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*)

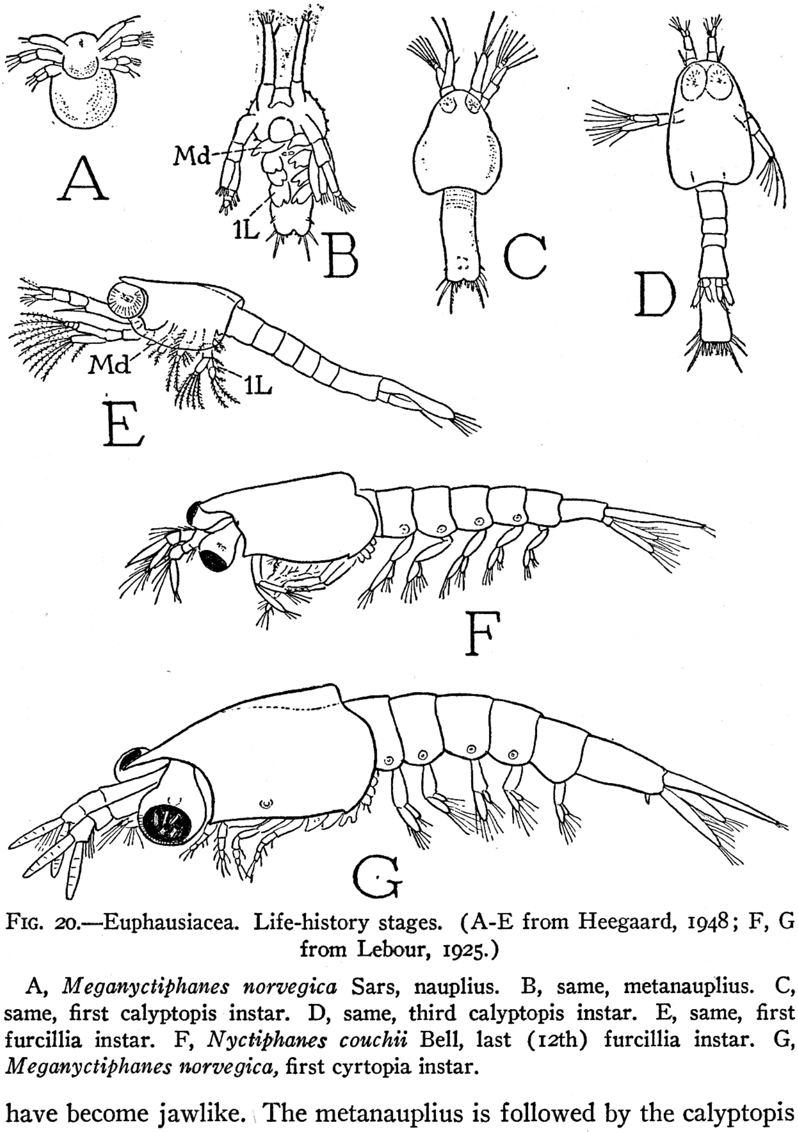

FIG. 20.—Euphausiacea. Life-history stages. (A-E from Heegaard, 1948; F, G from Lebour, 1925.)

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 pereiopods 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 *Meganyctiphanes* 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 pereiopods 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 pereiopods (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 pereiopods 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 pereiopods 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.

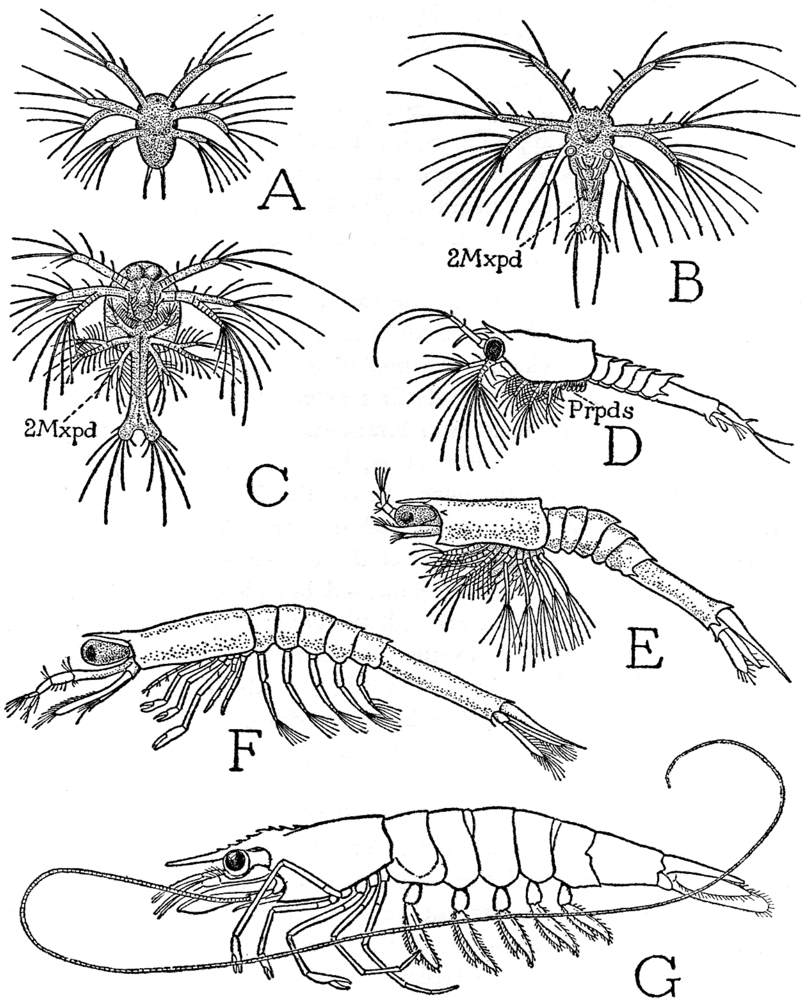

FIG. 21.—Decapoda: Penaeidea. Developmental stages of *Penaeus setiferus* (L.). (A-F from Pearson, 1939.)

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

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

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 pereiopods 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 pereiopods, 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 pereiopods 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 pereiopods. 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 zoeal 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

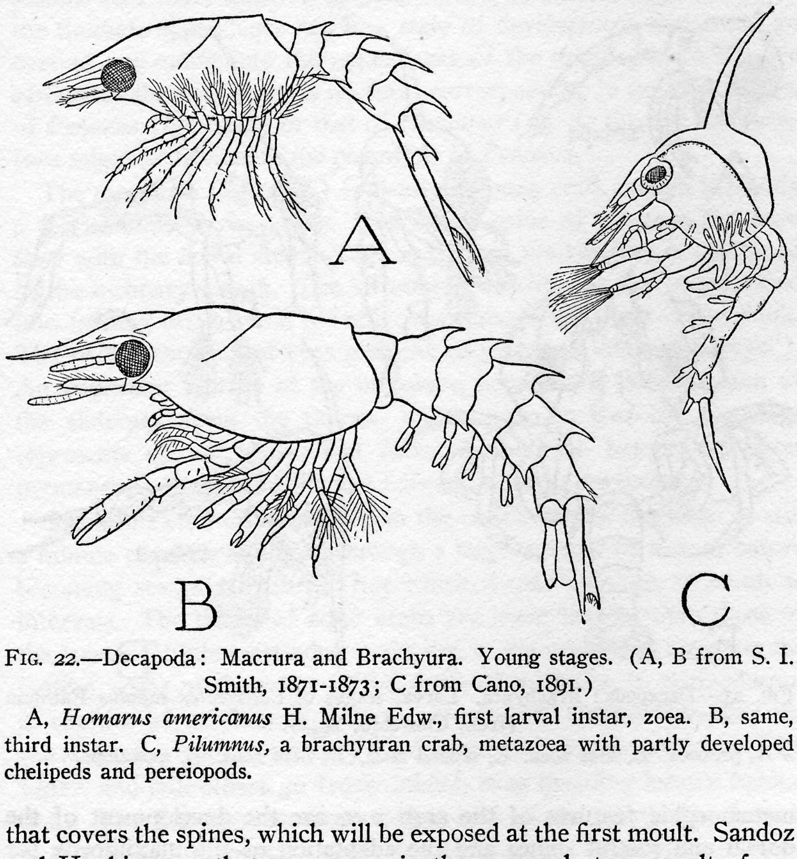

FIG. 22.—Decapoda: Macrura and Brachyura. Young stages. (A, B from S. I. Smith, 1871-1873; C from Cano, 1891.)

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 pereiopods.

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

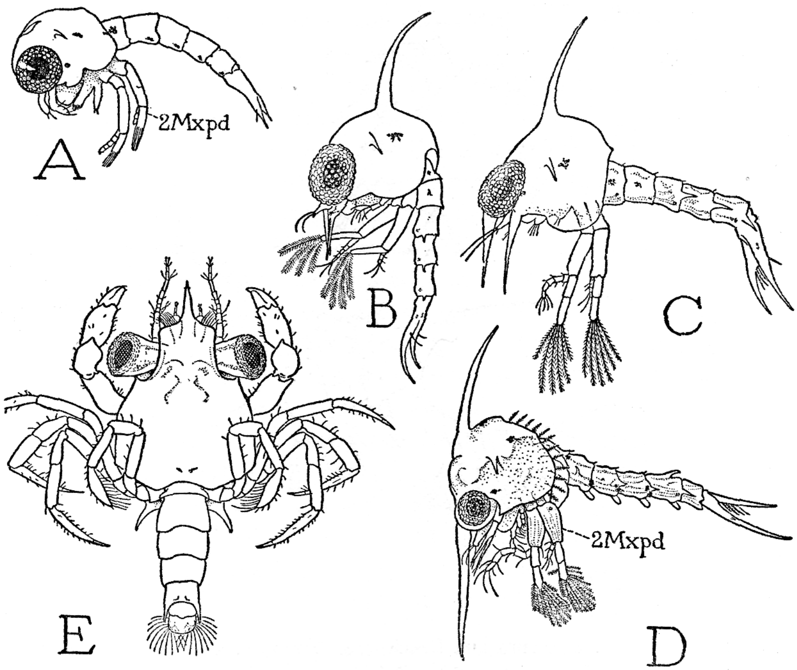

FIG. 23.—Decapoda: Brachyura. Larval stages of *Callinectes sapidus* Rathbun (from Churchill, 1942).

A, prezoea. 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 pereiopods 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 pereiopods, 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 (*2L*) 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 *Coronida,* and is termed by Giesbrecht an *antezoea.* This 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.

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