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CRUSTACEAN METAMORPHOSES

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U.S. Department of Agriculture



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INTRODUCTION

The review of crustacean metamorphoses given in this paper contains little that will be new to carcinologists, except perhaps a few accompanying unorthodox ideas. The paper is written for students in general zoology and is recommended reading for entomologists, who commonly think of metamorphosis as a phenomenon pertaining particularly to insects. It is true that the metamorphoses of insects and of crustaceans have no relation to each other, and have little in common, but a preliminary discussion of both will help in arriving at a general understanding of the nature of metamorphosis as it occurs in the arthropods.

The first treatise on metamorphosis was written by Ovid in about the year A.D. 7, but the metamorphoses that Ovid described were mostly the transformations of members of the human species into animals, trees, or rocks, willed by the ancient gods or goddesses in revenge against some mortal that had offended them. The metamorphoses imposed on animals by nature are not punishments, extreme as they may be in some cases, but are beneficent changes of form to better accommodate the individuals of a species temporarily to a more advantageous way of living. The young butterfly, for example, transformed in the egg into a wormlike caterpillar, is not an elegant creature as are its parents, but from a practical standpoint the caterpillar is perfectly adapted to its chief function, which is that of feeding.

The metamorphoses of Crustacea differ essentially from those of insects in that they pertain to a much earlier stage of development. The young insect hatches from the egg usually with the definitive number of body segments. The insects are thus *epimorphic*; but if the young insect has taken on a metamorphosed form in its embryonic development, it appears on hatching as a creature quite different from its parents. Yet a caterpillar, for example, is actually a winged juvenile stage of the butterfly corresponding with the so-called nymphal stage

of a grasshopper. The principal difference between the two is that the wings of the young grasshopper develop externally, and those of the caterpillar grow internally within pockets of the skin beneath the cuticle. Likewise, a "legless" fly maggot has legs developing in pouches of the skin covered by the cuticle. A young grasshopper goes over directly into a mature grasshopper; the caterpillar, the maggot, and others of their kind, when full grown with plenty of food stored in their bodies, must undergo a second transformation in a pupal stage to be restored to the parental form. This is the usual course of metamorphosis among the insects.

Most of the Crustacea, on the other hand, hatch at an early stage of embryonic development, though at varying periods of immaturity, when they have only a few body segments and corresponding appendages. During their development after hatching they successively add new segments and appendages until the definitive number is attained. The majority of crustaceans are thus *anamorphic* in their manner of postembryonic growth, though a few are epimorphic.

Anamorphosis involves a change of form during development, but it is merely a way of growing, common to crustaceans, diplopods, and some chilopods. It should not be confused with changes of form that have nothing to do with progressive development toward the adult; such changes constitute a true *metamorphosis*. The metamorphoses of Crustacea are changes of form that the growing animal may take on at successive stages of its anamorphic growth, including the sexually mature stage of many parasitic species. In such cases, metamorphosis has been superposed on anamorphosis. As Gurney (1942) has said, "it may be assumed that development in the 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 the larva and adult." Gurney notes an apparent exception to this rule in the Euphausiacea and some Penaeidae, in which the larva and the adult lead much the same kind of life. The successive phases of development in these two groups, however, are mainly stages of anamorphic growth; their only metamorphosis is the adaptation of the larval appendages for swimming.

Insect larvae may undergo metamorphic changes of form during their growth, but with the insects this larval *heteromorphosis*, commonly called "hypermetamorphosis," affects the fully segmented young insect, and is therefore not comparable to the heteromorphic larval growth of most Crustacea. Some metamorphosed young insects trans-

form directly into the adult, but most of them first undergo a reconstruction in a special, proimaginal pupal stage. Among the Crustacea there is no transformation stage strictly comparable to the insect pupa.

True metamorphic forms are not recapitulations of phylogenetic stages in the evolution of a species. An insect larva, though often wormlike in appearance, does not represent a worm stage in the ancestry of insects. A caterpillar has a modern insect head and mouth parts, a well-developed tracheal system, and wings growing beneath its cuticle. No worm, ancestral or otherwise, was ever thus equipped. Among the Crustacea also most juvenile forms assumed during the larval growth are temporary adaptations to a changed mode of life and are not phylogenetic recapitulations. Yet, it is true that former ancestral characters discarded somewhere along the line of evolution may appear in the ontogeny of the individual, and it is often difficult to determine what phases of development are recapitulatory and what are metamorphic aberrations. The following hypothetical example will make clear the distinction between the two, and will lead to a practical definition of metamorphosis.

If the eggs of birds regularly hatched into reptilelike creatures, which later transformed into feathered fowls, the change of form would literally be a metamorphosis; but, since birds have been derived from reptilian ancestors, it might be specifically a case of phylogenetic recapitulation. On the other hand, if there issued from the bird's egg a creature having no relation to anything in the avian line of adult evolution, but which still finally transformed into a bird, the change of form would be one of quite a different nature, and it is this kind of change that will be regarded as metamorphic in the following discussions. As here defined, therefore, *metamorphosis* is a structural change at any time in the life history of an animal that may be regarded as an aberration from the ancestral direct line of adult development which followed approximately the phylogenetic course of evolution of the species. In this case metamorphosis may affect the embryo, the larva, or the adult. Simple development without metamorphic interpolations might then be termed *orthomorphosis*.

In the higher Crustacea there is a tendency for hatching to take place at later and later stages of ontogeny, leaving a correspondingly lesser amount of development to be accomplished after the larva leaves the egg. Finally a condition is reached when body segmentation and appendage formation are complete or almost so at hatching; the animal then becomes epimorphic in its development. In an epimorphic arthropod, the embryonic development may proceed by the method of anamorphosis, or the entire body may be first laid down as a germ band.

In the second case segmentation appears later, usually progressing from before backward, suggesting that it represents a former anamorphic mode of segment formation in which the anterior segments are the oldest. Since anamorphic growth, either in the larva or the embryo, is characteristic of the annelid worms and recurs in so many of the arthropods, it was probably the primitive method of growth in the annulate animals.

The most immature larval form among the arthropods is the crustacean nauplius. For practicable purposes early hatching must be given up by terrestrial animals, unless they go back to the water to lay their eggs, as do the land crabs, frogs, and toads. The anamorphic myriapods do not quit the egg until they have acquired the adult type of structure and are equipped with a sufficient number of legs for terrestrial locomotion. The completely epimorphic spiders and insects are best fitted to cope at once on hatching with the conditions of their environment, and they have become the most successful of the land arthropods. Though some insects lay their eggs in the water and the young are aquatic, they are simply terrestrial forms that have become secondarily adapted in the larval stage for life in the water; they hatch at the same stage as their relatives on land.

The Crustacea are primarily aquatic animals; only a few have become adapted to a permanent life on land. The eggs of most species are laid in the water, and the newly hatched young must be capable of swimming; the adults can later adopt a bottom habitat if they acquire ambulatory legs. Considering the uniformity of the water environment of a swimming larva, there is relatively little inducement for a young aquatic animal to undergo adaptive metamorphoses. The metamorphoses of most crustacean larvae, therefore, are relatively simple as compared with those of insect larvae, which have a great diversity of habitats open to them. Parasitic crustaceans, however, are a conspicuous exception to this generalization.

As a rule small animals in the water are eaten by larger animals, but the small creatures have one recourse against their possible predators and that is to become parasitic on them. Parasites, however, have to be structurally adapted to a parasitic life, and consequently most parasites undergo metamorphic changes. Many of the smaller crustaceans have adopted parasitism, and the most extreme degrees of crustacean metamorphosis are found among such species, especially if the adults themselves remain parasites. Such adults in some cases have lost all resemblance to the ancestral forms of their race, even every mark of their crustacean ancestry. Moralists may cite the "degeneration" of such parasites as a warning of what parasitism may

lead to, but actually parasites are highly specialized for the life they lead by a simplification of structure and the elimination of all unnecessary organs, which were indispensable to their free-living ancestors. In fact, no sympathy need be wasted on "degenerate" parasites; give them credit for having found a simple and easy way of living, though at the expense of another creature. They have discarded all useless equipment, and some of them have devised most ingenious ways of attacking the host.

The control of metamorphosis by hormones has been extensively studied in insects, but apparently no comparable studies have been made on the role of hormones in the metamorphosis of crustaceans. It is well known that hormones are produced in the eyestalks of decapods, and the source of the eyestalk hormones has usually been referred to two organs known as the *sinus gland* and the *X organ*. However, from recent investigations (see Bliss and Welsh, 1952; Passano, 1953) it is now known that the so-called sinus "gland" is not a gland but a complex of the enlarged ends of nerve fibers proceeding from the X organ and from numerous neurosecretory cells in the brain, in the ganglia of the optic lobe, and in the thoracic ganglia. The sinus "gland" is therefore a receiving and distributing center for various hormones. Functions that have been attributed to these hormones include the movement of pigment in the compound eye, regulation of chromatophore activity in the integument, control of moulting, and the rate of development of the ovaries. Knowles (1953) gives evidence that the chromatophores are activated also by neurosecretory cells in the region of the tritocerebral commissure and the postcommissural nerves. The control of moulting by lengthening the period between moults was attributed by Passano to the X organ, which is itself a neurosecretory tissue in the proximal ventral part of the medulla terminalis of the optic lobe. Removal of both sinus "glands" has no effect on moulting since the hormone can escape from the cut ends of the nerves. Panouse (1946) also, in a study of *Leander*, had claimed that the "sinus gland" produces a hormone that normally blocks the growth of tissues and thus causes a lengthening of the intermoult period and retards the maturing of the ovaries.

From later work by Gabe (1953) and Echalier (1954), however, it now appears that moulting, at least in the Malacostraca, is controlled by a pair of ductless glands in the antenno-maxillary region. These glands, discovered by Gabe, are named by him the Y organs, and were demonstrated to be present in 58 malacostracan species, ranging from *Nebalia* to the decapods and stomatopods. In species in which the excretory gland is maxillary, the Y organs are in the antennal seg-

ment ; in those having antennal glands they lie in the second maxillary segment. Each gland is implanted on the epidermis by an enlarged base and is innervated from the suboesophageal ganglion ; in form it is conical, lenticular, or foliaceous. From their histological structure and changes during the intermoult period, Gabe shows that the Y organs are comparable to the thoracic endocrine glands of holometabolous insects, and he suggests that they have something to do with moulting. Following this suggestion, Echali er (1954) made experimental tests by removing the organs. He found that bilateral ablation of the glands, when not made too late after they had already discharged their secretion, resulted in a very great lengthening of the intermoult period, far in excess of the usual time between moults. Echali er, therefore, contends that the Y organs are crustacean endocrine glands for the control of moulting. That they do not disappear in the adult as do the thoracic glands of insects, Gabe points out, follows from the fact that the crustaceans continue to moult in the adult stage.

I. EVOLUTION OF THE ARTHROPODS

In any discussion of arthropod metamorphosis the question of recapitulation always comes up in relation to the larval forms. If there is any ancestral recapitulation in ontogeny, it then becomes necessary to have at least a theoretical concept of the evolution of the arthropods and some idea of what ancestral forms they had that might be recapitulated in the development of the individual.

The evolutionary origin of the arthropods is hidden in remote Pre-Cambrian times, so probably we shall never know the facts from visual evidence. There is, however, ample evidence from a study of modern forms to indicate that the early progenitors of the arthropods were closely related to the progenitors of the annelid worms, and that these two groups of annulate animals had a common ancestor. The fundamental characters preserved in the annelid-arthropod organization are: an elongate segmented body, an alimentary canal extending through the length of the body, a paired ventral nerve cord with segmental ganglia, a somatic musculature, and mesodermal coelomic sacs. We may therefore visualize the primitive annulate as a very simple, wormlike creature having these features. The mode of development was anamorphic, new segments being formed in a subterminal zone of growth. From this primitive segmented worm the annelids have been directly evolved with little addition other than the development of segmental groups of lateral bristles, which in the polychaetes have been carried out on movable lateral lobes of the segments, the so-called parapodia, that serve for swimming and burrowing.

By a different type of specialization for locomotion, members of another branch from the ancestral stock developed ventrolateral, lobelike outgrowths of the body segments, and thus became walking animals. These primitive legs eventually evolved into the jointed appendages of modern arthropods, the lobelike origin of which is still recapitulated in the embryo. At the lobopod stage of evolution (fig. 1 A) the animals resembled a modern onychophoran, and are

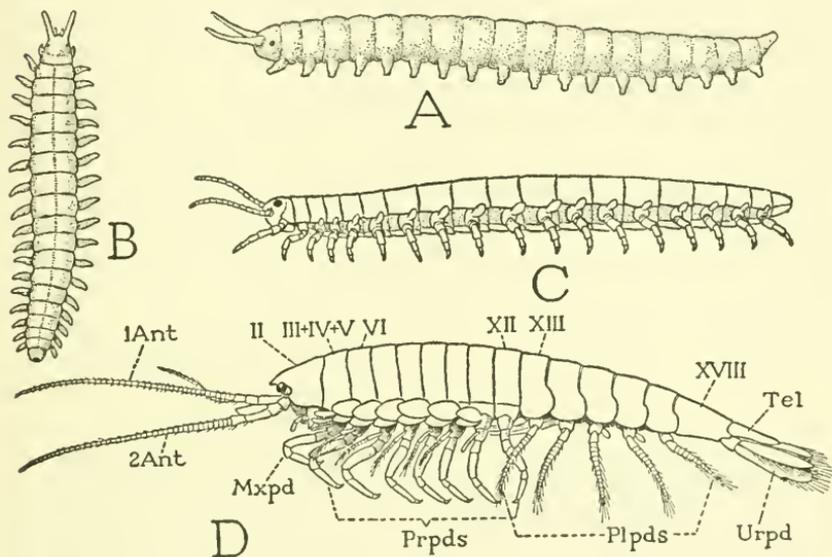


FIG. 1.—Theoretical evolutionary stages of the arthropods.

A, a primitive lobopod, common ancestral form of the Onychophora and Arthropoda. B, a derived form with longer and slenderer legs. C, a primitive arthropod with sclerotized integument, jointed legs, and gill lobes on the coxae. D, a fairly generalized modern crustacean, *Anaspides tasmaniae*.

1Ant, first antenna; 2Ant, second antenna; Mxpd, maxilliped; Plpds, pleopods; Prpds, pereopods; Tel, telson; Urpds, uropod; II-XVIII, body segments.

perhaps represented by such fossils as the Pre-Cambrian *Xenusion* and the Cambrian *Aysheaia*. The modern Onychophora are probably direct descendants from these early lobopods, and have structurally not progressed much beyond them. Others, however, acquired a sclerotization of the integument, which allowed the legs to become longer and slenderer (B), and finally jointed (C) for more efficient action in locomotion. These jointed-legged forms were the first true arthropods. The segmentation of the legs early took on a definite pattern, which has been preserved in both fossil and living arthropods, most of which retained the walking mode of locomotion, though some may also swim or fly.

From these early Pre-Cambrian arthropods (fig. 1 C) in which all the appendages were fully segmented ambulatory legs, the trilobites branched off by specialization of the body structure, but with no essential differentiation of the appendages. In the other derivative groups, however, the appendages took on different forms adapting them to various uses, but the number retained for walking is characteristic of the several modern arthropod groups. The myriapods use most of their postoral appendages for progression; the Malacostraca (D) use five or more pairs for walking, except where some of these have been modified for grasping; *Limulus* and the arachnids use four pairs, the insects three. That the ambulatory limbs, when limited in number, should in all cases be those of the middle part of the body, though not necessarily the same appendages, follows from the mechanical necessity of balance. The anterior appendages become sensory and gnathal in function; those of the abdomen have been modified for various purposes, such as respiration, silk spinning, copulation, egg laying, or swimming.

The modern arthropods comprise two distinct groups, the Chelicerata and the Mandibulata. In the chelicerates the first postoral appendages are a pair of pincerlike chelicerae that serve for feeding, and the ancestors of this group were probably closely related to the ancestors of the trilobites. The principal feeding organs of the mandibulates are a pair of jaws, the mandibles, formed of the second postoral appendages. The Mandibulata, including the crustaceans, the myriapods, and the insects, are certainly a monophyletic group, but their origin and their interrelationships are obscure.

Among the Crustacea the malacostracan type of organization (fig. 1 D), in which the thoracic appendages are typically ambulatory and the abdominal appendages natatory, would appear to be more primitive than the entomostracan types because it more closely conforms with the structure of other arthropods, and could be more directly derived from that of a primitive walking arthropod (C). The entomostracan forms, therefore, have been secondarily reconstructed for a purely pelagic life by a readaptation of the thoracic appendages for swimming.

If we accept the premise that the original arthropod (fig. 1 C) was a simple animal with jointed legs along the entire length of a uniformly segmented body, the crustaceans were derived from this common arthropod ancestor by specializations that established the generalized crustacean structure (D). Developmental recapitulation of adult crustacean structures, therefore, can go back only to the beginning of adult crustacean evolution. The embryo, however, starts its development from a single cell and the free larva completes development

up to the adult. The embryo and the early larva, therefore, represent pre-crustacean stages of arthropod evolution. The embryo, however, must reproduce its parental form. Hence the crustacean characters appear at a very early stage of ontogeny, but the resulting embryonic or larval stages are not recapitulations of adult crustacean evolution. The crustacean characters are simply precociously imposed on the anamorphic stages of ontogeny. Finally, if the embryo is set free as a larva at an early stage of development, it must be structurally adapted to a free life, and in its subsequent growth other adaptations may be necessary. Thus it comes about that metamorphosis still further complicates the course of ontogeny. The life histories of parasitic larvae best demonstrate that larval forms are metamorphic adaptations to a way of living, since the nonparasitic adult ancestors of such species can hardly be supposed to have had the larval form. Where a specialized adult structure has arisen since the crustaceans became crustaceans, there may be a true recapitulation of an earlier adult form, as in the megalops of the crabs. A further discussion of the nature of larval forms will be given in connection with the life history of a penaeid (p. 54).

II. THE NAUPLIUS AND THE METANAUPLIUS

Since among the crustaceans the young hatch at different periods of development, the youngest larvae may have very diverse forms in the various orders, representing different ontogenetic stages according to the degree of development they undergo within the egg. The earliest hatched larval form is the *nauplius*, which is particularly characteristic of the Entomostraca, but occurs also in the Euphausiacea and Penaeidea among the Malacostraca. The nauplius is usually followed by a *metanauplius*, which is the first stage of postembryonic growth. From the metanauplius on, development may be merely a matter of regular anamorphic growth by the successive addition of new segments and appendages, but in many species the larva takes on different forms as it develops. These ontogenetic changes differ so much in the various orders that no general description can be given, hence a discussion of them will be left to the next section of this paper. Special attention, however, must be given to the nauplius and the metanauplius.

The nauplius.—The nauplius is a minute creature, highly variable in form in different species, but typically ovoid or pyriform in shape with the larger end anterior (fig. 2 A). It has a pair of uniramous antennules, or first antenna (*1Ant*), typically biramous second antennae (*2Ant*) and mandibles (*Md*), and a median eye of two or more parts.

The antennae serve for locomotion. The internal organization includes usually an alimentary canal, a muscular system, a nervous system, and a pair of antennal excretory glands. The alimentary canal when fully developed consists of an endodermal mesenteron and an ectodermal stomodaeum and proctodaeum. The mouth is concealed above a large labrum; the anus is usually formed at a later stage. The nervous system includes three pairs of ganglia corresponding to the appendages. Though there is no visible segmentation in the ectoderm, the presence of appendages and ganglia shows that the nauplius is at

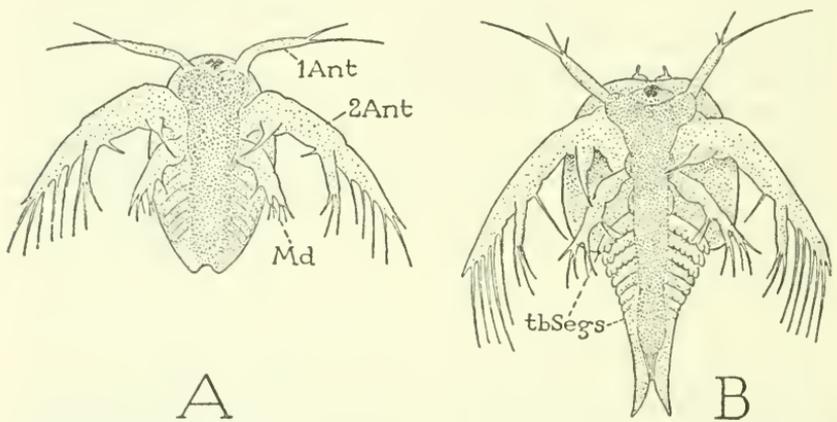


FIG. 2.—Nauplius and metanauplius of *Apus cancriformis* Bosc (from Claus, 1873).

A, nauplius, with first antennae (1Ant), second antennae (2Ant), and mandibles (Md), rudiments of teloblastic appendages seen through cuticle. B, metanauplius, appendages of teloblastic segments (tbSegs) exposed after first moult.

least a partly segmented stage of development. The region of the body behind the mandibles is that in which later the other segments will be formed, and their rudiments may be seen beneath the naupliar cuticle. When these segments are formed, however, they are generated by a different method from that which formed the anterior segments.

The nauplius is derived from a very early stage of embryonic development, represented in species that hatch at a later period by a simple embryo with rudiments of three pairs of appendages. The embryo still in the egg at this stage is clearly more simple in its structure than is the nauplius. The nauplius, therefore, is not merely an early hatched embryo—it has undergone a metamorphosis before hatching to adapt it to a free life in the water.

Our chief interest in the nauplius is the question of its theoretical value in phylogeny. The nauplius has been likened to the polychaete trochophore, and has been regarded as representing a primitive ancestral form of the Crustacea. The trochophore, however, is entirely unsegmented and does not have the internal organization of the nauplius. Later it becomes segmented by a direct division of the posterior part of its body into a few primary somites. Likewise the very young trilobite, known as a protaspis, at first shows no sign of segmentation, but it soon becomes marked by transverse grooves that divide it into a few primary segments corresponding with the segments in the prosoma of the adult. A similar early direct segmentation occurs also in the ontogeny of the Xiphosurida. The nauplius, therefore, would appear to represent the same stage of primary segmentation in crustacean ontogeny, though metamerism has not yet affected the ectoderm. It is reasonable then to infer, as contended by Iwanoff (1928), that the first somites in both the annelids and the arthropods were formed directly in the previously unsegmented body of the animal. The later extension of the body took place by the teloblastic generation of secondary somites from a subterminal zone of growth. The annelid and arthropod ancestors did not diverge until this method of anamorphic growth was fully established.

While the three larval forms discussed above do have a basic similarity of structure, which is primitive, it is evident that distinctive characters of more recent phylogenetic evolution have been impressed separately on each. The protaspis shows distinctly the definitive trilobite type of structure, the nauplius is clearly a crustacean, the trochophore is a young worm. The trochophore and the nauplius, moreover, are adapted in quite different ways for swimming at an early ontogenetic stage. The trochophore is not an adult ancestral form of the annelids, nor is the nauplius an ancestral form of the Crustacea.

The metanauplius.—The nauplius is the direct product of embryonic development. The further growth of the larva, or of the embryo if hatching occurs at a later stage, proceeds from a subterminal *zone of growth*, which becomes active before the naupliar cuticle is shed, so that rudiments of the new segments may be seen in the posterior part of the body of the nauplius (fig. 2 A). In the metanauplius (B), which appears after the last ecdysis of the nauplius, the posterior part of the body is much lengthened; it is now distinctly segmented and bears the rudiments of several pairs of new appendages. The postmandibular somites are the teloblastic segments (*tbSegs*).

Most studies that have been made on the larval development of Crustacea describe and picture the newly forming postnaupliar somites and appendages as they appear externally, without giving any information as to how they are formed. A paper by Fränsemeier (1939), however, describes the segment formation in the free-swimming metanauplius of the branchiopod *Artemia salina*, and papers by Sollaud (1923) and by Manton (1928, 1934) give details of the corresponding segmentation in the embryos of *Leander*, *Hemimysis*, and *Nebalia*.

In the anterior part of the nauplius the embryonic ectoderm is already differentiated into the tissues derived from it, and the mesoderm has been formed from the embryonic mesoblasts. The ectoderm of the body region behind the mandibles, however, is still undifferentiated and there is here no mesoderm distinguishable at this stage. At the posterior end of the body of *Artemia* the ectoderm forms a circumanal fold, the cells of which are the *ectodermal teloblasts* that will form the ectoderm of the new segments. From the ectodermal teloblasts, according to Fränsemeier, cells are given off into the interior of the body that become the *mesodermal teloblasts*, which will generate the secondary mesoderm. The naupliar mesoderm and the postnaupliar mesoderm of *Artemia* are thus distinct in their origin, though the formation of the second takes place 10 to 15 hours before the hatching of the nauplius. The teloblasts constitute the zone of growth, from which the new segments will be generated forward. The first segments formed from the teloblasts are said by Fränsemeier to be those of the first and second maxillae. As other segments are generated the anus-bearing region is carried posteriorly as a permanent telson. The proliferation zone remains active until the last segment is formed, when it is fully exhausted. The alimentary canal apparently simply lengthens posteriorly, the proctodaeum having been formed in the nauplius.

In the young naupliar embryo of the palemonine *Leander*, as described by Sollaud (1923), the postmandibular part of the body is a small anus-bearing lobe, or caudal papilla, which subsequently lengthens and projects free from the body in front of it and bends forward. A transverse row of large cells becomes differentiated in the ectoderm of the lobe before the anus, and later encircles the lobe. These cells are the ectodermal teloblasts. Below and a little before them is formed a corresponding ring of mesodermal teloblasts, which, according to Sollaud, are derived from the blastopore. The teloblasts generate the secondary segments in the usual manner, but in *Leander*, Sollaud says, the two maxillary segments are formed directly in the

larval body and not from the teloblasts, the first teloblastic segment being that of the first maxillipeds. In the Pericarida, however, he says the boundary between the primary tissue and the secondary tissue is between the segment of the mandibles and that of the first maxillae.

The accounts given by Manton (1928, 1934) of the embryonic process of secondary segmentation in *Hemimysis* and *Nebalia* are essentially the same as those of Sollaud for the embryo of *Leander* and of Fränsemeier for the larva of *Artemia*. Manton agrees with Fränsemeier that the teloblastic segments include both maxillary segments. In *Hemimysis*, she says, the naupliar and postnaupliar mesoderms are at first some distance apart, but later the teloblastic ectoderm and mesoderm extend forward as far as the first maxillary segment inclusive. The teloblasts of *Nebalia* are differentiated at the sides of the posterior blastoporic area, and the ectodermal teloblasts eventually form a complete circle around it. The mesodermal teloblasts, according to Manton, in agreement with Sollaud, are formed from the mesendodermal mass at the blastopore; Fränsemeier says they are proliferated from the ectodermal teloblasts. The ectodermal teloblasts, according to Manton, join the naupliar ectoderm between the mandibular and first maxillary segments, so that "all segments between the mandibular segment and the telson are formed by the teloblasts." The rudiment of each segment arises from one transverse row of descendants from the original ectodermal and mesodermal teloblasts. When the last abdominal segment is completed the teloblasts disappear in both *Hemimysis* and *Nebalia*.

Since the teloblastic generation of secondary somites added to the primary segmented body of the young larva or embryo is characteristic of the annelid worms and recurs in many of the arthropods, it must have been a way of lengthening the body developed in the very primitive wormlike ancestors of the two groups. The annelids and the arthropods, therefore, did not diverge until this method of growth was well established. Elsewhere the writer (1938) has suggested that telogenesis may have originated as a means of increasing the reproductive function by distributing the germ cells from the zone of growth through a larger number of segments.

III. EXAMPLES OF CRUSTACEAN METAMORPHOSES

The metamorphoses of Crustacea are so diverse that in a brief review of the subject we can include only a few examples representative of some of the principal orders. Since crustaceans that hatch at an early stage of ontogeny go through anamorphic phases of development

by the successive addition of segments and appendages, many of their changes are merely those resulting from the anamorphic manner of growth. In nearly all cases, however, there is some degree of metamorphosis superposed on the anamorphic stages, varying from a mere adaptation of the appendages for swimming to a total reconstruction of the animal for a parasitic way of life. The most striking examples of crustacean metamorphosis, therefore, occur in parasitic species. Among the Crustacea metamorphosis evidently has been developed separately in each order, and often independently in different members of the same order. There is no type of metamorphosis characteristic of large groups of orders, as in the holometabolous orders of insects. Moreover, since crustacean metamorphosis affects the juvenile anamorphic stages, except where it is carried over into the adult, the metamorphosis of Crustacea has no relation to that of the epimorphic insects. A brief but interesting account of the life-history problems of crustacean larvae is given by Gurney (1926).

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BRANCHIOPODA

The branchiopods undergo few changes during their larval development that are not the result of simple anamorphic growth by which the body and the appendages are completed and brought to the adult condition through successive instars. The branchiopods are thus of interest in showing a simple progressive development from nauplius to adult, which is accompanied, however, by a specialization of the postgnathal appendages for swimming. As an example we may take the life history of *Branchinecta occidentalis* Dodds as described by Heath (1924).

The newly hatched larva of *Branchinecta* is a typical nauplius (fig. 3 A) with three pairs of appendages, a median simple eye, and a large labrum, but the oval, unsegmented posterior part of the body is more than usually constricted from the forepart. The large second antennae are the principal swimming organs. Between the nauplius and the second instar, or metanauplius (B), a very considerable change takes place. Lateral compound eyes are now conspicuous by their pigmentation. The posterior part of the body has greatly lengthened, and bears rudiments of maxillulae, maxillae, and six or seven following pairs of appendages. In the third instar (C) the post-maxillary appendages have lengthened and the more anterior pairs

have taken on a leglike form; their mesal margins are indented, and each limb bears a conspicuous lobe, or flabellum, just proximal to an apical point. The body is more lengthened behind the appendages and

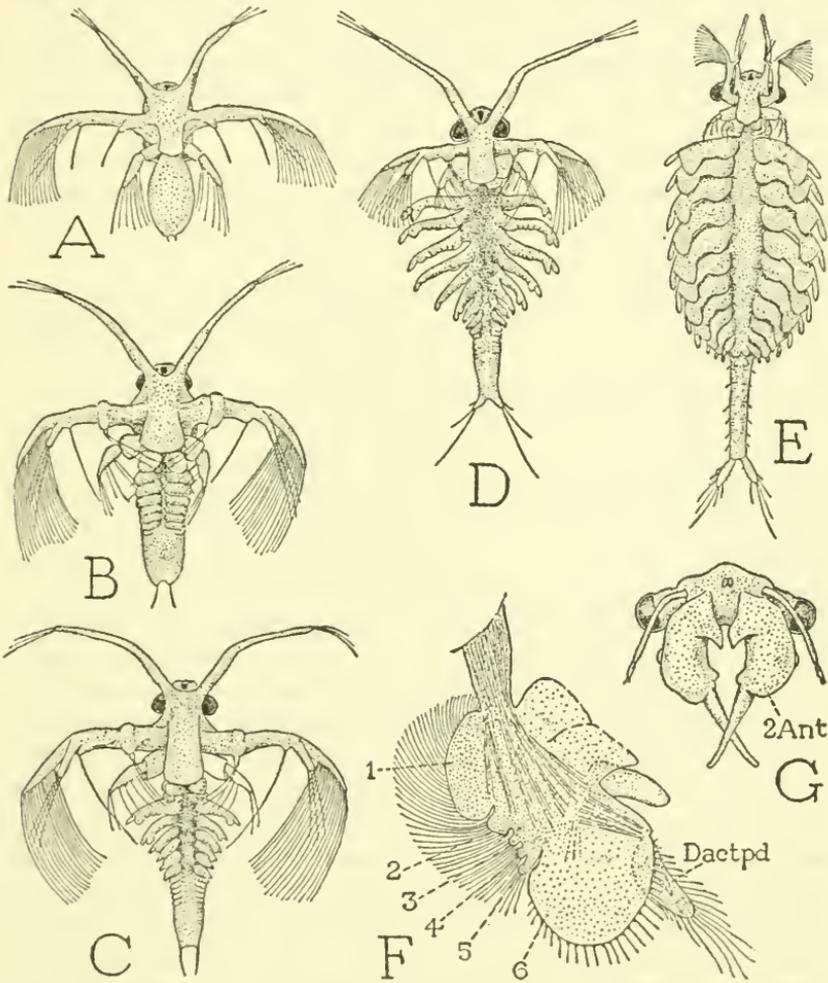


FIG. 3.—Branchiopoda. *Branchinecta occidentalis* Dodds, developmental stages (from Heath, 1924) and a thoracic limb of the adult.

A, newly hatched nauplius, length 0.4 mm. B, second instar. C, third instar. D, fifth instar. E, eighth instar, 2.9 mm. F, sixth left thoracic limb of adult male, with six endites (1-6) and a movable terminal lobe (*Dactpd*). G, head of adult male, anterior, with large second antennae (*2Ant*).

shows lines of further segmentation. After two more moults, the larva in the fifth instar (D) reaches an average length of 1.6 mm. The second antennae are relatively much shortened, but the legs have

increased in length and are more distinctly indented on their mesal margins. The slender posterior part of the body bears rudiments of four new appendages, and its apex is split into a pair of small caudal lobes. The postmaxillary appendages continue to develop through the sixth and seventh instars until 11 pairs are present. In the eighth instar (E) they have lost their leglike form and have become broad flat phyllopodia with large flabella and slender apical lobes. At this stage, as the thoracic appendages take over the swimming function, the second antennae are much reduced in size and are directed forward. Heath enumerates 17 instars in the larval life of *Branchinecta*, but development beyond the eighth instar merely brings about refinements toward the adult structure.

The larval stages of *Artemia* described by Heath (1924) are very similar to those of *Branchinecta*, as are those of *Branchipus* described by Oehmichen (1921). In the Concostraca and Cladocera the larval development is complicated by the formation of a bivalved shell.

The development of the branchiopod appendages is of interest because it suggests that the natatory phyllopodium has been evolved from a segmented ambulatory leg. The mature appendage of *Branchinecta* (fig. 3 F) is cut on its mesal margin into a number of lobes, of which five (1-5) are commonly described as endites, while the large, so-called flabellum (6) is interpreted as the endopodite, and the movable apical lobe as the exopodite. The same structure is seen in the limbs of *Branchipus* (fig. 27 A, B) and other anostracans. Since endites in general are lobes of the limb segments, the six mesal lobes of the phyllopodium suggest that they represent six leg segments, coxopodite to propodite. The movable, independently muscled apical lobe (*Dactpd*), therefore, should be the dactylopodite. There is thus in the phyllopodium evidence of the presence of the seven segments characteristic of the crustacean walking legs. In the second maxilliped of *Apus* (fig. 27 C) seven segments, including a terminal dactylopodite, are plainly evident, and each of the first six segments except the ischiopodite bears an endite. We can hardly escape the conclusion, therefore, that the phyllopodial limbs of the branchiopods have been evolved from 7-segmented walking legs. The metamorphosis of the appendages, therefore, has taken place since the crustaceans became crustaceans, and is recapitulated in the larval ontogeny. A more extensive discussion of the nature of the primitive arthropod limbs is given in section IV of this paper.

About the only metamorphosis in the life history of *Branchinecta* is the temporary adaptation of the antennae for swimming. It is hardly to be supposed that the primitive crustaceans swam with their

antennae. The nauplius has only three pairs of limbs, and, since it must swim, it has no choice but to use what appendages it has. As the body lengthens and the postmandibular appendages become broad and flat, these appendages assume the function for which they were modified in the branchiopod ancestors. The antennae then revert to a more simple form (fig. 3 E), and in the adult they are again modified, in the male (G) for grasping.

OSTRACODA

The ostracods, being enclosed in a bivalve shell from the time they leave the egg, go through no body changes of form that might be termed a metamorphosis; their appendages, however, give an impressive example of the extreme degree of structural modification that an ordinary segmented leg may take on.

The newly hatched ostracod larva is in the nauplius stage of development (fig. 4 A), since it has only the three usual pairs of naupliar appendages. It is not a typical nauplius, however; the antennae and mandibles are uniramous, and the body is already enclosed in a shell formed in the egg. Here is a good demonstration, then, that the crustacean nauplius, in addition to its primitive features, can take on a specialized structure characteristic of the order to which it belongs. During the postnaupliar stages, as shown in the series of drawings (fig. 4) here copied from Schreiber (1922) on the development of *Cyprinotus incongruens*, the postmandibular appendages are successively added until the definitive number of seven in all is present in the eighth instar (F), in which the larva has attained essentially the adult structure.

There is no question that the naupliar appendages are the antennules, the antennae, and the mandibles, but there has been some difference of opinion as to the identity of the postnaupliar appendages. In the Cypridae the first appendage after the mandible (fig. 5 B, 4) bears a large, flat, fringed lobe projecting upward in the shell cavity, and this appendage is commonly regarded as the maxilla. The next appendage (5) Schreiber termed the maxilliped. These two appendages on each side in *Cypris* arise side by side on the arm of the hypostome (D, 4, 5), and Cannon (1926) regarded them as the maxillula and the maxilla, respectively. In *Limnocythere inopinata* (A), however, as in other Cytheridae and in Nesideidae, appendage 5 is a typical leg well separated from 4. If, therefore, appendage 4 is interpreted as the maxilla, appendages 5, 6, and 7 are thoracic legs, and Kesling (1951) says this is now the accepted interpretation of

the ostracod limbs. Since we are here not particularly concerned with the identification of the appendages, they have simply been numbered on the drawings for purposes of comparison.

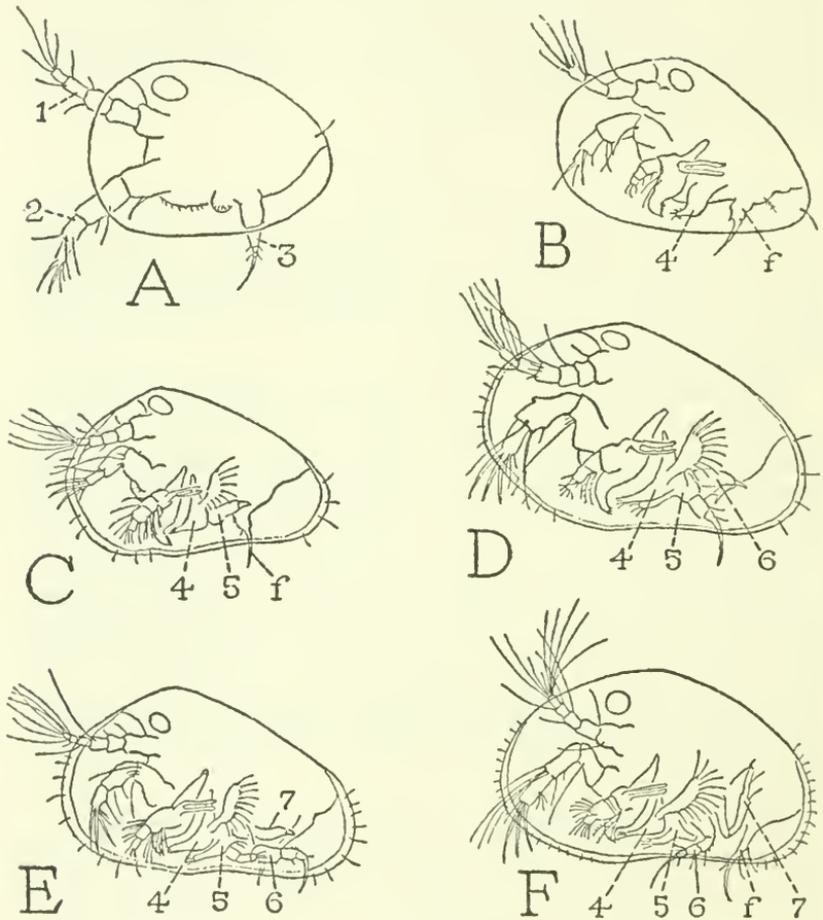


FIG. 4.—Ostracoda. Larval stages of *Cyprinotus incongruens* Ramdohr (from Schreiber, 1922).

A, nauplius, with three pairs of appendages. B, second instar, with one pair of added appendages (4) and caudal furca (f). C, fourth instar, with fifth appendages (5). D, fifth instar, with sixth appendages (6). E, sixth instar, with seventh appendages (7). F, eighth instar, essentially adult structure.

Inasmuch as in such forms as *Limnocythere* (fig. 5 A) the antennae and the last three pairs of appendages have the form of segmented legs, and in *Cypris* (B) the sixth and seventh appendages are typical legs (E), it may be inferred that the primitive ostracod appendages

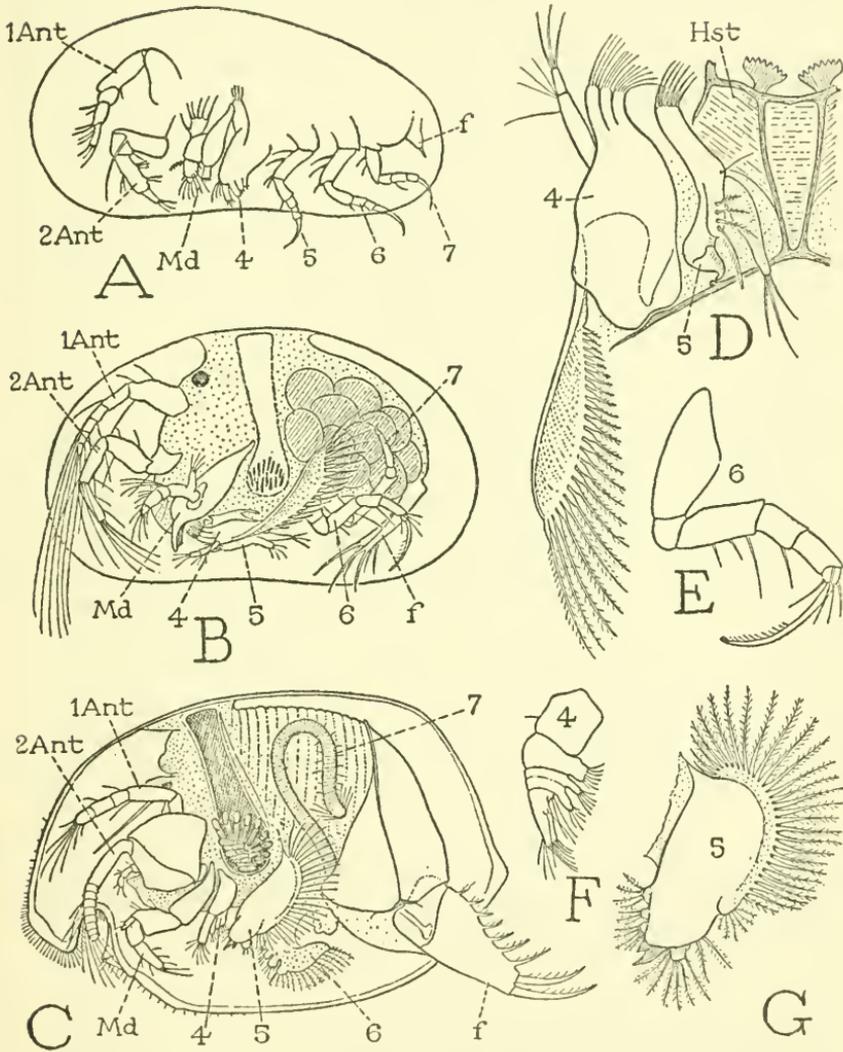


FIG. 5.—Ostracoda.

A, *Limmocythere inopinata* (Baird), eighth instar (from Scheerer-Ostermyer, 1940). B, *Cypris testudinaria* Sharpe, adult, left shell removed. C, *Philomedes globosa* (Lilljeborg), adult, left shell removed. D, *Cypris testudinaria*, fourth and fifth appendages of left side and hypostome (Hst), posterior. E, same, sixth appendage. F, *Philomedes globosa*, fourth appendage. G, same, fifth appendage.

were all ambulatory limbs. Moreover, since the legs of *Limnocythere* can be correlated with appendages of a very different structure in other genera, the ostracods give an actual demonstration of the changes that legs can undergo in adaptation to new uses. The very unleglike fifth appendage of *Cypris* (D, 5), for example, must have been evolved from a typical leg such as its representative in *Limnocythere* (A, 5). This same appendage in *Philomedes* (C, 5) is again quite different from the corresponding appendage in *Cypris*. The maxilla of *Cypris* (D, 4) is represented in *Philomedes* (C, F, 4) by an appendage still suggestive of its leg origin. The fifth appendage of *Philomedes* (C, G, 5), however, has no resemblance to its counterpart in *Limnocythere* (A, 5), though the presence of three small marginal lobes and an apical tooth might be taken as evidence of a former segmentation. The sixth appendage (C, 6) has likewise three small marginal lobes and a broad, fringed apical lobe, but otherwise it has departed far from the structure of a leg (A, 6). The seventh appendage of *Philomedes* (C, 7) has lost all semblance of a leg; it has become a long, flexible, vermiform cleaning organ armed with an apical brush of recurved bristles. The corresponding appendage in *Cypris* (B, 7) is likewise used for cleaning the shell chamber, but the only concession it has made to its function is an inversion of position. The sixth appendage of *Cypris testudinaria* (fig. 5 E) looks like a typical 7-segmented crustacean limb, counting the long terminal claw as the dactylopodite. The fourth and fifth podomeres of this appendage, however, are perhaps not true segments, since in *Cypridopsis vidua* Kesling (1951, fig. 20) shows that the muscles from the sixth podomere have their origins in the base of the fourth podomere.

The ostracods give no support to the theoretical phyllopod origin of crustacean limbs, and show clearly how simple segmented legs can be modified into very unleglike structures.

COPEPODA

The copepods include marine and fresh-water free-swimming species and a large number of parasitic species. They are nearly all very small crustaceans, mostly from 0.50 mm. to 10 mm. in length in the adult stage. The simpler free-swimming copepods seem to approach more closely the typical shrimplike form of the higher crustaceans than do any of the other entomostracans. The body of a generalized form such as the marine *Calanus* (fig. 6) is divided into a cephalothoracic region bearing the appendages, and a slender limbless abdomen. The cephalothorax includes an anterior unsegmented part

(*H*) known as the head, or cephalosome, and a posterior thoracic region of five segments. The head carries the two pairs of antennae, the mandibles, two pairs of maxillae, and the first pair of legs, or maxillipeds. The five segments of the thoracic region bear each a pair of legs, but the legs of the last pair may be much reduced. The genital ducts open on the basal segment of the abdomen.

The free-swimming copepods occur in such vast numbers in the ocean and in some inland lakes that they constitute a most important food source for many other aquatic animals from arrowworms to whales, but particularly for fishes. Being minute creatures themselves, the free copepods feed on the microscopic plant life of the water,

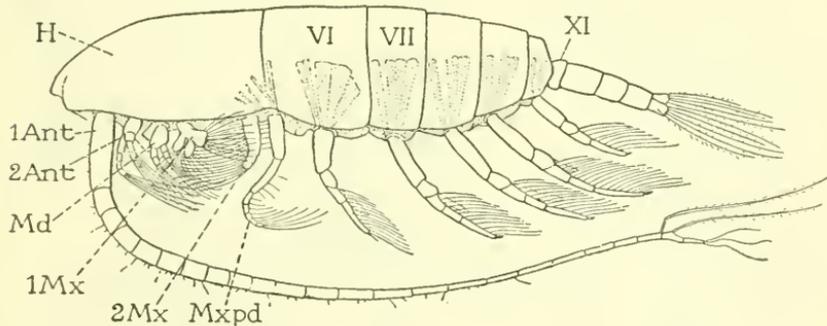


FIG. 6.—Copepoda. *Calanus cristatus* Kröyer, adult.

1Ant, first antenna; *2Ant*, second antenna; *H*, "head"; *Md*, mandible; *1Mx*, first maxilla; *2Mx*, second maxilla; *Mxpd*, maxilliped; *VI*, *VII*, *XI*, body segments.

which, elaborated in their own bodies, is thus passed on as food for the larger animals. It would seem, however, that the copepods have retaliated on the animals that eat them, since many species have become parasites of their potential enemies. Though fish are their favorite hosts, the parasitic copepods are not discriminative and attack almost every kind of creature that lives in the ocean. On the other hand, the copepods themselves are infested by numerous parasites, even by some of their own kind. Evidently life in the ocean is not a happy existence for either the predators or their victims.

The nonparasitic copepods go through no changes of form in their life histories that can truly be called a metamorphosis. Their environment is practically the same at all periods of their lives, and there is no call for adaptive modifications in either the larval or the adult stage. The successive developmental stages are merely steps in growth from youth to maturity. As an example, we may take the fresh-water

Cyclops and follow its life history as described by Dietrich (1915) and by Ziegelmayr (1925).

The *Cyclops* larva hatches from the egg as a typical nauplius (figs. 7 A, 8 A), which is followed by a second nauplius instar and four metanaupliar instars (fig. 8 B, C, D, E) in which the body lengthens, and finally (E) five pairs of appendages are added beyond the mandibles, including the maxillipeds (*Mxpd*) and two pairs of legs (*iL*,

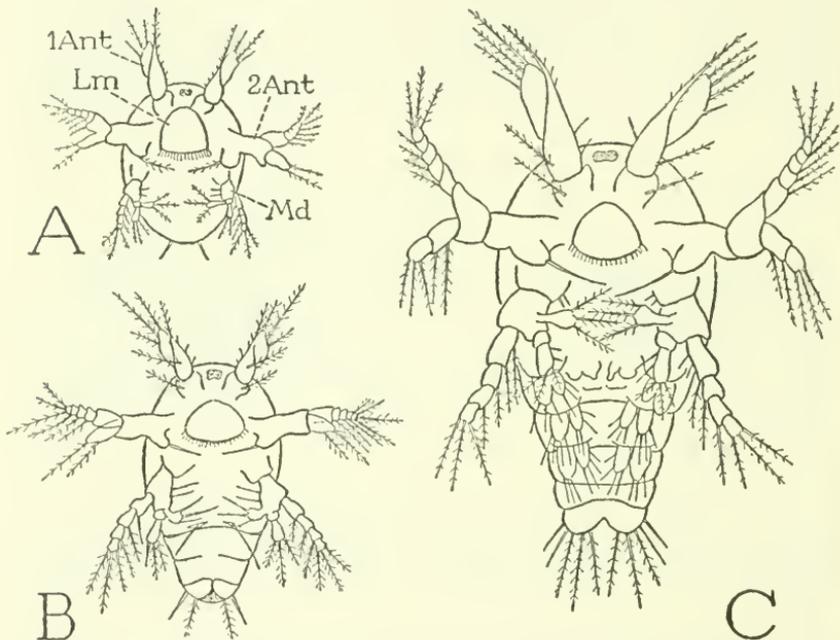


FIG. 7.—Copepoda. Nauplius and two metanaupliar instars of *Cyclops* (outlines from Ziegelmayr, 1925).

A, nauplius, ventral, showing three pairs of appendages and labrum (*Lm*). B, first metanaupliar instar. C, fourth metanaupliar instar.

zL). At the next moult the larva (F) begins to take on the form and structure of the adult (G) and is now termed a *copepodid*, the ending *id* signifying that at this stage the larva has become copepodlike. The first copepodid acquires a third pair of legs; with further growth it passes through six copepodid instars until at last it becomes a sexually mature adult (G). Among *Cyclops* species there is thus no abrupt change between the various stages of growth, but new segments are added and the appendages develop from simple rudiments to their definitive forms. According to Ziegelmayr the segments formed after the nauplius stage are generated in a subterminal zone of growth.

The genus *Calanus*, a typical free-swimming marine copepod of the suborder Gymnoplea, likewise develops from nauplius to adult by ordinary anamorphic growth without any metamorphic changes

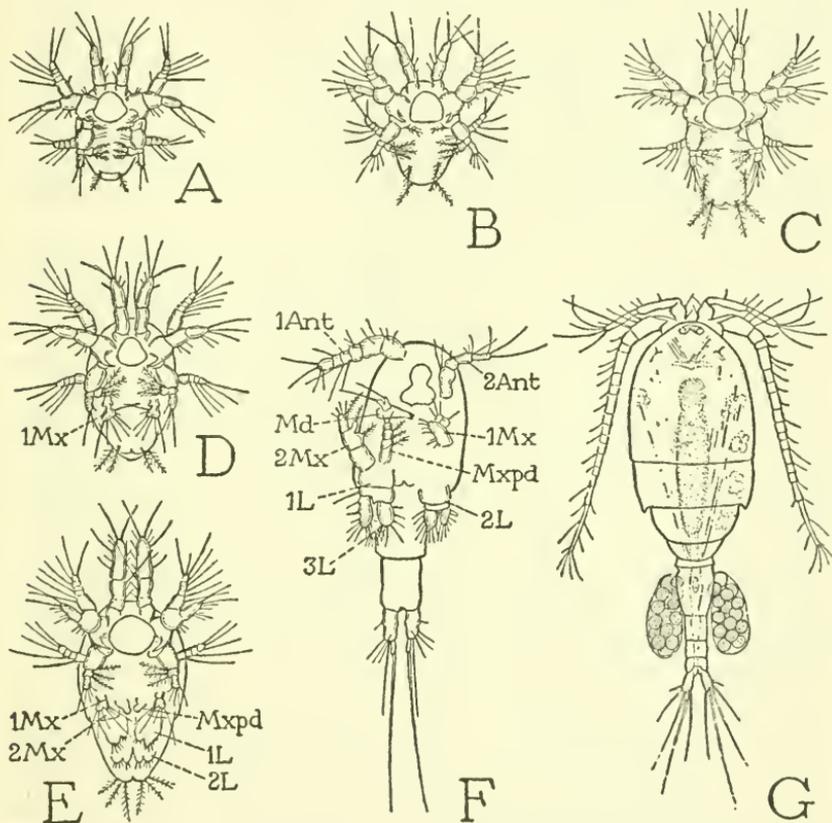


FIG. 8.—Copepoda: Podoplea. Developmental stages and adult of *Cyclops*. (A-F from Dietrich, 1915; G from Claus, 1863).

A, *Cyclops strenuus* Fischer, nauplius, 0.119 mm. B, same, first metanauplius. C, same, second metanauplius. D, same, third metanauplius. E, same, fourth metanauplius. F, same, first copepodid, 0.303 mm. G, *Cyclops coronatus* Claus, adult female with eggs, 3.50 mm.

1Ant, first antenna; 2Ant, second antenna; 1L, 2L, 3L, legs; Md, mandible; 1Mx, 2Mx, first and second maxillae; Mxpd, maxilliped.

adaptive to different ways of living at different stages. The life history of the common *Calanus finmarchicus* has been described by Lebour (1916). The first six instars the author calls nauplii, but some of them would ordinarily be regarded as metanauplii, since two posterior segments and indications of a third segment are said to appear in the

fifth stage, with traces of the fifth and sixth pairs of appendages. In the sixth instar, judging from related species, there are present second maxillae, maxillipeds, and two pairs of swimming legs. The next instar is that of the first copepodid, which has three pairs of legs; the fourth legs appear in the second copepodid instar, and the definitive number of five is present in the third copepodid. The fifth and last copepodid is essentially like the adult. The free-swimming copepods, therefore, have a typical anamorphic development. Being crustaceans, they are primarily constructed for life in the water, and so long as they maintain a free existence there is no need of metamorphic adaptations to any other way of living.

When now we turn to the parasitic copepods, the story is very different. An aquatic animal that hatches as a freely swimming larva and then becomes sedentary on another animal from which it extracts its food changes its environment and its mode of living in a very radical way. In some manner difficult to understand metamorphic changes of structure have been evolved that adapt the parasitic animal to its life of parasitism, and in many cases the transformation has been carried so far that the adult parasite could not be identified, or even recognized as a crustacean, if its early stages were not known.

A few copepods appear to be transitional in their habits between a free life and one of parasitism. Such species are termed semiparasitic by Wilson (1921b), who says they are found on worms, mollusks, echinoderms, and in the gill chambers of crabs. These species are capable of swimming freely in the water, and their residence on any one host may be temporary. Their mouth parts, according to Wilson, are not suitable for either chewing or sucking and appear to be adapted for licking nourishment from the animals to which they attach themselves. A species with biting mouth parts, however, could hardly resist sampling the blood of its host and then becoming an habitual parasite.

The truly parasitic copepods include a large number of species, all of which undergo striking metamorphic adaptations to the nature of the host or the part of the host attacked, and some of them lead a double life on two different species of hosts. Some parasitic copepods undergo their metamorphoses during the larval development and become again free living in the adult stage; others remain on the host and attain their highest degree of metamorphosis as adults. Most of them, however, hatch from the eggs as typical nauplii, and in this stage or the following copepodid stage they must find their proper hosts.

As an example of the life history of a parasitic copepod that returns to a free life in the adult stage, we may take the monstrillid *Cymbasoma rigidum* Thompson, described by Malaquin (1901) as *Haemocera danae* (Claparède), which in its larval stages lives in the blood vessel of the serpulid worm *Salmacina dysteri* Huxley. The nauplius (fig. 9 A) has the usual three pairs of naupliar appendages, but the mandibles are recurved hooks, and the young larva has no mouth or alimentary canal. It is poorly fitted for swimming, and Malaquin suggests that the females probably sow their eggs over a colony of the serpulids. When in contact with a worm the nauplius attaches itself by its mandibular hooks to the worm's integument, but it has no special organs for penetration. The skin of the worm, however, is delicate, and, a puncture once effected, the nauplius does a most surprising thing; it casts off its own cuticle and its appendages and forces its soft nude body into the host. Within the latter it becomes a shrunken, oval mass of undifferentiated cells (B), as if it had returned to an early embryonic condition to begin development all over again. In this form the parasite traverses the coelom of the host and makes its way into the ventral blood vessel. Here it secretes a new cuticle and then from its ventral side anteriorly there grow out two tapering, armlike processes (C) that extend posteriorly in the blood vessel of the worm and will serve the parasite as food-absorbing organs. Here, therefore, we see a metamorphic development adapting the parasite to its life in the host that certainly had no counterpart in the presumed free-living ancestors of its species. It is hard enough to believe the facts themselves, and we can speculate in vain as to how they all came about in evolution. The nauplius is prepared in advance for the life it is to lead by being provided with hooked mandibles, but what induces it to shed its cuticle and appendages and to squeeze itself into the worm?

With the growth of the young larva in the worm (fig. 9 H) the nutritive arms increase in length (D, E), the new cuticle is drawn out into a rostrum in front (E, R), and on the enlarged conical posterior part of the body it becomes armed with circles of spines directed forward. The organs of the future adult now gradually develop within the cuticle of the larva (F), and the abdomen forms as a ventral flexure (*Ab*) of the posterior part of the body. At an early stage the first antennae are regenerated (F, G, *1Ant*) and eventually penetrate into the rostrum (I) when the head tissue has receded from the latter. From this point on the parasite develops normally into the adult form within the cuticular sheath of the larva. Finally, when its development is almost completed (I), the parasite becomes strongly

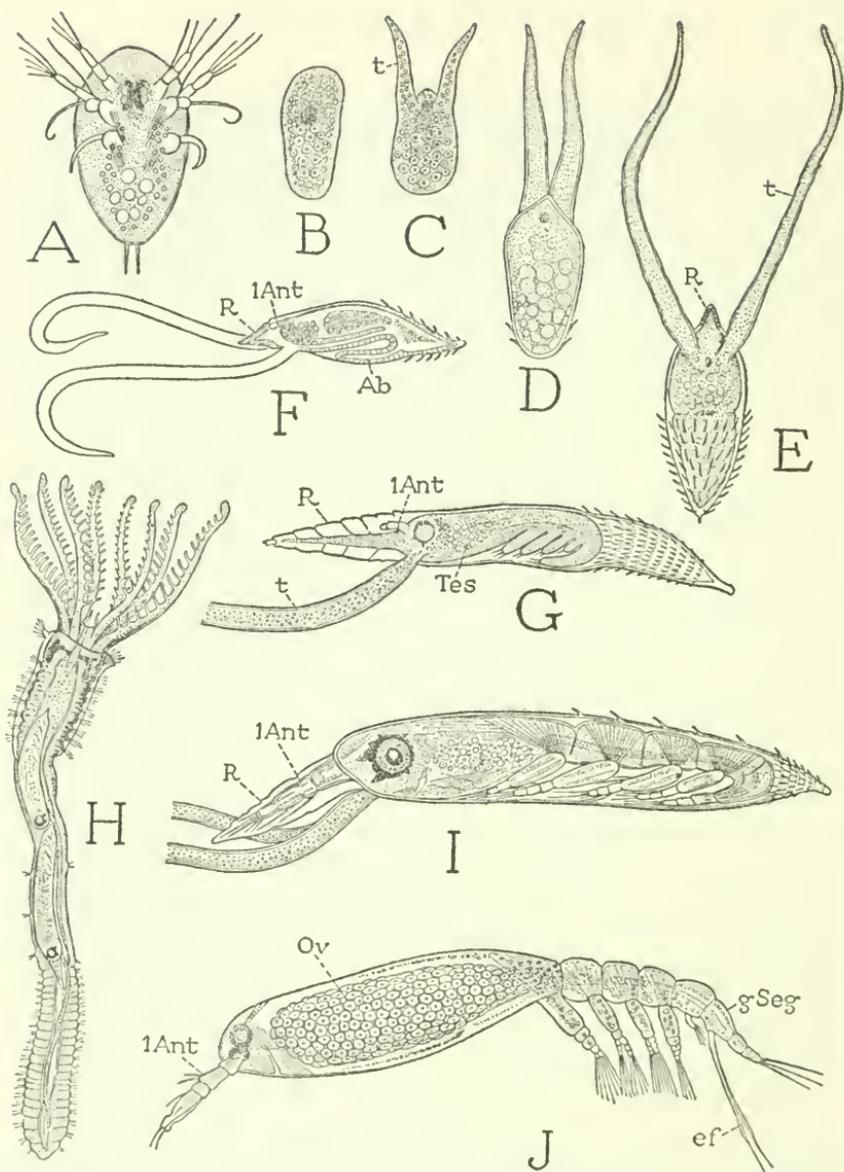


FIG. 9.—Copepoda: Monstrillidae. Larval stages and adult of *Haemocera danae* (Claparède) parasitic in the polychaete *Salmacina dysteri* Huxley (from Malaquin, 1901).

A, free nauplius. B, after penetration into host. C, same, with nutritive tentacles (*t*). D, same, later stage. E, later stage, with cuticular envelope, rostrum (*R*), and spines. F, beginning transformation to adult inside cuticular sheath, rudiment of abdomen (*Ab*) bent forward. G, later stage of male, showing testis (*Tes*). H, specimen of *Salmacina* with two parasites in ventral blood vessel. I, male parasite almost adult. J, adult female, free after shedding the sheath and leaving the host; *1Ant*, first antenna, *ef*, egg filaments, *gSeg*, genital segment, *Ov*, ovary.

active, doubling and straightening upon itself with the result that it ruptures both its enclosing sheath and the integument of the host. Then it escapes, leaving behind in its late host its spiny cuticle and its nutritive arms, which will no longer be needed. The monstrillid thus, according to Malaquin, makes during its life only two moults, one on entering the host, the other on leaving it. With its liberation the adult becomes at once an active free-swimming copepod (J). It now has only one pair of antennae and four pairs of swimming legs, and it lacks a complete alimentary canal. The body of the female, however, is mostly filled with a great mass of eggs (J, *Ov*); the business of the adult is the procreation of more parasites.

Members of the family Caligidae, mostly parasitic on fish, are also free in the adult stage, but, though the adults are at liberty to leave the host and are equipped with swimming legs, they still depend for their food on the host that nourished them as larvae or on some other fish of the same kind. They, therefore, live largely as free external parasites. The structure and habits of many species of Caligidae have been described by Wilson (1921a), and a detailed account of the larval stages of *Caligus curtus* (O. F. Müller) is given by Heegaard (1947).

In *Caligus curtus*, according to Heegaard, there are two naupliar instars, the second of which goes over directly into a first copepodid without an intervening metanaupliar stage. The first copepodid is followed by a second copepodid, and then come five larval stages in a form known as a *chalmus* before the individual becomes adult. The actively swimming first copepodid has the responsibility of finding a host, which will be a codfish. It grasps a scale or a fin ray of the fish by means of its clawed second antennae, and holds on with the maxillipeds. After attachment the copepodid moults into the second copepodid (fig. 10 A). In this stage a gland in the head produces a secretion which will be discharged from the frontal region as a filament (B), which becomes firmly fixed to a scale or a fin ray of the host. The parasite now becomes quiescent and takes no food as it hangs motionless on its attachment line, while within its cuticle a development takes place that will transform the copepodid into the first *chalmus*. This quiescent period of the copepod (B) is termed by Heegaard and some other writers a "pupa," but, though motionless and nonfeeding, it is not comparable to the pupa of an insect. The insect pupa is a stage in itself during which the metamorphosed larva reverts to the parental form. Each larval instar of any arthropod begins its development within the loosened cuticle of the preceding instar. The copepod "pupa," therefore, is merely the second copepodid

after completion of its own growth when the first chalimus is developing beneath its cuticle. An insect larva in a corresponding stage becomes quiescent and ceases to feed, but it is not a pupa. This concealed period in which any instar begins its development within the

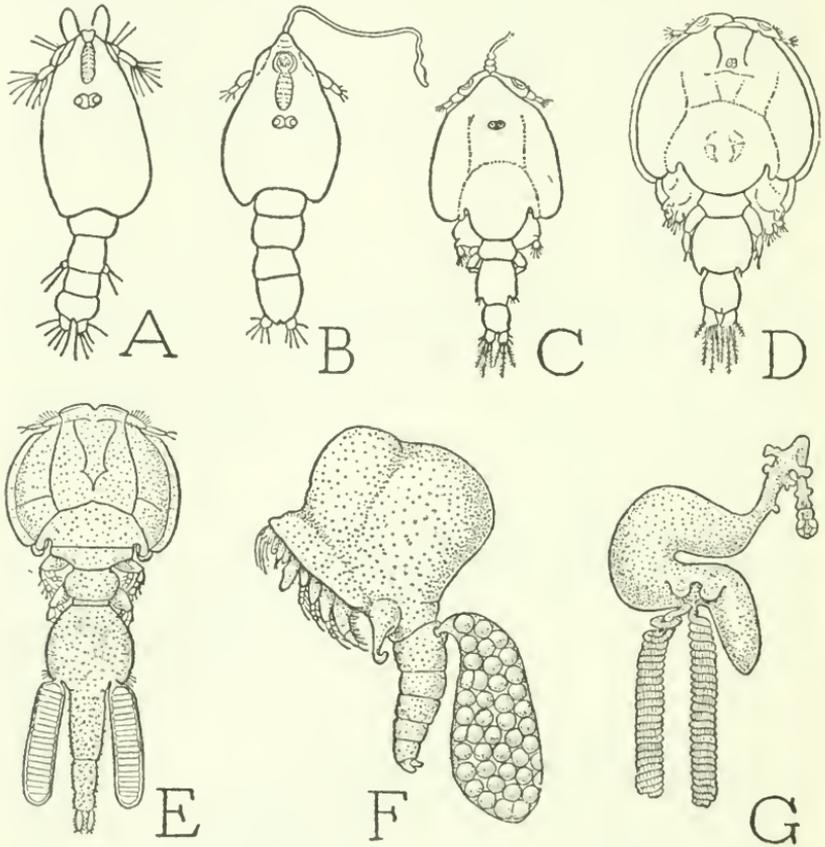


FIG. 10.—Copepoda. Larval and adult stages of fish parasites. (A, B from Heegaard, 1947; C, D from Wilson, 1905; E, F from Wilson, 1921a; G from Wilson, 1917.)

A, *Caligus curtus* (O. F. Müller), second copepodid. B, same, transforming stage of second copepodid. C, same, mature male chalimus. D, same, adult male. E, *Trebius latifurcatus* Wilson, adult female. F, *Blakeamus corniger* Wilson, adult female. G, *Haemobaphes cyclopterina* (Fab.), adult female.

cuticle of the preceding instar has been termed by Hinton (1946) the *pharate*, or cloaked, phase of development.

The young chalimus that emerges from the copepodid cuticle is not particularly different from the copepodid, though it is somewhat more advanced in development. Its first concern is to reattach itself to the

host, since the old filament remained with the discarded copepodid skin. Heegaard (1947) gives an interesting account of how the young chalimus with the pointed frontal lobe of its head bores a hole in a fin ray of the host. Into the wound thus formed is injected the secretion from the head gland, which hardens and holds fast, while the chalimus backs away and draws it out into a filament that secures the parasite to the host, but still allows it to move about on its tether. According to Heegaard each of the four succeeding chalimus stages reattaches itself in the same manner. The chalimus (C) was given its name because when first discovered it was thought to be the adult of an unknown species. Since the chalimus stages progressively develop from the second copepodid to the adult (D), they evidently represent the later copepodid stages of free-living copepods.

The adults of *Caligus curtus* (fig. 10 D) have pretty much the form and structure of an ordinary copepod, but, having no attachment to the host, both the males and the females are free to swim away. The egg-carrying female of another species with similar habits is shown at E of the figure. Since these copepods are dependent on a host for food in the adult stage, they retain their parasitic habits and are generally found crawling and feeding on the host, though they have not become specially modified in structure for a life of parasitism. This condition of dependence on a host, however, Wilson (1915) points out, constitutes the first step toward adult degeneration. If the adult parasite finds it advantageous to remain on the host, organs of locomotion become unnecessary, and in the end all that is needed are organs of nutrition and reproduction. The species shown at F, parasitic in an ascidian, still retains its appendages and a segmented abdomen, but the thorax has taken on a strange shape. The female at G, however, a permanent parasite on the gills of a fish, has degenerated from the copepod structure almost to the limit of simplification. Yet, as already noted, "degeneration" is merely adaptation by the elimination of unnecessary organs.

An example of an intermediate degree of degenerative simplification is seen in the lernaepodid fish parasite *Achtheres ambloplitis* (fig. 11) described by Wilson (1911). In this copepod, Wilson says, the naupliar and metanaupliar stages are completed in the egg, and the larva hatches as a copepodid (A). During the egg stage the head gland produces a filament, which is still coiled in the head of the emerging copepodid (A, f). The young larva has two pairs of feathery swimming legs, and its maxillipeds (*Mxp d*) are armed with strong hooks. It swims actively in search of a host, which must be a fish of the surface-swimming Centrarchidae. That the young copepod

deliberately presents itself to the head end of a fish has perhaps not been observed, but the fish unwittingly engulfs the copepod as food, which is of course just what the prospective parasite wanted it to do. To save itself from being swallowed the copepod grasps a gill arch of the fish with the hooks of its maxillipeds. Then it pushes its head into

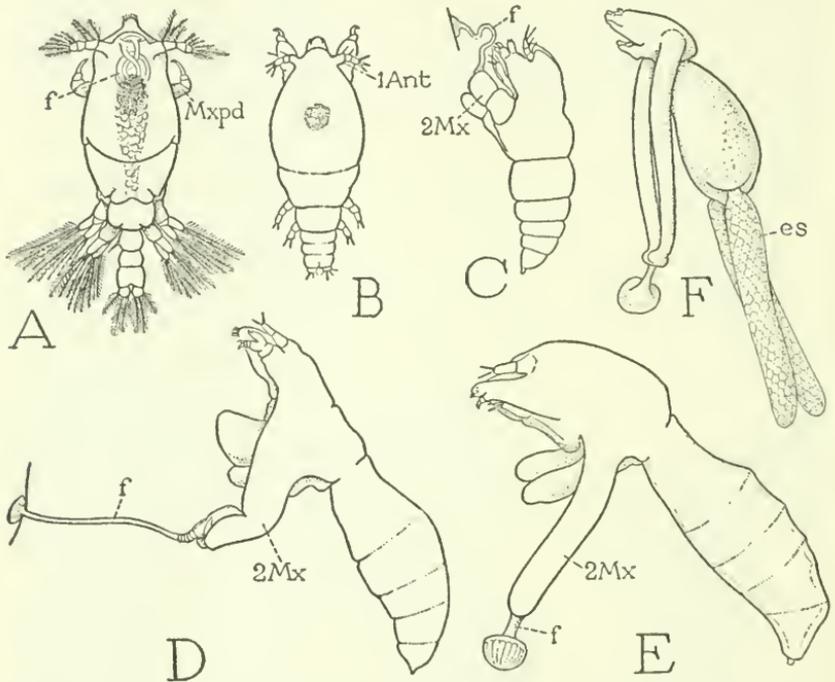


FIG. 11.—Copepoda: Lernaeopodidae. Developmental stages of fish parasites (from Wilson, 1910, 1915).

A, *Achtheres ambloplitis* Kellicott, first copepodid, with filament (*f*) in head. B, same, second copepodid. C, same, with filament extruded and attached. D, same, adult male. E, same, adult female. F, *Salminicola siscowat* (Kellicott), egg-carrying female.

the soft skin of a gill, which act breaks the cuticle over its head and releases the filament. The filament protrudes into the wound of the gill and the end spreads out into a disc that anchors the parasite inside the gill chamber of the fish.

The first copepodid larva of *Achtheres* (fig. 11 A) undergoes a moult and enters a second copepodid instar (B), which is decreased in size and has taken on a different shape. The swimming legs, being now useless organs, are greatly reduced and later disappear (C). The mandibles have become toothed piercing organs for feeding. The

large second maxillae (C, $2Mx$) are much thickened and securely grasp the base of the attachment filament (f) by means of hooks imbedded in apical depressions. Then the larva backs away and draws the filament out to its full length, and thus maintains its hold on the gill with sufficient freedom of movement for feeding. At the next moult the sexes are mature. The female grows to a length of 4 or 5 mm., but the male remains a pygmy not over 1 mm. long.

In the adult female (fig. 11 E) the maxillae are greatly lengthened, but the filament (f) is contracted so that only a short stalk projects beyond the maxillae. The maxillae of the male (D) are relatively not so long as those of the female, but the filament is unshortened. The filament, being a product of an internal head gland, is not shed and renewed at the moults; it retains its attachment and thus allows the parasite to complete its life in security within the gill chamber of the fish. The long filament of the small adult male permits the male to swing around on his tether until he comes in contact with a female, whom he grasps with his maxilliped claws and then lets go his hold on the filament, which remains attached to the gill. The female of another similar species of the genus *Salminicola* (F) is depicted by Wilson (1915) carrying her extruded eggs (es) in two long cylindrical sacs projecting from the gonopores while still attached to the gill of the fish. The newly hatched young presumably are carried out of the gill chamber in the expiratory currents of water.

A good example of a parasitic copepod that inhabits two hosts during its life is the well-known fish parasite *Lernaeocera branchialis* (L.), a member of the Lernaeopodidae. This species during its larval life is an attached parasite on the gills of a flounder, but when adult both the male and the female become free and leave the flounder. The male undergoes no further transformation, and, after mating with a female still on the flounder, his purpose is accomplished. The female, on the other hand, is not yet sexually mature, and some instinct now urges her to leave the flounder and to seek a cod on which to complete the development of her ovaries. Once attached in the gill chamber of a cod she goes through an adult metamorphosis by which she is functionally reduced to the bare essentials necessary for feeding and egg production. For an account of the life history of *Lernaeocera branchialis* we may draw on the work of Pedaschenko (1898), Scott (1901), Wilson (1917), Schuurmans-Stekhoven (1936), Sproston (1942), and Capart (1948).

There is some difference of opinion concerning the nature of the early forms of this species. Pedaschenko says the first larva is a metanauplius (fig. 12 B); Scott and Sproston observed only one early

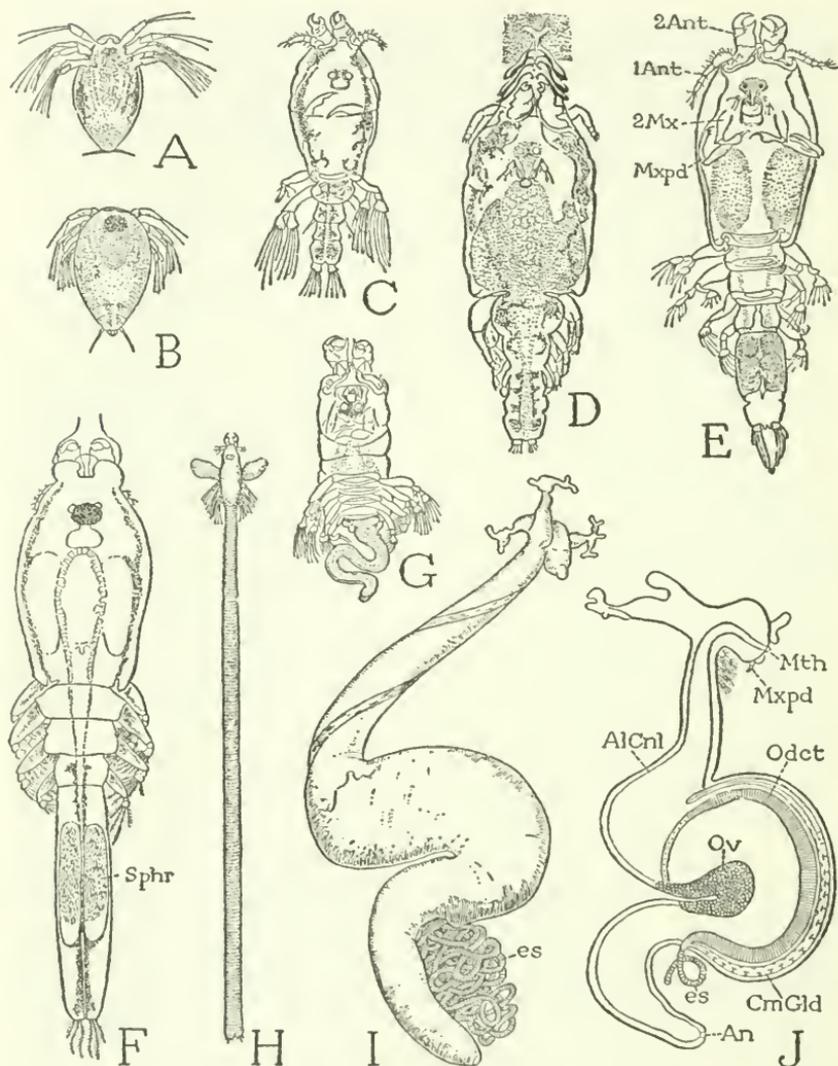


FIG. 12.—Copepoda. Developmental stages of the fish parasite *Lernaeocera branchialis* (L.). (A, C, D, E, G from Sproston, 1942; B from Pedaschenko, 1898; F, I from Capart, 1948; H, J from Scott, 1901.)

A, nauplius, 0.37 mm. B, metanauplius. C, free-swimming copepodid. D, third instar of chalimus stage on flounder. E, free-swimming adult male, 1.55 mm. F, young inseminated female on flounder. G, female on cod, beginning metamorphosis to penella stage. H, female in fully developed penella stage. 11.4 mm. I, adult egg-carrying female on cod, 40 mm. J, section of mature female.

An, anus; AlCnl, alimentary canal; 1Ant, first antenna; 2Ant, second antenna; CmGld, cement gland; es, egg string; Mth, mouth; 2Mx, second maxilla; Mxpd, maxilliped; Odct, oviduct; Ov, ovary; Sphr, spermatophore.

stage, and called this stage a nauplius (A); while Wilson and Capart record both a nauplius and a metanauplius. The matter is of no particular importance for us in a study of the metamorphosis of the species. Whatever the larva that hatches from the egg may be, it moults into a free-swimming copepodid (C). Though the copepodid is only about half a millimeter in length, it has the responsibility of finding a flounder and of fixing itself to the gills of the fish, for which latter purpose it is provided with strongly chelate second antennae. Its hold on the gill, Sproston says, is never relinquished, and becomes the anchorage of the parasite until the free-swimming adult stage is reached. The gill filaments, however, are grasped also by the second maxillae in order to bring the mouth parts into close contact with the tissues on which the parasite feeds.

When the copepodid moults the larva becomes a chalimus (fig. 12 D), but there is little change in form or structure. The chalimus, however, in its first instar acquires an additional attachment on the host in the form of a filament secreted by a gland in the head, which is anchored in the gill by two diverging branches that penetrate into punctures in the gill tissue. The rest of the secretion from the gland, Sproston says, falls back on the head of the larva where it hardens into a conical hood. The chalimus goes through four instars, and with each moult but the last a new hood is formed while the old ones remain, so that there are thus formed a set of overlapping caps corresponding in number with the moults. The third instar of the chalimus, to be identified as such by its three hoods, is illustrated at D of figure 12, redrawn from Sproston. The copepodid and the chalimus are metamorphic larval forms adapted to their respective functions of swimming and parasitic feeding. During its four instars the chalimus gradually approaches the adult structure, which is attained at the fourth moult after the copepodid stage.

The adult male of *Lernaeocera* (fig. 12 E) leaves the old attachment filament with the castoff chalimus cuticle hanging on the gill of the flounder, and goes off in search of a female. The female (F), however, awaits the coming of a male before she relinquishes her hold on the flounder. When the male finds a female still attached, mating takes place; two large spermatophores are inserted into the genital ducts of the female and are eventually lodged in her lengthened genital segment (F, *Sphr*). The female, still not sexually mature, then frees herself from the flounder and swims away to look for her second host, which should be a cod. On attaining a prospective victim, the female fixes herself to the bases of the gills by her second antennae, and now begins her metamorphosis into the final egg-producing stage.

After attachment on the cod the head of the female undergoes a curious transformation. Large branching, hornlike processes grow out from it and sink into the host tissue as anchoring devices (fig. 12 I). The proboscislike mouth region penetrates deeply in the flesh at the base of the gill until a large blood vessel is reached, from which the female will draw a rich nourishment for the maturing of her eggs. The first change of the body is a lengthening of the abdomen, principally the genital segment, which grows out in a twisted wormlike form (G), and finally (H) becomes a long, straight, slender appendage hanging from the thorax. At this stage the female is known as a penella from her resemblance to another adult copepod of that name. In the figure the penella stage shown at H is, of course, drawn on a much smaller scale than is the female at F or G. Next, the abdomen swells into a great, elongate, twisted bag (I). The female in her final stage is said by Wilson (1917) to attain a length of 40 millimeters when fully extended. From now on she is merely an egg-producing organism. Her internal organs (J) consist principally of the enlarged alimentary canal (*AlCnl*), the ovaries (*Ov*) and oviducts (*Odct*), and a pair of cement glands (*CmGld*) that form the casings for the eggs. The eggs are discharged in two long coiled strings (*es*), which, Wilson says, reach a length of 150 to 200 millimeters. Considering the number of eggs that the species produces, any flounder or cod may consider itself lucky if it escapes infestation. According to Schuurmans-Stekhoven there is only one generation of the parasite each year.

The metamorphosis of *Lernaeocera branchialis* affects principally the female on the secondary host. The less modified chalimus instars carry on the developmental processes while attached on the flounder as do the copepodid stages of free-living species. The adult male and the adult female on leaving the flounder are normal, swimming copepods. The transformation of the female on the cod involves, on the one hand, a simplification of the thorax until it becomes indistinguishable from the abdomen, except for the retention of the appendages; but, on the other hand, there is a new development of anchoring process on the head, and a great overgrowth of the reproductive part of the body. The metamorphosis of the female, therefore, is both recessive and progressive in an anatomical sense. A study of the development and metamorphosis should take into consideration not only the anatomical changes that the individual goes through, but also the changes in its instincts. The copepodid of *Lernaeocera*, for example, must have an instinctive urge to attach itself to a flounder; the adult female instinctively leaves the flounder and looks for a cod.

Copepod fish parasites are not all content with attacking the scales, fins, or gills of the host. Some make their abode in the nostrils of the fish; others penetrate through the skin into the body cavity where they attack the vital inner organs. The worst of them are members of the genus *Phrixecephalus*, several species of which are described by Wilson (1917). These parasites bore into the eyes of their victims in order to feed from blood vessels at the back of the organs. Parasites seem to have been endowed by nature with great versatility, but the life of a fish is nothing to be envied.

CIRRIPEDIA

The cirripeds include the familiar barnacles and several groups of parasitic species. The first-stage larvae in most cases are nauplii usually characterized by the presence of a pair of lateral *frontal horns* on the anterior part of the body. In some species the horns are merely short spines (figs. 14 B, 16 A, *fh*), in others they are long and either straight or curved, but when present the horns identify the nauplius as a young cirriped. The nauplius becomes a metanauplius; the metanauplius transforms into a free-swimming larval stage known as a *cypris* because its body is enclosed in a bivalve shell with a closing muscle, and thus resembles the ostracod of the same name. The cirriped cypris (fig. 14 C) has six pairs of swimming legs, a simple median eye, compound lateral eyes, and a pair of antennules projecting from the anterior end of the shell. After swimming freely for some time the cypris of most species attaches itself by the antennules to some solid object on which it remains permanently fixed and here develops into the adult form.

The barnacles in the adult stage (fig. 14 F, H) are sedentary on rocks, clam shells, wooden piles, ship bottoms, whales, or almost anything else in the ocean, and they get their food from the water. The parasitic cirripeds attach themselves to other animals and derive their sustenance from the host. The adult barnacles retain enough of their ancestral structure to be recognized as crustaceans; some of the parasitic cirripeds, on the other hand, undergo such extreme degrees of adult metamorphosis that their crustacean derivation is known only from their early larval stages.

The Ascothoracica.—The members of this suborder are of particular interest because as adults they appear to be equivalent to the cypris stage of other cirripeds. If they truly are cirripeds, therefore, they evidently are a primitive group of the order, and suggest that the cirripeds have been derived from cyprislike ancestors, perhaps re-

lated to the bivalved Ostracoda. From the standpoint of metamorphosis the Ascothoracica are of small interest, since whatever modifications some of them do undergo effect principally a simplification of the cypris structure. They are all minute creatures parasitic on Actinozoa and Echinodermata.

The least modified member of the Ascothoracica is *Synagoga mira* Norman (fig. 13 A), which lives externally on the black corals *Antipathes*, clinging to the host by the large antennules. Since *Synagoga* has well-developed setigerous legs, however, it appears probable that it can relax its hold and swim from one host to another. The species is known only from a few specimens described by Norman (1913). The head and thorax are enclosed in a large, oval bivalve shell, 4 millimeters in length, provided with strong adductor muscles, but the slender, five-segmented abdomen projects freely from the shell and bears a pair of long uropods. The large antennules (*1Ant*) are armed with apical hooks; the six pairs of thoracic legs bear long setae and are evidently adapted for swimming. The mouth parts as described by Norman are slender piercing organs enclosed in a large conical proboscis (*Prb*). Of all the Ascothoracica, *Synagoga mira* alone appears to have no metamorphosis and to have retained the ability to swim; no other species, therefore, has so good a claim to being a primitive cirriped.

A related member of the Ascothoracica is described by Okada (1938) as *Synagoga metacrinicola* (fig. 13 B). This species has the entire body enclosed in the shell, the abdomen being relatively short, but otherwise it is similar to *S. mira*. Okada finds well-differentiated males and females in *S. metacrinicola*, the sexes being separate in most of the Ascothoracica, in which the males are much smaller than the females. He reports that Norman's specimens, supposed to be females, are found on reexamination by sections to be males with mature spermatozoa. Okada thus demonstrates that the known examples of *Synagoga* are adult forms and not larvae of an otherwise unknown species, as some writers had suggested they might be.

The other Ascothoracica that are parasitic on horny corals appear as small budlike bodies on the coral stems. The shells are of various shapes and in some species are enclosed in a tunic derived from the host. In most of these forms the legs are more or less reduced and lack swimming setae. An ascothoracid described by Heegaard (1951) as *Ascothorax bulbosa*, found in specimens of an ophiuroid, or brittle starfish, has an oval shell (fig. 13 C), the small males being attached dorsally on the females beneath the cuticle of the latter. The body

of the animal (D, E) is somewhat deformed and the thoracic legs are reduced.

The greatest modification among the Ascothoracica occurs in the

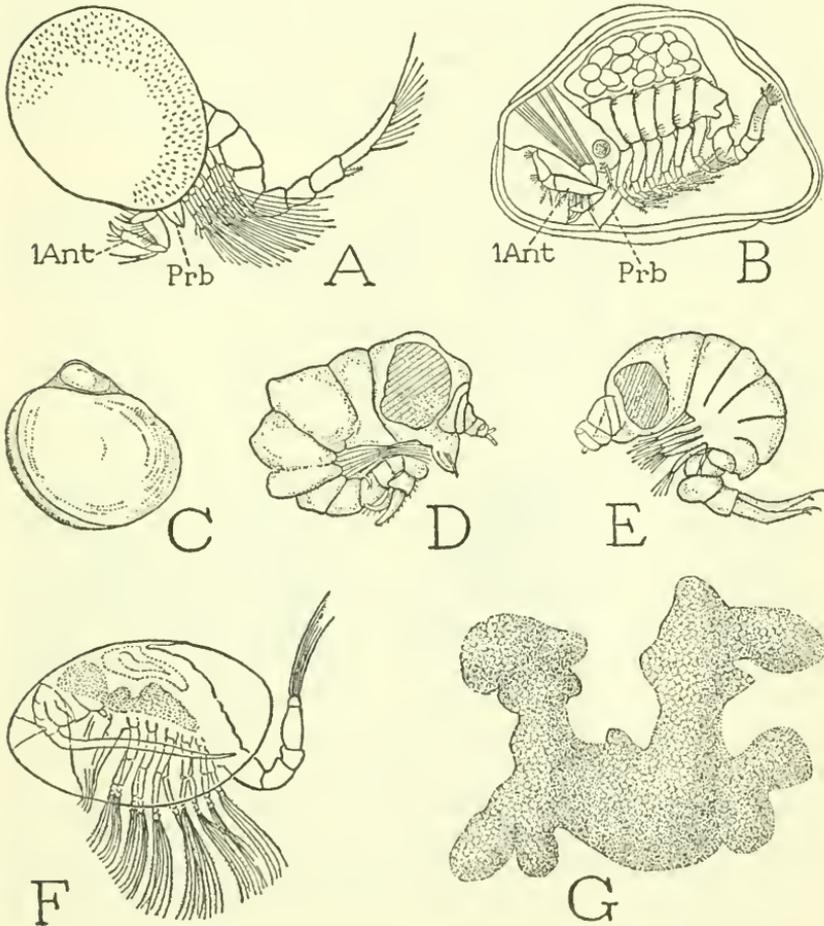


FIG. 13.—Cirripedia: Ascothoracica. (A from Norman, 1913; B from Okada, 1938; C, D, E from Heegaard, 1951; F, G from Knipowitsch, 1890.)

A, *Synagoga mira* Norman, adult. B, *Synagoga metacrinicola* Okada. C, *Ascothorax bulbosa* Heegaard, shell of female with small male on top, internal parasite of ophiuroid. D, same, female. E, same, male. F, *Dendrogaster astericola* Knipowitsch, cypris larva. G, same, adult enclosed in branched mantle, internal parasite of starfish.

Dendrogasteridae, which are internal parasites of echinoderms. *Dendrogaster astericola*, described by Knipowitsch (1890), is enclosed in a voluminous mantle (fig. 13 G) with large lateral lobes, which are penetrated by diverticula of the stomach. The cypris larva (F),

however, is a typical cirriped cypris, much resembling the adult of *Synagoga* (A). A species figured by Fisher (1911) as *Dendrogaster arbusculus*, found in a Californian starfish, has an elaborately branched structure.

The known nauplii of the Ascothoracica, according to Okada, differ from the nauplii of other cirripeds in the absence of the usual frontal horns, another feature that sets the ascothoracicans off as a primitive branch of the cirripeds. Some species hatch as nauplii, others as meta-nauplii, and still others in the cypris stage.

The Thoracica.—To this suborder belong the barnacles, which in the adult stage are enclosed in calcareous shells. Some are conical and sit flat on the substrate (fig. 14 F), others are flattened and supported on stalks (H). When either kind is broken open, however, there is exposed within the shell a shrimplike creature (G) lying on its back or standing on its head with its cirruslike feet, when active, sticking out of the top or side (H) with a waving movement.

The nauplius of a common barnacle such as *Balanus*, described by Runnström (1924-1925), has the typical naupliar structure (fig. 14 A) except for the pair of small horns (B, *fh*) on the anterior part of its body. Runnström describes two naupliar stages, but since the second becomes elongate and acquires rudiments of three postmandibular appendages it would ordinarily be called a metanauplius. After a few hours of swimming, the metanauplius abruptly transforms into a cypris (C) with a bivalve shell and long seta-bearing legs, wherewith it is better equipped for a pelagic life. Eventually the cypris fixes itself to a support by its first antennae (1*Ant*), each of which (E) is provided with an adhesive cup on the third segment. A cementing substance discharged through the antennae from glands in the head gives the cypris a permanent attachment. Then the cypris withdraws the hind part of its body and its legs into the shell, and now begins the formation of the plates of the adult barnacle. According to Runnström, the plates are first formed as chitinizations of the mantle and only later become calcified. When the plates have the essential adult pattern (D) the cypris shell is cast off, and with the moult the legs of the cypris are replaced by the cirri of the barnacle.

The metamorphosis of the cypris into the barnacle is not excessive. It is a structural adaptation to the permanently sessile condition within the shell, and the eyes are absorbed as now useless organs. The changes that take place in the body have been described by Doochin (1951). The shell-closing muscle of the cypris is retained (fig. 14 G, *mcl*), and the mantle supporting the plates of the shell is attached to

the body only around the ends of the muscle. The peduncle of the stalked barnacles is a product of the head and becomes occupied by connective tissue and muscles. The barnacles are hermaphroditic, but they generally live in crowded colonies and cross fertilization is made possible by a long, tubular penis arising at the base of the vestigial abdomen.

The Rhizocephala.—In this suborder of parasitic cirripeds we encounter the strangest metamorphic phenomena known in the whole

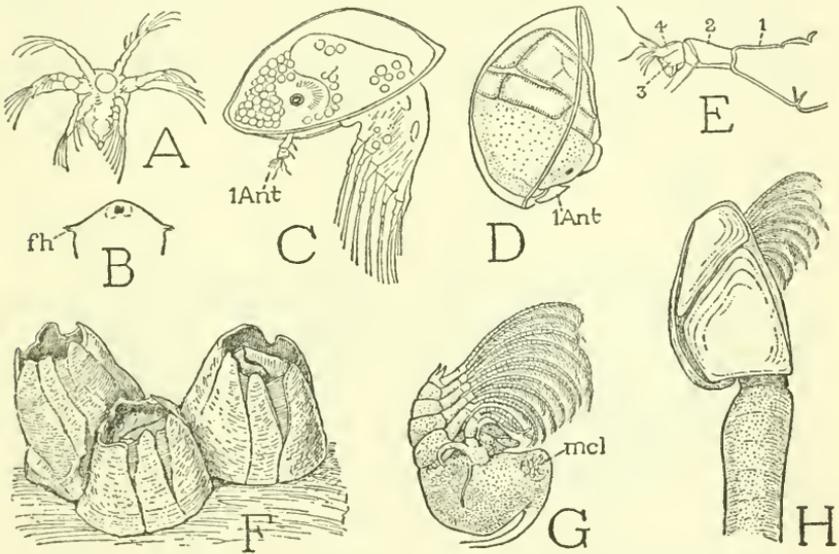


FIG. 14.—Cirripedia: Thoracica. (A-E from Runnström, 1924-1925.)

A, *Balanus balanoides* (L.), nauplius. B, same, anterior end of body with median eye and frontal horns (*fh*). C, same, cypris larva. D, same, later stage, barnacle plates formed inside cypris shell. E, same, first antenna of cypris with attachment cup on third segment. F, *Balanus eburneus* Gould, group of adults. G, *Lepas anserifera* L., adult animal in natural position removed from shell. H, same, stalked shell.

animal kingdom. The rhizocephalans include a number of genera, of which the best known are crab parasites of the genus *Sacculina*. The visible external evidence that a crab is parasitized by a sacculinid is the presence of a large saclike body attached ventrally on the crab at the base of the abdomen (fig. 15 A). This external sac is the reproductive part of the parasite containing the ovaries and the testes, but from it long, rootlike processes extend into the body of the crab and serve for the nutrition of the parasite. The eggs are fertilized and hatch within the external sac, giving rise to nauplii, which transform into typical cirriped cypris larvae. The free-swimming cypris

larvae escape through a hole in the sac, find another crab, and enter the latter after undergoing extraordinary transformation processes. The life history of *Sacculina carcini* Thompson was fully described and illustrated by Delage in 1884, and Delage's account has been verified, at least in part, by G. Smith (1906) and Veillet (1945). It still remains as the authentic history of a *Sacculina*, and the following story of the life and metamorphosis of this parasite is based on the papers by Delage and Smith, with illustrations taken from both.

The nauplius of *Sacculina* (fig. 16 A) has the characteristic frontal horns (*fh*) of cirriped nauplii, but it lacks an alimentary canal and has neither a mouth nor an anus. After several moults the nauplius becomes a cypris larva (B) with a length of 0.20 mm. On leaving

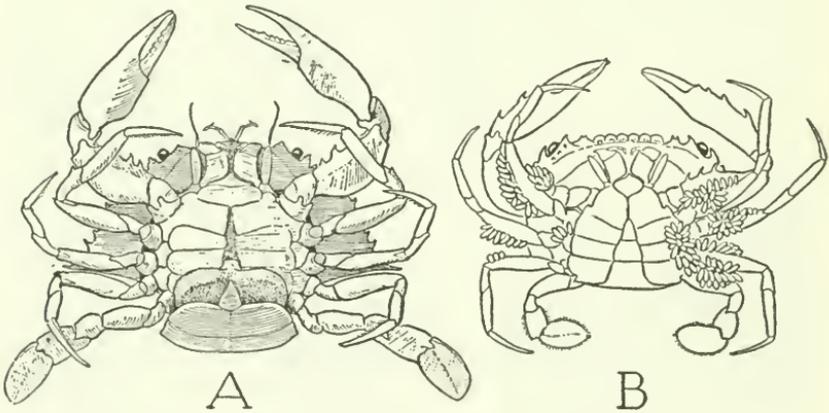


FIG. 15.—Cirripedia: Rhizocephala. External parasitic stages on crabs.

A, *Loxothylacus texanus* Boschma, a sacculinid on *Callinectes sapidus* Rathbun. B, *Thompsonia* on *Thalamita prymna* (Herbst) (from Potts, 1915).

the brood sac on the crab, the cypris leads a free life in the ocean for several days. Finally, on finding a young crab that has just moulted, it attaches itself to the latter by one of its antennules (*C*, *1 Ant*), which are provided with small suction cups. The point of attachment is usually in the membrane at the base of a hair (*HR*). When firmly secured the cypris begins violent swinging movements of the body, which detach the thorax (*Th*) along with the legs and the abdomen and throw the whole rear part of the body out of the shell (*Sh*). From the large hole thus left in the head end of the cypris are now expelled most of the internal tissues, leaving only a mass of cells containing the reproductive elements. Later the hole closes.

While this process of elimination has been going on, other changes take place. The body of the larva separates from the shell (*D*) and contracts to a sac walled by the ectoderm, which is much smaller than

the original cypris (B). Soon a new cuticle is secreted on the surface of the sac (D, *1Ct*) in continuity with the cuticle of the attached antenna, and the larva becomes a compact oval body still within the shell but now entirely free from it. Again, as if preparing for a moult, a second cuticle (*2Ct*) is formed beneath the outer one, and a small point (*d*) grows out from its anterior end into the hollow of the antenna. The body of the larva then retracts within the outer cuticle (E), and as it does so the cuticular point elongates into a long, hollow dartlike tube (*d*) with the narrow end cut off obliquely like the point of a hypodermic needle, and its widened base embedded in the body of the retracted tissue of the larva. This newly formed organ Delage called the *dart*, and the larva armed with the dart he termed a *kentrogon* (from Greek *kentron*, a dart, and *gonos*, a larva). The shell together with its loose inclusions is now thrown off, leaving the kentrogon, still enclosed in the outer cuticle, attached to the crab by the antenna (F).

The body of the larva again expands and pushes the dart into the antenna (fig. 16 F) until its tip comes into contact with the integument of the crab. Since the parasite is held fast by the antenna, the dart pierces the integument instead, pushing the larva away from it, and finally (G) projects into the body of the crab. Now the soft tissues of the larva contract away from the cuticle but remain still connected with the base of the dart. The remains of the larva thus have a free passageway into the body of the crab through the narrow channel of the dart, the orifice of which is said by Delage to be 3 to 6 microns in diameter. Though Delage says he did not observe the actual passage of the larval substance through the dart, globules are seen inside the dart and the parasite is next found inside the crab. By the method of the *Sacculina* a mouse might get into the pantry through the keyhole of the door, but once inside it would have to devise a new way of eating. This problem the *Sacculina* solves very easily—it simply adopts the feeding method of a plant by sending out absorbent roots among the organs of the crab.

Inside the crab the parasite becomes a small oval body consisting of a mass of cells enclosed in an ectodermal epithelium. It finds its way to the ventral side of the crab's intestine and here becomes attached. Now the principal concern of the parasite is to obtain nourishment from the host for maturing the germ cells which it has brought with it from the cypris stage. Incidentally, this will be the first food from an external source that the larva itself has had, since it was hatched without an alimentary canal. The larval body expands against the intestine of the crab (fig. 17 A) and sends out branching

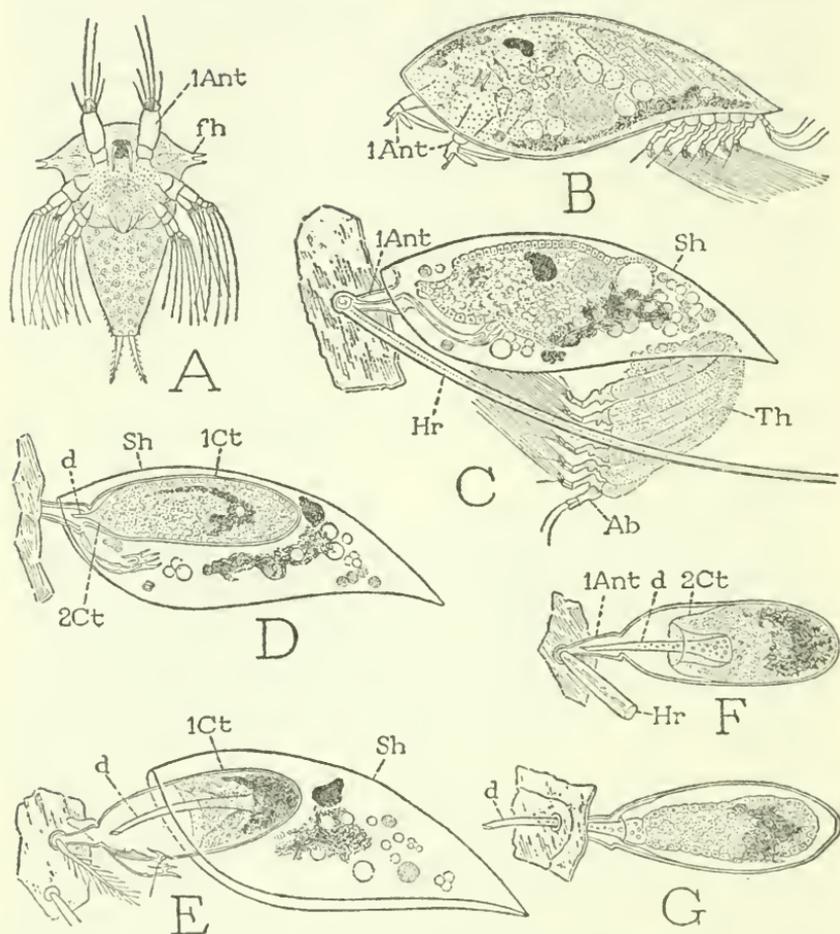


FIG. 16.—Cirripedia: Rhizocephala. Metamorphosis of *Sacculina carcini* Thompson (from Delage, 1884).

A, nauplius. B, free-swimming cypris stage ready to moult. C, cypris fixed by antenna at base of hair of crab, shell separated, thorax detached and thrown off with internal tissues. D, larva still in shell has formed a new cuticle (*1Ct*). E, shell being shed, larval body retracted within cuticle, with long, hollow "dart" (*d*) extended toward base of antenna. F, larva with a second inner cuticle (*2Ct*), the dart extended into antenna. G, larval body expanded, the dart has pierced the hair membrane of the crab.

Ab, abdomen; *1Ant*, first antenna; *1Ct*, outer cuticle; *2Ct*, inner cuticle; *d*, dart; *fh*, frontal horn; *Hr*, hair of crab; *Sh*, cypris shell; *Th*, thorax.

rootlike processes (*rhizai*), which continue to grow, branch, and unite until a network surrounds the intestine (B), from which branches penetrate between the other organs and extend out into the appendages. The roots do not enter the tissue of the crab, but Delage says only the heart and the gills are not attacked. These are the organs necessary for maintaining the life of the host and therefore that of the parasite, but how did the parasite ever learn to discriminate? The *Sacculina* at this stage has been aptly likened to a fungus. That a crustacean can be so transformed shows the unlimited potentialities of metamorphosis.

When nutrition has been fully provided for, attention must be given to the reproductive function. If the eggs were allowed to hatch inside the crab, the young larvae would find themselves in a prison from which there would be no escape. The body of the parasite, therefore, emerges through the ventral integument of the crab and becomes a brood chamber in which the eggs mature and from which the larvae are liberated into the ocean. The pressure of the parasite's body causes a dissolution of the crab's epidermis beneath it, and prevents the formation of cuticle at this point. Consequently at the next moult of the crab the *Sacculina* body containing the reproductive cells emerges and becomes external, but is still connected with the crab by a short peduncle giving passage to the feeding roots. The place of emergence is at the middle of an abdominal segment; if it were intersegmental, movements of the abdomen might constrict the peduncle and shut off the food supply of the parasite. It seems that the simpler a creature may be in its organization, the more does nature guard it against emergencies. It is interesting to note that the species shown at A of figure 15 is exactly modeled to fit into the pocket between the under surface of the thorax of the crab and the reflexed abdomen beneath it.

The external parasite, as seen in section (fig. 17 C, D) consists of a central mass of cells contained in a tunic suspended from the peduncle, and of an outer mantle (*mn*) that encloses a peripheral brood chamber (*bc*). The figures at C and D, taken from G. Smith (1906), depict a species of *Peltogaster*, but the structure is essentially the same in *Sacculina*. The cells of the central mass are the eggs in the ovary (*Ov*); above them is a pair of tubular testes (*Tes*) and a single nerve ganglion (*Gng*). The ripe eggs are discharged into the mantle cavity and here fertilized by spermatozoa from the testes, the parasites being necessarily hermaphroditic. The larvae escape in the cypris stage from an opening (D, *op*) in one end of the brood chamber. Successive lots of eggs are discharged and fertilized, and after each brood of larvae the cuticular lining of the brood chamber

is shed. The maturation of the sperm and the eggs and the fertilization of the latter are fully described by Smith, but here ends our discussion of the metamorphosis of *Sacculina*.

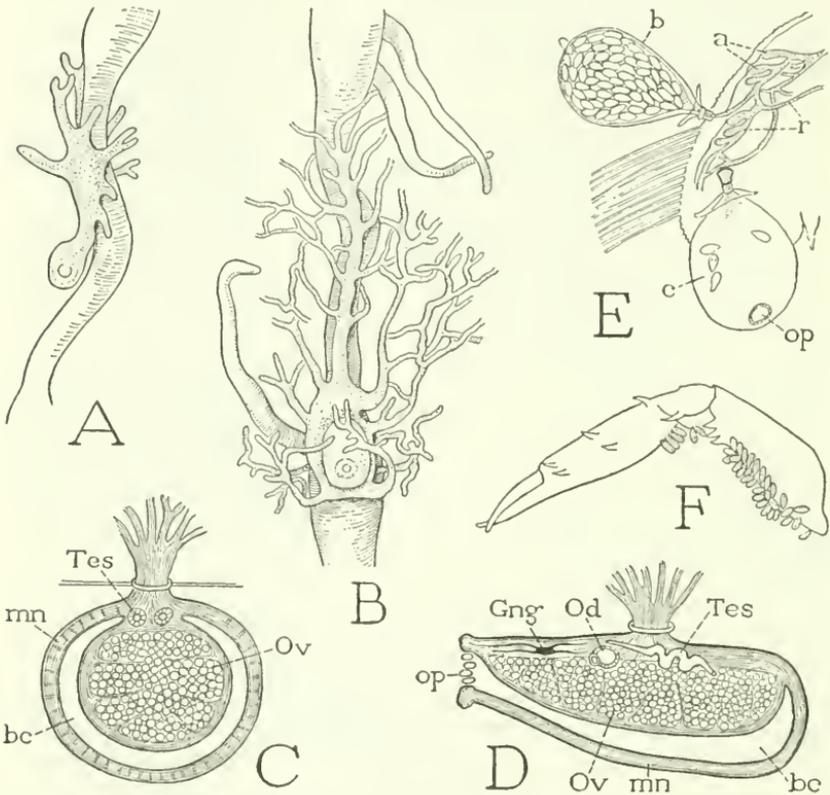


FIG. 17.—Cirripedia; Rhizocephala. Internal and external parasitic stages. (A-D from G. Smith, 1906; E, F from Potts, 1915.)

A, *Sacculina neglecta* attached on intestine of crab *Inachus scorpio*. B, same, later stage with root system developed. C, *Peltogaster* sp., diagrammatic cross section of parasite after emergence on ventral side of crab. D, same, longitudinal section. E, *Thompsonia* sp., part of root system in tail fan of crab *Synalpheus brucei*, with external brood sacs. F, same, external sacs on chela of *Thalamita prymna*.

a, internal reproductive buds; b, external brood sac containing cypris larvae; bc, brood cavity; c, external sac with all but a few larvae escaped through terminal aperture (op); Gng, ganglion; mn, mantle; Od, oviduct; op, external opening of brood cavity; Ov, ovary; r, nutritive roots; Tes, testis.

The parasitization of the crab by *Sacculina* adversely affects the gonads and results in structural changes of the host called *parasitic castration*. At the moult accompanying the emergence of the parasite, the male crab takes on certain female characters and the female suffers

a change from normal. Inasmuch as *Sacculina* produces only one reproductive body, the parasite has no concern with what happens to the host.

Peltogaster socialis, another rhizocephalan, differs from species of *Sacculina* in that a number of parasites, 2 to 30 of them, all in about the same stage of development, are found on the outside of one host. In his investigation of this species, G. Smith (1906) reported that each external parasite appeared to have its individual root system in the crab. Potts (1915) questioned the accuracy of Smith's observation, and suggested that more probably the several external parasites arise from a common root system, pointing out that *Peltogaster socialis* is a comparatively rare species and that it would seem unlikely that so many cypris larvae should attack the same crab at the same time.

That many external reproductive sacs may arise from one internal system of roots has been amply demonstrated by Potts (1915) in his study of the genus *Thompsonia*. Species of this genus, parasitic on various crabs, reach the ultimate in the conversion of an adult crustacean to the status of a fungus. The parasite within the host has the form of an extensive and intricate network of fine branching and anastomosing threads distributed principally on the ventral wall of the abdomen at both sides of the nerve cord, but also entering the thorax where the branches may extend up on the lateral and dorsal walls. The root threads, according to Potts, are from 10 to 20 microns in thickness. From the central network branches penetrate into the thoracic and abdominal appendages and into the lobes of the tail fan.

On the branches in the appendages are developed small budlike processes (fig. 17 E, *a*) that project outward against the integument. These buds contain the germ cells that will become ova. At the next moult of the crab they break through the soft new cuticle and become small external sacs (E, *b*, and F) standing on the surface. The sacs may be so numerous that the appendages, especially the legs, are loaded with them (fig. 15 B). These external sacs are the reproductive organs of the parasite, and might be likened to the spore-bearing bodies of a fungus mycelium. Since *Thompsonia* produces no male elements, the eggs are apparently parthenogenetic. They hatch directly into young cypris larvae (fig. 17 E), which, before the next moult of the crab, escape from the sac through an apical perforation (*op*). The empty sacs are carried off on the exuviae at the following moult of the crab. The development of the eggs, therefore, is so regulated that the larvae reach maturity during the time between moults of the host. At each moult a new crop of egg sacs breaks out on the

surface. *Thompsonia*, unlike *Sacculina*, appears to do no specific damage to its host, so that it can continue its parasitic life and indefinitely repeat its reproductive processes. The inoculation of the host by the free-swimming cypris has not been observed.

The *Thompsonia*-infested crab presents one of the most curious anomalies in the whole realm of nature. Here are two crustaceans, one inside the other, the crab a highly developed arthropod, the parasite, a crustacean relative of the crab, spread out inside the latter in the form of a network of filaments. Both host and parasite are adult animals, each being the reproductive stage of its species. Progressive and regressive evolution could hardly reach a greater degree of divergence.

Thompsonia is known to be a crustacean because it produces free-swimming cypris larvae, it is known to be a rhizocephalan because of its likeness to *Sacculina*, and *Sacculina* is known to be a cirriped because of the character of its nauplius. The barnacles and the rhizocephalans have in common the habit of attaching themselves to a support by the antennules in the cypris stage. From this point on they widely diverge. It would be highly interesting to know how the *Sacculina* larva learned to attach itself at the base of a hair on a crab, how it acquired the urge to get into the crab, and how it ever developed a self-reducing method for doing it. Halfway measures would be useless. Clearly there are problems in evolution for which natural selection does not offer a ready solution.

ISOPODA

Most of the Malacostraca are too large to be parasites. The majority are predatory, and few of them exhibit any considerable degree of metamorphosis. Most of them, moreover, hatch at a later period of development than do the Entomostraca, and some of them are almost completely epimorphic. A prominent exception to the general free mode of life, however, occurs among the isopods, a few species of which have adopted parasitism, and have become structurally adapted to a parasitic life in a degree equal to that of some of the entomostracans. This fact shows how readily metamorphosis can crop out independently in species that have adopted a new way of living.

The isopods in general are a conservative group in which the young hatch at a late stage of development with complete body segmentation and most of the appendages present. Among those that have become parasitic, however, varying degrees of adaptive metamorphosis occur

in the life history. Species that feed temporarily on the host only during the larval stages may undergo but little structural adaptation. On the other hand, species that are permanently parasitic are likely to go through a high degree of metamorphosis both in the larval and the adult stages. The two species described in the following pages, one belonging to the Gnathiidea, the other to the Epicaridea, may be taken to illustrate the two extremes of parasitic metamorphosis found among the isopods.

Paragnathia formica (Hesse).—This isopod, parasitic in its larval stage on fishes, gives us a good example of a parasite that undergoes but a minimum of metamorphic adaptation to life on its host. The developmental life history of *Paragnathia formica* has been amply described by Monod (1926) and the following account with accompanying illustrations (fig. 18) is taken from Monod's work.

The adult males and females live together in small burrows excavated in semihard mud banks of stillwater estuaries below the mean level of the ocean. Here the pregnant females in late summer or early fall give birth to active larvae. The newborn larvae leave the burrow, swimming with great speed by movements of the abdomen. Once in the open water they lose no time in attaching themselves to a fish; most any fish will do. The time between birth and attachment is a period of dispersal, during which the larva takes no food, subsisting on the remains of yolk in its alimentary canal. The larva attaches itself on the fish with its second maxillipeds, and the attack is made at any place that will readily yield blood, such as the membrane between the rays of a fin, the gills, or the mouth.

The swimming larva (fig. 18A) is a fully segmented young isopod with large compound eyes and a complete equipment of appendages. In its embryonic development it has been provided in advance with efficient piercing mouth parts and a sucking apparatus. The mouth parts (G) are enclosed in a large conical proboscis projecting forward from the head, formed of the epistome (*Epsi*) above and the first maxillipeds (*1Mxpd*) below. The long, strongly toothed mandibles (*Md*) are but little movable; they serve as harpoons to hold the parasite close to the fish while the sharp-pointed, freely movable first maxillae (*1Mx*), supported by the paragnaths (*Pgn*) beneath them, puncture the integument. The much reduced second maxillae (*2Mx*) have no recognized function in feeding.

When the young larva (fig. 18A) has once established itself on a fish and has begun to feed on the blood of the host, its form changes; the change is said by Monod to be effected without the intervention of a moult. The thorax lengthens, accompanied by a swelling of the

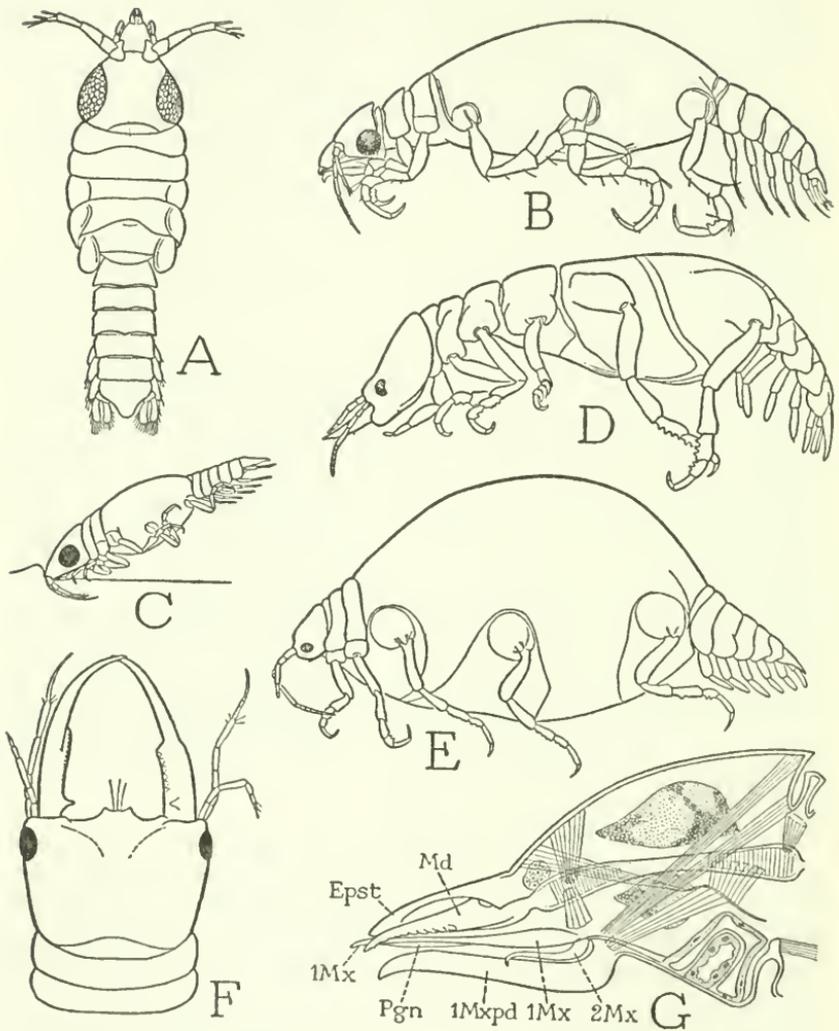


FIG. 18.—Isopoda: Gnathiidea. *Paragnatha formica* (Hesse) (from Monod, 1926).

A, first free-swimming larva. B, second form of larva parasitic on a fish. C, attitude of feeding larva. D, adult male. E, adult female. F, head of adult male, dorsal. G, section of larval head showing piercing mouth parts.

Epst, epistome; *Md*, mandible; *1Mx*, first maxilla; *2Mx*, second maxilla; *Mxpd*, maxilliped; *Pgn*, paragnath.

last three segments (B); the segmental limits disappear owing to the unfolding of the previously deeply infolded intersegmental membranes. This is the feeding stage of the parasite (B, C), called the *pranize* by Monod (L., prandium, lunch). Its meal lasts about six months.

At the end of winter or the beginning of spring the fully fed parasites leave the host and return to the bank of the estuary. The males individually dig burrows or take possession of empty ones in advance of the coming of the females. The completed burrows are 1.5 to 2.5 cm. in depth, sloping downward from the mouth to an inner chamber 4 or 5 mm. in diameter. When the females arrive they enter burrows already inhabited by a male; as many as 10 or more may consort with a single male. Within the burrows both the male and the females undergo their first and only moult, accompanied by a small degree of metamorphosis. The cuticle splits crosswise over the thorax, and the two ends are cast off separately. The sexes are now differentiated and the isopods enter their third functional stage, which is that of reproduction. The male (fig. 18D) retains a relatively slender figure, but the female (E) becomes greatly distended with the development of the ovaries. The mouth parts of both sexes are reduced, except the mandibles of the male (F), which are long prongs perhaps used for digging or for holding the female in mating. Subsistence is now at the expense of the food consumed during the parasitic stage.

The eggs develop into mature larvae within the ovaries of the female, which become distended into a pair of large, saclike uteri, compressing the empty alimentary canal between them. On the ventral surface of the female's thorax are several pairs of small overlapping oostegite plates, and above them is a large atrial cavity, into which the oviducts open, but this cavity does not serve as a brood chamber. When the young issue from the uteri through the oviducts into the atrium, the oostegites open and the larvae precipitate themselves head first through the aperture directly into the water, where they at once begin active swimming. After giving birth to the young, the females quickly die, but the males are longer lived and their metamorphosis is not so closely correlated with the season.

There is clearly in the life history of *Paragnathia formica* little that can be called a true metamorphosis. The change of form between the two larval phases is merely a distention and elongation of the thorax resulting from the unfolding of the intersegmental membranes. The metamorphosis at the moult to the adult stage involves principally a reduction of the mouth parts which are no longer used for feeding.

Since most isopods have biting and chewing mouth parts, the conversion of the mouth parts in the embryo of *Paragnathia* into piercing organs may be regarded as an embryonic metamorphosis preparing the future larva for its prospective life as a parasite.

Danalia curvata Fraisse.—This isopod belongs to the suborder Epicaridea, the members of which are parasitic on other crustaceans. It gives us an example of the sex versatility of some of the epicarideans in which the animal is first a functional male and then a functional female. In its female role *Danalia curvata* attaches itself to a crab infested with a rhizocephalan and feeds either on this parasite in its external state or on its roots in the host. Here the female is inseminated by a young free-swimming male, after which the male attaches to the crab and becomes a female. In this manner, though the species is hermaphroditic, it avoids self-fertilization. The following outline of the life history of *Danalia curvata* is taken from the work of G. Smith (1906) and of Caullery (1908).

The mature female (fig. 19 H) has no likeness whatever to a crustacean; she is little more than a sac full of eggs attached to the crab by a narrow stalk inserted into the crab's body. The young on hatching leave the brood pouch of the mother and become free-swimming larvae. At this stage the larva (A) is recognizable as an immature isopod, and is called a *microniscus*. The larva is distinctly segmented, has two pairs of antennae, five pairs of thoracic appendages, and five pairs of pleopods, but eyes are absent and the mouth parts are reduced to a pair of styliform mandibles enclosed in a small buccal cone. The microniscus larva may adopt a copepod as a temporary host, as do most of its relatives. After several moults it takes on a different form (B, C) and is now termed a *cryptoniscus*, presumably because its isopod characters are less evident. The body is more elongate and eyes have been developed, the appendages are retained; the cryptoniscus is a free-swimming stage. Within its body is a pair of large hermaphroditic sex organs (B), each of which contains in its anterior end a small ovary (*Ov*) and in its posterior part a large testis (*Tes*). The testes rapidly develop and become filled with an abundance of spermatozoa. The larva is now a functional male.

The male cryptoniscus seeks out a crab parasitized by a sexually mature female of his own species (G). After accomplishing the insemination of the female the larval male attaches himself to the crab or to the *Sacculina* on the crab by the first two pairs of his chelate pereopods. Then a moult takes place, the cuticle being shed in two pieces from the opposite ends of the body, and it is then seen that the larva has undergone a radical change of structure within the

cryptoniscus cuticle. The body has become a small cylindrical sac (D) about one and a quarter millimeters in length in which all trace of segmentation has disappeared. The eyes are gone, and all the

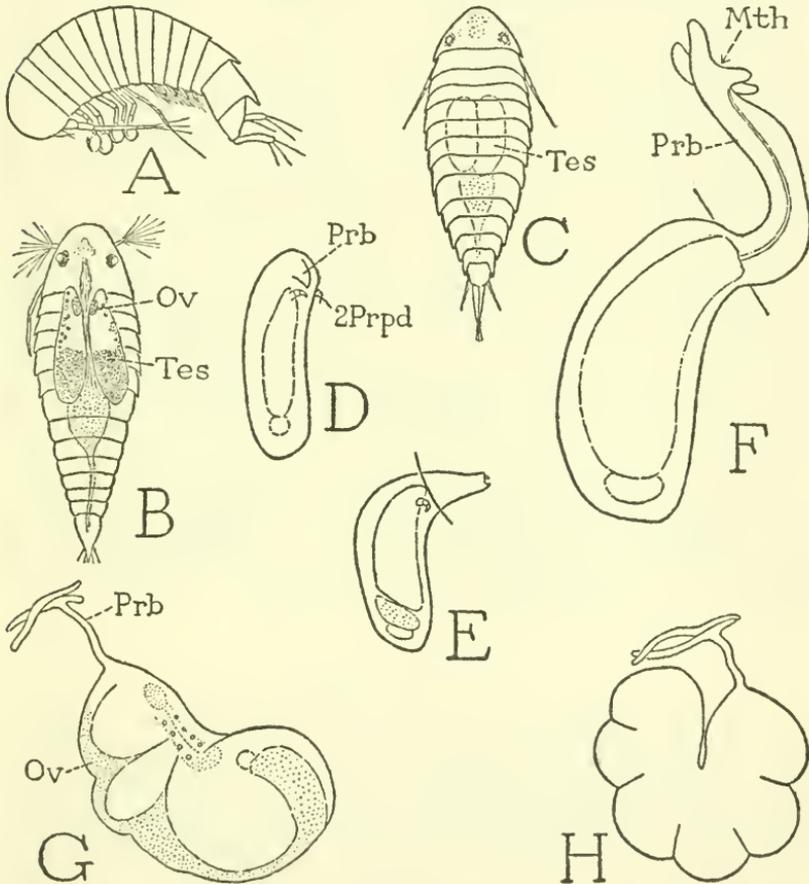


FIG. 19.—Isopoda: Epicaridea. Life history of *Danalia curvata* Fraisse. (A, C-H from Caullery, 1908; B from G. Smith, 1906.)

A, first instar larva. B, second free larval stage, with hermaphroditic sex organs containing small ovaries and large testes. C, larva with testes fully developed. D, parasitic larva on crab. E, same, with proboscis elongated. F, functional female stage, with testes degenerated, ovaries fully developed. G, female containing brood sac. H, female in final stage.

Mth, mouth; *Ov*, ovary; *Prb*, proboscis; *2Prpd*, second pereiopod; *Tes*, testis.

appendages have been cast off with the exuviae except a pair of small hooklike second pereiopods (*2Prpd*) with which the parasite maintains its hold on the host. A small conical proboscis (*Prb*) bears the mouth on its end. The testes, now that they have performed their

function, degenerate and the ovaries begin to develop, so that the former male larva thus changes functionally to a female.

As a female, the parasite begins to increase in size. First the proboscis elongates (fig. 19 E) and, though it is armed with only a pair of minute teeth, it penetrates the integument of the crab. Inside the host the proboscis stretches out to a long neck (F, *Prb*) until the mouth (*Mth*) at the end comes in contact with the roots of the *Sacculina*, and four diverging processes grow out around the mouth to anchor the proboscis in the tissues of the crab. The body of the newly feminized individual then takes on a saclike form (G). The ovaries (*Ov*) are now fully developed; the oviducts open on two pairs of ventral papillae. At this stage the female is inseminated by a cryptoniscus larva still in the male phase of development (C). The fertilized eggs are discharged into a large incubation chamber beneath the cuticle of the female. The process of forming the chamber is somewhat complex as described by Caullery, but essentially it appears that two lateral ingrowths of the ventral ectoderm extend inward around the sides of the body, and eventually close over the orifices of the oviducts. When the eggs are discharged into the incubation chamber, the female ceases to feed, doubles on herself in the form of a U (H) and becomes a mere inert sac in which the eggs complete their development.

EUPHAUSIACEA

The Euphausiacea and some of the Penaeidae are exceptional among the Malacostraca in that they are hatched as nauplii. They are both marine and entirely pelagic. The euphausiids go through many moults before reaching the adult stage. Students of the group commonly distinguish five immature stages in the life history of an individual. The first two are the nauplius and the metanauplius, the following three stages are termed the *calyptopis*, the *furcillia*, and the *cyrtopia*. These forms, however, are merely stages of growth characterized by different degrees of differentiation toward the adult structure (fig. 20 A-G). Except for the successive specialization of different groups of appendages for swimming there are few metamorphic changes involved in the development. The following condensed account of the typical life history of a euphausiid species is based on the papers by Heegaard (1948) and Lebour (1925), with illustrations taken from both. The order includes only a single family, the Euphausiidae.

The newly hatched euphausiid larva (fig. 20 A) is a typical nauplius of simple form with the usual three pairs of appendages, a simple

median eye, and a large labrum. The metanauplius (B) acquires three additional pairs of appendages, which are the first and second maxillae and the first pair of legs (*1L*), or maxillipeds. The mandibles (*Md*)

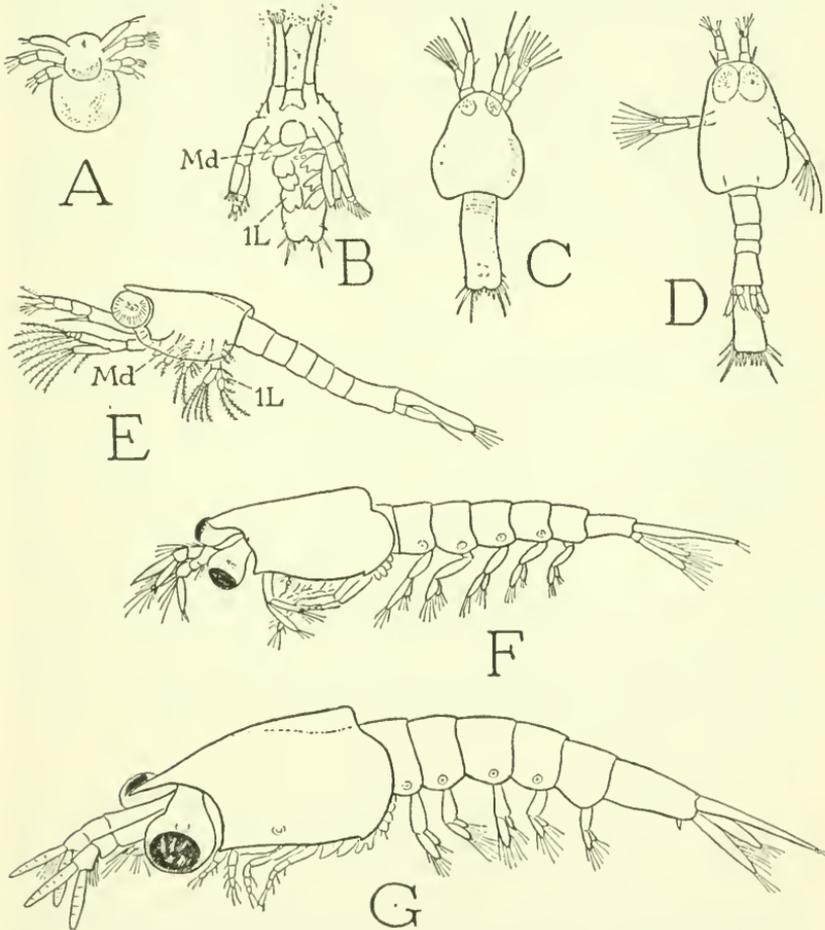


FIG. 20.—Euphausiacea. Life-history stages. (A-E from Heegaard, 1948; F, G from Lebour, 1925.)

A, *Meganyctiphanes norvegica* Sars, nauplius. B, same, metanauplius. C, same, first calyptopis instar. D, same, third calyptopis instar. E, same, first furcillia instar. F, *Nyctiphanes couchii* Bell, last (12th) furcillia instar. G, *Meganyctiphanes norvegica*, first cyrtopia instar.

have become jawlike. The metanauplius is followed by the calyptopis stage, which at an early instar (C) is characterized by the distinct development of the carapace and the elongation of the abdomen. The median eye is replaced by sessile rudiments of compound eyes concealed beneath the carapace. The appendages are those of the metanauplius. At a later calyptopis instar (D) the abdomen has become

segmented and the uropods are developed. In the furcillia stage (E, F) the larva begins to resemble the adult. The eyes are now stalked and project from beneath the carapace. The first furcillia instar (E) has still only the appendages of the metanauplius, but after the first moult the pereopods appear as simple papillae, which later enlarge (F, G) and finally become biramous appendages. At the same time the pleopods are formed. According to Lebour (1925) in *Nyctiphanes* and *Meganyciphanes* there are 12 furcillia instars separated by moults. In the final cyrtopia stage (G), after 8 to 13 moults according to the species, the young euphausiid acquires the adult structure with a complete set of appendages and luminescent organs.

DECAPODA

The decapod crustaceans include the shrimps, lobsters, crayfishes, and crabs. None of them exhibits any pronounced metamorphic changes during development or in the adult stage, but most of them go through stages of growth characterized chiefly by the successive development of sets of appendages. Only in the Penaeidae is there a free nauplius and a metanauplius. Most species hatch in a form called a *zoea*, in which the appendages following the second maxillipeds are as yet undeveloped or are present as rudiments. With the functional completion of the pereopods the larva is known as a *mysis* from its fancied resemblance to a member of the Mysidacea. Some species, however, go through the zoea stage in the egg and hatch as a *mysis*, and a few are almost completely developed in the adult form on leaving the egg.

The decapod larvae are free swimming, and in general are fairly uniform in structure with a fully developed carapace and a long segmented abdomen. A few, however, take on unusual forms. Among the Sergestidae many of the larvae are characterized by a great development of long, often profusely branched spines on the thorax and abdomen. The rounded carapace of the palinuran *Polycheles* larva looks like a spiny burr, and others of the same group, known as phyllosome larvae, are broad, flat, and leaflike in shape. Presumably such forms are adaptations to buoyancy or floating.

The Penaeidea.—In this order the family Penaeidae is of particular interest because it includes the only decapods that begin life as free-swimming nauplii. The fact that among the Malacostraca both the penaeids and the euphausiids hatch from the egg as nauplii may be taken as evidence that primarily all the crustaceans hatched at this early stage of development, and that later hatching among the higher Malacostraca is secondary, resulting from the earlier stages being

completed for better security in the egg. The life history of *Penaeus setiferus* (L.) is now well known from the studies of Pearson (1939) and Heegaard (1953), and will here be briefly reviewed from the papers by these two authors. The penaeid life history, moreover, will serve also as a good subject for a discussion of the significance of crustacean larval forms.

Both the nauplius and the metanauplius of *Penaeus* (fig. 21 A, B) have long swimming appendages, but the alimentary canal is not yet developed and the larvae in these stages subsist on the yolk derived from the egg. In the metanauplius (B), however, the mandibles have acquired gnathal lobes on their bases, and rudiments of four pairs of postmandibular appendages are present, the last being those of the second maxillipeds (*2Mxpd*). The metanauplius goes over into the zoeal stage, in which there are three instars. In the first zoea (C) the carapace has developed, the mandibles have become functional jaws, and the larva now takes its first external food. The following appendages have developed into biramous limbs, and the abdomen shows a faint trace of segmentation, but the larva apparently still swims by means of the antennae. In the third zoeal instar (D) the larva takes on something of the adult form (G). The carapace covers the thorax, and rudiments of the pereopods (D, *Prpds*) are present, the abdomen is fully segmented but pleopods have not yet appeared, and the antennae are still the chief organs of propulsion. The third zoea is followed by the so-called mysis stage, which goes through two instars. In the first mysis (E) the pereopods are all present and have long seta-bearing exopodites, which now assume the locomotor function, and the antennae are reduced. The abdomen has well-developed uropods, but pleopods are as yet absent.

The next stage (fig. 21 F), known as the *postmysis*, or *postlarva*, more nearly resembles the adult. The pereopods have lost their exopodites, and those of the first three pairs are chelate. Slender uniramous pleopods are present on the abdomen and are now the swimming organs as they are in the adult. In the adult (G) the pleopods have acquired the typical biramous structure, and a long filamentous flagellum arises from each second antenna.

The life-history stages of *Lucifer*, as described by Brooks (1882), are similar to those of *Penaeus*, except that the larva hatches as a metanauplius and the animal takes on a different form in its preadult and mature stages. Numerous examples of the bizarre larvae of Sergestidae, characterized by long, branched spines on the thorax and abdomen, are illustrated by Gurney (1924).

There has been much discussion among carcinologists as to whether or not the forms of decapod larvae have a phylogenetic significance.

Gurney (1942) has pointed out that "the larval stages of today provide evidence for phylogeny, but indirectly," since the ontogeny of an animal recapitulates the ontogeny of its ancestors.

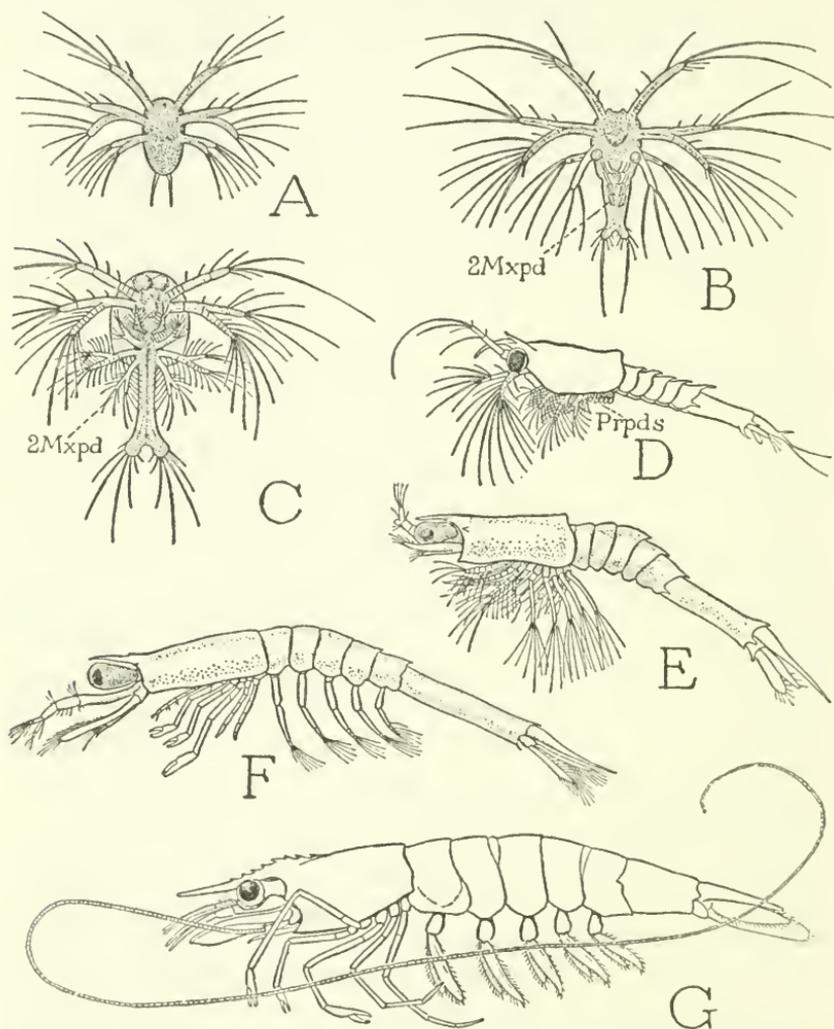


FIG. 21.—Decapoda: Penaeidea. Developmental stages of *Penaeus setiferus* (L.). (A-F from Pearson, 1939.)

A, first nauplius. B, metanauplius. C, first protozoa. D, third protozoa. E, first mysis. F, first postmysis. G, adult.

2Mxpd, second maxillipeds; *Prpds*, rudiments of pereopods.

It is true that ontogenetic stages of a species may represent in a modified way adult ancestral stages of phylogenetic evolution. The *adult* ancestry of a crustacean, however, can go back only as far as

the primitive adult arthropod from which the Crustacea were evolved. Life-history stages representing adult crustacean ancestors, therefore, can be recapitulations only of forms that intervened in evolution between the primitive arthropod and the modern crustacean.

On the assumption adopted in the early part of this paper as a basic concept, the primitive arthropod is presumed to have been an elongate, segmented animal with a pair of similar jointed appendages on each body segment (fig. 1 C). From such a progenitor all the modern arthropods were evolved by special modifications, particularly of the appendages, according to the adopted way of living. *Anaspides* (D) may be taken as an example of a fairly generalized modern crustacean, but other crustaceans go through no developmental stage resembling *Anaspides* or any other form that might be intermediate between their adult structure and that of a primitive arthropod. The megalops of a crab undoubtedly represents an early crab form, but there is little evidence that the Crustacea in general recapitulate adult stages of crustacean ancestry or the adults of other species of lower rank in taxonomy. There is no reason to believe that the likeness of the "mysis" stage of the penaeid (fig. 21 E, F) to an adult *Mysis* is anything more than a superficial resemblance. Foxon (1936) has shown that the decapod larvae do not go through a typical euphausiid or mysid stage, and that neither the structure nor the function of the mysid appendages is recapitulated in other groups. The precocious development of the uropods before the pleopods are formed is explained by Foxon (1934) as an adaptation to reverse movement.

Most crustaceans develop by anamorphosis, but the anamorphic method of growth was established in the remote progenitors of the arthropods before the arthropods became arthropods. The embryo in the egg goes through the preanamorphic stages of its ancestors, and if it is hatched as a nauplius, the following ontogenetic stages recapitulate the anamorphic steps of precrustacean evolution. The larva, however, is destined to be a crustacean, it carries the genes of its species, and its crustacean destiny is thus stamped on it before it leaves the egg. Hence, from the beginning of its development the larva takes on crustacean characters, but the forms it assumes are ontogenetic and not recapitulations of adult crustacean evolution. When the larva is set free at a very immature stage it must be structurally adapted to the exigencies of an independent life, and it may be modified for a way of living that was not at all that of its ancestors. Thus the normal ontogenetic stages may take on metamorphic aberrations having no relation to anything in the past history of the animal

or to its own future adult stage. Such nonancestral forms are particularly evident in parasitic species.

Gurney (1942), referring to the progressive shift of the swimming function in the larva from the antennae to the pereopods and finally to the pleopods, has expressed the idea that "the fundamental fact which determines the organization of the larva is the mode of locomotion." However, it is to be presumed that the use of the pleopods for swimming was first established in the adult ancestors of such species. The nauplius naturally cannot swim in this ancestral manner, and must use what appendages it has. As the larva grows by the addition of segments and appendages it can more efficiently swim by making use of the pereopods, and finally when the pleopods are developed it can swim in the adult manner. It is the progressive organization of the larva, therefore, that determines the mode of locomotion.

The Macrura.—The macruran decapods are the lobsters and the crayfishes. The lobster, *Homarus*, according to S. I. Smith (1871-1873) undergoes its early development in the egg and hatches at a stage when all the pereopods are present and are equipped with feathery exopodites. This first free stage of the lobster (fig. 22 A), therefore, corresponds with the mysis stage of *Penaeus* (fig. 21 E). In the next instar the larva increases somewhat in size, and rudiments of pleopods appear on the abdomen. In the third instar (fig. 22 B) the young lobster attains a length of 12 to 13 mm. and much resembles the adult; the chelae are well developed, the pleopods are biramous, but the exopodites are still present on the pereopods. Smith suggests that there is probably another instar intervening between the third and the adult when the exopodites are lost, as in the postmysis of *Penaeus* (fig. 21 F).

The fresh-water crayfishes, *Astacus* and *Cambarus*, hatch at a later stage of development than *Homarus*, when they have practically the adult structure except for the lack of the first and sixth pleopods.

The Brachyura.—The brachyurans, or "short-tailed" decapods, are the ordinary crabs, so named because of the small size of the abdomen, which in the adult is carried bent forward beneath the thorax. The zoal larvae are characterized in most species (fig. 23) by the presence of a long dorsal spine on the thorax and by the spinelike form of the rostrum, the two often projecting in a straight median line from opposite ends of the back. Some have also lateral spines. The larva swims with the large first and second maxillipeds, and the spines are supposed to assist in directing the course of the larva in the water or to help keep it afloat. The spines are absent in only a few species, as in the genus *Ebalia* and in members of the Pinnotheridae. The last

zoea transforms into a preliminary crablike stage known as a *megalops*.

The life history of the blue crab of the Chesapeake Bay, *Callinectes sapidus* Rathbun, has been studied by Churchill (1942), Hopkins (1944), and Sandoz and Hopkins (1944), and is typical of the development of most of the Brachyura. The young crab is sometimes hatched in a final embryonic stage called by Churchill a *prezoea* (fig. 23 A). It is still enclosed in a thin, transparent, closely fitting cuticle

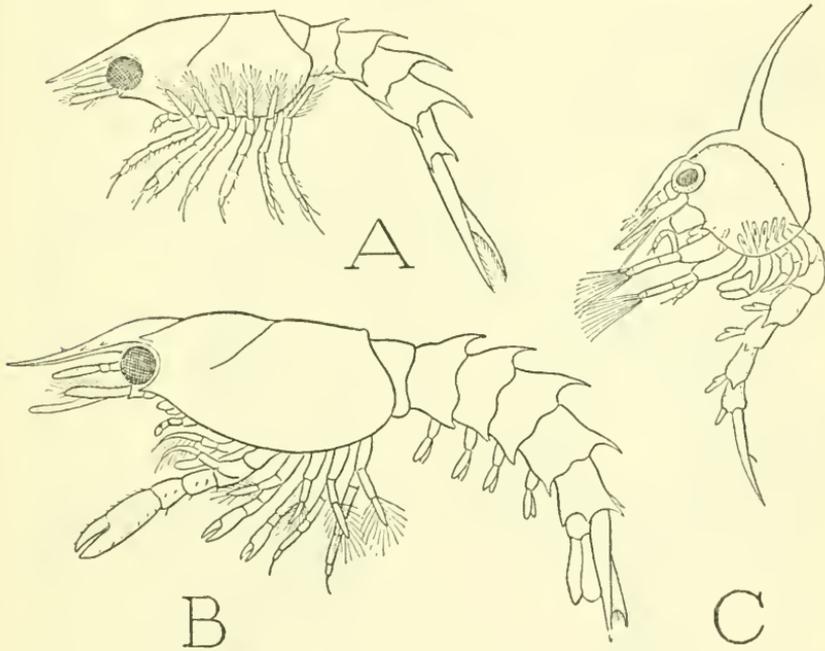


FIG. 22.—Decapoda: Macrura and Brachyura. Young stages. (A, B from S. I. Smith, 1871-1873; C from Cano, 1891.)

A, *Homarus americanus* H. Milne Edw., first larval instar, zoea. B, same, third instar. C, *Pilumnus*, a brachyuran crab, metazoea with partly developed chelipeds and pereopods.

that covers the spines, which will be exposed at the first moult. Sandoz and Hopkins say that emergence in the prezoeal stage results from unfavorable conditions at the time of hatching. The first free larva is a typical crab zoea (B) about 0.85 mm. in length. It has a short, rounded carapace and a long, slender, segmented abdomen. The last appendages are the large first and second maxillipeds, the exopodites of which are equipped with terminal fans of long featherlike bristles. The sixth segment of the abdomen is still united with the telson. In the second zoea (C) there is no essential change of structure, but the

body and appendages have increased in size. Churchill describes five zoeal instars in *Callinectes sapidus*, but his figures of the third, fourth, and probably the fifth instar are said by Hopkins (1944) to be larvae of some other crab. The differences, however, are slight and pertain mostly to the number of setae on the appendages and spines on the abdomen. In the fifth instar (D) the last abdominal segment is separated from the telson and pleopods are present. About the only

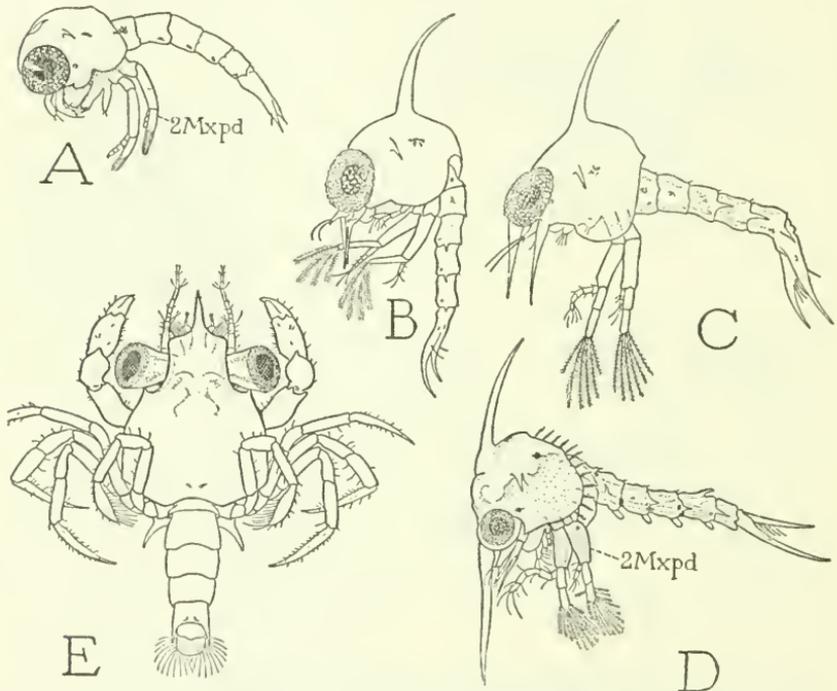


FIG. 23.—Decapoda: Brachyura. Larval stages of *Callinectes sapidus* Rathbun (from Churchill, 1942).

A, prezoa. B, first zoea. C, second zoea. D, fifth zoea. E, megalops.

metamorphic features of the crab zoea are the development of the dorsal and rostral spines and the adaptation of the maxillipeds for swimming.

During the zoeal stage buds of the third maxillipeds and of the pereopods appear on the thorax beneath the carapace and increase in length in successive instars, but they are not seen in Churchill's figures (fig. 23). It seems hardly likely that the zoea shown at D of the figure could go over directly into the megalops (E). In the final zoea of other crabs, sometimes called a *metazoea*, the appendages behind the second maxillipeds are well developed, as shown by Cano

(1891) in the metazoea of *Pilumnus* (fig. 22 C). The first and second maxillipeds still have the zoeal structure, but they are followed by the third maxillipeds and five pairs of pereopods, of which the first are strongly chelate. Moreover, all these newly developed appendages except those of the last two pairs support branchial lobes on their bases. Similar advanced larval instars are shown for several other species of Brachyura by Lebour (1928). Hence, we should assume that there must be in *Callinectes* a metazoeal instar in which the thoracic appendages are in a state of development that could go over at one moult into the appendages of the megalops. In the life history of the crab there is no form corresponding to the mysis stage of *Penaeus* (fig. 21 E) or that of *Homarus* (fig. 22 A), but the metazoea might be likened to the postmysis of *Penaeus*.

The megalops (fig. 23 E) is clearly a young crab, though it is only a few millimeters in length. The dorsal spine of the zoea has been shed with the larval cuticle (fig. 22 C) and the rostrum is shortened to the ordinary length. The swimming maxillipeds are transformed into feeding organs, and the other appendages are those of the adult. The prominent stalked eyes give the megalops its name ("bigeye"). An important feature of the megalops, however, is the extension of the abdomen from the thorax, which suggests that the megalops represents an adult ancestral form of the crab before the latter permanently flexed its abdomen forward beneath the thorax.

The adult crab on issuing from the cuticle of the megalops is still a minute creature and goes through a large number of instars before becoming sexually mature, after which it may continue to moult at intervals. The habits of adult crabs are more various than those of the larvae. While most adult crabs live in the ocean and crawl on the bottom, some of them live in the shells of mollusks, in echinoderms, in cavities of corals, and in tubes of worms. Others have left the water for the land, where they dig deep burrows in the sand above high water, and still others go freely inland, even invading human habitations. The famous anomuran robber crab of the South Sea Islands is said to climb cocoanut trees for their nuts. Regardless of their habits or the nature of their dwellings, however, the brachyuran crabs have undergone little structural adaptation. They vary in size and shape, in the relative size of the chelae, and in the length of their legs, but in general they retain the typical crab structure. Among the Anomura, however, a pronounced adaptive modification of the body occurs in the hermit crabs that live in snail shells. The carapace of these crabs is weak and flexible. The abdomen is a long, soft sac that

fills the cavity of the snail shell; pleopods are present generally on the left side only, but the uropods are strong, recurved appendages evidently serving to secure the crab in its house.

STOMATOPODA

The stomatopods are an individualistic group of malacostracans having some relatively primitive features in combination with so many structural specializations that it is difficult to give them a definite place in taxonomy. The head of the adult animal (fig. 24 G), projecting from beneath a small rostral lobe of the carapace, has a complex structure not found in any other crustacean. The short, narrow carapace covers only the gnathal region and the first four thoracic segments. The other four free segments of the thorax are symmetrical with the large abdomen, and appear to be a part of it except for the leglike appendages borne on the last three. The limbs of the first, third, fourth, and fifth thoracic segments are turned forward and each bears a small apical chela; but those of the second segment (αL) are huge raptorial organs in which the terminal segments are long, strongly toothed claws, each closing tightly against the penultimate segment, giving the stomatopod its likeness to the insect praying mantis (which is not responsible for its name). The large abdomen has five pairs of pleopods, and the stomatopod gills are borne on the pleopods. The uropods are large, biramous appendages; the telson is a broad spiny plate.

The adult stomatopods are mostly littoral in their habits. Though they swim freely, they live principally in burrows in the sand or mud of the bottom. The females lay their eggs in a mass beneath the fore part of the body, where they are held between the raptorial legs by the four small chelate legs of the thorax. The eggs are carried in this manner until the young larvae emerge, a period said by Giesbrecht (1910) to last for 10 or 11 weeks.

The young stomatopods are hatched in two different larval forms, which seem to have no developmental relation to each other. Our best source of information on the larval stages will be Giesbrecht's (1910) elaborate monograph on Mediterranean species. Gurney (1946) gives descriptions and good illustrations of various stomatopod larvae, but no full account of the life history of any one species. Alikunhi (1952) describes and figures particularly the last-stage larvae of Indian species.

The simpler first-stage larval form pertains to species of *Lysiosquilla* and *Coromida*, and is termed by Giesbrecht an *antozoea*. This

larva (fig. 24 A) is from 2 to 2.25 mm. in length. The thorax is fully segmented and is entirely covered by the carapace. The abdomen (*Ab*) is either unsegmented and entirely united with the telson (*Tel*)

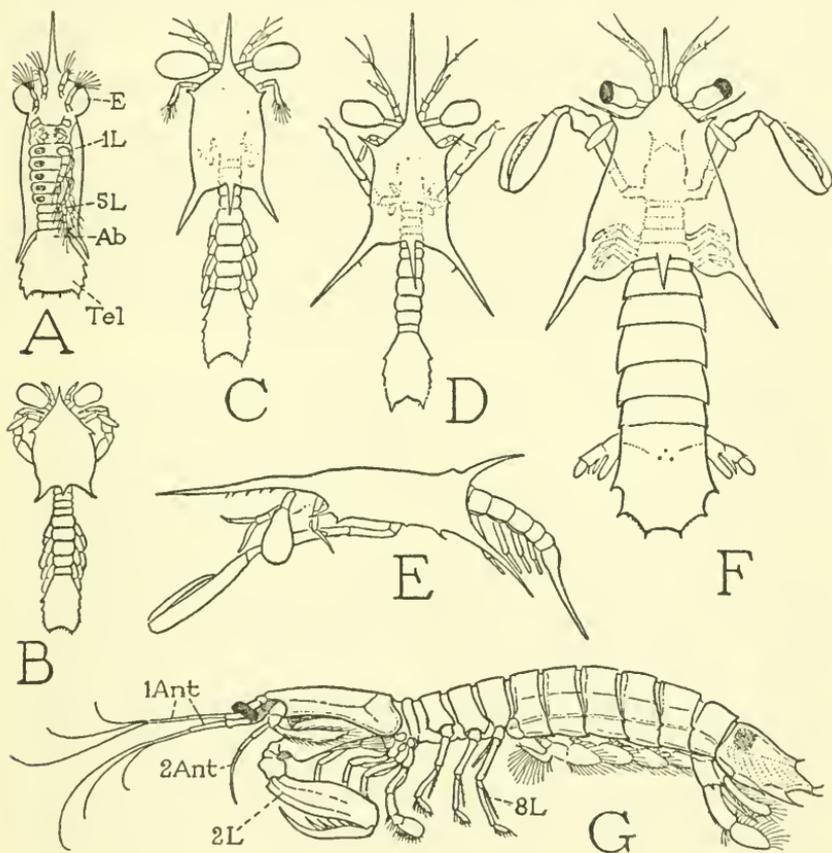


FIG. 24.—Stomatopoda. Larval stages and an adult. (A-E from Giesbrecht, 1910; F from Alikunhi, 1952.)

A, an antezoea larva. B, *Squilla mantis* Latr., first propelagic stage. C, same, second propelagic stage. D, same, first pelagic stage, dorsal. E, same, first pelagic stage, lateral. F, *Squilla latreillei*, last pelagic larval stage. G, *Squilla mantis*, adult male.

Ab, abdomen; *1Ant*, first antenna; *2Ant*, second antenna; *E*, eye; *1L*, *2L*, *5L*, *8L*, first, second, fifth, and eighth thoracic appendages; *Tel*, telson.

in a wide, fan-shaped plate, or one or two anterior segments may be free. The eyes (*E*) are large but sessile. The first five thoracic segments bear each a pair of small, biramous appendages (*1L*, *5L*) used for swimming. The antezoeal larva is pelagic. During subsequent

stages of its growth, the abdominal segments are successively separated from the telson and acquire pleopods. The five thoracic appendages lose their exopodites and take on the adult form, those of the second segment becoming typical raptorial fangs in the fourth instar. Later the appendages appear on the last three segments of the thorax. In the second instar the eyes are stalked.

The other first-larval form, termed a *pseudozoea* (fig. 24 B), occurs in species of *Squilla*, *Gonodactylus*, and probably of other genera. The eyes in this form are stalked at hatching. The thorax is fully segmented, but only the first two segments bear appendages, and those of the second segment are raptorial fangs. The short carapace has small spines on its anterior and posterior angles, and leaves four posterior thoracic segments uncovered. The abdomen has five free segments, of which the first four bear pleopods, but the sixth is still united with the telson.

Squilla mantis, according to Giesbrecht, goes through 10 larval instars. The first two live on the bottom, but after the second instar the larva becomes pelagic, swimming with the pleopods. In the second propelagic instar (fig. 24 C) there is little change from the first (B) except for an increase in size and a lengthening of the posterior carapace spines, which in the first pelagic instar (D, E) become much longer and widely divergent. In the third pelagic instar rudiments of the third, fourth, and fifth thoracic appendages appear, and become longer in the next stage, when also the appendages of segments six, seven, and eight are developed. The sixth segment of the abdomen becomes free from the telson in the seventh instar. The last pelagic larva (F) has essentially the structure of the adult (G) except for the large carapace, which now covers all but one of the thoracic segments. After about the fifth instar, Giesbrecht says, the two larval forms, originating with the antezoea and the pseudozoea, become structurally alike.

The principal structural changes during the life of the stomatopod take place at the transformation of the larva (fig. 24 F) into the adult (G). Even here, however, the only essential change affects the carapace, which is much shortened and narrowed and loses its posterior spines. Instead of covering most of the thorax as in the larva (D, F) the carapace of the adult leaves the last four thoracic segments exposed. In this respect the carapace reverts to its relative length in the first propelagic larva (B). It is evident, therefore, that the larval development of the back shield is a metamorphic adaptation to the pelagic life of the larva, probably to assist in keeping the larva afloat. The relative length of the larval carapace varies in different

species. In some forms the last four thoracic segments are not covered, as in the adult of *Squilla* (G), in others such as *Squilla latreillei* (F) only the eighth segment is exposed in the larva, while in species of *Lysiosquilla* the carapace of the last larva may cover the entire thorax and the first two abdominal segments. Probably these variations in the length of the larval carapace are only differences in the extent to which the free posterior margin is produced beyond the attachment of the plate on the third or fourth segment of the adult thorax. Otherwise the changes during the growth of the larva are merely developmental stages of growth and have no metamorphic value. It is difficult even to see any functional reason for the differences between the two larval forms on hatching.

IV. STRUCTURE AND EVOLUTION OF ARTHROPOD APPENDAGES

Inasmuch as changes in the form and function of the appendages are important features in the metamorphoses of Crustacea, and various conflicting views have been held concerning the primitive nature and the evolution of arthropod limbs, we must give some attention to this controversial subject.

Most studies on the comparative structure of the arthropod appendages, and deductions as to the origin and primitive form of the limbs give the impression that conclusions have resulted too much from an attempt to fit the facts into a preconceived theory. Widely accepted has been the idea that the primitive appendage was a biramous limb; and many carcinologists would derive all kinds of arthropod appendages from an original phyllopodial type of limb, such as that of the branchiopod crustaceans.

The trilobites are among the oldest known arthropods, and, with respect to their appendages, they are the most generalized, since all the postoral limbs are fully segmented legs. The base of each leg bears a branched lateral process (fig. 25 A, *Eppd*), which, arising on the coxa, is clearly an epipodite and hence cannot be an equivalent of the crustacean exopodite, which by definition is an exite of the basipodite. The trilobite limb, therefore, is not "biramous" in the manner of a crustacean limb, and hence does not relate the trilobites to the Crustacea. Raymond (1920), however, explicitly states the opposite view. "The trilobites," he says, "are themselves crustaceans, as is amply proven by their biramous appendages." More recently, Heegaard (1947) has argued that the trilobite limb is truly biramous, in spite of the evident coxal position of the "exopodite," and he further attempts to show that remnants of a primitive biramous structure are

to be found in various modern arthropods other than the Crustacea. His discussion, however, takes too many liberties with simple visible facts in an endeavor to fit them into a consistent scheme of structure. The studies of trilobite appendages by Störmer (1939) leave little doubt that the trilobite leg (fig. 25 A) is simply a uniramous, segmented limb with a coxal epipodite that was perhaps a gill. Störmer's contention, however, that a narrow ring at the base of the coxa is a

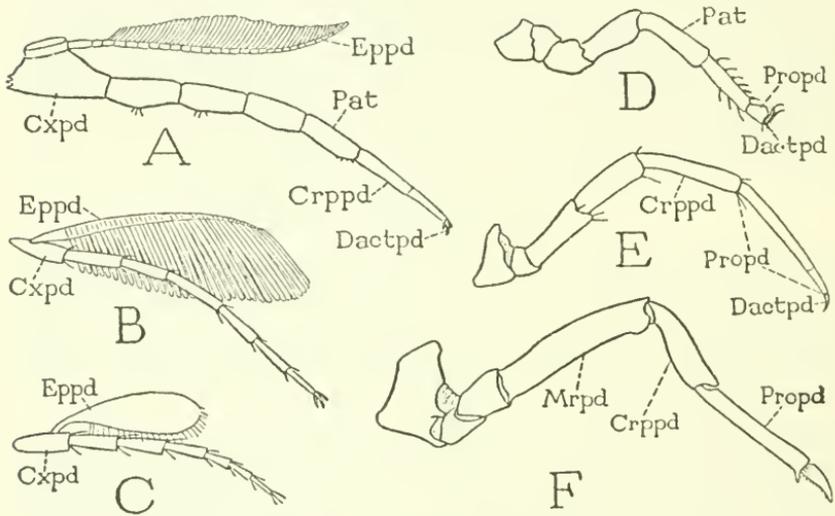


FIG. 25.—Examples of segmentation of arthropod legs.

A, leg of a trilobite (from Störmer, 1939). B, leg of *Marella* (adapted from Walcott, 1931). C, leg of *Burgessia* (from Walcott, 1931). D, leg of solpugid arachnid. E, leg of a chilopod, *Lithobius*. F, leg of a decapod, *Cambarus*.

Crppd, carpopodite (tibia); *Cxpd*, coxopodite (coxa); *Dactpd*, dactylopodite (pretarsus); *Eppd*, epipodite; *Mrpd*, meropodite (femur); *Pat*, patella; *Propd*, propodite (tarsus).

precoxal segment is questionable. The coxa of other arthropods is often marked by a circular groove near the base that forms an internal strengthening ridge giving attachment to the body muscles of the limb. In the trilobite leg the large coxopodite should be the movable basal segment of the limb and not the narrow "precoxa."

The idea that the primitive arthropod limb was a flat, lobulated appendage of the phyllopodial type has been accepted by some carcinologists regardless of the fact that the limbs of the trilobites (fig. 25 A) and of associated fossil forms such as *Marella* (B) and *Burgessia* (C) are slender jointed legs, as are those of nearly all modern arthropods (D, E, F), including the Malacostraca (F).

Walcott (1931), for example, in discussing his Burgess Shale fossils seems to accept this theory without question when he says: "The biramous limb of *Marella*, like that of the trilobite, undoubtedly passed through the foliaceous or multiramous limb stage in its evolution, probably in pre-Cambrian time." There is no disproving this idea, which should apply to the other arthropods as well, but such implicit faith in a theory is hard to understand.

On the other hand, Raymond (1920) says the theory of the phyllopod origin of the arthropod limb "has been completely upset" by the finding of such "undoubted branchiopods" as *Burgessia* in the Middle Cambrian with trilobitelike legs. The same idea has been expressed by Heegaard (1947) in his statement that the "undoubted branchiopods" found by Walcott in the Middle Cambrian having trilobite legs show that "it can no longer be held that the phyllopodial limbs are primitive." The writer fully agrees with this conclusion, but for different reasons than those given by Raymond and Heegaard. Such fossils as *Burgessia* and *Marella* are certainly not "undoubted" branchiopods. Walcott (1931) says of *Marella* that it is a less primitive form than the Apodidae and more primitive than the trilobites, but is nearer to the latter than to the former. Among the Middle Cambrian fossils, however, is a form, *Opabina regalis* Walcott, particularly studied by Hutchinson (1930), which evidently is an anostracan branchiopod with foliaceous appendages.

Another popular belief concerning the derivation of the arthropod limb, taken to support the theory of its biramous phyllopodial origin, is that the limb was evolved from the polychaete parapodium. Reasons have already been given in section I of this paper for believing that the annelids have only a remote connection with the arthropod progenitors. Certainly the arthropods can have no relation to modern polychaetes, which are highly specialized annelids and could give rise only to more polychaetes. The appendages of the worm, though they are bilobed flaps, have a lateral position on the body (fig. 26 A), and there is nothing in their structure having any likeness to an arthropod limb at any stage of its development. The parapodium bears two bundles of bristles supported on a pair of long internal rods giving attachment to muscles. Its only common feature with an arthropod limb is that, being a locomotor organ, it is movable forward and backward by body muscles. In short, the idea that the arthropod appendages were derived from annelid parapodia appears to be just another case of excessive zeal for generalization.

Among modern wormlike animals those closest to the arthropods are the Onychophora; some zoologists have even included the ony-

chophorans in the Arthropoda. Though a modern onychophoran shows no external segmentation of the body in the adult stage, the segmented repetition of internal organs and the complete body segmentation of the embryo leave no doubt that the Onychophora are

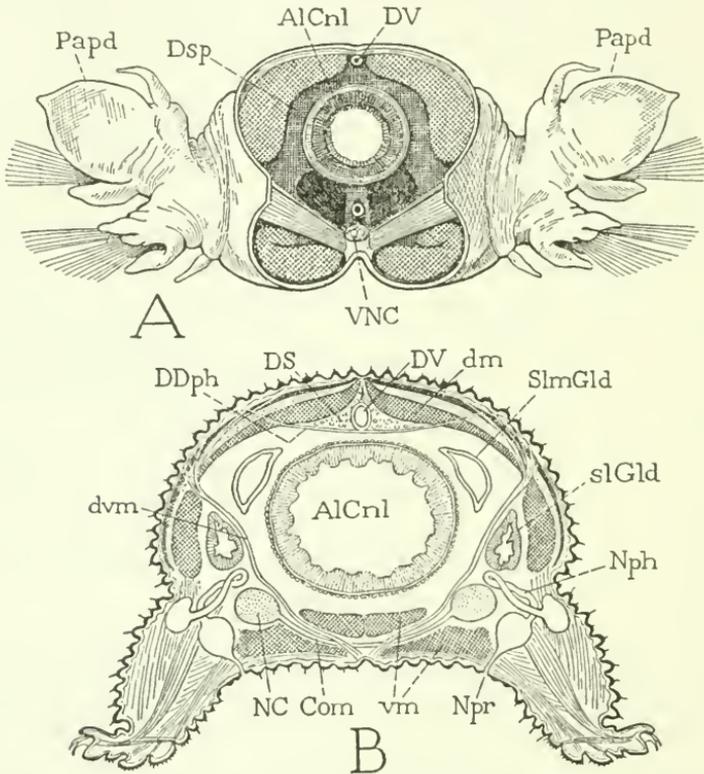


FIG. 26.—Diagrammatic transverse sections of *Nereus* (A) and *Peripatus* (B), showing comparative structure of the appendages of a polychaete annelid and an onychophoran.

AlCnl, alimentary canal; *Com*, nerve commissure; *DDph*, dorsal diaphragm; *dm*, dorsal muscles; *DS*, dorsal sinus; *Dsp*, dissepiment; *DV*, dorsal blood vessel; *dvm*, dorsoventral muscles; *NC*, lateral nerve cord; *Nph*, nephridium; *Npr*, nephropore; *Papd*, parapodium; *SlmGld*, slime gland; *vm*, ventral muscles; *VNC*, ventral nerve cord.

fundamentally metameric animals. The body cavity is undivided by dissepiments, the primitive coelom is represented only by the lumina of the nephridia and the gonads, and the embryogeny of the Onychophora gives the key to the early embryonic development of the arthropods. The onychophoran legs have a lateroventral position on the body (fig. 26 B) as in the arthropods, in contrast to the lateral posi-

tion of the polychaete parapodia (A). The nephridia (B, *Nphi*) and the primitive genital ducts open mesad of the leg bases suggestive of their openings on the coxae in many of the arthropods. Though modern Onychophora are terrestrial animals, there can be little doubt that they had aquatic ancestral relatives represented by the Cambrian *Aysheaia* of the Burgess Shale, and perhaps by the Pre-Cambrian *Xenusion* described by Heymons (1928).

The arthropod limbs are developed on the embryo from latero-ventral budlike rudiments that lengthen and become segmented. We may therefore suppose that from the ancestral onychophorans (fig. 1 A) a form was evolved with longer legs (B), which later, with sclerotization of the integument, became the jointed appendages of the ancestral arthropods (C). It then required a long period of Pre-Cambrian evolution to produce a trilobite on the one hand, and some ancestral form of crustacean on the other. The differentiation between the two groups, however, was first in the form of the body, not in that of the appendages, as seen in the legs of a trilobite (fig. 25 A) and those of *Marella* and *Burgessia* (B, C). Though there is no valid reason for regarding the primitive arthropod appendage as being a biramous limb, the crustacean appendages later acquired their characteristic biramous structure, which is usually lost in the ambulatory limbs (F).

Many carcinologists hold the view that the phyllopodial type of limb is primitive, at least for the Crustacea, and this concept has been well elucidated by Borradaile (1926a, 1926b). It is supposed that the primitive crustacean appendage was a flat, unsclerotized lobe with a fringe of hairs on the mesal border. Then the inner margin was broken up by the development of a series of endites. Next, the limb became more rigid by a sclerotization of the integument, but this necessitated lines of flexibility that led to a system of jointing, and naturally the joints were formed between the endites. Thus the endites are explained as the precursors of the later developed limb segments. Finally, with the departure from the phyllopodial form and the suppression of the endites, some of the limbs became slender, segmented, leglike appendages. In favor of this theory it may be noted that in many of the branchiopod appendages there are six endites on the mesal margin and a free lobe at the apex (fig. 27 A, B). If all the parts of such a limb became segments there would be seven segments in all, the terminal lobe becoming the dactylopodite, which gives the usual number of limb segments in the Crustacea generally, though Borradaile holds that the maximum number is nine, which would include the doubtful "precoxa" of the trilobite.

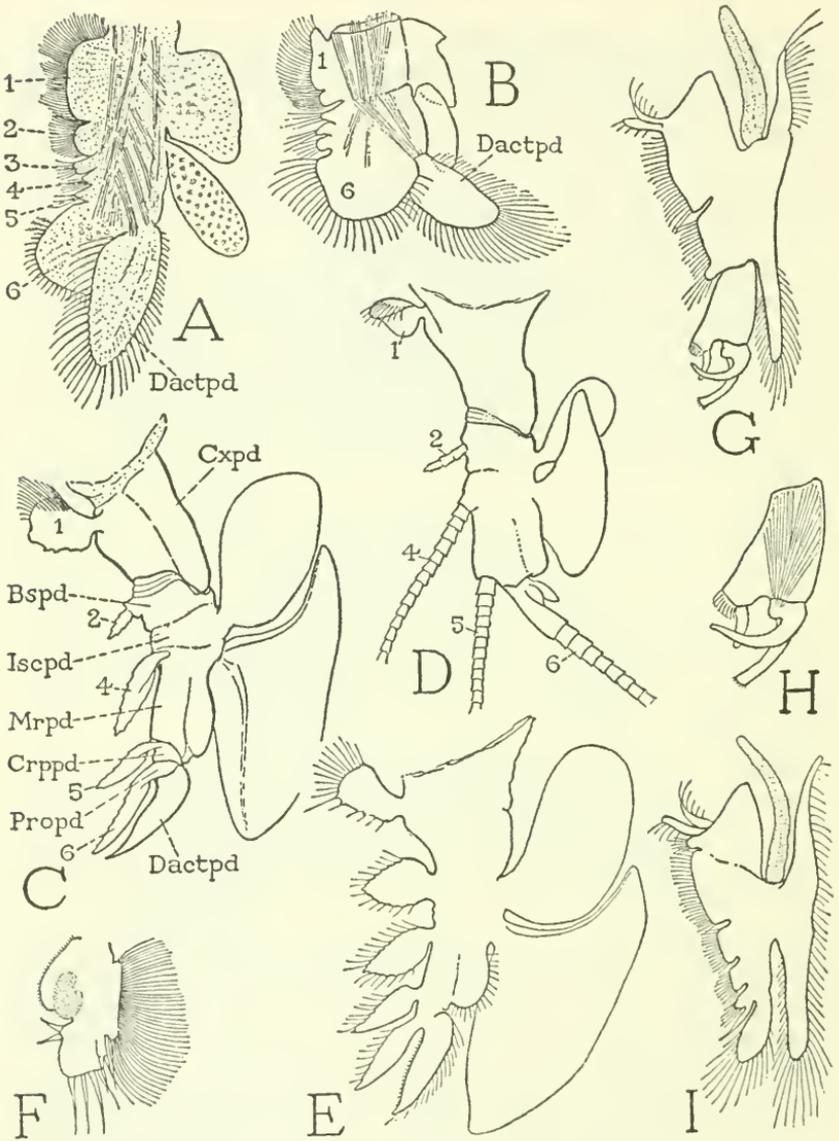


FIG. 27.—Examples of branchiopod appendages.

A, *Branchipus stagnalis*, Anostraca, thoracic limb (from Claus, 1873). B, *Branchipus serratus*, male, eighth thoracic limb. C, *Apus longicaudata*, Notostraca, second maxilliped. D, same, first maxilliped. E, same, thoracic limb from middle of body. F, *Daphnia magna*, Cladocera, third thoracic appendage (from Hansen, 1925). G, *Estheria clarkii*, Conchostraca, second thoracic limb. H, same, terminal segment. I, same, left limb from middle of body.

Bspd, basipodite; *Crppd*, carpopodite; *Cxpd*, coxopodite; *Dactpd*, dactylopedite; *Iscpd*, ischiodite; *Mrpd*, meropodite; *Propd*, propodite; 1-6, endites.

There are two chief objections to this phyllopod theory of the origin of jointed crustacean limbs. First, it gives no explanation of the origin of the similarly jointed legs of other arthropods, except by the wholly unsupported assumption that they likewise were developed from phyllopodial limbs. Second, the ontogenetic development of the crustacean appendages themselves gives no evidence of a phyllopodial origin, and suggests, on the contrary, that the phyllopodium has been evolved from an ambulatory leg.

The study by Heath (1924) of the postembryonic development of the branchiopod *Branchinecta occidentalis* shows very clearly that the limbs arise as simple, lateroventral lobes of the body segments (fig. 3 B). Instead of taking on a phyllopodial shape, the rudiments grow out first in a slender leglike form (C, D). On the inner margins of the appendages at this stage there are indentations suggestive of an incipient segmentation, and at the apex is a terminal lobe. Only at a later stage (E) do the appendages become broad overlapping flaps. Finally in the adult (F) the appendages have taken on the form of typical unsegmented phyllopodia with three large flat exites, six endites, and a free, independently muscled terminal lobe. Clearly, these appendages in their ontogenetic development undergo a metamorphosis from an ambulatory leg into a phyllopodium. Though Heath himself did not have this phase of the subject in mind, his pictures speak for themselves.

Conversely, as seen in Heegaard's (1953) account of the postembryonic stages of the decapod crustacean *Penaeus setiferus*, the rudiments of the pereopods develop directly into legs without undergoing any stage suggestive of a phyllopodial origin. The pereopods appear during the second protozoal stage as simple lobes on their respective body segments (fig. 28 A). In the third protozoa they take on a biramous structure (B), in which the protopodite, at first undivided, bears a short unsegmented endopodite and a longer exopodite. In the second mysis stage (C) the limbs attain a fully segmented structure by the division of the protopodite into two segments and the endopodite into five, with a terminal chela on each of the first three. The exopodites are now large seta-bearing branches of the basipodites used for swimming. In the postmysis (D) the pereopods have become essentially uniramous by the reduction of the exopodites to small lobes, and the swimming function has been taken over by the pleopods. This condition is retained in the adult. If the pereopods of *Penaeus* had a phyllopodial origin in their phylogeny, there is nothing to suggest it in their ontogeny. The mouth-part appendages proceed along their own lines of development to serve the special functions they have assumed

as organs of feeding. The pleopods (E) and the uropods (F), on the other hand, appear to remain in an early stage of development represented by the simple, unsegmented biramous stage of the pereopods (B).

The swimming appendages of the anostracan branchiopods so regularly have six mesal lobes (figs. 3 F, 27 A, B) and a movable terminal

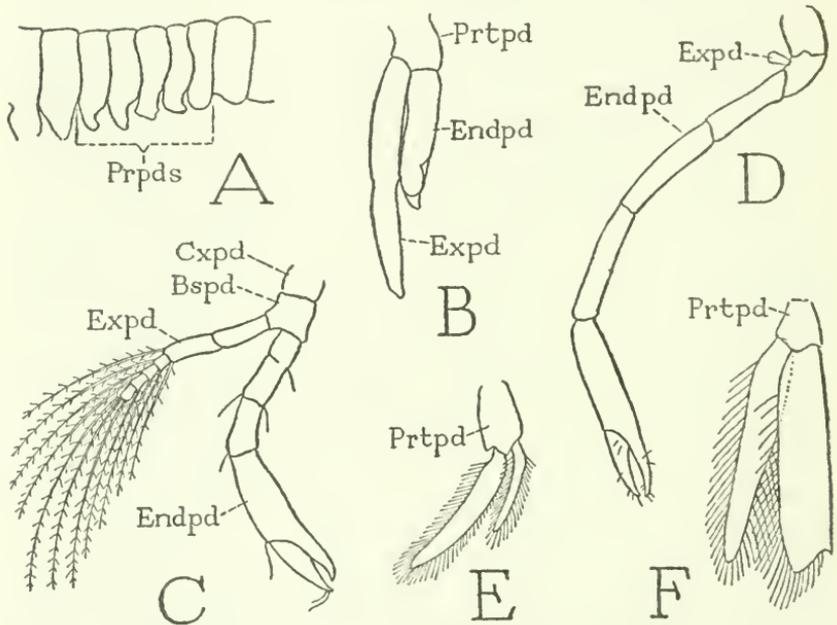


FIG. 28.—Development of the pereopods and pleopods of *Penaeus setiferus* (L.) (from Heegaard, 1953).

A, rudiments of pereopods on thoracic segments of second protozoa. B, pereopod of third protozoa. C, pereopod of second mysis instar. D, third pereopod of postmysis. E, second pleopod of young adult. F, uropod of postmysis.

Bspdp, basipodite; *Cxpdp*, coxopodite; *Endpd*, endopodite; *Expdp*, exopodite; *Prpds*, pereopod rudiments; *Prtpdp*, protopodite.

lobe as to suggest that the six endites represent the first six segments of a leg (coxopodite to propodite) and the independently muscled apical lobe the dactylopodite. Yet, the sixth endite is commonly interpreted as the endopodite and the apical lobe as the exopodite. In the notostracan *Apus*, however, the second maxilliped (fig. 27 C) is a seven-segmented leg ending with a clawlike dactylopodite (*Dactpd*) and having an endite on each of the other segments except the ischiopodite. The first maxilliped of *Apus* (D) is somewhat simpli-

fied, but the swimming appendages (E) clearly retain the structure of the second maxilliped. In other branchiopods the appendages may be variously reduced (F, G, H, I) obscuring the basic leg structure.

The segmentation of the arthropod legs is surprisingly constant; variations result from the elimination of segments, seldom from addition, though the propodite (tarsus) is generally rendered flexible by subdivision. If all the podomeres in the legs of the trilobite (fig. 25 A) and *Marella* (B) are true muscled segments, the ancient arthropods had eight limb segments, including a small apical dactylopodite, or pretarsus, and thus possessed all the segments that are present in any of the legs of modern arthropods. Among the latter, eight segments are present in the Pycnogonida and in some of the legs of the arachnid Solpugidae (D), but in most of the arachnids the leg has only seven segments by the elimination of the third segment from the base. The segment beyond the knee bend (D, *Pat*), which is the fifth segment in the trilobite leg (A), is called the patella, though it might appear to correspond with the carpopodite (tibia) in the leg of a centipede (E) or a decapod (F). Yet there are three segments beyond it in the spider leg, and only two in the other arthropods. In the latter, therefore, either two original segments in the distal part of the leg are united, or one has been eliminated. The legs of the chilopods and the decapods (E, F) have seven segments; the insect leg has only six segments because of the apparent union of the ischiopodite (second trochanter, or prefemur) with the meropodite (femur).

Though the primitive arthropods (fig. 1 C) undoubtedly were aquatic, they were walking animals provided with jointed limbs, and probably lived on plants in shallow water near the shore. Their habits may have been similar to those of the modern *Anaspides* (D). The typical jointed ambulatory leg has been retained in all modern arthropods, except in those crustaceans in which it has been modified for swimming, but even the phyllopodium preserves evidence of the seven-segmented structure of a walking leg. It would appear that the primitive arthropods had more legs than they needed for walking, and because of this fact their descendants have been able to reconstruct many of them into the great variety of appendicular organs possessed by modern forms. The arthropods owe what they are, as well as their name, to their jointed appendages.

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