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,

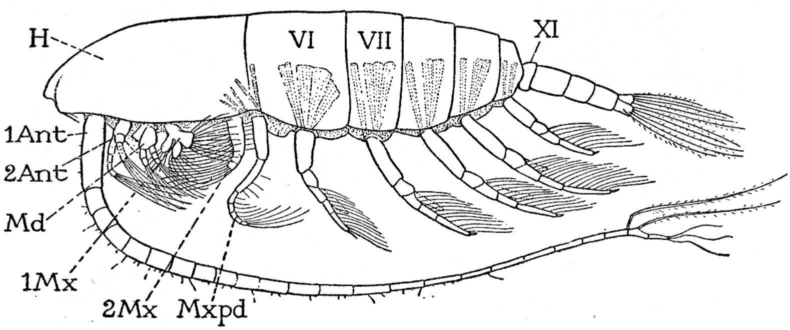

FIG. 6.—Copepoda. *Calanus cristatus* Kröyer, adult.

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 Ziegelmayer (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 (*1L, 2L*). 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 Ziegelmayer the segments formed after the nauplius stage are generated in a subterminal zone of growth.

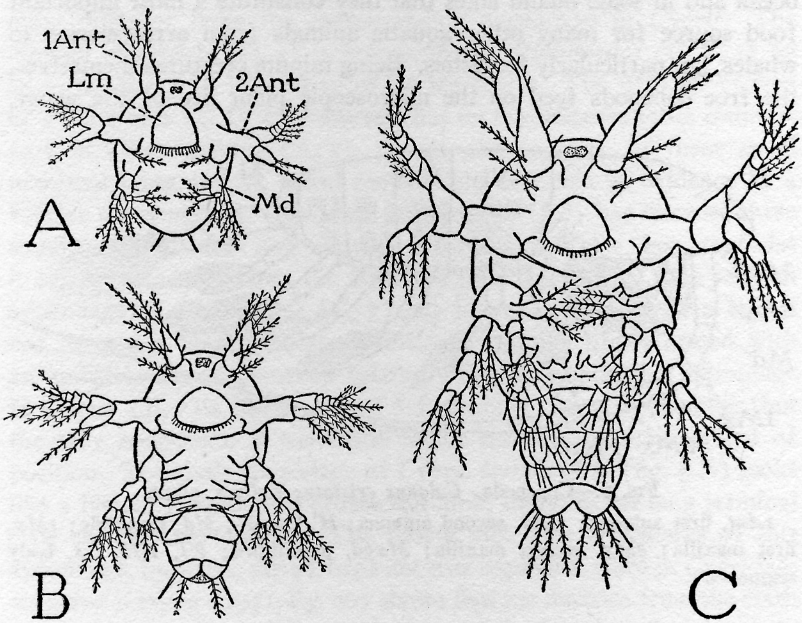

FIG. 7.—Copepoda. Nauplius and two metanaupliar instars of *Cyclops* (outlines from Ziegelmayer, 1925).

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

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

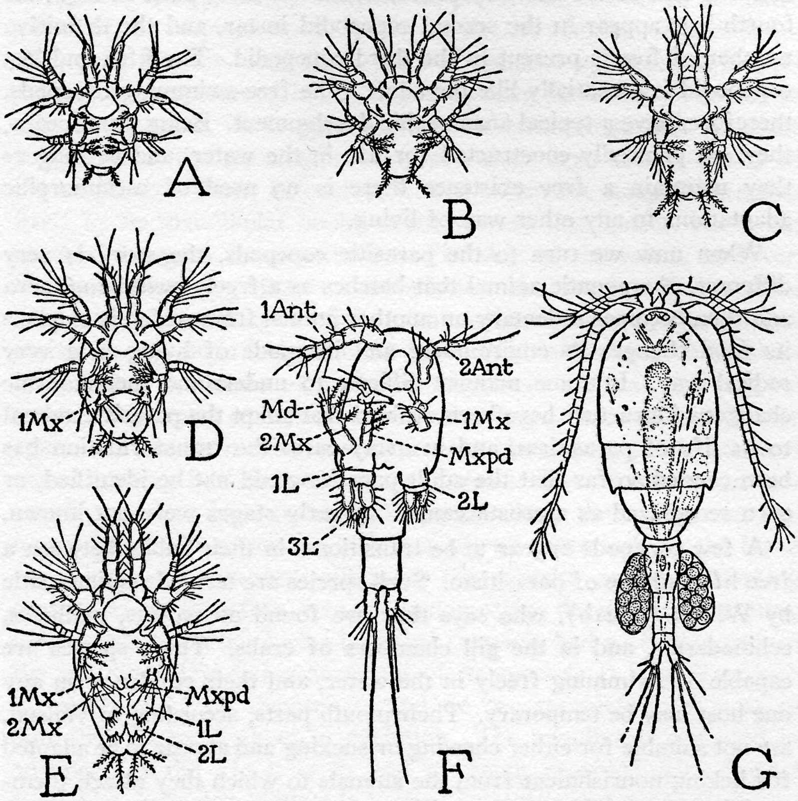

FIG. 8.—Copepoda: Podoplea. Developmental stages and adult of *Cyclops.* (A-F from Dietrich, 1915; G from Claus, 1863).

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

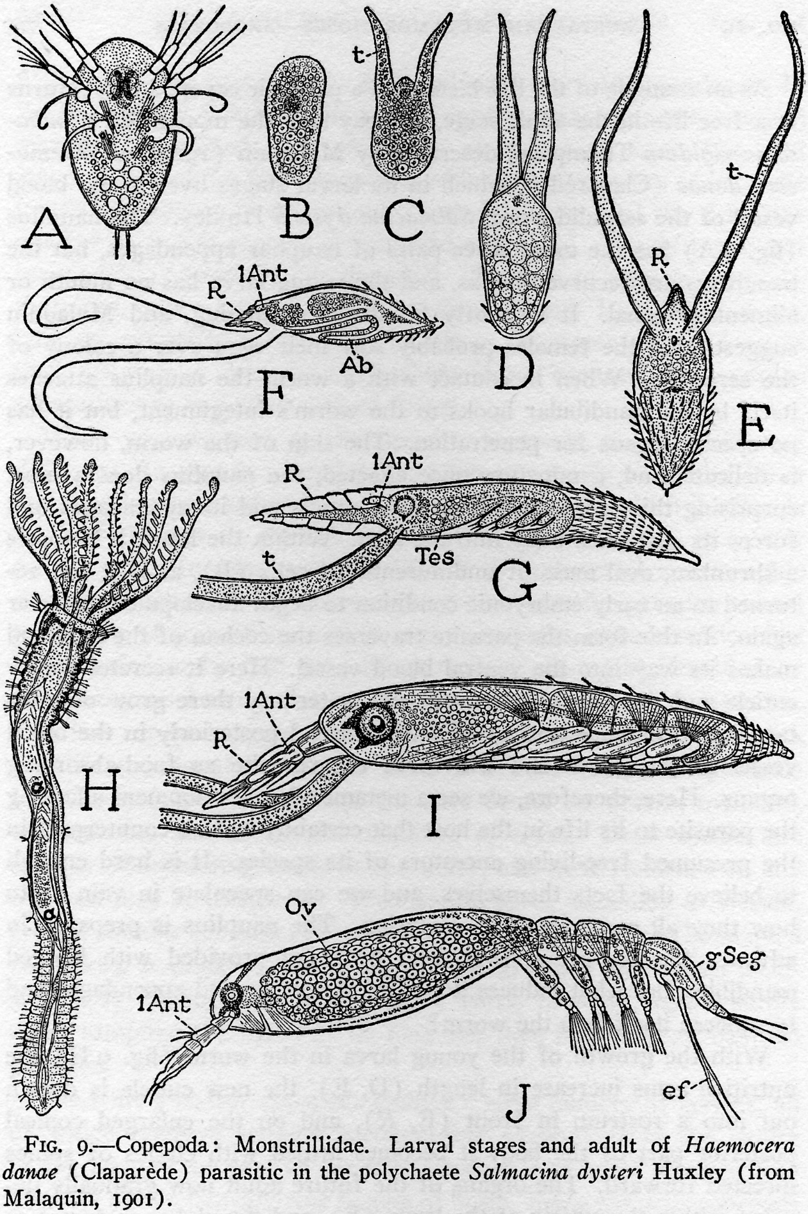

FIG. 9.—Copepoda: Monstrillidae. Larval stages and adult of *Haemocera danae* (Claparède) parasitic in the polychaete *Salmacina dysteri* Huxley (from Malaquin, 1901).

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 *chalimus* 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 chalimus. 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

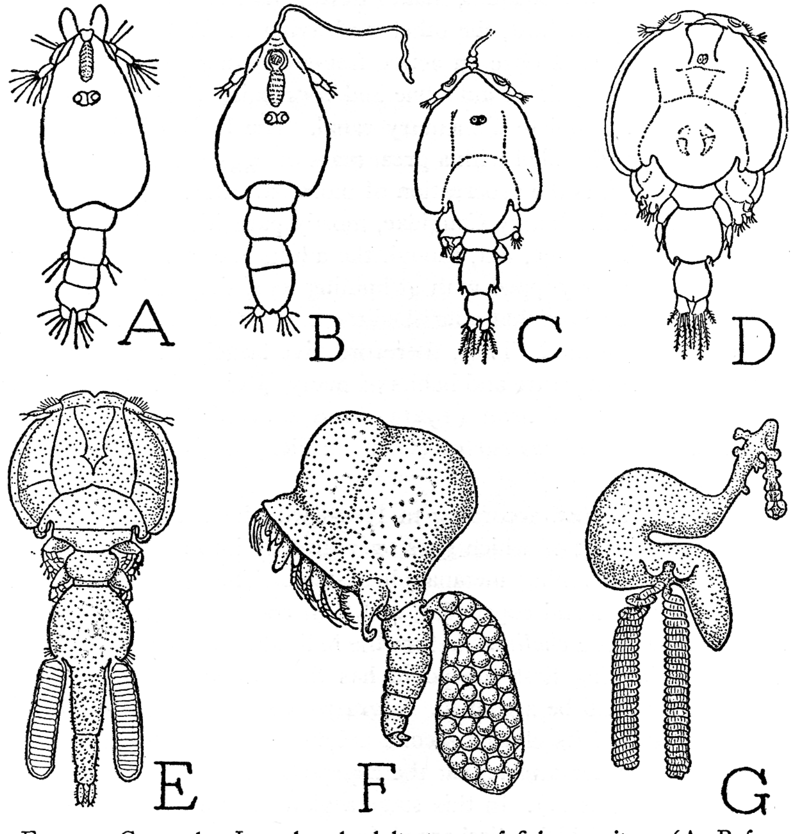

FIG. 10.—Copepoda. Larval and adult stages of fish parasites. (A, B from Heegaard, 1947; C, D from Wilson, 1905; E, F from Wilson, 1921a; G from Wilson, 1917.)

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, *Blakeanus 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 lernaeopodid 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 (*Mxpd*) 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

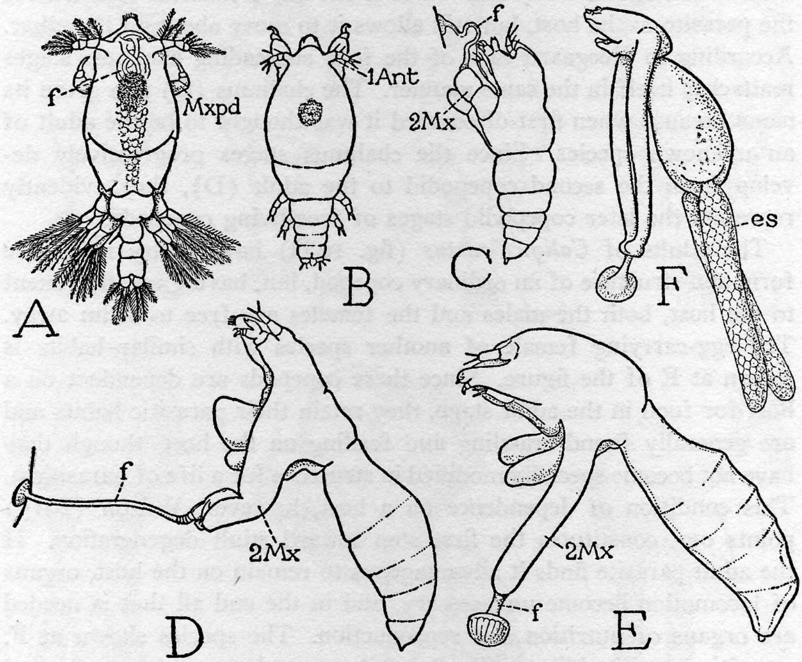

FIG. 11.—Copepoda: Lernaeopodidae. Developmental stages of fish parasites (from Wilson, 1910, 1915).

A, *Achtheres amblopltis* 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