecilogony was common in the genus *Synalpheus*, and not unknown in *Alpheus*. He said (p. 444), " on rencontre dans la même espèce a la fois les deux modes de développement, so bien que la poecilogenie, exceptionelle chez *Alpheus*, parait être devenue ici un processus normal." His own later work, however, led him to appreciate specific differences where he had previously regarded the individuals as of one species, and it is very doubtful if any case can really be shown to exist of individuals structurally the same having a different mode of development.

Coutière has suggested (1900, pp. 254, 314) that *Palaemon sintangensis*, De Man, from rivers in the centre of Borneo, may be a poecilogonetic form of *P. ritsemae*, De Man, from "more littoral" localities in Java and Madagascar. The former has large and the latter small eggs. Similarly *P. trompi*, De Man, with large eggs may be the same species as *P. superbus*, Heller, with small eggs.

Alcock (1901, p. 110) remarks of *Dorodotes reflexus* (Pandalidae) that the eggs are of two kinds, small brown ones and large pink ones. Presumably these are on different females, but it is not so stated. Stebbing (1914, p. 45) noted eggs of two kinds in *Nematocarcinus lanceopes*.

The only other example of possible poecilogony of which I am aware is that of *Spirontocaris gaimardi*. In this species the eggs of specimens from arctic localities (Greenland) are larger than those from boreal regions (Denmark) according to Thorson (1936, p. 68). In this case the larva hatched from a Scottish parent has been described (Lebour, 1940), but we do not know in what form the arctic representatives of the species leave the egg.

Edmondson (1929, p. 16) states that Atyidae when hatched in standing water in the laboratory pass through a free-swimming Zoea stage; but that if hatched in a strong current of water the "Zoea stage seems to be passed in the egg, as the young are released in the Mysis form." The species in question are not named, nor is any information given as to the size of the egg.

Poecilogony may be said to exist in *Caridina nilotica*. Bouvier, in his revision of the Atyidae (1925), divides the species into 14 varieties, some of which had previously been regarded as distinct species, and among these there are four—*typica*, De Man, *macrophora*, Kemp, *paucipara*, Weber, and *aruensis*, Roux—in which the eggs are conspicuously large. Within the same variety, *gracilipes*, there are differences in size of the eggs accompanied by differences in development (Gurney, 1927, p. 252); but nothing is known about the larvae of any of the other forms. Weber stated that his var. *paucipara* may occur in company with a form with small eggs of the var. *gracilipes*, and he drew attention to the parallel example of *Palaemonetes varians* as described by Boas. Bouvier states that var. *paucipara* abounds in Madagascar—" ou elle passe insensiblement à la forme typique." It is therefore true that poecilogony exists within the species *C. nilotica*, and it would seem that it may be impossible to distinguish by any other structural features the races bearing large eggs from those bearing small ones. It would be of interest if we could have observations on the spot of the biology of these forms.

DIMORPHISM.

The two Euphausid species, *Rhoda inermis* and *Thysanoessa neglecta* are now regarded as dimorphic forms of the same species *Thysanoessa inermis* (Lebour, 1926). The larvae of these two forms have been studied by Miss Lebour, who found that they could not be distinguished with certainty until the " 11th Furcilia " (with all pleopods setose), when the differences in the relative length of the legs which distinguish the adults became apparent. She found a very small difference in the shape of the telson in younger stages by which they could generally be separated.

Miss Webb (1919) distinguished two " classes " of larvae in *Upogebia deltaura* and *U. stellata*. Her class B differed from class A in stage 2 in being larger and in having more setae on the exopods of legs 1 and 2, while in stage 3 they were very much more advanced in the development of the legs, and moulted direct to post-larval. She suggested that this difference might be one of sex. I have examined large numbers of *Upogebia* larvae at Plymouth and have not found these classes to be sharply marked. Undoubtedly there are great differences in size and development between the smallest and the largest specimens in stage 3 (see Fig. 99, p. 247), and the largest do certainly moult to post-larval; but there are, in my own experience, so many transitional specimens that I cannot regard the facts as indicating more than an exceptional range of variability. The proportion of class B to class A was, in my material, much too small to permit of this being regarded as a case of sexual dimorphism. If any considerable proportion of the population consisted of class B, moulting direct to post-larval, the number of larvae in stage 4 should be, by that proportion, less than the number in stage 3. The actual numbers found in samples in which the two species were not distinguished were:

Stage 1	Stage 2	Stage 3	Stage 4	Total
48 .	60 .	58 .	94 .	260

ARTIFICIAL REARING.

It is easy to obtain the first larva by hatching from the egg, and it is not as a rule difficult to keep a larva alive during the time necessary for it to pass through a single moult, and in this way to follow the succession of stages; but it is very difficult to keep them alive for any length of time. It is essential that they should be kept at a low and even temperature, prevented from sinking to the bottom, and provided with adequate and suitable food. The moult is the critical period, and any loss of vitality at this stage leads inevitably to death. Overcrowding, with insufficient food, may cause great mortality, owing to the cannibalism of the larvae and the fouling of the water by dead bodies. The many experiments in lobster rearing made in Norway, the United States, Port Erin and elsewhere have resulted in methods of rearing this particular larva with success,* but it must be remembered that the larval life of the lobster is a short one, completed in three moults, so that the difficulty is not so great as it is for species less robust and with a longer larval life. At Wickford, Rhode Island, the lobster larvae are kept in large floating wooden boxes, in each of which a two-bladed wooden paddle rotates horizontally (see Barnes, 1911). It is found to be of the utmost importance that the current so caused should be of exactly the right strength to keep the larvae and their food moving without being strong enough to wash them against the sides of the box. The best food is found to be pulverized hens' eggs, but clam (*Mya*) meat is nearly as good. At Millport plankton, or ground-up crab, was used.

In the laboratory the "plunger jar" has proved most successful at Plymouth. In 1904 a number of larvae of *Pandalina brevirostris* were reared successfully up to the second post-larval stage, and *Portunus holsatus* from a late Zoea to a crab an inch across; but these were chance successes, and failure was the general rule. Miss Lebour has, however, brought this method of rearing to a point at which success is frequent rather than exceptional. She finds that in rearing crab-larvae living and moving food is very much preferred, and early larvae of the oyster provide the best diet. Larvae of echinoderms and worms obtained by artificial fertilization have also been used. She has found (1922) that the normal food in nature consists mainly of diatoms, of which the favourite genus is *Coscinodiscus*. Remains of larval molluscs and echinoderms were often traced among the diatoms. Later, unpublished, observations have shown that much débris is taken. On the other hand lobster larvae and Phyllosomas at all stages, and

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* The first successful experiments in rearing lobsters appear to have been made by Saville Kent in 1875.

the Megalopa stage of crabs, are carnivorous and feed upon Decapod larvae, Copepods or even young fish.

Miss Lebour informs me that she now regards animal food as essential for crab larvae. Diatoms are taken with the animals. The best rearing experiments were those in which the plunger jar contained diatoms, but living food was also given.

Remarkable success has been obtained by Mme. Heldt (1938) in rearing Penaeid larvae, using plankton as food. She fed the first Protozoea on the nauplii of Copepods hatched in the laboratory. An excellent source of food which has recently come into use is the larvae of *Artemia*, the eggs of which can be bought, and will hatch in normal sea water.

Larvae which hatch with some yolk still in the body will live easily so long as the yolk lasts. I found in Bermuda that the Nauplii of the Penaeid *Sicyonia* suffered very little mortality, but, as soon as they had moulted to the Protozoea, they all died off in a few hours.

Some species are very much more robust than others. For instance the larvae of *Lysmata intermedia* lived through several moults without difficulty, whereas those of *Brachycarpus biunguiculatus* all died in stage 2 under exactly the same conditions.

A certain amount of caution is necessary in accepting a series of stages as determined under artificial conditions as normal. I have found myself in the case of *Palaemonetes varians* that abnormal intermediate stages may be obtained in captivity (Gurney, 1924*a*), and the same appears to have been the case in Gauthier's artificially reared *Atyaëphyra* (Gauthier, 1924).

On the other hand, building up a series of stages from plankton material may not necessarily give a true picture, since it does not follow that a larva must pass through all the stages which can be distinguished. Where a long series of stages is found, as in *Palinurus* or *Processa*, it is desirable that it should be checked by keeping larvae through a moult to see if, for example, stage 7 does actually follow stage 6, or may arise from stage 4 or 5. In *Scyllarus* I have found that one of the stages established by Stephensen may be skipped, and in *Upogebia* Miss Webb has shown, and I can confirm her observation, that either stage 3 or stage 4 may moult to post-larval.

GIANT LARVAE.

Among the species of Decapoda of which the larval history is known larval life ends, as a rule, before any great size has been reached, and the discovery of pelagic specimens which retain certain larval characters at a size of 20 millimetres or more has given rise to the suggestion that these are larvae which have been carried far from their normal habitat, and have continued to grow without transforming to the adult structure. Bouvier (1905) has adopted this explanation for the large Pagurid larvae known as Glaucothoë, and Coutière (1907*b*) concluded that this explanation is necessary for such giant larvae as *Atlantocaris* and *Icotopus amplissimus*. Coutière suggested that the cause of the continued larval growth might be, not the external conditions, but an internal cause connected with delay in the maturation of the gonads.

The following table gives the size of a number of larvae of known parentage as compared with the adults, and it will be seen that the size of the larva bears very little relation to that of the adult. Whereas in some cases the larva is only about one-fifteenth the size of the adult (*Crangon vulgaris*) in *Caridion gordoni* and *Stenopus hispidus* it is about half.

In absolute size the largest larvae of known parentage and belonging to littoral species may reach the very respectable length of 30 mm. (*Pandalopsis dispar*).

In nearly all larvae of known species there is a marked difference between the last larva and the post-larval form. This is most strikingly the case in *Stenopus*, but it is true also, to a less extent, even in such a genus as *Pandalus*. On the other hand, some of the "proble-

Table showing Length of Larva as Compared with that of the Adult.

	Length of larva (in millimetres).	Length of adult (in millimetres).	Adult : larva.
Heterocarpus ensifer	53	87	1·6
Tozeuma sp.	31	—	—
Stenopus hispidus	31	50	1·6
,, ,,	21 (Lebour)	—	2·4
Pandalopsis dispar	30	215	7·0
Pandalus danae	17	55–114	3·0–6·6
,, *platyceros*	16	214	13·4
Pontophilus spinosus	16	64	4·0
Acanthephyra purpurea	13·4	103	6·7
Caridion gordoni	11–13	17–27	*ca.* 2·0
Processa canaliculata	9·5	68	7·1
Alpheus ruber	9·0	43	4·8
Caridion steveni	8·0	20–27	*ca.* 3·3
Leander longirostris	7·5	50–77	*ca.* 10·0
Palaemonetes varians	7·2	29–43	*ca.* 6·0
Crangon vulgaris	4·75	70	14·7

matical" Caridean larvae of the deep sea, while most clearly larval, have a solidity which one associates with maturity, and they also may have a form of rostrum and carapace which is more appropriate to the adult. For example *Procletes* (*Atlantocaris*) *gigas* reaches a size of 53 mm., and combines with obvious immaturity a form of carapace which is identical with that of *Heterocarpus.* Coutière suggested that it might be the larva of *Thalassocaris*, while Lenz and Strunck (1914) considered that the possibility of its reference to *Acanthephyra* could not be excluded. Ortmann also could only suggest that it might belong to some genus of Hoplophoridae. It can, I believe, be definitely proved that *Atlantocaris gigas* is the normal larva of *Heterocarpus ensifer* (Gurney and Lebour, 1941), and, if this, the largest known larva, can be satisfactorily disposed of, it is only a question of time before all others will be linked up with their appropriate adults.

Certain other large larvae, of unknown species, taken by the "Discovery," are so nearly mature that the *appendix masculina* of the male can be seen, although the legs and mouth parts are still in a larval condition. It may be noted here that, if this precocious appearance of sexual characters were so accentuated that sexual maturity occurred before metamorphosis, we should get at one step a new Decapod group the relationship of which would be most obscure, for the onset of maturity would almost certainly check any further bodily changes.

The contrast between the advanced development of some parts and the retardation of others in some of these forms is most marked. While, in such forms as *Leander*, the chelae of legs 1 and 2 may be traceable in stage 3, and are almost fully formed in the last larva, in some of the giant larvae there is no trace whatever of a chela on either leg, and even in *Atlantocaris* at a size of 40 mm. leg 1 has no chela at all, while that of leg 2 is exceedingly small.

In littoral forms there is considerable freedom as to the number of stages after stage 3, and it would not be surprising if the pelagic forms pass through a long series of larval moults and attain finally to structural and sexual maturity simultaneously or nearly so.

It seems probable that these large larvae may be of two kinds. Some, such as *Atlantocaris*, are those of deep-sea genera in which the change from larval to post-larval life involves no very great change of habit and none of habitat. Consequently there is nothing except the onset of sexual maturity to bring larval life to an end. Their size would then be perfectly normal, and metamorphosis would only take place after a long series of larval moults.

The position is much the same with the Stomatopoda. While the few littoral species of which the development is known have larvae of moderate size, some are known of very great length, *e.g. Alima hyalina* 50–54 mm., *Pseuderichthus elongatus* 47 mm. Hansen (1895) stated that there is no ground for regarding these as in any way abnormal, since it is only in the very largest individuals that the spines on the dactyl of maxillipede 2, which are an infallible indication of approaching metamorphosis, can be seen.

Until very recently there was no direct evidence for Coutière's and Bouvier's theory of " abnormality," but it is now proved that the larvae of some littoral species may grow to sizes very much larger than that at which metamorphosis normally takes place. The following examples are known :

(1) *Stenopus hispidus :* Miss Lebour (Gurney and Lebour, 1941) has obtained the post-larva from a larva of 21 mm. ; but lengths of over 30 mm. have been recorded.

(2) *Rhynchocinetes rigens :* The last larva, from which the post-larva has been obtained several times by moult, is about 8 mm. ; but others have been seen of over 14 mm. (*ibid.*, p. 119).

(3) In *Brachycarpus biunguiculatus* the larva goes on growing and moulting after having reached its final form. At present only one moult to post-larval has been obtained, from a larva of maximum size (*ibid.*, p. 142) ; but it is most probable that much smaller specimens may moult to post-larval.

(4) I have a larva of about 30 mm. from the neighbourhood of Bermuda (" Atlantis " station 1121) which appears to be an *Eretmocaris* which has grown far beyond the normal size of 6–8 mm. As the last legs are missing the identification is not beyond question, but I have no doubt myself, and would even suggest that it belongs to *Lysmata intermedia.*

This larva is so far advanced that there is a rudiment of the *appendix masculina* on pleopod 2.

As the largest *Brachycarpus* transforms to a perfectly normal adult form so, in all probablity, would all these larvae ultimately do, and in that sense they cannot be called abnormal. After reaching the stage at which metamorphosis normally occurs these larvae continue to grow without any important change in structure. Similarly the larva known as *Eretmocaris dolichops* has been seen to moult without any change whatever (Gurney and Lebour, 1941). The *Eretmocaris* mentioned above is an exception, since there are marked differences in the rostrum and some other parts from the oldest larva of *Lysmata intermedia* known.

I have been reluctant to accept any theory of abnormality (Gurney, 1924, p. 186), but, in view of these facts, it seems necessary to suppose that these large larvae of littoral species are abnormal in the sense that they have failed to metamorphose at the proper moment and have continued to grow. If this failure is due to their having been carried too far out beyond the littoral region we have to assume some sort of "depth-sense" which acts as an inhibitor of metamorphosis. On the other hand, in a situation like that of Bermuda, where abyssal depths are so close to the shore, it must be quite usual for larvae to find themselves over deep water at the time of metamorphosis. It is very desirable that the fate of these larvae should be further investigated, and the opportunity for doing so is offered at Bermuda.

CHROMATOPHORES AND COLORATION.

The systematic importance of the distribution of the chromatophores was made known by Keeble and Gamble (1904). They found that, in Mysidae, the chromatophores were arranged in three series :

(1) Neural group ; segmentally arranged in relation to the ganglia.

(2) Visceral group.

(3) Caudal group.

(4) Accessory group.

Nos. 1–3 constitute the primary system, the chromatophores of which are recognizable in the embryo (Fig. 16) and are specifically constant in number and position.

So constant are they that species otherwise separable with difficulty may be easily distinguished by their chromatophores. The accessory group is of very small importance in contributing to the colour pattern of the Mysidae, but becomes greatly developed in Decapoda. In them the primary group, homologous with that of the Mysidae, is retained throughout life and is conspicuous in the larva ; but the secondary system, homologous with the accessory system of the Mysidae, which is represented by but few chromatophores in the early Zoea, finally masks the primary system and is entirely responsible for the coloration of the adult. They found that the Euphausiidae in respect of their chromatophore

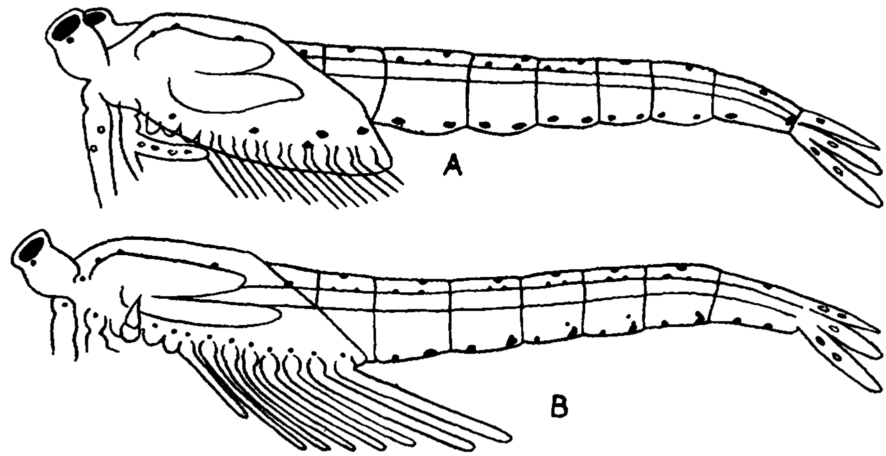

FIG. 16.—Embryo of *Macromysis neglecta* (A) and *M. flexuosa* (B), showing specific differences in the distribution of chromatophores. Primary chromatophores thus, ● ; secondary chromatophores thus, o. After Keeble and Gamble.

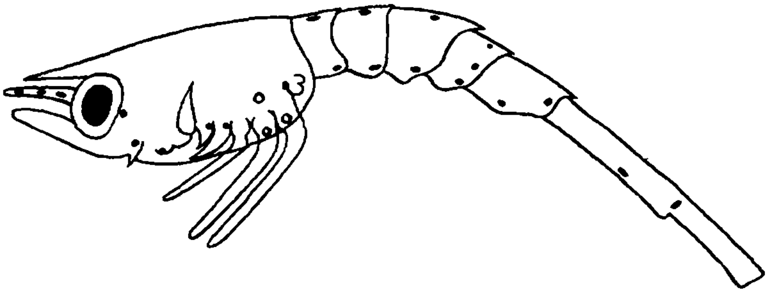

FIG. 17.—Larva of *Crangon vulgaris*, showing arrangement of primary and secondary chromatophores. After Keeble and Gamble.

system were more akin to the Decapoda than to the Mysidae—an important discovery in view of the fact that the separation of the Euphausiidae from the Mysidae and their relation to the Decapoda had not, at that time, been accepted.

The primary chromatophores in those Decapod Zoeas which were studied by Keeble and Gamble were found to be constant in position, and their number was definitely distinctive of the species.

The importance of coloration in distinguishing between larvae of allied species has been fully realized by Miss Lebour and other recent workers. Miss Lebour's coloured figures of Brachyuran larvae (1928) show admirably how readily the species may be separated in this way. Another good example is the colour distinction between the larvae of *Munida sarsi* and *M. tenuimana* shown by Huus (1935).

Stress has been laid rather upon coloration than upon the exact distribution of the chromatophores of the two systems, and Aikawa's tabulation of the individual chromatophores in each species studied is a notable advance in method (1929). Aikawa's table is reproduced here, and the same facts are summarized under the families in Table II. It will be seen that there are only three chromatophores or series of chromatophores which are invariably present, namely, those of the mandible and carapace and the abdominal series. Within a family, where several species are known, there is some diversity, but a significant agreement on the whole, and the complete identity in the two species of *Xantho* suggests that valuable evidence of relationship both of species and genera may be obtained in this way.

It is unfortunate that the pigments are generally destroyed by preservation and the chromatophores are sometimes very difficult to see even in life. In the condition of extreme expansion it is not always possible to distinguish the number of centres in a highly pigmented area, and in extreme contraction a small chromatophore may become almost or quite invisible. For

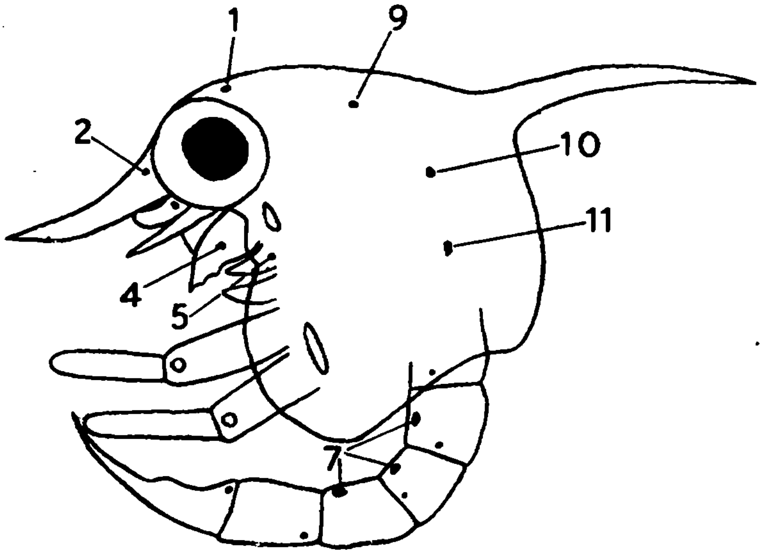

FIG. 18.—*Carcinus maenas* Zoea, showing distribution of primary and secondary chromatophores. After Keeble and Gamble.

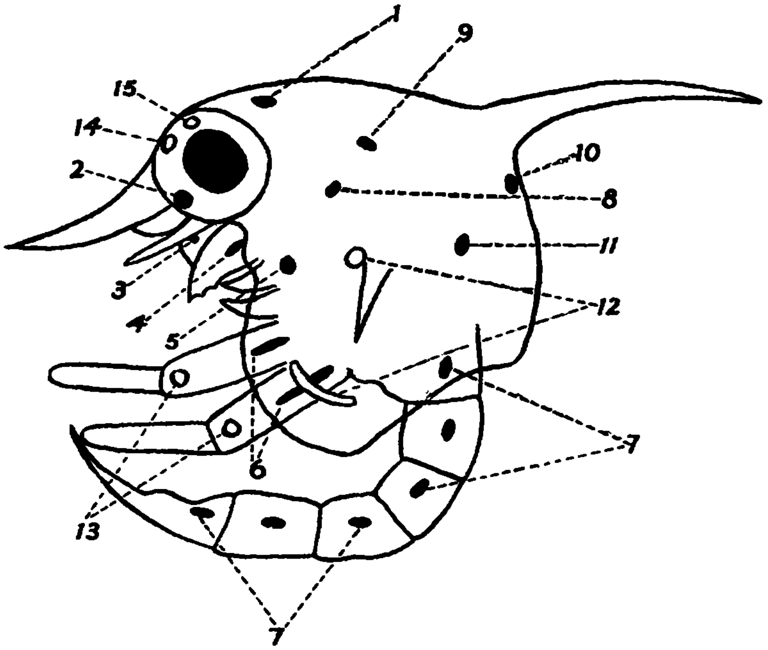

FIG. 19.—Diagram showing position of chromatophores in Brachyura. From Aikawa, 1929.

PRIMARY SYSTEM.
- A. Neural Group :
  - 1. Supracerebral.
  - 2. Antennal.
  - 3. Labral.
  - 4. Mandibular.
  - 5. Maxillar.
  - 6. Maxillipedal.
  - 7. Abdominal.
- B. Visceral Group :
  - 8. Median gastric.
  - 9. Precardiac.
  - 10. Subcardiac.
  - 11. Postcardiac.

SECONDARY SYSTEM.
- 12. Carapacial.
- 13. Maxillipedal.
- 14. Optic.
- 15. Median ocular.

Distribution of Chromatophores in Brachyura from Aikawa, 1929.

	Primary system.												Secondary system.					
	1.	2.	3.	4.	5.	6.	6′.	7.	8.	9.	10.	11.	12.	12′.	13.	13′.	14.	15.
EBALIIDAE.																		
1. *Philyra pisum*	o	/	/	o	o	o	o	o	o	/	o	o	o	/	/	/	/	o
2. *Ebalia* sp.	/	o	/	o	o	o	o	o	o	/	/	o	o	o	/	/	/	o
HYMENOSOMATIDAE.																		
3. *Rhynchoplax messor*	/	/	/	o	o	o	o	o	o	o	/	/	o	/	/	/	o	/
4. *Trigonoplax unguiformis*	/	/	/	o	o	o	o	o	o	o	/	/	o	/	/	/	o	/
5. *Halicarcinus septentrionalis*	/	/	/	o	o	o	o	o	o	o	/	/	o	/	/	/	o	/
INACHIDAE.																		
6. *Pugettia quadridens*	o	o	o	o	/	o	o	o	o	/	/	o	o	o	/	/	o	o
PORTUNIDAE.																		
7. *Neptunus*	/	/	o	o	o	/	/	o	/	/	/	o	o	/	/	o	/	/
MENIPPIDAE.																		
8. *Heteropanope*	/	o	o	o	o	o	o	o	o	/	o	/	o	o	/	/	o	/
9. *Pilumnus vespertilio*	/	o	o	o	o	/	o	o	o	/	/	o	o	o	/	/	/	o
10. ,, *minutus*	/	o	o	o	o	/	o	o	o	/	/	o	o	/	/	/	/	o
XANTHIDAE.																		
11. *Xantho exaratus*	o	o	o	o	o	/	/	o	/	/	o	/	o	o	o	o	o	o
12. *Xantho* sp.	o	o	o	o	o	/	/	o	/	/	o	/	o	o	o	o	o	o
GRAPSIDAE.																		
13. *Heterograpsus sanguineus*	/	o	o	o	o	/	/	o	o	/	o	o	o	/	o	o	/	o
14. ,, *penicillatus*	/	o	o	o	o	/	/	o	o	/	o	o	o	/	o	o	/	o
15. *Hemigrapsus longitarsis*	/	o	o	o	o	/	/	o	o	/	o	o	o	/	o	/	/	o
16. *Eriocheir japonicus*	/	o	o	o	o	/	/	o	o	/	o	o	o	o	o	/	o	o
17. *Platygrapsus depressus*	o	o	o	o	o	/	/	o	o	/	o	o	o	/	o	/	o	o
18. *Sesarma* sp.	/	o	o	o	o	/	/	o	o	/	o	o	o	/	o	/	/	o
OCYPODIDAE.																		
19. *Macrophthalmus dilatatus*	/	o	o	o	o	/	/	o	/	/	o	o	o	/	o	o	/	o
20. ,, *japonicus*	/	o	o	o	o	/	/	o	/	/	o	o	o	/	o	o	/	o
21. ,, *depressus*	/	o	o	o	o	/	/	o	/	/	o	o	o	/	o	o	/	o
22. *Scopimera globosa*	/	o	/	o	o	/	/	o	/	o	/	/	o	/	/	/	o	o
23. *Tympanomerus pusillus*	/	o	/	o	o	/	/	o	/	o	o	/	o	/	/	/	o	o
Frequency of occurrence	5	18	16	23	22	7	9	23	15	5	14	15	23	7	11	8	11	18

o = Presence. / = Absence.

Distribution of Chromatophores in the Families of Brachyura, Summarized from Aikawa's Table.

	No. of species.	Primary system.												Secondary system.					
		1.	2.	3.	4.	5.	6.	6′.	7.	8.	9′.	10.	11.	12.	12′.	13.	13′.	14.	15.
Ebaliidae	2	o	o	/	●	●	●	●	●	●	/	●	●	●	o	/	/	/	●
Hymenosomatidae	3	/	/	/	●	●	●	●	●	●	●	/	/	●	/	/	/	●	/
Inachidae	1	●	●	●	●	/	●	●	●	●	/	/	●	●	●	/	/	●	●
Portunidae	1	/	/	●	●	●	/	/	●	/	/	/	●	●	/	/	●	/	/
Menippidae	3	/	●	●	●	●	o	●	●	●	/	o	o	●	o	/	/	o	o
Xanthidae	2	●	●	●	●	●	/	/	●	/	/	●	/	●	●	●	●	●	●
Grapsidae	6	o	●	●	●	●	/	/	●	●	/	●	●	●	o	●	o	o	●
Ocypodidae	5	/	●	o	●	●	/	/	●	/	o	o	o	●	/	o	o	o	●

● = Present in all species. o = Present in some species. / = Absent in all species.

these reasons reliable results can only be obtained by examination of a number of healthy specimens under different conditions of expansion and retraction.

RATE OF GROWTH.

Brooks observed (1886), in the Stomatopod larvae studied by him, that the increase in length from moult to moult was so constant that "comparative measurements gave proof of identity which could hardly be made more conclusive by rearing the larvae." In this series, which he attributed to *Coronis*, he found the rate of growth to be an increase from stage to stage of five fourths, or a growth factor of 1·25. Actually the larvae dealt with did not all belong to the same genus. The early larvae were those of *Pseudosquilla*, while certain later larvae belonged to *Lysiosquilla* (*Coronis*).

Fowler (1909) termed this numerical relation between stages "Brooks's Law," and restated it thus: "During early growth each stage increases at each moult by a fixed percentage of its length, which is approximately constant for the species and sex."

Przibram and Megusar (1912) found in *Sphodromantis* that the weight doubled from moult to moult, and that the increase in length of the prothorax is, on an average, × 1·26. Przibram (1929), in a discussion of "Quanta in Biology," explains the doubling of weight as the result of doubling of the cells, which could be shown to occur in some tissues. A connection was thereby established between the growth factor 1·26 and a division of the volume of the cells, "whose linear dimensions would consequently increase as the cube root of 2" (Calvert).

Calvert (1929) has given a valuable summary of the published information on the rate of growth of Arthropods, particularly of insects, which makes it clear that Brooks's law is by no means of general application.

Seymour Sewell (1912) has found it to apply with astonishing exactness to certain marine Copepoda, but my own measurements of fresh-water Copepoda (1929, 1931) showed such great irregularity in the growth factor that very little reliance could be placed upon it.

In Copepoda and Decapod larvae there is a marked tendency for the growth factor to be about 1·26, but there is much irregularity, even when average figures can be taken, and the factor tends to decrease with age.

Few satisfactory figures are available for Decapod development, but the measurements given by Fraser (1936) for *Euphausia superba* are taken from an unusually large material, and should therefore provide a very good illustration of the working of the law. In this series only nine specimens of Nauplius 1 and 2 were available, and these do not permit the growth factor to be reliably found, but for the remainder the numbers are very large.

Growth Rate of Euphausia superba *from Measurements by Fraser* (1936).

Stage.	Number measured.	Length average.	Length range.	Growth factor.	Fraser's table.
Nauplius I	2	·62	..	..	IV
„ II	7	·66	·63–·70	1·03	V
„ III	432	·94	·84–1·08	1·42	VI
Calyptopis I	1263	1·71	1·42–1·92	1·82	VIII
„ II	559	2·71	2·13–3·33	1·58	IX
„ III	828	4·06	3·17–4·83	1·50	X
Furcilia I	507	5·30	3·50–6·50	1·30	XXIX
„ II	506	6·11	3·96–7·92	1·15	XXX
„ III	289	7·32	5·79–8·75	1·19	XXXI
„ IV	209	8·01	6·67–9·92	1·09	XXXII
Cyrtopia I	157	9·52	8·25–11·50	1·19	XXXV
„ II	284	11·34	8·00–15·5	1·19	XXXVII

It will be seen that the growth factor decreases rapidly from 1·82 to less than 1·2, the drop being very marked after the moult to the Furcilia.

Where there is great change of form, as between the Nauplius and Copepodid, measurements of length are apt to be misleading, and a better index of growth would be given by measurements of mass or weight. Bogorov (1935) has attempted such measurements of "biomass" in the Copepodid of *Calanus*, with rather surprising results. Whereas he found the index of linear growth to form a descending curve, the biomass, on the other hand, increased enormously up to stage 4, but then fell, and actually became negative at the moult from stage 5 to stage 6. This he assumed to be due to the maturation of the gonads. The difficulty of accurate determination of biomass is obviously great, but Bogorov's results seem to call for further study of the subject.

A good deal of attention has been paid to the rate of growth of the lobster (*e.g.* Ehrenbaum, 1908 ; Herrick, 1911) and of the shore crab (Brook, 1884 ; Williamson, 1903), but the observations deal chiefly with post-larval growth, and they are therefore not strictly relevant. The figures given by McKay and Weymouth (1935) for *Cancer magister* show a growth factor at the moult from the Megalopa of 1·86, but this high figure is no doubt due to the great change of shape.* At subsequent moults the factor decreases fairly regularly from 1·42 to 1·17 at the period when the sex became evident.

It may be said that Brooks's law is not sufficiently exact to be relied upon ; but, if its limitations are borne in mind, it may be a useful instrument when attempting to connect up into a series larvae taken in plankton. Thus, if the growth factor between any two stages assumed to belong to the same species exceeds 1·5 for example, there is at least a possibility that there has been an error in identification. The converse is, unfortunately, not true, since a growth factor of less than 1·26 has no such implication. Actual decrease in linear measurements at a moult has been observed.

MUTATION IN CARIDEA OF THE FAMILY ATYIDAE.

Among the species of the fresh-water shrimps of the family Atyidae there are some which show a remarkable degree of variation which Bouvier has called "evolutionary mutation." Bouvier's conclusions therefrom are of such far-reaching importance that the closest attention and criticism is called for.†

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* The measurements were of carapace width.

† For a full account of the facts and deductions therefrom see Bouvier, 1925.

His conclusion, shortly, is that the three genera *Caridina*, *Ortmannia* and *Atya* are an evolutionary sequence of which *Atya* is the culminating point, and that in certain species of *Caridina* the progeny of one female may include individuals having the characters of *Ortmannia*, and certain species of *Ortmannia* may, in like manner, produce young referable to the genus *Atya*. On the other hand, *Ortmannia* does not produce young reverting to *Caridina*, nor *Atya* young reverting to *Ortmannia*; that is to say, the mutation is irreversible.

The three genera are quite clearly definable, the most important character being the structure of the chelae. The essential differences between the genera are these:

(1) In *Caridina* the second pair of chelipeds differs from the first in having the carpus long and slender, and not excavated, whereas in *Ortmannia* the two appendages are the same, and the carpus is short and deeply excavated.

(2) In *Caridina* and *Ortmannia* the dactylo-propodal joint is normal, and situated at some distance from the carpo-propodal joint, whereas in *Atya* it is shifted proximally so that the chela "is composed of two similar parts, hinged together at one end, like the legs of a pair of compasses" (Calman, 1910).

Bouvier was led, by consideration of the intermixture of the two forms known as *Ortmannia alluaudi* and *Atya serrata* in the same localities, to suggest that the latter might be a mutant of the former, and this supposition was, as he believed, confirmed by Bordage, who found in the progeny of a female *O. alluaudi* ten young *O. alluaudi* and six young like *Atya serrata*. Another brood consisted of *O. alluaudi* only, while the progeny of *A. serrata* were all like the parent.

Similarly in the case of *Caridina richtersi*, with which is associated as a supposed mutant a form known as *Ortmannia edwardsi*, Charmoy obtained a brood from *C. richtersi* in which one out of 17 had the characters of *O. edwardsi*. On the other hand young obtained from *O. edwardsi* were all of the same form as the parent.

Bouvier's conclusions from the breeding experiments with *O. alluaudi* have been discussed and criticized by Calman (1910).

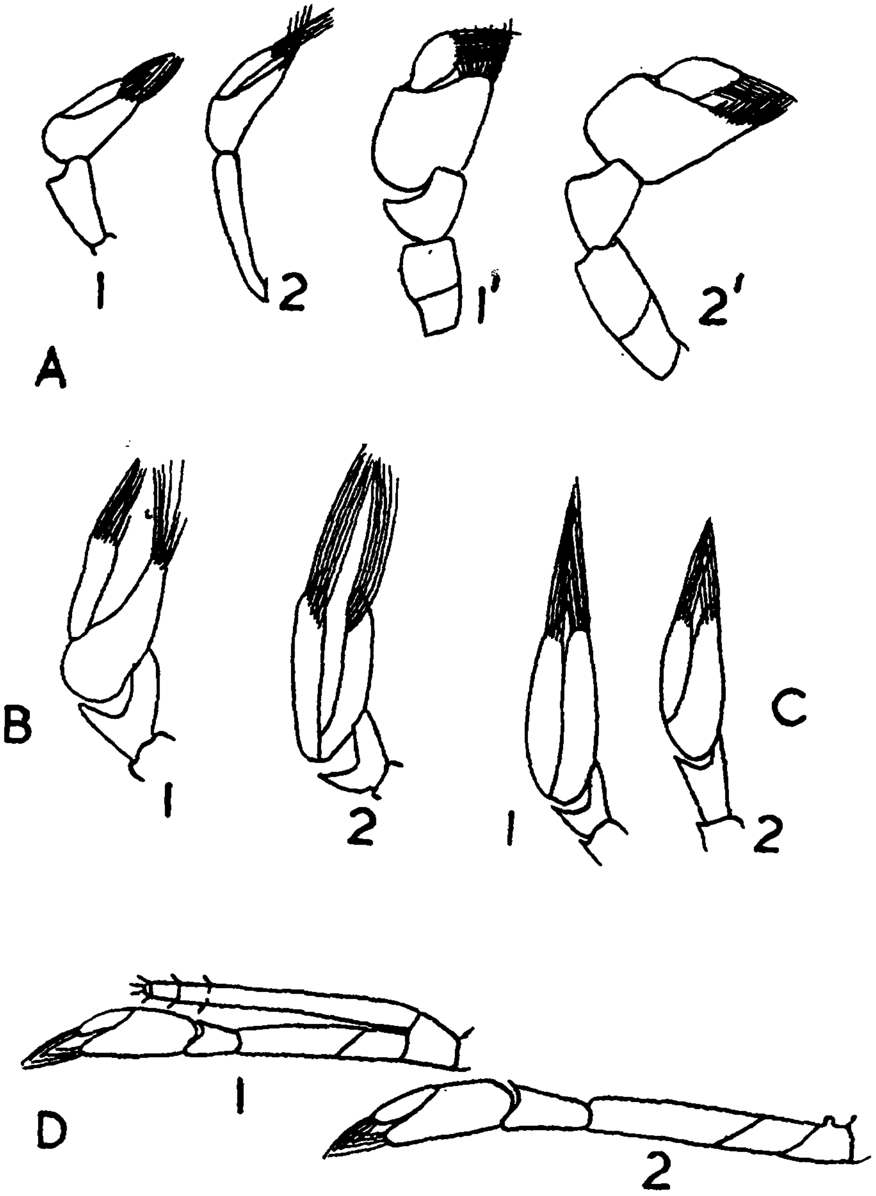

FIG. 20.—Mutation in Atyidae. After Bauvier, 1925, and Edmondson, 1929. A. 1, 2, Legs 1 and 2 of typical *Caridina richtersi*. 1', 2', The same of its mutant *Ortmannia edwardsi*. B. *Ortmannia alluaudi*. 1, Cheliped of typical form ; 2, the same of its mutant *Atya serrata*. C. *Atya bisulcata*. 1, Second cheliped before removal ; 2, the same (in *Ortmannia* form) after regeneration. D. *Atya bisulcata*. 1, First cheliped of young about 5 days old ; 2, second cheliped of young about a month old ; both of *Ortmannia* form.

Edmondson (1929) has investigated, on an extensive scale, the progeny of the two forms *Ortmannia henshawi* and *Atya bisulcata* in Hawaii, with results very different from those of Bouvier. From " about 25 " females of *A. bisulcata* over 1000 young were reared, and in every case the chelipeds shortly after hatching had the form typical of *Ortmannia*. From four females of *O. henshawi* 139 larvae were obtained, all of which had chelipeds of the same form as the parent. Edmondson concludes : " My experiments on regeneration and larval development show that the form called *Ortmannia henshawi* is the basis one, and that the one known as *Atya bisulcata*, by its reversion to the basic type, does not breed true and is not a fixed species. The evidence is sufficient to conclude that the generic or specific separation of the two forms cannot be sustained " (1929, p. 29). Edmondson's results answer in the affirmative the question posed by Calman—" whether there is any trace of an *Ortmannia* stage in the development of the *Atya*-form of cheliped."

Edmondson has shown that it is possible for specimens of *O. henshawi* to change into *Atya* by regeneration of the chelipeds into the *Atya* form, this being more frequent in old than in young specimens. But it is even more usual for *Atya* to regenerate the limbs in the *Ortmannia* form, in this case more frequently when young than when old. This reversion to the *Ortmannia* form is usually permanent, but the *Atya* form may be reacquired at a later moult. That the loss and regeneration of appendages is not frequent in nature was shown by the examination of more than 1000 specimens, in which less than 1 per cent. showed recent mutilation of the appendages.

It would seem beyond doubt that these two " species " are dimorphic forms of one species. Since all alike start life in the *Ortmannia* form it is to be expected that no specimen of the *Atya* form will be found less than a certain minimum size, and Edmondson concludes that the " fluctuations from *Ortmannia* to *Atya* occur most readily after the animals have reached a length of about 20 mm., and are from 9–12 months of age."

The actual proportion in numbers between the two forms can only be ascertained in collections made for the purpose and including all specimens obtainable at one spot. Such a collection of 1784 specimens from Hilo in Hawaii consisted of 1300 specimens of *Ortmannia*, 465 of *Atya* and *19 intermediates. Among* 2000 specimens of *O. henshawi* about 90 per cent. were males, whereas in *A. bisulcata* females predominate in about the same proportion.

Bouvier found a similar disparity in the sexes of *O. alluaudi* and *A. serrata.*

It is clear that, in the species dealt with by Edmondson, there is no mutation in Bouvier's sense. The change to the *Atya* form seems to be a phenomenon of differential growth associated with age and sex. On the other hand, the sequence *Caridina-Ortmannia-Atya* does appear to be an example of evolutionary progression, and it is probable that the *Ortmannia* and *Atya* forms have been independently evolved in different parts of the world from species of *Caridina* and *Ortmannia* respectively.

It is most desirable that more attention should be paid to the life history of other species of these genera, with special reference to early development and the changes which take place with growth.

Bouvier divided the known species of *Atya* into three categories. The first contains *A. serrata* and *A. bisulcata*, which, as he believed, were mutants of *Ortmannia*, and would ultimately supplant the parent. Secondly, *A. moluccensis* and *A. spinipes*, which, like the first group, are relatively small and lightly built, and are supposed to have been derived from and to have supplanted a parent *Ortmannia* in more or less remote times. The third group consists of seven species, all of which are large and depart in their heavy build, and in the loss of some epipods, from the *Caridina* type. These too may be supposed to have been derived from

Ortmannia at a very distant time. It would be of great interest to know if these established forms have retained any evidence of their parentage in the form of the chelipeds on hatching.

It is difficult to find any parallel to the phenomena seen in *O. alluaudi* and *A. bisulcata*, since it cannot be interpreted either as an example of high and low dimorphism as seen in *Forficula*, nor as dimorphism associated with a breeding phase as in *Inachus*. While the difference between the two forms is clear-cut, it affects only a single appendage, and it is not accompanied by increase of size or marked change towards the heavy form of the larger Atyidae.

It would seem that the nearest approach is to be found in certain Copepods (Sewell, 1912), where a proportion of the males seem to go a step further, as it were, in development, and "high dimorphs" result. The actual process by which these high dimorphs are produced is uncertain (Gurney, 1928).

Calman (1913, p. 930) compares the variability of the hepatic spine in *Palaemon hildebrandti* with the mutation of the Atyidae. In this case the presence or absence of the spine seems to be a local character, since all but one of the 19 specimens from one locality possessed a spine, whereas all 11 from three other places lacked it.

LOCOMOTION OF LARVAE.

The Nauplius and Protozoea of Penaeids were said by F. Müller (1863, p. 9) to swim in a vertical position by beating of the antennae. So far as my own observations go on *Penaeopsis*, *Sicyonia* and *Gennadas* they do not confirm this statement, since in all cases movement was horizontal in a forward direction. Mme. Heldt (1938, p. 129) also found the Protozoea to swim forwards, the rhythm of the beat of the antennae differing with the species. Whether the back is upwards or downwards is not certain, but my impression is that it is normally downwards. The post-protozoeal stages swim backwards, usually with the head somewhat down, and on their backs.

It appears that the usual position in Caridea is back down and the movement tail foremost. This is particularly well seen in *Leander* and other Palaemonidae. In *Lysmata intermedia* in stage 1 the larvae seemed to be indifferent as to whether the back was up or down, and, though they mostly swam tail forwards, this direction was often reversed. This orientation with back down is the same as that of most Branchiopoda, and probably of certain Trilobites.

The Zoea of *Crangon* swims head first, and usually back upwards, and the same is true of *Paratya compressa* (Yokoya). In *Homarus* the position is the same, but the direction of movement may have two components—a forward movement in the axis of the body, and a movement vertical to the dorsal surface (Bohn). The actual course in this case may be very irregular. In *Nephrops* the body is bent at right angles, and the animal moves tail first and back upwards (Foxon, 1934*a*). The orientation and direction of movement may therefore not be the same in closely allied forms. In *Porcellana* the larva may swim either forwards or backwards —usually the former.

The normal Brachyuran Zoea swims with the dorsal spine foremost. While it may be seen more or less keeping position in the water with dorsal spine uppermost, it is capable of very rapid horizontal movement with this spine forwards.

Foxon has made some notes on the rate of swimming of larvae of *Galathea*, *Eupagurus*, *Pandalus* and *Porcellana*. The results in each case are very much the same, namely a movement of 1 m. in 45–60 seconds, and he concludes that " the swimming actions of the larvae are sufficient to account for the migrations which actually take place in the sea " (1934*a*, p. 843).

Foxon suggests that the delay in appearance of pleopods and precocious development of the uropods may be due to " the early need of the reversal mechanism which all these larvae possess." This reversal is effected by flexure of the abdomen. The direction of movement effected by the pleopods is always forwards, whereas that of the thoracic appendages is usually backwards, consequently the pleopods cannot become functional until the exopods cease to be so at the post-larval moult.

Some Caridean larvae have the abdomen inflexibly bent (*Discias*, *Acanthephyra*, *Mesocaris*), and these are incapable of the sudden backwards jerk performed by other larvae by the sudden flexure of the abdomen. Miss Lebour informs me that these larvae may still make sideways jerks or springs of such vigour that they may leap out of the vessels in which they are contained.

Expansion of surface for the purpose of assisting flotation is effected by pronounced flattening of the thorax (*Phyllosoma*, *Amphion*), or by spines on the carapace or abdomen. Probably the long rostrum of some larvae also serves this purpose. A very spiny carapace is usual in the Acanthosoma of *Sergestes*, and much the same arrangement of spines is found in the Penaeid *Solenocera*.

In the Mastigopus (post-larva) and adult of *Sergestes* the immensely long antennal flagellum serves as an organ of suspension (see Pesta, 1914, p. 190); but it is not very long in the larva. In *Rhynchocinetes* the antennal flagellum is of remarkable length in the larva, with the distal segments dilated; but the only other instance of a very long flagellum is in a Carid of unknown family from the "Discovery" material (Gurney and Lebour, 1941). In this case the flagellum is one of the branches of the antennule.

Flattening or excessive size of some other parts are no doubt also provisions for flotation. In some Brachyura the spines of the carapace are flattened at the end; the antennal scale or the uropods may be very long or dilated (*e.g. Cerataspides longiremis*); or the propods of some of the legs may be expanded into large paddles (*Eretmocaris*).

THE INFLUENCE OF LIGHT UPON MOVEMENT.

Bohn (1905) states that lobster larvae when first hatched are attracted by light, but that they later become negatively phototactic, and Herrick (1911, p. 334) says that movement is always away from the light. In most cases, however, there is a strong attraction to light. Foxon (1934*a*) has shown that the influence of gravity is very slight as compared with that of light, and that in most cases the latter causes orientation with the eyes away from the light, and movement towards it—*i.e.* tail first. Bohn states that the lobster larva seeks a position in which the light falls on the dorsal side of the eye, and consequently with back upwards in normal conditions.

In the Brachyura Foxon found that, if the influence of white light is eliminated, the Zoeas remain with dorsal spine upwards " and they carry out random movements in this attitude." Experiments showed that this orientation depends upon the spines being intact, and it appeared possible that these spines may be the seat of a reaction to gravity similar to that of the statocyst. The real function of the spines remains obscure, since those forms which do not have them, *e. g. Ebalia* and *Pinnotheres veterum*, are quite commonly found in the plankton though, as Miss Lebour has pointed out (1928, pp. 536, 539), they show a preference for the bottom. Foxon has shown (p. 840) that the spines do retard sinking to a considerable extent, and they must be effective for the purpose in the larvae of *Sergestes* and *Solenocera* for example.

A particularly interesting observation of Foxon's was that the removal of the spines in Brachyura of the *Portunus* type does not affect the direction of movement as a reaction to light, but that all sense of direction is then lost in darkness.

Apart from the lobster the reaction to light of all Decapod larvae that have been tested has been strongly positive (Spooner, 1933). Spooner found that photopositive animals, such as Copepods and Decapod larvae, seek the source of light, and are but little influenced by its intensity. "Positive groups of the Plankton organisms investigated primarily collect around a point in the mean line of incidence of the light." "It is immaterial whether this happens to be the brightest region of the dish accessible, or not" (p. 427). Reversal of the direction of the light causes reversal of the direction of movement and of orientation; but, in the case of *Porcellana*, the reversal of direction is accomplished without change of orientation—*i.e.* by reversal of the swimming movements (Foxon, 1934*b*).

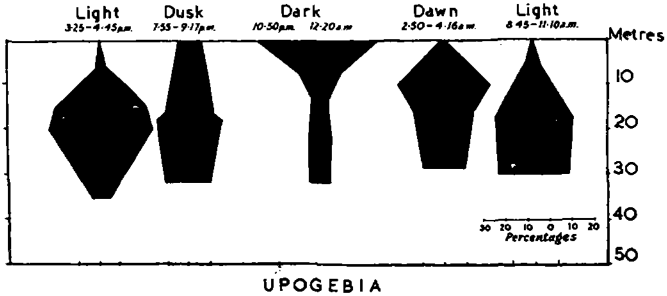

FIG. 21.—Vertical distribution of the larvae of *Upogebia*, July 15–16, 1924. The catch at each level is expressed as a percentage of the total number caught in the five hauls in each of the five series. After F. S. Russell, 1925.

Russell, in his series of papers on vertical movement of plankton organisms, has many references to Decapod larvae, and he has shown that they have a pronounced diurnal vertical movement. In the case of *Upogebia*, for example, he states (1928, p. 95): "On June 17 in daylight the majority of larvae were below a depth of 25 m. By dusk they were extending their distribution up to between 10 and 15 m., and in the dark they were most abundant actually at the surface." The post-larvae were not taken in the daytime, but only at night and at dawn in very small numbers. It would be of interest to know to what extent the successive stages differ in their reaction to light, particularly in Decapoda of the high seas. It is to be expected that the last stages of bottom-living forms would have a negative reaction; but this cannot be general, since these stages are quite commonly taken near the surface in daytime. As moulting generally takes place at night post-larval specimens should be found in the plankton only at that time. In my own experience there is a great difference between *Upogebia* and *Callianassa* in this respect. Post-larval specimens of the former are not uncommon in plankton; but I have never seen one of *Callianassa*.

There is some evidence among Copepoda that reaction to light changes with age. For instance, in *Diaptomus pacificus* the youngest stages were found by Kikuchi (1927, p. 186) nearest to the surface. This is also true of *Calanus finmarchicus*, where " the younger the stage of development the nearer the surface do the specimens live, as pointed out by Damas, Paulsen and Farran " (With, 1915, p. 28). Nicholls showed a marked difference in distribution with age (1933, p. 156). He says, " the stimulus to withdraw from bright light does not affect the Nauplii, but becomes increasingly effective as development proceeds." Russell (1931, p. 394) has shown a similar change in *Sagitta elegans*. Since the adults of *Calanus finmarchicus* are negatively heliotropic spawning must take place at night when they are near the surface.

Russell's work deals with the relatively shallow waters of the Channel and the larvae of littoral Decapoda, and little is known of the vertical distribution of the larvae of deep-sea genera, such as *Sergestes* and *Acanthephyra*.

While the adults of *Acanthephyra purpurea* appear normally to live below 800 m. during the day, and to rise to about 400 m. at night (Welsh, Chace and Nunnemacher, 1937, p. 191), the larvae, at all stages, may be taken between 25 and 100 fathoms, with the majority at 50 fathoms (Kemp, 1907, p. 211). Their distribution at Bermuda seems to be generally below 50 fathoms.

In the case of *Gennadas elegans* (Waterman, Nunnemacher, Chace and Clarke, 1939) the adult may reach the surface in small numbers at night, but the majority are at about 200 m. As egg-laying and hatching generally if not always take place at night under normal conditions, the first larvae may be expected to be found at the level of maximum frequency at night. All stages from the second Protozoea are fairly common in the upper 100 m. during the day, and it would seem that the Nauplius and first Protozoea probably do not reach the surface, at all events in any numbers. Whether there is any diurnal movement of later stages is not known, but Waterman *et al.* say that they found post-larval stages at 600 m. only, so that the last larvae must tend to leave the upper waters permanently.

The species of *Sergestes* are generally found at levels below 400 m., though some reach nearly to the surface. *S. atlanticus*, for example, has been taken at the surface, but lives during the day at about 800 m., rising during the night to 400 m. (Welsh *et al.*, 1937, p. 191). Larvae of this species in all stages from Protozoea to Mastigopus are, however, common in the upper 100 m. during the day at Bermuda. It seems that the larvae of these deep-living forms must rise very rapidly in the first hours after hatching.

Russell (1937) has shown that the larvae of different genera of Decapoda have distinct depth preferences, as shown in the accompanying diagram. He notes that the deeper the layer normally occupied the less, on the whole, is the diurnal movement. Savage (1926) found, on the fishing grounds of the east coast, that Decapod larvae in general were " very few in the surface waters down to 20 fathoms ; 89 per cent. of them were in the depths from 25–45 fathoms." His figures show some difference in distribution between different genera, and his results differ from those of Russell in that *Pandalina brevirostris* was found deeper than *Cheraphilus nanus*.

It is difficult to harmonize the facts of diurnal vertical movement with laboratory experiments on the influence of light, which show such a preponderant influence of the direction over the intensity of light. The fact that

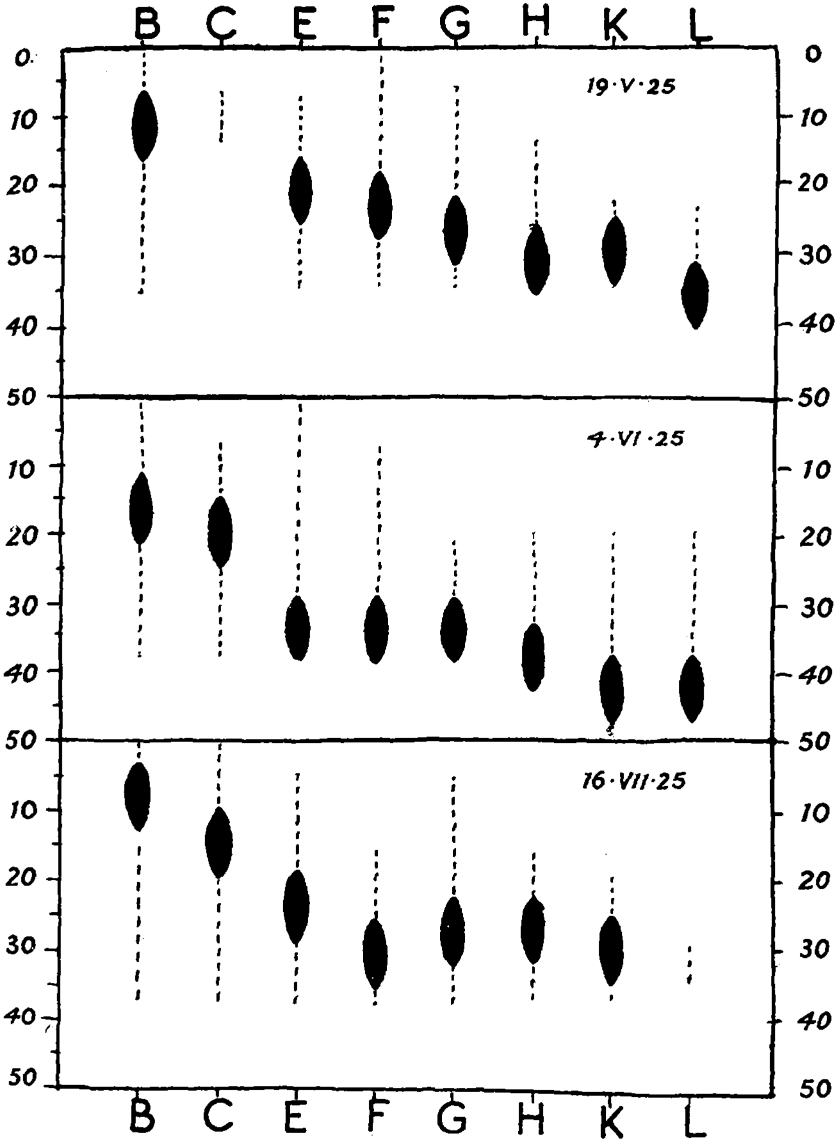

FIG. 22.—Diagram to show the vertical distribution of the undermentioned Crustacea on the three dates given. The ellipses show the region of maximum abundance, and the vertical broken lines the total range of distribution for each species. Depths in metres. B. *Calanus finmarchicus*. C. *Upogebia* spp. larvae. E. *Porcellana* spp. larvae. F. Galatheid larvae. G. Pandalid larvae. H. Pagurid larvae. K. Crangonid larvae. L. *Pontophilus spinosus* larvae. After Russell, 1927. In the original some of the ellipses are distinguished as being estimated rather than certain. The liberty has been taken of treating all alike.

in some cases animals are known to start movement up or down at times when there is no change of light seems to imply an innate rhythm which is difficult to accept. Russell (1927, p. 237) suggests that each species has an optimum intensity of light, which it follows upwards as the light fails. As the light falls below the optimum the animal tend to sink to lower levels of better temperature or salinity. At dawn they rise again to seek the increasing light, and again follow the optimum intensity downwards. He points out the limited application of laboratory results to conditions in the sea.

The factors concerned are evidently complex, and it is most difficult to determine their interaction.

The experiments of Foxon (1940) on *Hemimysis* show a curious interaction between phototaxis and geotaxis, which may perhaps be found to explain some of the anomalies observed.

DISTRIBUTION.

Since the fauna of the coast is much more varied than that of the deep sea, it is natural that the plankton of coastal waters should be richer in larvae in the neighbourhood of the coast than far out to sea (see Ortmann, 1893). This is not necessarily true of shallow inshore waters. In the Red Sea at Ghardaqa no larvae at all, and indeed scarcely anything living, could be found in plankton during the day within the outer reef, and plankton had to be sought in the deeper water some miles from the land. At night it was possible to obtain larvae close inshore, but never in large numbers. Much the same is true for the inshore waters at Bermuda. In both cases larvae must be hatching in thousands at night, and must be swept out to sea by the currents, to complete their transformation far out over the deeper water. It is true that there have been occasions when larvae in all stages have been taken inshore at Bermuda, just as on one occasion at Ghardaqa I obtained a rich plankton close inshore at night; but these catches must have been due to exceptional currents. Occasionally one may be fortunate in being present at the right moment and place. For instance, I have a sample taken by Dr. P. A. Buxton inside the reef at Samoa which is a mass of newly-hatched Decapod larvae, and at Bermuda I have seen swarms of newly-hatched larvae of *Pseudosquilla* and of *Albunea* at night.

At Plymouth the richest material of late larval stages is to be got in the Eddystone region, and the waters of the Sound contain few, and those mostly of relatively early stages.

While the swimming powers of some larvae are considerable they must be at the mercy of ocean currents, and these currents must have influence upon the distribution of the adults. Oceanic islands can only be populated by larvae whose period of development is long enough to survive the transit. Gardiner (1904) has discussed this point and concludes that development is, in fact, sufficiently prolonged to permit any bank in the Pacific or the Atlantic to be so colonized.

The lobster *Jasus lalandii* is found in New Zealand, the Cape, and Tristan d'Acunha. To reach Tristan from the Cape the larvae would have to traverse about 2000 miles of deep sea, which the adult could not possibly cross. The larvae have been taken at a number of places along a line about 33° S. as far as Tristan, but not west or south of Tristan. They are known to reach a large size and to pass through a number of moults (Gurney, 1936*c*), but we have no idea of how long their development lasts. If we assume it to be three months, which is probably too much, they would have to be carried at a steady average of 20 miles a day. I have been unable to find much evidence as to the speed of ocean currents; but the evidence of drift bottles in the North Sea, where the distances travelled are of the order of 3–4 miles a day, is very much against the possibility of such a rate of travel. On the other hand, the Agulhas stream is known to reach a speed of 7 km. an hour (Ekman, 1935, p. 274), and the speed of the

Gulf Stream at its origin is great. So far as concerns the direction of the current in the region in question there is no great difficulty, since the Benguela current flowing north up the coast of Africa sends off a western branch which sweeps round and joins the " West-wind drift " in a great eddy which may touch Tristan. Inasmuch as the late larvae are generally taken in deep water, it is doubtful if information on surface currents is really relevant, and very little seems to be known about deep currents. Ekman evidently believes that some species may have crossed the Atlantic as larvae, and gives as examples *Lysiosquilla scabricauda* and *Panulirus guttatus*.* It is, however, not impossible that the transport of *Panulirus* (and *Jasus*) may, in part, be effected in the post-larval, or natant, stage At Bermuda I have seen specimens of the natant stage of *Panulirus* (*argus* ?) taken at night in shallow water in plankton. They had probably been clinging to Sargassum weed, and might have been transported thus for a considerable distance.

A remarkable example of the relation of currents to the biology of a species has been worked out by Fraser (1936) in the case of *Euphausia superba*. The larval period is very prolonged, lasting from January to about October. By June a length of 10 mm. has been reached, and 24 mm. in a year or 14 months. During this period a very lengthy migration is effected. " The continued abundance of *Euphausia superba* in Antarctic waters and the replenishment of the stock of adolescents at the ice-edge is brought about by the rotary movement resulting from the assemblage of the earlier developmental stages chiefly in the southward flowing warm deep water and that of the later stages in the northward flowing Antarctic surface water " (Fraser, p. 167).

Reid (1935) has drawn attention to the very close correspondence between the distribution of the Sea-urchin (*Echinus esculentus*, L.) and the course of the

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* Another species found on both sides of the Atlantic is the crab *Euchirograpsus americanus* (Dollfus and Monod, 1927).

North Atlantic Drift; but the factors which effect this correspondence are not determined.

The present distribution of the Mitten Crab (*Eriocheir sinensis*) seems to offer another example of the influence of currents, in this case as a restriction upon distribution. This Chinese crab was first discovered in Europe in 1912, having, it is supposed, been introduced in the water ballast of ships. It has since spread far and wide up the rivers Rhine, Ems, Weser, Elbe and Oder as far as Mainz, Prague and Breslau, and has so multiplied that it is a serious pest. But it has not yet established itself anywhere on the British coast. A single adult specimen has been taken in the Thames at Chelsea ('Nature,' Oct. 26, 1935); but, so far as I know, no others have been seen. The larval life is spent in the sea, and there can be no doubt that it would have reached and invaded our eastern rivers if it were not for the fact that the prevailing currents of the North Sea set eastwards. It is the direction of the current which sets eastwards from the coast of Norfolk which "will explain the immense nurseries of young fish which are found in the eastern portions of the North Sea" (Allen, in Garstang, 1898, p. 201). No doubt the single British specimen was introduced in the post-larval state.

Panning (1936, p. 176) supposes that the metamorphosis of this crab from Zoea to Megalopa takes place in the region of the Elbe mouth and that the Megalopa, remaining on the bottom during the ebb tide, takes advantage of the flood to penetrate up the river. He estimates that, by using two tides, it could reach 30–40 km. up the river in one day, and all the way to Hamburg in 3–4 days.

Some observations of my own on the river Bure (1932) show that, in spite of the appearance of great speed, the maximum rate during the flood tide at the point of observation (about 10 miles from the sea) was 1525 yards per hour. Assuming a speed of double this amount (2 miles per hour) nearer the river mouth, and that the flood tide lasts six hours, the maximum penetration would be 12 miles (19 km.) in one tide. The possible distance during the succeeding tide would be very much less, since not only does the current rapidly diminish in speed, but the duration of the flood decreases. No doubt conditions in a large river, such as the Elbe, are unusually favourable, but Panning's estimate seems much too high, and it would seem that the colonization of the upper reaches is effected by active migration, or passive transport by boats, of post-larva or adult.

An interesting example of a species apparently on the way to become established in fresh water is that of the crab *Varuna litterata* (Kemp, 1915, p. 233). This crab is abundant in the Gangetic delta, and its Megalopas are carried in thousands to points at which the water is almost or quite fresh, and also into the pipes of the Calcutta water supply. It has not yet, in spite of the regularly recurring invasion, succeeded in colonizing fresh water.

Faxon (1879, p. 256) states that larvae of *Porcellana macrocheles*, *Calappa marmorata* and *Ocypoda arenaria* are carried northwards by the Gulf Stream beyond the range of the adults. Murray and Hjort (1912, p. 708) record the transport by the Gulf Stream of immense numbers of *Salpa fusiformis* north to beyond the Wyville Thompson Ridge, where they were dying off.

Rayner (1935, p. 243) mentions a swarm of *Munida gregaria* 300 miles from the nearest land and over water of 4000 m. depth. As the adult is a shallow-water species this swarm was being carried away to ultimate destruction.

To what extent Decapod larvae are at the mercy of currents or can control their own movements is not known; but the existence of swarms of larvae of single species, sometimes in late stages, is difficult to understand unless there is some sort of specific attraction. One may find in perfectly still fresh-water pools swarms of *Daphnia* or *Polyphemus*, or of *Calanus finmarchicus* at the surface of a glass-calm sea, where there cannot be eddies and currents aggregating them passively. The swarming habit of the *Grimothea* stage of *Munida gregaria* has attracted the attention of mariners since the sixteenth century (Matthews, 1932). The likeness of these swarms to swarms of bees has been more than once noted (Rayner, 1935, p. 242). It does not appear that the presence of these shoals has been attributed to the action of currents or eddies.

The larvae of *Crangon antarcticus* are numerous in the plankton taken by the " Discovery " and the " William Scoresby " in the Antarctic region. In any one sample the specimens are nearly always in the same stage.

If larvae in late stages have not the urge and power to move shorewards, it is rather difficult to account for the fact that they do return to inshore waters. I have myself been much struck by the fact that in estuarine waters in Norfolk the only larvae of *Leander* which I was able to obtain were either in stage 1—and these were exceedingly rare—or in the last larval stage. It seemed as if these larvae must actually migrate inshore and choose the flood tide to return to the habitat of the adult.

A good example of the influence of currents upon distribution is afforded by the Suez Canal. Fox (1929, p. 846) gives a table showing which members of the fauna of the canal have been derived from the Red Sea and which from the Mediterranean. Among those with floating larvae the great majority have come from the Red Sea, and this is due to the fact that from October to July the currents in the canal set northwards, and only in August and September do they run from north to south. Of the Decapod Crustacea three come from the Mediterranean and 23 from the Red Sea. The immigration from the Red Sea is also favoured by the strength of the tidal currents between Suez and the Bitter Lakes, in which so many species have established themselves. A number of species of fishes and Decapoda have now passed right through the canal and have spread out widely in the eastern Mediteranean. Monod (1930) gives the following species which are now found on the coast of Palestine and Syria : *Penaeopsis mono-*

ceros, *P. stebbingi*, *Penaeus semisulcatus*, *Myra fugax*, *Charybdis merguiensis*, *Neptunus pelagicus*. To what extent the migration has been effected in larval or adult condition it is impossible to say, since the Penaeidae are strong swimmers; but in the case of the Oxystome crab, *Myra fugax*, it is certain that it is the larva which has passed through the canal. The adult lives in sand and is incapable of active migration or of passive transportation.

Eggs and Egg-bearing.

The Euphausiacea either lay their eggs freely in the water, or carry them for a time in packets between the posterior thoracic appendages (*Nyctiphanes*, *Tessarabrachion*, *Nematoscelis* and *Stylocheiron*).

In *Lucifer* the eggs are few, and adhere to the last two pairs of legs in a mass which is very easily detached. In all other Penaeidea, so far as is known, the eggs are deposited in the water and, in some cases, if not usually, they sink to the bottom (*e.g. Sicyonia*). In other Decapoda the eggs are borne by some or all of the pleopods, and are more or less protected by the enlarged abdominal pleura. In the Palaemonid *Euryrhynchus* these pleura are so much enlarged that they entirely enclose the eggs and overlap each other below (Gordon, 1935, p. 334, fig. 21*c*). A similar brood pouch is found in *Paratypton siebenrocki* (Balss, 1914). An effective brood pouch is generally formed in Alpheidae; but *Automate* is exceptional in that the pleura are not at all enlarged, and the pleopods project freely carrying their eggs (Coutière, 1899, p. 299, fig. 377).

In the land crayfish *Engaeus* the posterior part of the abdomen can be bent downwards and forwards to cover the eggs completely. In *Leptochela bermudensis* the pleura of somites 1 and 2 are very much enlarged, and form a brood pouch closed behind by the second pair of pleopods, which take no part in egg-bearing.*

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* According to Kemp (1925, p. 250) the restriction of the eggs to the first two somites is characteristic of Pasiphaeidae in general.

The eggs may be borne upon all the pleopods, but, in Macrura, one or more of the posterior pairs are free from them. Usually only pleopod 5 is free, but in *Leptochela* the eggs are borne only upon pleopod 1 (Boone, 1935, p. 105; Gurney, 1939, p. 428).

The eggs are attached only to special ovigerous setae which are usually quite smooth, and generally have definite positions on the limb. In Caridea they may be in four groups on the basis as shown in Fig. 23; and there may also be a fifth group at the base of the endopod. Group A is apparently the most important and universal, and group C is generally present, but A^1, B and D are often absent. In *Systellaspis debilis* and *Acanthephyra purpurea* I have not seen any distinctly modified ovigerous setae, but, in the latter, the eggs seem to be attached mainly in the positions A and C. In the former the very large eggs seem to be held against the body, the underside of which is very hairy, and not to be firmly attached to the pleopods. In *Pasiphaea sivado* the eggs form a single mass, attached to the basal group of setae only, so that the pleopods can project freely from the brood chamber.

I do not know if these ovigerous setae have the same regularity of distribution outside the Caridea. In the lobster Herrick (1911, pl. 39, fig. 3) shows seven groups on pleopod 3, of which the three on the basis would correspond to groups A, A^1 and C of the Caridea. There are three groups on the endopod and one on the outer side of the exopod. In *Callianassa laticauda* (= *Stebbingi*) there is one group only on the basis and three on the endopod.

A detailed study of the distribution of these setae might produce results of systematic interest, but, unless moulted skins, or specimens freshly moulted and prepared for a new brood, are available, it is difficult to be quite sure of the arrangement of the setae, since they are so much hidden by the masses of eggs.

It has been noted in Palaemonidae (Sollaud, 1923, p. 15; Gurney, 1923, p. 120) that the pleopods are pro-

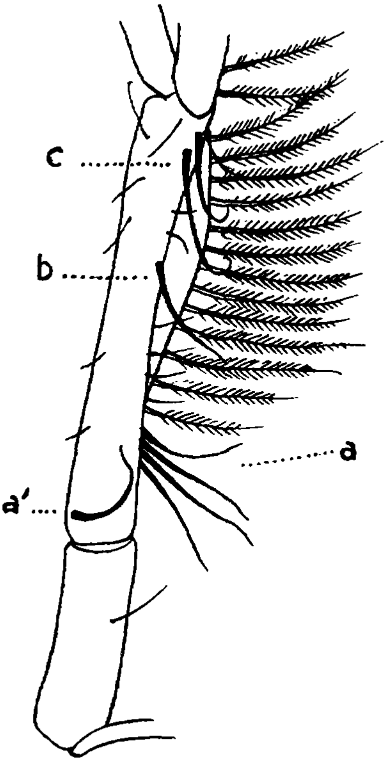

FIG. 23.—*Periclimenes americanus.* Pleopod 3 showing groups (A, A', B, C) of ovigerous setae.

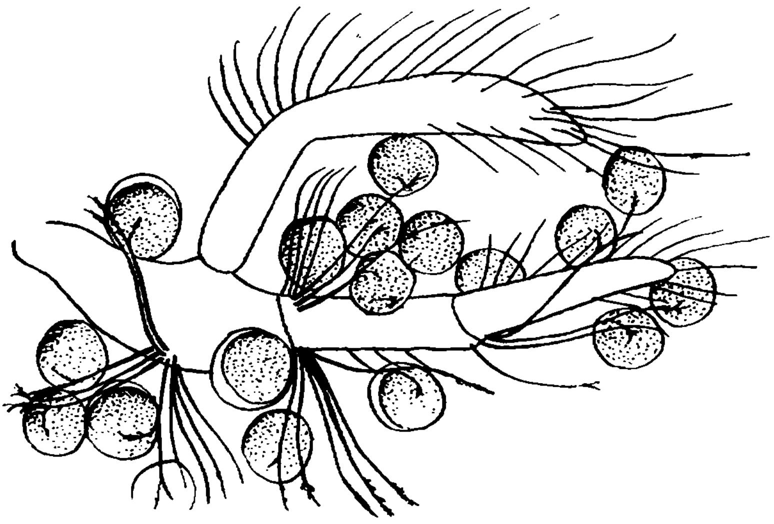

FIG. 24.—*Callianassa stebbingi.* Pleopod 2, carrying eggs.

foundly modified in the female at the moult which precedes egg-laying. Before this moult the outer margin of the basis is smooth, or with few setae, and the coxa, if traceable at all, is very small. At the moult the coxa, at least of pleopods 2 and 3, becomes very long, the outer margin of the basis becomes fringed with long setae, and the ovigerous setae appear. After hatching the female moults either at once, or after some days, and the pleopods revert to their normal form unless a second brood of eggs is to be laid. The same extension of the coxa in the breeding phase has been seen in other genera, but it is usually associated with a deep brood pouch and numerous eggs. For instance, in *Tozeuma armatum* the brood pouch is small and the coxa is short, while the eggs are confined to the base of the appendages. The coxa is also short in *Lysmata intermedia* and *Philocheras fasciatus*.

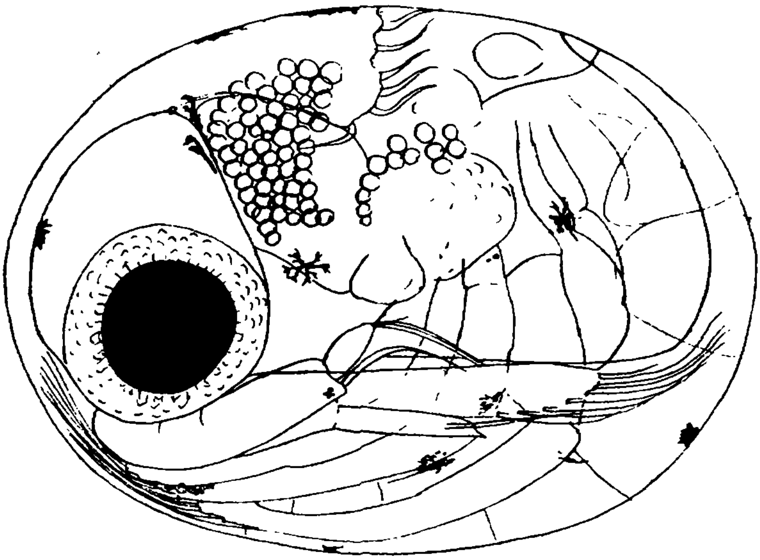

FIG. 25.—*Palaemonetes varians*. Young in egg.

Callan (1940) has found that these periodic modifications of the pleopods for egg-bearing are inhibited when the female is castrated by parasites or X-rays.*

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* For other references to ovigerous setae see Gurney, 1927, pp. 253, 260, 1936*b*, fig. 15 ; Sollaud, 1932*a*, p. 382 ; Lebour, 1939, figs. 17, 18.

The origin of the cement by which the eggs are fixed to the appendages and to each other has been a subject on which various views have been expressed (see Herrick, 1896, p. 126; 1911, p. 305; Broekhuysen, 1936, p. 21). Yonge (1938) has found that the outer membrane of the egg and the binding cement have the chemical characters of cuticle. This cuticle is secreted by glands in the pleopods which have ducts leading to the non-plumose ovigerous setae, and he says, " the circumstantial evidence in favour of the ducts from the cement glands opening along the sides of these setae is very strong " (p. 510). This supposition has since been confirmed (Lloyd and Yonge, 1940). If the cement were not confined to these setae it would be impossible to explain how the eggs come to be attached to them alone.

The position of the larva in the egg is the same in all Decapoda. It lies curled up so that the tail extends beyond the head and on to the back. The length of the larva on hatching is therefore more than twice the length of the egg.

Temporary Loss and Replacement of Appendages.

One of the most puzzling phenomena of larval development of Decapoda is the loss, or degeneration during one or more stages, of certain appendages, and their later reappearance in functional form. The following examples may be given:

(1) In some Palaemonidae (Sollaud, 1923; Gurney, 1924) at the moult to post-larval the exopods of maxillipedes 2 and 3 lose their setae, and regain them at the next moult. The same loss of setae from maxillipede 3 occurs in *Lysmata* (Gurney, 1937*b*).

(2) In *Atyaëphyra* at the same stage there is degeneration of the mouth parts, except for the exopod of the maxilla (Gauthier, 1924). A similar degeneration, though not so pronounced, occurs in *Upogebia* (Webb, 1919).

(3) In *Sergestes* legs 4 and 5 disappear entirely in

the Mastigopus stage, and are gradually regenerated in succeeding moults.

(4) In *Palinurus* maxillipede 1 is a large rudiment in the Prezoea, and disappears for a time (Claus, 1863).

(5) In Penaeinae and Sicyoninae the exopods of the maxillipedes and legs are lost in the post-mysis stage, and may be regained later (Burkenroad, 1934, p. 136).

(6) The non-appearance in the larva of *Leptochela* of pleopod 1 and the exopods of legs 4 and 5 are examples of the same thing.

(7) In the majority of the Decapoda the mandibular palp appears for the first time in the post-larval phase. As the mandibles of the Nauplius are biramous, this absence of the palp in the Zoea may be regarded as another case of the temporary loss of part of an appendage. Claus regarded it as evidence that the palp of the adult is a new acquisition not homologous with the larval appendage when present.

(8) Hyman (1920) found in the crab *Gelasimus* that the pleopods of the Megalopa disappeared entirely during the first three young crab stages, and that in the fourth stage pleopods of a " second series " appeared and developed directly into those of the adult. At this stage the sexes were distinguished, since the male had rudimentary appendages only on somites 1 and 2. Hyman's results require confirmation, since they are not supported by Cano (1892*b*) or Shen (1935).

Korschelt and Heider (1892, p. 496) note that temporary degeneration of an appendage may occur when a great transformation has to take place ; but such an explanation is certainly not generally applicable. It is not, of course, certain that the instances given are susceptible of a single explanation, and it is most difficult to conceive of any which would be applicable to all.

In the case of the Alpheidae the mouth parts may be undeveloped and functionless during one or more of the early stages, and in this case one supposes that there is sufficient yolk retained to enable the larva to grow without feeding. To suppress useless elaboration of appendages would economize energy. Something of the same kind seems to happen in *Atyaëphyra*, and to a less extent in *Leander*, namely, no function is required from the appendages for a time, and they appear at the moult in a modified form ; but this is no explanation. One needs to know how it can come about that these appendages are not in use at this stage.

There does not seem to be any deep phylogenetic significance in the phenomena, so much as simply adaptation to phases of larval life, the reason for which cannot be guessed at.

FRONTAL ORGAN.

A frontal sensory organ which may take the form of a pair of small papillae is generally present in Entomostraca in young or adult, or both ; but it appears to be absent from the early Nauplii except in Cirripedia, where it is a pair of long and conspicuous filaments. Zograf (1904, p. 36) concludes : "die Frontalorgane, sowie die Medianaugen, . . . sind uralte Organe, welche schon bei Urarthropoden entwickelt waren und von denselben auf die Crustaceen und Gigantostraken vererbt worden sind."

An homologous organ is found in most, if not all, Protozoeas of Euphausiacea and Penaeidea in stage 1. In *Sergestes* the papillae are placed in the region of the developing eye, and seem to be innervated from the optic ganglion (Fig. 26B). In stage 2, when the eyes are stalked, there is a similar papilla on the anterior lower side of each eye, which is usually retained throughout larval life. There seems to be no doubt that this papilla is the homologue of the frontal organ of the Entomostraca (Coutière, 1914). In Protozoea 2 of *Sergestes crassus* (Gurney and Lebour, 1940, fig. 16) there is a pair of very small papillae on the frontal lobe, innervated from the brain, and there is also a pair of ocular papillae. Consequently it seemed necessary to regard the former as the true frontal organ. While I have verified the presence of these papillae in *S. crassus*, I have not been able to find them in other species, and am forced to conclude that they are structures peculiar to this species, and not frontal organs. Though the homology of the papillae on the eyestalks with the frontal organ is reasonably certain, it is best to speak of them as " ocular papillae " since their position is so far removed from the front.

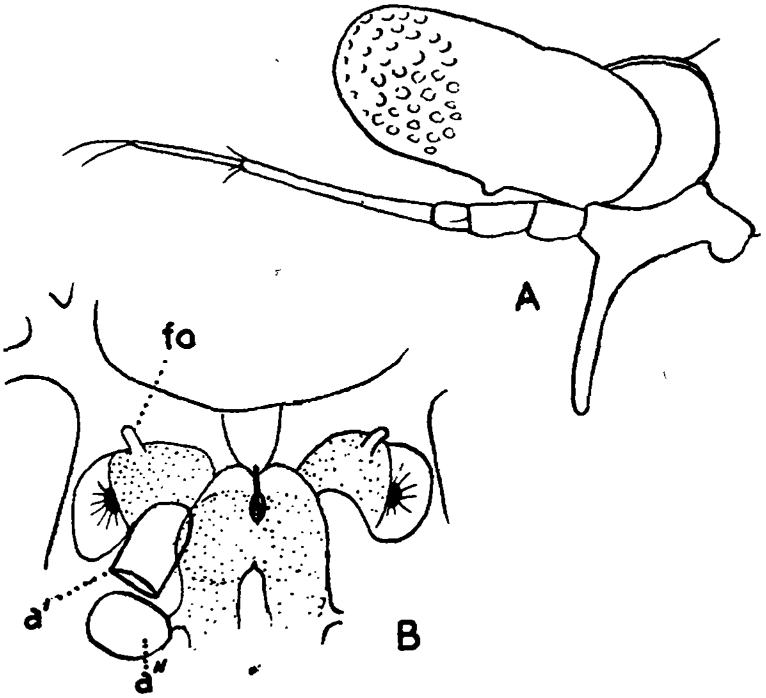

FIG. 26.—Frontal organ. A. *Macropodia aegyptiaca*, megalopa. B. *Sergestes vigilax*, Elaphocaris 1. Compound eyes under skin. FO. Frontal organ. A1, A2. Antennule and antenna.

The ocular papillae are placed on the lower side of the eye, and may not be easy to see ; consequently they may have been often overlooked, and their distribution is uncertain. So far as I am aware the only Caridean larva in which they have been seen is *Philocheras fasciatus* (Gurney, 1903, figs. 1, 2). I have not made an extensive search, but I have found a small ocular papilla in the last Zoea of *Portunus puber* and the Megalopa of *Macropodia aegyptia* (Fig. 26A), so that it is probably not uncommon in Brachyura. I have seen a small papilla in the Puerulus of *Panulirus argus*.

These papillae have been noted in many adult Malacostraca. Among Mysidacea they are present in certain deep-sea forms—*Gnathophausia*, *Eucopia*, *Caesaromysis*, etc.—but they are not generally seen in adult Euphausiacea. Among Decapoda they are particularly conspicuous in some Penaeidae, *e.g.* *Gennadas* and *Benthesicymus*. They are not present in the littoral genera, such as *Penaeus*. Bouvier noted the ocular papillae present in the adults of Hoplophoridae as an ancient feature, which is not found in the primitive family Atyidae. I have not found reference to the frontal organ in Macrura Reptantia, nor in Brachyura; but Doflein's figures (1904) of the eye of *Cyclodorippe uncifera* (pl. 46, fig. 6) and *Hypsophrys longipes* (pl. 49, fig. 4) show papillae which are no doubt homologous.

Bate (1888) supposed that he could see a small circular lens in the organ, and that its function was that of an "ocellus." Coutière (1914) denies the existence of any visual apparatus, but is unable to suggest any function.

DORSAL ORGAN.

Hansen (1921, p. 66) has noted the presence in some Decapod larvae of a dorsal tubercle, on the posterior part of the head or on the carapace, which he regarded as homologous with the dorsal organ of Entomostraca. He found that it was present also in the adult of most Penaeidae and Sergestidae, and in several Caridea, but that it was "scarcely to be found in Astacidae, Palinuridae, Galatheidae, etc." It is shown very definitely in Bouvier's figure of *Nephropsis atlantica* (1917, pl. i, fig. 2).

In Penaeidae it seems to be absent from the Protozoea, and small or absent from later stages also; but it is very large in *Solenocera* (Fig. 27B). It is generally traceable in the Protozoea of Sergestidae, though it may be absent, and it is particularly conspicuous in *S. corniculum*. In the Caridea it is always small, but it is generally present just behind the dorsal spines of the carapace, when these are present.

Among the Macrura Reptantia the organ has the form of a long slender papilla in *Eryoneicus*, but it is lost in the adult *Polycheles*. It is traceable in some Axiid larvae.

A dorsal organ can be traced either in embryo, larva or adult, in most groups of Crustacea, though the variety in structure and position makes it very doubtful if all are homologous.

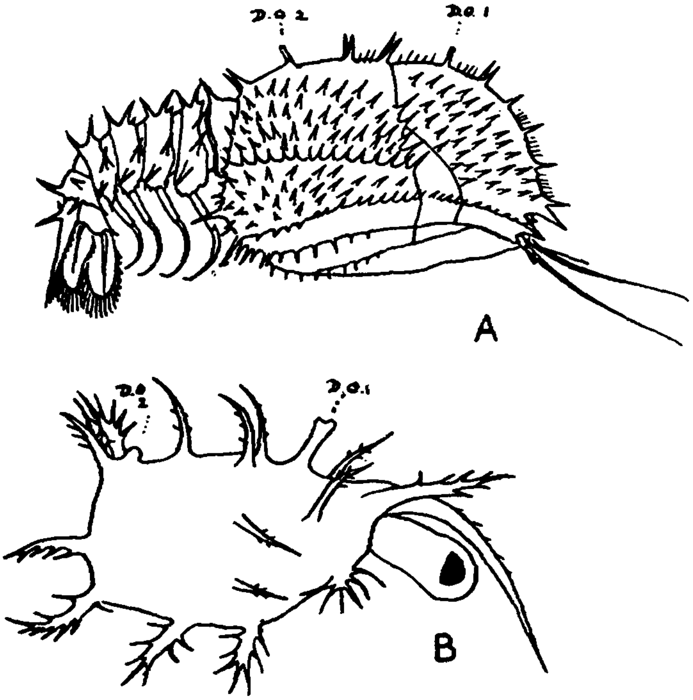

Fig. 27.—A. *Eryoneicus puritani.* After Bouvier. B. Solenocera, carapace. DO1, DO2. Anterior and posterior dorsal organs.

In Branchiopoda it is generally a large, flat, glandular organ; but in *Limnadia* there is a large papilla in its place.

In Trilobites (Raymond, 1920, p. 86) there is commonly a median tubercle in the region of the eye which has been compared to the dorsal organ of *Apus*. In some primitive forms this tubercle was developed into a long spine, and Raymond suggests that the tubercle is a vestigial organ, and that it " very strongly suggests the zoeal spine of modern Brachyuran Crustacea."

The function of the dorsal organ is disputed, and it is certainly not the same in all groups. In some Cladocera it is an adhesive organ (*e.g. Sida*), but in *Apus* it is supposed to be excretory (Bernard, 1892, p. 303). In some Malacostraca where it appears in the embryo alone it is supposed by its excretory action to assist in the moulting of the embryonic cuticle (Terao, 1919, *Panulirus* ; Piatakov, 1924, *Astacus*).

In the larvae of some Penaeidea and Caridea there is also a posterior unpaired dorsal papilla which is usually placed very near the posterior end of the carapace. It is small and inconspicuous, but it is present in *Eryoneicus*, and is then as prominent as the anterior dorsal organ. In *Panulirus* Terao mentions three dorsal organs, and it may be that this is the primitive number. Raymond states that there is a series of median tubercles in Trilobites which are exactly like the anterior dorsal organ.

CARAPACE.

The carapace in the first Protozoea of Penaeidea is a simple head-fold without rostrum which is not fused with the thoracic terga and does not entirely cover the thorax. In the Penaeidae (with the possible exception of *Solenocera*, of which stage 1 is unknown) there are no spines. In the Sergestidae *Lucifer* and *Petalidium*[*] have a rostrum and also dorsal and posterior lateral spines. In *Sergestes* and *Acetes* there is no rostrum at this stage, but there are anterior and posterior lateral spines and a posterior dorsal spine.

In stage 2 the rostrum appears, together with the supraorbital spines, if present at all ; but the thorax is not completely covered, and the thoracic terga remain free throughout the Protozoea phase (see Fig. 11).

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[*] The larva attributed to *Petalidium* (Gurney, 1924*c*) is probably *Sicyonella* (Burkenroad).

In the Euphausiacea the carapace of the Protozoea is without spines, except in *E. brevis* and its allies, which have a posterior dorsal spine. The rostrum is broad and hood-like, sometimes with serrated margin.

In other Decapoda the carapace is from the first fused with the thoracic terga, which are consequently completely covered. The rostrum is usually present even in stage 1, but there are very rarely any spines at this stage. The rostrum is usually at first a straight cylindrical rod which becomes compressed, and with dorsal and ventral spines only in stages later than the Protozoea. In some Macrura Reptantia it is flattened horizontally, and may then be serrated along its margins (*e.g. Callianassa*). In *Sergestes* alone, in Protozoea 2 and 3, it has long lateral and ventral spines, and in this respect resembles the Mysid *Caesaromysis*, which indeed has a general resemblance to a Sergestid larva (see Illig, 1905, (fig. 1).

In the Zoea stage (Acanthosoma) of Sergestidae the carapace bears large lateral spines, with secondary spinules, which probably serve the purpose of flotation, and in *Solenocera* there are similar lateral spines, while the surface is also covered with small spines. In fact the resemblance between the Zoea of *Solenocera* and that of *Sergestes prehensilis* for example is striking.

The great dilation of the thorax and the numerous spines on the carapace of *Eryoneicus* no doubt also assist in increasing buoyancy.

In *Amphion* and the Phyllosoma larva of Loricata the same effect is obtained by flattening of the thorax.

A supraorbital spine is generally present in the larva even when it is lost in the adult, and there is usually a spine at the anterior ventral angle (pterygostomial). The antennal, branchiostegal and hepatic spines would seem to belong properly to the post-larval phase, and their homologies are not clear. It has been suggested (Gurney and Lebour, 1941) that, in Palaemonidae at all events, the hepatic and antennal spines are the same, merely occupying different positions in different species;

but it is not certain that this interpretation can be extended to other groups. For instance *Acanthephyra valdiviae* has an hepatic spine and also a spine which appears to be equivalent to the antennal of Palaemonidae.

Whereas a dorsal spine and a pair of lateral spines are usual in Brachyura, they are very rare in other Decapoda. In some cases the carapace is produced on either side into a long posterior lateral spine (*Galathea, Porcellana*), and *Caridion steveni* is unique in having a pair of large procurved dorsal spines in the gastric region.

ABDOMEN.

In some genera somite 1 has a pair of lateral processes which overlap the edges of the carapace and appear to prevent lateral movement of the carapace (see Coutière, 1899, p. 290). This papilla or process is not homologous with the lateral or pleural spine so commonly found on abdominal somites, since it may be present when there is also a lateral spine. It seems to be absent from the larvae of all Caridea and Anomura, but present in many Penaeidea (*e.g. Gennadas, Sergestes*), *Stenopus*, and perhaps *Jaxea* among the Thalassinidea. The papilla in *Jaxea* may be only a modified lateral spine. In Penaeidae there may also be a similar papilla or spine on somites 2 and 3.

In Brachyura there is no process on somite 1, but it is generally, if not always, present on somite 2, and sometimes on other somites. In *Gonoplax* there are lateral papillae on somites 2–4.

Coutière has described a similar structure in the adult of *Alpheus*, and notes that it is also shown in Sars' figure of the Lophogastrid *Ceratolepis*.

A median ventral spine is present on all abdominal somites very rarely (*e.g. Parapenaeus longirostris*), but it is found on some somites in several Penaeidea. In *Sergestes edwardsi* there is one on each of somites 1–5, but it is confined in others to one or more of the first three somites (*e.g. Funchalia, Sergestes vigilax*).

The anal spine, which is often present on somite 6, may be one of the same series. It is often found in Caridea, even in stage 1, and may be retained in the adult. It is noted by Coutière as present in *Arete* and *Betaeus* alone among adult Alpheidae (Coutière, 1899, p. 308), and he regards it as homologous with the preanal spine of Euphausiidae. In some Stenopid larvae there is a large ventral spine on somite 5 only, and in some Penaeid Protozoeas there is a pair of very small anal spines; possibly these structures are not strictly homologous with the normal series.

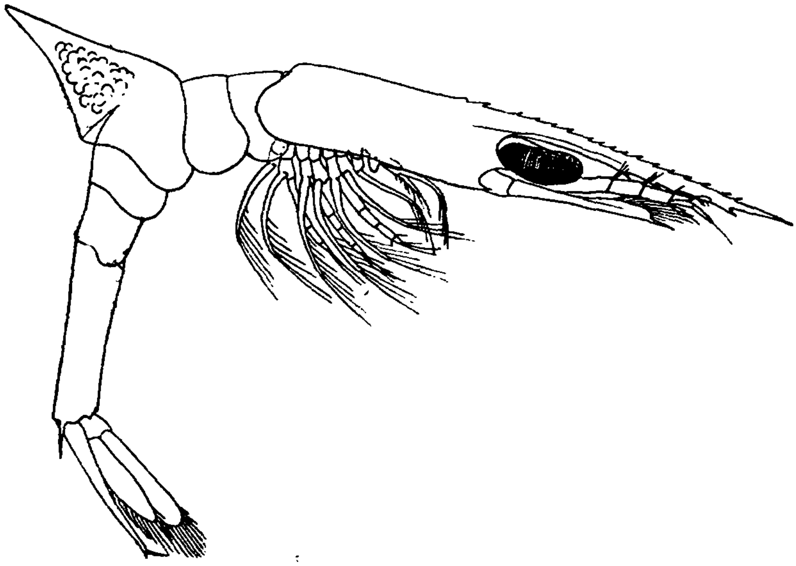

FIG. 28.—Caridean larva (Hoplophoridae) with large fat-filled projection of somite 3.

The abdomen is very generally flexed at the second or third somite, and one of these somites often bears a large dorsal spine (*e.g. Gennadas, Retrocaris*). In some cases somite 3 is very much produced dorsally. In *Acanthephyra* it takes the form of a more or less rectangular hood which overhangs somite 4, but in some deep-sea larvae of unknown parentage it is produced into a very large cone. A specimen of this type taken in Bermuda had the hump full of fatty globules, and floated when dead with the hump upwards. It would seem probable that in all cases the hump serves as an organ of flotation; but nothing definite can be said about it until specimens can be observed alive and uninjured.

TELSON.

The most primitive form of telson appears to have been a fork, with narrow arms, such as is found in certain Penaeid Protozoeas, and in an exaggerated form in some Sergestidae. In the Penaeidea the anus in the first Protozoea is terminal, in the depression between the arms of the fork. In *Nebalia* the telson, which is directly homologous with the telson of the Decapoda, bears a pair of movable appendages, corresponding to the furcal rami of Branchiopoda and Copepoda, and it seems reasonable to suppose that the two arms of the fork in Decapoda are homologous with the furcal rami of Copepoda for example.

Whereas in *Nebalia* and the Branchiopoda these arms bear numerous small setae, in Copepoda there is found almost universally among Calanoida, and in a large part of the Cyclopoida, an armature of six setae, which are remarkably constant in position. In the Decapoda the larva, when first hatched, has, in the great majority, seven spines or setae on either side of the telson, and this is true also for the Protozoea of many of the Penaeidea; but in the Sergestidae there are six only, and Conn has figured the telson of a Penaeid with this number.*

As is well known the prezoeal skin may show a telson of a different shape and with a different arrangement of setae from that found in the first free larva, and it is remarkable that, in all cases in which the prezoeal telson of Caridea has been seen, there are six setae, the inner, or sixth, containing within itself the 6th and 7th of the next stage.

I regard the Prezoea of the Caridea as the equivalent

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* *Amphion* seems to have only 6 + 6 spines in stage 1, but I have seen only one specimen of this stage, and no others have been recorded.

of the Nauplius phase of Penaeidea, and, inasmuch as it is passed through in the egg, and so exempt from the modifying influence of larval life, it is likely to have retained the primitive armature of the telson, whereas in the Penaeidae an additional inner seta has been developed. In the prezoeal telson all the setae are

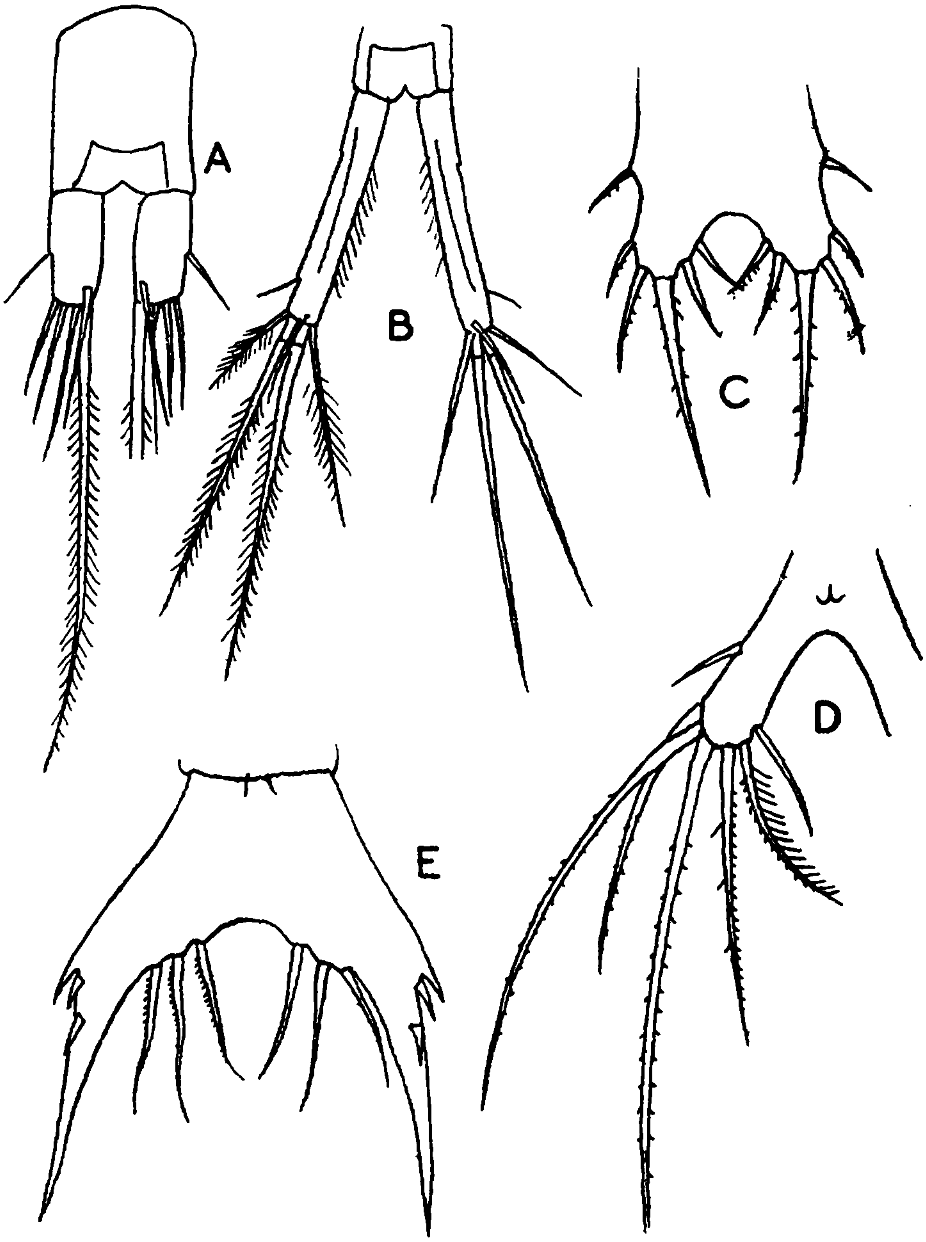

Fig. 29.—Telson. A, B, *Cyclops abyssorum*, copepodid and adult. C. *Petalidium*, Protozoea. D. Protozoea of a Penaeid. E. *Bathynectes* (Brachyura).

alike, large, profusely and delicately feathered; but in the Penaeid they may have definite positions and characters. Seta 1 is always lateral; setae 2, 5, 6, 7 are about equal and are feathered, whereas 3 and 4 are the longest and strongest, and are armed with small prickles.

It may be rash to attach importance to similarities in such widely separated groups as the Copepoda and the Decapoda appear to be, but there is a very striking similarity between them in the arrangement of these setae. In both cases seta 1 is lateral, and 3 and 4 larger than the rest.

There is, however, a serious difficulty in giving a phylogenetic significance to such similarities in number and arrangement of setae. In the development of *Cyclops*, for example, in the first Copepodid stage, seta 5 is very much the largest, and 2, 3 and 4 quite small—a condition which is retained in the adult *Ergasilus*. Again, in *Diaptomus* the terminal setae of the rami in Copepodid 1 are very different in size from those of succeeding stages (Gurney, 1931, fig. 142). Very little information is available as to the telson of other Calanoida, and there is no record of a marked difference in the size of the setae. The significance of the change in the proportions of the setae in Copepoda is unknown.

In *Hemimysis* a well-defined caudal furca is formed, each branch bearing setae; but it is lost at the first moult (Manton, 1928). This moult no doubt corresponds to the Prezoea of Decapoda, and the fact that the furca is lost with it does not necessarily imply that it is not represented by any structure in the following stage. Within the prezoeal skin of *Hemimysis* changes have been taking place in the direction of the " caridoid facies " and the telson grows out dorsally over the anus, while the uropods are carried backwards by the growth of the 6th somite below the 7th, till they reach their terminal position.*

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* For a discussion of the telson and the segmentation of the abdomen see Monod, 1926, p. 73. According to Tschetwerikoff (1911), whose paper I have not seen, the uropods belong to the seventh somite, the sixth being suppressed.

Where, as in Decapoda, great changes occur between successive moults, they are effected by growth within an already formed cuticle, and there is no gradual process of transformation of one structure into another. The intervening stages in phylogeny are not repeated, and can only be guessed at. In the Penaeid Protozoea stage 3 differs from stage 2 in many features, though retaining the same general form; but the anus is not now terminal, though the form of the telson is not strikingly different, and the arrangement of the spines is the same. It is clear that the primary forked telson is developing into the plate-like telson of the Zoea by growth backwards of the region between the forks. Granting that the forks are the homologues of the furcal rami of the Entomostraca or of *Hemimysis*, it is easy to see how they could in this way be absorbed into the telson and lose their individuality altogether, while their setae may be retained. With the compression of development in the Mysidae the intermediate steps have been completely suppressed, and the telson develops directly into the final form.

A curious example of the formation of a telson-like structure by fusion of caudal rami has been seen in *Cyclops* (Gurney, 1931, p. 77). In this case the anus remains dorsal, and it is most improbable that the telson of the Decapoda could have arisen by a process of fusion of this kind.

The Euphausiacea afford no evidence as to the origin of the telson. In most cases the telson of the larva is, from the first, a simple rectangular plate, with a formula of 7 + 7 spines, spines 3 and 4 being the largest. From Calyptopis 2 onwards there is also a median spine.

The normal armature of the telson in the free larva of the Decapoda is 7 + 7 spines in stage 1, and the size and arrangement of them sometimes provides useful evidence of relationship. In exceptional cases the telson is armed with numerous setae or spines, but where the number exceeds 7 + 7 in stage 1 the Prezoea may still have the primitive number, as in *Pandalopsis dispar*, where the Prezoea has 6 + 6, and the first larva 12 + 12 (Berkeley, 1930). A particularly interesting example is *Axius plectorhynchus* (Gurney, 1938, p. 303), in which the prezoeal telson shows traces of 7 primary spines on

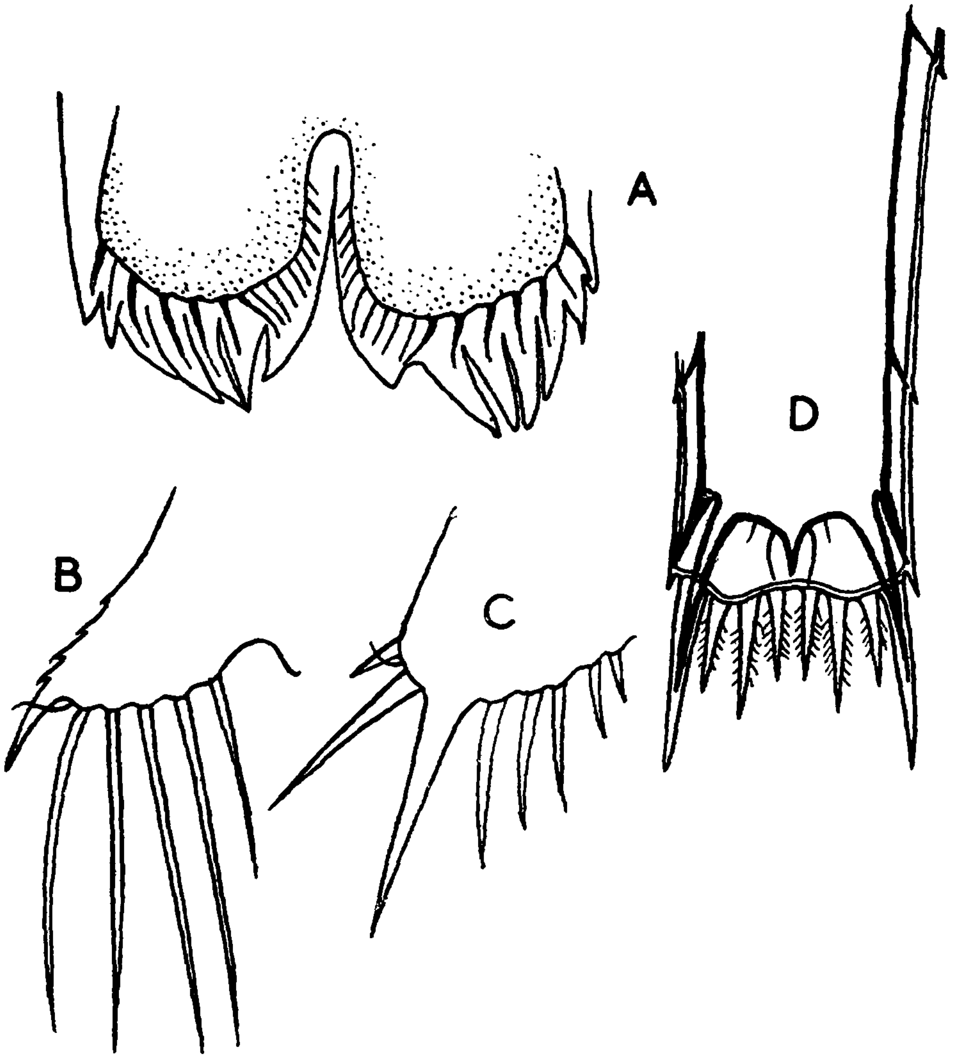

Fig. 30.—Telson. A. *Axius plectorhynchus*, Prezoea. B. *Stenopus hispidus*, stage 1. C. *Lithodes maia*. D. *Leander serratus*, about to moult to post-larval.

each side, each of which contains one of the spines of the zoeal telson, while numerous spines appear on the inner sides of the telson fork (Fig. 30A).

In stage 2 an additional spine appears at the inner end of the series, making a formula of 8 + 8. This number is not exceeded in later stages, but may be reduced by loss of the inner spine at the moult to post-larval.

Of the 7 original spines the first may remain on the outer margin, or may be reduced to a small spine on the outer angle of the telson plate, as in Paguridae. Sometimes, as in *Munida* stage 1 and *Jaxea*, it merges into an immense spinous prolongation of the outer angle.

Spine 4 is often greatly enlarged. This is seen among Euphausiacea and Penaeidea, and is characteristic of the later stages of Thalassinidea and Anomura; but it is most pronounced in Brachyura, where it forms the greater part of the fork of the telson.

Spines 5, 6, 7 are always relatively small, and form a distinct group, which is always preserved in Brachyura, even when 1–3 are reduced or absent.

In the Caridea it is a general rule that the spines or setae form three groups, namely, the single outer spine, spines 2–4, which may be placed at the apex of a more or less forked telson, as in *Pontophilus spinosus* (Fig. 83), and 5–7 on the posterior, or inner, margin. The arrangement is very much the same as in the Protozoea of Penaeidea, to which the first Zoea actually corresponds.

Spines 1 and 2 in stage 1 are generally feathered only on their inner side. Spine 2 is reduced to a hair in *Stenopus*, Thalassinidea and Anomura, though it may be of normal size in the Prezoea.

The significance of the median spine, when present, is uncertain. It appears to be present in all Euphausiacea, but not in the first Protozoea, so that it may not be a primitive character. In the Decapoda it is found in some Penaeidae, Homaridea and, according to Cano, in *Homola*, *Latreillia* and *Dynomene*, but the identification of these larvae is subject to doubt. It is present in some species of *Porcellana* and some Thalassinidea. A median spine often appears in the Caridea in the first post-larval stage, and may, perhaps, be the homologu of the median spine of the Euphausiacea, but delayed in development. It cannot be claimed that this spine is always an adult character thrown back into larval life, since it may be present in the larva and absent in the adult (*e.g. Upogebia*).

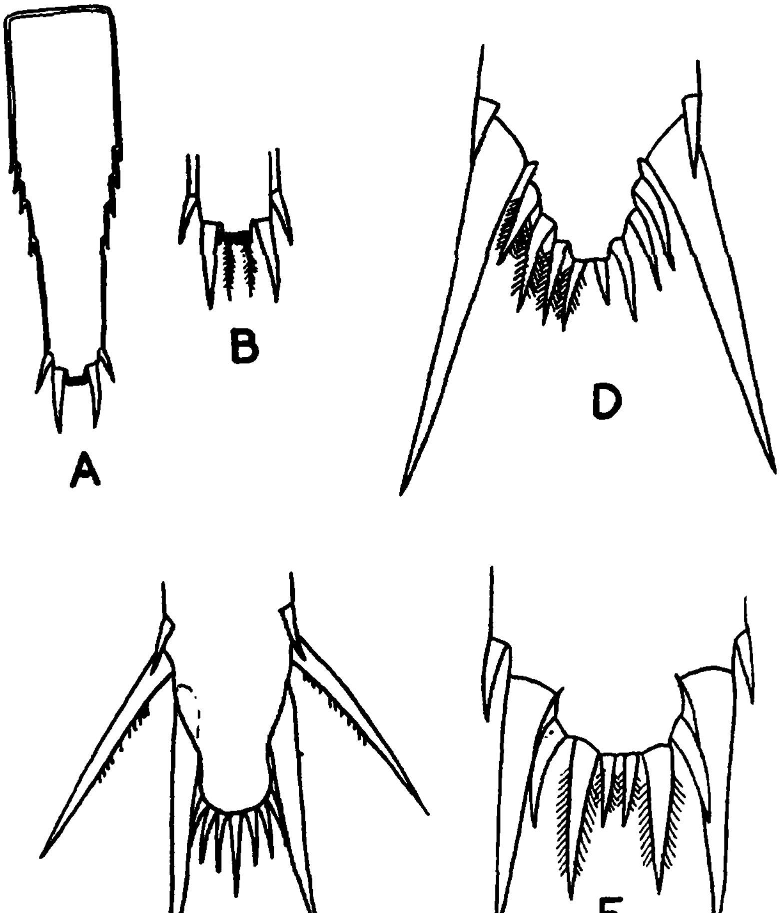

FIG. 31.—Telson. A, B. *Lophogaster typicus.* After Sars. C. *Thysanopoda cristata*, Furcilia 3. D, E. Two species of Caridean larvae (*Caricyphus*).

In Caridea the broad triangular telson becomes narrower at each moult after the appearance of the uropods until it is transformed into the parallel-sided form of the adult. During the transformation spines 1 and 2 move up along the outer margin, while spine 3 remains at the angle. Spine 4 may become relatively very large (Fig. 65). The remainder are generally reduced, and some, or all, may be lost at the moult to post-larval. Normally the number 8 + 8 is not exceeded. When the total number exceeds 16 they may be said to be "indefinite." This is only the case when larval development is more or less abbreviated—*e.g. Pasiphaea tarda*, *Sabinea septemcarinata*, *Axius stirhynchus*.

A peculiar form of telson is seen in some Euphausiacea (*Thysanopoda tricuspidata*). Here the part of the telson lying between the enlarged fourth pair of spines is produced, and bears six small spines and a median spine. An almost exactly similar form of telson is seen in certain Hoplophorid larvae (Coutière, 1905, *Caricyphus bigibbosus*) and also in adult *Lophogaster*. The resemblance is so close that it is difficult to believe that it can be without significance. This form of telson only appears in *Caricyphus* in the post-protozoeal phase, and in the Furcilia of Euphausiacea, which is about equivalent. Inasmuch as the Hoplophoridae are the most primitive Caridea it is possible that it is a primitive form of telson preserved from a predecapod ancestor.

EYE.

The compound eyes are always sessile in the first Protozoea of Penaeidea and stage 1 of all other Decapoda, becoming stalked in stage 2. The eyestalk may be very elongated in some Sergestidae and Caridea. This elongation of the eyestalk is the main characteristic of the larval genus *Eretmocaris*, but the genus is a composite one, and the long eyestalk has no doubt been independently acquired in genera not very closely related. The most extreme case is that of *E. dolichops*, in which the eye and stalk are as long as the whole body, and the stalk itself is jointed.

I have specimens of a Euphausid larva which may belong to *Stylocheiron*, in which the eyes are on long stalks. It is curious that a similar tendency to stalked eyes is found in the larvae of some fishes. These are all taken in depths of less than 500 metres (Murray and Hjort, 1912, p. 683).

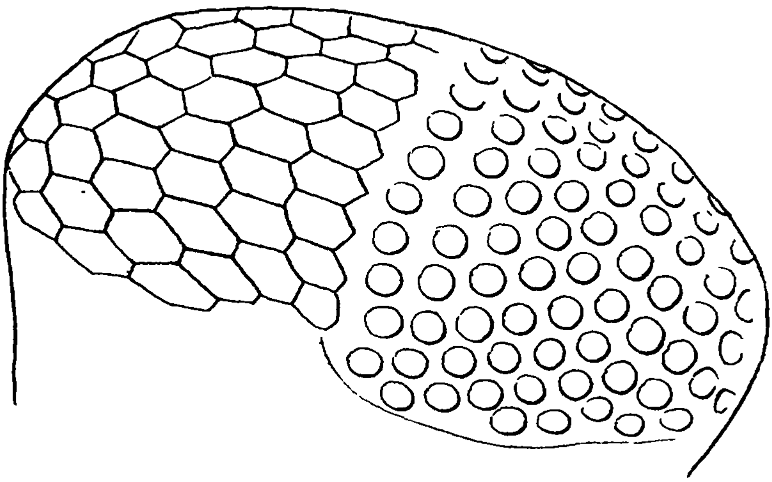

FIG. 32. *Eupagurus prideauxi.* Eye drawn from moulted skin.

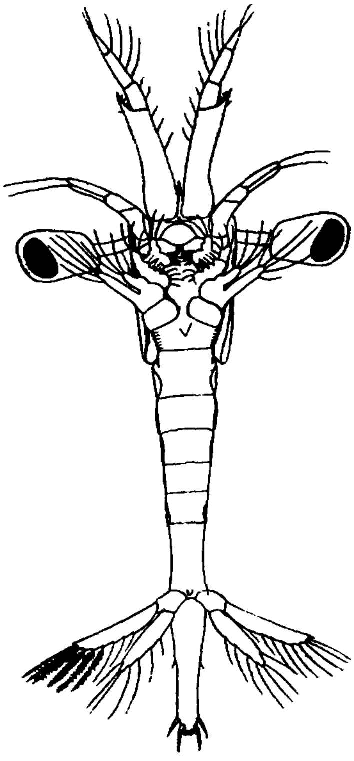

FIG. 33.—Euphausid larva with stalked eyes.

The ommatidia are often of different sizes in different parts of the eye. This is notable in some Euphausid larvae, *e.g. Thysanopoda* (Sars, 1885, pl. 31). In some species of *Sergestes* the eye of the larva has the ommatidia much longer in the posterior part, which consequently bulges out behind. Claus (1885, p. 65) noted that in Thalassinidea and Anomura the posterior ommatidia are longer than the anterior. I have noted in *Eupagurus prideauxi* that the anterior facets are of a different shape from the posterior facets; but I have not been able to repeat the observation on other species.

ANTENNULE.

The antennule of the early Nauplius of the Penaeidae is entirely unsegmented, though it may be ringed at the base. In the last Nauplius and first Protozoea a distal segment is clearly marked off from a peduncle of two segments, the first of which has four or five annular markings. The distal segment bears at its end two long setae, a short slender seta and two aesthetes.

The antennules are true preoral appendages and, as such, not built on the same plan as the others (see Calman, 1909, p. 11; Sollaud, 1923, p. 327). As pre-eminently sensory organs they were probably primitively unsegmented and uniramous, as they are in the Nauplius.

In all other normal Decapoda in stage 1 the peduncle is unsegmented, and it becomes three-segmented later. The third segment is separated first, the division between segments 1 and 2 being often very indistinct in stage 2.

The distal segment, which becomes the outer flagellum, seems to bear a constant number of setae and aesthetes, though they very in size. In a number of Caridea of different genera it was found that there was always an inner feathered seta and four aesthetes, of which two are longer than the rest. The innermost of them is short, and may taper to a fine point; but in some genera (*Lysmata*, *Saron*) there is a delicate membrane on either side, which may widen distally into a sort of spoon shape. The total number is therefore the same as in Penaeidae, and is probably universal, at least in early protozoeal stages.

The third segment of the peduncle bears dorsally in most, if not in all, Decapod larvae a structure which may be called the antennular lobe. This is a small rounded prominence bearing four or five feathered setae. This structure is found in the adult of most Decapoda and also in Mysidae, *Euphausia*, and probably in other Malacostraca. Its absence in the Nauplius and early Protozoea seems to show that it is primarily an adult structure.

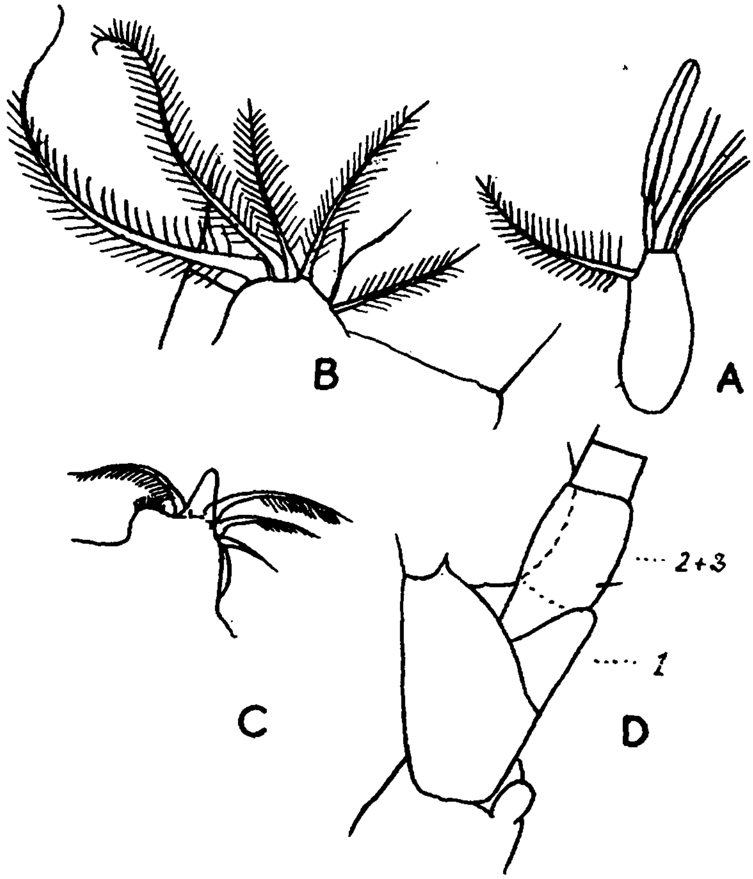

FIG. 34.—A. End of antennule, *Saron marmoratus*. B. Antennular lobe, *Lysmata*. C. Antennular lobe, *Neomysis vulgaris*. D. Antenna, *Leander longirostris*, last larva.

ANTENNA.

There are two views as to the homologies of the basal segments of the antenna. Coutière (1899, p. 146) and

Calman (1909, p. 265) regard the sympod as of two segments, and the flagellum as having three large basal segments. These three segments are articulated in a zigzag manner in the Decapoda, which makes their relation to the protopodite obscure. Borradaile (1917, p. 354) and Fraser (1936, pp. 60, 93) suppose that the apparent first segment of the endopod is actually a part of the basis—metabasipodite. Hansen (1924, p. 130) regards the two segments of the protopodite in Decapods as homologous with the second and third segments of

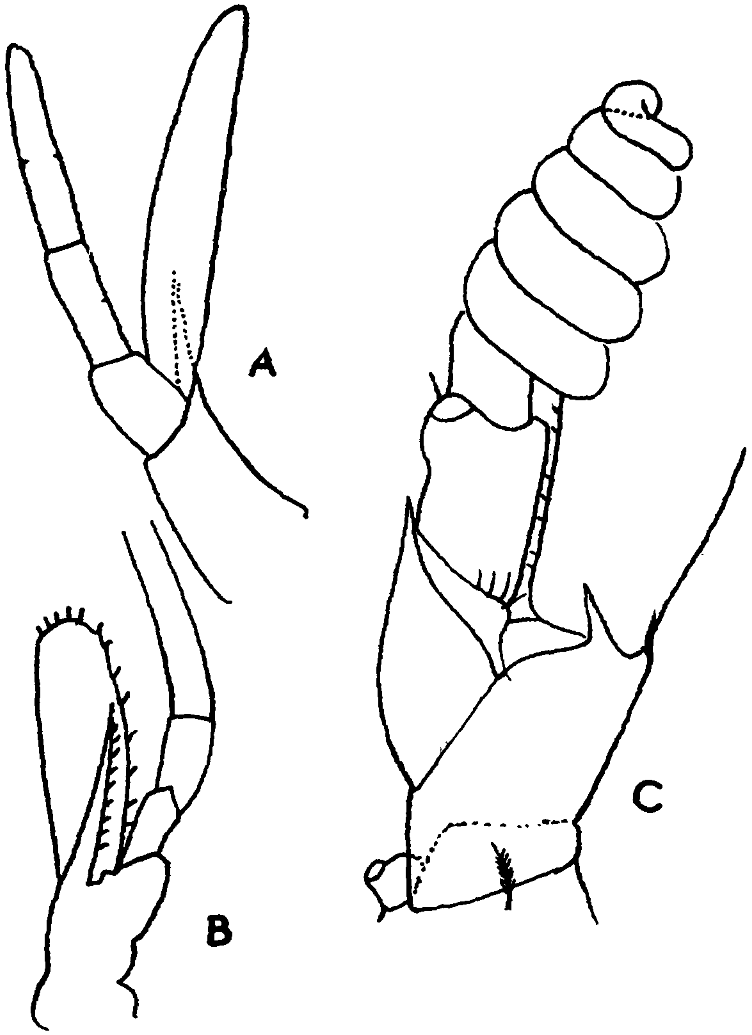

FIG. 35.—A. *Euphausia superba*, Cyrtopia 1, antenna. B. *Euphausia brevis*, Cyrtopia 2, antenna. C. *Rhynchocinetes rigens*, last larva. Antenna with flagellum regenerating.

Mysidacea and, inasmuch as the latter have three peduncular segments in the endopod, it is to be supposed that he interpreted the segments in the Decapoda in the same way as Calman and Coutière.

The development of the antenna in Caridea entirely supports Borradaile's interpretation, since the basal segment of the endopod can be seen to arise by splitting off of a part of the basis. This is particularly well seen in *Rhynchocinetes* (Fig. 35c), where this part of the basis has a distal inner spine, and is obviously not really a part of the endopod.

In the Euphausiacea it is very difficult to determine with certainty the origin of the segments. In the Furcilia there are two distinct segments in the protopod; but in the Cyrtopia it would seem that these two segments have fused into one, which bears an outer spine, as the second segment in Decapoda generally does. The origin of the basal segment of the endopod by splitting from the basis is less obvious than it is in the Decapoda, but it is the easiest interpretation.

The segmentation of the exopod has been discussed elsewhere (p. 23).

MANDIBLE.

A remarkable feature of Decapod development is the early loss of the mandible palp. In Euphausiacea the biramous palp is lost in the third Nauplius, and in the Penaeidea it disappears at the moult to the Protozoea. In all other Decapoda it is absent until a relatively late stage of the larva, and in many cases it does not appear at all until the post-larval phase is reached. Even then it may be delayed through several moults. In *Spirontocaris occulta* the first rudiment is seen in the 4th post-larval stage (Lebour, 1936, p. 100).

Claus noted the disappearance of the palp, and suggested that "von den Gliedmassen war der Mandibularfuss wahrscheinlich im Laufe der Entwickelung geschwunden, aber schon durch einen secundär erzeugten Taster ersetzt worden" (1876, p. 23).

This loss and reappearance of the palp is probably only an extreme example of the loss and replacement of parts mentioned above.

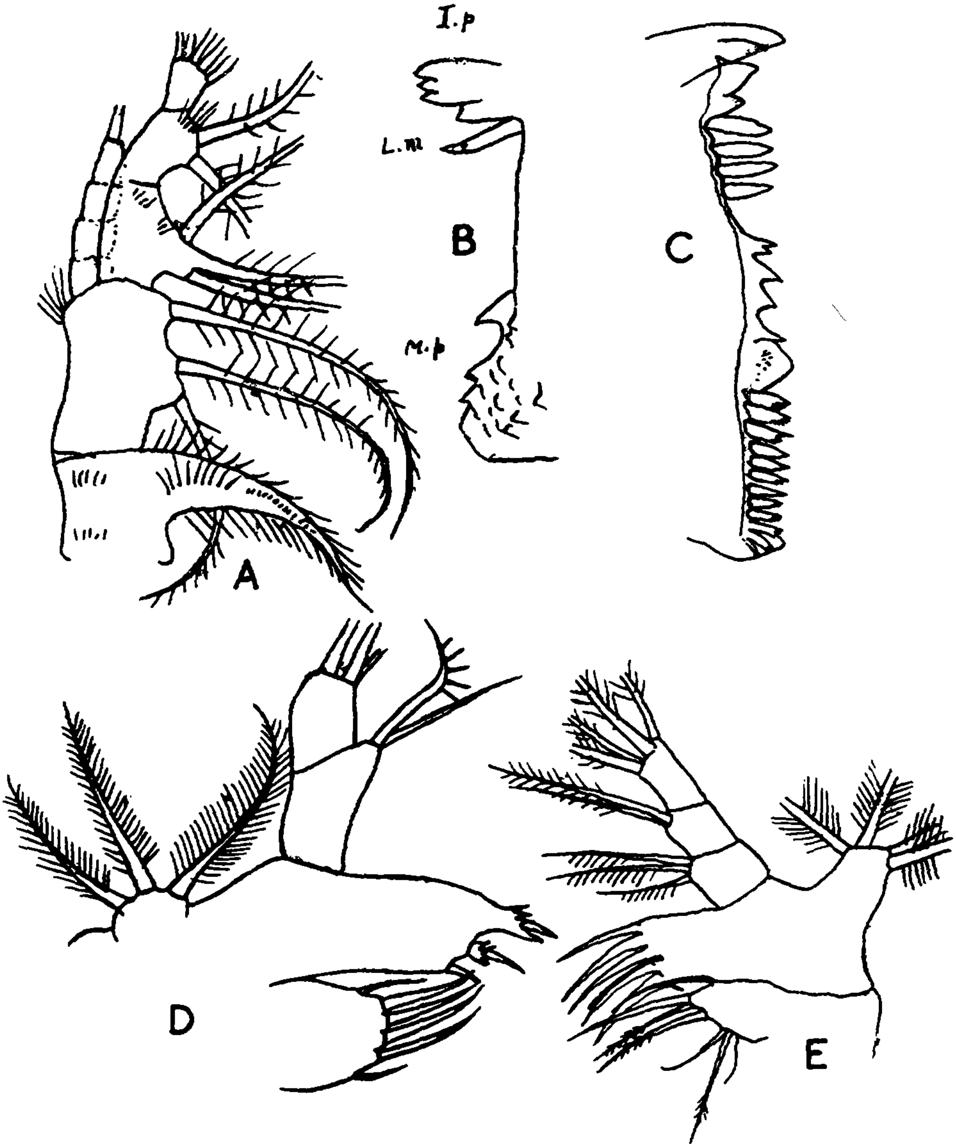

FIG. 36.—A.–C. Mandible. D.E. Maxillule. A. *Lepas*, Nauplius. B. *Pandalus montagui*. *I.p.*, incisor process ; *L.m.*, *lacinia mobilis* ; *M.p.*, molar process. C. *Acanthephyra purpurea*. D. *Rhynchocinetes rigens*. E. *Sergestes* sp., acanthosoma.

According to Hansen the *corpus mandibulae* is the precoxa, and this view is also accepted by Borradaile (1917, p. 58). Balss (1927) regards it as the coxa. Borradaile interprets the incisor process of the Malacostracan mandible as representing the coxa. The development of the limb in Decapoda throws no light on the homologies of the parts, since there is no distinct segmentation of the stem in the Nauplius.

I am unable to appreciate the evidence offered by Hansen for the homologies of the parts in Ostracoda and Copepoda ; indeed the evidence seems very strongly against his view (Fig. 37). In *Polycope setigera* Skogsberg's figure (1920, fig. 102) shows the *corpus mandibulae* quite clearly as coxa, and Hansen himself (1925, pl. 3, fig. 1*c*) is unable to show a coxal segment distal to it. In *Cypridina* there is a mandibular process on both coxa and basis, and between the two a very small sclerite can be detected. Hansen gives no reason for claiming this obscure sclerite as coxa. In the Nauplius of Copepoda and Cirripedia the limb obviously consists of coxa and basis, without trace of precoxa (Fig. 36), and it seems quite unjustifiable to assume that at the metamorphosis to the Copepodid in the former a large new proximal segment appears and a large distal segment is reduced to a minute sclerite or disappears altogether.

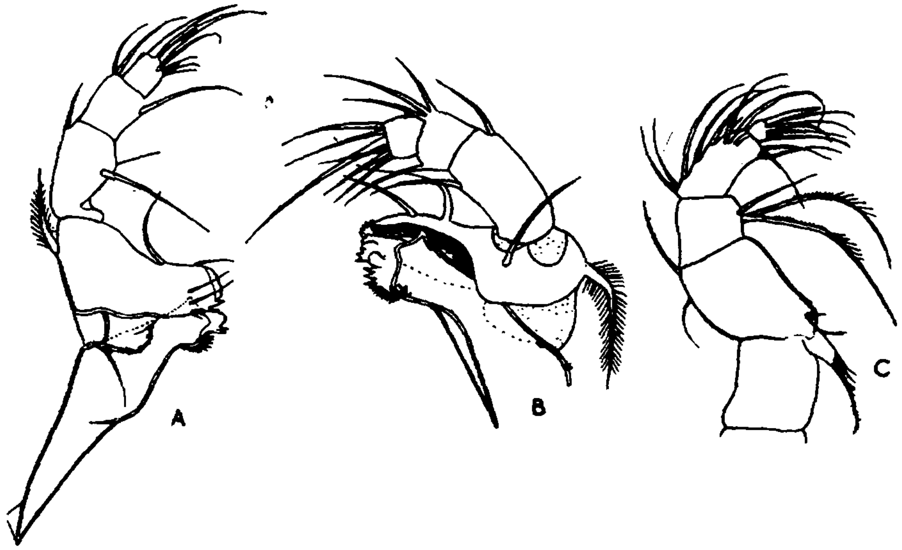

Fig. 37.—Mandible of Ostracoda. A. *Conchoecia* ; B. *Halocypris* ; C. *Asterope.*

There is in the Decapod larva from the first usually a differentiation into molar and incisor parts, but there is no deep cleft between the two, and no evidence that the two parts represent endites of two segments as Borradaile has postulated.

There is no reason to suppose that a mandible in which molar and incisor parts are undivided from each other is more primitive than one in which they are distinctly separated.

There are usually one or more movable spines adjacent to the incisor part, and representing the *lacinia mobilis*, on one mandible.

A striking departure from the usual type of larval mandible is seen in the Thalassinidae of the family Laomediidae (*Jaxea*, *Naushonia*) (Fig. 101). Here the incisor part of the left mandible is drawn out into a long pointed sickle, and the paragnath of the same side is similarly modified. Nothing of the kind is known in any other group, and its purpose is unknown. Modification of the mandible into a piercing organ has taken place in the adult Penaeid *Funchalia* and the limnetic Cladoceran *Leptodora*. Piercing mandibles are common among parasitic Copepoda.

MAXILLULE.

In the Penaeidea the endopod is long and of three segments, while there is an outer lobe with four long setae representing the exopod. In other Decapoda the endopod is more or less reduced, and the exopod is absent except in a few primitive forms. An exopod with two setae is shown by Ishikawa (1885) in *Paratya compressa*, but Yokoya (1931) in his description of the same species does not mention nor figure it. Presumably it disappears after stage 1. A very small vestige, with two setae, is found in *Caridina nilotica* (Gurney, 1927, p. 255). In *Atyaëphyra desmaresti* there is a relatively large exopod in stages 1–3, with three large setae. I have described an exopod on the maxillule of a larva attributed to *Acanthephyra* (1924c), but now proved to belong to *Rhynchocinetes*. The exopod

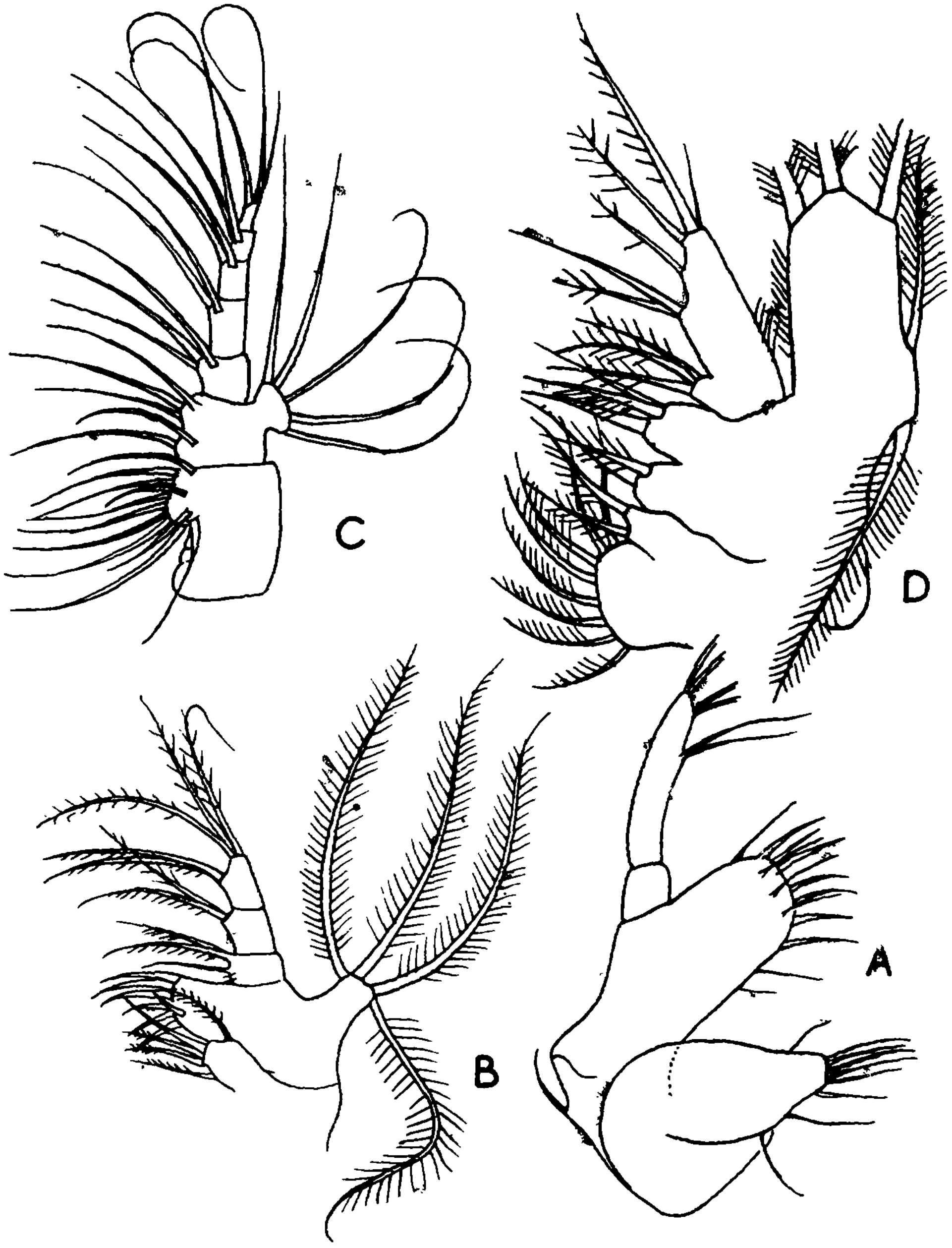

FIG. 38.—A.B. Maxillule. C.D. Maxilla. A. *Cancer pagurus*. B. *Sergestes* sp. C. *Sergestes* sp. D. *Tozeuma carolinense*.

is not present in *Acanthephyra* (Gurney and Lebour, 1941). In a Stenopid recently described by Miss Lebour (Gurney and Lebour, 1941) as "Stenopid A" there is a small exopod with setae. In some Caridea (*Processa*, *Hippolyte*, *Pandalus*) and some Brachyura there is an outer seta on the second segment which may be the vestige of an exopod.

The "pseudexopod" which is found in the adult of Euphausiacea and some Eudecapoda does not appear in the larva.

The maxillule and maxilla of Penaeidea are so much alike that it is necessary to suppose that the endites belong to homologous segments. In the maxilla these are, according to Hansen, coxa and basis; but he regards them as belonging in the maxillule to precoxa, with which the coxa is fused, and basis. In other Malacostraca they are supposed by him to represent precoxa and basis, the coxa being represented by a small intermediate sclerite. It seems to me that Hansen attached too much importance to these obscure sclerites, and that the two endites belong, as in the maxilla, to coxa and basis.

MAXILLA.

There is a very marked difference between the Euphausiacea and the Decapoda in the structure of the maxilla, for in the former there is no exopod in the larva, and the respiratory current is presumably caused by the exopods of the maxillule and maxillipede 1.

In the Penaeidea the coxa and basis each bear a pair of well-developed inner lobes. The endopod consists of five segments, and the exopod is very small in the Protozoea, and bears five setae only. In the Caridea there is a strong tendency to reduction of the distal coxal lobe, but it is entirely lost only in the Palaemonidae and Alpheidae. The endopod, outside the Penaeidea, is often unsegmented, but has inner seta-bearing lobes which indicate lost segments. In *Rhynchocinetes rigens* there is a distinct basal segment and three more indicated by setae. In *Processa edulis* there are four lobes, and a line of segmentation between 2 and

3. Usually there are not more than three lobes in Caridea (*e.g. Tozeuma*), and the endopod may be reduced to an unsegmented process with only apical setae (Palaemonidae and Alpheidae). In some Palaemonidae

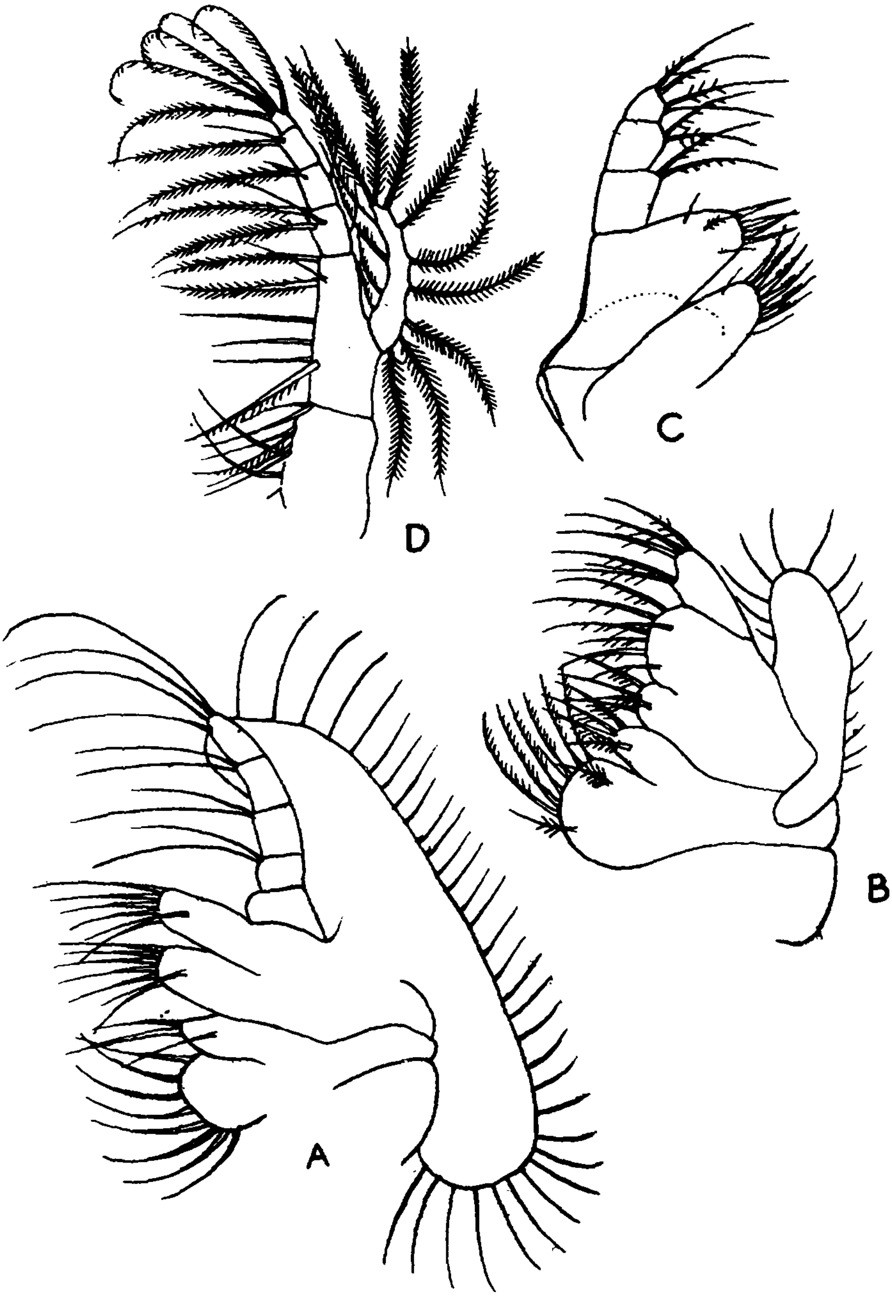

FIG. 39.—Maxilla. A. *Solenocera* (late Zoea). B. *Upogebia stellata*. C. *Upogebia stellata*, maxillule. D. *Sergestes* sp., maxillpede 1.

there may be a small basal lobe which is partly jointed off.

In Macrura Reptantia the two coxal lobes are usually both well developed, and the endopod may be three-segmented (*e.g.* some Axiidae). In this case five segments may be indicated by setae. In the Brachyura the coxal lobes are both present, but the endopod is reduced.

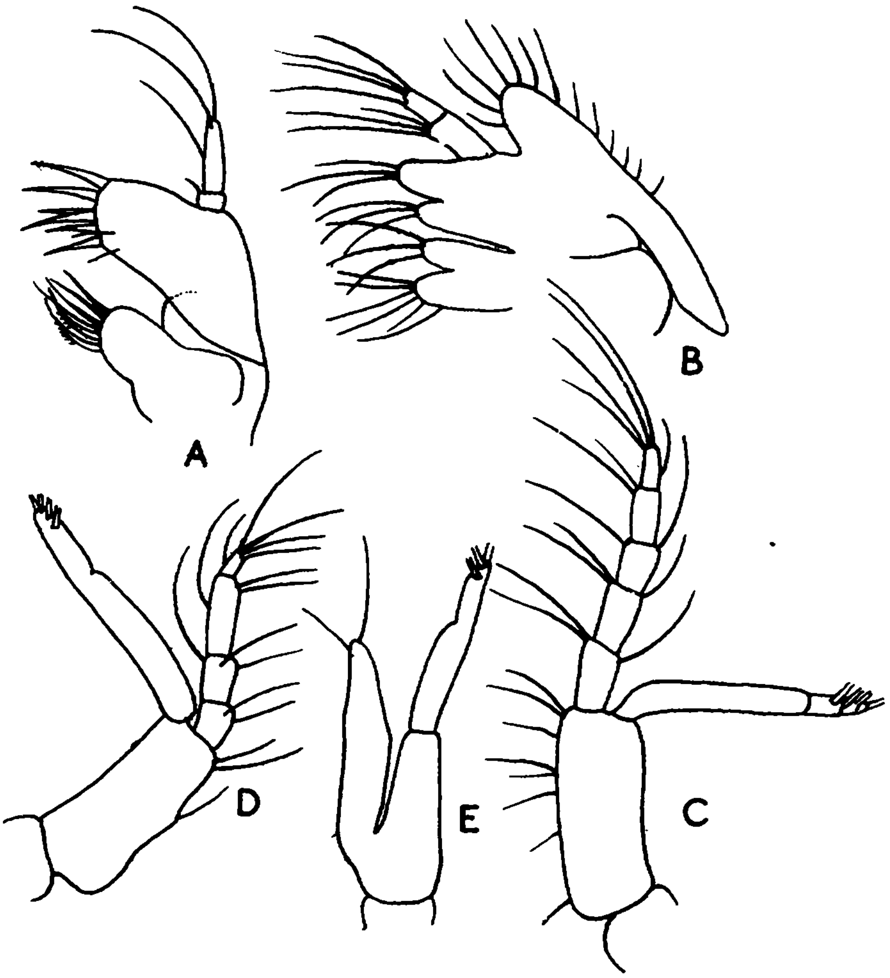

FIG. 40.—***Eupagurus*** **sp.** A. **Maxillule.** B. **Maxilla.** C. **Maxillipede 1.** D. **Maxillipede 2.** E. **Maxillipede 3.**

The exopod in stage 1 of the Caridea has no proximal extension, and only five setae, as in the Protozoea of the Penaeidea. In later stages the proximal extension soon develops, usually bearing one or more very large apical setae. This proximal part is quite bare of setae in Paguridae, *Upogebia* and *Naushonia*.

Hansen's interpretation of the structure of the maxilla is without doubt correct. For other views see Coutière, 1905, p. 27; Williamson, 1905, p. 75; Borradaile, 1917, p. 336.

MAXILLIPEDES.

In the Protozoea (Calyptopis) of Euphausiacea only one thoracic appendage is functional, and there may be no trace of any others until the succeeding Furcilia phase. In the Penaeidea the first two pairs are functional in the Protozoea, and the third is present as a rudiment. In Brachyura, Anomura and the Anomuran section of the Thalassinidea (*Upogebia*, etc.) only maxillipedes 1 and 2 are functional at first, the third remaining rudimentary or, at most, developing a setose exopod. The Caridea, Nephropsidea, Axiidae and *Callianassa* have three pairs of functional exopods from the first, while the endopod of maxillipede 3 is also well developed as a rule. The Phyllosoma larva of the Loricata has maxillipedes 2 and 3 functional, while the first pair is quite rudimentary at first.

The exopods of maxillipedes 2 and 3, like those of the legs when they appear, usually have four apical setae symmetrically disposed in stage 1, the number being increased from stage to stage. In Brachyura, when there is the full number of five stages, the numbers of setae are, with few exceptions, 4, 6, 8, 10, 12 (Lebour, 1934, p. 477). In some Caridea, in *Homarus* and in Phyllosoma the setae may be numerous, and probably indefinite in number.

In some Caridea in stage 1 there are only three apical setae instead of four, but this asymmetrical arrangement does not seem to have systematic significance, since both numbers are found within the family Hippolytidae. The following list of genera shows the distribution of the two arrangements so far as is known:

	3 apical setae.	4 apical setae.
Hippolytidae .	*Hippolyte.* *Spirontocaris.* *Caridion.* *Lysmata.* *Tozeuma.* *Chorismus.*	*Saron.* *Latreutes.*
Atyidae .		*Caridina.* *Paratya.* *Caridella.* *Limnocaridina.*
Pasiphaeidae .	*Leptochela.*	
Palaemonidae .		*Leander.* *Palaemonetes.* *Brachycarpus.*
Alpheidae .		*Alpheus.* *Athanas.*
Pandalidae .	*Pandalus.* *Pandalina.* *Chlorotocella.*	
Processidae .	*Processa.*	
Crangonidae .	*Crangon.* *Pontophilus.*	
Amphionidae .	*Amphion.*	

In the Penaeidea maxillipedes 1 and 2 are slender swimming limbs with coxa and basis not very unequal and very setose. The endopod is longer than the exopod, and of four or five segments. The exopod is short, with two or three pairs of apical setae, and also two or three unpaired setae on the outer margin. The form remains unchanged until the Zoea phase, when, in Penaeidae, a large epipod appears on maxillipede 1, and the exopod becomes nearly as long as the endopod. A great transformation takes place at the moult to post-larval, when, even though the appendage may be reduced and apparently functionless, it has the general form of the adult. In *Penaeus trisulcatus* where, according to Mme. Heldt, it is difficult to point to a sharp division between larval and post-larval phases, the maxillipedes in stage 5 differ profoundly from those of stage 4, and I regard that moult as the limit of the larval phase. In *Sergestes* and some Penaeidae the limit is quite definite.

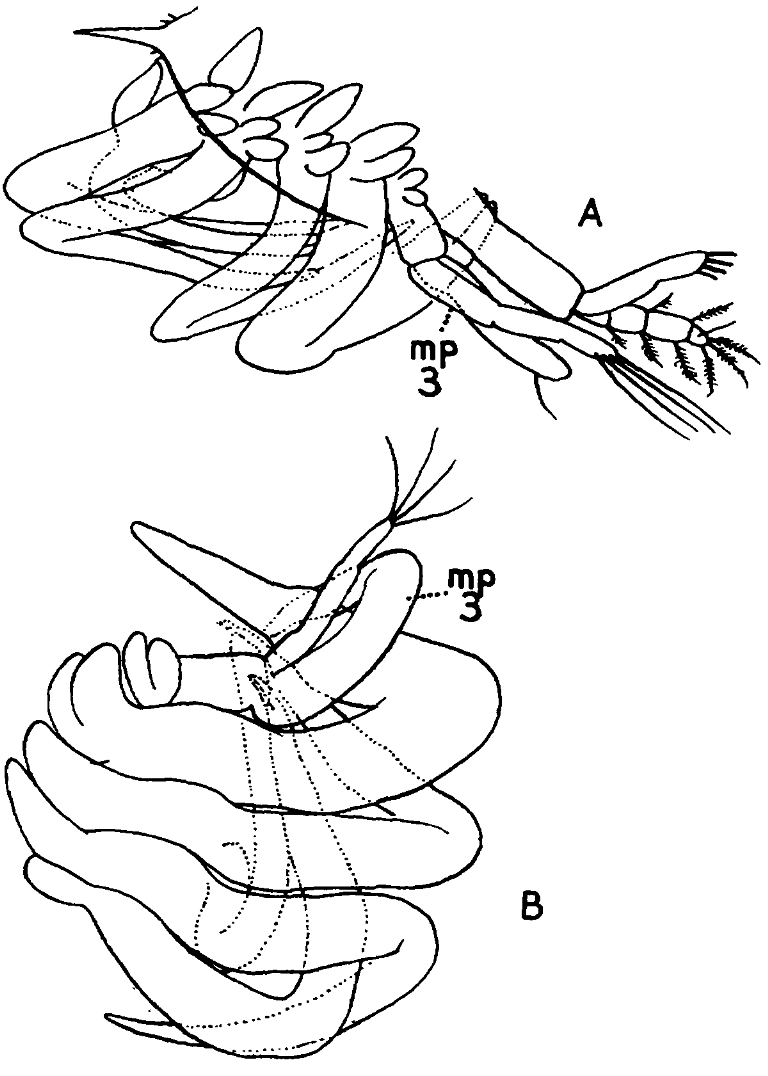

FIG. 41.—Maxillipede 3 and legs. A. *Galathea* sp. B. *Porcellana* sp.

In the Caridea maxillipedes 1 and 2 are almost exactly the same as in the Penaeid Zoea, but the exopod is always longer than the endopod, and does not have setae along its outer margin until in late stages the proximal expansion in maxillipede 1, which is characteristic of the group, may appear. The endopod of maxillipede 1 is never of more than four segments.

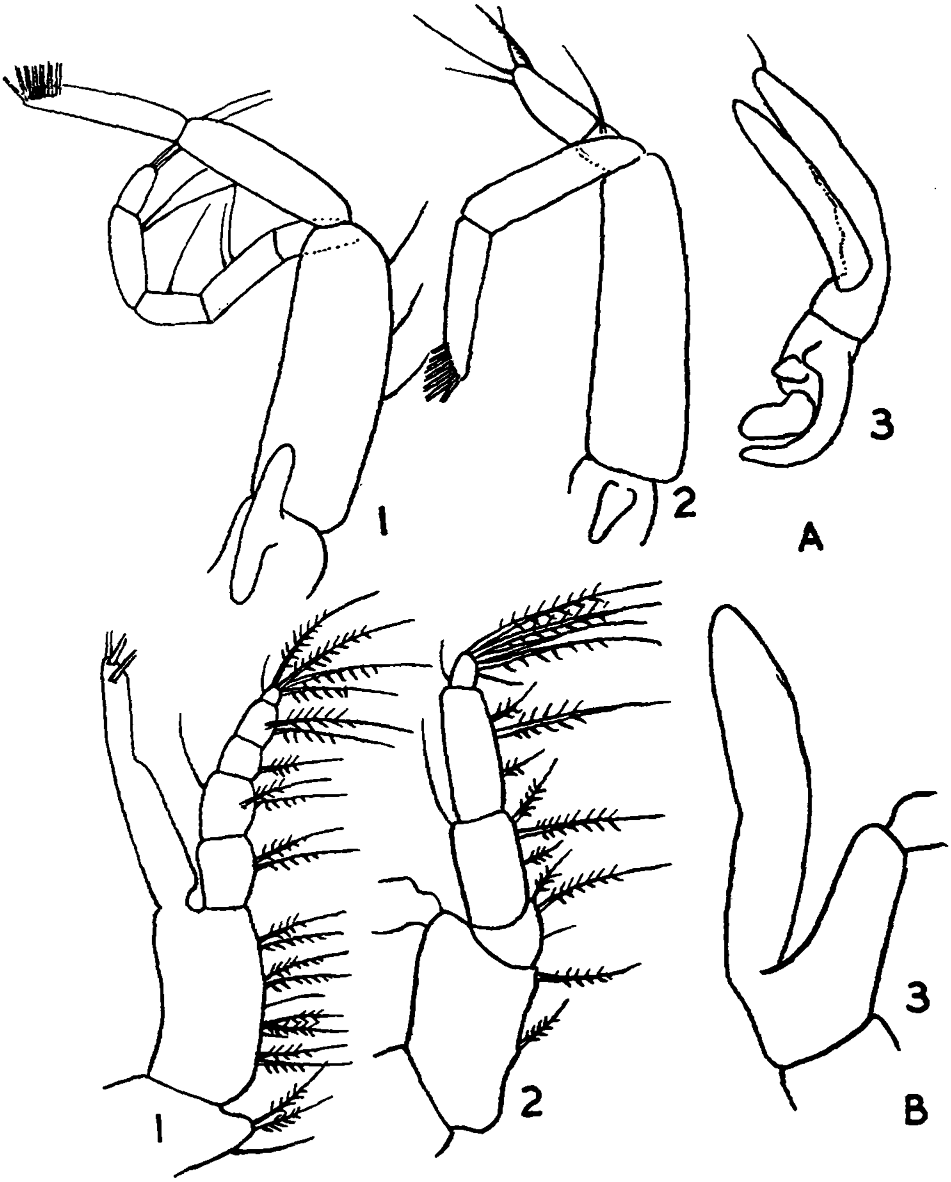

Fig. 42.—Maxillipedes 1–3. a. *Cancer pagurus*, Zoea. b. *Upogebia stellata*.

There is a tendency, which is very marked in Palaemonidae and Alpheidae, to a reduction of the coxa.

In Anomura, Thalassinidea of the Anomuran section, and Brachyura the coxa is very small, the basis long and cylindrical, while the exopod is generally divisible into a proximal and distal part, though not, perhaps, definitely segmented.

Maxillipede 3 in Penaeidea becomes a normal biramous limb like the legs, and the exopod does not go through a stage in which it resembles that of maxillipedes 1 and 2.

In Caridea the endopod is always longer than that of maxillipede 2, and generally closely resembles the following appendages, the dactyl having a single strong terminal spine. In some Palaemonidae in stage 1 there are two long slender spines instead of one large one—*e.g. Periclimenes grandis* (Gurney, 1938*b*, p. 17). In *Leander tenuicornis* there is the same arrangement, and this and other differences suggest that this species should be separated as a distinct genus. In *Alpheus* and *Athanas* this maxillipede in stage 2 has the dactyl produced into a very long spine, which reaches forwards to the labrum, and is very similar to leg 5 when the latter develops. In later stages it becomes normal. In *Synalpheus*, where development is more or less abbreviated, this modification of maxillipede 3 does not occur.

In Nephropsidea, Axiidae and *Callianassa* maxillipede 3 is quite normal and of the same type as in the Caridea ; but in other Thalassinidea and Anomura it is much modified. It is rudimentary in stage 1 and, when it develops, it is only the exopod which becomes functional. The endopod remains undifferentiated and springs from near the proximal end of the basis (Fig. 40E). In the Brachyura this maxillipede is rudimentary throughout larval life, but the endopod is normally placed.

In some Euphausiacea maxillipedes 2 or 3 may be very much longer than the other appendages. In *Thysanoessa* maxillipede 2 (leg of first pair, Sars) is very long, but not otherwise much modified. In *Nematoscelis* the same appendage is extremely long and slender, with a group of stout apical spines. In *Stylocheiron* it is the next appendage (leg of 2nd pair, Sars) which is hypertrophied, and may end in a prehensile chela.

LEGS.

It is only among the Penaeidea, Nephropsidea, Axiidae and some Caridea (Pasiphaeidae and Hoplophoridae) that functional exopods are found on all the legs of the larva. In the majority of the Caridea that of leg 5 is lost, and there is a tendency to lose others also. In the Pandalidae the exopod of leg 4 is generally lost, and there may be exopods only on legs 1 and 2 (*P. danae*, *P. hypsinotus*).* In *Chlorotocella* only leg 1 has an exopod (Gurney, 1937*c*). In the Crangonidae there are usually exopods on legs 1 and 2, but only on leg 1 in *Crangon vulgaris*. The number of exopods is not always the same in all the species of a genus, since in *Spirontocaris occulta* there are exopods on four legs, and only on three in *S. cranchii*, while in *Processa* there may be three or four. It is particularly notable that *Leptochela bermudensis* has exopods on legs 1–3 only in the larva though they are present on all the legs in the adult.

In *Troglocaris* the number of exopods seems to increase with age (see p. 203).

Among the Thalassinidea there may be a well-developed exopod on leg 5 in larvae supposed to belong to the Axiidae (Gurney, 1938*c*),† and they are present on legs 1–4 in some species of *Callianassa*. Even in the Anomuran section of the Thalassinidea they are found on three or four pairs. In the Anomura and Brachyura, however, they are absent from all the legs, except in *Dromia*, in which there is a setose exopod on leg 1 and rudimentary exopods on legs 2–4 (Lebour, 1934*b*).

In Penaeidea, Caridea and Thalassinidea the endopods may be slender, segmented, and setose, presumably having some function to perform in collecting food. Even in some Penaeidae such as *Penaeus trisulcatus* (Heldt, 1938, fig. 83) they are more or less undifferen-

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* An exopod is present on leg 4 in *Parapandalus richardi* and perhaps in *Plesionika* (Lebour, 1941).

† One of these larvae has now been proved to belong to *Paraxiopsis* by Miss Lebour.

tiated and apparently functionless in larval life. Similarly in some Caridea they develop directly to the adult form without apparently becoming functional (Crangonidae). In some Thalassinidea (Axiidae and Callianassidae) the endopods may be fully segmented and setose in the larva; but in *Upogebia* and *Jaxea* they are undifferentiated rudiments, seated low down on the basis in the larva. The same is the case in *Stenopus* where there are exopods on legs 1–3, and the endopods are large twisted rudiments (Gurney, 1936*c*) in the same position as in *Upogebia* for example. In all Anomura and Brachyura the endopods develop directly without being functional in the larva.

Abbreviation of larval life tends to the suppression of exopods on the legs. This is well seen in Palaemonidae, where Sollaud (1923) has given examples of progressive abbreviation. For instance in *Palaemonetes varians occidentalis* there are four exopods, whereas there are only two in *P. v. lacustris*, and none in *P. punicus*.

When development is abbreviated the legs usually appear all together, and develop directly to the adult form, the chelae not being functional till the post-larval phase. In *Homarus* the chelae of leg 1 would seem to be functional in stage 2, while in *Nephrops* they are well developed even in stage 1 (Jorgensen, 1925). A remarkable instance of precocity in the appendages is seen in a larva allied to *Nephrops*, but of unknown genus, from the Barrier Reef (Gurney, 1938*c*). This larva, though only in stage 2, has leg 1 very large in comparison with the body and the rest of the appendages, and with a fully developed chela. These chelae are almost equally large in *Enoplometopus* at a stage which is intermediate between larva and post-larva, but with legs 2–5 in larval form (Gurney, 1938*c*, p. 297).

In Palaemonidae and Alpheidae leg 5 may develop before legs 3 and 4, and become a very long appendage bent forwards and reaching with its long terminal spine beyond the mouth. It may even be longer than the whole body in some larval Palaemonidae. In larvae believed to belong to the Palaemonid genus *Anchistioides* it reaches its maximum development, and the terminal spine becomes a bent claw (Gurney, 1938*b*).

In the Hippolytid genus *Lysmata* leg 5 develops in stage 2, before legs 3 and 4, and becomes extremely large; but in this case the propod widens out into a large paddle-shaped structure (Caroli, 1918). In an unknown species allied to *Lysmata* leg 4 also has a paddle-like propod, but the limb is not so long as leg 5 (Gurney, 1937*b*, fig. 42). Another species from Bermuda has also the propod of leg 3 enlarged (Gurney and Lebour, 1941). There is a tendency to enlargement of the propods in *Caridion* (Sars, 1899; Lebour, 1930*a*); but in this case it is in legs 1 and 2.

A peculiar feature of the late larvae of Anomura is the position of leg 5, which is displaced inwards and forwards, so that it is entirely hidden by leg 4 (Fig. 41). It is not hidden in this way in Brachyura.

GILLS.

The homologies of the epipodial structures of Decapoda are made clear by the existence in *Eiconaxius* of a remarkably complete branchial series (Coutière, 1908). In a species of this genus from Barbados legs 1–5 have a pleurobranch, two arthrobranchs, recurved mastigobranch and setobranch. In leg 1 the setobranch has a branchial outgrowth, so that it is clear that the setobranch is of the same branchial system as the epipods or gills. Coutière concluded that the original epipod of the coxa has given rise by two successive divisions to four structures, anterior podobranch with setobranch, and posterior podobranch with mastigobranch. Of these four structures one or more is generally lost. The two arthrobranchs and the pleurobranch are, on his view, derived from the pre-epipod.

Borradaile (1907) had already expressed the opinion that four structures have been derived from the epipod —mastigobranch, setobranch, podobranch and anterior arthrobranch. Coutière, in earlier papers, had regarded the arthrobranch as derived from the epipod but, as Borradaile admits, there is no actual evidence of such derivation. It is frequently situated at some distance from the coxo-pleural joint (*e.g. Sicyonia*), and its derivation from the pre-epipod seems much more probable than its migration across a joint. Borradaile suggests that there may have been three rows of epipods and that the anterior arthrobranch represents the middle row.

It might be expected that some evidence would be found in larval development of the relation of the three series of gills to the primitive epipods, and that in those species in which the gill formula is reduced, rudiments of the lost gills might be traced. Of such "recapitulation" there is no evidence (see p. 27).

Gills are, in fact, structures special to the adult,* and it is commonly the case that they do not appear at all until the close of larval life. The series may, indeed, not be complete until late in the post-larval phase, *e.g. Pasiphaea* (Calman, 1902), *Parapasiphaë* (Kemp, 1910, p. 52), *Pandalus* (Berkeley). Their appearance in the larva is an example of the modification of larval structure by the precocious appearance of adult structures.

Claus in 1885 described and figured two stages in the development of the gills in Penaeid larvae of the *Euphema* type (= *Gennadas*). In young stages, before the pleopods develop, there are two series of gill rudiments, one above the other, on maxillipede 3 and legs 1–4, while maxillipede 2 has only one, apparently of the upper series. At a later stage a third series of rudiments appears on each appendage from maxillipede 2 to leg 5, in front of and at the same level as the uppermost of the earlier pair. Claus regarded the rudiments of the first two series as anterior and posterior arthrobranchs, and the third series as pleurobranchs; but

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* Bouvier (1908, p. 14) regarded the exceptionally rich gill-formula of *Cerataspis* as a larval character.

he pointed out that this terminology which Huxley introduced as a result of the study of *Astacus* is not

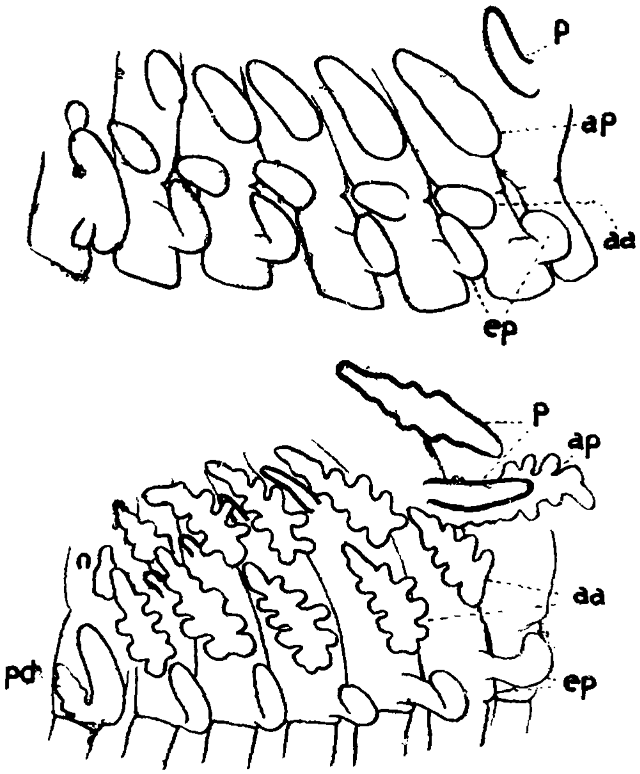

FIG. 43.—Two stages in the development of the gills in the Penaeid *Gennadas*.

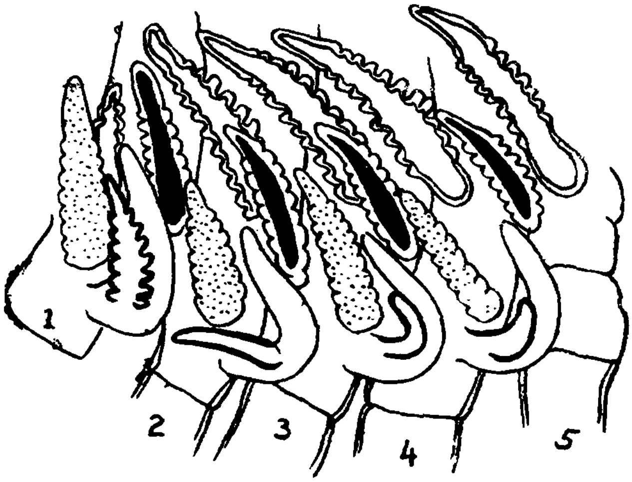

FIG. 44.—Gills of *Homarus*, stage 1.

applicable to the Penaeidae, since the two gills of the dorsal series are placed side by side in the position of pleurobranchs (Fig. 43).

In my own description of the larva of *Gennadas* (Gurney, 1924*a*, p. 58) I have referred to the dorsal rudiments of the earliest stage as pleurobranchs, since they are inserted so far above the arthrobranch, and I supposed the last series to appear was that of the posterior arthrobranchs. Burkenroad (1934, p. 117) states that the upper of a pair of arthrobranchs is always placed behind the lower one, and that the upper gill in front of the lower arthrobranch must be a pleurobranch. Renewed examination of the larvae of *Gennadas* shows that he is right, but it should be noted that, in many early larvae, at the time when the arthrobranchs only have appeared on legs 1–4, there is a perfectly distinct gill rudiment on leg 5, which appears to be one of the dorsal series of arthrobranchs. In later stages this gill is large and foliated when the pleurobranchs of the anterior legs are small rudiments. This gill on leg 5 is always regarded as a pleurobranch, and it has to be supposed that it appears precociously on this limb before the other gills of the same series.

Claus supposed his larvae to belong to *Penaeus*, and was consequently forced to assume that certain gills found in the larva disappeared in the adult; but it is clear that he was actually dealing with *Gennadas* and that there is no such disappearance of gills.

Williamson (1901, p. 113) stated that, in *Crangon vulgaris*, the gills appear first as podobranchs, pass through a stage in which they have the position of arthrobranchs, and finally become pleurobranchs. Such a shifting of position during development has not been seen in any other species, and nothing of the kind takes place in the closely allied *Philocheras trispinosus* (Gurney, 1903, p. 27). Coutière (1905) stated that the podobranch of maxillipede 3 in Caridea has been displaced on to the coxo-pleural joint, so that there appear to be two arthrobranchs on this limb, but I do not know of any evidence for this assumption.

Burkenroad (1939, p. 316) states that the dorsal gills of Caridea occupy the position anterior to the arthrobranchs, when the latter are present, characteristic of pleurobranchs, and points out the contrast in the appearance of pleurobranchs before the arthrobranchs in Caridea as compared with their delayed appearance, or absence, in Penaeidae. He also states that the order of appearance of the gills in Stenopidea is the same as that in the Caridea.

How far this difference in development of the gills can be regarded as significant is not clear. The fact that the gill on leg 5 in Penaeidae is accepted as a pleurobranch and yet appears in *Gennadas* at the same time as the arthrobranchs seems to show that there is no fundamental difference in the order of appearance, but that the contrast is due to a general tendency to loss of pleurobranchs in Penaeidae, whereas this series is the more important in Caridea.

On the other hand, the suggestion may be put forward that, in spite of their position anterior to the arthrobranchs, the dorsal gills of Caridea may actually be arthrobranchs of the dorsal series. It should be noted that when the arthrobranchs are present in Caridea there is never more than one on any leg—which was assumed by Claus to be the anterior one of the pair. There may be two on maxillipede 3, but in this case there is never a pleurobranch also.

Claus says of the gills of Caridea that they are, by position, pleurobranchs, but " indessen durfte die Lage allein nicht fur diese Deutung entscheidend sein."

There is a marked tendency in most other Decapods to a reduction or disappearance of the pleurobranchs, and it may be said to be more likely that they have disappeared (except perhaps for the gill on leg 5) in Caridea than that the Caridea should be exceptional in their early appearance and survival.

The following series of gill-formulae may be found useful in dealing with advanced larvae of unknown parentage. They are taken from many sources, and I have checked very few of them myself. In the Penaeidae it will be noticed that the two gills of maxillipede 2

Table of Gill-formulae.

Ep, epipod ; a. arthrobranch ; p, pleurobranch ; m. mastigobranch ; m l, mastigobranch with podobranch ; r, rudimentary.

	Mxp. 1.		Mxp. 2.			Mxp. 3.			Leg 1.			Leg 2.			Leg 3.			Leg 4.			Leg 5.
	Ep.	a.	Ep.	a.	p.	Ep.	a.	p.	Ep.	a.	p.	Ep.	a.	p.	Ep.	a.	p.	Ep.	a.	p.	p.
PENAEIDEA.																					
PENAEIDAE.																					
Solenocera	m	..	m l	2	..	m	2	1	m	2	1	m	2	1	m	2	1	m	2	1	1
Penaeus	m	1	m l	2	..	m	2	1	m	2	1	m	2	1	m	2	1	..	1	1	1
Trachypenaeus	m	..	m l	2	..	..	2	1	m	2	1	m	2	1	m	2	1	..	1+r	..	..
Xiphopenaeus	m	r	m l	2	..	..	2	1	m	2	1	m	2	1	m	2	1	..	1	..	..
Parapenaeus	m	r	m l	2	..	..	2	1	m	2	1	m	2	1	m	2	1	..	1	1	..
Penaeopsis	m	r	m l	2	..	..	2	1	m	2	1	m	2	1	m	2	1	..	1+r	1	..
Sicyonia	m	..	m l	1	1	..	2	1	m	2	..	m	2	..	m	2	..	..	1+r	..	..
Benthesicymus	m	1	m l	1	1	m l	2	1	m l	2	1	m l	2	1	m l	2	1	m	2	1	1
Gennadas	m	1	m l	1	1	m l	2	1	m l	2	1	m l	2	1	m l	2	1	m	2	1	1
Aristeus	m	1	m l	1	r	m l	2	r	m l	2	r	m l	2	r	m	2	r	..	2	r	1
SERGESTIDAE.																					
Sergestes	m	..	m l	r	..	..	1+r	..	..	1+r	..	..	1+r	..	..	2	..	..	2	..	..
Sicyonella	m	..	m l	..	..	..	1+r	..	..	1+r	..	..	1+r	..	..	2	..	..	2	..	..
CARIDEA.																					
PASIPHAEIDAE.																					
Pasiphaea	m	..	..	..	..	..	..	..	..	1	1	..	1	1	..	1	1	..	..	1	1
Sympasiphaea	m	..	r	..	..	r	1	..	..	1	1	..	1	1	..	1	1	..	1	1	1
Parapasiphaë	m	..	m	..	..	m	2	..	..	1	1	..	1	1	..	1	1	..	1	1	1
Psathyrocaris	m	..	m l	..	..	m	2	..	..	1	1	..	1	1	..	1	1	..	1	1	1
Leptochela	m	..	m	..	..	m	2	..	..	1	1	..	1	1	..	1	1	..	1	1	1
BRESILIIDAE.																					
Bresilia	m	..	m	..	..	..	..	..	..	..	1	..	..	1	..	..	1	..	..	1	r

HOPLOPHORIDAE.																					
Acanthephyra .	m	..	m 1	..	..	m	2	..	m	1	1	m	1	1	m	1	1	(m)	1	1	1
Ephyrina . .	m	..	m 1	..	..	m	2	..	m	1	1	m	1	1	m	1	1	(m)	1	1	1
ATYIDAE.																					
Caridina . .	m	..	1	..	..	m	1+r	..	m	1	1	m	..	1	m	..	1	m	..	1	1
Atyaëphyra . .	m r	..	1	..	..	m	1	..	m	..	1	m	..	1	m	..	1	m	..	1	1
Limnocaridina .	..	..	..	..	..	..	..	..	..	..	1	..	..	1	..	..	1	..	..	1	1
NEMATOCARCINIDAE.																					
Nematocarcinus .	m	..	m 1	..	..	m	2	..	m	1	1	m	1	1	m	1	1	m	1	1	1
PSALIDOPODIDAE.																					
Psalidopus . .	m	..	m	..	..	m r	r	..	..	r	1	..	r	1	..	r	1	..	r	1	1
PANDALIDAE.																					
Pandalus . .	m	..	m 1	..	..	m	2	..	m	1	1	m	1	1	m	1	1	m	1	1	1
Plesionika . .	m	..	m 1	..	..	m	2	..	m	1	1	m	1	1	m	1	1	m	1	1	1
Pandalina . .	m	..	m 1	..	..	m	2	..	m	..	1	m	..	1	m	..	1	m	..	1	1
Heterocarpus . .	m	..	m1	..	..	r	1	..	r	1	1	r	1	1	r	1	1	r	1	1	1
ALPHEIDAE.																					
Alpheus (*strenuus*) .	m	..	m	..	..	m	1	..	m	..	1	m	..	1	m	..	1	m	..	1	1
Synalpheus . .	m	..	m	..	..	..	1	..	..	..	1	..	..	1	..	..	1	..	..	1	1
PALAEMONIDAE.																					
Leander . . .	m	..	m 1	..	..	m	1	1	..	..	1	..	..	1	..	..	1	..	..	1	1
Palaemonetes . .	m	..	m 1	..	..	m	1	..	..	..	1	..	..	1	..	..	1	..	..	1	1
HIPPOLYTIDAE.																					
Hippolyte . .	m	..	m	..	..	..	..	..	..	..	1	..	..	1	..	..	1	..	..	1	1
Spirontocaris . .	m	..	m 1	..	..	m	..	..	m	..	1	m	..	1	m	..	1	m±	..	1	1
Caridion . .	m	..	m	..	..	m	..	..	m	..	1	m	..	1	m	..	1	m	..	1	1
Latreutes . .	m	..	m	..	..	r	..	..	m	..	1	m	..	1	m	..	1	m ±	..	1	1
Leontocaris . .	m	..	m	..	..	..	1	..	..	..	1	..	..	1	..	..	1	..	..	1	1
THALASSINIDEA.																					
AXIIDAE.																					
Axius . . .	m	..	m 1	r	..	m 1	2	..	m 1	2	..	m 1	2	1	m 1	2	1	m 1	2	1	r
Calocaris . .	m	..	m r	r	..	m 1	2	..	m 1	2	..	m 1	2	..	..	2	..	..	2	..	..
Calocarides . .	..	..	m r	1	..	m 1	2	..	m 1	2	..	m 1	2	..	m 1	2	..	m	2	..	..
Eiconaxius . .	..	..	m	..	..	m 1	..	..	m 1	2	..	m 1	2	1	m 1	2	1	m	2	1	..
Paraxius . .	..	..	mr 1	2	..	mr 1	2	..	mr1	2	..	mr 1	2	..	..	2	..	..	2	..	..
Iconaxiopsis . .	m	..	mr	r	..	m 1	2	..	m 1	2	..	m 1	2	1	m 1	2	1	m	2	1	..

	Mxp. 1.		Mxp. 2.			Mxp. 3.			Leg 1.			Leg 2.			Leg 3.			Leg. 4.			Leg 5.
	Ep.	a.	Ep.	a.	p.	Ep.	a.	p.	Ep.	a.	p.	Ep.	a.	p.	Ep.	a.	p.	Ep.	a.	p.	p.
CALLIANASSIDAE.																					
Callianassa subterranea	m	..	mr	..	..	..	2	..	..	2	..	..	2	..	..	2	..	..	2	..	..
UPOGEBIIDAE.																					
Upogebia . .	..	..	m	..	..	mr	2	..	..	2	..	..	2	..	..	2	..	..	2	..	1±
LAOMEDIIDAE.																					
Jaxea . . .	m	1	m 1	2	..	m 1	2	..	m 1	2	..	m 1	2	..	m 1	2	..	m	2	..	..
Naushonia . .	m	1	m 1	2	..	m 1	2	..	m 1	2	..	m 1	2	..	m 1	2	..	m	2	..	..
AXIANASSIDAE.																					
Axianassa . .	m	..	m 1	2r	..	m 1	2	..	m 1	2	..	m 1	2	..	m 1	2	..	m	2	..	..
THALASSINIDAE.																					
Thalassina . .	..	..	m	1	..	m	2	..	m	2	..	m	2	..	..	2	..	..	2	..	..
NEPHROPSIDEA.																					
NEPHROPSIDAE.																					
Nephrops . .	m	..	m 1	..	..	m 1	2	..	m 1	2	..	m 1	2	1	m 1	2	1	m 1	2	1	1
Homarus . .	m	..	m 1	..	..	m 1	2	..	m 1	2	..	m 1	2	1	m 1	2	1	m 1	2	1	1
Phoberus . .	m	..	m 1	..	..	m 1	2	..	m 1	2	..	m 1	2	1	m 1	2	1	m 1	2	1	1
Nephropsis . .	m	..	m	..	..	m 1	2	..	m 1	2	..	m 1	2	1	m 1	2	1	m 1	2	1	1
ASTACIDAE.																					
Astacus . . .	m	..	m 1	1	..	m 1	2	..	m 1	2	..	m 1	2	r	m 1	2	r	m 1	2	r	1
Cambarus . .	m	..	m 1	1	..	m 1	2	..	m 1	2	..	m 1	2	r	m 1	2	r	m 1	2	r	..
Astacopsis . .	r	..	m 1	1	..	m 1	2	..	m 1	2	..	m 1	2	1	m 1	2	1	m 1	2	1	1
Astacoides . .	r	..	m 1	r	..	m 1	1	..	m 1	1+r	..	m 1	1+r	..	m 1	1+r	..	m 1	1+r	..	1
PALINURA.																					
ERYONIDAE.																					
Polycheles . .	m	..	..	..	..	r	1	..	m 1	2	..	m 1	2	1	m 1	2	1	m 1	2	1	1
PALINURIDAE.																					
Panulirus . .	m	..	m 1	1	..	m 1	2	..	m 1	2	..	m 1	2	1	m 1	2	1	m 1	2	1	1
Palinurus . .	m	..	m 1	1	..	m 1	2	..	m 1	2	..	m 1	2	1	m 1	2	1	m 1	2	1	1
SCYLLARIDAE.																					
Scyllarus . .	m	..	m	..	..	m 1	2	..	m 1	2	..	m 1	2	1	m 1	2	1	m 1	2	1	1

STENOPIDEA.																					
Stenopidae.																					
Stenopus . .	m	l	m l	l	..	m	2	1	m	2	1	m	2	1	m	2	1	m	2	1	1
Spongicola inermis (Bouvier)	m	..	m lr	..	..	..	1	1	..	1	1	..	1	1	..	1	1	..	r	1	1
S. venusta M.-Ed. and Bouvier	m	..	m l	l	1	m	2	1	m	2	1	m	2	1	m	2	1	m	2	1	1
Spongicoloides .	m	r	m lr	r	...	m	1	1	..	1	1	..	1	1	..	1	1	..	1	1	1
GALATHEIDEA.																					
Galatheidae.																					
Galathea squamifera	m	..	..	..	..	m	2	..	m	2	..	m	2	1	m	2	1	..	2	1	1
Ptychogaster } *Uroptychus* } .	..	..	..	..	..	..	2	..	..	2	..	..	2	1	..	2	1	..	2	1	1
PAGURIDEA.																					
Paguridae.																					
Eupagurus } *Lithodes* } . .	..	..	..	..	..	m	2	..	..	2	..	..	2	..	..	2	..	..	2	..	1
DROMIACEA.																					
Dromiidae.																					
Dromia . . .	m	..	m l	..	..	m	2	..	m	2	..	..	2	1	..	2	1	..	1	1	1
Conchoecetes . .	m	..	m l	..	..	m l	2	..	m	2	..	..	2	1	..	2	1	..	1	1	1
Homolodromiidae.																					
Homolodromia .	m	..	m l	l	..	m l	2	..	m l	2	..	m l	2	1	m l	2	1	..	2	1	1
Arachnodromia .	m	..	m *l*	r	..	m *l*	*2*	..	m *l*	*2*	..	m *l*	*2*	*l*	m *l*	*2*	*l*	m±*l*	*2*	*l*	*l*
Homolidae.																					
Homola . . .	m	..	m l	l	..	m	2	..	m	2	..	m	2	1	m	2	1	..	1	1	..
Latreillia . .	m	..	m l	..	..	m	2	..	..	2	..	..	..	1	..	..	1	..	..	1	..
BRACHYURA.																					
Cancer . . .	m	..	m l	l	..	m l	2	..	..	2	..	..	..	1	..	..	1	..	..	..	..
Ocypoda . . .	m	..	m l	..	..	m l	2	..	..	2	..	..	..	1	..	..	..	..	..	..	..
Pinnotheres . .	m	..	..	..	..	m	1	..	..	2	..	..	..	..	..	..	..	..	..	..	..
Ilia	m	..	r	..	..	r	2	..	..	2	..	..	..	..	..	..	..	..	..	..	..

may be regarded by some as arthrobranchs and by others as arthrobranch and pleurobranch. In the Sergestidae the gills are given as pleurobranchs by Hansen and others, while Burkenroad (1937, p. 511) regards them as both arthrobranchs.

PLEOPODS.

The pleopods, though they may be large, and may rarely have short setae, do not seem ever to be functional in Decapoda until the moult to the post-larval phase. In *Penaeus trisulcatus* the fourth zoeal (or Mysis) stage has setose pleopods and these are, from that stage, the effective organs of locomotion (Heldt, 1938, p. 143). In this species there is no clear distinction between larval and post-larval phases, at all events in the sequence observed in the laboratory, and I am not prepared to agree with Mme. Heldt in the limits which she assigns to each.

In the Euphausiacea the limit between larval and post-larval phases is also by no means sharply defined, and the pleopods become setose and functional in succession during the zoeal (Furcilia) stages.

In the Decapoda the pleopods appear simultaneously except in the Sergestid genus *Acetes*, and in the Penaeid *Gennadas* and allied genera. In *Acetes* (Müller, 1869, fig. 33, and Menon, 1933) they appear first as non-setose rudiments and then as setose appendages, as they do in Euphausiacea, the sequence being as follows :*

	Non-setose.	Setose.
Stage 4 (" Mysis ")	3	0
,, 5 (Mastigopus)	0	3
,, 6	1	3
,, 7	1	4
,, 8	0	5

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* This table is compiled from Menon's figures. In the text he mentions rudiments of pleopod 5 in stages 5 and 6, but they are not shown in his figures, and must be very small. Müller's excellent figure of stage 6 shows a minute rudiment of pleopod 5 and a very large one of pleopod 4.

In *Gennadas* pleopod 1 appears before the rest, in a peculiar bulbous form.

As a general rule the pleopods appear after the uropods, but the order may be reversed when development is shortened and the larva has all the appendages except the uropods when first hatched (*e.g. Palaemonetes varians lacustris* ; Sollaud, 1923, fig. xviii).

In Penaeidea and Caridea there are always the full number of five pairs, with the single exception of *Leptochela*, in which pleopod 1 does not appear at all in larval life (Gurney, 1936*a*).

In Stenopidea pleopod 1 seems generally if not always to be delayed in appearance till the end of larval life (Lebour in Gurney and Lebour, 1941).

In all Macrura Reptantia, Anomura and Brachyura the first pair is absent, but they are usually present, and paired, on somites 2–5. In *Eryoneicus*, which is the natant stage of *Polycheles*, pleopod 1 is present, and may even be modified as in the adult male ; but, in the earliest stages known, it is absent (Balss, 1921, p. 196).

In *Spiropagurus* (= *Anapagurus*) *chiroacanthus* (Sars, 1889) there are three pleopods only, that of somite 5 being absent, while in *Diogenes pugilator* there are only two, on somites 3 and 4 (Gurney, 1927, p. 282). In the first post-larval stage of this species there are still only two pairs, whereas in *S. chiroacanthus* there are four at this stage. In the Galatheid *Diptychus nitidus* the pleopod of somite 5 is absent (Bouvier, 1892), as it is also in *Porcellana platycheles* and *P. longicornis*. On the other hand, this appendage is present in *P. inaequalis* (Gurney, 1938*a*) and in some other Porcellanid larvae which have been described. Larvae of *Porcellana* with four pairs of pleopods are known from Plymouth, but the adult has not yet been found. Pleopod 2 disappears in the adult female of *Porcellana*, but it persists in the male.

In the primitive symmetrical Pagurids of the genus *Mixtopagurus* there are paired pleopods in both sexes on all the segments of the abdomen in the adult (Boas, 1926).

In the Brachyura four pairs are always present, and are functional in the Megalopa.

In the Paguridea generally one of each pair is lost in the adult, and the number retained is not the same in male and female. In *Eupagurus longicarpus* (Thompson, 1903) the male loses the pleopod of somite 2 6–12 days after the Glaucothoë (1st post-larval stage) stage. But in *E. bernhardus* (Giard, 1886) the male when parasitized by the Bopyrid *Athelges* has pleopods on this somite as in the female. As Thompson points out, if the post-larval development is the same as in *E. longicarpus*, the male must be parasitized very early, or this pleopod must reappear. In *Lithodes maia* all the pleopods are lost in the male, and the female has four unpaired. This loss takes place in *Neolithodes* at the moult from the Glaucothoë stage (Marukawa, 1933). The post-larval development of the pleopods in *Munida subrugosa* has been described by Rayner (1935, p. 218). In the second post-larval stage the exopod has dwindled and lacks setae, while the protopod is proportionately enlarged and setose. The exopod finally disappears and the endopod develops into a two-segmented appendage which, in the female, is finally longer than the protopod.*

In the male pleopod 2 becomes specially modified, but retains a very small exopod. Pleopod 1 appears early in post-larval life and develops into a copulatory appendage. Pleopods 3–5 are arrested in development at about the same condition as in the female in stage 2. The fate of the pleopods is very much the same in *Galathea* according to Perez (1927).

The pleopods offer an exception to the rule that appendages not present in the adult are not developed in the larva ; but they survive in the larva because they are functional in the first post-larval stage. It is very remarkable that in *Diogenes pugilator* and some *Por-*

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* Milne-Edwards and Bouvier (1894, p. 221) regarded the distal segment as the *appendix interna* of a one-segmented endopod.

cellana there should be fewer pleopods in the larva than in the adult.

The pleopods of Anomura and Brachyura have the endopod reduced to a small *appendix interna* bearing the usual hooks. Their post-larval development, with reference to sexual differences, has been described in Brachyura by Hyman (1920, *Gelasimus*), Cano (1892*b*, *Portunus*), and Shen (1935, *Carcinus*). According to Hyman all the pleopods of the Megalopa dwindle away, and are replaced in the fourth crab stage (5th post-larval) by pleopods of a " second series " on somites 1 and 2 in the male and 2–5 in the female. Cano and Shen agree in their account, but that of Shen is very much the fuller. In *Carcinus* the sex is shown in the second crab stage when pleopod 1 appears in the male, while 3–5 begin to disappear. In pleopod 2 the exopod disappears, and the copulatory appendage is derived from the endopod. In the female the pleopods remain biramous, but the endopod becomes longer than the exopod; and is divided into several segments.

In the pleopods of the Brachyuran Megalopa the setae are usually disposed along the whole of the inner margin of the exopod and half the outer margin. In *Macropodia aegyptia* there are only eight setae, all close together at the apex of the exopod, which is narrow and parallel-sided. It is possible that this difference may hold good for all Oxyrhyncha as compared with other crabs, but I have not material for examination.

The uropods appear in stage 3 except in a few cases of abbreviated development (see p. 50). At this stage the endopod is not jointed to the stem, and has few, or no, setae.* The jointing of the endopod and appearance of setae upon it is a clear mark of stage 4 in normal development. In *Porcellana* the uropods do not appear until the first post-larval stage, but a larva having the general appearance of *Porcellana*, but with uropods, has been described from Australia (Gurney, 1924, p. 178).

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* In *Crangon antarcticus* the uropods appear in stage 3, but the endopod is then fully developed and setose.

In Brachyura a pair of rudimentary appendages appears on somite 6 in the larva, and is small and uniramous, but setose, in the Megalopa ; but it is lost in the crab stage. In *Dromia*, which is generally placed among the Brachyura, there are well developed uropods in larva and Megalopa (Cano, 1893 ; Lebour, 1934*b*), and there are also uropods in the larva *Acanthocaris*, Claus, which may belong to the Raninidae. Uropods do not appear at all in *Lithodes maia* (Sars, 1884), but they are present, as uniramous appendages, in *Paralithodes*, in larva and 1st post-larval (Marukawa, 1933).

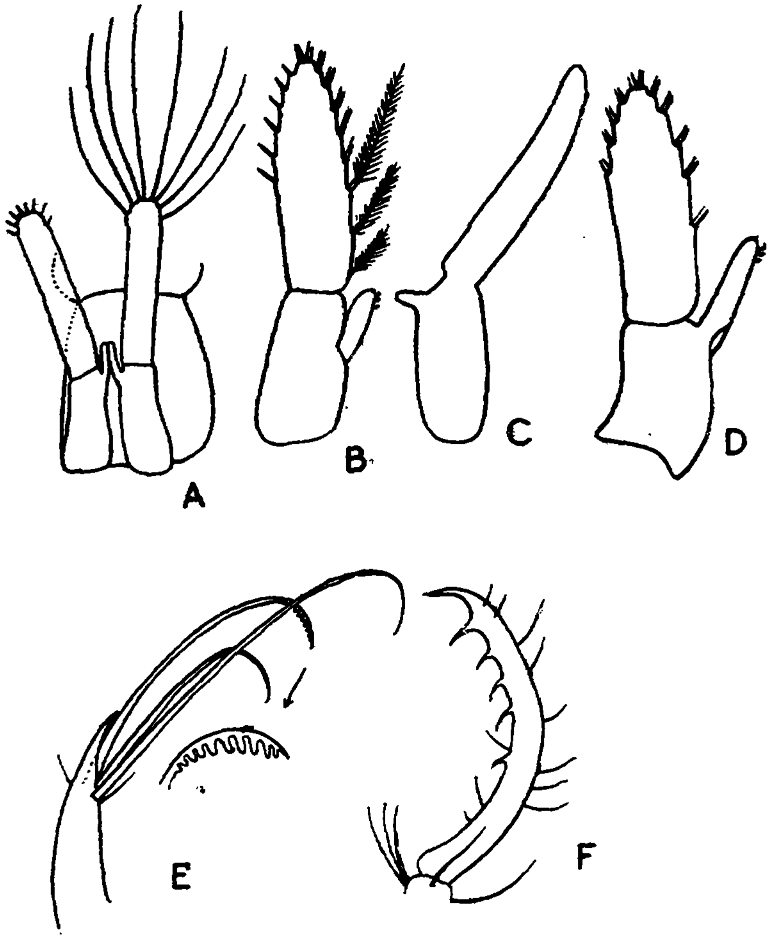

FIG. 45.—Pleopods. A. *Macropodia aegyptia*, megalopa ; pleopod somite 2. B, *Portunus* sp., megalopa ; pleopod somite 3. C. *Portunus* sp., first young crab ; pleopod 2. D. *Ebalia* sp., megalopa ; pleopod 4. E. *Portunus* sp., megalopa ; dactyl of leg 5. F. *Macropodia aegyptia*, first crab ; dactyl of leg 5.

The shape of the uropods is very uniform throughout, the exopod having much the same form as the exopod of the antenna, with large apical spine. In *Ceratasspides longiremis* it has become an enormous appendage, much longer than the whole body (see fig. 56, p. 185).

INTERNAL ANATOMY.

I have not thought it necessary or desirable to set out what is known about the internal structure of the Decapod larva since it does not seem to differ materially from that of the adult (Claus, 1885). Daniel (1930, 1931) has made extensive research on the muscular system of Malacostraca including the Zoea, and it appears that the musculature of the larva differs in no important features from that of the adult. In the crab Zoea the abdominal muscles are already reduced as they are in the adult.

DEVELOPMENT OF THE EUPHAUSIACEA AS COMPARED WITH THE EUDECAPODA.

In supporting the separation of the Euphausiacea from the Mysidacea, proposed by Boas and Hansen, Calman (1909, p. 251) pointed out their close affinity with the Decapoda, thus : " The differences in structure which justify the separation of the Euphausiacea from the Mysidacea have already been insisted on. . . . The resemblance between the members of the present Order and some of the lower Decapoda, especially the Penaeidea, are of much greater importance. The complex copulatory armature of the first pleopods has a general resemblance to that of the Penaeidea, the larval development of the two groups is closely parallel, and the presence in some Sergestidae of phosphorescent organs resembling, though differing in details from, those of the Euphausiacea may also be an indication of affinity."

Our knowledge of the development of the Euphausiacea is extensive and detailed, and we now know all the essential facts about the Penaeidea. The resemblance between the two groups is remarkably close.

Phase.	Euphausiacea.	Sergestidae.	Penaeidae.
I	Nauplius, 3 stages.	(Nauplius ?)	Nauplius, 3 or more stages.
II	Calyptopis, 3 stages	Elaphocaris, 3 stages	Protozoea, 3 stages
III	Furcilia, 3–5 stages	Acanthosoma, 2 stages	Zoea, 2 or more stages
IV	Cyrtopia	Mastigopus	Post-larval.

While there is exact correspondence in phases 1 and 2, this is not the case after that point. There are only two Acanthosoma stages, with pronounced metamorphosis to the Mastigopus, but the number of stages in the Penaeidae does not seem to be fixed, and, in the Euphausiacea, the number is not the same even within the same genus (*Euphausia*). The transition from Furcilia to Cyrtopia is not a change involving all appendages equally, but is somewhat arbitrarily based upon a change in the form of the antenna, which is presumed to accompany a change in the manner of swimming.

Although no exact parallel exists in the number of stages, the general similarity in development is apparent, and the difference between Euphausiacea and Decapoda is not greater than that between different groups of the Caridea, where the number of post-protozoeal stages is very variable.

While so close a correspondence in the phases and stages of development seems to prove a very close relationship between Euphausiacea and Decapoda, it is impossible to say how conclusive such evidence is, for the reason that no other Malacostraca, except the Stomatopoda, have free larvae with which comparison can be made. The developmental sequence surviving in the two groups may be no more than a heritage from ancestors near the root of the phylogenetic tree.

In nearly all Euphausiacea the thoracic somites are almost as compressed and obliterated as they are in the higher Decapoda, and the thoracic appendages are very much delayed in their appearance. This is, however, not the case in *Euphausia superba*, in which all the thoracic appendages of the adult are represented as large rudiments even in the last Calyptopis stage, exactly as they are in the last Protozoea of Penaeidae. The resemblance is very striking, since in both cases the simultaneous appearance of all these limbs contrasts with their appearance in order from in front backwards in nearly allied species.

Whereas maxillipede 2 is fully developed, and maxillipede 3 is rudimentary in the Penaeid Protozoea, neither appears at all in the corresponding stage of Euphausiacea, and when they develop they, and also the legs, grow directly into the adult form. Only those limbs which are functional in the Calyptopis have a form peculiar to the larva.

In the higher Decapoda the maxillipedes, and often the legs also, have a different form in the larva from that seen in the post-larval phase ; but it is to be noted that this is not always the case, and particularly when development is abbreviated the legs develop directly into the final form.

In the Sergestidae, as in the Euphausiacea, the appendages have the same form in phases 2 and 3 (Elaphocaris and Acanthosoma), and there is then an abrupt change to semi-adult form in the Mastigopus, instead of the gradual transformation in the Cyrtopia phase.

There is a tendency in some Penaeidae for the early transformation of the appendages from the protozoeal form towards that of the adult. In the Euphema type of larva (belonging to *Gennadas* and allied genera) even the exopod of the maxillule is absent, and there is little in the maxilla to recall the form of it in the Protozoea ; but some other Penaeidae, with development of the Penaeopsid type, retain the protozoeal form of appendages into the next, or zoeal, phase. On the other hand, the endopods of the legs may not have an intermediate larval form, but may develop directly to that of the adult.

It would seem that, in development at all events, the Euphausiacea come very close to the Sergestidae. In the latter the last two pairs of legs are reduced to vestiges in the first Mastigopus, and reappear in the adult except in *Lucifer*. In Euphausiacea these legs may not appear at all and are always more or less reduced. When they are present they develop directly, without temporary suppression.

In all Decapoda, with the exception of certain Penaeidea (*Acetes*, *Gennadas*), the pleopods appear simultaneously. In *Gennadas* pleopod 1 appears before the rest. In *Acetes* they appear in succession much as in the Euphausiacea (see p. 152). The Euphausiacea have retained a mode of development of these appendages which was probably general, but has been lost in nearly all Decapoda.

In Euphausid development there is no well-marked metamorphosis, and the stages succeed one another with such small differences that ontogeny approaches continuity. In Penaeidea the three phases are marked by changes in swimming, the locomotor appendages being first cephalic, then thoracic, and finally abdominal; whereas in Euphausiacea it seems that the thoracic appendages are never effective swimming organs, and there are only two functional phases—Nauplius-Calyptopis-Furcilia and Cyrtopia.

DEVELOPMENT OF THE STOMATOPODA.

In the early stages of development there are two types of larva distinguished by Giesbrecht (1910) as Pseudozoea and Antizoea, but the differences between them disappear in later stages. The two types may be defined as follows:

Antizoea: Hatching with biramous appendages on first five thoracic somites; abdomen unsegmented or only partly segmented, without setose appendages. Develops into a larva of Erichthus type.

Pseudozoea: Hatching with thoracic appendages 1 and 2 only, the second being in the form of a large raptorial claw, and both without exopods; abdomen fully segmented, and bearing functional pleopods.

Develops into a larva either of Erichthus or Alima type.

The distribution of these larval types within the group is as follows (Giesbrecht):

(1) Lysiosquillinae: First larva of Antizoea type, developing into Erichthus. *Lysiosquilla* and *Coronida.*

(2) Gonodactylinae: First larva a Pseudozoea with five pairs of pleopods. Developing into Erichthus. *Gonodactylus* and *Odontodactylus.*

(3) Squillinae: First larva a Pseudozoea with four pairs of pleopods. Developing into Alima. *Squilla.*

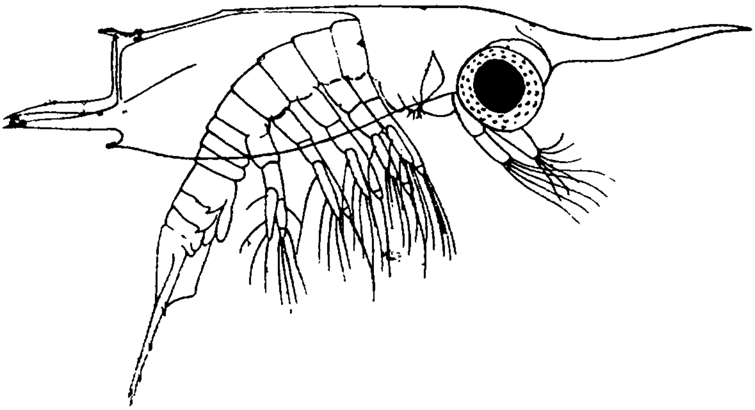

FIG. 46.—*Lysiosquilla eusebia,* Antizoea, from Plymouth.

The full sequence of development is known with certainty only in *Squilla, Gonodactylus* and *Lysiosquilla.* In the former there are two "propelagic" stages, and seven or eight pelagic. In *Gonodactylus* there are also two propelagic stages (Gurney, 1937), and probably not more than six or seven stages in all. In *Lysiosquilla* there is no propelagic stage, and there are nine stages in all in *L. eusebia* and *L. occulta* (Giesbrecht).

The two forms of Pseudozoea, Erichthus and Alima, are commonly distinguished by the broad flattened form of the carapace in the latter, but there are intermediate forms which make such a distinction invalid. Giesbrecht gives the following characters of the two types:

Alima.—Telson with four or more spines between the two lateral spines and the hindmost, or submedian,

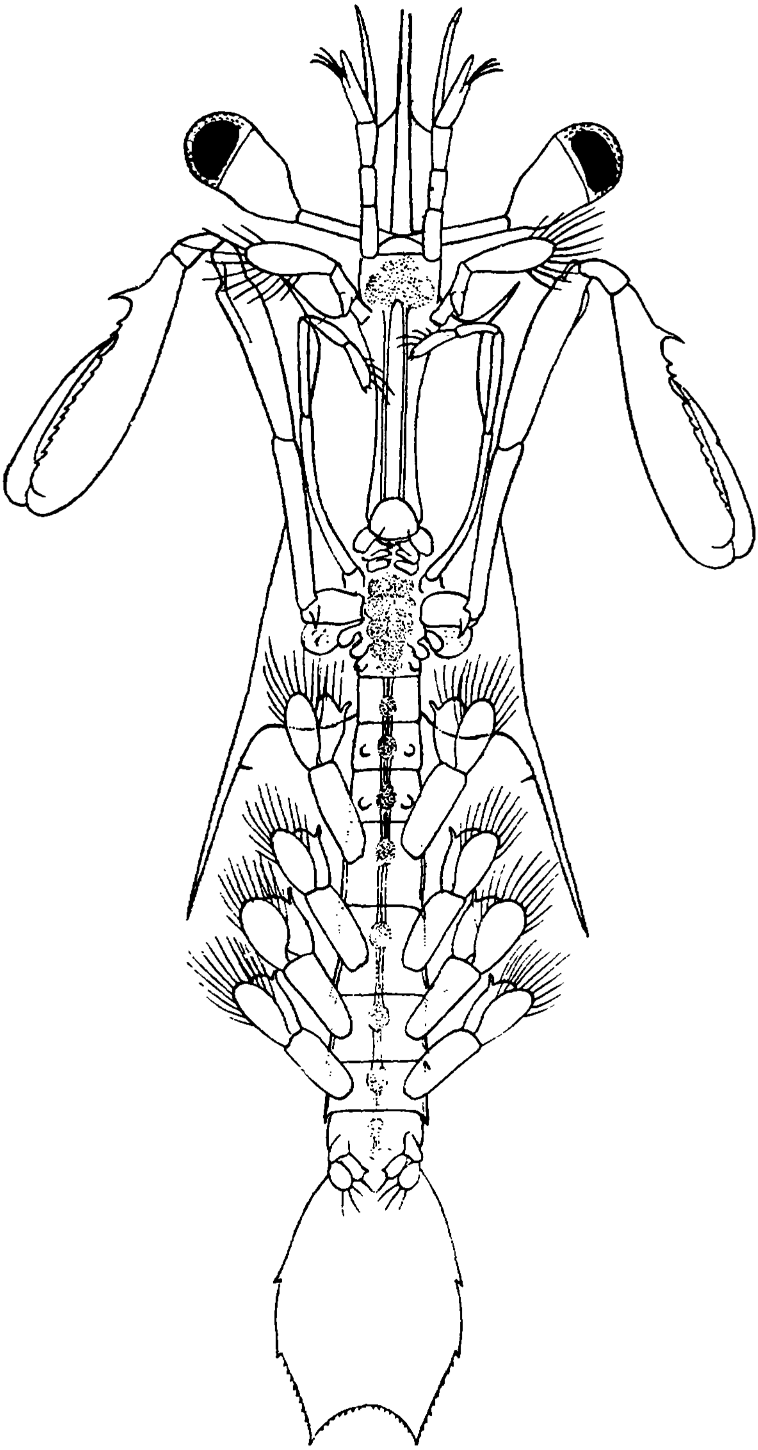

FIG. 47.—*Squilla mantis*, Pseudozoea.

spine. Antennular somite generally with median spine. Posterior lateral spine of the carapace with accessory spine. Eyestalk generally long. Basis and exopod of antenna elongated. Pleopods 1–5 without setae on border of proximal part of exopod. Exopod of uropod longer than endopod. Youngest larva with four pairs of pleopods only.

Erichthus.—Telson with one spine between lateral and terminal spines. Antennular somite without median spine. Posterior lateral carapace spine without accessory spine. Eyestalk short. Basis and exopod of antenna generally thick-set. Pleopods 1–5 with setae on proximal margin. Youngest larva with five pairs of pleopods.

In the Antizoea of *Lysiosquilla* the pleopods develop in succession, thus :

	L. occulta.		*L. eusebia.*	
	Pleopods.		Pleopods.	
	Non-setose.	Setose.	Non-setose.	Setose.
Stage 1	..	..	2	..
,, 2	2	..	2	2
,, 3	2	2	1	4
,, 4	1	4	..	5
,, 5	..	5	..	5

The phylogenetic position of the Stomatopoda remains doubtful. The opinions of previous authors are summarized by Grobben (1919).

Grobben's view is that the Stomatopoda have a number of primitive characters, some inherited from the Leptostraca, and that they are an offshoot of a " Protomalacostracan " stem. In his earlier work (1892) he had regarded them as sprung from an " Urschizopod " stem, and considered the Antizoea (Erichthoidina) afforded evidence of such descent.

The larval forms do not provide any very secure basis for speculation. The simple fact that it is only in the Eucarida and Stomatopoda among Malacostraca that there is a series of free larvae, and that there is a rough general similarity among them, suggests an ultimate common origin, but detailed comparison of the Stomatopod larva with the rest reveals many fundamental differences.

There is a close correspondence in the number of stages passed through, but in Stomatopoda these stages follow one another without separation into phases such as are so clear in Euphausiacea and Decapoda. The thoracic appendages in the Pseudozoea and Erichthus develop directly into the adult form without assuming a distinct larval structure, and this is also true for the head appendages. The maxilla, for instance, has a very simple unsegmented form, without exopod in the larva, and changes gradually into that of the adult. At all stages it resembles the Euphausid maxilla more than that of any other Malacostracan.

In Euphausiacea the appendages of the head and the first thoracic somite have a distinct larval facies ; but the following thoracic appendages do not. In the Decapoda as a rule all the head and thoracic appendages have a distinct larval form ; but this is more or less suppressed when larval life is shortened, and the appendages may then develop directly to the adult form.

The appearance in the Stomatopoda of the uropods later than the preceding pleopods is probably a primitive feature, and a point of difference from the Eucarida ; but the manner in which the pleopods appear in succession, first non-setose and then setose, is a striking point of resemblance to the Euphausiacea.

So far as evidence can be drawn from the larvae, it seems that the Stomatopoda may be an offshoot from the Malacostracan tree close to the origin of the Euphausiacea, retaining the primitive freedom of some of the somites from the carapace, which is also perpetuated in the larval life of the Penaeidea. The larvae themselves have become modified by a process akin to the " condensed development " of Decapoda, which leads to the suppression of purely larval characters by the early appearance of adult features.

PART II.—DESCRIPTIVE

DECAPODA

EUPHAUSIACEA

In most species of Euphausiacea it is known or presumed that the eggs are shed freely in the water, but in some species they are carried for a time attached to the thoracic appendages. In *Nyctiphanes couchii* the eggs are borne in a gelatinous sac (Holt and Tattersall, 1905, pl. 17). Some species, such as *Euphausia brevis*, spawn at the surface, where eggs and larvae at all stages can be taken; but others, such as *E. superba* (Fraser, 1936), probably spawn at depths below 250 fathoms.

The development of the egg was first described by Sars (1898). He found two kinds of "propagating spheres" which he called oospheres and spermatospheres. In the latter there is a central sphere attached to the outer envelope by a number (from 1 to 6) of chitinous ducts which have funnel-like ends attached to the central sphere, and apparently open at the surface of the outer envelope. Sars suggested that the central body "represents the spermatic matter destined to fecundate the ova contained in the oospheres." The fact that spermatophores are frequently found attached to the female renders this interpretation improbable. I have myself seen among unidentified Euphausiid eggs taken at Bermuda some which resemble those figured by Sars. I was unable to see the funnel-like structure figured by Sars. None of these eggs developed any further, although numerous Nauplii were hatched from the normal eggs. It seems possible that these "spermatospheres" are only dead eggs attacked by fungal hyphae.

NAUPLIUS.

The Nauplius is known in the following species:

Meganyctiphanes norvegica (Sars, 1898; Lebour, 1924; Macdonald, 1927).

Nyctiphanes couchii (Lebour, 1924).
N. australis (Sars, 1885 ; Dakin and Colefax, 1940).
Thysanoëssa raschii (Macdonald, 1928).

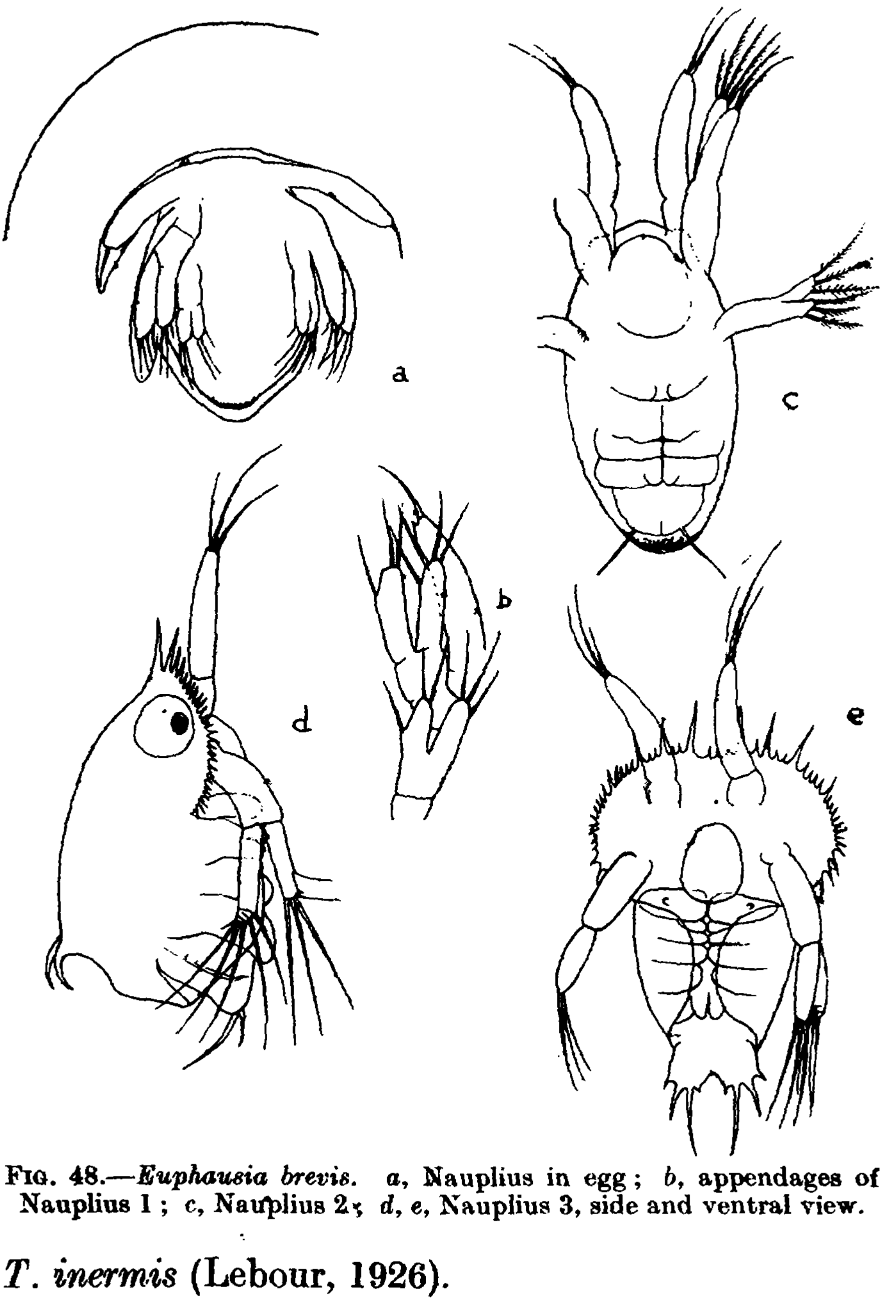

FIG. 48.—*Euphausia brevis.* *a*, Nauplius in egg ; *b*, appendages of Nauplius 1 ; *c*, Nauplius 2 ; *d*, *e*, Nauplius 3, side and ventral view.

T. inermis (Lebour, 1926).
Euphausia mülleri ? (Metschnikoff, 1869).
E. krohni (Sars, 1885 ? ; Lebour, 1926).
E. superba (Fraser, 1936).
E. brevis (Gurney, 1935, unpublished).

In *Stylocheiron carinatum* the eggs are very large (Sars, 1885, pl. 26, fig. 1). Nothing is known about the early stages of the larva, and it is possible that there is no Nauplius.

The number of Nauplius stages is uncertain. In *E. superba* Fraser found three, and I have found three only in *E. brevis*, but there seem to be four in *M. norvegica*, and four in *N. couchii*, but in this case the first two moults take place within the egg pouch (Lebour).

The Nauplii have very much the same form in all species. In stages 1 and 2 there is a biramous mandibular palp, except in *N. couchii*, and the exopod of the antenna is unsegmented.

In stage 3 the form is changed, a large rostral hood appears which may be deeply serrated (*e.g. E. brevis*), and the telson is differentiated. The exopod of the antenna becomes segmented at the end, and the mandibular palp is reduced to a small papilla. Behind it appear rudiments of maxillule, maxilla and maxillipede 1,* and these may be partly covered by a shell fold. There are no masticatory processes on antenna and mandible, and it would seem that the Nauplius does not feed.

CALYPTOPIS (PROTOZOEA).

The Calyptopis phase, which corresponds to the Protozoea of Penaeidea, differs from the Nauplius in having acquired three pairs of functional post-mandibular appendages, and in having the thoracic somites distinct, though much compressed. There are invariably three stages, but no new thoracic appendages are acquired. In stage 1 the abdomen is unsegmented; in stage 2 its somites are distinct, but the telson is not separated from somite 6; in stage 3 the telson is separated, and

---

* Since there is no distinct modification of any thoracic appendages as maxillipedes it is the general practice not to use the term "maxillipede" for any of the appendages in Euphausids. In view of the close relationship between the Euphausiacea and Decapoda there is some convenience in designating the first three thoracic appendages as maxillipedes in both groups, even when there is no morphological distinction between them and the succeeding appendages.

the uropods appear, but there are no pleopods. The telson is usually a rectangular plate, without posterior

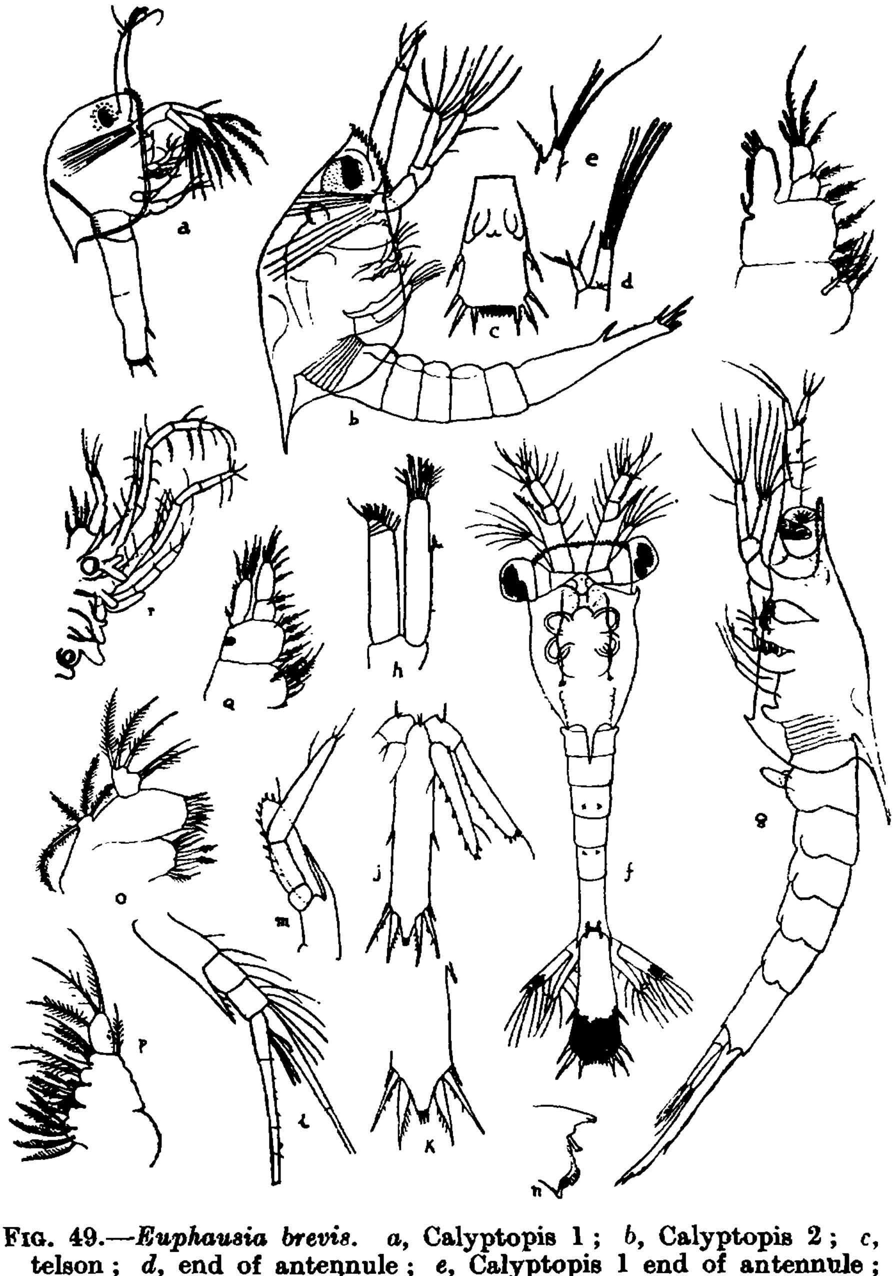

FIG. 49.—*Euphausia brevis.* *a*, Calyptopis 1; *b*, Calyptopis 2; *c*, telson; *d*, end of antennule; *e*, Calyptopis 1 end of antennule; *f*, Furcilia 1, dorsal, specimen with very red telson; *g*, Furcilia 1, side view, specimen with telson colourless; *h*, antenna; *i*, maxillipede 1; *j*, Furcilia 4, telson; *k*, ditto; *l*, antennule; *m*, antenna; *n*, mandible; *o*, maxillule; *p*, maxilla; *q*, maxillipede 1; *r*, legs.

indentation, and with 7 + 7 spines. In stage 2 a median unpaired spine appears, which persists in the adult. The structure of the appendages is very much the same in all species known. The mandible may have a conical process representing the palp. The maxillule has a small unsegmented endopod and a lobe bearing four setae which is the exopod. In the maxilla the exopod is represented only by a single outer seta, and the endopod is unsegmented. The maxillipede has large coxa and basis, and very short branches. The endopod is of two segments only, longer than the exopod, which has four apical setae and a small outer proximal seta.

FURCILIA (ZOEA).

The Furcilia phase is distinguished from the Calyptopis by the development of the eyes, which are now stalked and movable, and the appearance of thoracic and abdominal appendages. The limit between this and the following Cyrtopia (post-larval) phase is ill-defined. Fraser (1936) and John (1936) accept no distinction, but I think there is advantage in regarding, as Sars did, the stage at which the antennae become modified and cease to be natatory as the first Cyrtópia stage, and the equivalent of the first post-larval stage of *Eudecapoda.*

The number of Furcilia stages varies even within the species of *Euphausia,* and in some species, particularly *E. superba* (Fraser), there is so much individual variation in the development of the appendages that a separation of distinct stages is not easy. These stages are generally separable according to the number of setose or non-setose pleopods, combined with the arrangement of spines on the telson.

Fraser showed that there is a definite rule that the pleopods appear first as non-setose rudiments, these rudiments of one stage becoming setose at the next moult. As the order of their appearance varies a great deal with the species the " pleopod formula " may provide useful systematic evidence. I have drawn up a table showing the pleopod succession in all the species in which the development is known. This table also shows the number of spines at the end of the telson, and it will be seen that there are great differences in the stage at which the final form, with one apical spine, is reached.

The appendages present in the Calyptopis remain almost unchanged through the Furcilia stages, but new thoracic appendages are added, though they do not all develop completely in this phase as a rule.

In *Euphausia brevis*, for example, the third, or last, Furcilia has maxillipedes 2 and 3 well developed, with setose exopods, and bilobed gill rudiments. Leg 1 is a fairly large biramous rudiment, and there are simple rudiments of gills corresponding to legs 1–3. The luminous organs have appeared in maxillipede 2 and abdominal somite 1.

Fraser's work on *E. superba* is the most complete account of the development of a Euphausid that we have ; but it is an exceptional species, partly by reason of the great individual variability, and partly from the very early development of all the thoracic appendages.

Within the genus *Euphausia* there are three distinct " pleopod formulae " thus :

		Stage 1.	Stage 2.	Stage 3.		
Group I .	Non-setose	1	4	0		*E. krohni, E. brevis.*
	Setose	0	1	5		
Group II .	Non-sétose	4	1	0		*E. vallentini, E. frigida, E. triacantha, E. superba,* E. distinguenda?*
	Setose	0	4	5		
		St. 1.	St. 2.	St. 3.	St. 4.	
Group III .	Non-setose	1	3	1	0	*E. longirostris, E. spinifera, E. similis ?*
	Setose	0	1	4	5	

* In *E. superba* the usual succession is $\frac{5}{0}$ $\frac{0.}{5}$

Hansen (1911) has distinguished four groups within the genus *Euphausia*, mainly upon the characters of the petasma. Of these groups " a " includes those species related to *E. krohni*, and the development of the two species known confirms their close relationship. Of

Table showing Development of Pleopods and Number of Apical Spines on the Telson at Successive Stages of the Furcilia.

	Stage I.			Stage II.			Stage III.			Stage IV.			Stage V.			
	Pleopods.		Telson.	Pleopods.		Telson.	Pleopods.		Telson.	Pleopods.		Telson.	Pleopods.		Telson.	
	N.	S.	Spines.	N.	S.	Spines.	N.	S.	Spines.	N.	S.	Spines.	N.	S.	Spines.	
ysanopoda aequalis	0	0	7	2	0	5	2	2	3	1	4	3	0	5	1*	Lebour, R. G.
cutifrons	3	0	7	2	3	7	0	5	7	0	5	7 C	..	..	..	Frost.
ristata	3	0	7	2	3	7	0	5	7	..	..	..	..	..	..	R. G.
gassizi	..	..	..	3	2	5	..	...	..	..	..	..	..	..	..	Hansen.
rientalis	..	..	..	..	..	..	0	5	5	..	..	...	..	..	..	,,
tipahnes couchii	3	0 ?	7	2	3 ?	7	0	5 ?	7	0	5	5	0	5	3 C	Lebour.
ganyctiphanes norvegica	3	0	7	2	3	7	0	5	7	0	5	7	0	5	7 C	Lebour, Macdonald.
phausia brevis	1	0	7	4	1	7	0	5	7	0	5	3 C	0	5	1	R. G.
krohni	1	0	7	4	1	7	0	5	7	0	5	3 C	0	5	1	Lebour, Frost.
ongirostris	1	0	7	3	1	7	1	4	7	0	5	7	0	5	4–6 C	John.
spinifera	1	0	7	3	1	7	1	4	7	0	5	7	0	5	3	,,
vallentini	4	0	7	1	4	7	0	5	5/7	0	5	5 C	0	5	3	,,
frigida	4	0	7	1	4	7	0	5	7	0	5	5 C	0	5	3	Rustad, John.
riacantha	4	0	7	1	4	7	0	5	7	0	5	7 C	0	5	5	John.
superba	4/5	0	7	1/0	4/5	7	0	5	7	0	5	5	0	5	3 C	Fraser, R. G.
ysanoessa raschi	0	0 ?	7	1–5 ?	0	7	1–4	1–5 ?	7	0	5	7	0	5	7 C ?	Macdonald.
inermis	0	0 ?	7	5	0 ?	7	0	5 ?	7	0	5	7	0	5	7 C ?	Lebour.
macrura	0	0	7	5	0	7	0	5	7	0	5	5	0	5	5 C ?	Rustad.
gregaria	0	0	7	5	0	7	0	5	7	0	5	5	0	5	3 C	R. G.
natoscelis microps	1	0	7	3	1	7	1	4	3–5	0	5	1	0	5	1 C	Sars, Lebour, R. G.
megalops	2	0	7	3	2	7	0	5	5	0	5	1 C	0	5	1	Frost.
ocheiron suhmi	0	0	6	1	0	6	2	1	6	2	3	6	0	5	4†	Lebour, R. G.
bbreviatum	..	..	..	..	..	..	2	1	7	2	3	7	0	5	5†	,,
ongicorne	0	0	7	1	0	7	2	1	7	2	3	7	0	5	7†	Frost.

N. = Non-setose ; S. = setose. C = Cyrtopia * Cyrtopia 1 at Stage VI. † Cyrtopia 1 at Stage VII (probably).

the three remaining groups Hansen himself regarded group "d" as well established, but groups "b" and "c" as less certainly related. John has discussed the relationship of the five southern species. Group "d" includes four species, *E. triacantha*, *E. longirostris*, *E. spinifera*, *E. hanseni*, and the development of the first three is known. Two, *E. longirostris* and *E. spinifera*, agree so closely that their relationship cannot be doubted; but *E. triacantha* differs not only in the pleopod sequence, but also lacks the serration of the carapace found in the other two. In its adult structure it appears to be an aberrant member of the group, and its position is therefore questionable. So far as pleopod succession is concerned *E. triacantha* falls into the same group as *E. superba*, *E. vallentini* and *E. frigida*, which are members of John's southern group.

It may be suggested that the pleopod succession in groups 2 and 3 is not really different, since group 2 might be derived from group 3 by combining stages 1 and 2 in one stage in such a way that the first four pleopods appear together instead of in succession. In that case the difference between them becomes a matter of abbreviation of development rather than a deep-seated specific distinction. In *E. superba* a further step in abbreviation is taken, since not only do all the pleopods usually appear simultaneously, but also all the appendages of the adult are present as equally large rudiments in Furcilia I.

CYRTOPIA.

The Cyrtopia stage is thus defined by Sars: "antennular flagella becoming elongate and distinctly articulate. Antennae transformed, so as not to serve the purpose of locomotion. Posterior legs and gills successively appearing" (1885, p. 150). The first Cyrtopia stage may be the fourth, fifth, sixth or seventh stage after the Calyptopis, so that there may be from seven to eleven post-naupliar stages.

As has already been said, the distinction between Cyrtopia and Furcilia has to be based upon a single character, and is not accepted by Fraser; but it is still more difficult, and indeed impossible, to distinguish between Cyrtopia and post-larval or adolescent forms. Fraser is forced to rely upon the presence or absence of the posterior lateral spines of the telson in *E. superba*. I am convinced that, if we are to look at the development of the Euphausiacea as proceeding upon the same lines as that of the Decapoda, it is necessary to recognize a first Cyrtopia stage as the first of the post-larval series leading, without any important changes between moults, to the adult. As Miss Lebour says (1925, p. 815), " so gradually does the Cyrtopia change into the adult that it is almost impossible to fix a so-called post-larval stage—for specimens may be mature before the limbs are perfect." The change in the antenna is definite and distinctive; but it does not necessarily take place at the same time as the other changes which characterize the post-larval phase. Of these the most important is the change in maxillipede 1 from the larval form which it has retained through Calyptopis and Furcilia. In *E. brevis* the beginning of the change is traceable in Cyrtopia I (Fig. 50); but it is not really marked till stage 3.

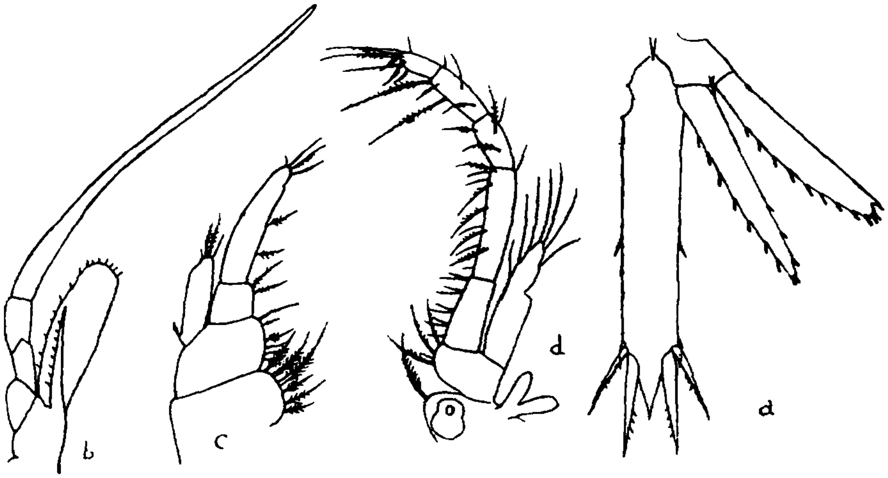

FIG. 50.—*Euphausia brevis*, Cyrtopia 1. *a*, Telson; *b*, antenna; *c*, maxillipede 1; *d*, maxillipede 2.

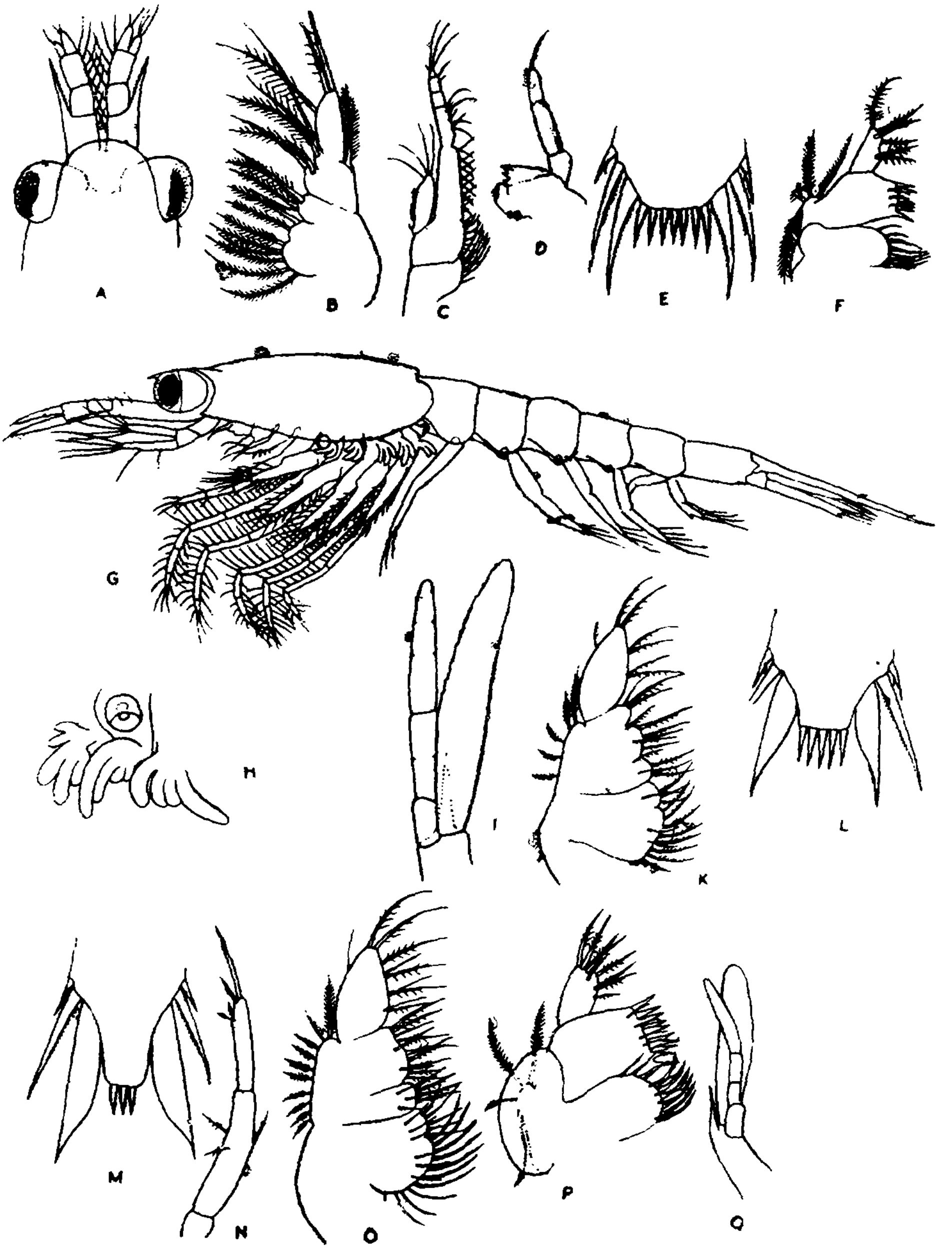

FIG. 51.—*Euphausia superba.* *a*, Furcilia 1, head from above; *b*, maxilla; *c*, Furcilia 3, maxillipede 1; *d*, mandible; *e*, Furcilia 3, telson; *f*, maxillule; *g*, Furcilia 3, 7·7 mm.; *h*, Cyrtopia 2, gills; *i*, Cyrtopia 1, antenna; *k*, maxilla; *l*, Furcilia 3, telson; *m*, Cyrtopia 1, telson; *n*, mandible palp; *o*, maxilla; *p*, maxillule; *q*, antenna.

The exopod of the maxillule may be retained even to the same stage in *E. brevis*. In *E. superba* it is still present in the first Cyrtopia (fifth Furcilia of Fraser) though the exite of the adult has appeared (Fig. 51, *p*; but it is lost at the next stage.

The change in the antenna either coincides with the moult at which all the pleopods become functional, or takes place at the next moult, that is to say it does correspond to a definite change of method of locomotion, whereas the other changes, in the mouth parts, are of subsidiary importance and spread over several moults. The changes in the telson are relatively unimportant, and should not have much weight in determining stages in development.

EUDECAPODA

Everyone who has been concerned with zoological systematics will have met with the difficulty of framing a definition for any large group. Specific distinction is generally easy, but distinction becomes more and more difficult as more species, genera or families are brought in, and more allowance has to be made for exceptions. This is sadly true for Decapod larvae, and I am unable to offer any definition which will cover, for example, all Caridea and distinguish them from all Penaeidea or Macrura Reptantia. A definition in which each clause has to be qualified by " usually," " generally " and so on ceases to define. In practice it is generally possible to identify a larva as that of Carid, Penaeid or other group with tolerable certainty; but it is not easy to give unequivocal reasons for one's verdict. Actually no doubt one relies to a great extent upon characters which are not larval—for example, the number of chelae, or the gills, and these characters cannot legitimately be used in a definition. Certain fundamental points of distinction may not be of practical use—for instance, the presence of Nauplius and

	Antennal scale segmented.	Maxillule with exopod.	Maxillipede 1 endopod segments.	Maxillipede 3 functional in stage 1.	Telson spine 2 reduced.	Telson with median spine.	Telson spine 4 enlarged, often fused with telson.
Penaeidea	+	+	4–5	+	–	±	–
Caridea	+	±	4 (or r)	+	–	–	–
Nephropsidea . . .	–	–	2 r	+	–*	+	–
Scyllaridea	–	–	3–4	+	–	–	–
Stenopidea	+	±	2–3 r	+	+	–	–
Callianassidae . . .	–	–	4	+	+	+	+†
Axiidae	–	–	4	+	+	+	+†
Upogebiidae *Laomediidae* . . .	–	–	5	–	+	±	±
Galatheidea	–	–	5	–	+	–	+
Paguridea	–	–	5	–	+	–	+
Hippidea	–	–	5	–	+	–	–
Dromiacea	–	–	5	–	+	–	–
Brachyura	–	–	5	–	–	–	+

* Spine 2 is slightly reduced in *Homarus*.

† Spine 4 is not very markedly larger.

Protozoea in Penaeidea, or the presence of six spines in the prezoeal telson of Caridea.

For these reasons I have not attempted to define the larval characters of the major groups. The following table summarizes the distribution of certain easily observable characters, and may be of some help in placing a larva. It must be noted that it does not necessarily follow that any character is observable throughout development. For instance the segmentation of the antennal scale disappears in late stages.

MACRURA NATANTIA

PENAEIDEA

PENAEIDAE.

See Hudinaga, 1935 ; Heldt, 1938 ; Pearson, 1939.

It is only of quite recent years that the full life history of any species of Penaeid has been satisfactorily described, and we now know all the stages from Nauplius to post-larval of several species. The Nauplius and Protozoea stages are very much alike in all these forms, though generic, if not specific, differences can readily be found. The differences are much greater in the zoeal phase.

NAUPLIUS (Fig. 9, A).

The number of Nauplius stages appears to vary considerably. Hudinaga found six in *Penaeus japonicus*, while Mme. Heldt described eight in *P. trisulcatus*, and Pearson five in *P. setiferus*. In *Sicyonia* Mme. Heldt found eight, Pearson five, and I myself three only. The Nauplius is of very simple pear-shaped form, with a pair of furcal setae in stage 1 and no carapace fold. The three pairs of appendages are, in stage 1, without distinct segmentation, and there are no masticatory hooks on the antenna and mandible. The body is full of yolk, and no food is taken throughout the phase. The whole series of stages is passed through in 24–36 hours (Pearson), or 68 hours (Heldt), or 23 hours (Hudinaga). In *Sicyonia wheeleri* the Nauplii had reached the last stage in about 24 hours after hatching in Bermuda. The changes between moults are small, but the last Nauplius has a shell fold, rudiments of maxillae and maxillipedes 1 and 2, while the bifurcate telson of the Protozoea is partly developed, with 7 + 7 spines.

PROTOZOEA.

The Protozoea differs from the Nauplius in having the carapace developed as a fold from the somite of the maxilla free from the thoracic tergites. The last five thoracic somites are uncovered in *Sicyonia*, and in all species some are uncovered. The thoracic somites are all distinct in stage 1, but the abdominal somites are fused until stage 2. The telson is bifurcate, the two branches slender in *Sicyonia* and *Gennadas*, each bearing seven spines. The rostrum appears in stage 2, when supraorbital spines also appear if present at all. In stage 3 dorsal and lateral spines may develop on the abdominal somites. The eyes appear not to be functional in stage 1, but are stalked in stage 2. The antennules are long and slender, unsegmented in stage 1, but ringed at the base, and with long apical setae. It appears to be a rule that the apex bears two aesthetes and three long setae. The relative length of the antennule and of the setae are useful systematic characters.

The mandible loses its palp at the moult from the Nauplius, and the new palp does not appear till the Zoea. Maxillule and maxilla are on much the same plan, each with a small exopod bearing four and five setae respectively, but the endites of coxa and basis are each divided into two lobes in the maxilla. Maxillipedes 1 and 2 have short exopods with four apical setae and two or three outer marginal setae. Maxilli-

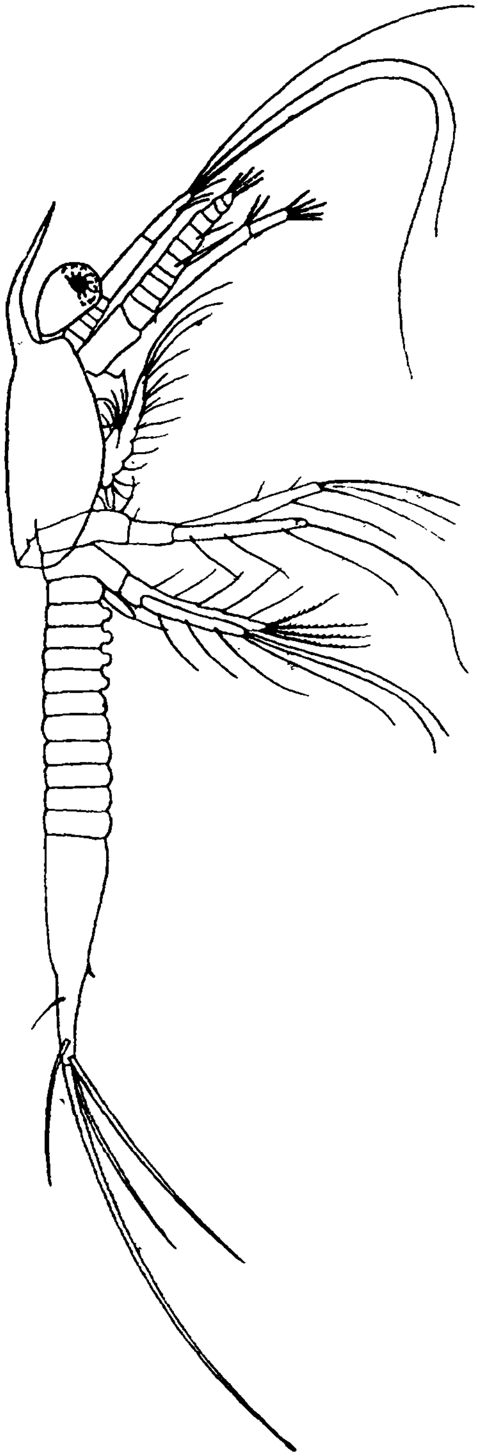

FIG. 52.—*Gennadas*, Protozoea 2.

pede 3 is rudimentary or absent. These appendages remain unchanged through the Protozoeal phase, and, in some species, into the zoeal phase. In stage 3 there are rudiments of all the legs, and the uropods are developed.

ZOEA.

With the moult from Protozoea 3 the difference between genera are greatly increased. The number of zoeal stages differs considerably in the different genera, and the distinction between Zoea and Post-larval is far from clear in some forms (Heldt). There are also great differences in the extent to which the carapace is fused with the thoracic tergites in Zoea 1. The following list shows the species which are known, the condition of the carapace, and the number of stages :

	Carapace fused with tergite of—	Zoeal stages.
Penaeus trisulcatus . . .	Mxp. 3 (H.) .	4 (H.)
P. setiferus	All thorax (P.) .	2 (P.)
P. japonicus	,, (Hu.) .	?
Trachypenaeus constrictus . .	,, (P.) .	2 (P.)
Parapenaeus longirostris . .	Leg 3 (H.) .	16 (H.)
,, ,, . .	All thorax (P.) .	4 (P.)
Penaeopsis sp.	Mxp. 3 (G.) .	3 ? (G.)
Metapenaeus stebbingi . . .	,, 3 (G.) .	3 (G.)
Solenocera membranacea . .	All thorax ? (H.) .	2 (H.)
Sicyonia carinata . . .	Mxp. 3 (H.) .	4 (H.)
S. wheeleri	,, 2 (G.) .	3 ? (G.)
Gennadas elegans . . .	All thorax (H.) .	4 (H.)

* H. = Heldt, Hu. = Hudinaga, P. = Pearson, G. = Gurney.

In *Sicyonia* the protozoeal form of the mouth parts, including maxillipedes 1 and 2, is retained in Zoea 1 and 2, though the antennules and antennae are changed. All the legs are functional, with exopods, and the pleopods appear in stage 2. This carrying over of the protozoeal form of the appendages into the zoeal phase seems to take place in *Penaeus*, *Trachypenaeus* and *Parapenaeus*, but in *Solenocera* and *Gennadas* there is a sudden change at this point.

The larvae hitherto described may be said to fall into three types ; but I am aware of other types which do not fit the definitions here given for the Zoea phase.

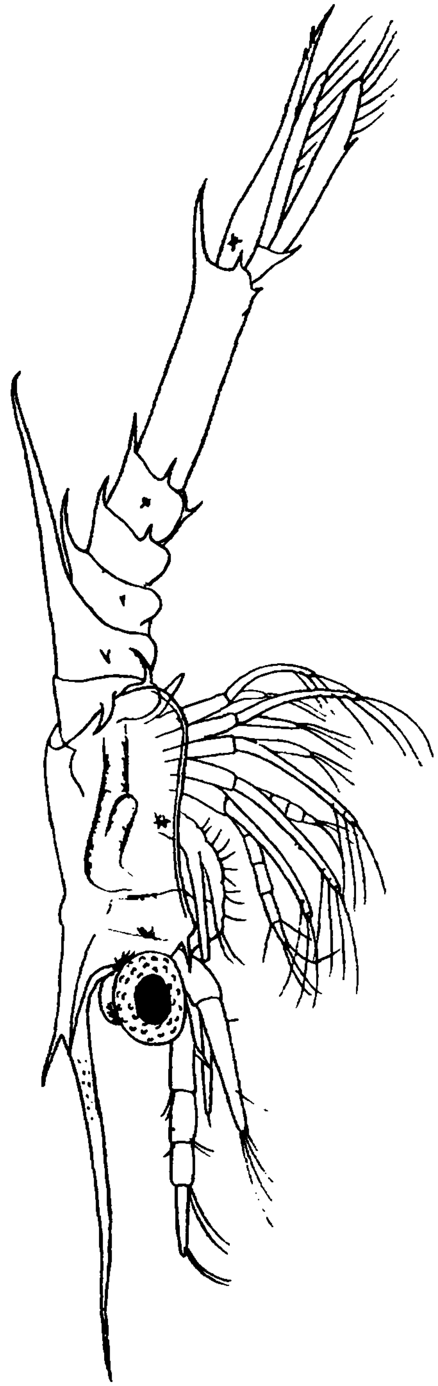

FIG. 53.—*Gennadas*, Zoea.

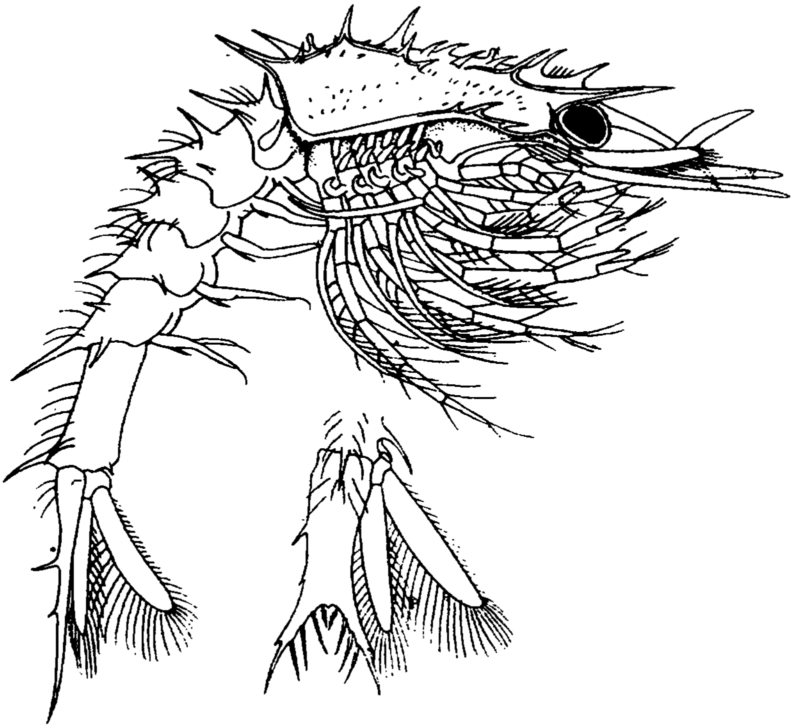

Fig. 54.—*Solenocera*, Zoea.

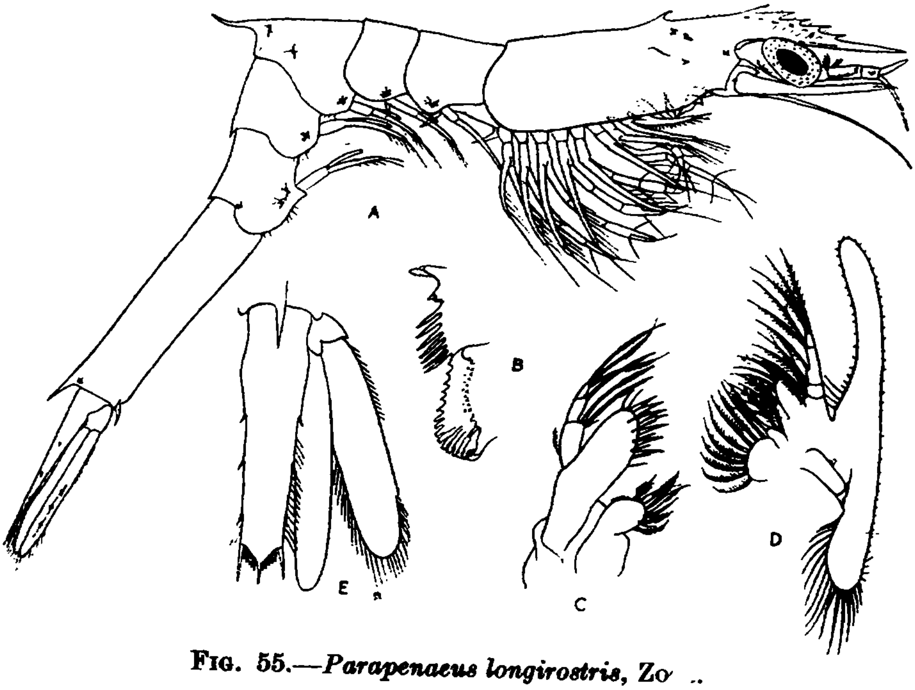

Fig. 55.—*Parapenaeus longirostris*, Zo ..

(1) *Penaeus*, *Parapenaeus* and allied genera: Body slender and not strikingly bent. Carapace with rostrum not longer than antennules, and with dorsal teeth in last stage. Abdomen with small dorsal spines on three or more somites. Telson parallel sided, or widening distally, sometimes with median spine. Gills delayed in appearance and very small. Pleopods appearing all together.

(2) *Solenocera*: Body stouter. Carapace and abdomen with numerous small dorsal spines, the former also having a series of anterior lateral spines. Rostrum without dorsal spines, except for one at the base. Telson deeply forked. Gills larger, but not in full adult number. Pleopods appearing all together.

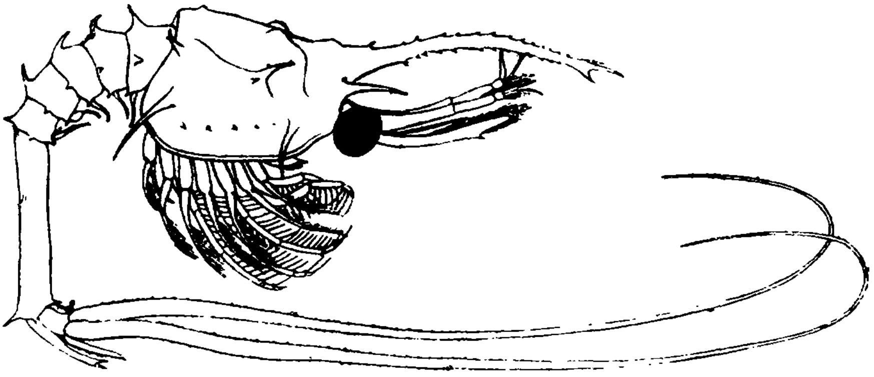

FIG. 56.—*Ceratuspides longiremis.*

(3) *Gennadas* and allied genera: Body stout, abdomen generally bent at right angles to thorax. Rostrum very long, without dorsal spines except for spine at base. Abdomen with very long spine on somite 2. Leg 5 rudimentary in Zoea 1. Gills appearing early, very large, and in some species in full adult number in last larval stage. Telson narrowed behind, ending either in a small fork or deeply cleft, the arms parallel.

SERGESTIDAE.

See Hansen, 1922; Gurney and Lebour, 1940.

The development of *Lucifer*, *Acetes* and *Sergestes* is now fully known, and a very distinct type of larva has been referred to *Petalidium* (Gurney, 1924c), but may really belong to *Sicyonella*.

In *Lucifer* the eggs are carried for a time on the last legs, and a Nauplius has been described (Brooks, 1882d). According to Soejima (1926) there is also a Nauplius in *Acetes*. Nakazawa (1916) has claimed that there is a Nauplius in *Sergestes* also, but further evidence is required before his statement can be accepted.

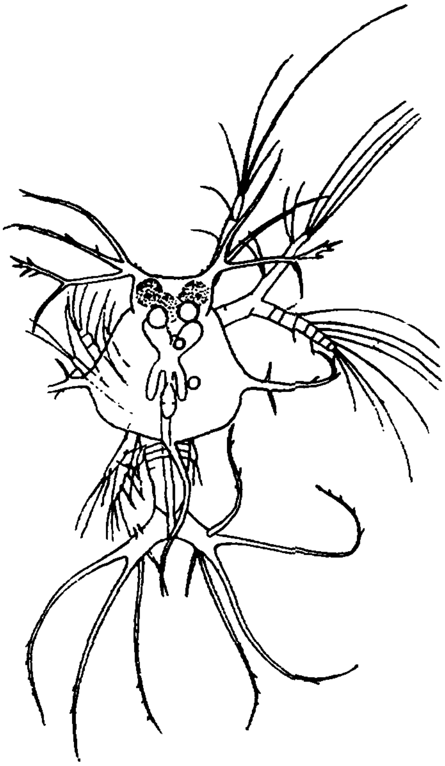

FIG. 57.—*Sergestes cornutus*, Protozoea 1.

In *Sergestes* and *Lucifer* there are three Protozoea stages (Elaphocaris) and two Zoea (Acanthosoma) stages. In *Acetes* there is apparently only one Zoea (Menon, 1933, stage 4).

Sergestes.

The first Protozoea has no rostrum, but the carapace has a pair of large branched processes, a pair of lateral processes and a posterior dorsal process or spine. The abdomen is unsegmented, and the telson has two slender arms bearing six spines each, of which the anterior one is very small and nos. 3–5 long and spiny.

At the moult to stage 2 the outgrowths of the carapace are so completely changed that it would be impossible to connect the two if the moult were not observed, or the colour in life. In stages 2 and 3 there are three quite distinct types of Protozoea (Gurney and Lebour, p. 6). The following description applies to the commonest type, of which *S. cornutus* is an example :

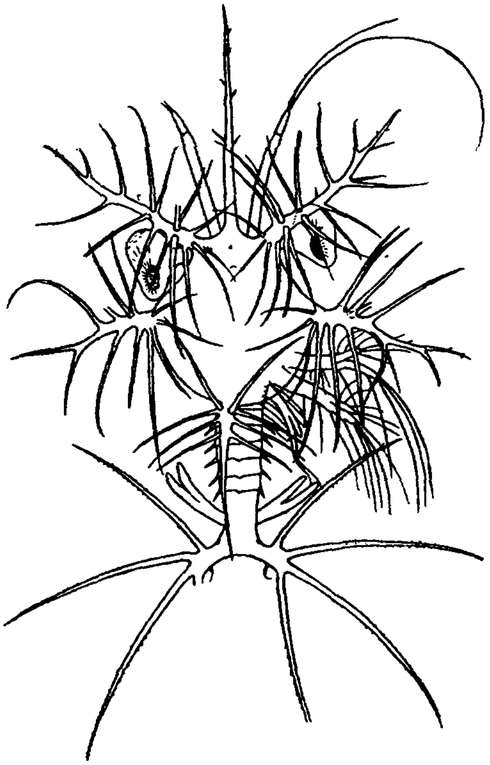
FIG. 58.—*Sergestes cornutus*, Protozoea 3.

There is now a long rostrum, with lateral and ventral spines ; a pair of large lateral processes, each with a series of long spines, and a posterior dorsal process with a group of spines at its base. The abdomen is not segmented. The telson arms are shorter, but there is the same number of spines. The eyes are stalked.

Stage 3 differs from stage 2 in having the rostrum simple, without spines, but a pair of large spiny supra-orbital processes has appeared. The lateral and dorsal processes remain about the same. The abdomen is segmented, and there are now large rudiments of the legs. The uropods have appeared, though they are not functional, and there are no pleopods.

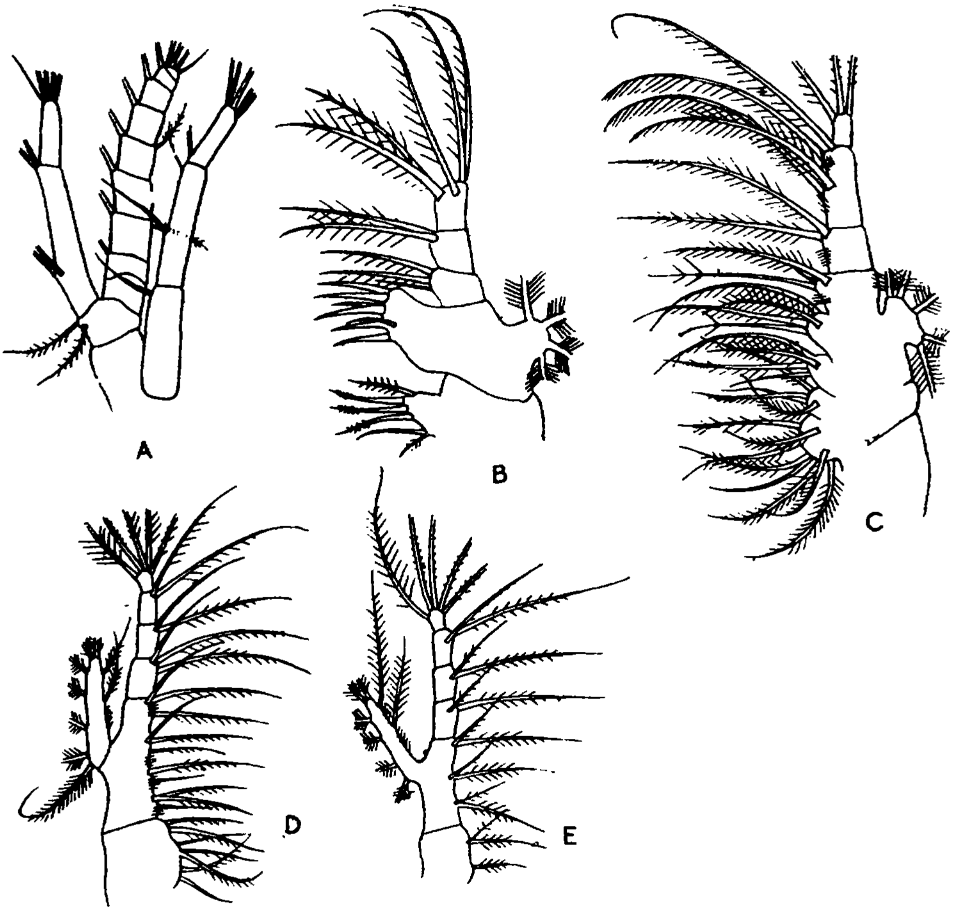

FIG. 59.—*Sergestes cornutus*, Protozoea 3, appendages. A, Antennule and antenna; B, maxillule; C, maxilla; D, maxillipede 1; E, maxillipede 2.

The appendages of the Protozoea and Zoea are very much the same as in the Penaeidea.

A second, very different type, belonging to *S. crassus*, is shown in Fig. 60.

ZOEA (ACANTHOSOMA).

The Zoeas of the various species differ so much from each other that it cannot be said that one example is typical for the genus, though the appendages are the same in all. In all species the carapace is now fused with the thoracic terga. In *S. corniculum*, for example,

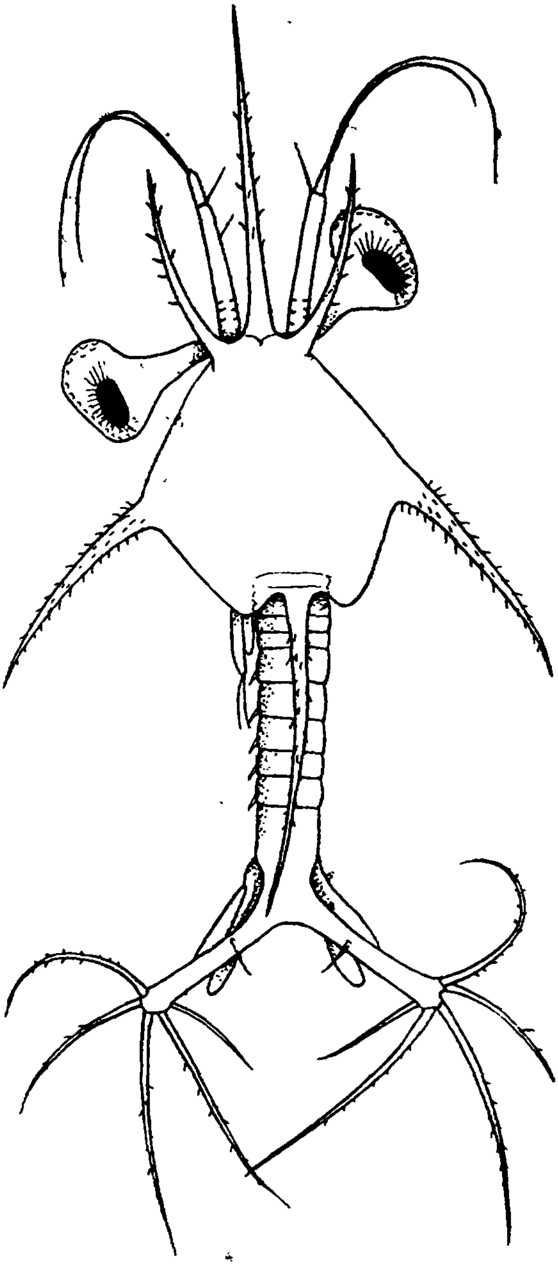

FIG. 60.—*Sergestes crassus*; Protozoea.

the carapace bears two pairs of large lateral and one pair of dorsal spines in addition to the large supraorbital and rostral spines; but there is no posterior dorsal spine, as there is in most species. The abdominal somites have large dorsal and lateral spines, and the telson is long, constricted in the middle, and deeply forked. The appendages of the thorax are fully formed and biramous, but the mouth parts are as in the Protozoea. The pleopods are present in both stages. Stage 2 differs from stage 1 very little, but can be distinguished by the form of the antennal scale, which has an outer apical spine.

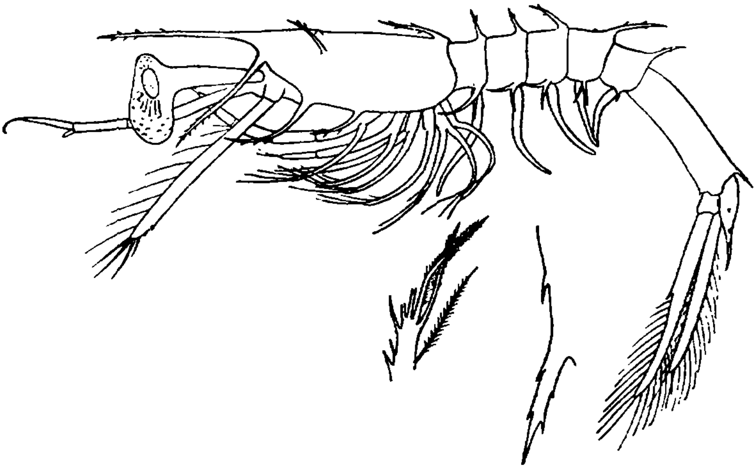

FIG. 61.—*Sergestes atlanticus*, Acanthosoma 2.

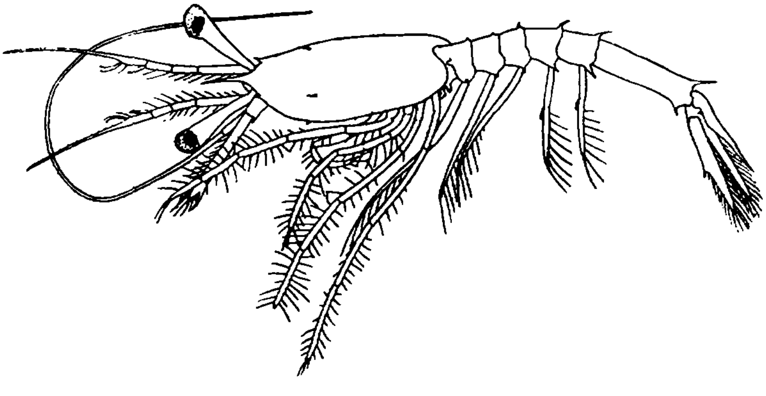

FIG. 62.—*Sergestes robustus*. Mastigopus, showing loss of legs 4 and 5.

POST-LARVAL (MASTIGOPUS).

At the moult to post-larval, or Mastigopus, phase the spines of thorax and abdomen are lost or reduced, and the telson approaches the adult form. The appendages change completely towards the adult form, the exopods are lost from the legs, or remain as vestiges in stage 1, and legs 4 and 5 disappear, or are reduced to minute stumps. The pleopods become setose and functional. In the first stage the antennal flagellum is usually not very long and lacks the peculiar setae which characterize the flagellum of the adult. Legs 4 and 5 are redeveloped during subsequent moults. There may be several moults before the adult form is finally reached, and the Mastigopus phase is a very distinct one in *Sergestes*. The most striking change is in the eyes, which are usually on long stalks in larva and Mastigopus.

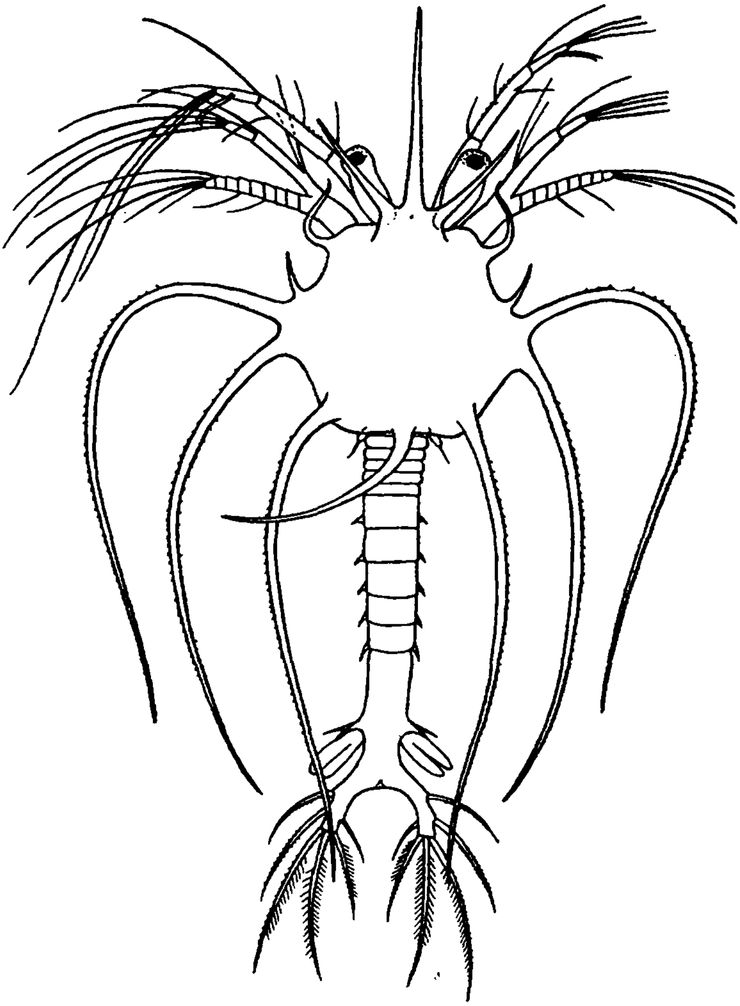

FIG. 63.—Sergestid ? Protozoea. Barrier Reef.

While the development of *Sergestes* follows much the same course as in Penaeidae, and the appendages are the same, the larvae are always readily distinguishable. The only Penaeid larva which could be confused with those of *Sergestes* is that of *Solenocera*, which has a very spiny carapace and abdomen, and a telson which, in the last Zoea, is remarkably like that of some *Sergestes*. A very unusual form of Sergestid Protozoea from the Barrier Reef is shown in Fig. 63, in which the telson differs from the normal form and somewhat approaches that of a Penaeid. As all the genera of Sergestidae are now accounted for except either *Petalidium* or *Sicyonella*, it would seem that this must belong to one of these or to a genus as yet unknown.

CARIDEA

Larvae of species representing nearly all the families of Caridea are now known. No concise definition which will be applicable to the whole group can be framed, but the following characters are generally applicable :

(1) Prezoeal telson with six spines on either side.

(2) Rostrum cylindrical or laterally compressed, never horizontally flattened throughout.*

(3) Antennal scale usually segmented in stage 1, and the endopod with one long apical seta. This seta may be fused with the endopod to form a long spine. There may be also a small spine or another seta, but never two equally long setae as in Thalassinidea for example.

(4) Mandibular palp rarely appearing before the end of larval life.

(5) Maxillule rarely with exopod ; the endopod usually of two segments, or reduced.

(6) Endopod of maxilla seldom distinctly segmented, sometimes much reduced. Distal coxal lobe reduced or lost.

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* In *Thor* the rostrum is a flat plate not extending to the end of the eyes (Lebour, 1940). I do not regard this as a serious exception, since this plate may be said to correspond to the broad base of the rostrum in *Hippolyte* without the rostral point.

(7) Three pairs of maxillipedes functional on hatching.

(8) Maxillipede 1 with coxa and basis large, flattened; the endopod small, of four segments, or unsegmented.

(9) Maxillipedes 2 and 3 with endopod longer than that of maxillipede 1; exopods often with three apical setae in stage 1.

(10) Legs appearing in succession, except when development is abbreviated; but leg 5 may develop before legs 3 and 4 in Alpheidae, Palaemonidae and some Hippolytidae. Exopods on some or all of the legs; endopods of legs usually segmented and setose.

HOPLOPHORIDAE.

See Gurney and Lebour, 1941.

Among the known genera of Hoplophoridae *Acanthephyra* and *Notostomus* have small eggs, and *Hoplophorus*, *Systellaspis*, *Ephyrina* and *Hymenodora* have very large yolk-filled eggs and abbreviated development.

1. *Acanthephyra.*

Larvae of *Acanthephyra* have been described by Kemp (1907), but the whole series in *A. purpurea*, including the post-larval stage obtained by moult, has been studied with living material by Miss Lebour at Bermuda.

The number of stages seems to be indefinite. Miss Lebour distinguished seven, but between the seventh at 7 mm. and the last of 12 mm. there appear to be several moults.

The carapace has a long rostrum in stage 1, and the anterior and posterior margins are denticulate. The abdomen has no spines, except lateral spines on somite 5, but the pleura of somites 1 and 2 are denticulate in late stages. Somite 4 projects into a rounded hump full of fat, the body being sharply bent at this point. The development of the telson is shown in Fig. 65. The triangular form of the first stage becomes parallel-sided in stage 4, and progressively narrower. In stage

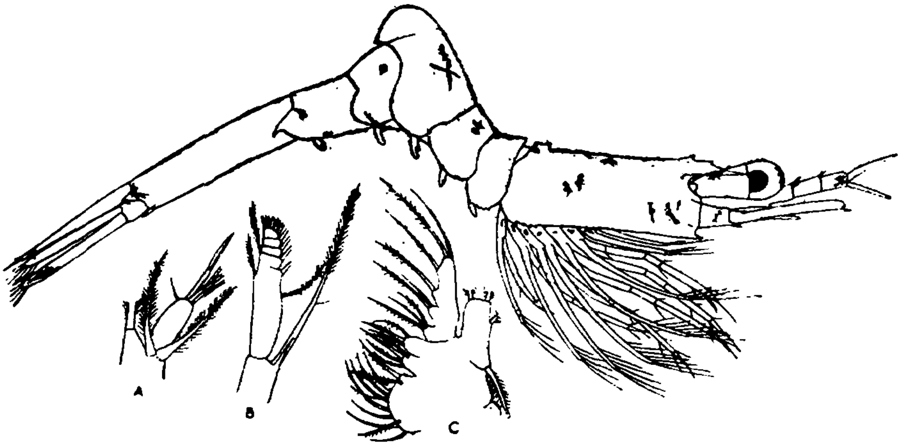

FIG. 64.—*Acanthephyra purpurea.* Stage 8 ?, 8·75 mm. A–C. Stage 2: A, Antennule; B, Antenna; C, Maxilla.

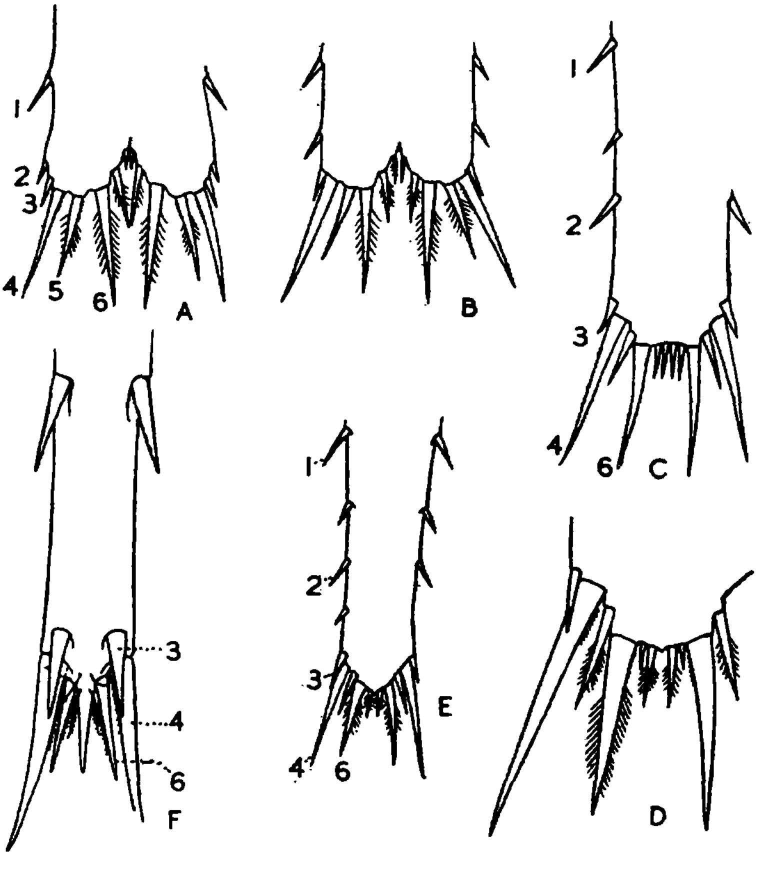

FIG. 65.—*Acanthephyra purpurea*, growth of telson. A. Stage 4, 5·75 mm. B. Stage 5. C. Stage 8 ? D. Stage 9 ?, moulted from C. E, Penultimate stage. F. Adult.

4 it has the appearance of having two closely apposed arms, but the median concavity flattens out and is finally replaced by a median spine. The primary eight spines on either side of stage 2 are retained throughout, though the two outer ones move far up the sides. Between spines 1 and 2 and 3 and 4 a new pair of lateral spines appears, making the full number of four dorso-lateral spines characteristic of the species; but the terminal spines are finally reduced by the loss of nos. 5, 7 and 8.

The antennal scale is segmented, and the endopod has a single apical seta in stage 1. The mandibular palp appears at about the eighth stage. The maxillule has no setose exopod.* The maxilla has four inner lobes, and unsegmented endopod. It is not known if the exopods of the maxillipedes have three or four apical setae. The legs are not all developed until stage 7, and all have exopods. Legs 1 and 2 are not chelate in the last larva. Epipods are present in the last stage.

The rostrum is very short in the first post-larval stage, but lengthens with age. Its post-larval growth has been described by Coutière (1906*a*).

2. *Species with Large Eggs.*

The larvae of *Hymenodora*, *Systellaspis* and *Hoplophorus* are only to be found at considerable depths—1000 m. or more. The body is full of yolk, and all appendages are present on hatching. In spite of this, there are five stages in *Hymenodora* (Stephensen, 1935) and *Hoplophorus*, stage 3 as usual being the first with uropods. In *Systellaspis* the number of stages is less certain, and it is possible that the first stage actually corresponds to the normal stage 2 (Gurney and Lebour, 1941). In *Systellaspis* and *Hoplophorus* all the leg rudiments are biramous from the first, and there is a rudimentary mandibular palp; but in *Hymenodora* in stage 1 there is no palp and legs 4 and 5 are uniramous.

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* The larva described by me (1924*c*, fig. 37) with setose exopod is not *Acanthephyra* but *Rhynchocinetes*.

The palp appears in stage 3 and the exopods of legs 4 and 5 in stage 2.

The mouth parts appear not to be functional in larval life. An interesting point in the development of *Systellaspis* and *Hoplophorus* is the presence of a labral spine—a structure general in Penaeid larvae, but not found elsewhere except perhaps in *Rhynchocinetes*.

In *Hoplophorus* the exopods of legs 2–5 are without setae in stage 4, and have only small setae in stage 5. In its first post-larval stage the exopods of the maxillipedes and all legs are without setae. It is not certain if the exopods have three apical setae in stage 1 in *Systellaspis* and *Hoplophorus*, as I have seen no undamaged material; but there are three in *Hymenodora* (Stephensen, 1935, fig. 26).

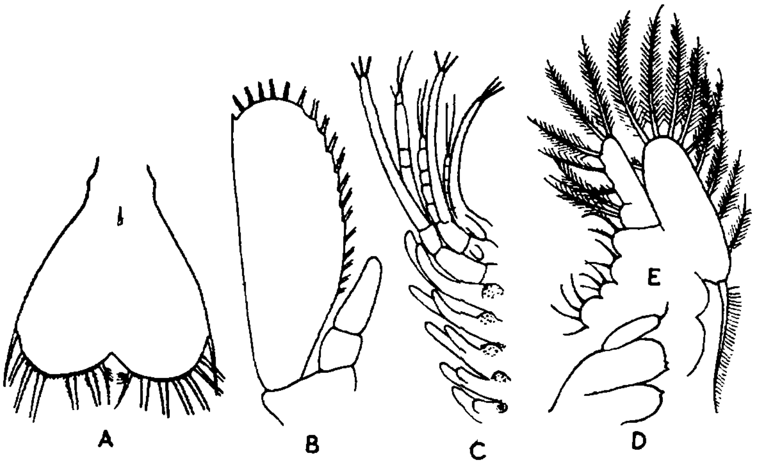

FIG. 66.—*Hymenodora glacialis*, stage 2. A. Telson. B. Antenna. C. Maxillipedes and legs. D. Maxillule. E. Maxilla.

I am indebted to Dr. Stephensen for larvae of *Hymenodora*, among which is one specimen apparently in stage 2, but having some of the characters of stage 1. The antennal scale has a small spine and the telson has eight spines on one side and seven on the other, while legs 4 and 5 are biramous. On the other hand, the eyes appear to be sessile, the exopod of the maxilla has fewer setae than Stephensen shows in stage 2, and the exopods of the maxillipedes have only three setae. The mandible has no palp, and the maxillule is rudimentary.

DISCIADIDAE.

See Gurney and Lebour, 1941.

The family contains the single genus *Discias*, with three species, the position of which is disputed. I have suggested (1938, p. 392) that it is related to *Bresilia* and the Hoplophoridae, and Miss Lebour, who has now discovered the larva, agrees with this conclusion. The larva is a very distinctive form, and closely resembles one described by Ortmann as *Anisocaris dromedarius*. The larval genus *Anisocaris* has been regarded by Coutière as probably belonging to the Pasiphaeidae, but Miss Lebour's discovery disposes of this suggestion.

In *Discias atlanticus* there are nine larval stages. The body is bent at a sharp angle at somite 3, and the sutures between somites 1, 2 and 3 are so difficult to see that it would seem little movement is possible between them. The carapace has a long straight rostrum, without dorsal teeth, and its margin is serrated in front and behind. The pleura of somites 1 and 2 are serrated, and somite 5 has a pair of lateral spines in late stages. The antennule has a very large ventral spine. The antennal scale in stage 1 is segmented, and the endopod is a short rod with two small apical setae. The mandible has a small rudiment of a palp in the last stage. The maxillilule has no exopod. Maxillipede 1 has coxa and basis large and broad, with bilobed epipod in the last stage; the endopod is short, stout, with four segments. The exopods of the maxillipedes have three apical setae in stage 1. Legs 1 and 2 in the last stage have chelae like those of the adult, and there are exopods on all legs.

Miss Lebour has described two other forms of which one (form D) has legs modified as in *Discias*, but with lateral teeth on the rostrum. The other (form C) has the legs not modified, and a dorsal recurved spine on

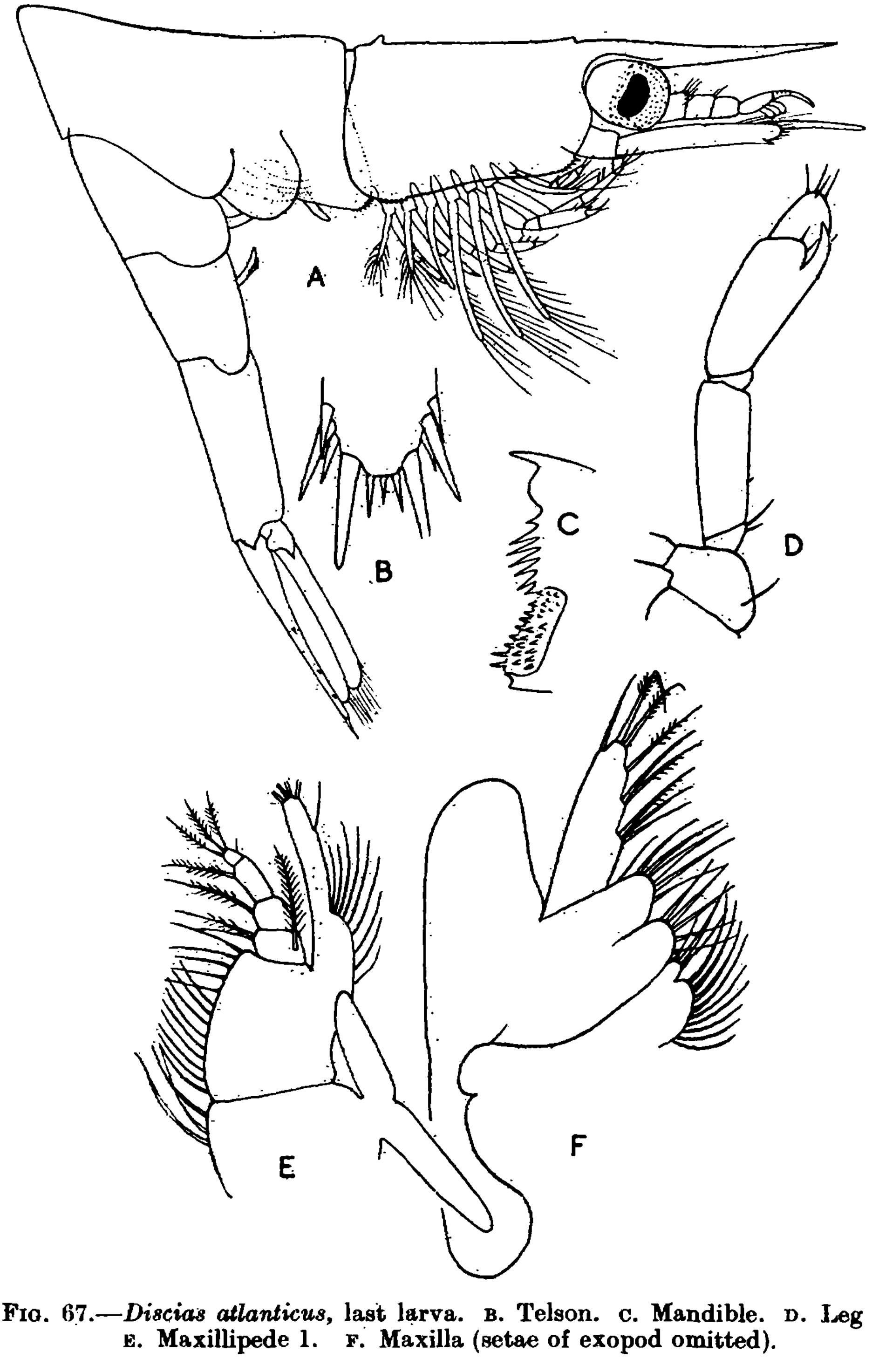

Fig. 67.—*Discias atlanticus*, last larva. B. Telson. C. Mandible. D. Leg 1. E. Maxillipede 1. F. Maxilla (setae of exopod omitted).

somite 3. A specimen of this species from the " Discovery " material has legs 4 and 5 very stout, and with strong spines on ischium and merus. The rostrum has dorsal teeth. I have seen a very similar form, with dorsal spine on somite 4, from the Red Sea.

All these forms seem to belong to the same family, though probably to different genera. Species C may perhaps belong to the genus *Lucaya*, Chace, as Miss Lebour suggests.

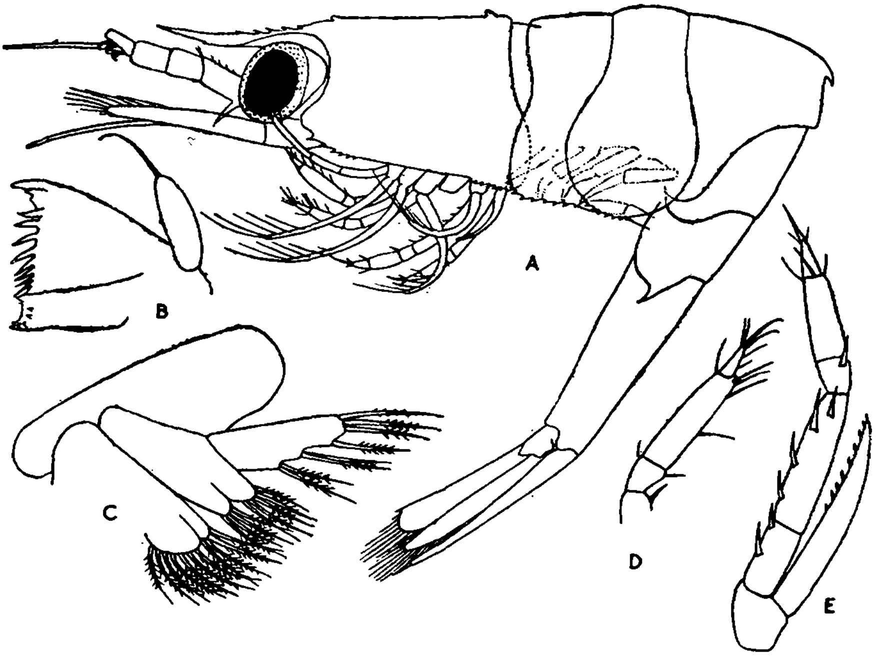

FIG. 68.—*Anisocaris* sp. C (Lebour). B. Mandible. C. Maxilla (setae of exopod omitted). D. Leg 2. E. Leg 5.

RHYNCHOCINETIDAE.

See Gurney and Lebour, 1941.

The family includes only one genus, *Rhynchocinetes*, the systematic position of which has remained uncertain. The evidence from the larvae points strongly to a close relationship with the Hoplophoridae, and this evidence is supported by some points in the adult anatomy.

Ten larval stages have been distinguished, but, although larvae of 7 mm. moult to post-larval, larval life may continue until a length of 14 mm. is reached.

There is a long rostrum in stage 1. The abdomen has no dorsal or lateral spines at any stage, and it is not sharply flexed. The telson, in the last stage, has three pairs of lateral spines and 6 + 6 terminal, disposed upon a rounded projection. The antennal scale is segmented in stage 1, and the endopod has a long apical seta, with a small spine at its base. The endopod of the antenna is as long as the scale in stage 3, and becomes thereafter of remarkable length. In stage 9 it is nearly as long as the whole body, and in stage 10 it is much longer, with the last segments expanded and bent on each other. Detached flagella presumed to belong to large specimens have been seen of 34–46 mm.

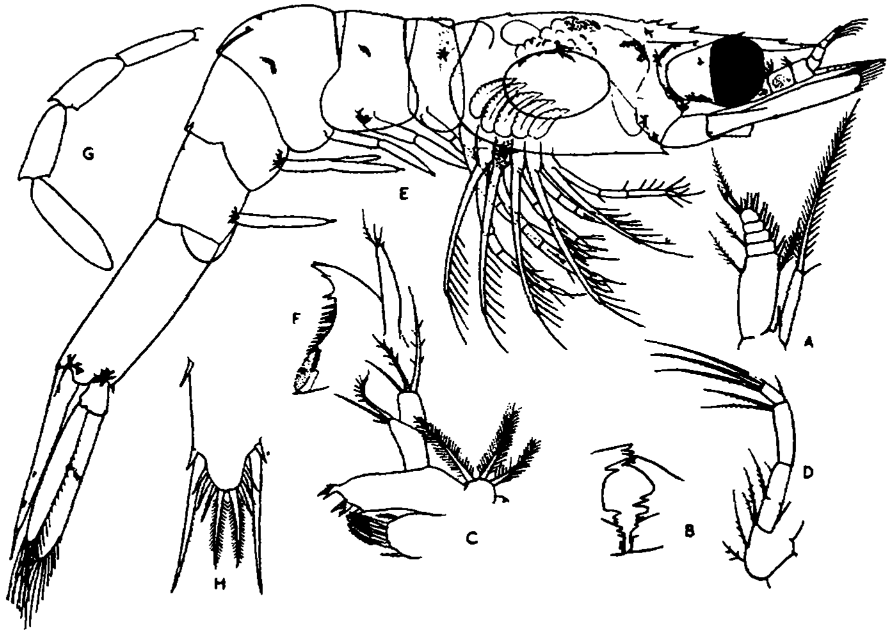

Fig. 69.—*Rhynchocinetes rigens*. A–D. Stage 1: A, Antenna; B, Mandible; C, Maxillule; D, Maxillipede 3. E. Last stage 11 mm. F. Mandible. G. End of antennal flagellum of 33·5 mm. H. Telson.

The mandible has an unsegmented palp in the last stage. The maxillule has an exopod with three setae in stage 1. The exopods of the maxillipedes have three apical setae in stage 1. The legs are not all developed until stage 8, when there are setose exopods on legs 1–4 and leg 5 has a rudimentary exopod. There are no chelae on legs 1 and 2 in the last stage, and leg 5 has lost its exopod.

ATYIDAE.

See Gauthier, 1924 (*Atyaëphyra*); Gurney, 1927 (*Caridina*); Yokoya, 1931 (*Paratya*).

The family is regarded as primitive, with relation to the Hoplophoridae. All the genera are confined to fresh water, but, in spite of this, a normal series of free larvae is preserved in at least three genera. In the most evolved genera *Ortmannia* and *Atya* the free larva has been almost or quite suppressed.*

A Zoea from Lake Tanganyika, and attributed with doubt to *Limnocaridina*, is described by Sars as "the most primitive Caridean larva that I have ever met with." I have seen stage 2 of this form, and find that it has, even then, no rudiments of appendages behind the maxillipedes.

Atyaëphyra desmaresti.

Gauthier's description is most complete. He noted much difference between larvae later than stage 3 reared in the laboratory and those taken in natural conditions. In those conditions there are six stages.

Stage 1 has a small rostrum and the carapace has no marginal denticles. The abdomen has no spines, but there is an anal spine. The antennal scale is segmented, and the the endopod has one long seta and a small spine. The maxillule has an exopod with three large setae. The exopods of the maxillipedes have four apical setae. Leg 1 is a small bilobed rudiment, and leg 2 scarcely visible.

The exopod of the maxillule persists in stage 3, and is then lost. In the last stage there are supraorbital spines, but no spines on the rostrum. Legs 1–3 have exopods with setae, and there are rudimentary exopods on legs 4 and 5 which are lost at the moult to post-

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* For supposed mutation in Atyidae see p. 83.

larval. In post-larval stage 1 the mouth parts, including maxillipede 1, are reduced and not functional, except the exopod of the maxilla; but the exopods of the maxillipedes do not lose their setae. Leg 3 has a setose exopod, and a vestigial exopod may be retained on this leg in the adult.

I have a few larvae of this species in stages 1, 2, 4, 5 from a pool by Lake Tiberias, and these differ considerably from those described by Gauthier from Algeria. In stages 1 and 2 there is no trace of an exopod on the maxillule, and the maxilla has nine setae on the exopod instead of five. There is no anal spine in stage 1. Legs 1 and 2 are large biramous rudiments in stage 1, and leg 1 is fully functional in stage 2, instead of being quite rudimentary. Antennule and antenna are much more developed in stage 2.

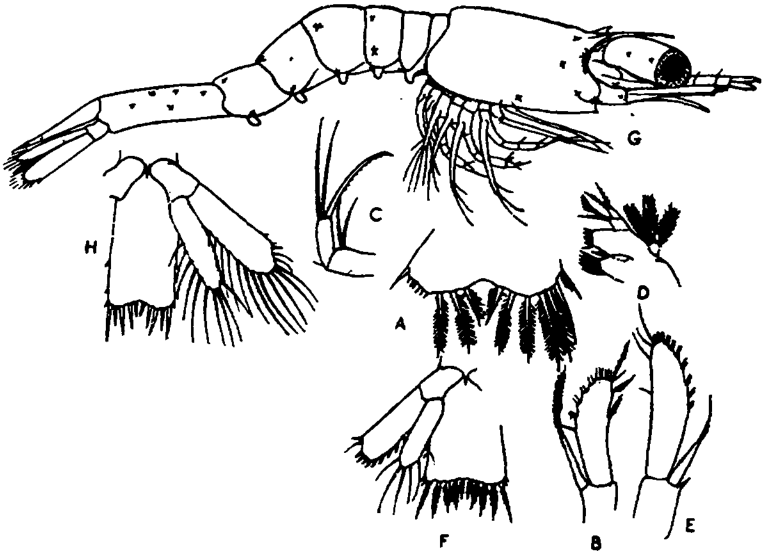

FIG. 70.—*Atyaëphyra desmaresti*. Palestine. A–C. Stage 1: A, Telson; B, Antenna; C, Maxillipede 3. D, E. Stage 2: D, Maxillule after Gauthier; E, Antenna. F. Stage 4, telson. G. Stage 5. H. Telson.

There is evidence that there are differences between the larvae of *Caridina nilotica* from different localities (Gurney, 1927, p. 252), and the same may be true of *Paratya compressa*, since Ishikawa (1885) figured an exopod on the maxillule, while Yokoya's specimens had no trace of it. In *Caridina nilotica* there is a very small exopod on the maxillule in Egyptian specimens, and the shape and arming of the last segment of maxillipede 3 is exactly the same as in *Atyaëphyra* (Fig. 70, *c*). In *Caridina* there are exopods on legs 1–3 only.

An interesting point in the post-larval development of *Troglocaris schmidti* is noted by Stammer (1932, p. 607). In the smallest specimens of 6–8 mm. there were exopods only on legs 1–3 and, in the largest specimens, on 1–4. There is presumably no free larva in this subterranean form. Birstein (1933, p. 150) found an exopod even on leg 5 in specimens of 30 mm., so that the exopods are here, so far from being larval, developed on more and more legs with increasing age. The number of exopods has been used for separating new genera allied to *Troglocaris*, but apparently the number is simply a matter of age.

PASIPHAEIDAE.

See Kemp, 1910 ; Bjorck, 1911 ; Stephensen, 1935 ; Gurney, 1936*a*.

The family is generally regarded as primitive, owing to the presence of exopods on all the legs ; but there is no other primitive character except, perhaps, the form of maxillipede 2. The " undivided " mandible is certainly not primitive.

All the genera known except *Leptochela* have large eggs and abbreviated development. Ortmann and Coutière have attributed to the family certain larvae which Ortmann called *Anisocaris*, but one of these is now known to belong to *Discias*, and it becomes most improbable that any of them are Pasiphaeidae.

The development of *Pasiphaea tarda* and *Parapasiphaë sulcatifrons* is known, and they are very much the same. In both species the eggs are very large (about 3 mm.) and the larvae have the thorax full of yolk and the cuticle soft. They very closely resemble the larvae of *Systellaspis* and are, no doubt, confined to deep water below 800 m.

Parapasiphaë sulcatifrons.

Stage 1 8·5 mm. (Kemp). The antennae have no spine, and the endopod is about one-third as long as the scale. Maxillipedes 1–3 and legs 1 and 2 are developed but 3–5 are just buds. Pleopods and uropods are absent. In stage 2 the mouth parts are rudimentary, but all the legs are present, unsegmented, with rudimentary exopods without setae. Stephensen has described a third stage still without uropods. It is so unusual for stage 3 to lack uropods that it seems probable, in spite of the differences mentioned by Stephensen, that this and Kemp's stage 2 are the same. In stage 3 (Stephensen's stage 4) legs 1 and 2 are chelate and segmented, the pleopods are large, and there are large uropods. In a specimen kindly sent me by Dr. Stephensen there are setae on the exopods of maxillipede 3 and leg 1, but not on the other legs. The number of stages is uncertain. Stephensen's stage 6 may be called post-larval, and it would seem there are either 4 or 5. None of the appendages at any stage have a distinctively larval form, and development may be said to be direct. Apparently no food is taken during the larval phase.

Kemp noted the very late appearance of arthrobranchs and mandibular palp.

Leptochela.

The eggs are small, and there are five normal larval stages. In stage 1 the carapace has a long straight rostrum; abdominal somite 5 has a pair of lateral spines, and the telson is of unusual form, more or less oval instead of triangular. The antenna has a large spine on the exopod, which is exceptional at this stage. The maxillule has no trace of an exopod. There is a rudiment of leg 1 only.

In the last stage legs 1 and 2 are chelate, leg 1 with setose exopod, and leg 2 with an exopod without setae. Legs 3–5 are rudimentary, without exopods. There are large pleopods on somites 2–5, but none on somite 1. The delayed development of legs 3–5 and suppression of pleopod 1 are very remarkable features, especially in a genus belonging to a family supposed to be primitive.

In the first post-larval stage leg 2 has a setose exopod, but legs 3–5 have no exopods, though they are present in the adult. Pleopod 1 appears as a rudiment in stage 2.

Development of four species is known. I have myself seen larvae of *L. bermudensis*, *L. pugnax* and *L. aculeocaudata*. Menon (1937) has described larvae attributed to *L. aculeocaudata*, and Dakin and Colefax (1940) the larval and post-larval stages of *L. sydniensis*, n. sp. There is no important difference between the species.

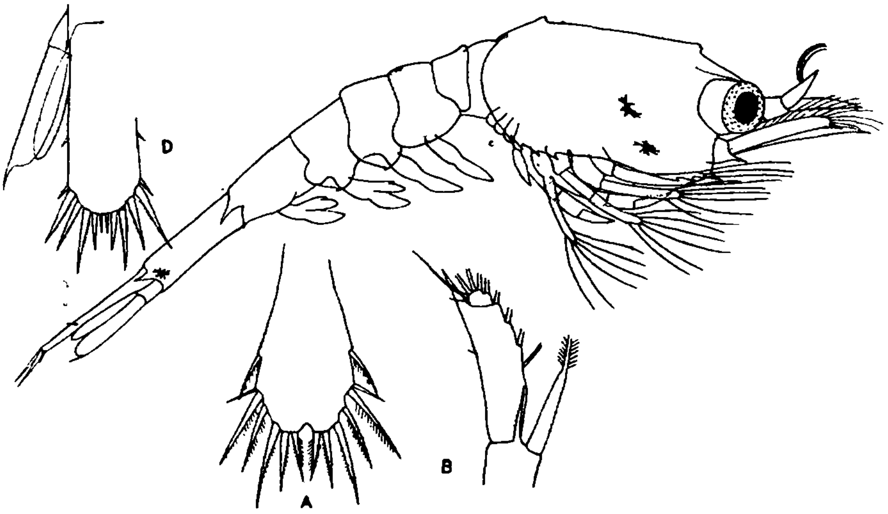

FIG. 71.—*Leptochela bermudensis*. A. Stage 1, telson. B. Antenna. C. Stage 5. D. Telson.

PANDALIDAE.

See Berkeley, 1930; Lebour, 1940.

The development is now known of eight species of *Pandalus* and of species of the genera *Pandalina*, *Parapandalus*, *Pandalopsis* and *Chlorotocella*. The characters of these genera are summarized by Miss Lebour. It does not seem that there is any purely larval character by which the Pandalidae can be separated on the one hand from the Hippolytidae, and on the other from the Processidae. From the Hoplophoridae they are distinguished by the loss of the exopod from leg 5, and there is a tendency to a loss of the preceding exopods,

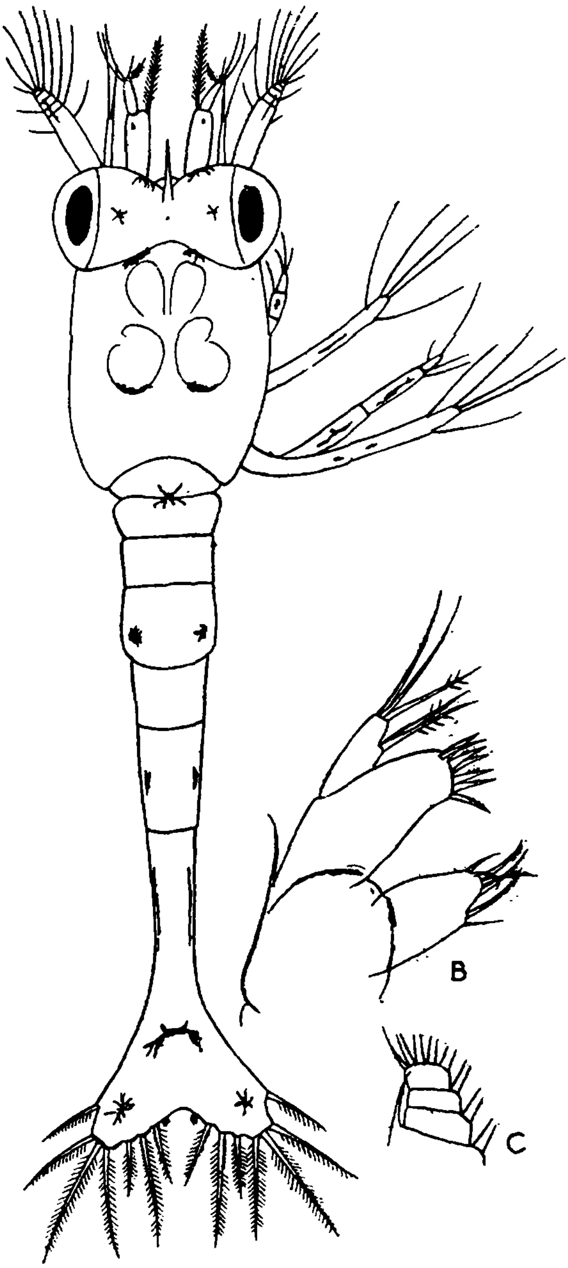

FIG. 72.—A. *Pandalina brevirostris*, stage 1. B. *Pandalus montagui*, stage 2, maxillule. C. Antenna, end of scale.

reaching its end in *Chlorotocella*,* which has an exopod on leg 1 only.

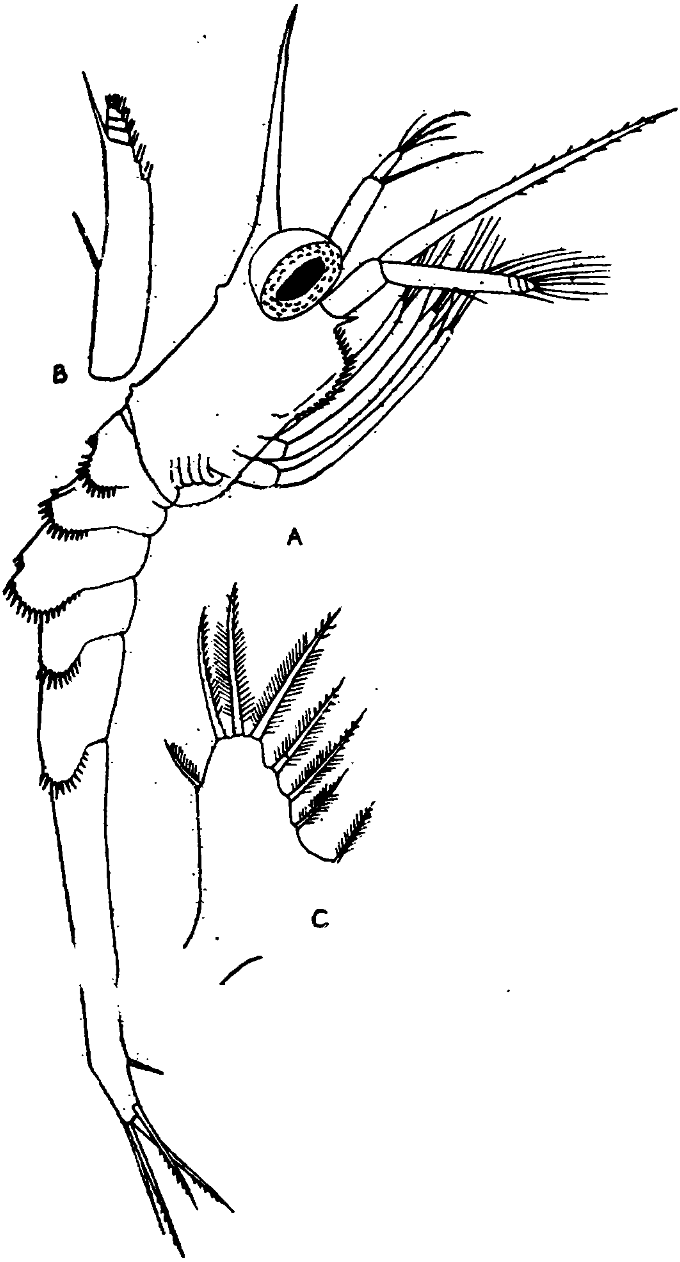

FIG. 73.—A. *Pandalus stenolepis*, stage 1. B. Antennal scale. C. Telson.

The following definition is quoted from Miss Lebour (1940, p. 240): " Caridea with rostrum in all stages;

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* Dakin and Colefax (1940, p. 157) describe some stages in the development of *C. leptorhynchus* (Stimpson), which they consider may be the same species as *C. gracilis*, Balss.

antennular peduncle concave on the outer margin (except sometimes in the first stage); antennal flagellum a simple rod ending in a seta with or without an accessory seta; mouth parts well developed; 5th leg never prematurely developed; none of the legs oar-shaped. No exopod on leg 5. Rostrum toothed in late stages. Legs 3–5 ending in simple dactyls. Leg 1 simple or with rudimentary chela. Leg 2 chelate in late stages."

The antennal scale is usually segmented, and it is not strictly correct to say that the endopod has always an apical seta, since in *P. stenolepis* it is a long spiny rod (Fig. 73), and in *Pandalopsis dispar* it is a long segmented flagellum in stage 1. In those species which I have seen myself (*Pandalina brevirostris*, *Pandalus montagui*, *P. stenolepis*) there is an outer seta (vestigial exopod ?) on the basis of the maxillule in stage 1. It is not present in *Chlorotocella*, and is not shown in figures of other species.

There are various larvae which have been described under generic names and referred to Pandalidae. The most striking of these is *Procletes* (*Atlantocaris*) *gigas*, Ortmann, which reaches a length of about 50 mm. This is now identified with *Heterocarpus* (Gurney and Lebour, 1941). Nothing is known about its early stages.

The following key to the larvae known gives a partial summary of the characters, but does not arrange them in a systematic way. Miss Lebour's summary shows that they may be arranged in order of increasing specialization.

1. Margin of carapace coarsely serrated, and some of the abdominal somites with a fringe of teeth . . . . 2.
   No fringe of teeth on abdominal somites . . . . 4.
2. Rostrum in stage 1 with dorsal spines; antennal endopod scarcely longer than scale . . . . *P. platyceros*.
   Rostrum smooth in stage 1 . . . . 3.
3. Dorsal fringe of spines only on somites 3 and 4; somite 5 with dorso-lateral spines . . . . *P. propinquus*.
   Dorsal fringe on somites 1—5; no dorso-lateral spines on somite 5 . . . . *P. stenolepis*.

4. Antennal scale not segmented in stage 1; legs rudimentary in stage 1; exopods on legs 1–3 . *P. borealis.*
   Antennal scale unsegmented; legs fully formed in stage 1. Exopods on legs 1 and 2 . . . . 5.
   Antennal scale segmented; legs rudimentary or absent in stage 1 . . . . 6.
5. Rostrum toothed. Telson with 24 spines in stage 1 *Pandalopsis dispar.*
   Rostrum smooth; telson with 14 spines . { *P. danae.* *P. hypsinotus.*
6. No legs present in stage 1 . . . . 7.
   Rudiments of legs present in stage 1 . . . . . 8.
7. Exopods on legs 1–4 . . . . *Parapandalus richardi.*
   Exopods on legs 1–3 . . . . *Pandalina brevirostris.*
8. Margin of carapace denticulate; somite 5 with dorsolateral spines . . . . . . *P. bonnieri.*
   Carapace smooth; not spines on somite 5 . *P. montagui.*

HIPPOLYTIDAE.

See Lebour, 1931*b*, 1936*a*, 1940*b*; Gurney, 1937*b*.

The larvae of the following genera are known wholly or in part: *Hippolyte* (6 species); *Spirontocaris* (10 species); *Thor* (1 species); *Caridion* (2 species); *Chorismus* (1 species); *Saron* (1 species); *Tozeuma* (1 species); *Latreutes* (1 species); *Lysmata* (2 species) *; *Trachycaris* (1 species).

In some species of *Spirontocaris* and in *Bythocaris* and *Cryptocheles* development is abbreviated or the free larva completely suppressed.

The larvae of Hippolytidae show such diversity that it is impossible to frame any definition which will distinguish them as a whole from other Caridea. They approach the Pandalidae very closely, but can be separated from them when the adult features of the legs begin to appear.

The examples of *Hippolyte* and *Lysmata* are taken to illustrate this diversity.

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* Including *L. intermedia* (from Bermuda), unpublished.

Hippolyte.

Rostrum present in stage 1, remaining simple and broad at the base. Carapace without supraorbital spines, or with very small spines in late stages; margin of carapace denticulate. Abdominal somite 5 with a pair of dorsal spines. Anal spine present in late stages only. Antennal scale with tendency to lose segmentation; endopod spine-like in stages 1 and 2. Maxillule with outer seta on basis. Exopods of maxillipedes with three apical setae in stage 1. Exopods on legs 1 and 2 only. Four to nine stages.

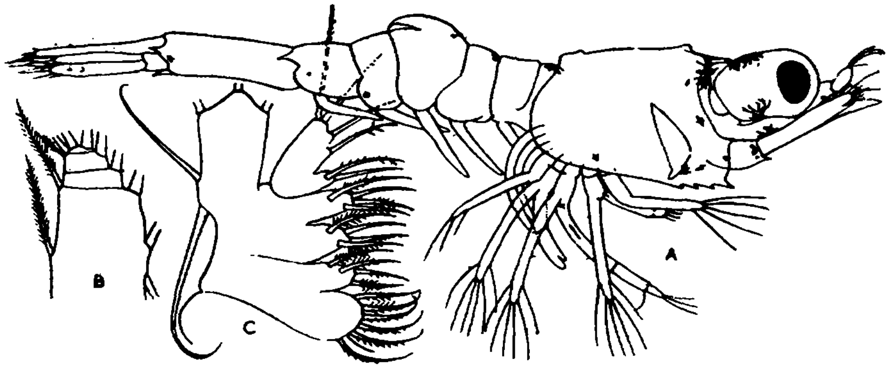

FIG. 74.—A. *Hippolyte pleuracantha*, stage 5. B, C. *H. acuminata*, stage 1: B, Antenna; C, Maxilla.

Lysmata.

Rostrum long and slender in stage 1. Carapace with supraorbital spines and denticulate margin. Abdominal somite 5 with or without dorsal spines. Anal spine absent. Eyes borne upon long stalks. Antennal scale segmented in stage 1: the endopod a rod with one seta and a small spine. Maxillule without outer seta. Exopods of maxillipedes with three terminal setae in stage 1. Exopods on legs 1–4. Leg 5 appearing before leg 4 and of enormous size, the propod greatly expanded. Probably nine stages.

The larva of *Lysmata* comes within the larval genus *Eretmocaris*, Bate, but the latter includes forms of very problematical position. In particular *E. dolichops* may perhaps belong to *Nematocarcinus* or to an unknown Pandalid (Lebour in Gurney and Lebour, 1941). The systematic relationships of the genera are still unsettled, and the knowledge of the larvae has so far contributed little to a solution of the difficulty.

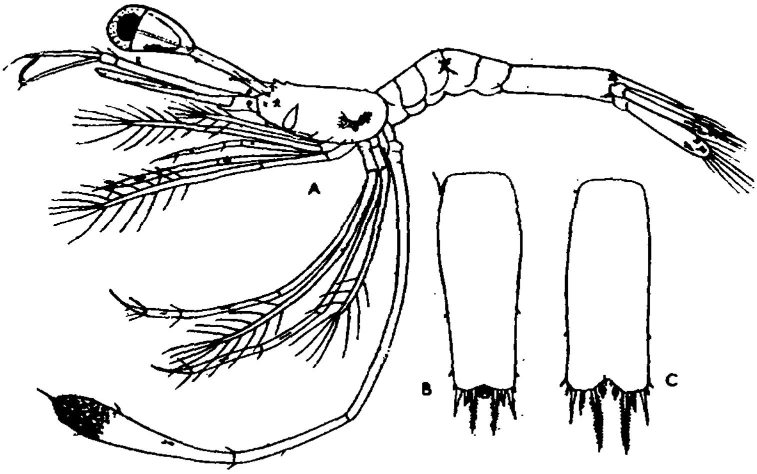

FIG. 75.—A. *Lysmata intermedia*, stage 5. B. Telson. C. Telson, stage 4.

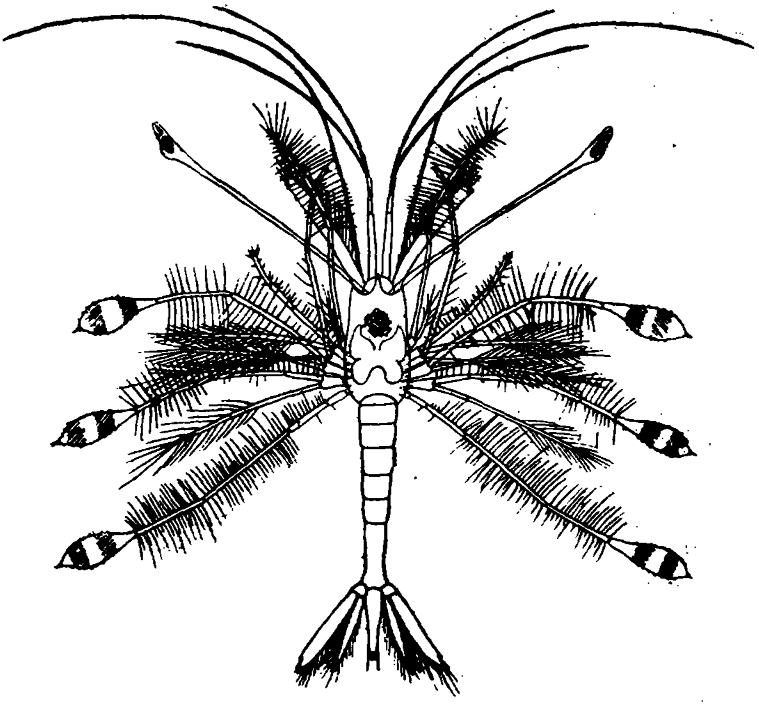

FIG. 76.—*Eretmocaris X*, after Lebour. Bermuda.

A figure is given of a remarkable larva allied to *Eretmocaris dolichops* (*Eretmocaris* X, Lebour) in which there are the same long jointed eyestalks, but the propods of legs 3, 4 and 5 are all expanded.

PROCESSIDAE.

See Lebour, 1936*b*, 1941 ; Gurney, 1936*d*, 1937*a*.

The family includes the two genera *Processa* and *Nikoides*, which can only be separated by the possession by the latter of an exopod on leg 1. The larvae are known of four species of *Processa* and of *Nikoides danae*. Their characters may be summarized thus :

Carapace without rostrum in stage 1, or with minute rudiment of it ; anterior margin serrated ; supraorbital and branchiostegal spines present, generally large. Abdominal somite 5, and sometimes 4 also, with a pair of dorsal spines. Stem of antennule very curved in late stages. Antennal scale unsegmented in stage 1 ; the endopod in stage 1 a simple pointed rod. Maxillule with outer seta on basis. Exopods of maxillipedes in stage 1 with three spical setae. Legs 3–5 with propod not expanded. Leg 5, and sometimes leg 4, also without exopod. Eight or nine stages.

The species *P. edulis*, *P. canaliculata* and *P. bermudensis* are very much alike, but the last has no exopod on leg 4. Late larvae of *P. aequimana* differ considerably from all the rest in having a median dorsal spine on abdominal somites 3 and 6, and an unusually large branchiostegal spine. It has also no exopod on leg 4. The larva of *N. danae* differs very little from that of *P. edulis*, for example.

Certain larvae which are undoubtedly Processids have been described under the generic name of *Hectarthropus*, and these are strikingly different in the large size of the supraorbital, branchiostegal and abdominal spines (Gurney, 1937a, p. 96). Another very different form from the Indian Ocean (" Discovery " Expedition) is shown in Fig. 78. The left leg 1 is not chelate, which makes it almost certain that it is a Processid; but it differs a great deal from the normal type, and also from *Hectarthropus*. It is probable that these very distinct

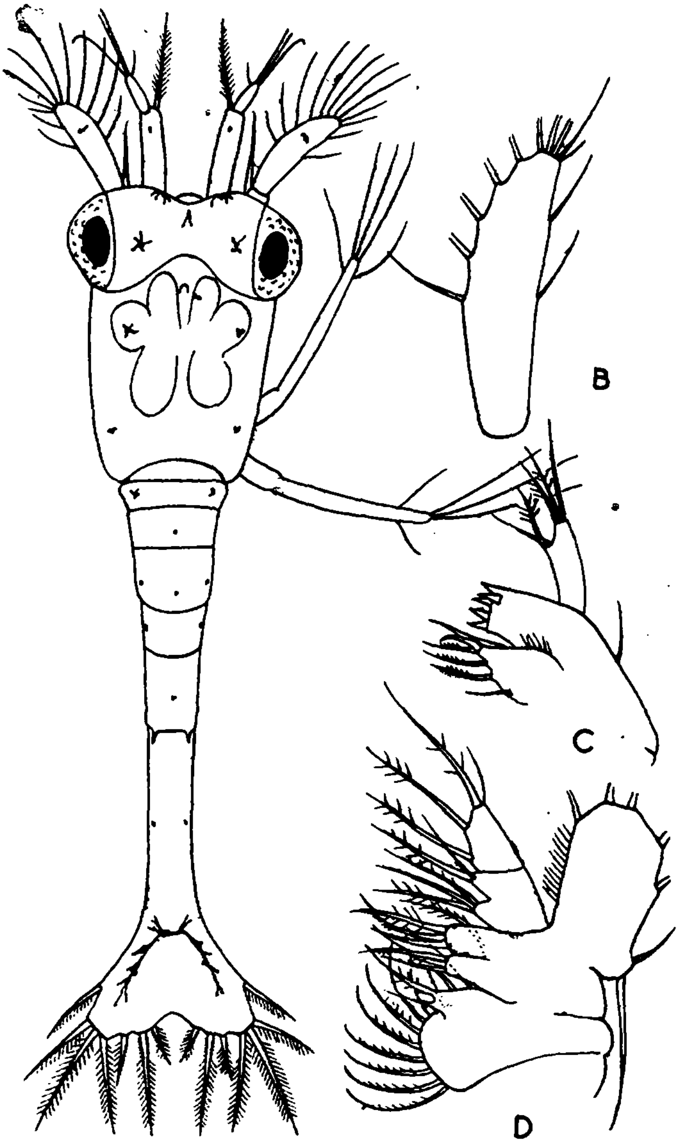

FIG. 77.—A. *Processa edulis*, stage 1. B. Antenna. C. Stage 2, maxillule. D. Maxilla.

types of larva represent genera as yet undiscovered, perhaps inhabiting deep water.* The habit of the adult

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* Miss Lebour (1941) has now shown that a larva of the Hectarthropus type may give rise to an adult (*P. wheeleri*, sp.n.) differing very little from *P. edulis* or *P. canaliculata*.

of some species of lying hidden in sand during the day makes them escape capture by a light trawl.

FIG. 78.—Processid. "Discovery" Station 1580.

ALPHEIDAE.

See Brooks and Herrick, 1892; Lebour, 1932*b*; Gurney, 1938*b*.

In *Alpheus* and *Athanas* development follows its normal course, with as many as nine stages in some species; but in *Synalpheus* there is a strong tendency to abbreviation of development. Herrick (1892, p. 379) drew attention to the relation between habitat and length of larval life, and found that in "*Alpheus saulcyi* var. *longicarpus*" (= *Synalpheus longicarpus*) the young might hatch actually in adult form. He believed that different races of the same species might differ in development, but Coutière has shown that he did not correctly discriminate between species. Poecilogony in Alpheidae has not, in fact, been proved to exist (see p. 64).

For normal Alpheidae, such as *A. ruber*, the following definition holds good:

Carapace with or without supraorbital spines, the rostrum short as a rule, widened at its base, and without dorsal teeth. Abdominal somites without dorsal teeth, and generally without pleural spines. Antennal scale segmented, and endopod with apical seta and small spine in stage 1. Mandible poorly developed in early stages. Palp of maxillule unsegmented, very small; no outer seta on basis. Maxilla with three inner lobes only, the endopod small and unsegmented. Maxillipede 1 with endopod very small and unsegmented. Maxillipede 3 in stage 2 with very long apical spine. Exopods with four apical setae in stage 1. Leg 5 developed before leg 4, very long and slender, the apical spine very long and serrated at the end. Legs 1–4 with exopods.

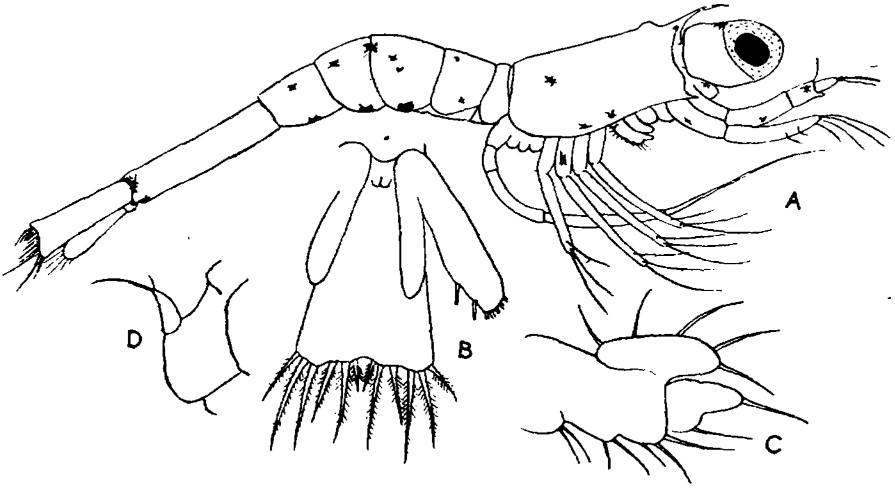

FIG. 79.—A. *Athanas nitescens*, stage 3. B. Telson and uropods. C. Maxilla. D. Maxillipede 1.

There is no really satisfactory account of abbreviated development in Alpheidae, but that of Brooks and Herrick (1892) of "*Alpheus saulcyi* var. *brevicarpus*" (*Synalpheus brevicarpus*) is adequate. In this form there are apparently only two stages. Stage 1 has all legs and pleopods, legs 1–4 having exopods without setae. Leg 5 is large, blunt-ended and bent forwards.

The telson is oval, with 7 + 7 spines. The mouth parts are rudimentary, and the exopod of the maxilla has a proximal lobe without setae. Stage 2 has setae on the exopods and large setose uropods. It is most desirable that further investigation should be made of this type of development in Alpheidae. I have followed the development of *S. goodei*, which differs in some important points from Herrick's account. A description of this species will be published by Mr. J. C. Armstrong.

It is evident that there are great differences in development within the genus *Synalpheus*. In *S. triunguiculatus* (Gurney, 1938*b*) there are 4 or 5 stages, and a more or less normal larva. It is probably characteristic of abbreviated development in this genus that the telson in stage 2 has only 7 + 7 spines.

The genera *Anebocaris*, Bate, and *Diaphoropus*, Bate, are larval Alpheidae. Few larvae which can be recognized as Alpheids depart widely from the general form and structure of *Alpheus ruber* for example; but some are known which, by reason of the shape of the rostrum or of the abdominal pleura, have a rather distinctive appearance, and no doubt belong to genera other than *Alpheus*. I have described one very remarkable form which unites the characters of Alpheid and Palaemonid larvae (Gurney, 1938*b*, p. 56). A strange form, in which the head region is greatly elongated is figured by Dakin and Colefax (1940, fig. 252). This is a large species of 20 mm.

PALAEMONIDAE.

See Sollaud, 1923*b*; Gurney, 1938*b*; Gurney and Lebour, 1941.

1. PALAEMONINAE.

In the fresh- and brackish-water species Sollaud has described examples of increasing abbreviation of development, but, although all the appendages of the adult, except the uropods, may be present on hatching (*e.g.*

Palaemon potiuna), the larva is never entirely suppressed, and there are not less than three stages.*

It is interesting also to note that in these species the telson remains broad and triangular, without narrowing, until the post-larval stage is reached (Sollaud).

The number of stages in marine species may be as many as eight (*Leander serratus* according to Sollaud), but I have not found more than five in *L. longirostris* and *L. squilla*. In *Brachycarpus biunguiculatus* eleven stages have been distinguished (Gurney and Lebour, 1941), but the number is by no means certain. It is impossible to frame any definition for the Palaemonidae as a whole which will distinguish them from the Alpheidae, though, for the most part, they are, in fact, easily separated. In the Palaemonidae maxillipede 3 is never modified as it is in most Alpheidae. The characters of the larvae of *Leander* and *Palaemon* have already been summarized (Gurney, 1938*b*, p. 15), but in order to frame a definition of the subfamily it is necessary to bring in the group of larvae included in "*Cryptoleander*," since one of them has been shown to be *Leander tenuicornis* (Species B.R. IX, Gurney, 1938 ; see Gurney and Lebour, 1941).

Definition of Palaemoninae.

Body not greatly flexed. Carapace with supra-orbital and one or more median dorsal spines. Abdominal somite 3 sometimes with dorsal process. Somite 5 usually with lateral spines ; anal spine usually absent. Antennule with ventral spine. Antenna in stage 1 with exopod segmented, and endopod with apical seta and small spine. Endopod of maxillule small, unsegmented, with one or two small apical setae. Maxilla with three inner lobes only ; the exopod fringed with setae throughout ; the endopod with, or rarely without, a basal lobe. Basis of maxillipede 1 without strong spines ; endopod usually with few or no distinct segments. Leg

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* An apparent exception is *Conchodytes biunguiculatus*. Boone (1935) states that she has found 100 young in the brood-pouch of this species.

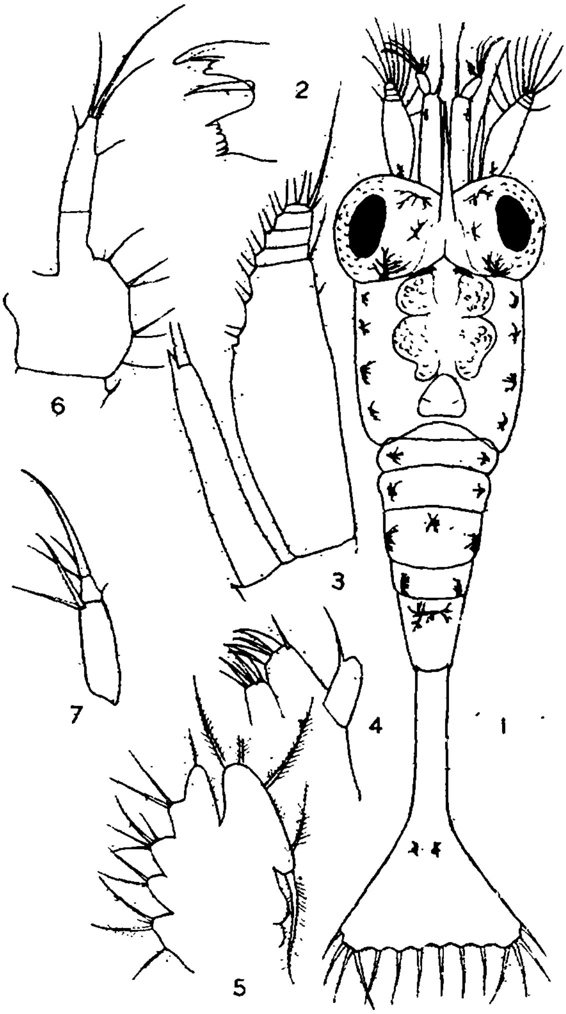

FIG. 80.—*Leander pacificus*, stage 1. 2. Mandible. 3. Antenna. 4. Maxillule. 5. Maxilla. 6. Maxillipede 1. 7. Maxillipede 3.

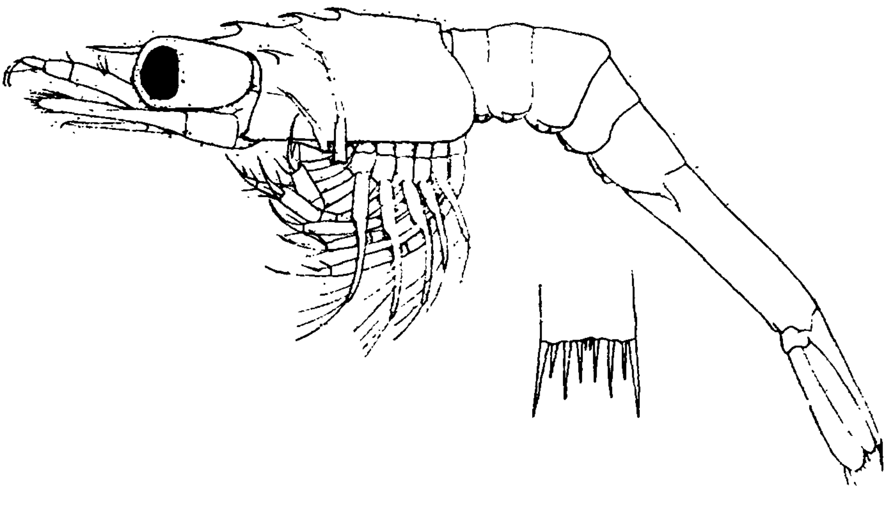

FIG. 81.—*Leander squilla elegans*, Egypt. Stage 4.

4 usually developing after leg 5, with exopod except in *L. longirostris* and *Cryptoleander*. Leg 5 larger than leg 4 and often more than twice as long; its dactyl with basal spine.

2. PONTONIINAE.

The larvae which are supposed to belong to the Pontoniinae differ so much among themselves that a precise definition to cover all of them cannot be framed. Since so little is certainly known about this subfamily only a description of *Periclimenes* subg. *Ancylocaris* is given here. The larvae of five species of this subgenus are known, and others unnamed, but closely related.

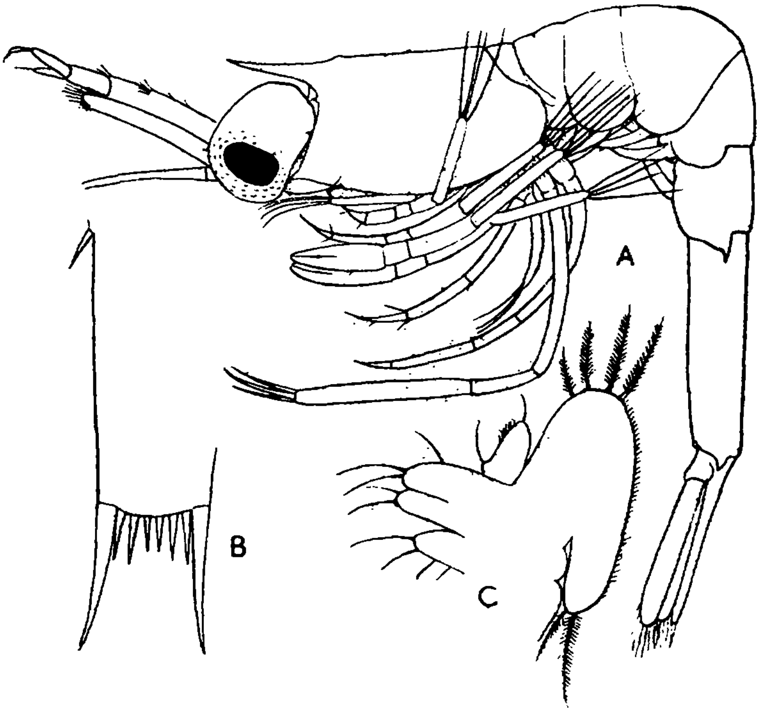

FIG. 82.—*Periclimenes* (*Ancylocaris*) sp. Red Sea. Last stage. B. Telson C. Maxilla.

Periclimenes subg. *Ancylocaris*.

Body not sharply flexed at junction of thorax and abdomen. Rostrum short, usually without dorsal spines. Carapace without dorsal spines, and with or without small supraorbital spines. Abdomen without dorsal spines; somite 5 with lateral spines. Anal spine absent. Endopod of maxilla with basal lobe; the exopod without setae on outer margin. Maxillipede 1 with basis protuberant, without strong spines; the endopod usually not distinctly segmented. Leg 4 without exopod. Leg 3 shorter than legs 4 and 5, which are subequal, or leg 4 longer than leg 5. Dactyl of leg 5 without basal spine.

A series of larvae which have been included in a "*Mesocaris* group" (Gurney and Lebour, 1941) differ very much from *Ancylocaris*, particularly in the marked flexure of the body and the flattening of the thorax. Legs 4 and 5 are not longer than leg 3. This group certainly includes species of *Periclimenes* which must be referred to the subgenera *Periclimenes* and *Periclimenaeus*; but it also probably includes *Harpilius* and *Coralliocaris*. Much more information is required about the larvae of the Pontoniinae. It seems very probable that the grouping of the adults will have to be much modified.

Only stages 1 and 2 of *Anchistioides* are known with certainty (Gurney, 1936*d*). Stage 2 has very large supraorbital spines and a pair of posterior spines on the carapace. Abdominal somite 3 has a dorsal process. The mouth parts are much reduced. Two very strange late larvae have been referred to the genus with doubt (Gurney, 1938*b*). If these are correctly identified *Anchistioides* must be excluded from the Pontoniinae and a new subfamily, the Anchistioidinae, must be founded for it.

CRANGONIDAE.

See Sars, 1890; Lebour, 1931*b*.

The following summary of the characters of the Crangonid larvae is adapted from that given by Miss Lebour.

There are not more than five stages. Rostrum present in stage 1, usually short, but long and slender in *Pontophilus*. Carapace without supraorbital and (except in *C. antarcticus*) dorsal spines; its anterior

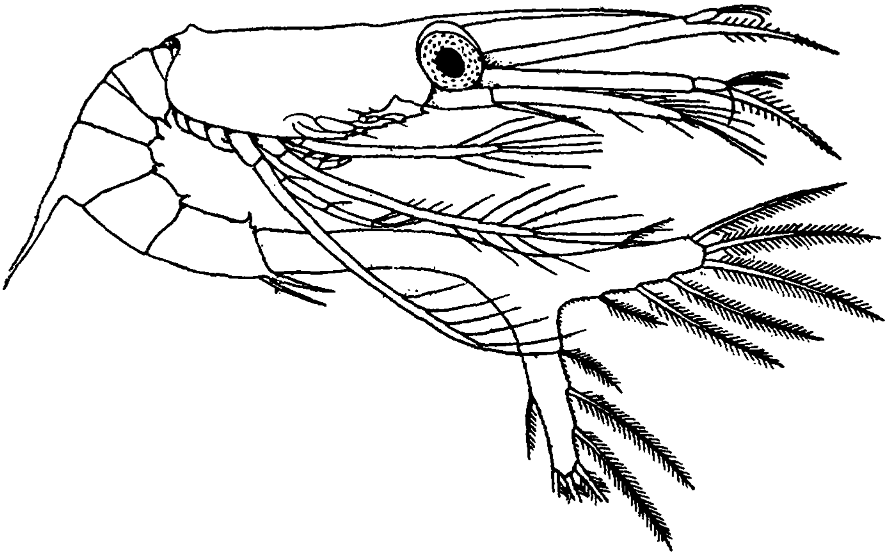

FIG. 83.—*Pontophilus spinosus*, stage 1.

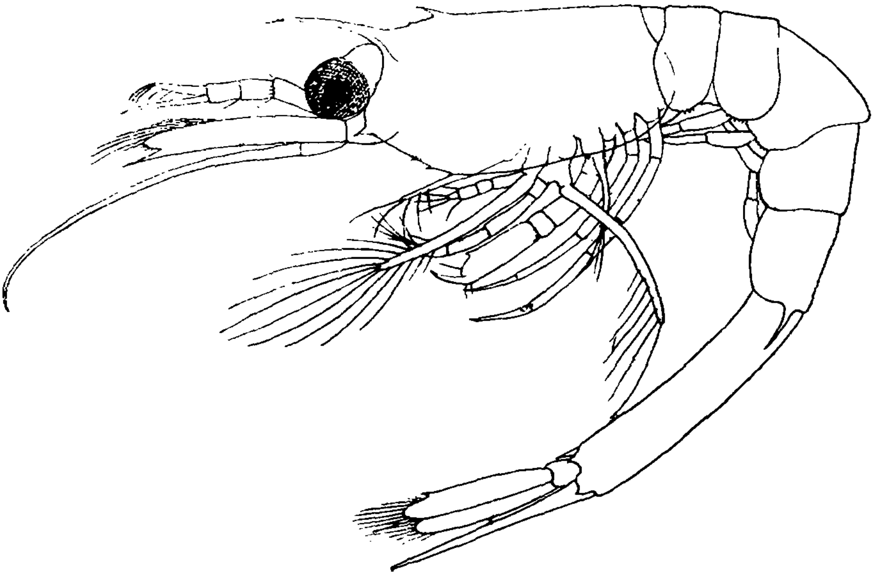

FIG. 84.—*Crangon antarcticus*, stage 3.

ventral margin usually denticulate. Abdomen usually with a pair of lateral spines on somite 5; somite 3 with or without dorsal or lateral spines. Anal spine appearing in stage 4, or in stage 3 in *C. antarcticus*. Antennule with inner branch a straight pointed process in stage 1. Antennal scale unsegmented; endopod a thick rod at first, swollen at base, without apical seta. Maxillule without outer seta on basis; endopod unsegmented, with three inner lobes. Exopods of maxillipedes with three apical setae in stage 1. Exopods on leg 1 or on legs 1 and 2, never on 3–5. Endopods of legs without setae, and apparently not functional.

In *Sabinea septemcarinata* there are three stages only (Sars), and the larva differs from others in the pointed abdominal pleura and numerous setae on the telson. The prezoeal telson, however, has only five spines (Sars, pl. v, fig. 20).

The larva of *Crangon antarcticus* differs from all other Crangonidae in having a dorsal spine on the carapace in stages 2 and 3, and from other species of *Crangon* in the very long rostrum, the long lateral spines of abdominal somite 5, and the denticulate abdominal pleura. It resembles *Sabinea* in having only three stages, and in the very small size of leg 2, which has no exopod and is hidden behind legs 1 and 3. As in *Sabinea* the first larva has rudiments of all the appendages, long antennal flagellum and very large telson. The exopod of the maxilla also has numerous setae from the first. The peculiarities of the larva support the separation of the species as a distinct genus, or subgenus, *Notocrangon*, Coutière. Borradaile (1916, p. 89) was of opinion that it is most nearly allied to *Sclerocrangon*.

In *Sclerocrangon* there is no free larva, and the young hatch in the adult form, and with the last two pairs of legs modified for clinging to the parent. As is the case in *Astacus*, this first stage has no uropods, but nothing is known about later moults (Wollebaek, 1909).

A curious difficulty is raised by Grieg (1932), who has recorded numerous larvae of *Sclerocrangon boreas* as having been taken in plankton. It would not seem possible for the young figured by Wollebaek to be planktonic, but it would seem equally impossible for Grieg to identify his specimens wrongly

AMPHIONIDAE.

See Bate, 1888; Gurney, 1936c.

The family includes only *Amphionides* and the larval genus *Amphion*. The systematic position of *Amphion* has been in dispute, but I am convinced that it is the larva of *Amphionides*. They are undoubtedly Caridea.

Amphion is a member of the oceanic plankton, but it is not confined to deep water. *Amphionides* has only been taken in great depths.

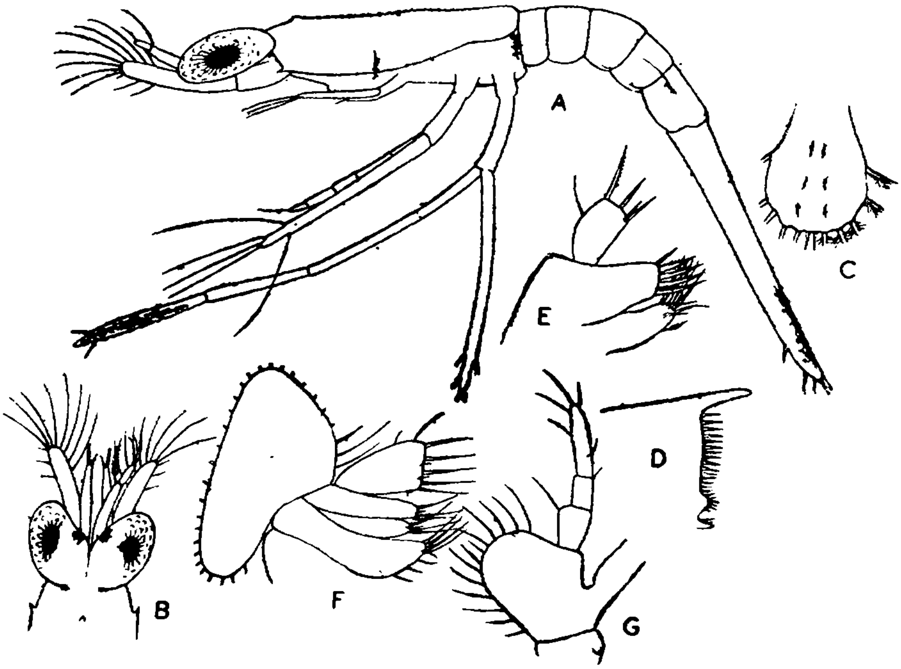

FIG. 85.—*Amphion*. A–C. Stage 1 : B, Head ; C, Telson. D–G. Late stage : D, Mandible ; E, Maxillule ; F, Maxilla ; G, Maxillipede 1.

The youngest stage described is stage 2 (Dohrn, 1870*b*, p. 16, fig. 10), and the total number of stages is uncertain, but it is probably nine.

I have seen one specimen of stage 1, from deep water at Bermuda.

The carapace is very much flattened, especially in late stages. There is no rostrum in stage 1, and it is always minute when present. The abdomen has no spines.

The telson is narrow, with 6 + 6 spines in stage 1, becoming pointed and without spines in the last stage. Antennal scale unsegmented from the first, the endopod long, and ending in a seta and spine in stage 1. The endopod in late stages is very long, with peculiar nodes at intervals. Maxillule without outer seta on basis, and

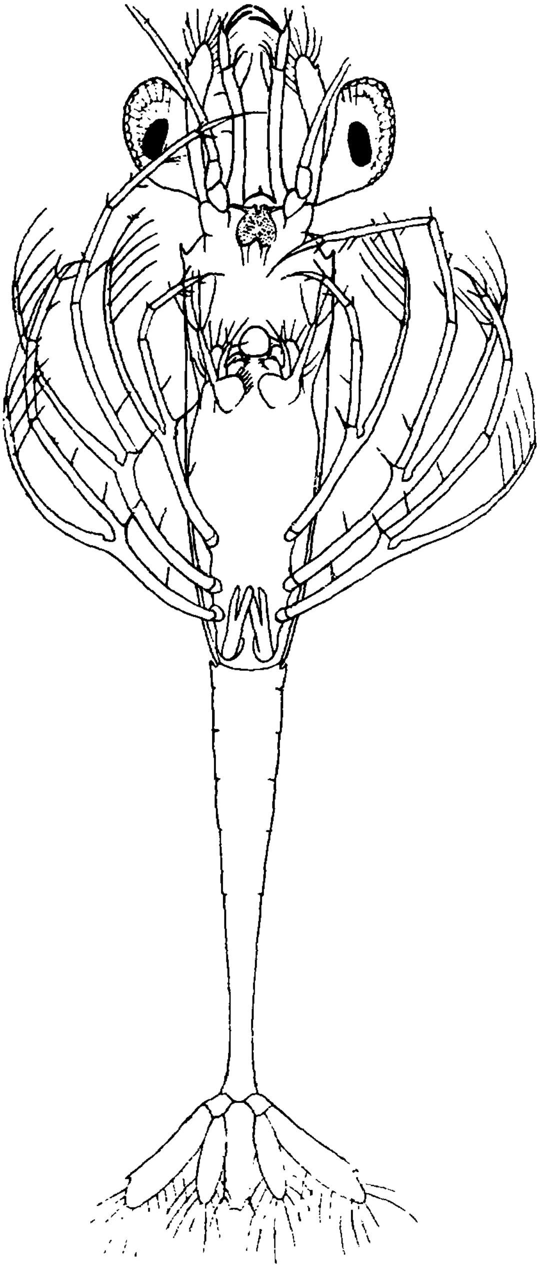

FIG. 86.—*Amphion*, stage 4.

with broad unsegmented endopod. Maxilla with three inner lobes only; the endopod unsegmented and very broad. The exopod is very broad in front in late stages. Coxa of maxillipede 1 almost obsolete, the basis very protuberant; the endopod with distal part unsegmented. Maxillipede 2 widely separated from maxillipede 1. Exopod of maxillipedes with three apical setae in stage 1. Maxillipedes 2 and 3 and legs 1–4 with very small coxa and very long cylindrical basis. Legs 1–4 with long exopods. Legs 1 and 2 are not chelate. Leg 5 very small, and altogether absent in some specimens, which are presumed to be males. Pleopod 1 is uniramous in those specimens which lack leg 5.

The post-larval form *Amphionides valdiviae*, Zimmer, has the whole thorax so excessively delicate that it is distorted beyond possibility of reconstruction in most specimens. Although I have now seen seven specimens I am still in doubt as to the real form, but I am inclined to think that the carapace is flattened and not inflated as I had supposed (1936*c*, p. 397). The figure which I have given is, I think, otherwise fairly correct for what is supposed to be the male. In this form there are only four pairs of legs, all very much reduced, and with vestigial exopods. Pleopod 1 is developed into an immense, uniramous, flattened structure which reaches forwards nearly to the mouth. In other specimens, which are assumed to be female, the legs are rather less reduced, the fifth leg being present, and pleopod 1 differs from the succeeding pairs only in the small size of the endopod.

A description of this most remarkable species, based on undistorted material, is most desirable.

MACRURA REPTANTIA

NEPHROPSIDEA

NEPHROPSIDAE.

Nephrops norvegicus.

See Sars, 1884 ; Jorgensen, 1925*b*.

There are only three larval stages, all with the same general form. In stage 1 the rostrum is large, but there are no supraorbital spines. These spines appear in stage 2. Abdominal somites 3–5 each have a dorsal spine, those of somites 4 and 5 very long and bent slightly forwards. The pleura are pointed. Somite 6 has a pair of long dorsal spines. The telson is a narrow crescent, each arm of which is about four-fifths the length of the body without rostrum. The posterior margin has a large median spine and about 30 setae on either side ; the anterior margin has 11–13 short spines.

The antennule is unsegmented. The antenna has a narrow unsegmented exopod and a flagellum about 1½ times as long as the scale. The mandible has an unsegmented palp. Maxillipedes 1 and 2 have exopods without setae. All the legs are present, each with setose exopod, and legs 1–3 chelate. Pleopods and uropods are absent.

Stage 2 differs very little, but has large rudimentary pleopods on somites 2–5. In stage 3 the uropods are present and the pleopods are setose. The first pleopod is still absent in the first post-larval stage.

There is a very close resemblance between the larvae of *Nephrops* and *Homarus*, in which there are also normally only three larval stages ; but *Homarus* lacks the very long dorsal spines on the abdomen, and the telson, though it has the median spine and numerous setae, is not drawn out into a sickle shape. Spine 2 of the telson is slightly reduced (Fig. 87. B). It differs also in having the exopod of maxillipede 1 setose.

A very remarkable form of larva from the Great Barrier Reef has been referred, with much doubt, to *Nephrops* or an allied genus. Only stage 2 is known, but leg 1 is fully developed, with a huge chela, while antennae and telson are of a form normal for this stage (Gurney, 1938*c*).

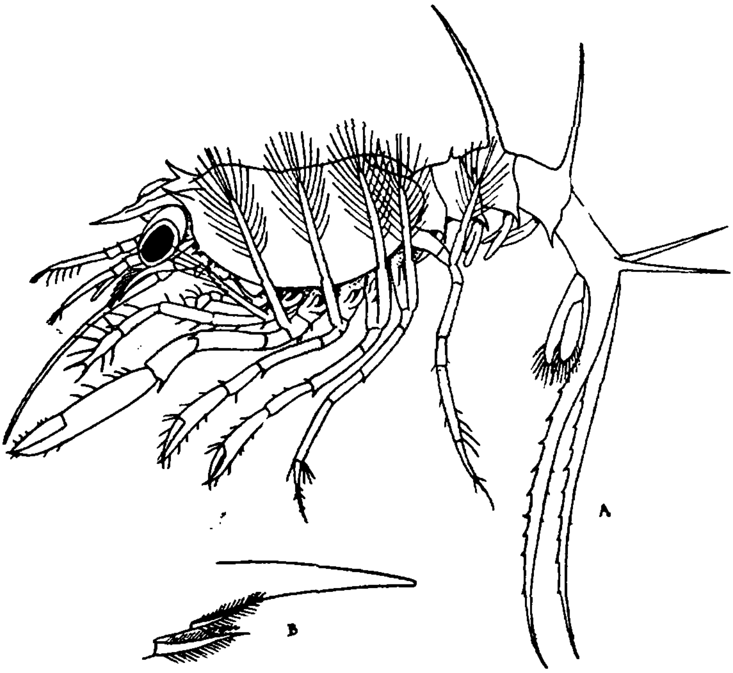

FIG. 87.—A. *Nephrops norvegicus*, stage 3. B. *Homarus*, end of telson, showing reduced seta 2.

ASTACIDAE.

In all Astacidae and Parastacidae the young when hatched have all the appendages of the adult except the first pleopods and the uropods, and they remain for a time attached to the pleopods of the parent (see p. 63). None of the appendages have a larval form, and even the antennule is like that of the adult, with open statocyst, in stage 1. The fact that the uropods do not appear until the second moult (stage 3), as in all normal larval series, shows that a reminiscence of three free stages, as in *Homarus*, is retained in ontogeny. Pleopod 1 appears in stage 4 in *Astacus leniusculus*.

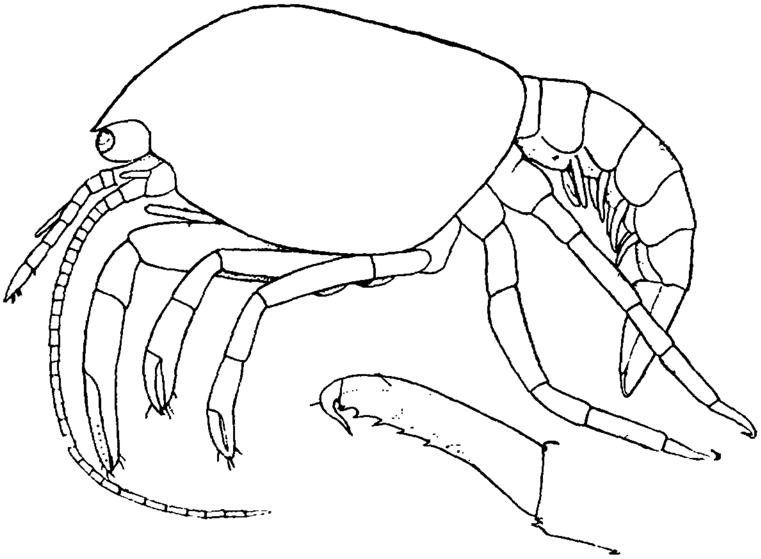

FIG. 88.—*Engaeus fossor*, just hatched.

ERYONIDEA

See Selbie, 1914; Balss, 1925; Stephensen, 1935.

It is now fully established that *Eryoneicus* is the post-larval, or natant, stage of *Polycheles*, but nothing is known of the earliest stages, and the transformation to the adult form has not been seen. Since the eggs are not large there are presumably a number of early stages to be discovered, but the great depths at which the adults live make discovery difficult. The earliest larva known is that described by Selbie (1914, p. 40), which was 7 mm. long, with large globular carapace, covered with spines, like that of the full-grown *Eryoneicus*, but with a long rostrum. The antennae and mouth parts are of the adult type, but maxillipedes 2 and 3 have exopods, which are lost later, and legs 1 and 2, though large and chelate, have exopods. There are no other thoracic appendages. Pleopods are present, but small, but it is not stated if there is one on somite 1. Balss has described a similar form with a carapace

5 mm. long (1925, p. 195). In this specimen there were rudiments of legs 3–5.

The smallest specimen known, with a carapace of 3·5 mm., was described by Stephensen (1925, p. 45). The appendages are as in Selbie's specimen, but there are rudiments of legs 3–5. Pleopods are present on all somites, but there are no uropods. The latter appear to be present in Selbie's figure.

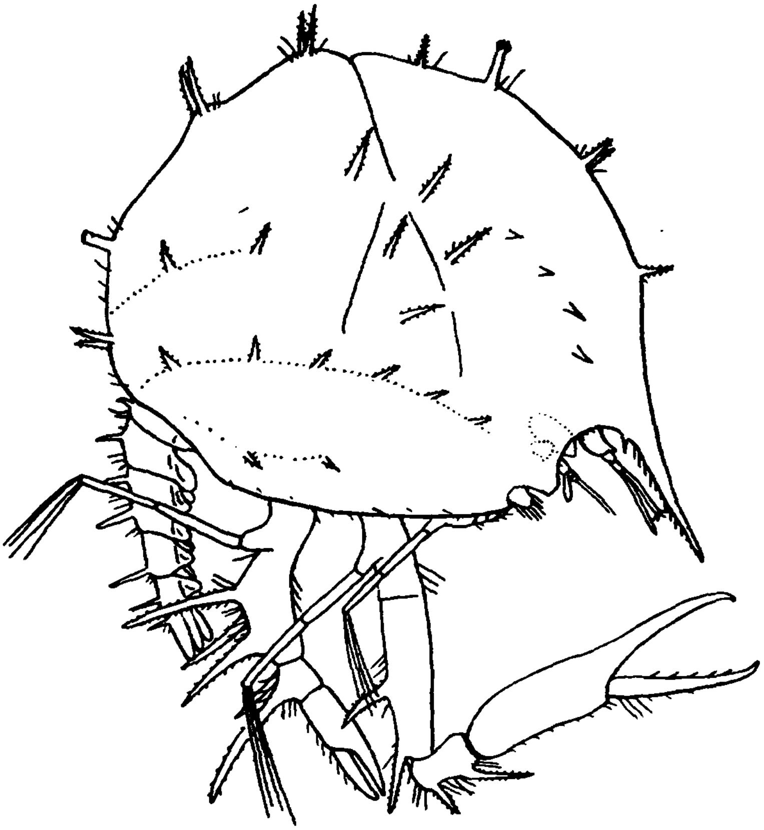

Fig. 89.—*Eryoneicus* sp., early stage. After Selbie.

Apart from the possession of exopods on legs 1 and 2 the young *Polycheles* has, therefore, from the earliest stage known, no special larval features. It would seem to be a case of direct development, but with the exceptional features of the absence of some of the thoracic legs.

The great dilation of the thorax and the numerous spines borne upon it and the abdominal somites serve the purpose of increasing surface and assisting flotation. All the specimens known have been taken at great depths.

SCYLLARIDEA

See Bouvier, 1914*a*; Stephenson, 1923; Gurney, 1936*c*.

All the genera of this group have the characteristic larva known as Phyllosoma. Although numbers of Phyllosomas have been described since the genus was founded by Leach in 1817, the adult species to which they belong is known in very few cases. The larvae characteristic of *Palinurus*, *Panulirus*, *Jasus*, *Scyllarus* and *Scyllarides* are known with certainty or probability, but there are others which cannot be identified. The whole series of stages has been described only for *Palinurus vulgaris* and *Scyllarus arctus* (Bouvier, 1914; Santucci, 1925*a*; Stephensen, 1923), but there are discrepancies in the two accounts of the former which cannot be reconciled. The first post-larval stage was described by Boas in 1880, but it was not until 1914 that Bouvier demonstrated in *P. vulgaris* the transformation of the Phyllosoma to the post-larval form.

Palinurus vulgaris.

Stage 1: The whole body is flattened and transparent. The carapace partly overlaps the somite of maxillipede 3, and the tubes of the liver extend into its folds. The abdomen is very small, unsegmented, and without distinct telson. The eyes are long and pear-shaped, but without a defined stalk. The antennule is unsegmented, and the antenna has a long unsegmented endopod and a small tooth in place of an exopod. The mandible and maxillule have no palp. The maxilla is small, without inner lobes, and the exopod, bearing five setae, is apical rather than an outer appendix. Maxillipede 1 is a minute rudiment. Maxillipede 2 is large, but without exopod. Maxillipede 3, like the following legs, has a long basis and the endopod is not distinctly jointed to it. It has a long exopod. Legs 1-3 are developed, with exopods; but the exopod of leg 3 has no setae. Leg 2 has the dactyl extremely long. Legs 4 and 5 are small buds.

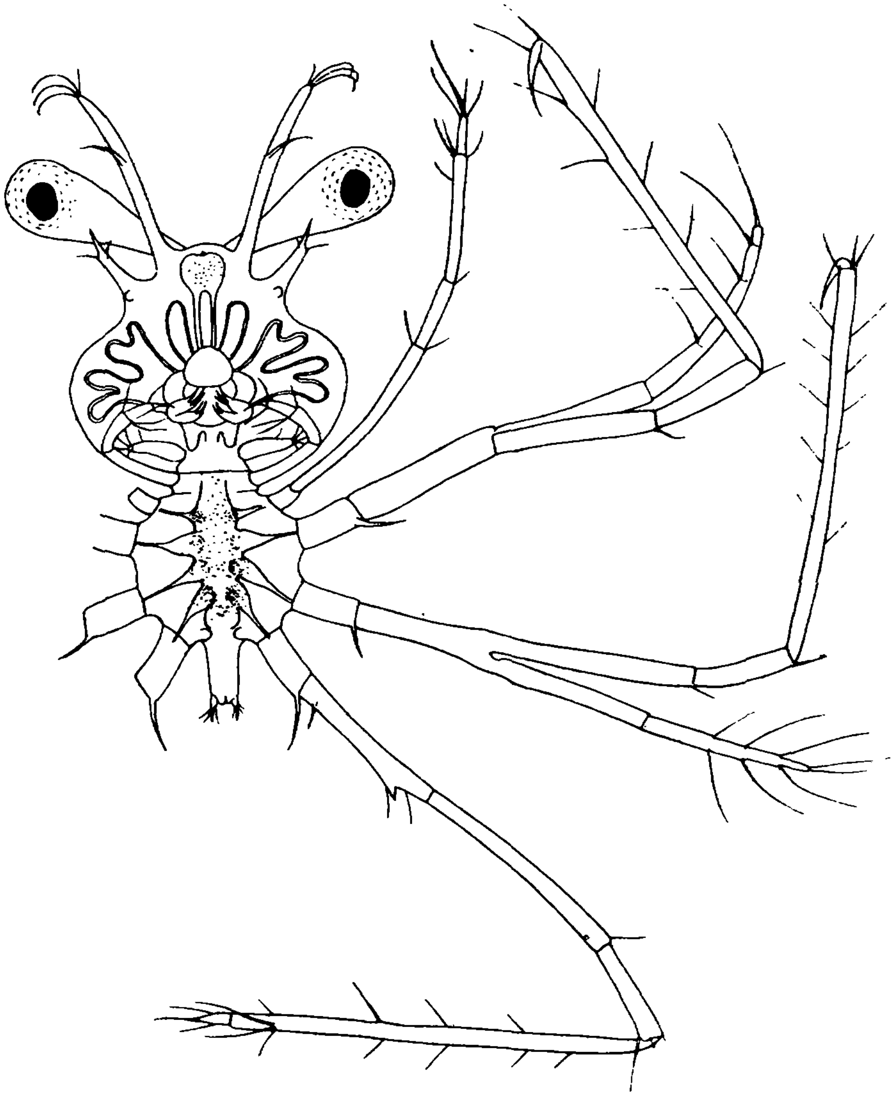

FIG. 90.—*Scyllarus arctus*, stage 1. Alexandria.

The general form at this stage is much the same in all species known, but there are differences in detail. In *Scyllarus*, for example (Fig. 90), the form of the maxilla is very different, and there is no exopod on maxillipede 3 or leg 3.

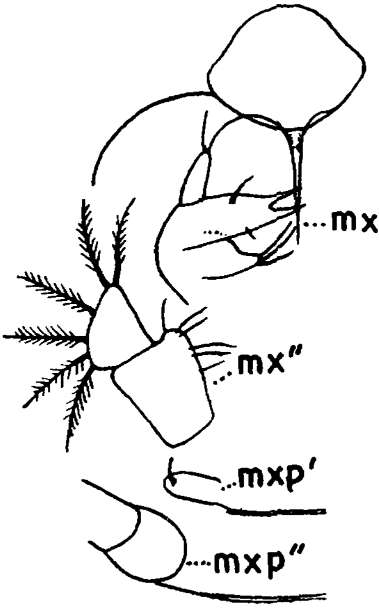

FIG. 91. *Palinurus vulgaris*, stage 1. Mouth parts.

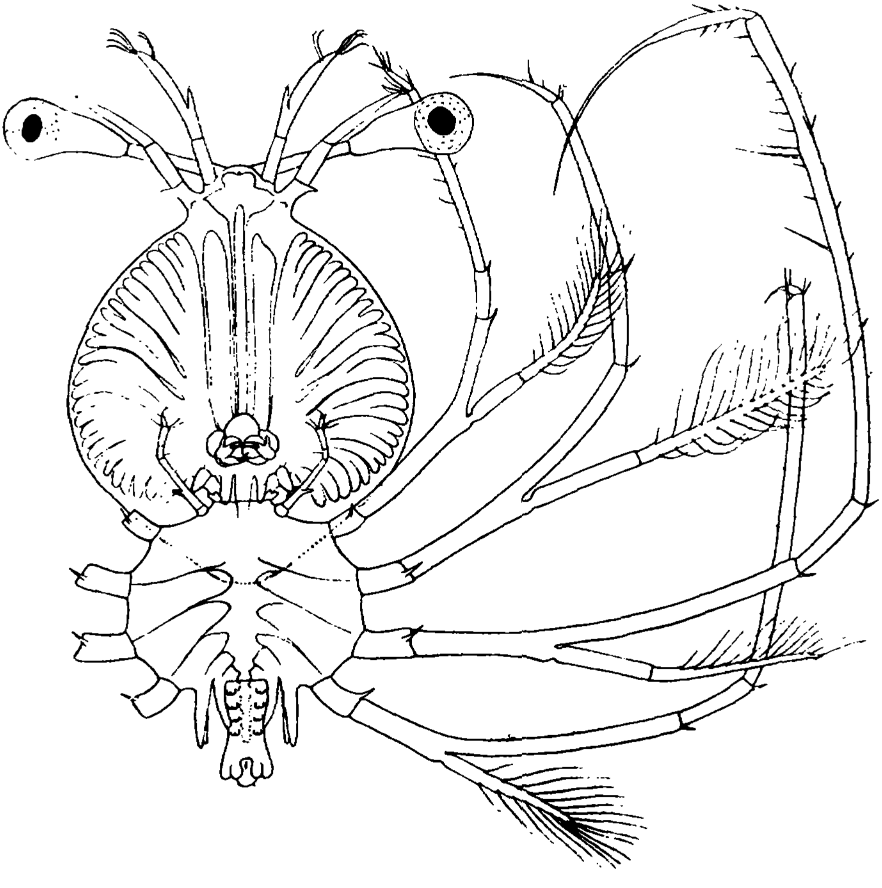

FIG. 92.—*Palinurus vulgaris*, stage 3.

In *P. vulgaris* Bouvier distinguished 10 stages and Santucci 9. I have myself, with limited material, been able to find only 8. Stephensen found 9 stages in *S. arctus*, but I have had a specimen corresponding to his stage 7 which moulted to his stage 9.

LATER STAGES.

In stage 2 the eyes are stalked, the abdomen slightly larger, and with bilobed rudiments of uropods. The maxillule has a small endopod. In some species the endopod is not developed at all.

In subsequent stages the growth of the abdomen continues, and in the last stage it approaches adult form. The maxilla acquires a large setose exopod, but the inner lobes are not distinct. Maxillipede 1 develops a long exopod without setae, and maxillipede 2 has a long setose exopod. Leg 4 has an exopod, but leg 5 has none. The gills are small, but in the full adult number in the last stage. There is no pleopod on somite 1.

The last Phyllosoma of *Scyllarus* has the carapace broader than long, and the antennae are short and flattened. The maxillule has no endopod, and maxillipede 2 has only a very small rudiment of an exopod. Maxillipede 3 has barely a trace of an exopod. The abdomen is as broad at its base as the thorax, and the telson is very broad, with a large curved spine at each angle.

It is not known if these differences are distinctive of the two families Palinuridae and Scyllaridae. For instance, *Jasus* (Palinuridae) has no exopod on maxillipede 3, and the carapace is wider than long, while Phyllosomas attributed to *Thenus* (Scyllaridae) have the same form of body as in *Panulirus*, and the antennae are intermediate. In one form tentatively referred to *Parribacus* (Gurney, 1936*c*, p. 437) there is an exopod on leg 5.

The Phyllosoma is a larva which cannot easily be compared with any other. It is unique in the flattened form of the whole thorax, and the complete freedom of most of the thorax from the carapace is a character of the Protozoea. This freedom of the thoracic somites

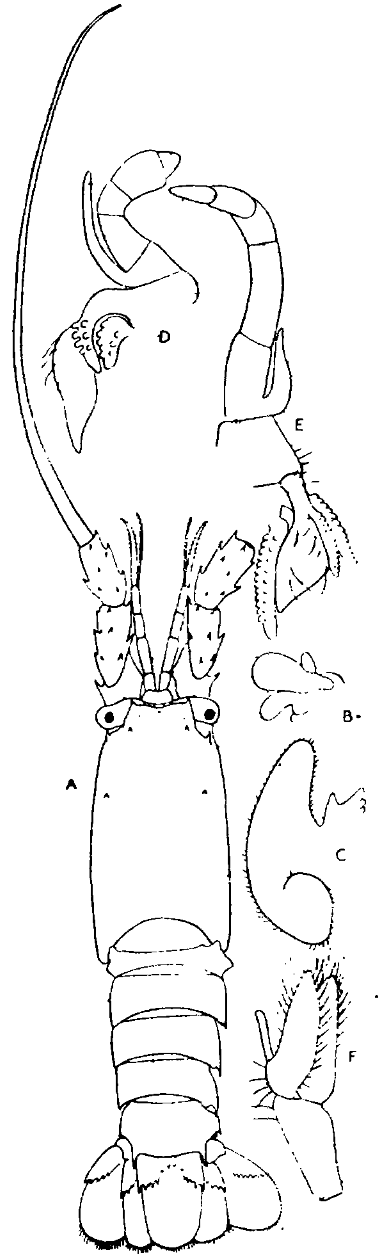

Fig. 93.—*Panulirus argus*, natant stage. Bermuda. B. Maxillule. C. Maxilla. D. Maxillipede 2. E. Maxillipede 3. F. A pleopod.

must be supposed to be a retention of the protozoeal form in spite of great specialization in all other respects, and the development of three pairs of legs in stage 1 is a curious example of precocity. The presence of an exopod on leg 5 in one genus is a primitive feature retained also in the Nephropsidea.

POST-LARVAL.

The most profound transformation at a single moult known among Decapoda is that of the Phyllosoma to the post-larval stage of the Scyllaridea. Bouvier was fortunate in obtaining a Phyllosoma actually moulting, and Fedele (1926) observed the moult of *S. arctus* in the laboratory. The first post-larval stage has received undue notoriety, since it actually differs less from the adult than many other first post-larval stages. Ortmann's genus *Puerulus* was founded mainly upon specimens in this stage (Calman, 1909*a*)[*], and it is, for that reason, commonly called the Puerulus-stage ; but the term " natant " was given to it by Boas in the belief that it was a free-swimming stage. Whether it does habitually swim is uncertain. I have seen specimens of the Puerulus of *Jasus* taken in plankton far out to sea. Fage had nine specimens of *P. vulgaris* taken from the stomach of a pelagic fish, *Centrolophus niger.* Orton and Ford (1933) supposed that *P. vulgaris* lurks on the bottom in the daytime and swims at night. I have two specimens of this stage of *Panulirus argus* taken in plankton at night at Bermuda, but it is possible that they were actually attached to *Sargassum*, and they did not swim freely in the laboratory. These two specimens were perfectly transparent when taken, but gradually developed the brown colour of the adult.

The Puerulus stage does not differ from the adult in any important respect, but the carapace lacks the grooves and most of the spines of the adult, and has a lateral ridge which the adult has not got. In *P. argus* the mouth parts appear not to be functional. The maxillule and maxilla have more or less the adult form,

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[*] *P. angulatus,* the type of the genus *Puerulus,* is a valid adult species. The other species are in the natant stage, and one of them, *P. spiniger,* is identified by Calman as *Panulirus versicolor.*

but no spines, and the mandible is degenerate and without palp. Maxillipede 1 has a large exopod, but the endopod is vestigial. Maxillipedes 2 and 3 have the exopod small, without setae. The exopods of the legs have almost disappeared, but can just be traced.

Bouvier and Fedele describe the carapace of *P. vulgaris* as inflated, but this inflation is not natural, and was, no doubt, due to decay or method of preservation. Actually it is depressed, and more or less quadrangular in section owing to the lateral ridges.

Bouvier (1917, p. 108) has described two post-larval stages of *Scyllarus*. These two stages had been named by Sarato *Nisto asper* and *N. laevis*, and it is remarkable that, in contrast to *Palinurus*, the first stage is more spiny and rugose than the second. The appendages are not described.

STENOPIDEA

See Gurney, 1936*c*; Gurney and Lebour, 1941.

The only species of which the development is known* are *Stenopus hispidus* and *S. spinosus*, but thirteen different larval forms have been described from the Atlantic. Only ten adult species are known from this region, and all those of the genera *Spongicola* and *Richardina* known have large eggs and probably abbreviated development. It does not necessarily follow that they have no free larvae, but they would at all events be hatched in an advanced condition. In *Spongicola koehleri* Kemp described what was probably the newly hatched young (1910, p. 409). These very closely resembled the adult, but had conspicuous exopods on legs 1–3, and no uropods. Stage 1 is known only in the two species of *Stenopus* and two of the unknown forms, so that the characters of that stage are not well established. The following summary of the characters

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* Miss Lebour has followed the development to post-larval of two species at Bermuda, but it is not possible to identify them.

of all these larvae is based upon that given by Miss Lebour:

(1) Rostrum very long, and supraorbital spines very prominent (except in stage 1).

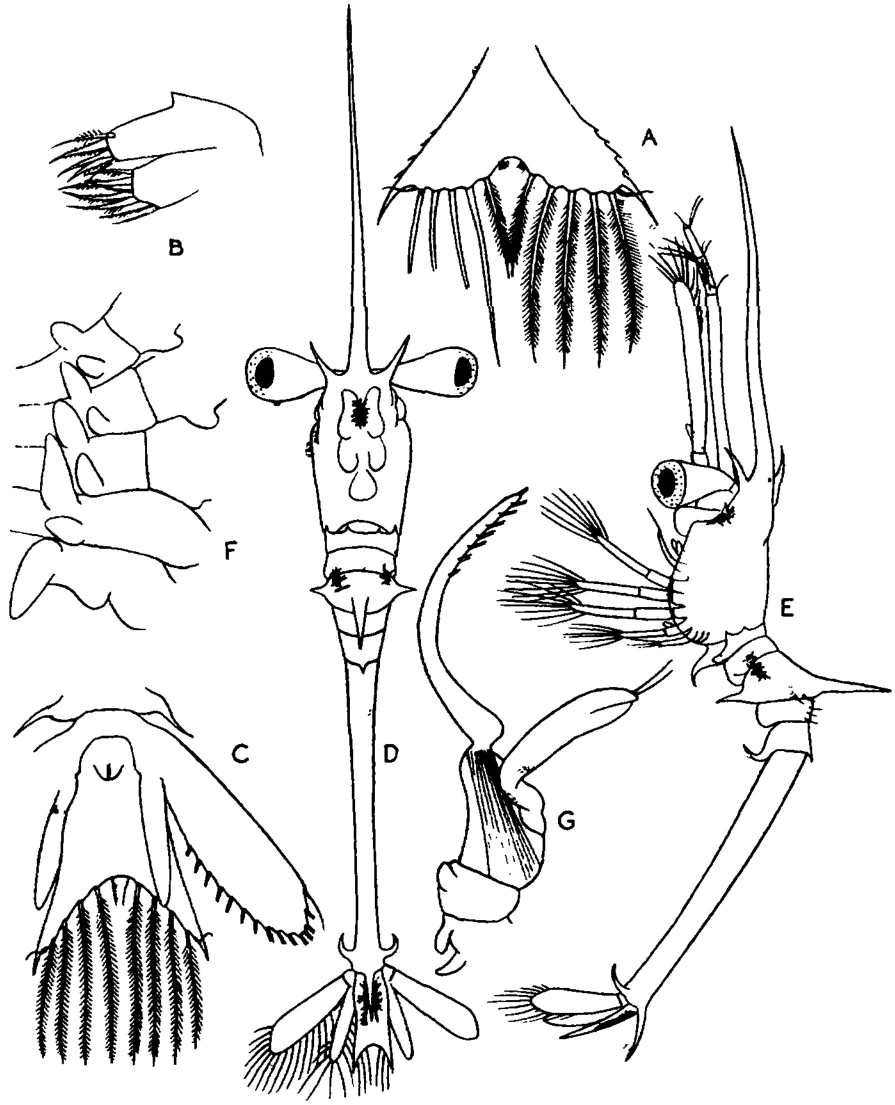

Fig. 94.—*Stenopus hispidus*. Red Sea. A. Telson, stage 1. B. Maxillule. C. Telson, stage 3. D, E. Stage 4. F. Stage 7 ? (11·0 mm.), gills. G. Leg 1, last stage, 15 mm. without rostrum (Atlantic).

(2) Telson more or less deeply indented in stages 1 and 2; spine 2 reduced; outer margin serrated in some species. In later stages hind margin almost straight, with a short spine at each angle, and four or six long setae between.

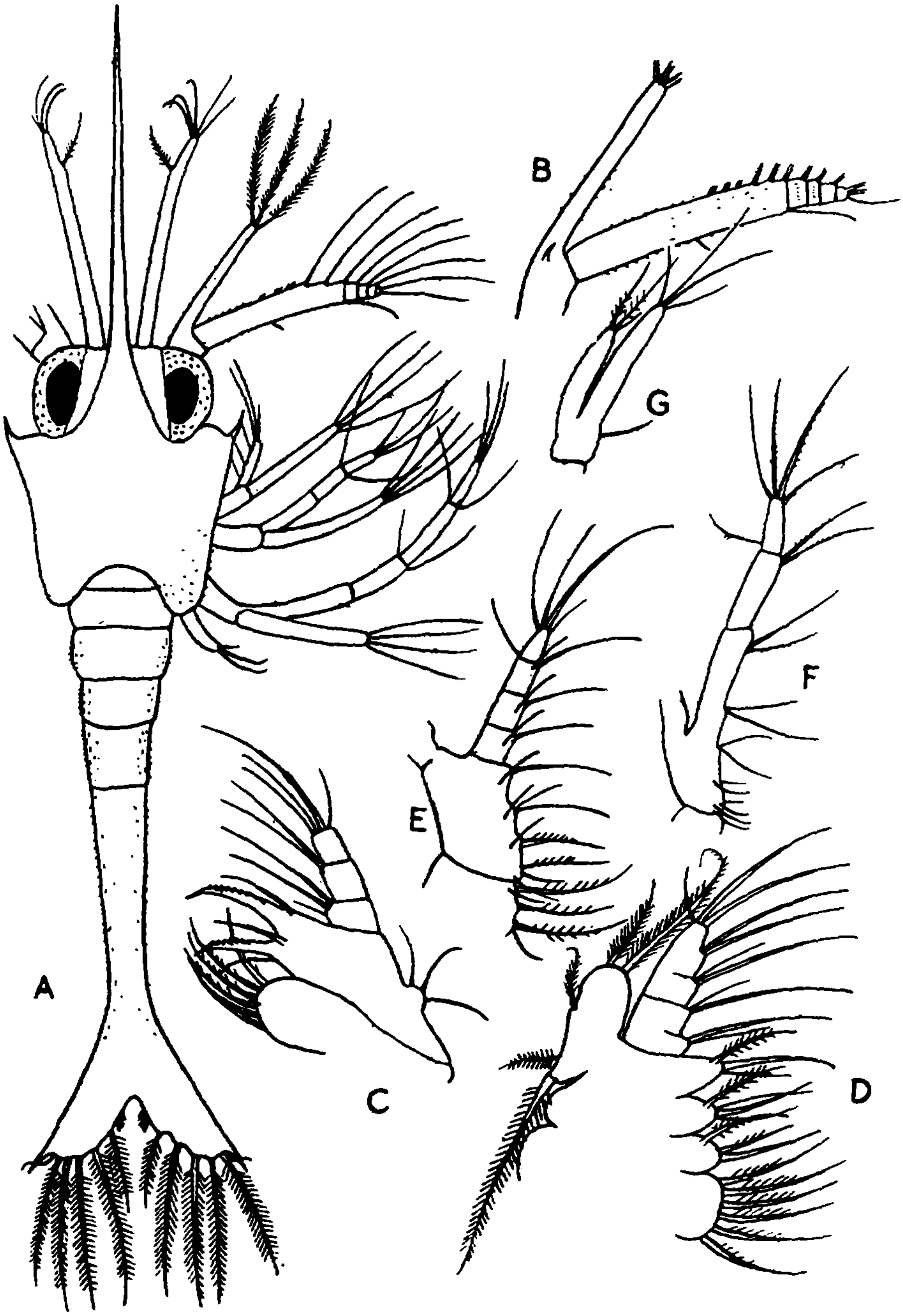

Fig. 95.—Stenopid A (Lebour). A. Stage 1, dorsal. B. Antenna. C. Maxillule. D. Maxilla. E. Maxillipede 1. F. Maxillipede 2. G. Leg 1.

(3) Abdomen in later stages bent almost at right angles at somite 3 ; pleura sometimes pointed. Somite 5 often with median ventral spine.

(4) Antennal scale, in stage 1, segmented ; endopod with two or three long apical setae.

(5) Mandible very large and fitting into a deep notch in the carapace.

(6) Maxillule usually with endopod vestigial.

(7) Maxillipedes with four apical setae on exopods in stage 1.

(8) Stage 1 with leg 1 already well developed, with setose exopod.

(9) Endopods of legs not functional, and the posterior pairs not appearing till late. Endopods of legs 1–3 springing from below middle of basis.

(10) Pleopod 1 delayed in appearance.

A particularly interesting form, of which only stage 1 is known, is described by Miss Lebour as Stenopid A. Whereas in all other forms the endopod of the maxillule is vestigial, in this species it is fully developed, and there is also an exopod with three setae, a rare and primitive character. The endopods of the maxilla and maxillipede 1 are more developed in this species than in *S. hispidus*.

The Stenopid larvae hitherto made known have characters which suggest relationship with certain Thalassinidea (Gurney, 1936*c*), but the possession of so primitive a maxillule in one species is difficult to reconcile with such a view. Ortmann (1896, p. 426) says that the Stenopidea "den gemeinsamen Stammform der Natantia und Reptantia unter den lebenden Decapoden am nächsten stehen." Apart from this primitive maxillule there is nothing in the structure of these Stenopid larvae to support Ortmann's statement. Too much importance should not be attached to this particular larva until more is known of its later stages ; but there is no reason to doubt that it is a Stenopid, and I can offer no plausible explanation for it alone having this primitive character.

THALASSINIDEA

The larvae are known of species representing all the families of the Thalassinidea except the Thalassinidae and Axianassidae, each of which includes one genus only. The larvae that are known provide evidence that there is a fundamental cleavage between the Callianassinae and the Upogebiinae,* which are regarded as members of one family, and that the genera may be arranged in two groups, thus :

Homarine Group : Axiidae and Callianassidae.

Anomuran Group : Laomediidae and Upogebiidae (Gurney, 1938).

AXIIDAE.

See Webb, 1921 ; Gurney, 1938*c*.

In the two species of which the development is known —*Axius stirhynchus* and *Calocaris macandreae*—the eggs are large and development abbreviated. Large eggs and abbreviated development would appear to be the rule in the species known, but there are exceptions such as *Calocaris alcocki*, the figure of which shows numerous small eggs. On the other hand, a number of larvae have been assigned to the Axiidae which show no evidence of abbreviation, though the number of stages in any of them is not known. Miss Lebour (1941) has obtained from one of these larvae a post-larva which could be identified as *Paraxiopsis*, so that some, at all events, of them have been correctly placed. The resemblance of some of them to *Callianassa* is so close that the only distinguishing character which can be relied upon is the presence of an exopod on leg 5 in Axiidae.

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* In discussing the relations between Upogebiidae and Callianassidae (1938*c*, p. 341) I have not taken account of the evidence from faecal pellets (Moore, 1932). These do not support a separation of *Callianassa* from *Upogebia*. On the other hand, as they equally clearly indicate absence of relationship between Paguridae and Galatheidae I do not feel that the evidence can have much weight.

Axius stirhynchus.

The Prezoea has large feathered setae on the antenna, the endopod having three. The telson has seven processes enclosing the seven outer setae of the larva.

The larva has a very long rostrum which is flattened, with marginal teeth, in stage 2. The carapace has a large spine at the anterior angle, and no supraorbital spine. Abdominal somites 2–4 and 6 have small median dorsal spines, somite 5 having two dorsal pairs. The telson is very broad, with strong median spine, and 14–16 small spines on either side ; spine 2 is reduced to a hair.

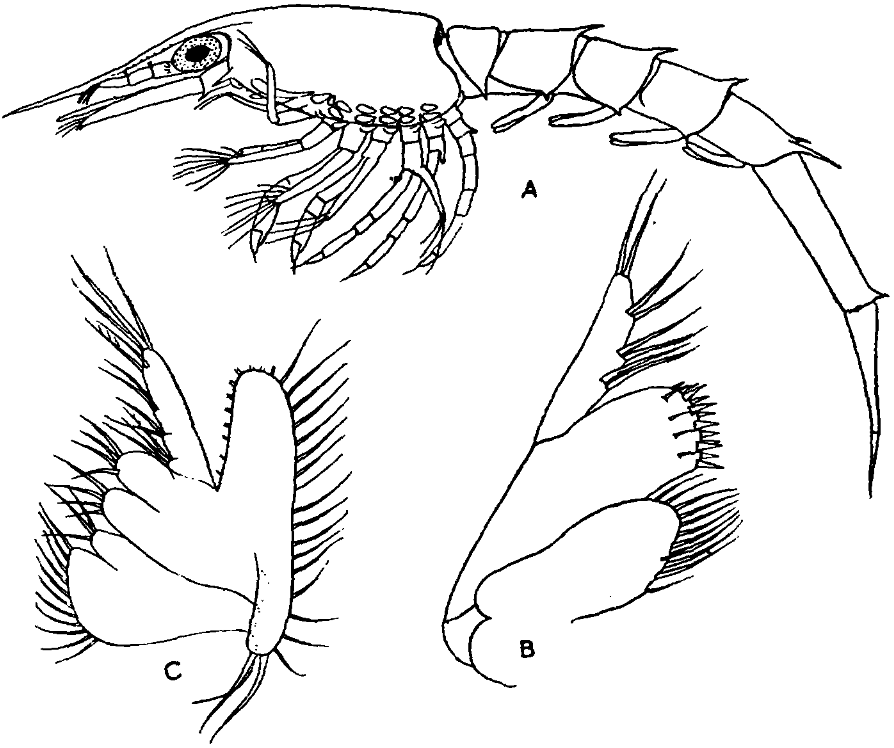

FIG. 96.—*Axius stirhynchus.* A. Last larva. B. Maxillule, stage 2. C. Maxilla, stage 1.

The antennal scale is not segmented, and the endopod has no terminal setae in stage 1. The mandible has a rudimentary palp in stage 1. The maxillipedes have four apical setae on the exopods.

In stage 2 legs 1–3 have setose exopods, legs 4 and 5 having small rudiments of exopods. There is no pleopod on somite 1, and the uropods are absent until the moult of stage 2 to post-larval. Vestiges of the exopods are visible on all the legs in post-larval stage 1.

Calocaris macandreae.

There appear to be three stages, of which I have myself seen only stages 2 and 3. The first stage, hatched from the egg, is described by Bull (1934). The eggs are large, and the larva when hatched is inert. The rostrum is bent down between the eyes. The endopod of the antenna is unique in having four setae (Bull, fig. 3). All the legs are present, leg 1 and 2 being chelate, and there are exopods on all of them. The mouth parts are undeveloped and functionless throughout larval life. There are pleopods on somites 2–5. This stage moulted to stage 2 in 48 hours. I have seen two specimens of stage 2 which, though capable of swimming, were very sluggish and remained on the bottom.

Stages 2 and 3 differ very little from stage 1. In stage 2 the rostrum is very long, flat, with a few lateral teeth at the end. The abdomen has no dorsal spines except a small one on somite 6. The telson is broad, with no median spine and 17 spines on either side, spine 2 reduced to a hair. In stage 3 there is a small median spine. The exopods of all the legs are reduced and without setae in stage 2, but those of legs 1–3 are setose in stage 3. The pleopods are very large in stage 2 and the uropods appear to have the exopod free. In stage 3 both branches are free, but without setae, and functionless.

The larvae of unknown genera which are supposed to belong to the Axiidae have the rostrum very long, flat, and with lateral teeth. The abdominal somites have relatively small dorsal spines, and usually pointed pleura. The telson in late stages is parallel-sided, with three or four lateral spines, a large median spine and a group of small spines on either side of it. There is an exopod on leg 5 and epipods on the legs. The palp of the maxillule is 2- or 3-segmented, and that of the maxilla 3-segmented. The antenna usually has a very large spine on the basis, and an outer seta near the base of the scale.

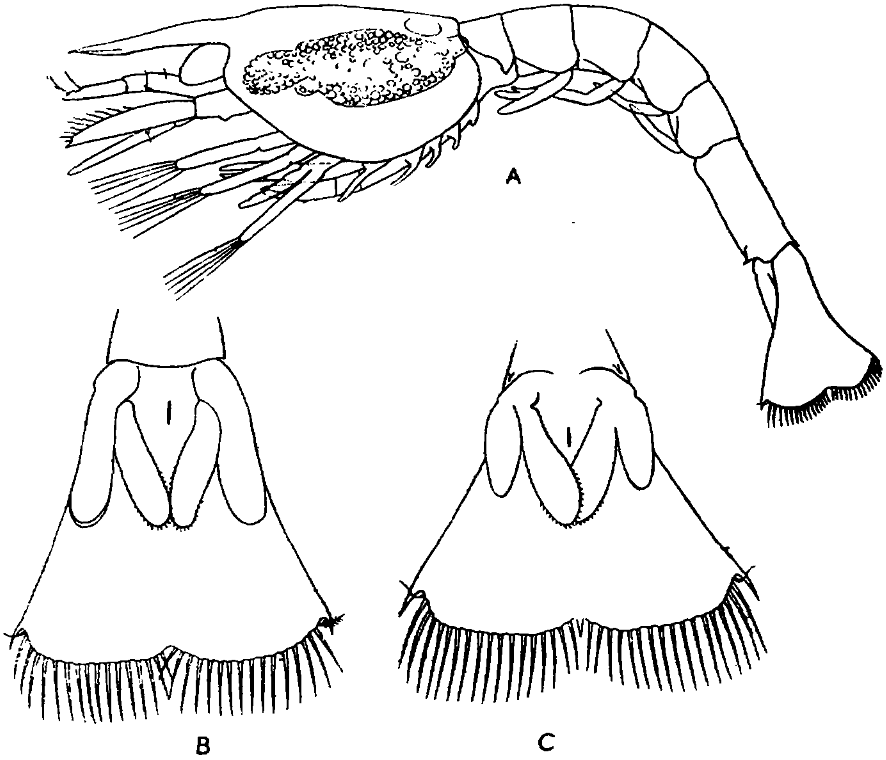

FIG. 97.—*Calocaris macandreae.* Millport. A. Stage 2. B. Telson, stage 2. C. Telson, stage 3.

CALLIANASSIDAE.

See Sars, 1884 ; Cano, 1891 ; Gurney, 1937*c*.

Very little is certainly known of the parentage of the larvae which have been referred to *Callianassa*. They are of two distinct types (Gurney, 1937*c*, p. 326). The older references to *Callianassa* may be summarized thus :

TYPE I.

C. (*Cheramus*) *subterranea*. Claus, 1861, 1876, p. 44, figs. 14–18 (as *Hippolyte*). Sars, 1884, pls. 6, 7 (as *Calocaris*).

C. (*Trypaea*) *truncata*. Cano, 1891, pl. 2 (as *Axius*).*

TYPE II.

C. (*Callichirus*) *laticauda* (= *stebbingi*). Cano, 1891, pl. 3 (as *C. subterranea*).*

C. (*Callichirus ?*) sp. Claus, 1876, p. 54, pl. 8, figs. 1–7 ; 1885, pl. 5, fig. 42 (as *Callianassa*).

Miss Lebour (1938) has described the first larva of *C.* (*Trypaea*) *affinis*, and Dakin and Colefax (1940) that of *C.* (*Trypaea*) *australiensis* ; both are of type I.

There is good reason to doubt if the accepted subgenera of *Callianassa* are well founded, and useful evidence would be obtained if our knowledge of the larva could be extended.

TYPE I.—*C. subterranea.*

There are five stages.†

The rostrum is very long, flattened, and with lateral teeth in stage 2 and later. The carapace has the anterior margin serrated. Abdominal somite 3 has a very large dorsal spine, and somites 3–5 have a dorsal denticulate ridge. The telson is at all stages widened behind, with a very large median spine, and seven spines on either side of it in stage 1 ; spine 2 is reduced to a hair. The antennal scale is not segmented in stage 1, and the endopod bears two apical setae and a hair. There is a large spine on the basis. The endopod of the maxillule has three segments. The exopod of the maxilla has a narrow proximal lobe bearing setae. In maxillipede 1 coxa and basis are flattened and nearly equally large ; the endopod is of four segments, with delicate setae, and an outer seta on segment 1. Maxillipede 3 is present and functional in stage 1. All the legs are

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* The identification of these larvae is due to Caroli (1921), who hatched the eggs of *C. laticauda*, and of a species of *Trypaea* which he has informed me in a letter was later identified as *T. truncata*.

† Dakin and Colefax describe six stages in *C. australiensis*, but their stage 1 is the Prezoea.

present in stage 3, with setose exopods on legs 1–4; the endopods are normally placed at the end of the basis. There are pleopods on somites 3–5 only.

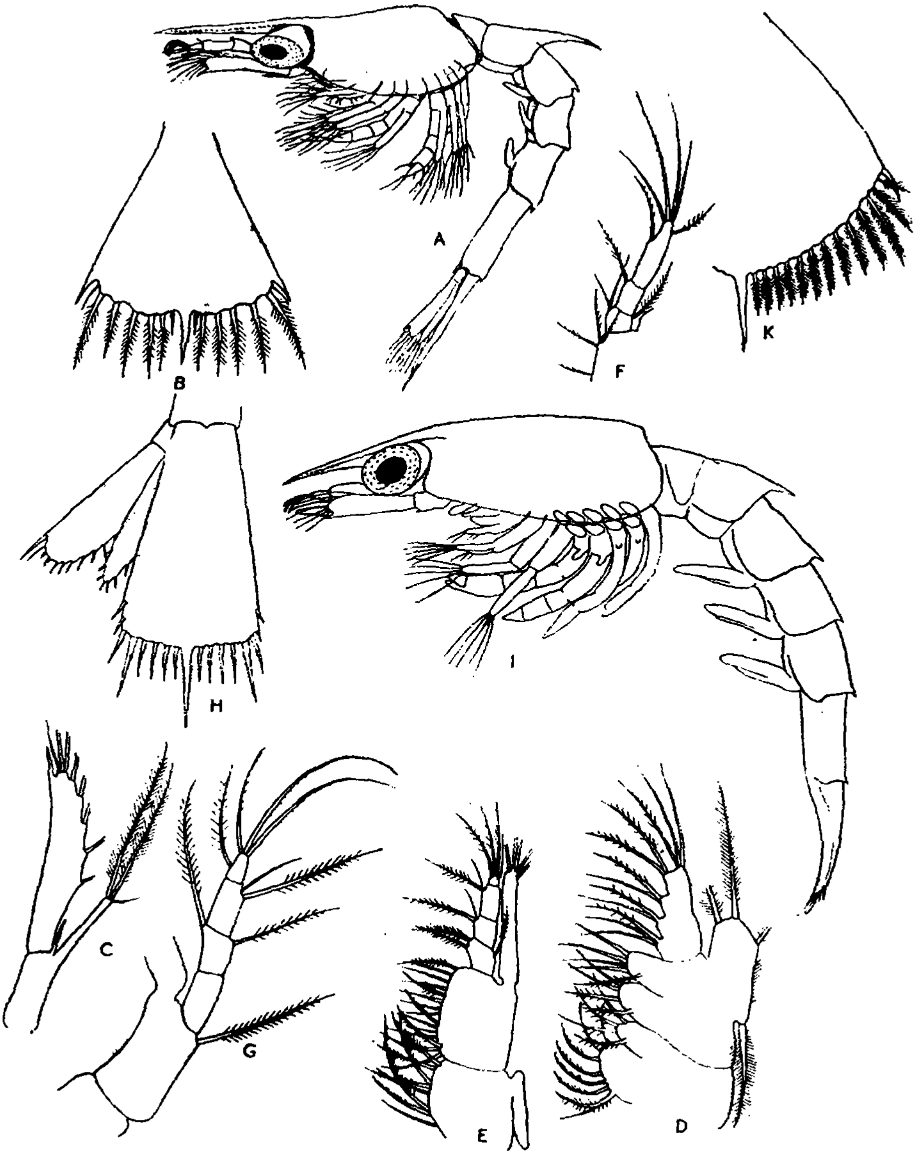

Fig. 98.—*Callianassa subterranea.* A. Stage 5. B. Telson, stage 2. C–G. Stage 1: C, Antenna; D, Maxilla; E, Maxillipede 1; F, Maxillipede 2; G, Maxillipede 3. H. Telson, last larval. I. *Callichirus* sp. ? ("Claus's larva"), stage 2. 4·4 mm., Alexandria. K. Its telson.

Type II.—*C. laticauda* (= *stebbingi*).

Cano described three stages.

The rostrum is long, flat and serrated. There are dorsal spines on somites 2–4, that of somite 2 not much larger than the others, and somites 3–5 are not ridged. The telson is very broad, convex, with small median spine and 14 small spines on either side of it; spine 2 is reduced to a hair. In stage 2 all the legs are present as large rudiments, with rudimentary exopods on legs 1 and 2. In a specimen from Alexandria, which I believe to belong to this species, there are traces of exopods also on legs 3 and 4 in stage 2. The exopods of legs 1 and 2 are setose in stage 3. The closely allied species figured by Claus has very small rudiments of exopods on legs 1–4 in stage 2, but it is not known if there is a third stage with setose exopods. I have seen specimens of this form, from Alexandria, which agree exactly with Claus's figure. There are large pleopods on somites 3–5 in stage 2, and free uropods in stage 3.

In certain forms of this type from the Red Sea (Gurney, 1937*c*) and Indian Ocean (Menon, 1933) there are only two stages, stage 2 being observed to moult to post-larval. In all these forms the mouth parts were undeveloped. The three forms from the Red Sea are of interest since they have four pairs of pleopods, and in one of them there is a setose exopod on leg 4. In Menon's species there are three pairs of pleopods and an exopod on leg 4.

I have described (1938*c*) a series of larvae from the Atlantic and Barrier Reef which belong to or are related to *Callianassa*. The four forms of Group IID resemble Type 2, but it is very doubtful if all belong to this genus. One of them (B.R. XI), while having the general form and telson of *Callianassa*, has the leg rudiments more like those of *Upogebia*.

UPOGEBIIDAE.

See Sars, 1884; Webb, 1919; Gurney, 1937*a*, 1938*c*.

The development of the following species of *Upogebia* is known:

U. deltaura. Sars, 1884 (as *U. littoralis*); Webb, 1919.

U. littoralis. Cano, 1891.
U. stellata. Webb, 1919.
U. danai ? Gurney, 1924*c*.
U. savignyi. Gurney, 1937*a*.
U. major. Miyazaki, 1937.
U. pugettensis. Hart, 1937.

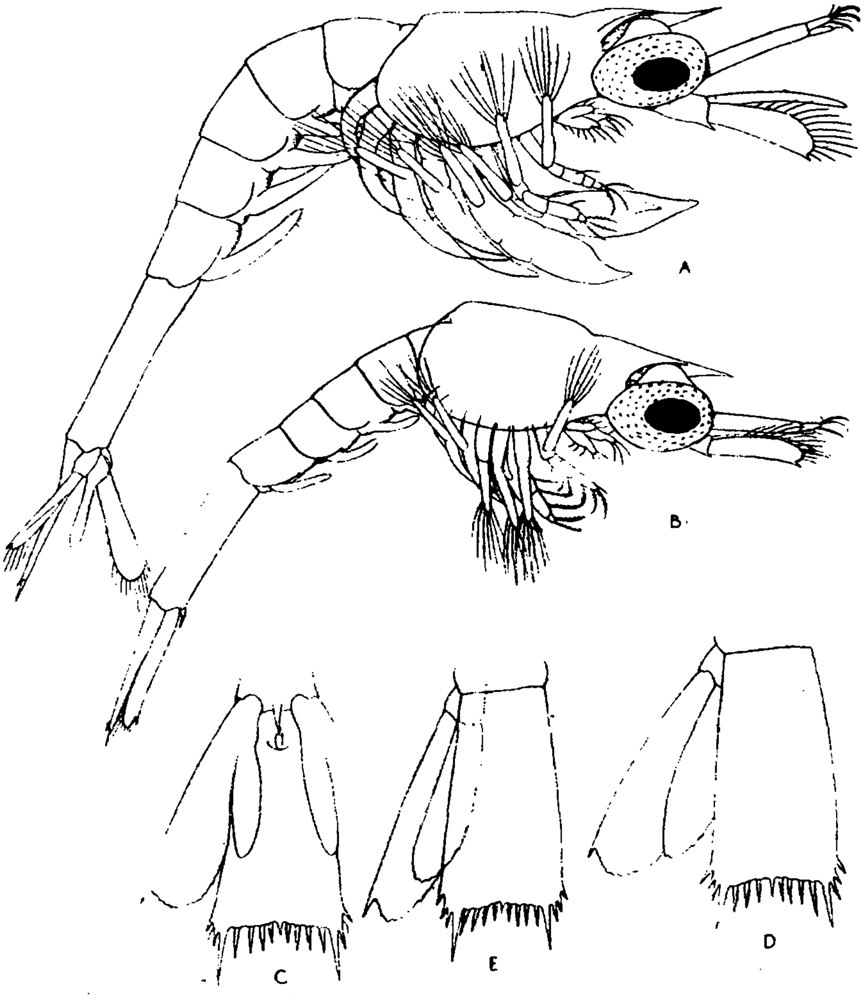

FIG. 99.—*Upogebia deltaura*. A, B. Two specimens in stage 3, drawn to same scale. C, D. Telson, stages 3 and 4. E. *U. stellata*, telson, stage 4.

The larva referred to the Upogebiinae by Menon (1933) developed into a post-larval form with epipods on the legs and an appendix interna on the pleopods—two characters which definitely exclude it from the family as at present defined.

The following description applies, with some exceptions noted, to all species.

There are three or four stages except in *U. savignyi*, in which there is no free-swimming larva.

The rostrum is small, not flattened nor serrated. The abdominal somites have no dorsal spines or ridges, except in a form from the Barrier Reef supposed to be a Upogebiid, which has spines on somites 2–6 (Gurney, 1938*c*, p. 332). The telson has spine 2 reduced to a hair, and a small median spine after stage 1. It is parallel-sided in the last stage, with 8 + 8 spines, of which spine 4 is the largest. The antennal scale is

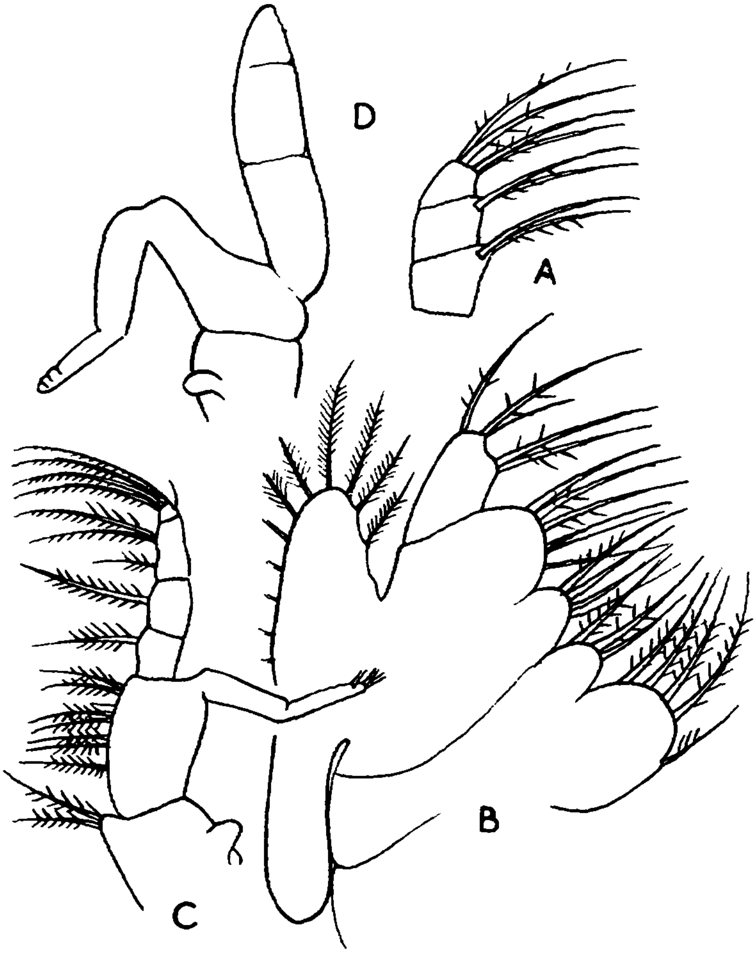

FIG. 100.—*Upogebia stellata*, last larva. A. Palp of maxillule. B. Maxilla. C. Maxillipede 1. D. Maxillipede 3.

unsegmented; the endopod with three setae in stage 1. The mandible has no palp, except in *U. pugettensis*, where it is present in stage 2. The maxilla has a narrow proximal extension which may be bare of setae as it is in Paguridae. Maxillipede 3 is rudimentary in stage 1, and the endopod remains undifferentiated and springing from low down on the basis. Legs 1–3 have setose exopods, and the endopods placed as in maxillipede 3. There are no pleopods on somite 1. In maxillipedes 1 and 2 the basis is much longer than the coxa and not flattened; the endopods bear stiff, coarsely plumose setae and resemble those of Anomura. A rudiment of an epipod has been seen on maxillipede 1 in *U. danai*, but it is absent in the adult.

In *U. deltaura* and *U. stellata* there are such great differences in size and development between individuals in stage 3 that Miss Webb distinguished two classes which she supposed might represent the two sexes. I have examined about 300 larvae from Plymouth, and do not think the differences amount to more than individual variation, since there is every transition between the extremes. The more vigorous and larger larvae may moult to post-larval from stage 3, whereas the others pass through an additional stage. The two species can be distinguished at all stages, the most reliable character being the length of the uropods.

LAOMEDIIDAE.

See Thompson, 1903*a*; Caroli, 1921, 1924; Gurney and Lebour, 1939; Dakin and Colefax, 1940.

The family includes only the genera *Laomedia*, *Jaxea* and *Naushonia*, the first two with one species each, and the third with three, or possibly four. The larvae of *Jaxea* and *Naushonia* are known, and an unidentified form with a general resemblance to *Upogebia*, but certainly related to *Jaxea*, has been described (Gurney, 1928*c*, p. 337).

The characters of *Jaxea* and *Naushonia* are as follows :

(1) There are six stages in *Jaxea* according to Caroli, and five in *Naushonia*.

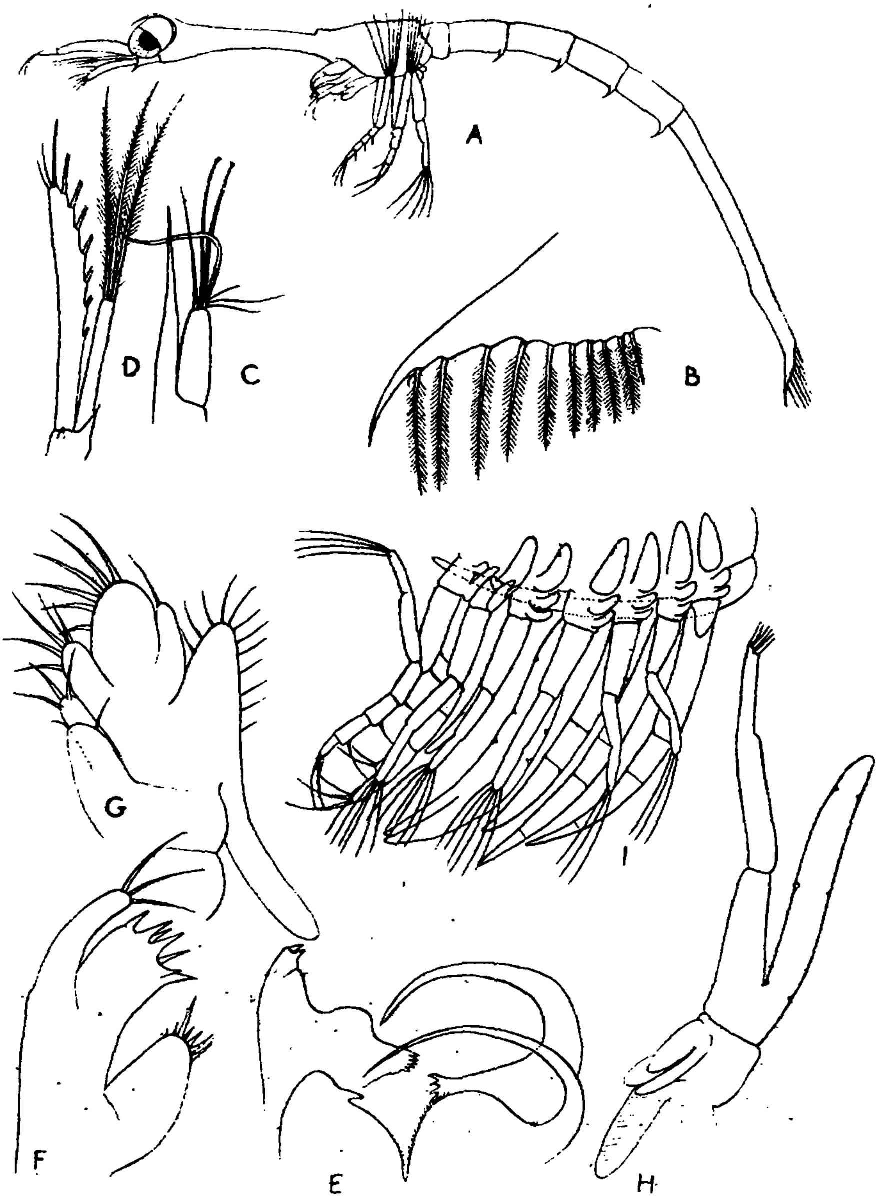

FIG. 101.—*Jaxea nocturna*. A–D. Stage 2. B, Telson; C, Antennule: D, Antenna. E–I. Stage 6 : E, Mandibles and paragnaths ; F. Maxillule ; G, Maxilla ; H, Maxillipede 3 ; I, Legs.

(2) There is a tendency in *Naushonia* to a lengthening of the region between mouth and antennna which becomes extreme in *Jaxea*. In *Jaxea* the whole body is remarkably long and slender.

(3) The rostrum is very small, and upturned in *Naushonia*.

(4) The abdominal somites have no dorsal spines, but the pleura of some or all the somites are drawn out into procurved hooks.

(5) The telson is deeply incised in stage 1, when it has the normal formula of 7 + 7 spines, the second reduced to a minute hair. In *Jaxea* the spines become numerous in late stages. There is no median spine.

(6) The antennule in *Jaxea* has a pointed process representing the endopod in stage 1.

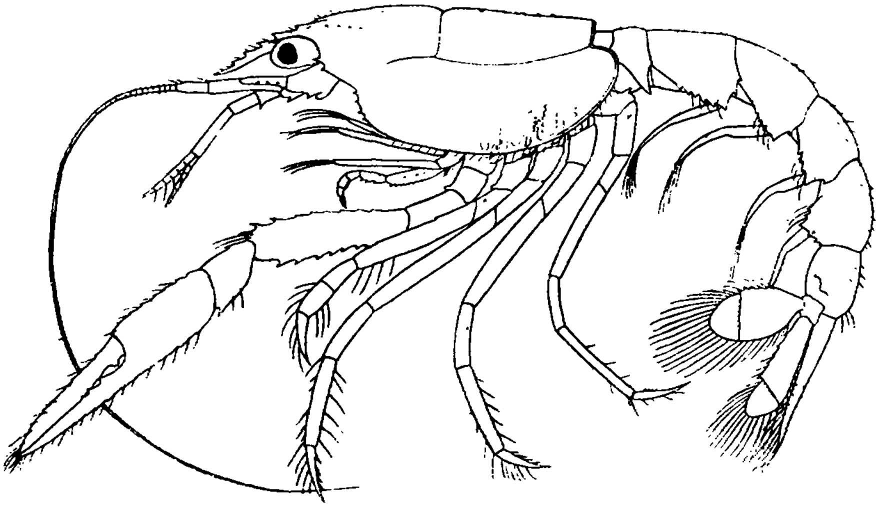

FIG. 102.—*Jaxea nocturna*. 1st post-larval, showing vestiges of exopods on legs 1–3.

(7) The antennal scale is unsegmented; the endopod with three apical setae in stage 1.

(8) The mandibles are asymmetrical, the incisor part on the right side drawn out into a sharp sickle; the paragnath on the same side is similarly modified.

(9) The endopod of the maxillule is unsegmented.

(10) The endopod of the maxilla is very much reduced. The exopod in late stages has a proximal extension without setae.

(11) Maxillipedes 1 and 2 have the basis long and cylindrical, but the setae of the endopod small and delicate.

(12) Maxillipede 3 is rudimentary in stage 1. The endopod remains undifferentiated and seated low on the basis.

(13) The endopods of the legs remain unsegmented and inserted low on the basis. There are setose exopods on legs 1–4 in *Naushonia*, but the exopod on leg 4 in *Jaxea* is rudimentary.

(14) There is no pleopod on somite 1.

The post-larval stage 1 of *Jaxea nocturna* (Fig. 101) (for which I am indebted to Prof. Tattersall) differs very much from the adult in the large size of the rostrum and eyes. It is remarkable that a large rostrum with serrated margin should appear at this stage when the rostrum of the adult is so small.

ANOMURA

GALATHEIDEA

AEGLEIDAE.

The single member of this family, *Aeglea laevis*, lives in streams in South America, preferring those parts of the stream where the bottom is stony and the current rapid. Müller (1880, 1892) noted that its development was shortened as in some fresh-water prawns, and Mouchet (1932) states that the young hatch in the form of the adult. No description of embryo or young has been published.

UROPTYCHIDAE.

The species of this family are confined to deep water, and, according to Milne-Edwards and Bouvier (1897), the eggs are large and may give rise to young of adult form.

Bouvier (1892) has described the embryo of *U. concolor* and *U. nitidus*. The mouth parts of the late embryo begin to have the characters of the adult, and there are rudiments of pleopods, but no pleopod on somite 5.

GALATHEIDAE.

See Sars, 1889 ; Huus, 1934 ; Rayner, 1935.

The development is known of all the British species of *Galathea* (Lebour, Bull), and Huus has fully described

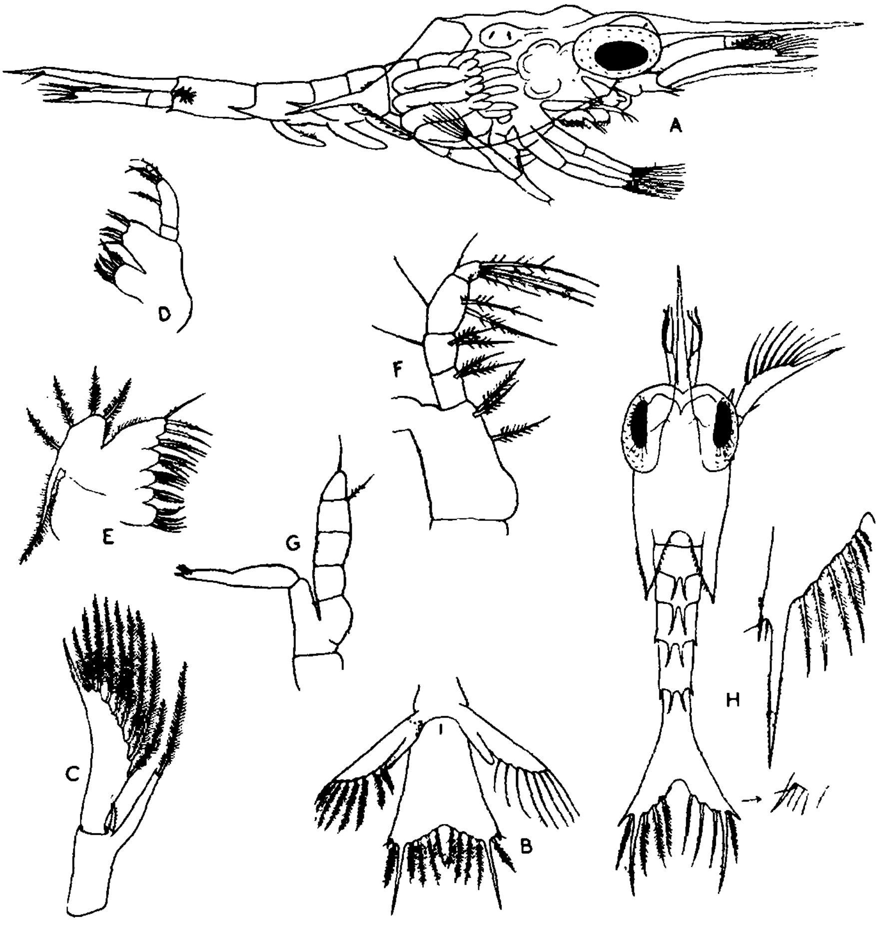

FIG. 103.—A. *Galathea strigosa*, stage 4. B. *G. intermedia*, telson, stage 3. C–G. *G. squamifera*, stage 1 : C, Antenna ; D, Maxillule ; E, Maxilla ; F, Maxillipede 2 ; G, Maxillipede 3. H. *Galathea* sp. Melbourne Harbour. Stage 1, with part of later telson.

it in the three northern species of *Munida*. There are no important differences between either larvae or adults in these genera. In *Munidopsis* (*Galathodes*) *tridentata* development is somewhat shorted, and the larva is very distinct from that of *Galathea* and *Munida* (Sars, 1889, pl. 4).

The following characters are common to these two genera :

(1) There are four, or rarely five, stages.

(2) The rostrum is long, not flattened nor serrated.

(3) The carapace is produced into a spine behind on either side, and its margins are serrated behind.

(4) The stem of the antennule remains unsegmented throughout.

(5) The antenna has a large spine on the basis ; the endopod with one apical seta and a small spine, or without setae.

(6) The mandible has a palp in the last stage.

(7) The endopod of the maxillule is unsegmented or of two segments.

(8) The proximal extension of the exopod of the maxilla bears setae ; the endopod is unsegmented.

(9) Maxillipedes 1 and 2 have the basis much longer than the coxa, cylindrical ; the endopod has stiff, coarsely feathered setae. The exopods have four setae in stage 1.

(10) Maxillipede 3 is rudimentary in stage 1 ; the endopod later unsegmented and seated low on the basis.

(11) The legs have no expods, and are not functional.

(12) Leg 5 is hidden behind legs 3 and 4.

(13) There is no pleopod on somite 1.

(14) The abdominal somites usually have the posterior margins toothed, and lateral spines on somite 5, or 4 and 5.

(15) The telson has seta 2 reduced, with formula 7 + 7 in stage 1. In the last stage spine 4 is longer than the rest, and the formula 8 + 8. Spines 1–3 may be much reduced in late stages (*Munida*).

While these characters apply to all European species, they will probably not be found to hold good universally. I have seen larvae which may be assumed to belong to the Galatheidae but differ in some points.

One species from the Barrier Reef has the antennal scale enormously developed, parallel-sided but expanded at the end. A species from Bermuda has the rostrum flattened and serrated along the margins. A species from Melbourne Harbour has a pair of long dorsal spines on somites 2–5, and in stage 1 spine 4 of the telson is enlarged, as it is in later stages of other species. Probably these forms belong to genera other than *Galathea* and *Munida*.

While the first post-larval stage of *Galathea* and *Munida* differs very little in form and habit from the adult, there is one exception to the rule—*Munida gregaria*. In this species this stage differs from the adult in several details (Matthews, 1932, p. 475), and was placed by Leach in a new genus *Grimothea*. This *Grimothea* stage is pelagic, and frequently found in swarms at the surface. The adult may also be found swarming at the surface at times. In the closely allied *M. subrugosa* the first post-larval stage does not normally swim though the adult may do so. An allied species *Pleuroncodes planipes* may also be taken in shoals at the surface. This species and *M. gregaria* are important as the food of some species of whales, and they are known as " Lobster Krill." For a full account see Matthews, 1932.

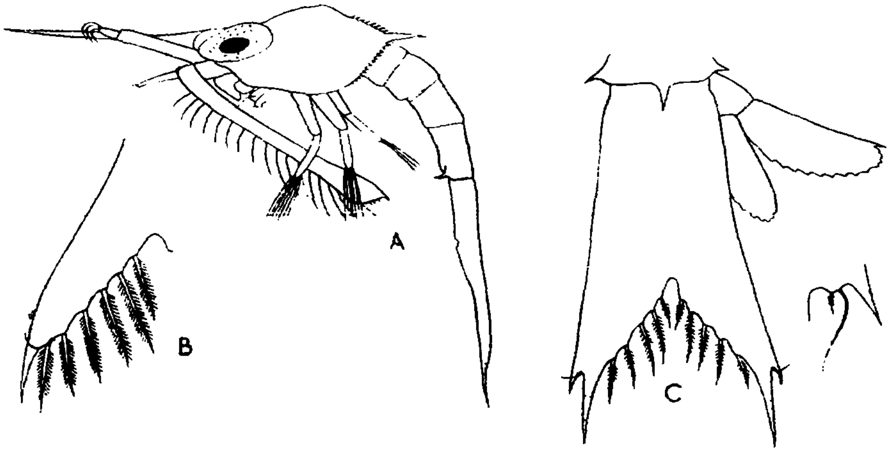

FIG. 104.—*Galatheid*, stage 2. Barrier Reef. B. Telson. C. Telson of later stage and enlarged outer portion.

PORCELLANIDAE.

See Sars, 1889 ; Cano, 1893*a* ; Gurney, 1924*c*, 1938*a*.

While there is a general similarity with *Galathea* the larvae of *Porcellana* and allied species differ as follows :

(1) The number of stages is not certainly known, but it is believed to be two or three.

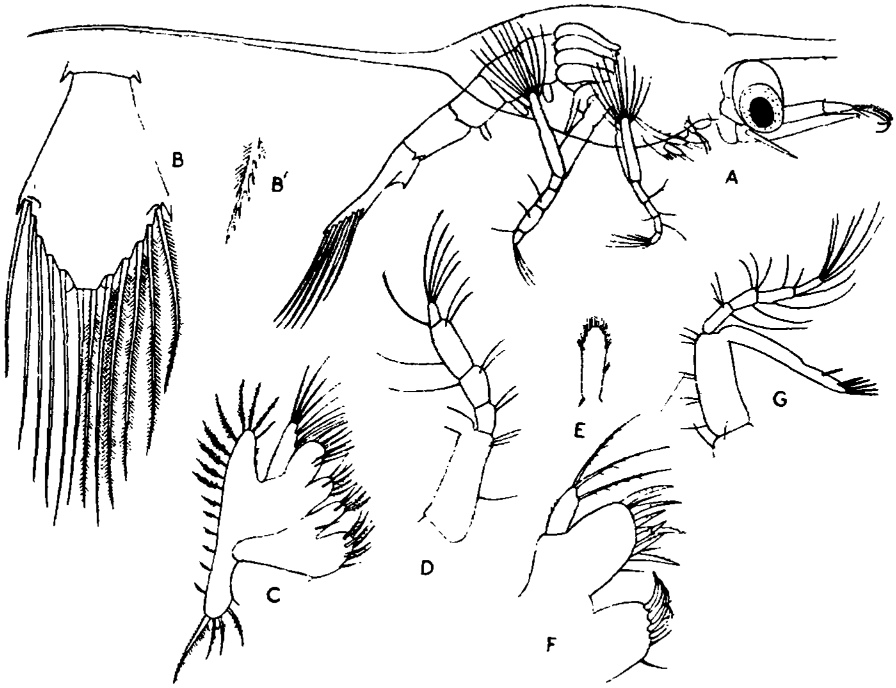

FIG. 105.—*Porcellana* sp. Plymouth. A. Stage 2 ?. B–G. Last stage : B, Telson ; B′, Part of outer spine ; C, Maxilla ; D, Maxillipede 2 ; E, End of exopod ; F, Maxillule ; G, Maxillipede 2.

(2) The rostrum and posterior spines of the carapace are enormously long, the rostrum not flattened. The margins of the carapace are not serrated.

(3) The abdominal somites are usually smooth.

(4) The telson has the posterior margin convex, and sometimes with median spine.

(5) The antennal scale is reduced to a spine.

(6) The setae of maxillipedes 1 and 2 are not stiff nor coarsely feathered ; there are sometimes outer setae on all the segments.

(7) Somite 5 sometimes has no pleopod (as in *Uroptychus* according to Bouvier). This is the case in the two British species *P. platycheles* and *P. longicornis*.

(8) There are no uropods.

A larva from Melbourne Harbour described by me (1924*c*, p. 178) has the general form of *Porcellana*, but a telson of quite different form, and well developed uropods.

PAGURIDEA

PAGURIDAE.

See Sars, 1889; Thompson, 1903*b*; Hart, 1937.

The development of only a few of the many genera of Paguridae is known. There are many references to Pagurid larvae, but few of them are of value. It is particularly desirable that the development of one of the symmetrical genera should be made known.*

In *Cancellus typus* (Pagurinae) the larva is entirely suppressed and the young cling to the abdomen of the parent (Hale, 1927, p. 95). Development is somewhat shortened in *Paguristes*. Issel described two larval stages only in *P. oculatus* (1910), but Miss Hart found three in *P. turgidus*, and suggested that Issel may have missed stage 1. There are four stages in *Eupagurus* (Thompson), and this is probably the normal number in the group.

DESCRIPTION.

(1) The rostrum is not flattened nor serrated.

(2) The carapace usually has a pair of short downturned posterior spinous processes, and the margin is not serrated.

(3) The abdominal somites rarely have small dorsal spines; but the margins are sometimes toothed. Somite 5 often has a pair of lateral spines.

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* *Orthopagurus*, of which the larva is described by Hart, is one in which the abdomen has become straight secondarily.

(4) Spine 4 of the telson is usually the largest, and fused with the telson. Spine 2 is reduced to a hair and there is no median spine.

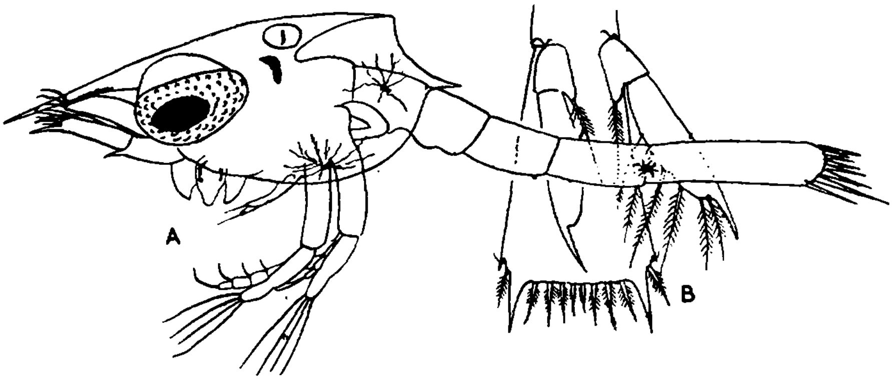

Fig. 106.—a. *Anapagurus hyndmani*, stage 1. b. Telson, last stage.

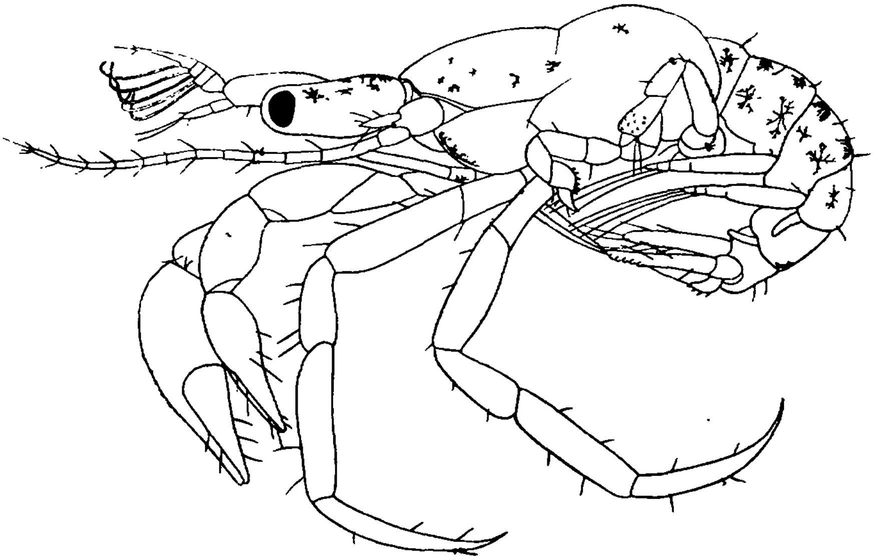

Fig. 107.—*Anapagurus hyndmani*, post-larval. Showing reduction of pleopods.

(5) The peduncle of the antennule remains unsegmented.

(6) The scale of the antenna is unsegmented; the endopod with two, or rarely three, setae, or without setae.

(7) The mandible has a small palp in the last stage.

(8) The endopod of the maxillule has three segments.

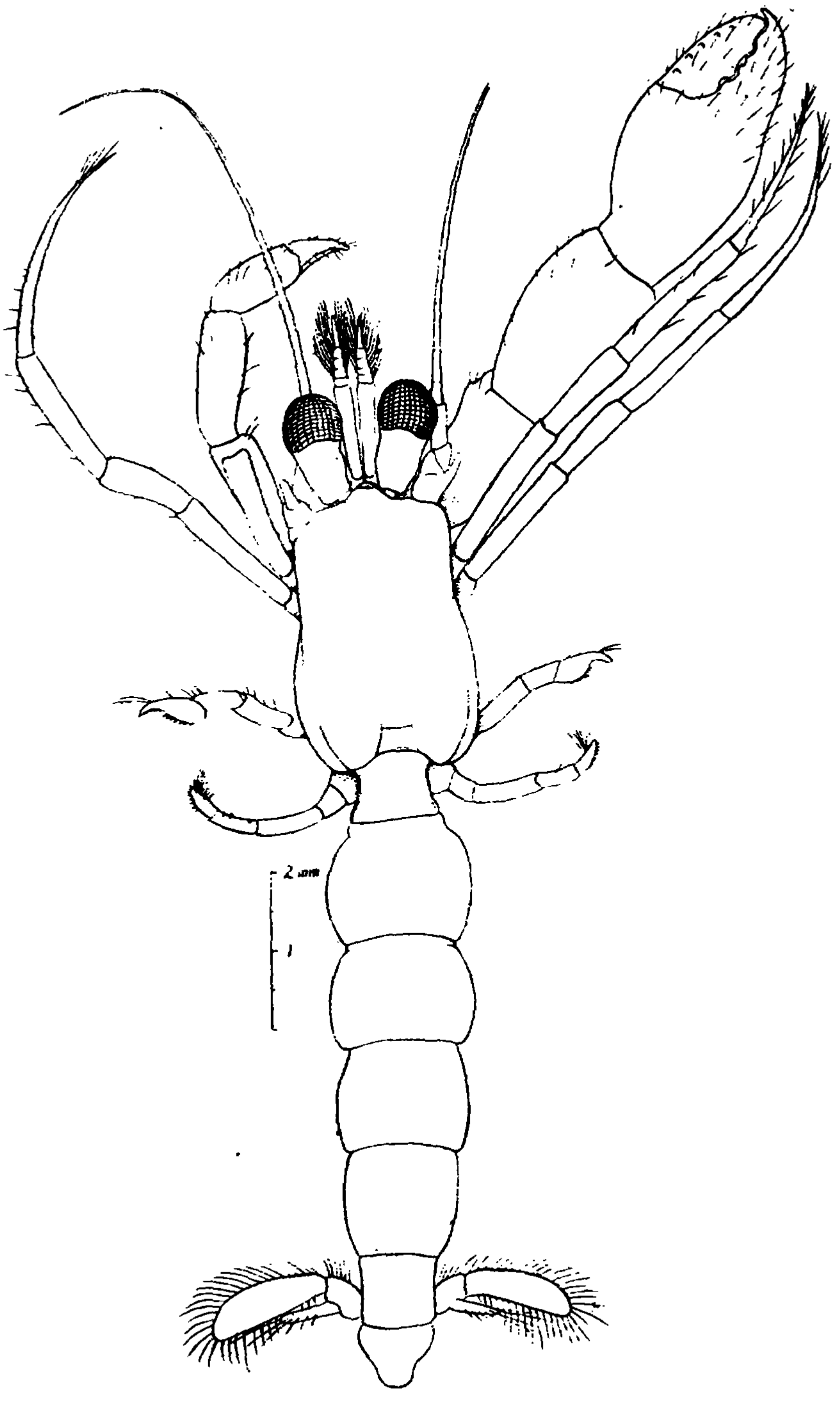

FIG. 108. *Glaucothoë peronii.*

(9) The proximal extension of the exopod of the maxilla is bare of setae.

(10) Maxillipedes and legs as in Galatheidae.

(11) The endopod of the uropod is much reduced.

(12) There are two or three pairs of pleopods only.

The first post-larval stage of the Paguridae is known as the Glaucothoë stage from the genus *Glaucothoë* established by Milne-Edwards for *G. peronii*, a large post-larval Pagurid. Whereas the Glaucothoë stage of *Eupagurus longicarpus*, for instance, is only about 3 mm. and changes finally to the adult form at the next moult, the species of *Glaucothoë* may be as much as 20 mm. long. One, *G. peronii*, is known to have the same form from a size of about 7 mm., and therefore evidently moults often without change. These large larval forms have symmetrical abdomen, large eyes, and no ocular scales.

Bouvier (1891, 1905) supposed the large Glaucothoës to be larvae which had failed to follow the normal course of development, and had continued to moult and grow without change of form. The contrary has been maintained—that they are normal larvae, perhaps of deep-sea genera not yet known (Gurney, 1924*c*, p. 186). No new evidence has been brought to bear on this problem. I have seen many of these large larvae in the " Discovery " material, but, until one of them has been kept alive and moulted to post-larval, no new light is likely to be shed on the question. I have seen none alive at Bermuda.

During the Glaucothoë stage in *Eupagurus* great changes take place in the internal anatomy (Thompson, 1903, p. 157). While free-swimming at first, the Glaucothoë may take to a shell before the moult to stage 2. In *Birgus* it is apparently the rule for the Glaucothoë to take a shell and come to land protected in this way (Harms, 1937).

The Paguridae are divided by Melin (1939) into two groups—the *Pagurus* Group and the *Eupagurus* Group. Of the former we have adequate descriptions of *Pagu-*

ristes and *Diogenes*[*] but no satisfactory description of *Pagurus*.[†] Of the second group several species of *Eupagurus* and *Anapagurus* have been described. The available information is far from sufficient, but it is of interest to note that there seems to be a very close relation between the larvae of *Paguristes* and *Diogenes* on the one hand, and *Eupagurus* and *Anapagurus* on the other. The former agree in having the carapace rounded behind, spine 4 of the telson not enlarged nor fused with the telson, and the endopod of the antenna with three setae. One of these setae is reduced in *Diogenes*, and *P. oculatus* is said to have four. In *D. pugilator* and *P. turgidus* there are dorsal spines on the abdomen, whereas there are none in any other species.

Taking the Paguridae as a whole the only characters which will in all cases distinguish their larvae from those of the Galatheidae are the absence of serrations on the carapace margin ; reduction of the endopod of the uropod ; the three-segmented maxillular palp ; and the absence of setae from the proximal extension of the maxillar exopod.

KEY TO PAGURID LARVAE OF KNOWN SPECIES.

1.	Carapace rounded behind	2.
	Carapace with posterior spines	4.
2.	Two pairs of pleopods	*Diogenes pugilator*.
	Four pairs of pleopods	3.
3.	Dorsal spines on somites 2–5 . .	*Paguristes turgidus*.
	No dorsal spines	*Paguristes oculatus*.
4.	Three pairs of pleopods . .	*Anapagurus chiroacanthus*.
	Four pairs of pleopods	5.
5.	Endopod of antenna without apical setae in stage 1 .	6.
	Endopod with two setae	7.
6.	Somite 5 with lateral spines . .	*Eupagurus* { *pubescens* *beringanus*.
	Somite 5 without lateral spines . . .	*E. bernhardus*.

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[*] The identification of the larvae attributed to *Diogenes* is not beyond dispute.

[†] It must be understood that I use here the nomenclature which has been accepted in Europe for a century. The transference of *Pagurus* to *Eupagurus* is sheer sabotage.

7. Spine 4 in last stage larger than the rest . . . . 8.
   This spine not larger . . . . *Eupagurus longicarpus.*
8. Telson in last larva more than twice as long as it is wide *Orthopagurus schmitti.*
   Telson as wide as it is long. *Spiropagurus spiriger.**

LITHODIDAE.

See Sars, 1889; Marukawa, 1933.

In *Lithodes maia* the egg is large and the larva is full of yolk and has large rudiments of the legs on hatching.

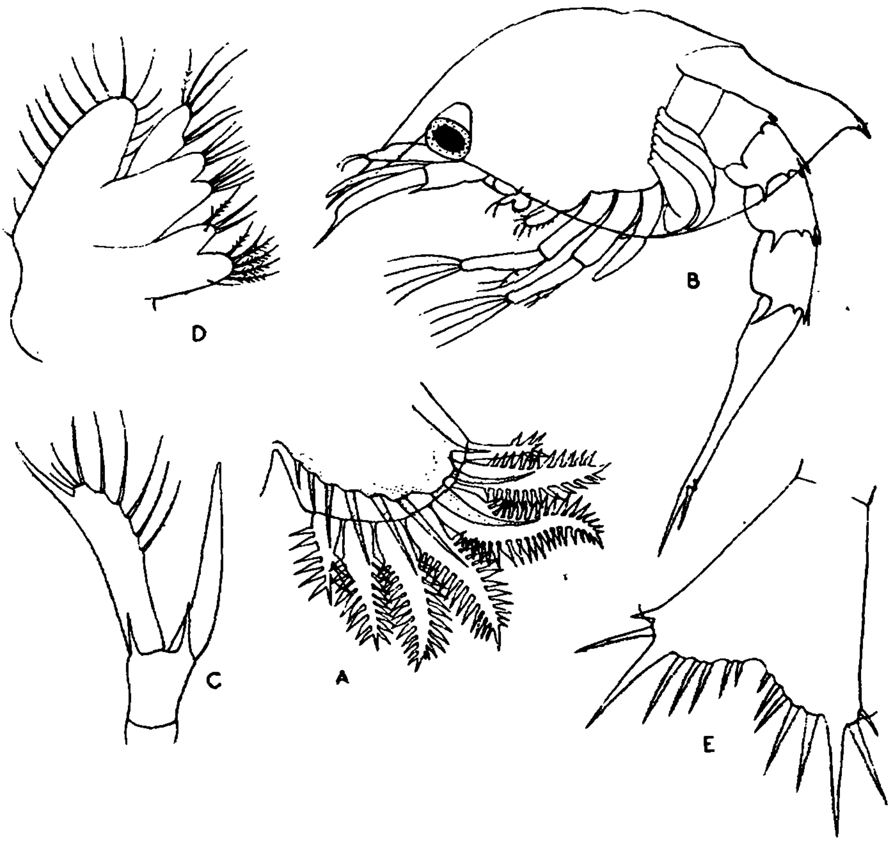

FIG. 109.—*Lithodes maia.* From Millport. A. Prezoeal telson. B. Stage 1. C. Antenna. D. Maxilla. E. Telson.

Sars describes only two free stages. In *Paralithodes* there are four (Marukawa).

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* The shape of the telson in this form, as figured by Menon, is so different from that of *Anapagurus* (*Spiropagurus*) *chiroacanthus* as figured by Sars that I find difficulty in accepting Menon's identification. His larvae were not obtained from the egg.

The larvae of these two genera are very much alike, but whereas in *Lithodes* apparently the uropods are not developed at all, in *Paralithodes* they appear in stage 3 as very slender, uniramous appendages.

The post-larval stage described by Bouvier as *Megalope grimaldii* (1923, p. 37) is regarded by him as belonging to *Neolithodes*. It differs from *Paralithodes* at the same stage in having biramous uropods.

Apart from the reduction, or disappearance, of the uropods there is no definable difference between the larvae of the Lithodidae and those of the Paguridae of the *Eupagurus* Group. Boas (1880) and Bouvier (1896) agree in regarding *Lithodes* as descended from *Eupagurus*. *Lithodes* is, according to Boas, " un *Eupagurus* richement modifié pour vivre sans coquille " (1880, p. 192).

HIPPIDEA.

See Faxon, 1879*a* ; Menon, 1933, 1937.

Knowledge of the group is not very satisfactory, since it is only in *Hippa talpoida* that the larva has been obtained from the egg. There can be little doubt that the larvae described as *Albunea* have been correctly identified ; but it is desirable that this identification should be confirmed, particularly as some doubt has arisen as to the fate of the gills (see p. 28). Menon's identification of his larvae as those of *Hippa asiatica* and *Albunea symnista* was founded only upon the fact that these species alone are known from the Madras coast. I have not myself seen any larvae of *Hippa* ; but I have specimens of two quite distinct types in stage 1 from Bermuda, and advanced larvae from the " Discovery " material, which apparently belong to *Albunea*.

DESCRIPTION.

(1) There are five stages (Menon).

(2) The rostrum is large and smooth. The carapace

has a pair of large posterior lateral spines. In *Hippa* these spines appear in stage 2.

(3) The abdomen has no dorsal spines, and is with or without lateral spines. The abdomen consists of five somites only (including telson) in stage 1.

(4) The telson is very broad, with convex margin and a spine at each outer angle. There are numerous short marginal spines, but no median spine. Spine 2 may be reduced to a hair.*

(5) The antenna has a very large spine on the basis. The exopod is setose in *Albunea*, but vestigial in *Hippa*. The endopod is absent in early stages.

(6) The mandible has no palp.

(7) The endopod of the maxillule is reduced and unsegmented.

(8) The exopod of the maxilla is very large, the proximal extension partly bare; the inner lobes are usually vestigial, but well developed in a species of *Albunea* from Bermuda (Fig. 110, D).

(9) Maxillipede 3 is absent in stage 1 or present as a very small rudiment. It is biramous in stage 3 in *Albunea*, with the endopod low down on the basis, but uniramous in *Hippa*.

(10) There are no exopods on the legs. Leg 5 is hidden.

(11) There are biramous pleopods on somites 2–5.

(12) Uropods are present in stage 3, uniramous throughout in *Albunea* but becoming biramous, without setae on the endopod, in *Hippa* (Menon).

The two species from Bermuda are shown in Fig. 110. It is impossible to name either, since there is only one species, *Albunea oxyophthalma*, known from there. Species A has a very short rostrum and lateral spines, and no spines on the abdomen except on somite 5. The scale of the antenna is very broad, the maxilla has no endites, and there is a very distinct rudiment of maxillipede 3. Species B has very long rostrum and lateral

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* This hair is present in the two species from Bermuda. It is not mentioned by Faxon or Menon.

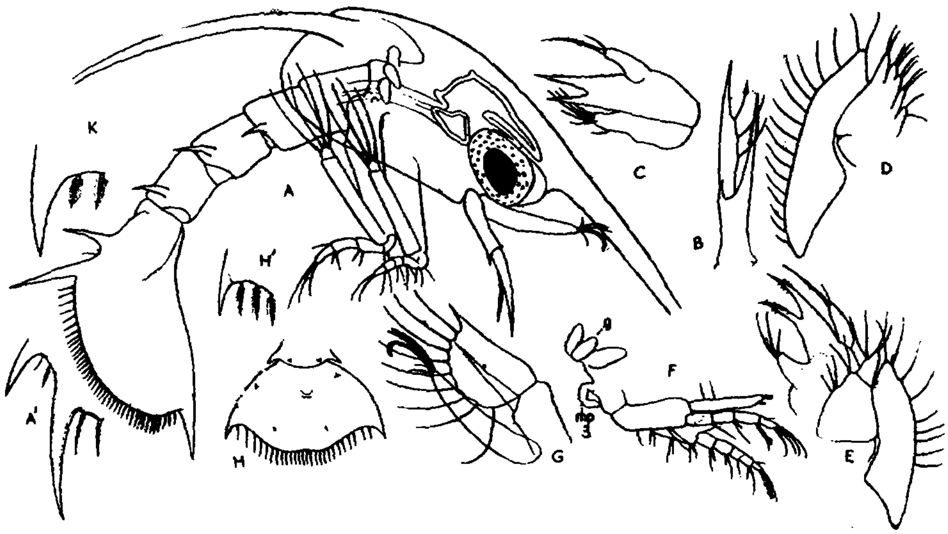

FIG. 110.—*Albunea.* A–D. Species B, Bermuda: A, Stage 1; A′, Part of telson; B, Antenna; C, Maxillule; D, Maxilla. E–H. Species A: E, Maxillule and maxilla; F, Maxillipedes and gills (*g*); G, Antennule and antenna; H, Telson; H′, Outer angle of telson. K. Outer angle of telson of *A. symnista*, stage 2 (specimen from Dr. Menon).

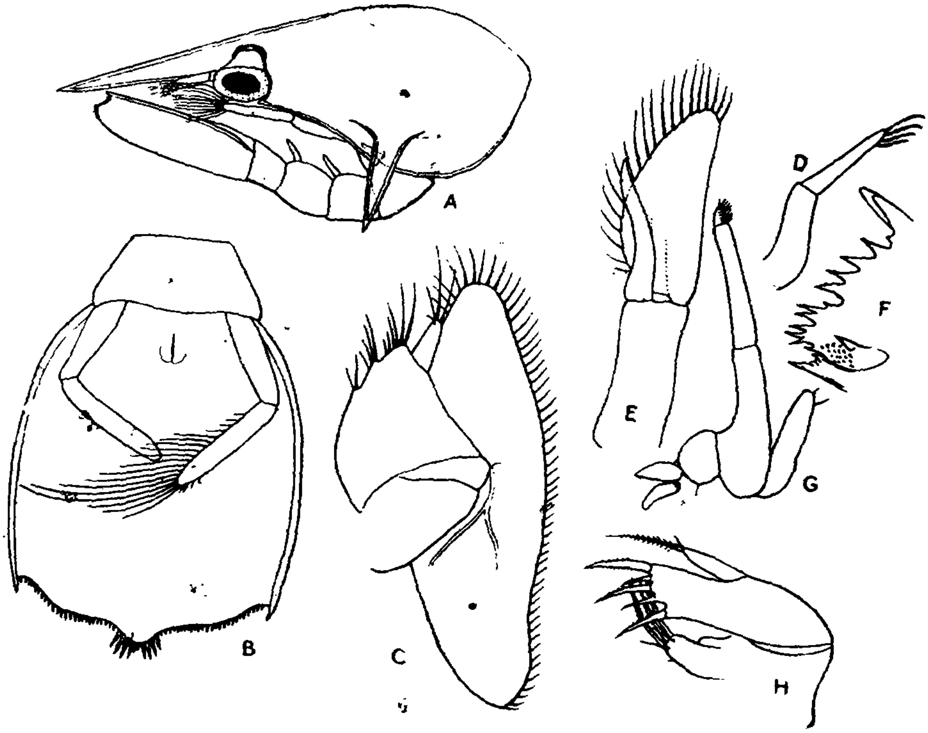

FIG. 111.—A. *Albunea* sp., stage 5. B. Telson. C. Maxilla. D. Antennule. E. Antenna. F. Mandible. G. Maxillipede 3. H. Maxillule.

spines, lateral spines on the abdominal somites, distinct endites on the maxilla, and no trace of maxillipede 3. The telson is very different. In both species there are three large rudiments of gills. This early appearance of gills, before the legs have appeared, is remarkable.

Fig. 111 shows stage 5 of an unnamed species with uniramous uropods taken about 300 miles from the coast of South Africa.

Smith (1877) regarded the larva of *Hippa* as essentially the same as the Brachyuran Zoea, and Claus (1885, p. 71) also noted a close resemblance; but he pointed out the differences in the presence of biramous pleopods and of uropods. In view of the presence of uropods in the crab-like Zoea *Acanthocaris* (see p. 272) the latter difference is not fundamental. There is a resemblance in general form, due to the large lateral spines on the carapace. The disappearance of the endopod and reduction of the scale of the antenna, with the large size of the spine on the basis, make the appendage approach that of the Brachyura. The reduction of the somites of the abdomen is another Brachyuran feature. The Hippidea, Dromiacea and Gymnopleura seem all to have some affinity with Brachyura due to a common pre-Brachyuran ancestry.

DROMIACEA

See Cano, 1893*a*; Gurney, 1924*c*; Lebour, 1934*b*.

The larval development of *Dromia vulgaris* is fully known (Cano, 1893*a*; Lebour, 1934*b*), and Cano has described stages in the development of *Homola*, *Dynomene* and *Latreillia*. Aikawa (1937) has figured the first stage from the egg of *Latreillia phalangium* and *Paromola japonica* which are almost identical, and differ so much from Cano's *Latreillia* that the latter's identification must be supposed to be wrong. I have seen a similar form from the Barrier Reef which I regard as a Pagurid. Bouvier (1896, p. 105) was at great pains to prove that Cano's larva had no affinity with the Paguridae, but accepted the identification without question. Cano's *Dynomene* cannot be accepted without further evidence, his identification being purely speculative. Aikawa has described a larva and Megalopa of *Homola*, but it is not stated if the latter was moulted from the larva, so that the genus remains in doubt. The larva has the same general form as his *Latreillia*, and Cano's *Homola*, though very different, might well be related. Boas has also described a larva attributed to *Homola*.

In view of Aikawa's figures I think the two larvae described by me (1924*c*, p. 189) as " Dromiacea 1 and 2 " can be referred to *Latreillia* or closely allied genera. Both have the serrated carapace margin which seems to be characteristic.

There is a tendency to abbreviation in larval development. In *Dicranodromia* there is presumably a free larva, but with all the appendages present at first (Caustier, 1895) ; but in *Cryptodromia octodentata*, *Petalomera lateralis*, and probably also in *Platydromia thomsoni* development is direct, and the young hatch with most of the characters of the adult (Hale, 1925).

In view of the uncertainty about some, and the incompleteness of knowledge of other genera, only *Dromia* can safely be taken into account in considering the bearing of the larva upon classification.

Dromia vulgaris.

The carapace has a large rostrum, and postero-lateral spines as in Paguridae. The abdominal somites have no spines. The telson has no median spine. There is a small spine at each angle and a spine formula of not more than 8 + 8. Spine 2 is reduced to a hair and spine 4 is not larger than others. The peduncle of the antennule is not segmented. The antennal scale is large, with setae or hairs on its outer margin ; the basis spine is small. The endopod has three apical setae in stage 1. The mandible has a palp in the last stage. The endopod of the maxillule is of two segments. The exopod of the maxilla has setae on its proximal extension. The coxa of maxillipedes 1 and 2 is small, the basis long and cylindrical. The endopod is of five segments on maxillipede 1 and of four in the second. The exopod is of two segments, with four setae in stage 1 and eight in stage 5.* Maxillipede 3 is rudimentary in stage 1, with small endopod and larger exopod without setae ; the endopod is seated low on the basis in later stages. Leg 1 has a functional exopod ; legs 2 and 3, and perhaps leg 4, have small rudiments of exopods in stage 5. The uropods have two large setose branches in stage 5. The pleopods in the larva are biramous. In the Megalopa they have a small endopod with hooks.

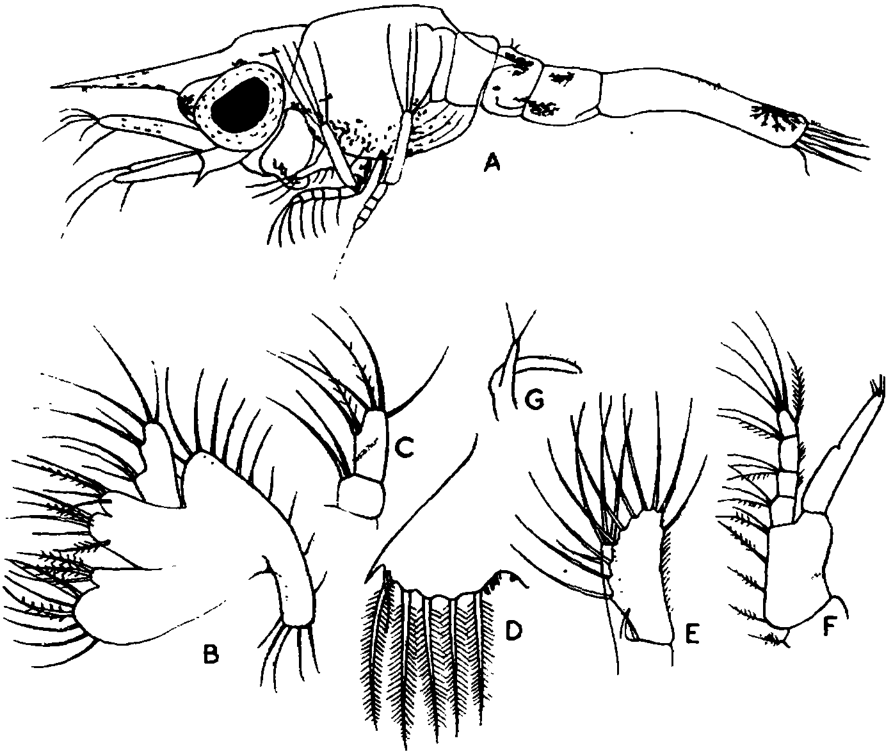

FIG. 112.—*Dromia erythropus* ? Bermuda. Stage 1. B. Maxilla. C. Palp of maxillule. D. Telson. E. Antenna. F. Maxillipede 2. G. Maxillipede 3.

Miss Lebour notes that the rich orange-red colour of

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* Miss Lebour points out that this number of setae agrees better with Anomuran or Thalassinid than with Brachyuran relationship (1934, p. 242).

Dromia vulgaris is the same as is so general in Anomura and Thalassinidea but very rare in Brachyura.

The specimen figured is of an unnamed species from Bermuda. The only species recorded from Bermuda is *D. erythropus*. It differs from *D. vulgaris* in having an additional inner seta on the endopod of the antenna, and in the greater size of the reduced spine of the telson.

In *Latreillia* (Aikawa) there are only two setae on the antennal endopod, and the spine on the basis is extremely large, as in *Galathea* and Brachyura. The exopod of the maxilla has relatively few setae and one large one on its proximal end in stage 1.

The larva of *Dromia* could hardly be suspected of belonging to a crab. Miss Lebour has summarized the points of difference from Brachyura and resemblance to Thalassinidea and Anomura. There are certain features, such as the presence of setae on the outer margin of the antennal scale, and the form of the telson in the last stage, which are peculiar, and the presence of exopods on legs 1–3 (and perhaps 4), though functional only on leg 1, would make it improbable that it would belong to an Anomuran. The presence of these exopods makes derivation from any existing Anomura impossible, but points to a close relation between the ancestral Dromiid and the Anomuran section of the Thalassinidea.

Bouvier treated the evidence from larval forms (1897, p. 99) in a manner which is difficult to understand except on the assumption that he found it peculiarly awkward to bring within his argument. When he says that the larva of *Homarus* does not differ from that of the Thalassinidea except in the presence of exopods on the last two legs, one is prepared to accept the relationship, if not the statement, provided it is restricted to the Axiidae and Callianassidae; but when he goes on to say "it is therefore quite as logical to connect the development of *Dromia* with that of the Homaridae as with that of the Thalassinidea," one can only disagree. That the Homarids are not far removed from the ancestral Reptant Decapoda may be accepted; that one section of the Thalassinidea has close affinity with the Homarids is almost certain; but the other section has diverged far in the direction of the Anomura, and it is probable that it was from this stock that the Dromiacea sprang.

Arguing from adult anatomy, Ortmann considered that the parent stem of the Dromiacea arose from an Anomuran intermediate between Galatheidae and Paguridae, while Boas has postulated an ancestor between Anomura and Thalassinidea. Larval development and adult anatomy combine to prove descent from an Anomuran-Thalassinid stock.

While that might be generally conceded, there seems to be a general conviction that the Brachyura are descended from the Dromiacea, and that the origin of the Brachyura is solved when that of the Dromiacea is accounted for. Bouvier's thesis on the Homarid origin of the crabs is founded wholly on the assumption that the Dromiacea are the parents. Pesta alone of recent authors (1918), so far as I can find, gives the Dromiacea a division separate from the Brachyura, from which he also excludes the Oxystomata.

My own opinion, expressed in 1924 and supported by Miss Lebour, is that the Dromiacea should be excluded altogether from the Brachyura.

BRACHYURA

See Lebour, 1928*b*, 1931*c*; Aikawa, 1929.

The great majority of Brachyura have a typical Zoea larva with long rostral, dorsal and lateral spines on the carapace, slender curved abdomen, and forked telson. The first to attempt a comprehensive survey with the object of discovering specific and generic differences among them was Miss Lebour (1928*b*). Aikawa (1929, 1933, 1937) has made use of characters not systematically used by Miss Lebour, such as chromatophores, setae on the maxilla, etc., to group the

Zoeas of Brachyura, but without, in my opinion, greatly advancing our knowledge. . He has formed certain groups—Inachizoea, Grapsizoea, Xanthozoea, etc.—according to the form of antenna, telson, etc., but these groups do not profess to include only species related phylogenetically. For instance, under Inachizoea he includes species of *Inachus*, *Pilumnus*, *Heteropanope* and *Gonoplax*, while Grapsizoea is of even more diverse composition. I am unable to see that any purpose is served by setting up such a series of heterogeneous groups. Miss Lebour, on the other hand, has made use of all the facts at her disposal to throw light upon the systematic grouping of the adults, with interesting results.

In spite of the great extension of our knowledge of crab larvae of recent years, it is still not sufficient to have any dependable influence on classification. The group is so large and varied that the proportion of known to unknown genera is small, and there are serious difficulties which only time and much extended research can remove. For example, we have descriptions of the larvae of *Heteropanope tridentata* (Tesch, 1913) and of *H. glabra* (Aikawa, 1929), and they differ so much that one can only believe either that the two species do not belong to the same genus, or that larval characters have no significance at all.* Similarly the differences between the species of *Pinnotheres* and allied genera with regard to telson and carapace are such that it is difficult to believe that the systematics of the adults can be correct. If typical Zoeas of Pinnotherid, Ebaliid and Hymenosomatid crabs are taken they are found to have so many points of agreement that they must be supposed to be related; and yet each is now placed in a group widely separated from the others.

Miss Lebour has rightly used the Megalopa stage in defining specific and generic characters; but I have not dealt fully with this stage. The Megalopa is a post-

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* A third alternative, that the parents were not correctly identified, is just possible.

larval stage, and consequently not strictly relevant, but it may have characters which are not found in the adult, and may therefore be regarded as larval. On the other hand there are so many genera in which the Megalopa is unknown that its value is limited.

GYMNOPLEURA

RANINIDAE.

We do not know the development of any species of Raninidae* ; but the larva described by Claus under the name of *Acanthocaris* (1876, 1885) was regarded by him as perhaps belonging to a Raninid. This identification was accepted by Cano (1892*b*, p. 21 ; 1893, p. 18), and may well be correct. Westwood's *Zoea gigas* is certainly the same form. I am much indebted to Miss Lebour for a specimen of this form in stage 1 from Bermuda, from which the accompanying figures are taken.

Aikawa (1933) has described three Zoeas of this type under the name of *Lithozoea*. He gives as examples for this group *Lithodes*, *Homola* and *Dromia*, but it is not clear if he means to imply relationship, since his other groups are very heterogeneous. Two of the species which he describes have normal Brachyuran carapace spines, but the third rather approaches the form of *Latreillia*. In none of them is there any trace of relationship to *Lithodes*.

In its general appearance *Acanthocaris* is a normal Brachyuran Zoea, but it differs from all others in having a normal antennal scale and endopod, and a setose uniramous uropod. The telson is also quite different, though it may be regarded as transitional to the Brachyuran fork. The maxillule, maxilla and maxillipedes are of normal Brachyuran form, the endites of the maxilla being deeply cleft. The exopod of maxillipede 3 has

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* Miss Lebour informs me that the Zoea of *Ranina* has now been described by Aikawa (1941), but I have not seen this paper.

no setae, and there are no exopods on the legs. The gill formula is somewhat uncertain, but it seems there is a podobranch on maxillipede 2. Claus's figure shows three small gills, which he supposed were about to disappear, and which he regarded as two arthrobranchs and a pleurobranch. Apart from these gills the formula is the same as that of a normal Brachyuran. Claus regarded his larva as indicating a descent of the Raninidae from the Anomura.

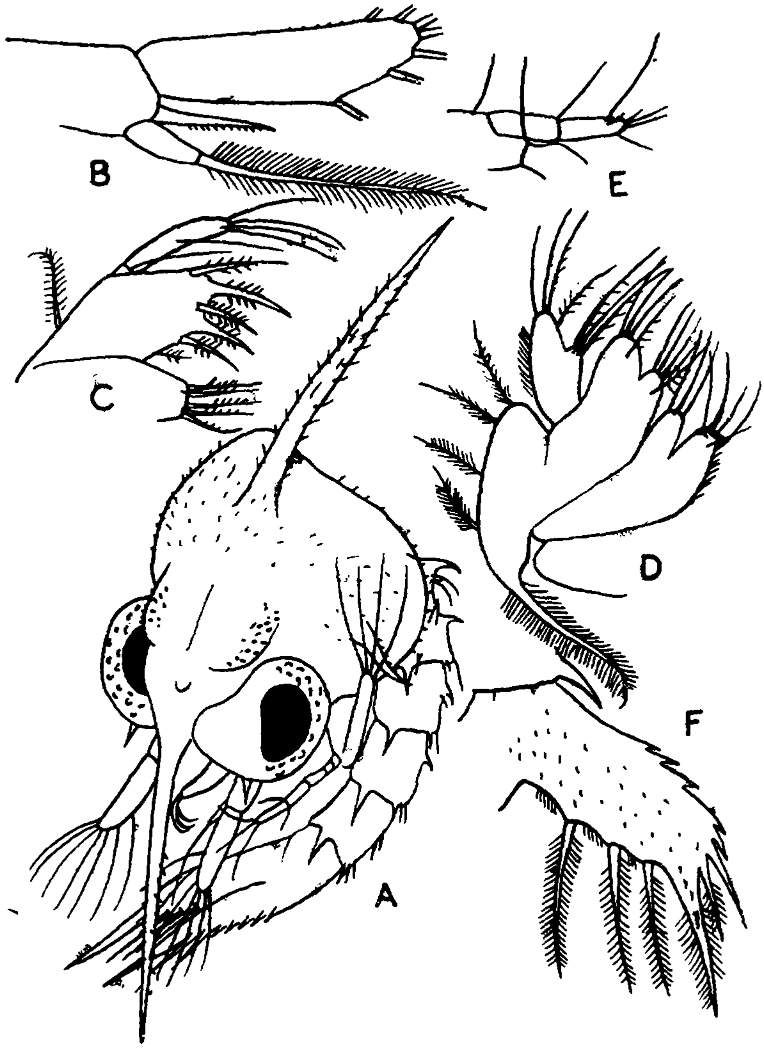

FIG. 113.—*Acanthocaris* (Raninid ?), stage 1 (Bermuda). B. Antenna. C. Maxillule. D. Maxilla. E. Maxillipede 2, endopod. F. Telson.

Bourne's opinion was thus expressed: "Although not descended from crabs, but from lobsters, the Ranidae have been so similarly modified, in one direction or another, that they must be classed with the crabs, with which they have no relationship save that of a remote common ancestor which was itself not a crab" (1922, p. 56).

BRACHYGNATHA

BRACHYRHYNCHA

Apart from the Pinnotheridae, which present peculiar difficulties, the Zoeas of the Brachyrhyncha are so much alike that the distinctions which can be made between

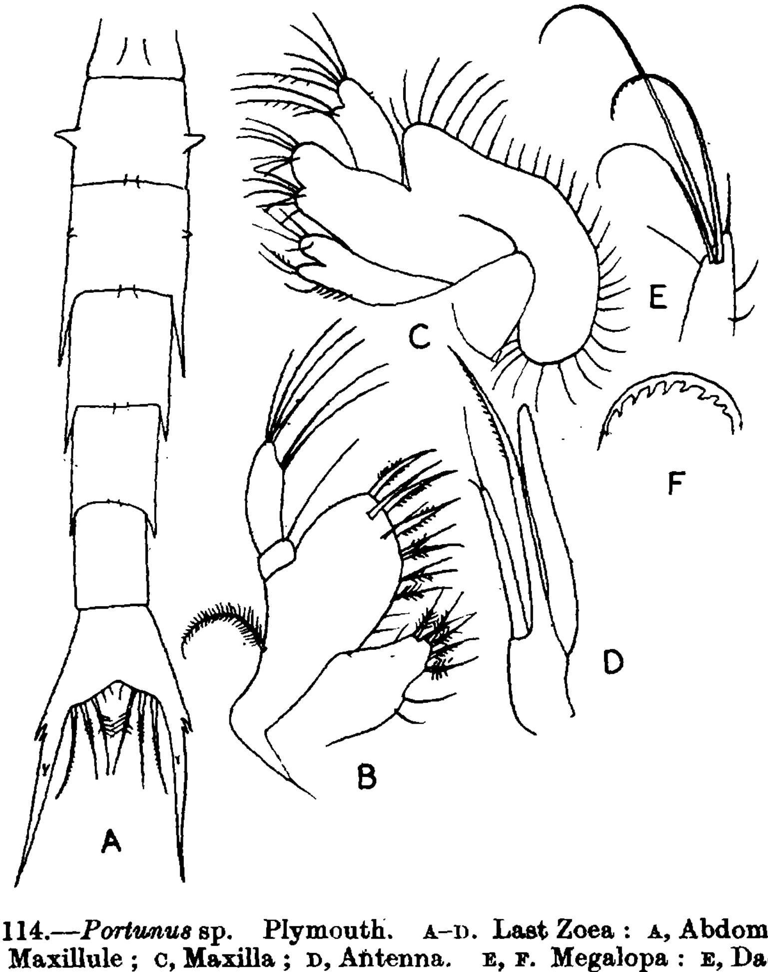

FIG. 114.—*Portunus* sp. Plymouth. A–D. Last Zoea : A, Abdomen ; B, Maxillule ; C, Maxilla ; D, Antenna. E, F. Megalopa : E, Dactyl of leg 5 ; F, End of one "feeler."

families are very small. The genus *Palicus* (= *Cymopolia*) is included by Rathbun (1918) among the Grapsoid crabs, but its Zoea is described by Cano (1891*b*) and is unmistakably a Dorippid. Cano does not state that the Zoea was hatched from the egg, but there is no reason to doubt his identification. The genus was regarded by Ortmann as belonging to the Dorippidae, and it is in that family that it should surely remain.

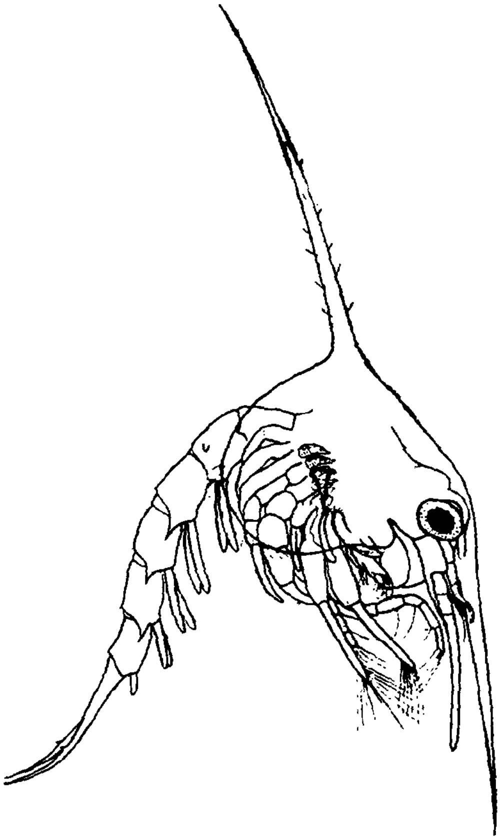

FIG. 115.—*Corystes cassivelaunus*, last Zoea.

The following are the characters of the Brachyrhynch Zoea as given by Miss Lebour. Four or five stages, with 4, 6, 8, 10, 12 setae on the exopods of the maxillipedes in the respective stages. In *Corystes* the number in stages 3–5 are 10, 12, 14. Antenna with well developed exopod and spinous process. The antennal flagellum, pleopods and long lateral spines on the abdominal somites do not usually appear until stage 3.

The telson is forked. There are five abdominal somites in addition to the telson in the first, and usually the second, stage.

The Megalopa has "feelers" on the dactyl of leg 5.

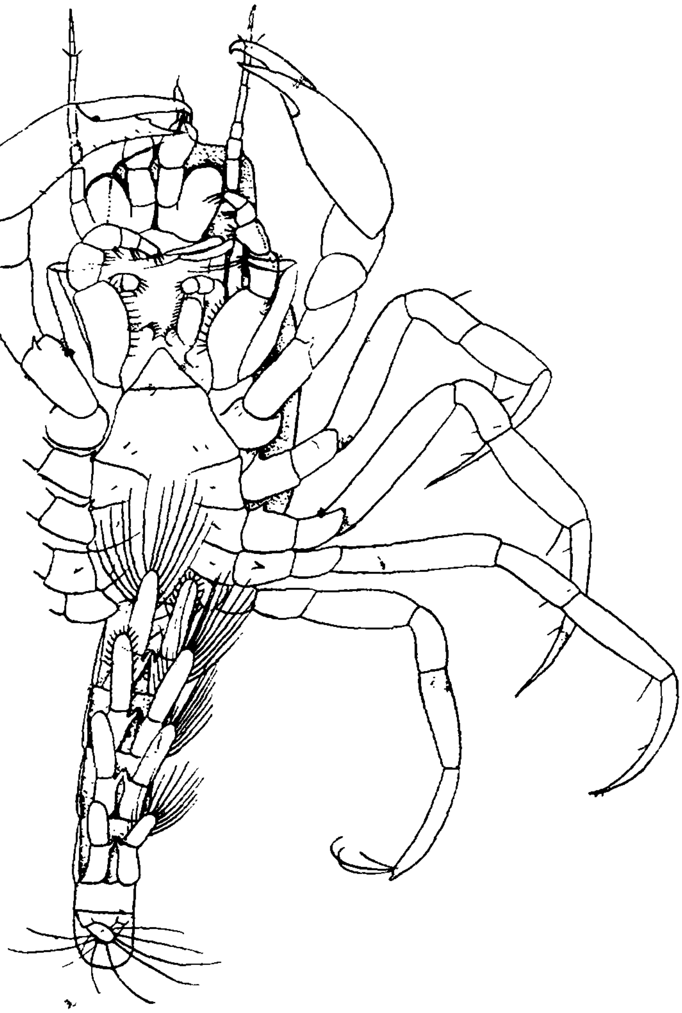

FIG. 116.—*Portunus* sp. Plymouth. Megalopa.

These feelers are three stiff setae curved at the end, one of which is toothed like a saw in the curved portion (Fig. 114, F). The presence or absence of these feeler effectively distinguishes between Brachyrhynch and Oxyrhynch Megalopas of British crabs* ; but it is not certain if the distinction holds good always. Aikawa,

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* These setae are correctly shown in Latreille's figure of the Megalopa called *Ocypode ceratophthalma* (1826, pl. 275, fig. 1).

for example (1937, fig. 26), describes a *Portunus* in which they are absent. Inasmuch as the identification is open to question, not much weight can be placed on this exception.

EXAMPLE.—*Portunus*.

There are five stages. The carapace has well developed dorsal, lateral and rostral spines. The abdomen has knobs on somites 2 and 3 ; somites 3–5 have lateral spines in late stages. The telson is forked, with three outer spines, one of which may be lost in late stages (*e.g. P. puber*) ; *there are two extra pairs of inner spines* in the last stage. The exopod of the antenna is about half the length of the spine. The palp of the maxillule is of two segments, segment 1 with a seta ; there is an outer feathered seta on the basis. Both endites of the maxilla are bilobed, and the endopod is bilobed at the end. The endopod of maxillipede 2 is of three segments.

The carapace of the Megalopa is without a dorsal spine and conspicuous protuberances. The rostrum is a small point on a rectangular projection, usually bent downwards. The uropod has 7–10 setae.

The lateral spine may be absent (*Carcinus, Portumnus*), or there may be two lateral spines (*Tetralia glaberrima*). One of the lateral spines of the telson is absent in *Corystes* and *Thia*, and one or more may be lost in some Xanthidae. It is characteristic of the Xanthidae that the exopod of the antenna should be reduced, but there are exceptions.

The Pinnotheridae differ so greatly from other Brachyrhyncha in their larvae that their relationship to the rest seems to be remote. No definition of the family as a whole can be given, since the only peculiar feature that they have in common is the great reduction of the antenna, and that reduction they share with the Leucosiidae (Oxystomata). There is a tendency to lose one or more of the spines of the carapace, and in this respect also there is resemblance to the Leucosiidae.

The telson is of two quite distinct types, the one with the fork obsolete and a median prominence, and the other with a more or less normal fork, but without outer spines. The forked telson is found in *Dissodactylus* and in three species of *Pinnotheres*, while *Pinnixa chaetopterana*, *Ostracotheres tridacnae* and four species of *Pinnotheres* have the trilobed type. In a *Pinnixa* of unknown species (Faxon, 1879*a*) the telson has no median prominence, but otherwise is like that of *P. chaetopterana*, which has one. In these two species somite 5 is greatly expanded—a feature otherwise found only in Hymenosomidae (*e.g. Elamena*). The Hymenosomidae are characterized by the reduction of endite 1 of the maxilla, and in this respect they differ from Leucosiidae and Pinnotheridae; but all alike have this endite undivided.

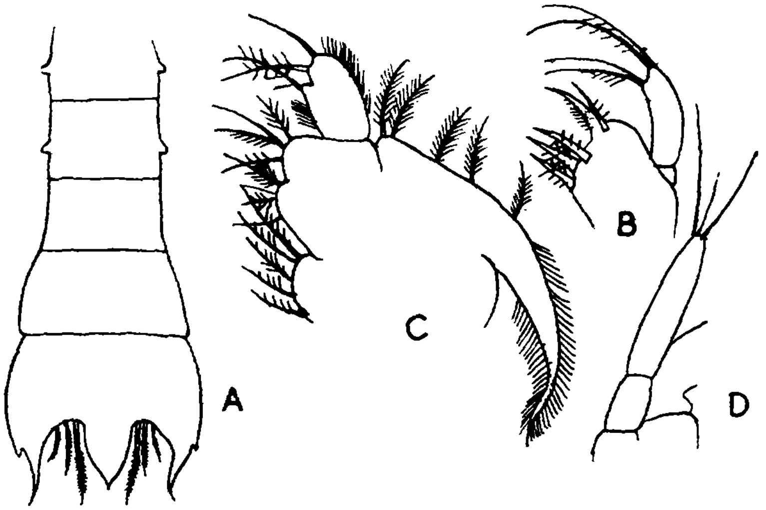

FIG. 117.—*Pinnotheres veterum*, stage 1. A. Abdomen. B. Part of maxillule. C. Maxilla. D. Maxillipede 2.

In *P. chaetopterana* the last Zoea is said to moult direct to the young crab (Faxon). The only Megalopa described is that of *P. veterum* (Lebour, 1928, p. 537). It lacks the feelers on leg 5 found in all other Brachyrhyncha and closely resembles in this and other respects the Megalopa of *Ebalia* (Lebour, 1928*a*). Miss Lebour has drawn attention to the points of agreement between the two genera. It would seem that the larval characters point to a relationship between Pinnotheridae, Leucosiidae and Hymenosomidae, and also suggests that the genus *Pinnotheres* should be divided.

OXYRHYNCHA

See Cano, 1893*b*; Lebour, 1927, 1928*b*.

Rathbun (1925) follows Borradaile in including the Hymenosomidae in the Oxyrhyncha. The larvae of four genera of this family are known, and they have no apparent affinity with the other two families—Maiidae and Parthenopidae. Rather they seem to be related to the Leucosiidae and Pinnotheridae. In *Paranaxia serpulifera* (Pisinae) the young are hatched in the form of the parent (Rathbun, 1914, p. 661). This is the only case of direct development known among marine Brachyura (excluding Dromiacea) (see p. 5). While there appears to be no doubt that this crab is correctly placed in the Pisinae, its generic name (*Naxia*, *Paranaxia* or *Naxioides* seems to be a matter of choice.

The following definition is taken from Miss Lebour: Prezoëa with the usual seven embryonic spines on each side of telson, two on antennule and four on antennae, with simple sheaths for spinous process and flagellum. Two zoeal stages, one Megalopa. First Zoea far forward in development, showing antennal flagellum and pleopods. Lateral spines on abdominal somites 3 to 5. Horns of fork of telson with spicules. Megalopa with rostrum; without feelers on last joint of last legs.

The differences in the Zoea from the Brachyrhyncha are, in fact, only those which accompany some abbreviation in development, but they are distinctive of all British species. As Miss Lebour has pointed out to me, the combination of four setae on the exopods of the maxillipedes with small pleopods, and of six setae with long pleopods, which is found in stages 1 and 2 of British Oxyrhyncha distinguishes them at once from Brachyrhyncha.

The definition does not apply to the genus *Lambrus* (Parthenopidae), which has a simple Zoea having no character to distinguish it from a Brachyrhynch (Aikawa, 1937, *L. validus*).* Similarly *Paratymolus pubescens* and *Tiarinia cornigera* have neither leg rudiments nor pleopods when hatched. It seems impossible to find any character, or combination of characters, which will, without fail, distinguish the Oxyrhynch from the Brachyrhynch Zoea.

The Zoea of *Chionoecetes opilio* has been described by Aikawa (1937, Prezoea) and Stephensen (1935, last Zoea from plankton). Aikawa's identification must be accepted, as he had eggs and parent, but the Prezoea had no appendages behind maxillipede 2, and apparently no prezoeal spines, so that it does not fit the definition given above. Stephensen's Zoea cannot belong to the same species and cannot very well be an Oxyrhynch, owing to the numerous setae on the exopods. As the only other Brachyura found in the region of West Greenland belong to *Hyas*, and this Zoea certainly does not, its identity remains a mystery.

EXAMPLES.

1. *Maia squinado.*—Maiidae.

There are two zoeal stages only. The carapace has dorsal, lateral and rostral spines. The abdomen has lateral knobs on somite 2 only, and somite 6 is fused with the telson in stage 1, but free in stage 2. Somites 3–5 have short lateral spines. The telson fork is rather narrow, with three outer spines, and spine 4 is covered with small spicules. The antennal spine is nearly as long as the rostrum, and the exopod about half as long as the spine, with three terminal setae ; the endopod is present on hatching. The maxillule has a two-segmented endopod and no outer seta on the basis. The coxal and basal endites of the maxilla are bilobed, but

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* The Parthenopidae have been variously placed. Miss Rathbun regards them as Oxyrhyncha ; Ortmann as Brachyrhyncha (Cyclometopa) ; Strahl as Oxystomata ; Flipse as transitional from Oxyrhyncha to Brachyrhyncha.

the endopod is not cleft at the end. The exopods of the maxillipedes have four setae in stage 1 and six (or rarely five) in stage 2. Rudiments of the legs are present in stage 1.

The Megalopa has no spines on the carapace, but many protuberances. The tips of legs 2–5 are pointed and armed with short spines. The uropods bear five setae.*

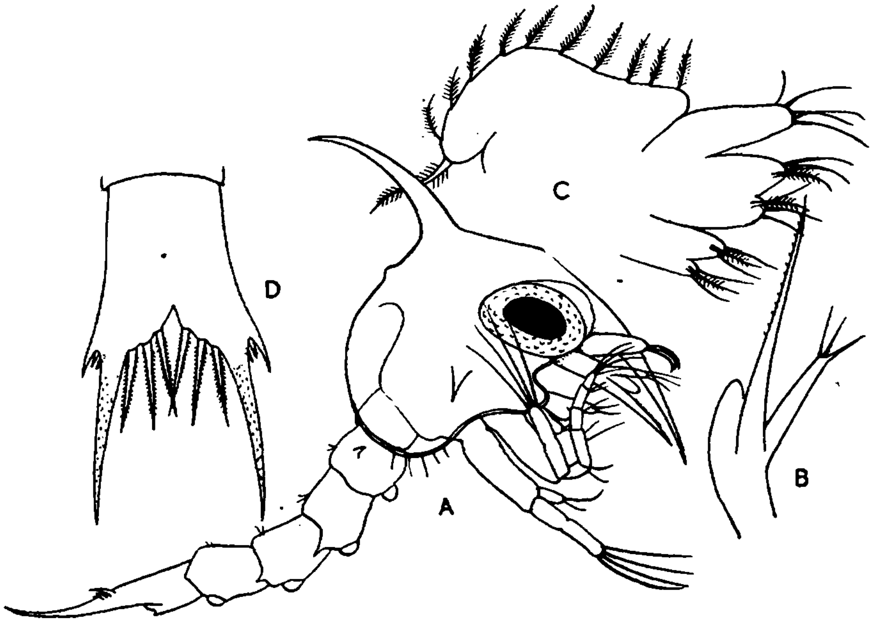

Fig. 118.—*Maia squinado*, stage 1. B. Antenna. C. Maxilla. D. Telson.

In *Inachus* and *Macropodia* rostral and lateral spines are absent. *Maia* may be regarded as one of the more primitive Oxyrhynch Zoeas, since in *Inachus* and *Macropodia* there is also a reduction in the abdominal somites, and in some other forms the number of outer spines on the telson is reduced.

2. *Elamena mathaei*.—Hymenosomidae.

The carapace has no dorsal or lateral spines, and the rostrum is very short. The abdomen has no lateral knobs, but somites 2–4 have lateral ridges, the ridge of

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* The arrangement of setae on the pleopods in the Megalopa of *Macropodia* differs from that of Brachyrhyncha, see p. 155.

somite 5 very broad and produced backwards on either side of the telson. The telson is fused with somite 5, and is parallel-sided, with six terminal spines within the narrow fork; there are no outer spines. The antenna is reduced to a minute knob. The endopod of the maxillule is of two segments, with a seta on segment 1.

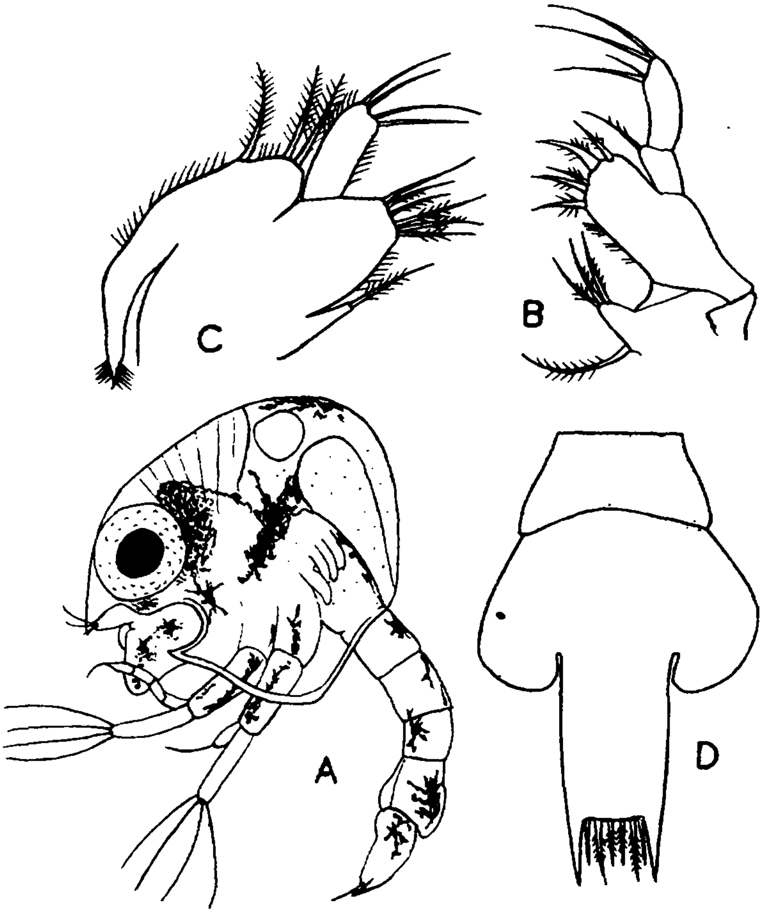

FIG. 119.—*Elamena mathaei*, stage 1. B. Maxillule. C. Maxilla. D. Telson.

In the maxilla the proximal endite is vestigial, and endite 2 is not bilobed. The endopod of maxillipede 2 is of two segments only. There are rudiments of maxillipede 3 and the legs.

It will be seen that this Zoea has little in common with the typical Oxyrhynch Zoea, and provides strong evidence against the inclusion of the Hymenosomidae in the Oxyrhyncha.

OXYSTOMATA

It is generally accepted that the Oxystomata are true crabs and that the group contains the families Dorippidae, Calappidae, and Leucosiidae. The Raninidae were removed by Bourne (1922) to a new group Gymnopleura, but were still included in Oxystomata by Balss in 1927. The Dorippidae were regarded by Bouvier and by Ihle as having relation with the Dromiacea and descended from the Dynomenidae. The Calappidae Ihle (1918) considered to be more primitive than the Leucosiidae and sprung from a common stem with the Dorippidae. Miss Lebour (1928*b*, p. 538) placed *Ebalia*, the only British Oxystome genus, between *Pinnotheres* and the Oxyrhyncha, to emphasize the resemblance between larva and Megalopa of the two genera.

The group seems to be a most unnatural one* founded, in the main, upon structures which may owe their similarity to convergence due to a common habit of burrowing in sand. The larvae of *Dorippe* and *Ebalia* have nothing in common but their general Brachyuran character, and cannot be nearly related. The Zoea of *Calappa* (Aikawa, 1937, p. 102) has all the characters of the Brachyrhyncha.

I am unable to carry criticism of the grouping of these families further by discussion of the adult structure, but the system cannot be very securely founded when the genus *Cymopolia* (= *Palicus*), which has been generally regarded as a member of the Oxystomata, and has a larva of Dorippid form, can be placed by Miss Rathbun in the Brachyrhyncha (1918, p. 182).

DORIPPIDAE.

See Menon, 1937 ; Aikawa, 1937.

EXAMPLE.—*Ethusa.*

There are four stages. The carapace has very long

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* Miers, 1886, p. ix : " A somewhat heterogeneous group, which it will perhaps be found hereafter impossible to sustain in its entirety."

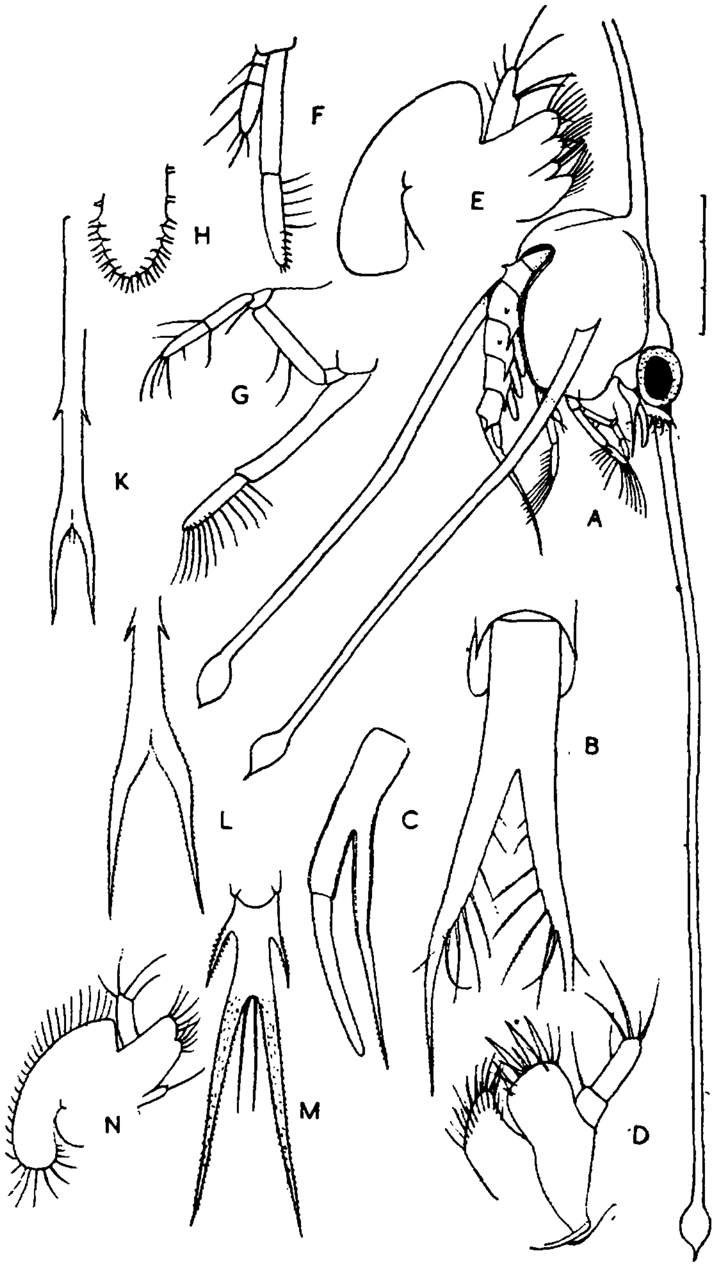

FIG. 120.—A–H. Brachyuran Zoea (*Pluteocaris*, Claus). "Discovery" Station 1578: A, Last Zoea, with scale of 3 mm.; B, Telson; C, Antenna; D, Maxillule; E, Maxilla, setae of exopod omitted; F, Maxillipede 2; G, Maxillipede 1; H, End of exopod, maxillipede 2. K. *Zoea clavata*, Leach (type), telson. L. Telson of Zoea allied to *Z. clavata*, with expanded ends to the spines. "Discovery" Station 254. M. *Dorippe* ?, Barrier Reef, Telson. N. Maxilla of same.

dorsal and rostral but no lateral spines. The abdomen is very slender, of five somites and telson in stage 1, and with lateral knobs on somite 2. There are no lateral spines. The telson has one pair of lateral spines, and spine 4 is extremely long and prickly, forming a narrow fork, within which is one pair of setae. Spine and exopod of the antenna are equally long. The maxillule has an unsegmented endopod and no outer seta. The proximal endite of the maxilla is much reduced, and not bilobed—as in the Hymenosomidae. The endopod of maxillipede 2 is of two segments, and the exopods have 4, 6, 8, 10 setae in stages 1–4.

Whereas in *Dorippe* and *Ethusa* the telson in front of the lateral spines is very short (Fig. 120, M), there are Zoeas with exactly the same kind of forked telson, but with the anterior part very much extended (see Gurney, 1924*c*, fig. 77). Leach's *Zoea clavata* has the same form of telson, and is doubtless closely related, but its long carapace spines have spoon-like expansions at the ends. A very similar form, from "Discovery" station 254, with expanded ends to the spines, has the same form of telson, but has lost the inner pair of setae (Fig. 120, L). It is remarkable that spines with expanded ends should be found in other Zoeas not related to the Dorippidae. I have given figures of a very large and striking form of this kind from "Discovery" station 1578 (11° 25′ S., 42° 03′ E.), in which the rostrum is about 18 mm. long. The telson and appendages show that it is not a Dorippid, and I am unable to say to what group it belongs. It is closely related to the form described by Claus as *Pluteocaris* (1876, pl. xii).* Another similar form was figured by Dohrn (1870*c*), and was given the name *Fissocaris*† by Claus (1876, p. 65).

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* Williamson (1915, p. 567) states that this is the same as *Zoea boscii*, Guérin-Méneville.

† I regret that this was omitted from the list of larval genera in my bibliography.

LEUCOSIIDAE.

See Lebour, 1928*a*, *b*; Menon, 1937.

EXAMPLE.—*Ebalia* (*tuberosa*).

There are four stages. The Zoea curls up into a ball, and has rudimentary rostral and lateral spines only. The abdomen has five somites, and telson, in all stages, with lateral knobs on somites 2 and 3. The telson is a triangular plate with posterior margin nearly straight, and with six spines in the middle. There may be one or more small spines at the angles. The antenna is reduced to a small stump. The endopod of the maxillule is unsegmented, and there is a small outer seta on the basis. The proximal lacinia of the maxilla is small and entire, but the distal one may be bilobed or entire. Maxillipede 2 has the endopod unsegmented and very small. The exopods have 4, 6, 6, 8 setae in successive stages (Lebour). There are only four pairs of pleopods (Lebour).

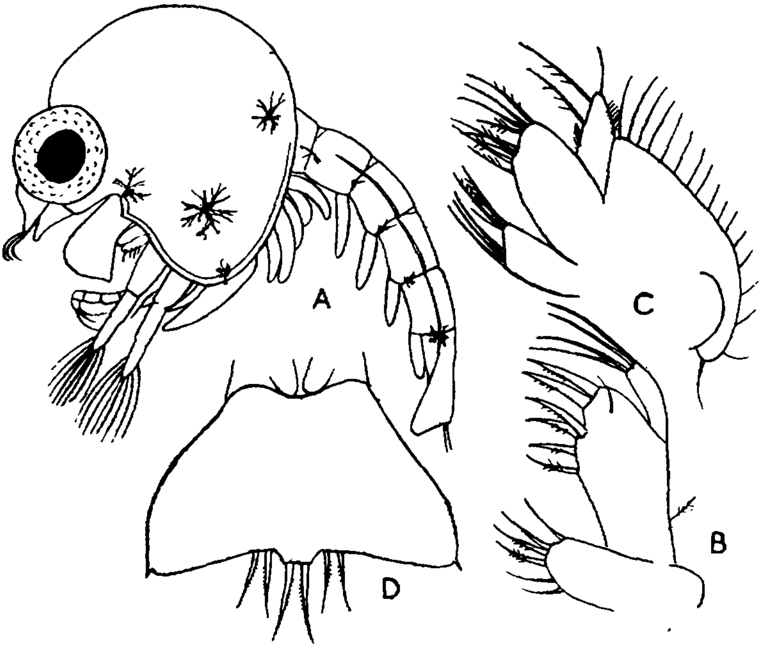

FIG. 121.—*Ebalia* sp. Plymouth. Last Zoea. B. Maxillule. C. Maxilla. D. Telson.

The Megalopa has no rostrum or dorsal spines. Leg 5 has no feelers. There are five pairs of pleopods, the last (uropods) with six setae.

The general form and the appendages are very much the same throughout the Leucosiidae, but the carapace may have well-developed dorsal and rostral spines (*Philyra*) or rostral and lateral (*Leucosia*). The abdominal somites may have lateral ridges. The Megalopa of *Philyra* has a dorsal spine and a pair of peculiar blunt-ended anterior dorsal processes.

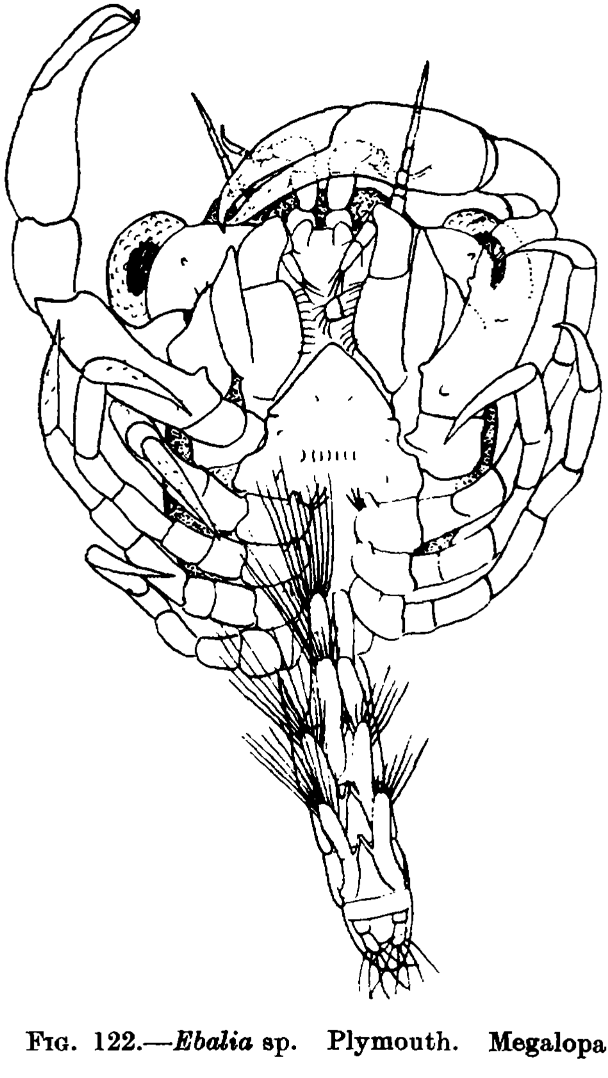

FIG. 122.—*Ebalia* sp. Plymouth. Megalopa.

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