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
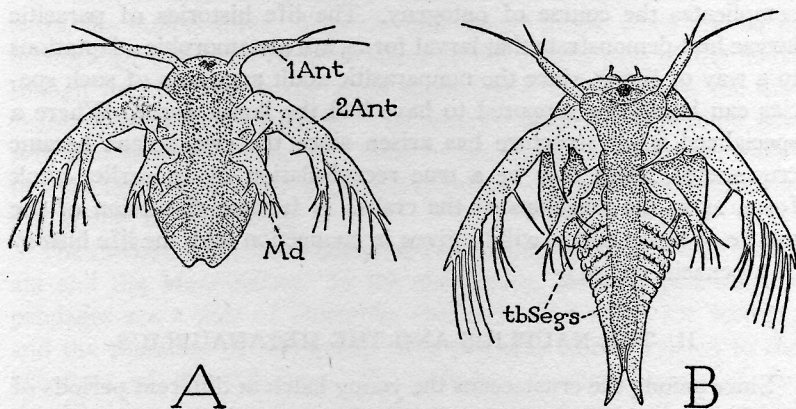

FIG. 2.—Nauplius and metanauplius of *Apus cancriformis* Bosc (from Claus, 1873).

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).

For much assistance in preparing this section of the paper the writer is indebted to Dr. Fenner A. Chace, Jr., and his associates in the division of marine invertebrates of the U. S. National Museum.

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
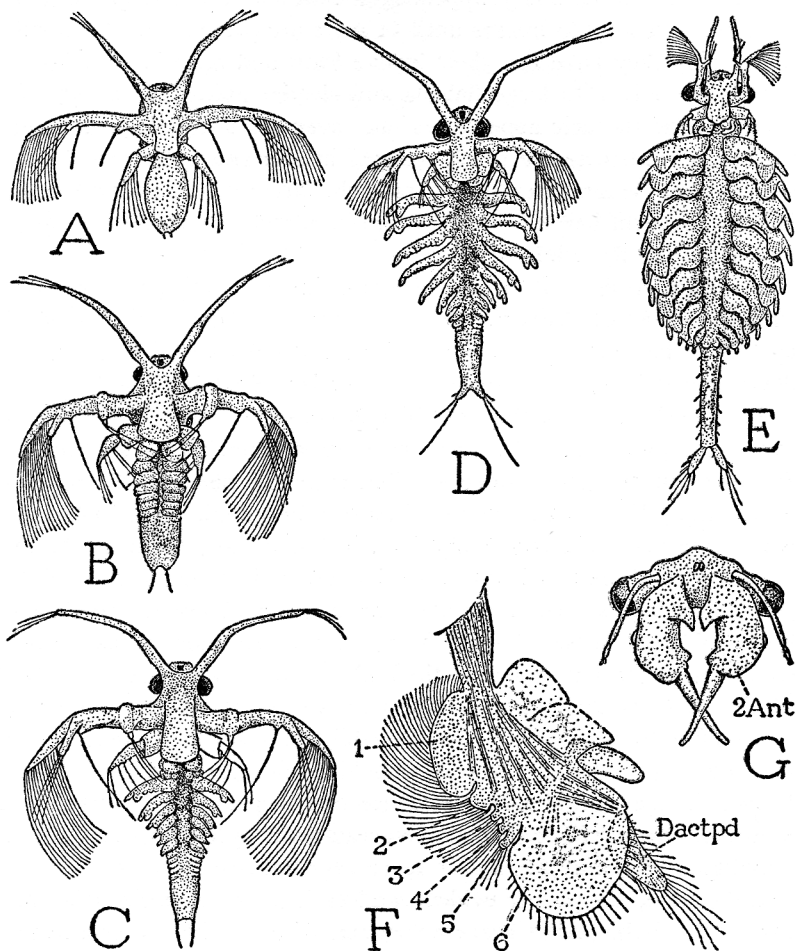

FIG. 3.—Branchiopoda. *Branchinecta occidentalis* Dodds, developmental stages (from Heath, 1924) and a thoracic limb of the adult.
   A, newly hatched nauplius, length 0.4 mm. B, second instar. C, third instar. D, fifth instar. E, eighth instar, 2.9 mm. F, sixth left thoracic limb of adult male, with 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 musculated 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.
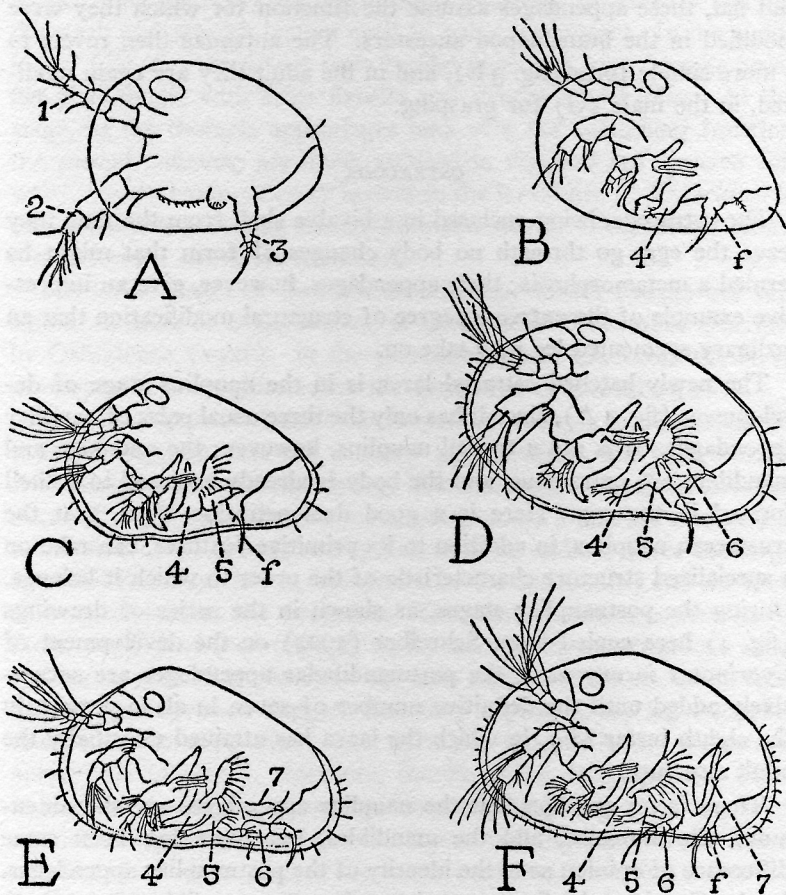

FIG. 4.—Ostracoda. Larval stages of *Cyprinotus incongruens* Ramdohr (from Schreiber, 1922).

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
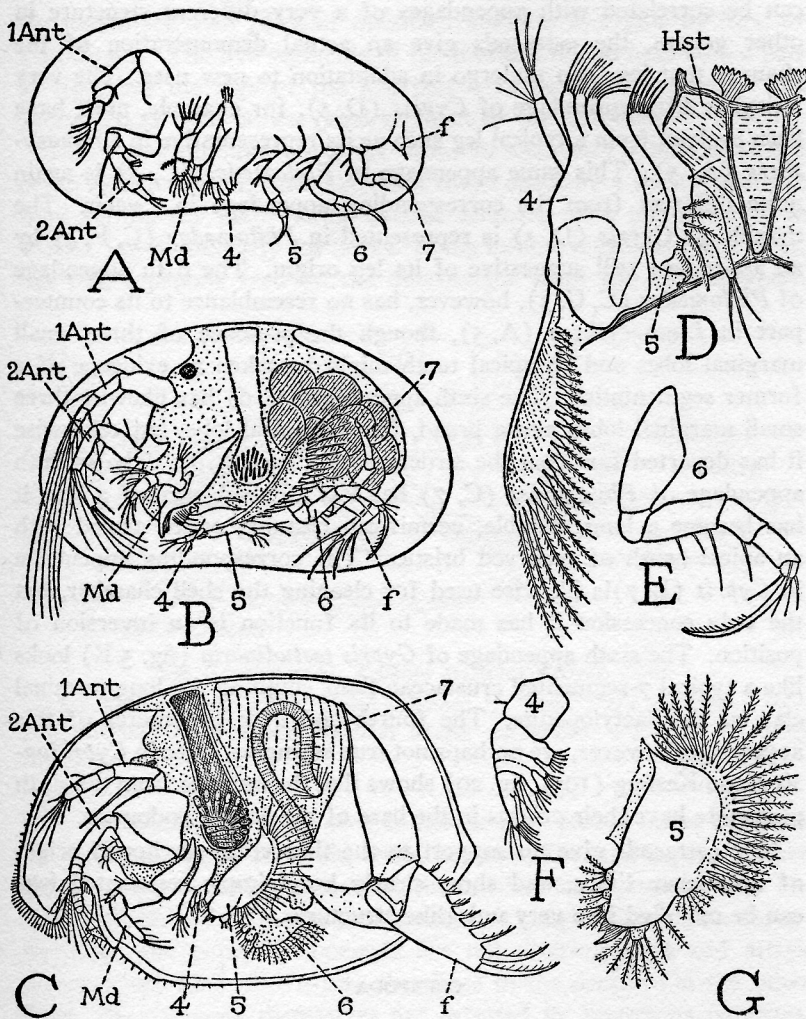
FIG. 5.—Ostracoda.

A, *Limnocythere 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.