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

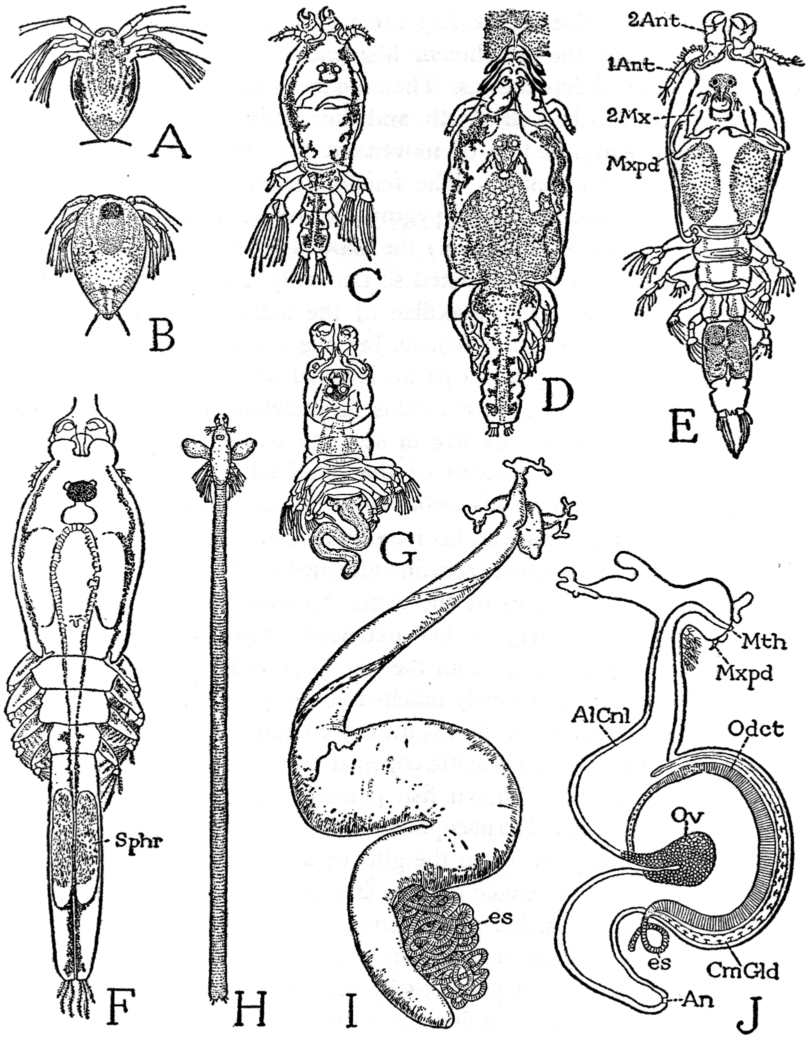

FIG. 12.—Copepoda. Developmental stages of the fish parasite *Lernaeocera branchialis* (L.). (A, C, D, E, G from Sproston, 1942; B from Pedaschenko, 1898; F, I from Capart, 1948; H, J from Scott, 1901.)

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 lenth 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 anatomcial 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 *Phrixocephalus,* 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 related 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

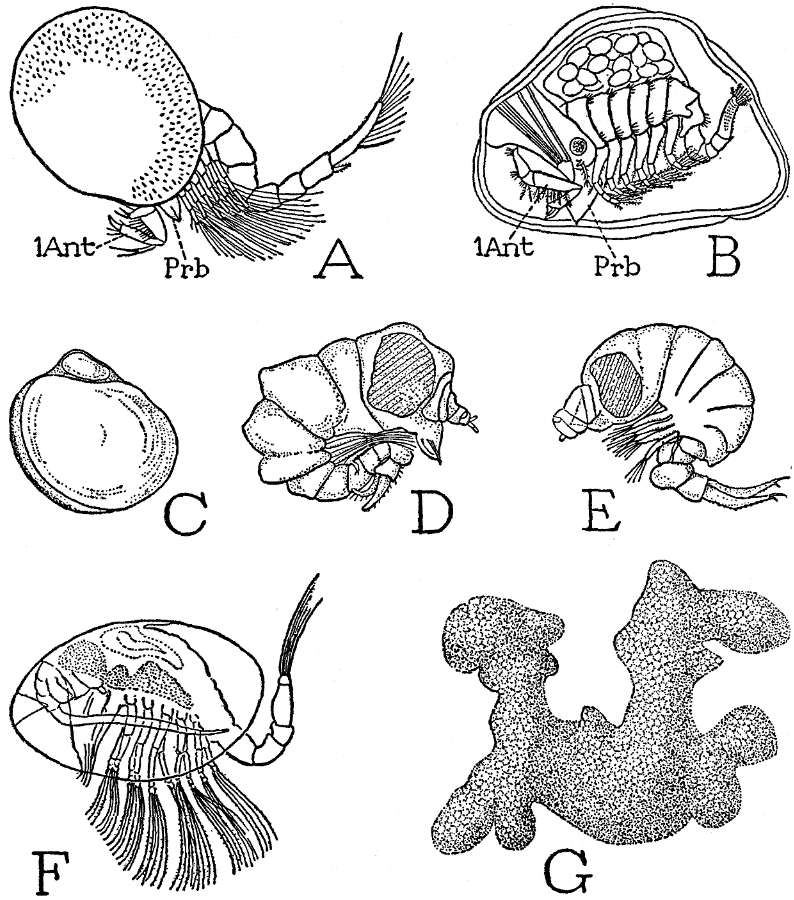

FIG. 13.—Cirripedia: Ascothoracica. (A from Norman, 1913; B from Okada, 1938; C, D, E from Heegaard, 1951; F, G from Knipowitsch, 1890.)

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 metanauplii, 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 (*1Ant*), 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

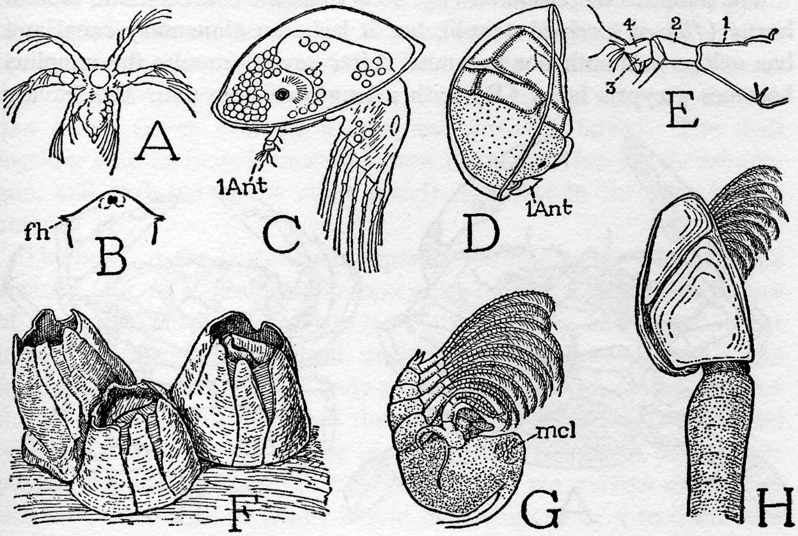

FIG. 14.—Cirripedia: Thoracica. (A-E from Runnström, 1924-1925.)

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

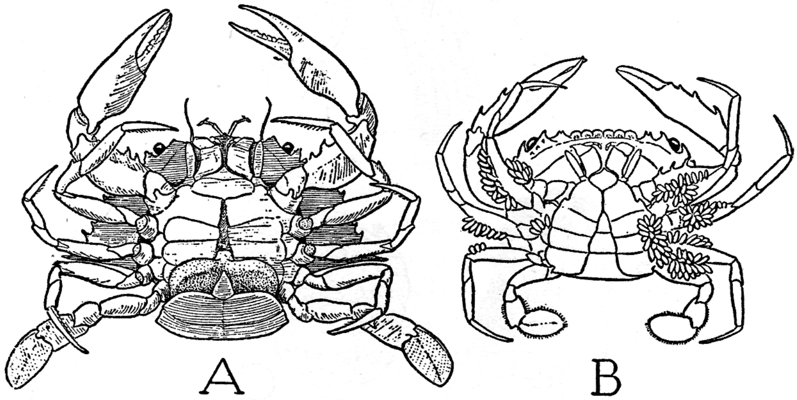

FIG. 15.—Cirripedia: Rhizocephala. External parasitic stages on crabs. A, *Loxothylacus texanus* Boschma, a sacculinid on *Callinectes sapidus* Rathbun. B, *Thompsonia* on *Thalamita prymna* (Herbst) (from Potts, 1915).

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, *1Ant*), 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