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

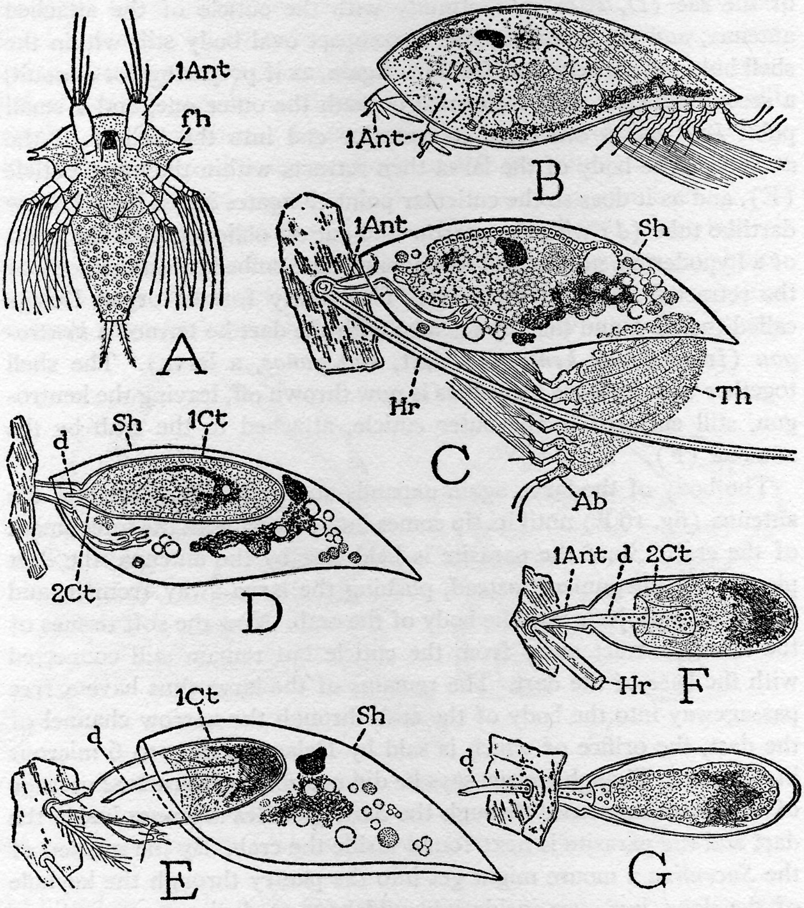

FIG. 16.—Cirripedia: Rhizocephala. Metamorphosis of *Sacculina carcini* Thompson (from Delage, 1884).

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.*

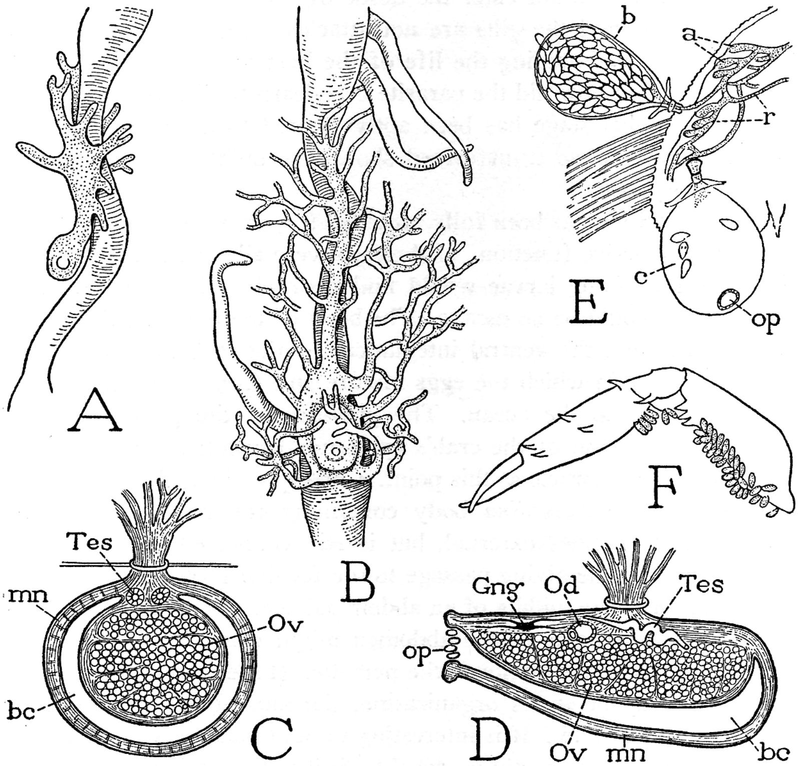

FIG. 17.—Cirripedia; Rhizocephala. Internal and external parasitic stages. (A-D from G. Smith, 1906; E, F from Potts, 1915.)

A, *Sacculina neglecta* attached on intestine of crab *Inachus scorpio.* B, same, later stage with root system developed. C, *Peltogaster* sp., diagrammatic cross sction 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 nycellium. 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. 18 A) 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 (*Epst*) 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. 18 A) 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

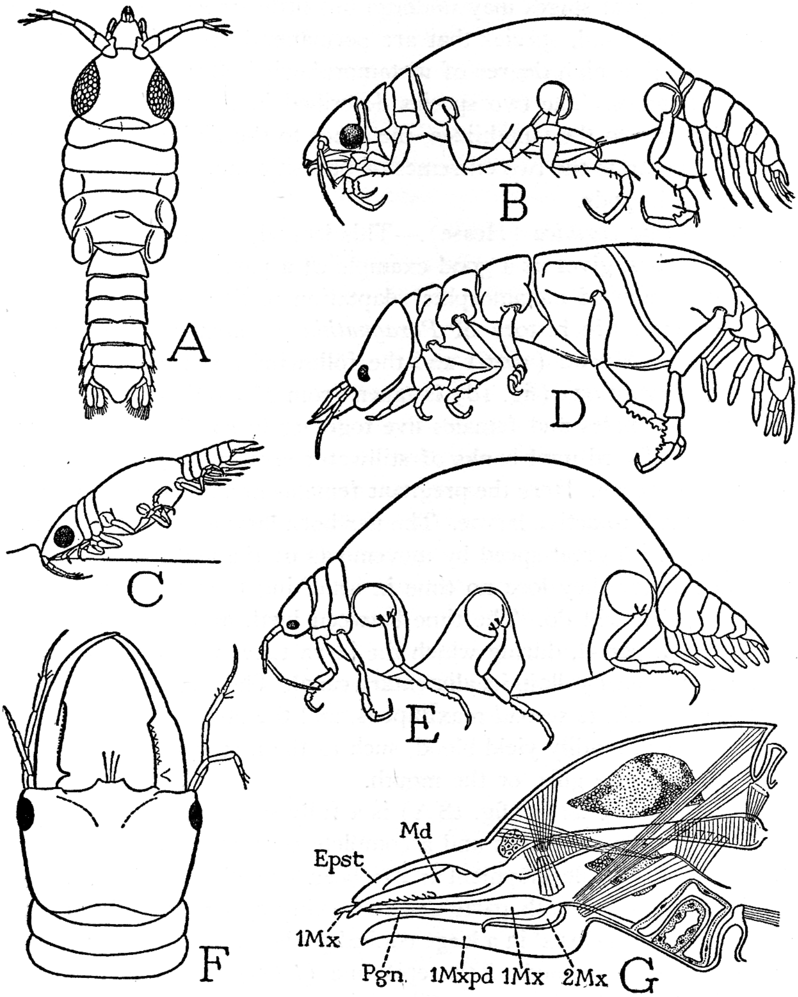

FIG. 18.—Isopoda: Gnathiidea. *Paragnatha formica* (Hesse) (from Monod, 1926).

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. 18 D) 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 pereiopods. 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

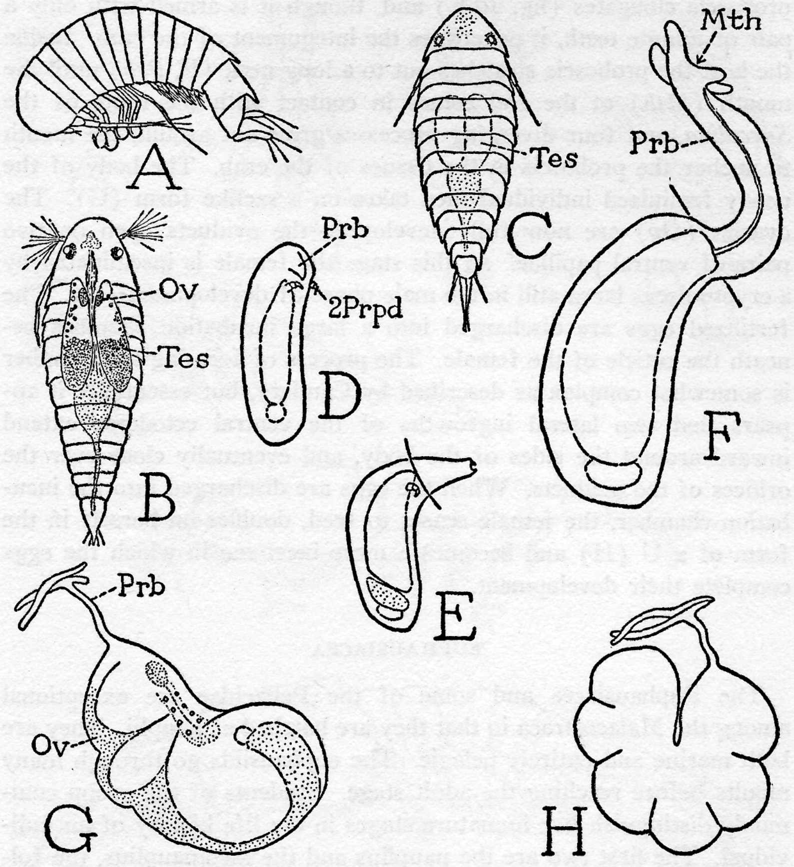

FIG. 19.—Isopoda: Epicaridea. Life history of *Danalia curvata* Fraisse. (A, C-H from Caullery, 1908; B from G. Smith, 1906.)

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