CHAPTER XV

THE DECAPODA

Order **Decapoda**, Latreille (1802).

Sub-Order 1. **Natantia.**

Tribe 1. PENAEIDEA.
„ 2. CARIDEA.
„ 3. STENOPIDEA.

Sub-Order 2. **Reptantia.**

Section 1. PALINURA.
Tribe 1. ERYONIDEA.
„ 2. SCYLLARIDEA.

Section 2. ASTACURA.
Tribe NEPHROPSIDEA.

Section 3. ANOMURA.
Tribe 1. GALATHEIDEA.
„ 2. THALASSINIDEA.
„ 3. PAGURIDEA.
„ 4. HIPPIDEA.

Section 4. BRACHYURA.
Tribe 1. DROMIACEA.
Sub-Tribe 1. DROMIIDEA.
„ 2. HOMOLIDEA.
Tribe 2. OXYSTOMATA.
„ 3. BRACHYGNATHA.
Sub-Tribe 1. BRACHYRHYNCHA.
„ 2. OXYRHYNCHA.

Definition.—Eucarida in which the caridoid facies may be retained or may be greatly modified; the exopodite of the maxilla is very large (scaphognathite); the first three pairs of thoracic limbs are specialised as maxillipeds; branchiae typically in several series, attached to the coxopodites of the thoracic limbs (podobranchiae), to the articular membranes (arthrobranchiae), and to the

lateral walls of the thoracic somites (pleurobranchiae), very rarely absent; young rarely hatched in nauplius-stage.

Historical.—The great majority of the larger and more familiar Crustacea belong to the Decapoda, and this Order received far more attention from the older naturalists than any of the others. A considerable number of species are mentioned by Aristotle, who describes various points of their anatomy and habits with accuracy, and sometimes with surprising detail. A long series of purely descriptive writers who have added to the number of known forms without contributing much to a scientific knowledge of them begins with Belon and Rondelet in the sixteenth century, and perhaps does not altogether come to an end with Herbst's *Naturgeschichte der Krabben und Krebse* (1782-1804). Among the most noteworthy of early contributions to anatomy are Swammerdam's memoir on the Hermit-Crab (1737), and that of Roesel von Rosenhof on the Crayfish (1755). Réaumur's observations on the phenomena of ecdysis and the regeneration of lost parts in the Crayfish (1712-1718) have become classical. The foundations of classification were laid by J. C. Fabricius (1793), who divided the Linnean genus *Cancer* into a large number of genera, the majority of which are still recognised. Latreille, to whom the name of the Order is due (1802), also began its subdivision into sub-orders and families. In this more than in any other group of Crustacea the works of H. Milne-Edwards, and especially his *Histoire Naturelle des Crustacés*, may be taken as marking the beginning of the modern period, and his classification of the Decapoda has been that most generally accepted until very recently. Almost contemporaneous with Milne-Edwards's great work, and often surpassing it in morphological detail and systematic insight, was de Haan's volume on the Crustacea of Japan (1833-1849). The first important departure from the general plan of classification laid down by these authors was made by Boas in 1880, and his system has been further elaborated by Ortmann and by Borradaile. J. Vaughan Thompson's discovery of the larval metamorphosis of Decapoda (1828-1831), confirming the earlier observations of Slabber and Cavolini in the eighteenth century, gave rise to a curious controversy in which Westwood and others denied the possibility of such a metamorphosis, basing their arguments chiefly on Rathke's memoir on the development of the Crayfish (1829). F. Müller in 1863 made the highly important discovery that *Penaeus* is hatched from the egg in the form of a nauplius, and the clue thus given to the interpretation of the other larval stages was followed up especially by Claus. The development of deep-sea exploration within the last thirty years has resulted in the discovery of a large number of important new types of Decapoda, which have been described by Spence Bate, Miers, Henderson, A. Milne-Edwards, Bouvier, Faxon, Alcock, and others. The numerous

species of fossil Decapoda have been little studied from the point of view of phylogeny, but reference may be made to Bouvier's essay on the origin of the Brachyura as an example of the results which may be obtained in this department. Among other papers which have been fruitful in suggesting lines of research for later workers may be mentioned Huxley's memoir on the classification and distribution of the Crayfishes (1878); A. Milne-Edwards's note on the transformation of the ocular peduncle into an antenna-like organ in a Palinurid (1864), the forerunner of much recent work on regeneration and abnormalities; Giard's papers on parasitic castration; and Faxon's discovery of the alternating dimorphism in the males of *Cambarus*.

Morphology.

Amid the great diversity of general shape exhibited by the Decapoda, two chief types may be distinguished. In the first or Macrurous type the general caridoid facies is retained, the body is elongated and subcylindrical, the abdomen is long and terminates in a tail-fan. In the Brachyurous type (which is not confined to the Brachyura, but recurs in several groups of Anomura) the cephalothorax is greatly expanded laterally and more or less depressed, while the abdomen is reduced and folded underneath the cephalothorax. A very peculiar modification is found in most Paguridea, where the abdomen is markedly asymmetrical and spirally coiled, in correlation with the habit of living in the empty shells of Gasteropod Molluscs.

The carapace coalesces dorsally with all the thoracic somites and overhangs on each side as a *branchiostegite*, enclosing the branchial chamber within which the gills are concealed. Anteriorly it may be produced into a rostrum, which in a few genera of Caridea (*Rhynchocinetes*, etc.) is movably articulated. In most Brachyura the rostrum is reduced to a short but broad frontal plate, of which the relations to the adjacent parts will be described below. In some Macrura (Scyllaridae) and in many Anomura and Brachyura, where the cephalothorax is flattened from above downwards, the lateral portions of the carapace are abruptly bent inwards towards the bases of the legs. The lateral margin thus produced is commonly toothed or otherwise armed.

The surface of the carapace is commonly marked by depressions and grooves corresponding in part to the insertions of various muscles, but in part independent of these. In this way several regions of the carapace are defined which, especially in the Brachyura, may be still further divided into sub-regions. For convenience of systematic description these various areas are denominated according to a scheme of terminology introduced for the most part by H. Milne-Edwards (1851). More recently the furrows of the

carapace have been studied by Boas and by Bouvier. Only a few points can be mentioned here. In the lobsters and crayfish a conspicuous groove (Fig. 145, *c*) crosses the dorsal surface of the carapace transversely about the middle of its length and curves forwards on either side. This groove, named the "cervical groove" by Milne-Edwards (*c* in Boas's terminology, the "branchial groove" of Bouvier), was supposed by him to indicate the line of division between the portions of the carapace arising from the antennal and mandibular somites respectively. Other writers, for instance, Huxley, regarded it as marking the limits of the cephalic and thoracic regions. There appears to be no ground, however, for regarding this groove as of greater importance than some of the other grooves of the carapace. In some cases an equally conspicuous transverse groove (*e* of Boas, "cervical groove" of Bouvier) (Fig. 145, *e*, *e'*) crosses the carapace a little in front of the cervical, and as this is the only transverse groove, apparently, to be found in any of the lower Macrura (Stenopidea, Caridea), it seems at least as likely to afford an important morphological landmark. In some cases portions of the carapace may be separated by a longitudinal groove or uncalcified line, which may even form a movable hinge. Of this nature are the *linea thalassinica* (Fig. 146, *l.t*) of the Thalassinidea, with which the *l. homolica* of the Homolidae may perhaps be identical, and the *l. anomurica* (*l.a*) of many Anomura, identified with the *l. dromiidica* of Dromiidae and the unfortunately named "epimeral suture" of other Brachyura.

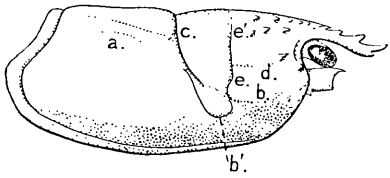

FIG. 145.

Carapace of the Norway Lobster (*Nephrops norvegicus*) from the side. (After Boas.) The letters referring to the grooves of the carapace are those used by Boas. *e*, *e'*, the "cervical groove" of Bouvier, "anterior cervical groove" of Borradaile; *c*, "branchial groove" of Bouvier, "posterior cervical groove" of Borradaile.

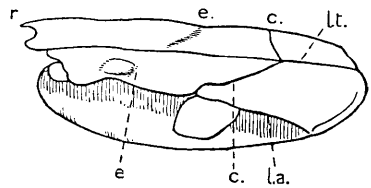

FIG. 146.

Carapace of *Callianassa novaebritanniae* (Thalassinidea) from the left side. (After Borradaile.) *e*, *e*, the grooves so lettered by Boas (see Fig. 144); *l.a*, *linea anomurica* (perhaps also the *linea dromiidica*), the front part of which is the line *b* of Boas; *l.t*, *linea thalassinica* (perhaps also the *linea homolica*), the front part of which is the line *d* of Boas; *r*, rostrum.

The sternal surface of the cephalothorax is very narrow in many Macrura, but is often broad in those which have a depressed form. It is broad in many Anomura and in all Brachyura, with the exception of Raninidae. The thoracic sterna are usually clearly distinguishable, and, in the lower forms, seem to preserve a certain

degree of mobility. In the higher forms they become firmly united, with the exception of the last thoracic sternum, which may be movable (Astacidae, Parastacidae, and Anomura).

In front of the mouth, regions representing the sterna of the three preoral "somites" can be distinguished, but on account of the "cephalic flexure" the ophthalmic and antennular sterna are directed forwards, or even upwards. The antennal sternum is mainly represented by the *epistome*, a plate of varying shape lying between the labrum and the bases of the antennae. In the Natantia the epistome is comparatively narrow, and on each side is separated from the lateral portions of the carapace by the exhalent branchial channels. In most of the Reptantia the epistome (Fig. 147, A, *ep*) is broad and comes in contact with the carapace on each side, and in the Brachyura it becomes firmly united with it. In this way there is defined more or less distinctly a *buccal frame* within which lie the mouth-parts, and which in most Brachyura is closed by the operculiform third maxillipeds. The sides of this buccal frame are formed by the free antero-lateral margins of the carapace (Fig. 147, B, *l.m*), while in front it is more or less distinctly delimited by the epistome itself, or by a transverse ridge (Fig. 147, B, *a.m*) which divides the epistome into two parts, the epistome proper and the *endostome* or palate (*end*). In most Brachyura also (except the Dromiacea) the proximal segments of the antennae are fused with the epistome. In the Macrura the anterior margin of the carapace forms on each side of the base of the rostrum a more or less distinct "orbital notch," within which the eye rests when it is turned outwards. In the Brachyura this transverse direction of the eye-stalks is permanent, and the orbit is usually (except in Dromiacae) completed by the downgrowth of a process (*l.p*) from the front, external to the antennules, which unites either directly or, more usually, by intervention of the second segment of the antenna, with the sub-orbital lobe (*s.o*) of the carapace. Further, in all the Brachyura the rostrum or frontal plate sends downwards in the middle line a process (*m.p*) which unites in front of the ophthalmic and antennular sterna with the epistome, and separates from one another the basal segments of the antennules. The greater part of the ophthalmic peduncle is in this way concealed in a kind of sheath, and only the terminal segment appears and is movable within the orbit.

In the Dromiacea the second segment of the antennal peduncle is free and there is no corresponding process of the front, so that the orbits are incompletely or not at all defined. The arrangement is hardly more complete in certain Oxyrhyncha (*Macrocheira*) (Fig. 147, B), but in most Brachyura the antennal peduncle joins with the front to form a partition separating completely the orbits from the "antennular fossae," into which the antennules

may be withdrawn. There is, however, great diversity in the details of structure of the "facial" region among the Brachyura, and these are of considerable value as systematic characters.

In the Scyllaridae among the Macrurous groups the cephalic

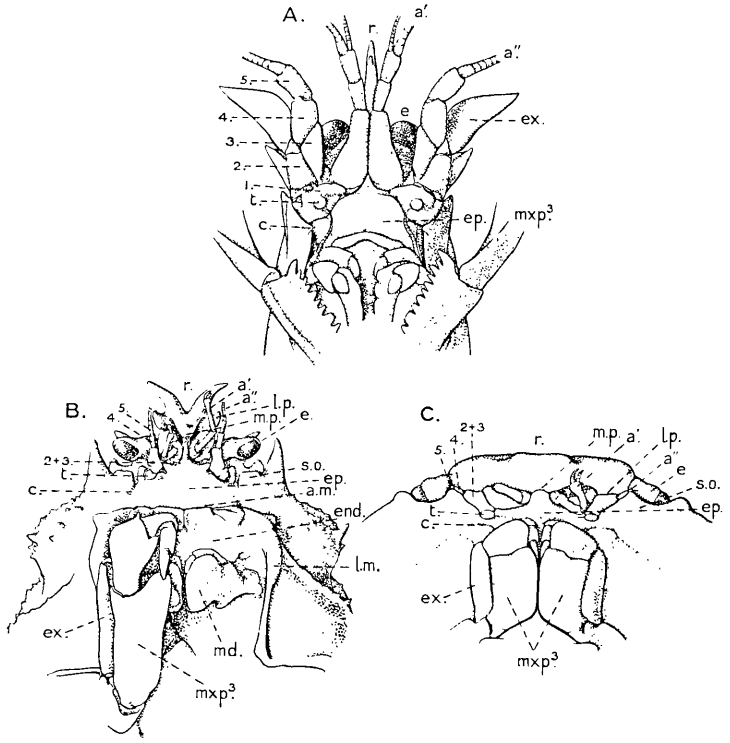

FIG. 147.

Head and anterior part of body from below. A, *Nephrops norvegicus*. B, *Macrocheira Kaempferi*. C, *Carpilius convexus*. (Drawn by Miss G. M. Woodward.) *a'*, antennule; *a''*, antenna; *a.m*, ridge forming anterior margin of the mouth-frame and dividing the epistomial area into epistome proper and endostome; *c*, point where the lateral wing of the carapace touches, or, in B and C, fuses with, the epistome; *e*, eye, in C retracted into, and partly concealed by, the orbit; *end*, endostome; *ep*, epistome; *ex*, exopodite; *l.m*, lateral margin of buccal frame; *l.p*, lateral process of rostral plate, which in C comes in contact with the basal segment (2+3) of the antenna; *md*, mandible; *mp*, median process of the front (in B and C) uniting with anterior process of epistome; *mxp³*, third maxilliped; *r*, rostrum or (in C) frontal plate; *s.o*, suborbital lobe forming floor of orbit; *t*, in A, tubercle bearing opening of antennal gland, in B and C, operculum covering the opening and probably representing the reduced first segment of the antenna; 1-5, the segments of the antennal peduncle.

region is modified in a way that at first sight suggests the Brachyurous type, the eyes being widely separated and lodged in complete orbits. In this case, however, the front unites in the middle line not with the epistome but with the greatly enlarged antennular somite.

In the Alpheidae (Caridea) the anterior margin of the carapace

is modified in a very peculiar manner, growing over and, in most cases, completely enclosing the eyes.

The differences in the development of the abdominal region are no less conspicuous than in the case of the cephalothorax, and have been utilised as affording characters for the primary subdivisions of the Order. In the Natantia the abdomen is large and, with its appendages, forms the chief organ of swimming. It is generally more or less compressed and its somites have well-developed pleura. It is dorsally humped or bent between the third and fourth somites in many Caridea (Eukyphotes, Boas) (Fig. 148), but the character is not so constant as to justify great

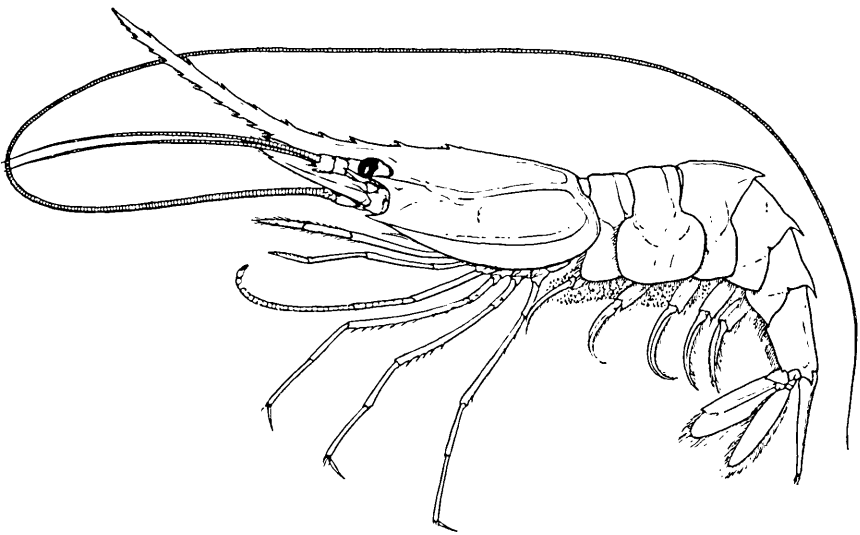

FIG. 148.

Heterocarpus Alphousi (Caridea, Pandalidae), showing the "humped" form of the abdomen and the multiarticulate meropodite and carpopodite of the second leg. (From Alcock, *Naturalist in Indian Seas.*)

systematic importance being attached to it. In the Palinura and Astacura the importance of the abdominal appendages as natatory organs is generally reduced, and the abdomen itself is not humped.

Among the Anomura, the Thalassinidea (Fig. 149) have retained the extended abdomen of the Macrurous groups, but the pleura are more or less reduced; the Galatheidea (Fig. 150) have the abdomen more or less closely flexed under the cephalothorax but not greatly modified; the Paguridea, with the exception of some interesting transitional forms (Pylochelidae) (Fig. 151), have the abdomen and its appendages more or less unsymmetrically developed and its somites imperfectly indicated. In the hermit-crabs (Paguridae and Coenobitidae) the abdomen is soft-skinned and spirally

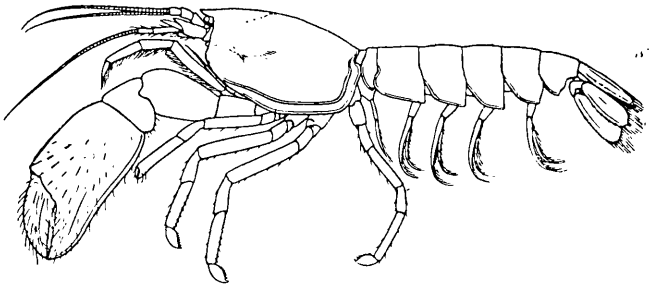

FIG. 149.

Iconaxiopsis andamanensis (Thalassinidea). (From Alcock, *Naturalist in Indian Seas.*)

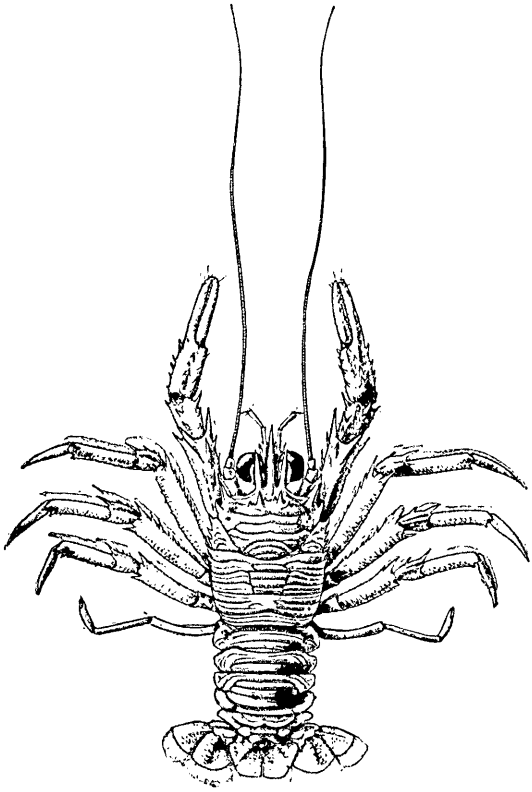

FIG. 150.

Munida andamanica (Galatheidae), abdomen extended.
(From Alcock, *Naturalist in Indian Seas.*)

coiled to fit into the Gasteropod shells inhabited by the animals. Only the sixth somite and the telson are fully calcified, the tergal portions of the other somites being merely indicated by widely

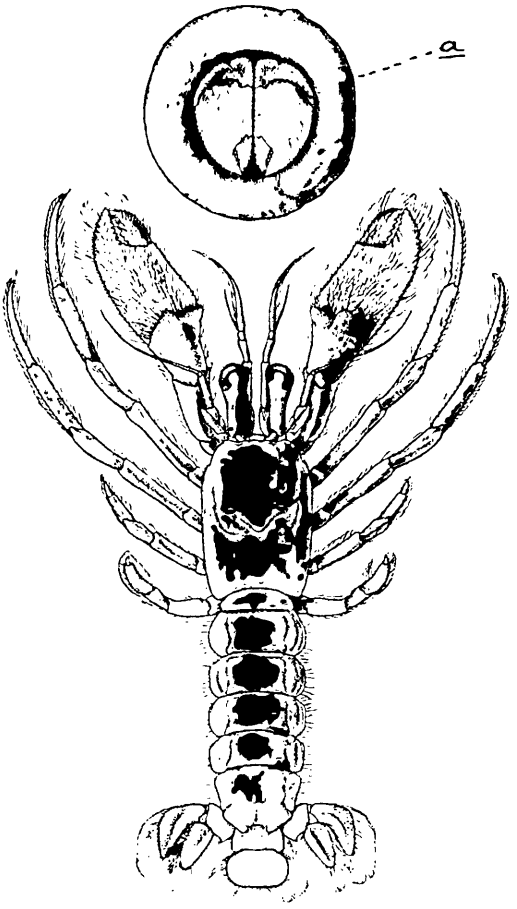

FIG. 151.

Pylocheles Miersii (Paguridea). *a*, end view of the animal lodged in a tube of water-logged mangrove or bamboo, its chelipeds closing the opening. The lower figure shows the animal in a conventional attitude after removal from its refuge. (From Alcock, *Naturalist in Indian Seas.*)

separated chitinous plates in the membranous investment of the dorsal surface. In the coco-nut crab *Birgus* (Coenobitidae) (Fig. 152), which has abandoned the use of a covering for the hinder part of the body, the abdomen, though short, is symmetrical and its terga are well calcified. In the Lithodidae (Fig. 153),

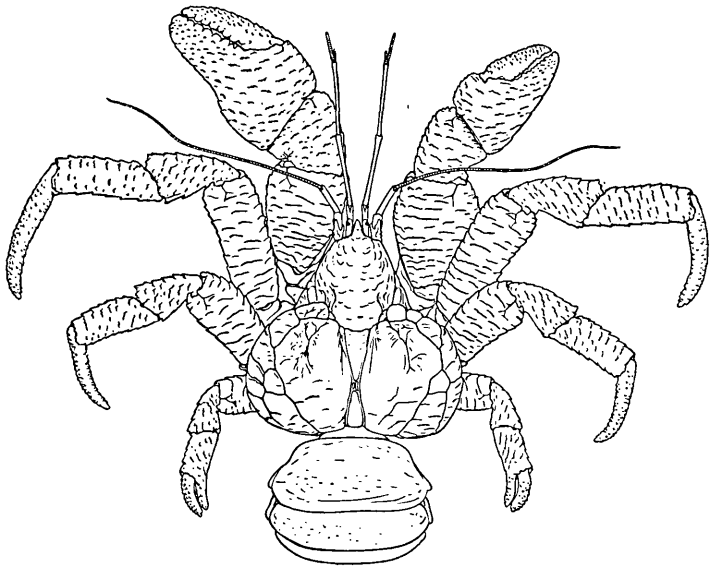

FIG. 152.

Birgus latro, ♂, about ⅛th natural size. The last pair of thoracic legs are folded out of sight in the branchial chambers. (From Alcock, *Naturalist in Indian Seas.*)

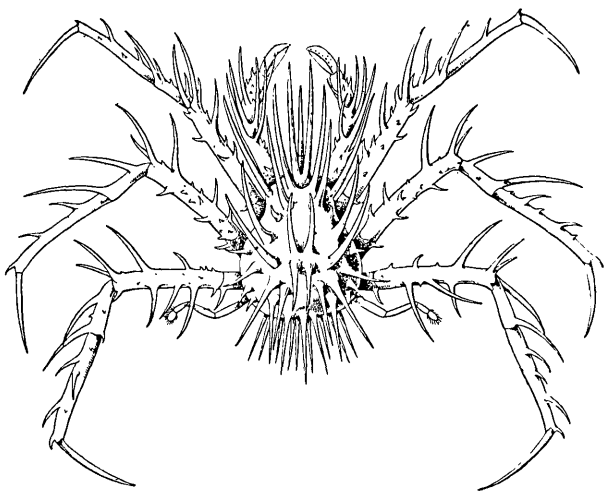

FIG. 153.

Neolithodes grimaldii (Lithodidae). (After Milne-Edwards and Bouvier, from *Ency. Brit.*)

which afford a remarkable instance of "convergence" in the assumption of the Brachyuran facies, the relationship to the hermit-crabs is shown by the fact that the short abdomen, which is closely bent up under the cephalothorax, has the terga incompletely calcified, and is, in the female, more or less unsymmetrical, bearing appendages only on one side.

Among the Brachyura the abdomen is always closely flexed under the cephalothorax, and is much reduced in size. The shape usually differs much in the two sexes, being narrow in the male but broad and often excavated for the reception of the eggs in the female. The terga of all the six somites, as well as the telson, may remain distinct, but very often two or three of the somites may become coalesced, especially in the male sex.

In the region of the thorax a system of internal skeletal structures is developed by infoldings of the cuticle (apodemes) forming the *endophragmal system*. In the Natantia, with feebly calcified integument, this system is but slightly developed, but in the Palinura and Astacura, and especially in the Brachyura, it attains a great degree of complexity. A "sternal canal" may be formed by the meeting of the sternal apodemes of opposite sides above the nerve-cord, and in the anterior part of the thorax this may give a firm plate or "entosternite" lying between the nerve-cord and the alimentary canal. It is not certain whether this entosternite involves any elements other than those supplied by the ectodermal and cuticular infoldings forming the apodemes; if it does not it can hardly be regarded as homologous with the entosternite already mentioned in Branchiopoda (p. 44), which appears to be of mesodermal origin.

In the Brachyura a sternal canal is not formed, the union of the apodemes being confined to one or two of the posterior thoracic somites, where it gives rise to a transverse bar known as the "sella turcica."

Appendages.—Among the Decapoda the *ocular peduncles* (Fig. 154) assume more the character of limbs than they do in any other Crustacea, since they are generally (perhaps always) divided into two, or more rarely three, movable segments. Instances of extreme development of the eye-stalks occur among Caridea and Brachyura, sometimes the first (*Podophthalmus*, Fig. 154, C) and sometimes the second segment (*Macrophthalmus*, Fig. 154, D) being elongated. The corneal surface is generally terminal, but may be oblique and even lateral, the peduncle running out beyond it into a styliform process which may equal in length the rest of the eye-stalk (*Ocypoda*, Fig. 155). In certain species of *Gelasimus* one of the ocular peduncles terminates in a long process of this kind while the other does not. In cases where the eyes are atrophied, as in abyssal or cavernicolous decapods, the peduncle often persists in a reduced state (Figs. 161, 162).

The *antennules* have the three segments of the peduncle always distinct, and as a rule both flagella are present. In many Caridea

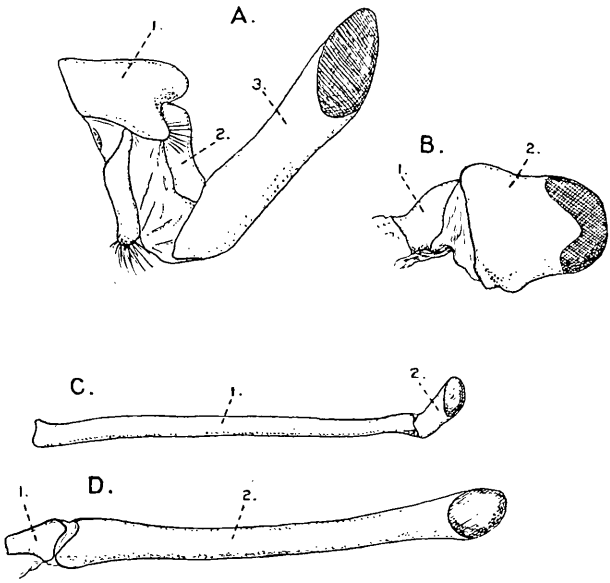

FIG. 154.

Ocular peduncles of Decapoda. A, *Ranina scabra* (Brachyura). B, *Astacus fluviatilis* (Astacura). C, *Podophthalmus vigil* (Brachyura). D, *Macrophthalmus pectinipes* (Brachyura). 1, 2, 3, successive segments of the peduncle.

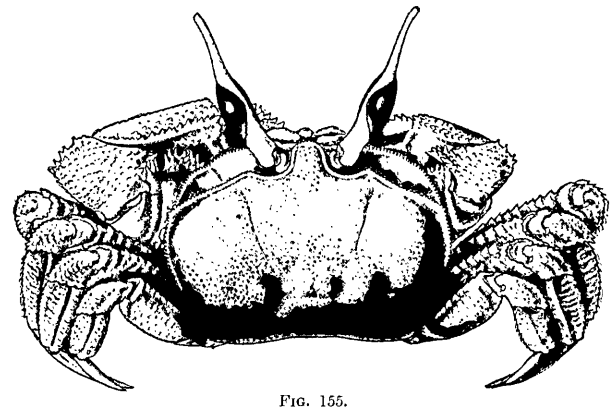

FIG. 155.

Ocypoda macrocera (Brachyura) in a natural attitude with the eyes elevated, showing the styliform prolongation of the ocular peduncles. (From Alcock, *Naturalist in Indian Seas.*)

(Fig. 156, A) the outer flagellum is bifurcated near the base, and in some cases the three flagella appear to arise separately from the

end of the peduncle. The proximal segment of the peduncle, which in most cases lodges the statocyst, possesses in the Natantia a very characteristic expansion of its outer margin in the form of a rounded lobe or spiniform process known as the *stylocerite* (*sty*). In the Brachyura the flagella are very short or quite vestigial; the basal segment is enlarged and generally firmly fixed in the antennular fossa, and the other two segments fold up beside it.

Certain special modifications of the antennules may be mentioned here. In the Sergestidae the outer flagellum of the male is bifurcated and forms apparently a prehensile organ. In *Hymenocera* (Caridea) the inner flagellum is broadly foliaceous. In *Solenocera* (Penaeidae) the same flagellum is in the form of a

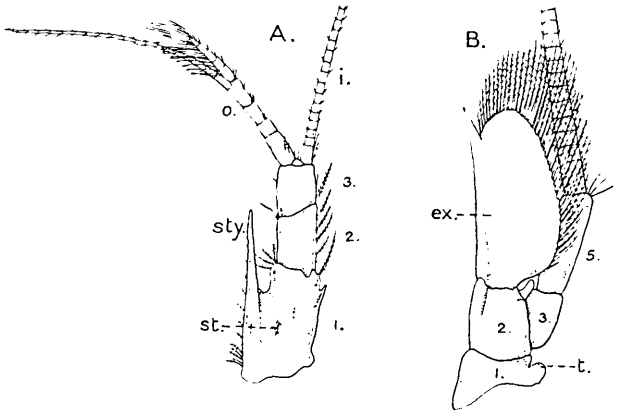

FIG. 156.

A, antennule, B, antenna, of *Athanas nitescens*. (After Sars.) 1-5, segments of the peduncle (the fourth segment in the peduncle of the antenna is not visible from above); *ex*, "scale" or exopodite of antenna; *i*, inner flagellum; *o*, outer flagellum of antennule with its inner branch bearing olfactory filaments; *st*, statocyst in basal segment of antennule; *sty*, stylocerite; *t*, tubercle bearing aperture of antennal gland.

half-tube ensheathing the outer flagellum and forming with its fellow of the other side a long siphon supposed to have a respiratory function. In *Albunea* (Hippidea), where by a rare exception only one flagellum is present, a respiratory siphon is formed by the apposition of the two antennules, which bear each a double longitudinal row of setae.

In the lower Decapoda the peduncle of the *antenna* has five segments, the two segments of the protopodite and the first three of the endopodite, but the segments are usually more or less displaced so as to articulate with each other in a zigzag manner (Fig. 156, B). The exopodite (*ex*) forms a large foliaceous "scale" (squama) in the Natantia. In most Reptantia the number of peduncular segments is reduced by the fusion of the second and

third, and the exopodite, when present, is often reduced to a spine-like "acicle." In the Scyllaridea the number of free segments is further reduced by the coalescence of the proximal segment with the epistome. In the Brachyura, the proximal segment is only distinct in the Dromiacea; in the other groups it is either fused with the epistome or, perhaps, represented by a small operculum (Fig. 147, B and C, *t*) which covers the external opening of the antennal gland. The exopodite is absent in all the Brachyura except possibly in certain Dromiacea (Homolodromiidae), where an immovable spiniform process is supposed to represent it. The flagellum is very short in most Brachyura and may disappear altogether. In some Corystidae the two flagella form a long respiratory siphon in much the same way as the antennules do in *Albunea*. In the Palinuridae not only the peduncle but also the flagellum is very stout, and in the Scyllaridae the whole appendage is expanded and flattened, and the flagellum is represented by a broad, shovel-like plate.

The *mandibles* never have a distinct lacinia mobilis, although, in some of the lower types (Atyidae), they may have a group of setae or spines on the inner edge. The incisor is widely separated from the molar process in many Caridea (Fig. 157, A), but in the other groups the two cannot be distinguished or are separated only by a groove. In some Caridea the incisor process is wanting. A palp of three segments is usually present, but the number of segments is sometimes reduced, and among the Caridea the palp is not unfrequently entirely absent either in isolated genera (*Hippolyte*, *Palaemonetes*) or throughout whole families (Crangonidae, Atyidae). In the Penaeidae the palp is expanded and lamellar, and apparently takes part in enclosing the respiratory passages.

The *maxillulae* (Fig. 157, B, and Fig. 9, B, p. 13) have two inwardly turned endites, and a palp which is sometimes divided into two, and even, in some species of *Penaeus* (Fig. 158, A), into three or four, segments. An outwardly turned plate (*ex*) directly connected with the proximal endite, and having the same relations as the large external plate of the maxillula of Euphausiacea, can sometimes be observed, but only exceptionally (*e.g. Caridina*) is it of considerable size. The chief difference from the maxillulae of the Euphausiacea consists in the absence of a distinct second segment, which here appears to be fused with the first.

The *maxillae* are closely comparable to those of Euphausiacea, though the relative proportions of the parts are very different. In the typical form such as we find in the Crayfish (Fig. 9, C, p. 13) the two endites are each divided into two by a deep incision, there is an unsegmented palp, and a very large lamellar expansion on the outer side to which the name *scaphognathite* is given. According to Hansen, the two bifid endites arise here, as in the Euphausiacea,

from the second and third segments of the limb. Coutière, however, states that in some primitive Caridea the double proximal

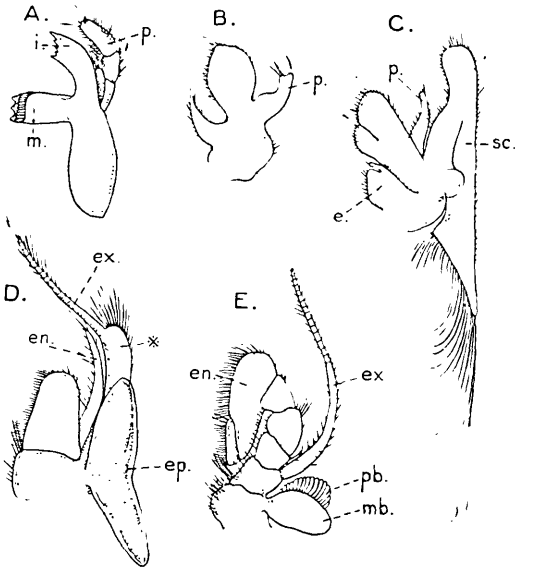

FIG. 157.

Mouth-parts of *Pandalus borealis* (Caridea). (After Sars.) A. mandible; B, maxillula; C, maxilla; D, first maxilliped; E, second maxilliped. *e*, proximal endite of maxilla (according to Boas, the small distal lobe alone represents the endite and the large proximal lobe does not represent the proximal division of the endite in other Decapoda); *en*, endopodite; *ep*, epipodite; *ex*, exopodite; *i*, incisor process; *m*, molar process of mandible; *mb*, mastigobranchia; *p*, palp; *pb*, podobranchia; *sc*, scaphognathite of maxilla; *, lobe on exopodite of first maxilliped characteristic of Caridea.

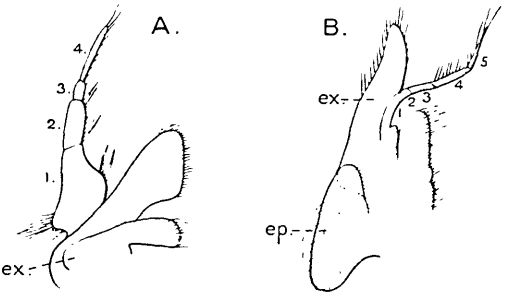

FIG. 158.

A, maxillula of *Penaeus caramote*; 1-4, palp of four segments; *ex*, exite connected with proximal endite. B, first maxilliped of same; 1-5, endopodite of five segments; *ep*, epipodite; *ex*, exopodite. (After Boas.)

endite can be seen to belong to the first segment, and that the other two lobes are independent of each other, belonging respectively

to the second and third segments. The scaphognathite has been variously interpreted as an epipodite or as consisting of epipodite and exopodite together. A comparison with the maxilla of the Euphausiacea shows, however, that it must be regarded as an extreme development of the plate which in the latter case is identified as the exopodite.

The modifications which this typical form undergoes within the Order are not very striking nor do they afford much material of systematic value. An undivided proximal endite is characteristic of the Caridea, in which group (with some few exceptions) it is also greatly reduced in size (Fig. 157, C). In the Pasiphaeidae both endites disappear.

It is characteristic of the Decapoda that the first three pairs of thoracic limbs are more or less distinctly differentiated from the others as *maxillipeds*. It must be noted, however, that the line of demarcation between the two groups of appendages is not always sharply drawn, and that in the Penaeidea and Caridea the third maxillipeds are often distinctly pediform.

In all Decapods, however, the *first maxilliped* (unlike the corresponding appendage of the Euphausiacea) has completely lost its pediform character. The endopodite is greatly reduced in size, and the coxopodite and basipodite are produced inwards as broad endites of which the proximal is often divided by an incision. The most primitive condition is found in certain Penaeidae (Fig. 158, B), where the endopodite presents the full number of five segments. In other Decapoda the number of segments is never more than two and the endopodite is often unsegmented. The exopodite is always present; in the Caridea (Fig. 157, D) it presents a characteristic lamellar expansion of its outer margin (lobe *a* of Boas), the narrow distal part corresponding apparently to the flagellum, which in the higher forms is segmented off from the peduncle and may be divided into numerous articulations. The epipodite is rarely absent (*e.g.* in many Anomura) and is especially large in the Brachyura (Fig. 159, A).

The *second maxilliped* departs less from the general type of the thoracic limbs than does the first. The proximal segments are not produced inwards as distinct endites. The endopodite is relatively short, permanently flexed inwards, and its distal part is commonly more or less flattened.

In the family Stylodactylidae (Caridea) the second maxillipeds appear to present an anomalous structure, two terminal segments articulating side by side on the end of the fifth segment. In the great majority of the Caridea (Fig. 157, E) the terminal segment articulates, not with the distal end but with the inwardly turned (morphologically the outer) margin of the preceding segment. The number of distinct joints is not infrequently reduced by the fusion

of the basipodite and ischiopodite. The exopodite is rarely absent (Sergestidae, Pasiphaeidae), and is often divided into a peduncle and a multiarticulate flagellum.

The *third maxilliped* may, in the Natantia, even exceed in length the next succeeding pair of appendages. The coxopodite and basipodite are almost always connected by an immovable articulation. In the Caridea the ischiopodite is quite coalesced with the meropodite, and the dactylopodite is obsolete or coalesced with the preceding segment. A serrate ridge or "*crista dentata*" (Fig. 147, A, *mxp*^{3}) is commonly present on the third segment, but no endites are developed from the first and second segments. Among the Brachyura (Fig. 147, B, C, *mxp*^{3}) the third maxillipeds become greatly modified to form an oper-

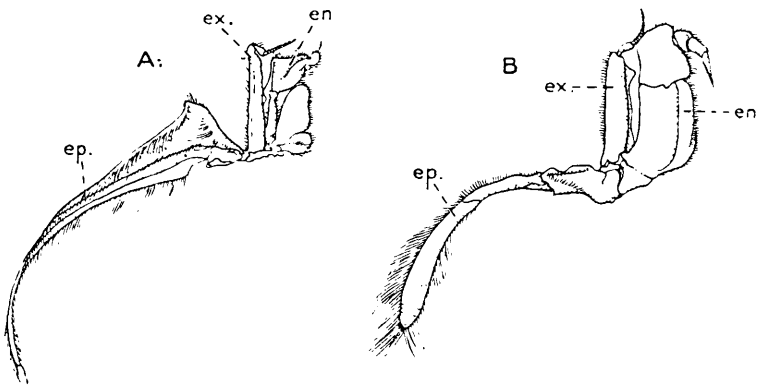

FIG. 159.

A, first, B, third maxilliped of *Neptunus pelagicus* (Brachyura). (After de Haan.) *en*, endopodite; *ep*, epipodite (mastigobranchia); *ex*, exopodite.

culum to the buccal frame and entirely lose their pediform character. The ischiopodite and meropodite become broad plates and the terminal three segments are often hidden behind the meropodite. The peduncle of the exopodite may also be expanded and share in forming the operculum. Its terminal flagellum is either folded out of sight or may be entirely lost. The epipodite forms a long curved blade in most Brachyura (Fig. 159, B, *ep*).

The remaining five pairs of thoracic appendages (*pereiopods*) are typically ambulatory legs, composed of the usual seven segments. Exopodites may be present on some or all of them in some Penaeidea and Caridea (Pasiphaeidae, Fig. 160, Hoplophoridae, some Atyidae, and Crangonidae), but elsewhere they are wanting. As a rule one or more pairs are chelate or sub-chelate, except in the Scyllaridea (where, however, the last pair are imperfectly chelate in the female sex) and in some Hippidea. The first three pairs are chelate in

most Penaeidea and in the Stenopidea and Astacura (Fig. 161), the first four or all five pairs in the Eryonidea (Fig. 162), the first two

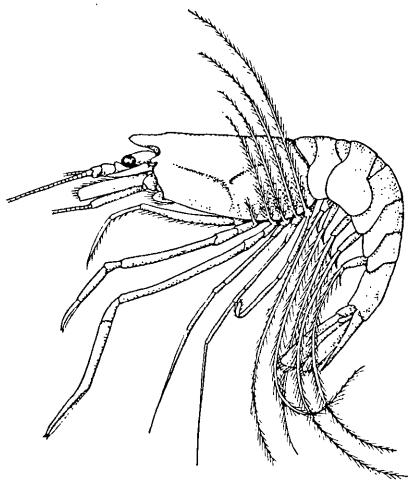

FIG. 160.

Psathyrocaris fragilis (Pasiphaeidae), showing the greatly developed exopodites of the thoracic legs (a "Schizopod" character) and of the pleopods. (After Alcock.

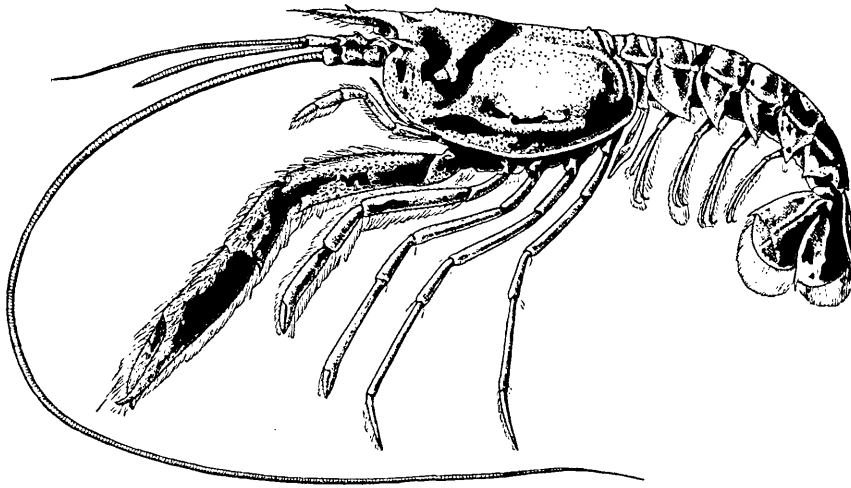

FIG. 161.

Nephropsis Carpenteri (Nephropsidae), ♂. A deep-sea species in which the eyes have almost disappeared but the vestigial eye-stalk can be seen below the rostrum. (From Alcock, *Naturalist in Indian Seas.*)

in most Caridea, the first or the first two in Thalassinidea (Fig. 149, p. 260), and the first pair only in the other Anomura (Fig. 150,

p. 260) and the Brachyura. In most Anomura the last pair, and in a few Brachyura the last or the last two pairs, are subchelate. A very remarkable form of chela is found in the genus *Psalidopus* (Caridea) (Fig. 163), in which *both* fingers are movably articulated with the propodite, an arrangement resembling that found in the second maxilliped of *Stylodactylus*.

In most of the Reptantia, where the first pair of legs are chelate and much larger than the others, they are commonly referred to as the *chelipeds*, and the following four pairs are distinguished as walking-legs. Frequently the chelipeds are asymmetrical in size and shape on the two sides, the larger chela having the fingers armed with blunt crushing-tubercles, while the smaller has sharp cutting-teeth. In many cases, as, for instance, in the lobster, the larger crushing-chela may be on the right or the left side indifferently, but in some Brachyura it is constantly on the same side of the body. A curious reversal of asymmetry sometimes occurs as a result of the loss of the larger chela; at the next ecdysis the remaining chela assumes more or less completely the characters of a large crushing-chela, while the regenerating limb has the form of a small cutting-chela.

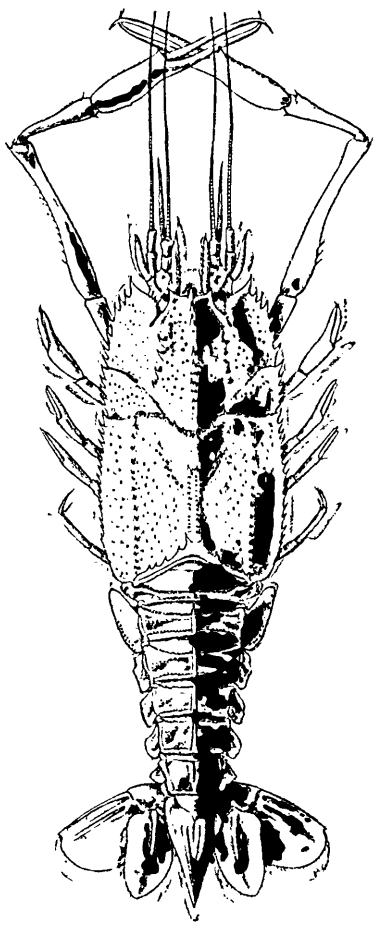

FIG. 162.

Pentacheles Hertii (Eryonidea). The vestigial eye-stalks are fixed in notches in the front of the carapace. (From Alcock, *Naturalist in Indian Seas.*)

A modification of some of the legs as swimming-paddles occurs in various groups, for instance, in the Portunidae (Brachyura), where the last pair are so modified. In some Natantia and in one genus of Hippidea one pair of legs may become multiarticulate and flagelliform. This modification occurs especially in the second pair of many Caridea (formerly grouped together as Polycarpinea) (Fig. 148), where the

carpopodite and sometimes also the meropodite and ischiopodite are subdivided into small articulations.

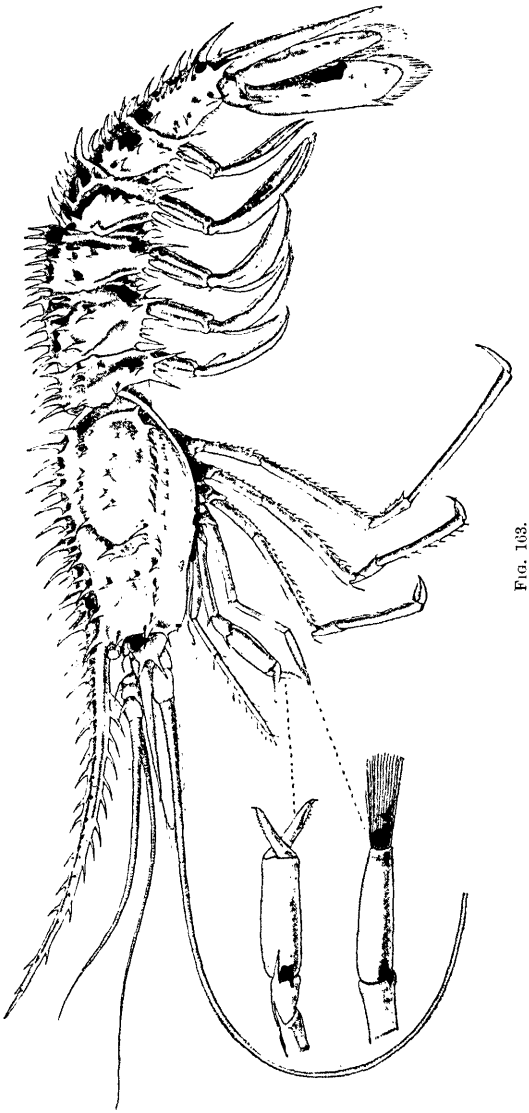

FIG. 103.

Psalidopus spinivendris (Caridea). As shown in the enlarged figures at the side, the first legs have peculiar chelae in which both fingers are movable, while the second legs terminate in a brush of setae. (From Alcock, *Naturalist in Indian Seas.*)

While in the Natantia, with few exceptions, all the seven segments of the limb are distinct and movable, among the Reptantia

this is only the case in the Eryonidea. In the Astacura the first pair, and in the remaining Reptantia all the five pairs, of legs have the basipodite and ischiopodite immovably united. Perhaps correlated with this fusion is the presence of a "fracture plane" in the basipodite, at which separation of the limb takes place in autotomy in many Reptantia.

In a few Decapoda some of the legs become quite vestigial or even disappear altogether. In the Sergestidae the last two pairs are reduced, and in *Acetes* the last pair and in *Leucifer* the last two are quite absent. In the Pinnotheridae (Brachyura) the last pair may be rudimentary or absent. In many Crangonidae the second pair are smaller than the others, and in *Paracrangon* they disappear entirely. This case is especially noteworthy since the suppression of members of a meristic series rarely occurs except at one end of the series.

The epipodites and associated structures of the thoracic limbs will be described below in connection with the branchial system.

The *pleopods* of the Decapoda present typically the same structure as those of the Euphausiacea. Of the two segments composing the protopodite the first is usually small, often apparently absent, the second elongated and often stout. The two rami may be multiarticulate and flagelliform, more often flattened and unsegmented, and bear a marginal fringe of natatory setae. The endopodite may bear on its inner margin an *appendix interna* tipped with a group of coupling-hooks.

It is interesting to note that the Penaeidea and Stenopidea, which, on the whole, take the lowest place among the Decapods, never possess an appendix interna (except in so far as an element derived from it may possibly share in forming the copulatory appendage on the first pair of pleopods in the male), though the presence of that organ in the Leptostraca, Euphausiacea, and Stomatopoda shows that its possession must be reckoned a primitive feature among the Malacostraca.

The pleopods are most strongly developed in the Natantia, where they form the chief swimming-organs. In the Reptantia the natatory function is less important and the pleopods are generally feebler, though in some fossorial Thalassinidea they are of considerable size. An appendix interna is wanting except in some Thalassinidea and in the Scyllaridea, where the pleopods are peculiarly modified. In the Anomura, excluding the Thalassinidea, the pleopods are generally feeble, often uniramous, and are sometimes absent from the first somite, as they are also in the Scyllaridea and Parastacidae. They are absent altogether in the males of Hippidea, Lithodidae, and of some other Paguridea; when present in the Paguridea, they are, as a rule, developed only on one side of the body and an appendix interna is sometimes present. In the Brachyura the first and second pairs (which are specially

modified, as described below) alone persist in the male, while in the female the second to the fifth pairs are (with rare exceptions) developed as egg-carrying appendages, with short protopodite and long and slender rami; the first pair are absent in the female except in the Dromiacea. In *Callianidea* (Thalassinidea) the rami of the pleopods are fringed with long filaments, apparently branchial in function; this isolated case forms a curious parallel to the development of branchial filaments on the pleopods in the Stomatopoda and in *Bathynomus* among the Isopoda.

Sexual modifications are commonly presented by the pleopods, most constantly by those of the first and second pairs, which in the male assume a copulatory function. In the case of the first pair the difference may be slight, as in most Caridea, where the endopodite is reduced to a small leaflet, differing more or less in shape in the two sexes, and in the male armed with a group of coupling-hooks. In the Penaeidea the first pair of the female have the endopodite small or wanting; in those of the male it is represented by a membranous plate, often of large size and complicated structure, attached to the inner side of the peduncle, and bearing (as in the Caridea) a group of coupling-hooks which interlock with those of the other side. To this apparatus the name of *petasma* has been given by Spence Bate. In the Reptantia the appendages of this pair are never biramous. In the female sex they are greatly reduced in size or altogether absent. Occasionally they are absent in both sexes (Parastacidae, Scyllaridea, some Paguridea, and Hippidea), but more commonly they are developed in the male into copulatory appendages, usually styliform, with a spoon-shaped or tubular terminal part. In some Thalassinidea (*Upogebia*), by a rare exception, these appendages are present (uniramous) in the female but absent in the male sex.

The second pair in the female sex are almost always similar to those which follow. In the male sex, however, this is rarely the case (some Scyllaridea, Parastacidae, *Upogebia*). As a rule, they are modified by the development of an accessory process, the *appendix masculina* (Boas), from the inner edge of the endopodite. This appendix is small in the Penaeidea and Caridea (in which latter it may coexist with the appendix interna), but in the other groups it increases in importance, the terminal part of the endopodite diminishing, as does also the exopodite, until in the Brachyura (and some Anomura) there remains only a styliform appendage of two segments, the proximal representing the protopodite and the distal the endopodite together with its appendix masculina.

The *uropods* retain in the Macrurous[1] groups the general characters of the caridoid type, having a short protopodite and broad lamellar rami, forming with the telson a tail-fan. As a rule the exopodite is more or less distinctly divided by a transverse

joint, and very rarely as in *Laomedia* (Thalassinidea) the endopodite is similarly divided.

Among the Anomura the uropods are variously modified. In the Galatheidea they retain more or less the type of structure which they showed among the Macrura. In most Paguridea they become modified as organs for fixing the posterior end of the body in the shell or other lodging carried by the animal, the rami are stout and curved, with roughened, "file-like" surfaces which are pressed against the shell, and the appendages of the two sides share in the asymmetry of the whole abdomen. In the Lithodidae alone among Anomura the uropods are wanting. This is all but universally the case also among the Brachyura, where only in certain Dromiacea (Dromiidea) are there found traces of uropods in the form of small plates intercalated on each side between the last abdominal somite and the telson.

Branchial System.—With the single exception of the aberrant genus *Leucifer*, all Decapoda possess branchiae connected with some or all of the thoracic somites and lying in the cavities enclosed by the branchiostegites on each side. The typical number of branchiae which may be present on each side of a somite is four, arranged as follows: One is attached to the lateral wall of the somite dorsal to the articulation of the appendage (*pleurobranchia*), two to the articular membrane between the coxopodite of the appendage and the body-wall (*arthrobranchiae*), and one, representing a differentiation of part of the epipodite, is inserted on the coxopodite itself (*podobranchia*).

Four series of gills corresponding to these can be traced in a more or less incomplete form throughout the whole series of the Decapods. They are, however, not invariably distinguished from each other by the position of attachment in the manner just described. In particular, the distinction between arthrobranchiae and pleurobranchiae is often very difficult to draw in practice, and there are some cases where an arthrobranchia in one species is plainly homologous with a pleurobranchia in another. Claus has shown that in the development of *Penaeus* three bud-like outgrowths appear on the proximal part of most of the thoracic limbs (Fig. 164, A). The distal one (*a*) gives rise to the epipodite with its podobranchia and the two others (*b*, *c*) are the arthrobranchiae. As development proceeds an apparent change in the position of these last is brought about by coalescence of the proximal part of the appendage with the body, so that the branchiae no longer appear as outgrowths of the limb but spring from that part of the body-wall which afterwards forms the articular membrane of the joint. The pleurobranchia appears a little later than the other two (Fig. 164, B, *d*), but its place of origin is very close to if not actually on the basal part of the limb itself. Williamson has observed a

similar transference of the gills from the limb to the body-wall in the development of *Crangon* (Caridea), and Bouvier in *Uroptychus* (Galatheidea). Claus concludes from these observations that not only the podobranchiae but also the arthro- and pleurobranchiae are originally appendages of the limb. The absorption of the proximal part of the limb into the body-wall is of importance in view of Hansen's recognition of a pre-coxal element in the appendages of various Crustacea.

The origin of the podobranchiae by differentiation of part of the epipodite is also clearly shown in the development of *Penaëus*. The most distal of the three outgrowths mentioned above early becomes bilobed. The distal lobe, which lies in front of the

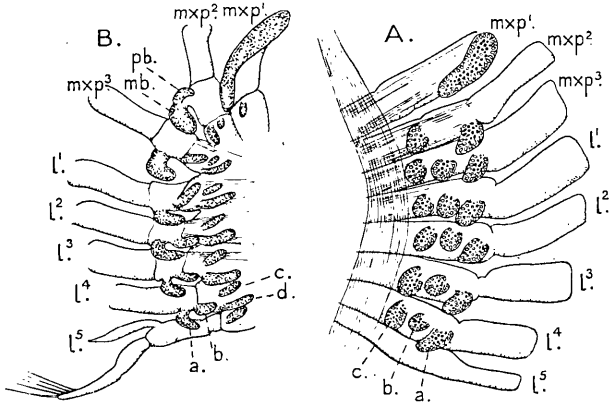

FIG. 164.

Two stages in the development of the branchial system of *Penaeus*. (After Claus.) A, early stage; B, later stage after appearance of the rudiments of pleurobranchiae. *mxp*¹-*mxp*³, maxillipeds; l^1-l^5, legs; *a*, distal series of rudiments giving rise to mastigobranchiae and podobranchia (on *mxp*²); *b*, *c*, rudiments of arthrobranchiae; *d*, rudiments of pleurobranchiae. In B the distal rudiment on *mxp*² is dividing into podobranchia (*pb*) and mastigobranchia (*mb*).

proximal one, develops in the case of the second maxilliped (Fig. 164, B, *mxp*²) into the podobranch (in the other appendages it disappears), while the proximal and posterior lobe becomes the epipodite or *mastigobranchia* of the adult, a bilobed membranous lamina which extends upwards into the branchial chamber between the gills. On the first pair of maxillipeds the distal lobe remains simple and persists as the distal part of the laminar epipodite of the adult. It is remarkable, however, that in the only cases in which the epipodite of the first maxilliped develops branchial filaments (in some Parastacidae), these are borne, not by the distal part which appears to represent the podobranchia, but by the proximal division.

In most Reptantia the podobranchiae have a similar relation to the mastigobranchiae to that just described in *Penaeus*. In the

Astacidae, however, the axis of the gill coalesces with the mastigobranchia, which has the form of a folded membranous lamina from which the branchial filaments spring directly. In the Parastacidae this lamina is greatly reduced or disappears.

In the Caridea, the mastigobranchiae, when present, have usually the form of short curved rods, directed backwards, each ending in a hooked process which grasps a tuft of long slender setae on the coxopodite of the next succeeding appendage. This tuft of setae, which is also present in some Reptantia, springs from a small papilla which Coutière has compared with the setiferous epipodial process found in *Gnathophausia* (Mysidacea) (Fig. 106, *ep*, p. 176), and which he regards as a distinct element of the branchial system (*setobranchia* of Borradaile). In a species of *Eironaxius* (Thalassinidea) Coutière has found that the coxopodite of the first leg bears *two* podobranchiae, one attached as usual to the base of the mastigobranchia, the other close to, if not actually inserted on, the setobranchia. In no other Decapod is more than one podobranchia found on any limb.

As regards their structure, each branchia consists of a stem or axis which is attached at or near one end and bears numerous lateral branches. According to the form and arrangement of these latter, three main types of gills have been distinguished, which, however, are connected by intermediate forms. In the *trichobranchiate* type (Fig. 165, B) the branches are filamentous, and are arranged in several series around the axis. In the *phyllobranchiate* type (Fig. 165, C) the branches are flattened laminae, and as a rule only two opposite series are present. The *dendrobranchiate* type (Fig. 165, A) is characterised by the fact that the biserial primary branches are themselves ramified, sometimes in a very complex fashion. The dendrobranchiate type is peculiar to the Penaeidea, but each of the other two types recurs in widely separated groups. Thus the Caridea have phyllobranchiae, as have also all the Brachyura, with the exception of some of the primitive Dromiacea, which have trichobranchiae. The Stenopidea, Palinura, and Astacura have trichobranchiae. Among the Anomura, phyllobranchiae are the rule, but *Aegleа* among the Galatheidea, and the Pylochelidae, with several genera of Paguridae among the Paguridea, have trichobranchiae, and the gills of some Thalassinidea are intermediate in character.

In the number and arrangement of the gills very great differences exist, which afford valuable systematic characters. At the same time, the important divergences sometimes presented by closely allied forms render it necessary to use caution in estimating the value of these characters (compare, *e.g.*, *Caridina* and *Limnocaridina*, or *Pandalus* and *Pandalina*). The last thoracic somite is invariably destitute of mastigobranchia, podobranchia, or arthro-

branchiae, though it may carry a pleurobranchia and a setobranchia. As a rule no gills are present on the first thoracic somite, but in some Penaeidea, Stenopidea, Astacura, and Thalassinidea, a minute arthrobranchia (? pleurobranchia) is present, while in some Parastacidae the epipodite bears some branchial filaments and is, in fact, a rudimentary podobranchia.

On the remaining somites the podobranchiae are the most frequently suppressed. It is characteristic of the Scyllaridea and Astacura that they possess a full series of podobranchiae, and less complete series are found in the more primitive Penaeidea (Ceratospinae and Aristeinae), in the Eryonidea and some Thalassinidea, and in the primitive Homolodromiidae among the Dromiacea. In

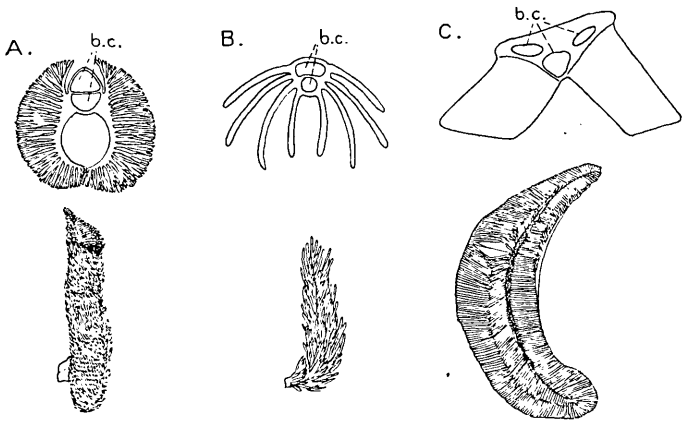

FIG. 105.

Branchiae of Decapoda. The lower figures show the complete branchiae, the upper figures transverse sections of the same. A, dendrobranchiate type (*Penaeus canaliculatus*). B, trichobranchiate type (*Astacus fluviatilis*). C, phyllobranchiate type (*Palaemon lar*). *b.c*, blood-channels in axis of branchia.

all other Decapods they are absent from the legs and, except in Brachyura, from the third, though not uncommonly present on the second, maxillipeds. Apart from the podobranchiae, the mastigobranchiae and setobranchiae may persist in a more or less complete series, especially in the Caridea. The pleurobranchiae are stated to extend forwards to the somite of the third maxilliped in some Caridea, and to that of the second in the Penaeidae; but it must be noted that the distinction between pleuro- and arthrobranchiae in the crowded anterior part of the branchial chamber is often obscure. They form the chief part of the gill-system in the Caridea, where five are usually present, and, on the other hand, they are quite wanting in most of the Thalassinidea. In the Brachyura a formula of nine branchiae on each side is found in all the main subdivisions; but while it is practically universal in the Oxyrhyncha

and in those families of the Brachyrhyncha formerly grouped together as Cyclometopa, it suffers reduction in many of the Catometopa, especially in terrestrial and parasitic forms, and in the majority of the Oxystomata.

The table on p. 280 gives the branchial formulae in a series of representative forms.

The arrangements for maintaining a current of water through the branchial chamber and for preventing the ingress of foreign particles are very varied and often complex. The branchial current is caused by the vibratory movements of the scaphognathite or exopodite of the maxilla, and as a rule it sets from behind forwards, though it appears that in some cases, especially in Decapods which burrow in sand or mud, the direction of the current is periodically reversed. In the simplest cases, as in most of the Macrurous groups, the water enters along the lower margin of the branchial chamber, which is protected by setae, and in particular by those of the setobranchiae. The exhalent current passes out at the sides of the oral region in front. This arrangement is modified in the Brachyura by the free edge of the branchiostegite fitting closely to the bases of the legs on each side, only leaving an aperture for the ingress of water in front of the base of the cheliped. This aperture is provided with an opercular valve formed by the base of the long epipodite of the third maxilliped. These arrangements may be further complicated in various ways, especially in the case of burrowing forms. The exhalent passages, which in some cases may by reversal of the current become inhalent, are not unfrequently prolonged towards the front of the head by the apposition of various appendages. In many Penaeidea the lamellar mandibular palps, the antennal scales, and the antennular peduncles co-operate to this end; in the Brachyura and some Anomura the flattened third maxillipeds carry the exhalent channels at least as far as the anterior margin of the buccal frame; the flagella of the antennules in some Hippidea and of the antennae in the Corystidae form a long exhalent (or inhalent) siphon; and in the Leucosiidae among the Brachyura the inhalent as well as the exhalent channels are carried forwards to the front of the head beneath the expanded maxillipeds. Some special adaptations for aerial respiration will be described below in connection with the circulatory system.

Alimentary System.—The stomodaeal "stomach" of the Decapods is developed into a triturating and straining apparatus of great complexity. The simplest form of the gastric armature appears to be found in the Penaeid genus *Cerataspis* (Fig. 166), recently studied by Bonnier. Here the chitinous lining of the stomach, although provided with numerous internally projecting ridges armed with setae and spinules, is nowhere indurated or calcified to form distinct sclerites such as are found in other Decapods, and in so far it

Table of Branchial Formulae.

Note. The numbers indicate well-developed branchiae. m. = mastigobranchia; r. = vestigial branchia.		Maxillipeds.									Legs.														Total.
		I.			II.			III.			IV.			V.			VI.			VII.			VIII.			
		Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	Podobranch.	Arthrobranch.	Pleurobranch.	
Penaeidea	*Penaeus (caramote)*	m.	1	0	1 m.	1	1	m.	2	1	m.	2	1	m.	2	1	m.	2	1	0	1	1	0	0	1	19+6 m.
	Benthesicymus	m.	1	0	1 m.	1	1	1 m.	2	1	1 m.	2	1	1 m.	2	1	1 m.	2	1	m.	2	1	0	0	1	24+7 m.
	Sergestes	m.	0	0	1 m.	0	r.	0	0	1 r.	0	0	1 r.	0	0	1 r.	0	0	2	0	0	2	0	0	0	8+4 r. +2 m.
Stenopidea	*Stenopus*	m.	1	0	1 m.	1	0	m.	2	1	m.	2	1	m.	2	1	m.	2	1	m.	2	1	0	0	1	19+7 m.
Caridea	*Pandalus*	m.	0	0	1 m.	0	0	m.	2	0	m.	1	1	m.	1	1	m.	1	1	m.	1	1	0	0	1	12+7 m.
	Palaemon	m.	0	0	1 m.	0	0	m.	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	8+3 m.
	Spirontocaris (spinus)	m.	0	0	1 m.	0	0	m.	0	0	m.	0	1	m.	0	1	m.	0	1	0	0	1	0	0	1	6+6 m.
	Hippolyte (viridis)	m.	0	0	m.	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	5+2 m.
	Crangon (vulgaris)	m.	0	0	m.	0	0	m.	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	6+3 m.
	Hoplophorus	m.	0	0	1 m.	0	0	m.	2	0	m.	1	1	m.	1	1	m.	1	1	m.	1	1	0	0	1	12+7 m.
	Atya	m.	0	0	1	0	0	m.	2	0	m.	1	1	m.	0	1	m.	0	1	m.	0	1	0	0	1	9+6 m.
	Limnocaridina	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	4
	Pasiphaea (sivado)	m.	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	1	0	0	1	0	0	1	8+m.
Astacura	*Homarus*	m.	0	0	1 m.	0	0	1 m.	2	0	1 m.	2	0	1 m.	2	1	1 m.	2	1	1 m.	2	1	0	0	1	20+7 m.
Palinura	*Palinurus*	m.	0	0	1 m.	1	0	1 m.	2	0	1 m.	2	0	1 m.	2	1	1 m.	2	1	1 m.	2	1	0	0	1	21+7 m.
Anomura	*Thalassina*	0	0	0	1 m.	1	0	1 m.	2	0	1 m.	2	0	1 m.	2	0	m.	2	0	m.	2	0	0	0	0	15+6 m.
	Axius	m.	0	0	1 m.	r.	0	1 m.	2	0	1 m.	2	0	1 m.	2	1	1 m.	2	1	m.	2	1	0	0	r.	18+2 r. +7 m.
	Upogebia	0	0	0	0	0	0	0	2	0	0	2	0	0	2	0	0	2	0	0	2	0	0	0	0	10
	Galathea (squamifera)	m.	0	0	0	0	0	m.	2	0	m.	2	0	m.	2	1	m.	2	1	0	2	1	0	0	1	14+5 m.
	Coenobita	0	0	0	0	0	0	0	r. r.	0	0	r. r.	0	0	2	1	0	2	1	0	2	1	0	0	1	10+4 r.
	Eupagurus and *Lithodes*	0	0	0	0	0	0	0	2	0	0	2	0	0	2	0	0	2	0	0	2	1	0	0	0	11
Brachyura	*Homolodromia*	m.	0	0	1 m.	1	0	1 m.	2	0	1 m.	2	0	1 m.	2	1	1 m.	2	1	0	2	1	0	0	1	20+6 m.
	Dromia	m.	0	0	1 m.	0	0	m.	2	0	m.	2	0	0	2	1	0	2	1	0	1	1	0	0	1	14+4 m.
	Cancer	m.	0	0	1 m.	1	0	1 m.	2	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	9+3 m.
	Ocypoda	m.	0	0	1 m.	0	0	1 m.	2	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	7+3 m.
	Ilia	m.	0	0	m. r.	0	0	m. r.	2	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	0	6+3 m.
	Pinnotheres	m.	0	0	0	0	0	m.	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3+2 m.

resembles that of many of the more primitive Malacostraca. A deep transverse infolding of the dorsal surface, which marks the division into the larger anterior or cardiac and the smaller posterior pyloric chamber, is produced internally into a strong median tooth (*m.t*). The floor of the cardiac chamber presents internally a median (*m.r*) and a pair of lateral (*l.r*) longitudinal ridges defined by deep foldings of the cuticle and representing elements which in other forms become calcified sclerites; just above these on each side are series of stout denticles (*d*), of which a posterior group in the vicinity of the "median tooth" appear to correspond to the "lateral teeth" of other Decapods. The pyloric division has its lumen greatly reduced by infoldings of its walls, and may be regarded as being divided by a longitudinal fold (*r*) on each side into a dorsal and a ventral portion,

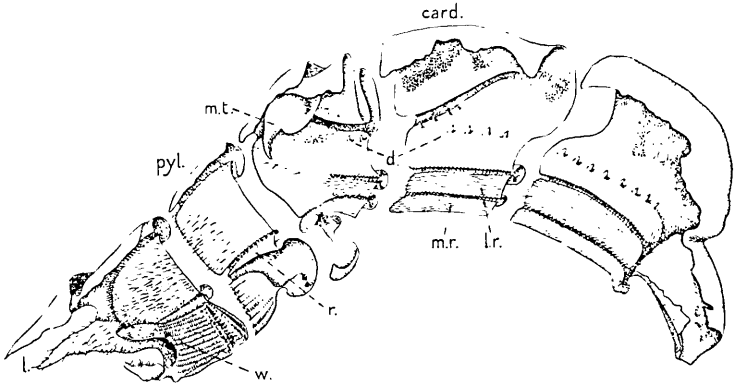

FIG. 166.

Dissection of the stomach of *Cerataspis monstruosus* (semi-diagrammatic). *card*, cardiac chamber; *d*, lateral denticles; *l*, terminal lappets projecting into mid-gut; *l.r*, lateral ridge; *m.r*, median ventral ridge of cardiac chamber; *m.t*, median tooth; *pyl*, pyloric chamber; *r*, longitudinal ridge separating dorsal and ventral divisions of pyloric chamber; *w*, wedge-shaped ridge with straining apparatus. (After Bonnier.)

of which the former is a direct continuation of the cardiac chamber, while the latter is a diverticulum closed in front and communicating with the dorsal chamber only by a narrow slit between the setose margins of the longitudinal ridges. The ventral chamber has its cavity again divided into two portions by a strong median wedge-shaped ridge (*w*) which rises from its floor and is produced posteriorly into a tongue-like process overhanging the apertures of the hepatic ducts into the mid-gut. The lateral surfaces of this ridge are provided with a characteristic armature which seems to act as a straining apparatus; it consists of numerous parallel plate-like ridges running longitudinally and standing at right angles to the surface, each bearing on its edge a comb-like fringe of setae lying parallel with the surface and covering in the groove lying between each ridge and the next. This wedge-shaped ridge and

straining apparatus appear to be very constant throughout the group, and are no doubt homologous with the very similar structures found in other orders of Malacostraca. At its posterior end the chitinous lining of the stomodaeum terminates in four tongue-like lappets (*l*) (much elongated in *Penaeus*) which project freely into the cavity of the mid-gut.

In the other Penaeidea the stomodaeal armature is much more complex than that just described. A large number of sclerites, more or less calcified, are differentiated in the walls of both cardiac and pyloric chambers. A dorsal and a ventral series can be distinguished, the dorsal and dorso-lateral pieces of the cardiac chamber being in relation to the strong median and lateral teeth. From this arrangement of the parts found in the Penaeidea, that characteristic of the Reptantia may be easily derived, the chief differences being due to the appearance of additional sclerites, and especially of a series of intermediate pieces on the lateral walls of the two chambers. The elements of the dorsal series are the more important, forming as they do a system of levers moving the dorsal and lateral teeth.

The great majority of the Caridea diverge more widely from the Penaeid type owing to the disappearance of the whole of the dorsal series of sclerites and of the dorsal and lateral teeth associated with them, the roof of at least the cardiac chamber remaining quite membranous. Only the Atyidae and one or two others among the families of Caridea hitherto examined possess certain elements of the dorsal series well developed, but they are differently arranged from those of the other Decapods.

Mention must be made here of the gastroliths or "crab's eyes," which are discoidal calcareous nodules in the lateral walls of the cardiac division of the stomach in Crayfish (*Astacus*) and Lobsters (*Homarus*). They are periodically formed shortly before ecdysis takes place, and are shed into the cavity of the stomach, to be broken up and dissolved, apparently providing some of the material necessary for the calcification of the new integument. No similar structures are definitely known to occur in any other group of Decapods.

The mid-gut varies very much in length in different Decapoda, but exact observations have been made only on a few types. In the Crayfish (*Astacus*) it is exceedingly short, so that the dorsal lappet which terminates the cuticular lining of the stomodaeum extends through it into the beginning of the proctodaeum. In most, if not all, Brachyura it is also very short. In the Lobster (*Homarus*), however, it occupies five-sixths of the post-gastric part of the alimentary canal. In species of *Alpheus* (Caridea) the mid-gut extends as far as the last somite, and in *Paguristes* it is longer than the proctodaeum. From the upper surface of the mid-gut

there arises anteriorly in Astacura and most Thalassinidea a short unpaired caecum. In *Callianassa* among the Thalassinidea and in most Paguridea a pair of longer or shorter caeca are present, and in most Brachyura they form two long and convoluted tubules. In the Caridea and Galathaeidea and in *Pagurisles* (Paguridea) no caeca are found. *Dromia* possesses a single short caecum, and so resembles the Astacura and differs from the other Brachyura.

An unpaired caecal tube of considerable length springs from the dorsal surface of the intestine in the Brachyura, and a shorter caecum is present in the Lobster, in the Thalassinidea, and in some Paguridae. It is probable that in all these cases the caecum arises from the posterior end of the mid-gut. In *Alpheus*, according to Coutière, the mid-gut is produced backwards beyond its junction with the narrower hind-gut into a number of blind saccules.

Groups of gland-cells on the walls of the oesophagus, on upper and lower lips, and on the maxillulae and maxillae, have been regarded as salivary glands. Quite similar glands, however, may occur throughout the whole length of the hind-gut also, and they are identical in structure with the dermal glands which occur in various situations on the surface of the body.

With the single exception of *Leucifer*, which possesses only two pairs of hepatic caeca, the voluminous "liver" of the Decapods consists of a mass of minutely ramified tubules, lying mainly in the thorax. It communicates with the anterior part of the mid-gut by, as a rule, a single duct on each side, but in *Alpheus* (Coutière) three ducts are present. In Paguridae the hepatic glands are displaced backwards, and lie for the most part in the abdominal region.

Circulatory System.—The heart in all Decapods is short, polygonal in outline, and situated under the posterior part of the carapace. As a rule there are three pairs of venous ostia, of which one, or in the Brachyura two pairs are situated on the upper surface. Coutière has demonstrated the existence of two additional pairs in certain Caridea, and possibly further research will show that these are present in other cases.

Anteriorly the heart gives off a median ophthalmic artery which runs forward to supply the region of the eyes. On each side of this originates an antennal artery, which, besides supplying the antennae, sends branches also to the rostrum, eyes, and adjacent parts. In *Astacus*, Bouvier finds that terminal branches of the antennal arteries unite in front of the brain in a median vessel which runs backwards to anastomose on the walls of the oesophagus with branches of the sternal (subneural) artery—an arrangement which recalls the circumoesophageal vascular ring of some Isopoda and Amphipoda. A second pair—the hepatic arteries—arise from the sides of the heart a little way behind the antennal arteries, and are distributed to the hepatic glands and adjacent viscera.

Posteriorly the heart sends off a median vessel, the superior abdominal artery, while the unpaired descending artery (sometimes called the sternal artery) may arise separately from the heart (Brachyura) or may branch off from the superior abdominal artery just beyond the valves which mark its origin from the heart.

The descending artery passes on one side (either to right or left) of the intestine and pierces the ventral nerve-chain in nearly all Decapods, passing between the connectives uniting the sixth and seventh thoracic ganglia. Only in some of the Brachyura, where the concentration of the nervous system reaches its highest point (Oxyrhyncha and some Brachyrhyncha), this perforation of the nerve-mass does not take place, the artery passing behind instead of through it. On arriving at the ventral surface the artery bifurcates in the median plane, a large branch, to which the name of sternal artery is commonly applied, running forwards to supply the ventral surface of the thorax and its appendages, while a smaller branch running backwards also beneath the nerve-chain is the inferior abdominal artery (absent only in Paguridea). These two arteries taken together form a median longitudinal trunk quite comparable to the subneural vessel of Isopods, and, like it, may communicate with the dorsal system of vessels by a circumoesophageal ring. A further communication is very often present at the posterior end of the abdomen, where a vascular ring encircling the intestine unites the superior and inferior abdominal arteries. A pair of posterior lateral arteries arising from the superior abdominal artery near its origin from the heart, and often unsymmetrically developed, are of importance since they irrigate the branchiostegal regions of the carapace which have a respiratory function.

A venous sinus in the mid-ventral line receives the blood from the lacunar system of the body and appendages and distributes it to the gills, whence it is returned to the pericardial sinus by branchio-pericardial channels running in the inner wall of the branchial cavity. A minor circuit for the blood is afforded by the lacunar network of the branchiostegites, which, receiving blood partly from arteries and partly from adjacent venous sinuses, return it directly to the pericardium by special channels.

In terrestrial Decapods various modifications of the respiratory and circulatory systems are met with. In those most completely adapted to a terrestrial life (*Birgus*, *Cardisoma*) the lining membrane of the branchial cavity is very vascular and covered with minute villi. The supply of venous blood to the sinuses of the branchiostegal regions is more important and more definite than in aquatic Decapods, and the apparatus no doubt functions as a lung. In the terrestrial Hermit-crabs (*Coenobita*) a very peculiar respiratory organ is found. A rich vascular network is developed

in the delicate skin of the abdomen, especially on the dorsal side anteriorly. Two pairs of venous trunks running along the sides of the abdomen return the blood to the pericardium, a pair of rhythmically contractile vesicles at the base of the abdomen serving to accelerate the flow.

Excretory System.—In all Decapods the antennal gland is well developed, and generally presents a complexity of structure not found elsewhere among Crustacea. It has in most cases lost its original tubular form and assumed that of a compact gland. Three divisions are commonly distinct—the saccule, the labyrinth, and the bladder, with its efferent duct leading to the exterior. The saccule, which represents the end-sac of the typical antennal gland, may retain its simple saccular form, but more commonly it is complicated either by the development of partitions dividing up its cavity, or by numerous branches which ramify through the mass of the labyrinth. The labyrinth may be considered as derived from a sac which, by the rich development of partitions and trabeculae from its walls, has been converted into a spongy mass traversed by a complex system of canals. In the Crayfish (*Astacus*) the structure is still further complicated, mainly by the elongation of a portion of the labyrinth into a whitish cord of spongy substance which is convoluted upon itself, forming the "medullary" portion of the gland, the greenish "cortical" layer representing the proximal portion of the labyrinth which communicates with the end-sac. The bladder may retain, as in the Crayfish, the form of a simple vesicle communicating with the exterior by a short duct. In many cases, however, it sends off prolongations which may extend through a great part of the body. In some Caridea this vesical system is very extensive, lobes from the two sides uniting with each other to form an unpaired vesicle above the stomach. In the Brachyura three main lobes are given off from the bladder, which are very constant throughout the group, such differences as do occur being correlated with the differences in shape of the carapace. In the Paguridae, however, the vesical system reaches its greatest complexity (Fig. 167). The bladder sends off prolongations which ramify between the organs and anastomose to form delicate networks and arborisations in the region of the thorax, and two long diverticula, which may unite with each other, pass backwards to traverse the whole length of the abdomen. In *Palinurus* an accessory gland not found in any other type opens into the duct of the bladder. The external aperture is in most cases placed on a papilliform elevation on the proximal segment of the antennal peduncle. In the Brachyura the aperture is covered by an operculum (Fig. 147, B and C, *t*), capable of being opened and closed by special muscles. It has been shown that this operculum in all probability represents the

reduced proximal segment of the antenna, and the muscles attached to it have been identified with those which move the proximal antennal segment in the lower Decapods. This structure was described by Audouin and Milne-Edwards as a kind of auditory ossicle.

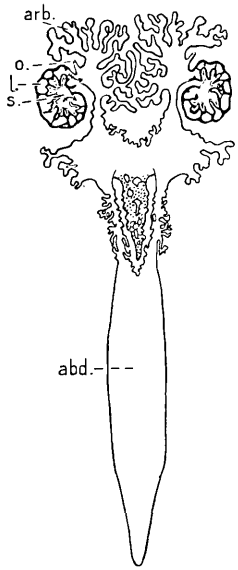

FIG. 167.

Diagram of the excretory system of *Eupagurus bernhardus*. *abd*, unpaired vesicle lying in abdomen; *arb*, arborisations of the vesical system in thorax; *l*, labyrinth; *o*, external opening; *s*, saccule. (After Marchal.)

No trace of the maxillary gland is known to persist in any adult Decapod, though it is frequently well developed in the larval stages.

Traces of glandular organs, presumed to be homologous with the antennal and maxillary glands, have been observed in embryonic stages in certain other somites of the trunk. In addition, certain other structures are found in adult Decapods, the excretory functions of which have been demonstrated physiologically, although their morphological significance remains obscure. The most important of these are the "branchial glands," which are masses of connective-tissue cells surrounding the venous channels in the axis of the gills and are devoid of ducts. Other glands of the dermal type also occur in connection with the gills.

Nervous System.—Great differences exist in the number and disposition of the ganglia composing the ventral chain. Among the lower Decapods the six ganglia corresponding to the six abdominal somites are distinct, but those of the cephalothorax may be more or less coalesced. The largest number of distinct ganglia appears to be found in the Astacura, where those of the five posterior thoracic somites are well separated, the remaining cephalothoracic ganglia being more or less completely coalesced to form a large suboesophageal ganglion. In other cases coalescence has taken place to a greater extent, and in the Scyllaridea and some Caridea, at least, all the cephalothoracic sternal ganglia form a single mass. Among the Anomura the degree of coalescence varies, and sometimes the first abdominal ganglion is approximated to the thoracic mass. Among the Brachyura the concentration of the nervous system reaches its highest point; the whole of the sternal ganglia are united into a rounded mass lodged in the thorax, from which the nerves radiate outwards. As a rule this mass is perforated in the centre for the passage of the descending artery. In the more primitive Dromiacea, however, the concentra-

tion is somewhat less complete, the outlines of five pairs of ganglia can be distinguished in the central mass, while posteriorly is a shortened chain of five pairs of ganglia corresponding to the abdominal somites, although not extending beyond the posterior limits of the thorax.

A system of visceral nerves is well developed in the Decapoda. A gastric plexus is formed by anastomosis of three nerves, a median one arising from the posterior surface of the cerebral ganglia and a pair from the oesophageal commissures. Special nerves to the rectum are given off by the last abdominal ganglion.

Sense-Organs.—The paired eyes are well developed in the great majority of Decapods, although, as already mentioned, they may be reduced or entirely absent in deep-sea and cave-dwelling forms as well as in some parasitic and burrowing species. The cornea is generally distinctly faceted, the facets being square or hexagonal in outline. Sometimes they are square in the centre of the corneal area and hexagonal towards the margin. As a rule the crystalline cone is formed by four cells, and there are seven retinular cells enclosing a quadripartite rhabdome. The *nauplius-eye* has been found to persist in a vestigial condition in the adult in many of the lower Decapoda.

A pair of *statocysts* lodged in the proximal segment of the antennules occur in the great majority of Decapods (Fig. 156, A, *st*, p. 265). Only in certain Caridea do these organs appear to be entirely wanting (*Pandalus*, *Hippolyte*). The statocyst develops as an invagination of the integument, and in most of the lower Decapods it remains in communication with the exterior, sometimes by a wide aperture (*Crangon*), more commonly by a narrow slit. Rarely among the Natantia the statocyst appears to be quite closed (*Leucifer*, *Sergestes*), and this is the case also in the Galatheidea and Hippidea among the Anomura and in the whole of the Brachyura. In the Brachyura, after ecdysis, the statocyst is open to the exterior by a narrow slit, which, however, soon closes by coalescence of the newly formed cuticle covering its edges. In this group also the cavity assumes a complex form by the folding of its walls. In those cases where the statocyst remains open it contains a number of foreign particles, sand-grains, which act as statoliths, and are in some cases agglutinated together into a mass by an organic substance secreted by dermal glands on the inner surface of the sac. In this mass the tips of the sensory setae are embedded. When ecdysis takes place the chitinous cuticle lining the statocyst is thrown off and with it the contained sand-grains, and it has been shown that fresh grains are introduced by the animal either burying its head in the sand or placing the grains in position by means of its chelae. When the statocyst is without external opening it usually contains no solid particles.

This is the case in the Brachyura and the majority of the Anomura. In the few Natantia, however, which have closed statocysts, solitary statoliths, probably of organic composition, are present, which are no doubt formed *in situ*. As with the open statocysts, the lining membrane, and with it the statolith, is cast and renewed at each ecdysis. In all cases the inner surface of the statocyst bears plumose sensory setae arranged in one or more rows. In *Leucifer* the tips of the sensory hairs are embedded in the substance of the statolith.

The development of the statocysts has been traced in the Lobster and the Shore-crab. In both cases the functional state is assumed rather suddenly; at the fourth larval stage in the lobster and the first Megalopa-stage in the Crab. In the latter the statocyst is at first open to the exterior and sand-grains are found in it.

Sensory filaments occur in most cases on the external flagellum of the antennules, commonly in larger numbers in the male than in the female sex. In many Caridea they are confined to a specially thickened portion of the flagellum, and when the flagellum bifurcates the filaments are borne by the secondary branch (Fig. 156, B, p. 265). In some terrestrial species (*Coenobita*) the filaments are very short, forming a close fur.

Phosphorescent organs are now known in a number of deep-sea Decapoda (Sergestidae, Penaeidae, Hoplophoridae, Pandalidae, Eryonidae), but the nature of the organs differs widely in the different groups. In *Aristeus coruscans* (Penaeidae) (Fig 168) and *Heterocarpus alphonsi* (Pandalidae) (Fig. 148, p. 259) Alcock observed a luminous fluid to be emitted from the base of the antennae, apparently from the orifices of the antennal glands. This case may be compared with that of *Gnathophausia* among the Mysidacea, where a luminous secretion is produced by a gland on the maxilla which may possibly be the excretory maxillary gland. *Polycheles phosphorus* (Eryonidae) was found by the same observer to be "luminous at two points between the last pair of thoracic legs, where there is a triangular glandular patch." Numerous phosphorescent organs have been found by Coutière on the body and limbs of various Hoplophoridae, but their structure has not been examined. In *Sergestes challengeri* Hansen has found an extraordinary number of luminous organs (about 150) on the body and limbs, although they are not found in other species of the genus. In this case the structure recalls that found in the Euphausiacea. Each organ has, internally, a reflector, composed apparently of concentric lamellae, enclosing a mass of cells. There is nothing corresponding to the "striated body" of Euphausiacea, and the "lens" is double, the outer part being formed by a thickening of the cuticle which has no counterpart in the Euphausiacea.

Reproductive System.—The *testes* as a rule lie partly in the thoracic region and partly in the abdomen, and, except in some Paguridae, are connected with each other across the middle line. In the simplest cases, as in some Caridea, they are tubular in form, but as a rule they send off numerous caecal diverticula. In *Leucifer* the two testes unite with each other to form an unpaired mass lying below the intestine. In the Paguridae they are displaced backwards so as to lie wholly in the abdominal region, where they are unsymmetrically placed on the left side, either fused into a single mass or entirely separated from each other, the right testis lying in front of the left.

The vas deferens presents typically three divisions (which, however, are not distinctly defined in many Caridea): (1) a narrow

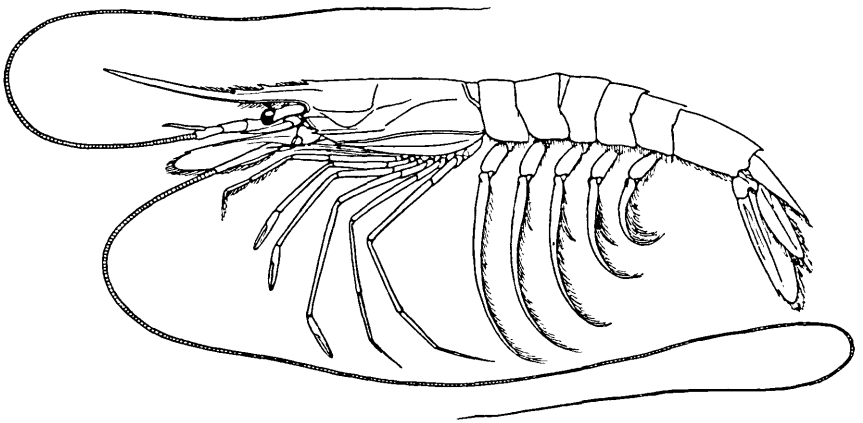

FIG. 168.

Aristeus coruscans (Penaeidae). (From Alcock, *Naturalist in Indian Seas.*)

efferent duct leading from the testis; (2) a glandular part, with wider lumen, often convoluted; (3) a terminal ductus ejaculatorius with muscular walls. In Brachyura (except Dromiidae) the distal portion of the second or glandular division is provided with caecal diverticula which in some cases are very numerous, forming a large glandular mass. In *Leucifer* the structure of the vas deferens is very complex, and there are two distinct glandular regions.

In nearly all cases the terminal portion of the vas deferens perforates the coxopodite of the last pair of legs, or emerges on the arthrodial membrane between the coxopodite and the body. In the majority of cases no penes are formed, but in some genera of Paguridae (*Spiropagurus*, etc.) a membranous tubular penis is present on one side only. In all Brachyura a pair of penes are present, the tips of which lie within the grooves of the first pair of abdominal appendages. In those families of Brachygnatha formerly

grouped together as Catometopa these penes either lie for a short distance from their base within grooves excavated in the last thoracic sternum, or else they perforate the sternum directly, the vasa deferentia in this case not entering the coxopodites of the legs at all, as they do in most other Decapods.

In most Macrura and in the Dromiidae the spermatozoa when discharged are enclosed by a sheath of secretion which sets to a firm membrane, forming a continuous cord-like mass. In *Scyllarus* and in the Anomura this is broken up into separate spermatophores attached by one end in a row on a strip of membrane. In the Brachyura (except the Dromiidae) the spermatophores are quite separate.

The spermatozoa are remarkably varied and complex in structure. As a rule they are provided with stiff radiating processes which serve to attach them to the surface of the egg, and, in some cases, an "explosive" apparatus is present which effects penetration of the egg-membrane.

The *ovaries* generally resemble the testes in shape and position. In the Penaeidae they may extend through the whole length of thorax and abdomen, but in most cases they are of less extent. In *Leucifer*, and in most if not all Thalassinidea and Paguridea, they lie wholly in the abdomen. They are always united across the middle line, sometimes at more than one point. In the Crayfish the two ovaries (like the testes) are joined together posteriorly so that the organ has a trilobed form. Except in *Leucifer* and in the Brachyura, the oviducts are simple in form and open on the coxopodites of the sixth thoracic appendages (third legs). In *Leucifer*, which is peculiar in so many points of structure, the oviducts have receptacula seminis connected with them and unite to open by a median aperture on the sternal surface of the thorax. In the Brachyura, where intromittent organs are developed in the male, the terminal part of the oviduct is of considerable length and serves as a vagina, while a lateral pouch, sometimes double, with glandular walls, forms a receptaculum seminis. In the Dromiacea the receptaculum seems to be a temporary structure formed at the time of copulation. In the Brachyura, with exception of the primitive Dromiacea and of certain Oxystomata (Raninidae, some Dorippidae), the oviducal apertures are removed from the coxopodites of the legs and open on the sternum of the corresponding somite.

In addition to the internal receptacula seminis mentioned above, an external organ having apparently the same function is found in certain Decapods. It is best known in the Penaeidae, where it has been named the *thelycum* and affords characters of systematic importance. It lies on the sternal surface of the thorax and appears to be formed by two or more outgrowths from the last

thoracic somite enclosing a cavity within which may sometimes be found the large foliaceous spermatophores deposited by the male. In the Lobster (*Homarus*) (Fig. 169) a median pouch enclosed by three processes on the sterna of the last two thoracic somites has the same function, and in the Crayfishes of the genus *Cambarus* (but not in *Astacus*) a more complicated organ in the same position is known as the "annulus ventralis." These structures have not hitherto been studied from a comparative point of view, but it seems likely that an investigation of their morphology and their relation to the structures occupying a similar position in the Syncarida would yield important results.

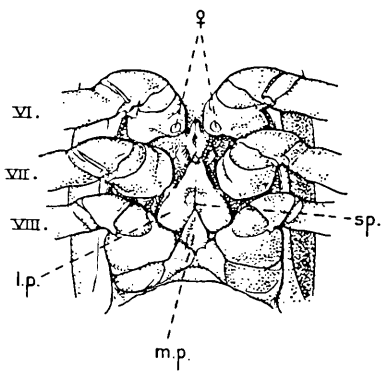

FIG. 169.

Sternal surface of posterior thoracic somites of female Lobster (*Homarus gammarus*), showing the receptaculum seminis. VI-VIII, bases of the last three pairs of legs; ♀, external openings of oviducts; *l.p*, lateral process on penultimate sternum; *m.p*, median process on last thoracic sternum; *sp*, slit-like opening of receptaculum.

In the great majority of Decapods the eggs after extrusion are carried by the female attached to the abdominal appendages. Only in the Penaeidea they appear to be shed free into the water immediately on extrusion, or carried for a short time only, as in *Leucifer*, where they have been found attached to the posterior thoracic limbs. The attachment of the eggs to the abdominal appendages of the parent is effected by means of a cementing material. As a rule this material seems to be produced by dermal glands, which are found abundantly developed on the inner faces of the pleural plates of the abdomen and on the uropods. In some cases (*Stenopus* and Thalassinidae), where the pleural plates are slightly developed, the glands occur mainly on the pleopods, and in the Paguridae they are distributed over the ventral integument of the abdomen. In the Brachyura, however, such glands are absent or only little developed, and the function of producing the cementing material is stated to be discharged by the receptaculum seminis.

Secondary sexual characters among the Decapods are numerous and varied. In many cases the males are distinguished from the females by the greater size and different shape of the chelipeds and by the narrower abdomen. Dimorphism of the males has been noted in many cases, and Faxon discovered that in Crayfishes of the genus *Cambarus* the two forms are alternating breeding and non-breeding phases in the life-history of the same individual. A closely similar series of changes has been found by Coutière and by

G. Smith in the males of some Oxyrhyncha, and it is very probable that it may occur also in other groups of Decapoda.

Mention may be made here of the remarkable phenomena of "parasitic castration," discovered by Giard in Decapods infested by Rhizocephala, Entoniscidae, and other parasites, and more recently investigated by G. Smith. The latter observer finds that, in Brachyura infected with *Sacculina*, the females show very little modification of external characters beyond a reduction in size of the pleopods, although the gonad is reduced in size or even completely eradicated. Infected males, however, assume in various degrees the secondary sexual characters proper to the female; the chelipeds (in species with dimorphic males) remain in the form of the non-breeding phase and resemble those of the female; the abdomen becomes more or less broadened and may assume completely the female form; the copulatory styles (first and second pleopods) are greatly reduced, and small pleopods may appear on the third to the fifth abdominal somites. In the most completely modified specimens only the reduced copulatory styles remain to show that they once were males. The very remarkable observation has been made that these completely modified males, in the rare cases when they recover sufficiently from the parasitic infection to regenerate a gonad, become perfect hermaphrodites, the gonad producing both spermatozoa and ova.

Observations, as yet unpublished, made by A. Wollebaek, seem to indicate that certain deep-water Decapoda are normally hermaphrodite.

Development.

With some noteworthy exceptions to be mentioned below, the Decapoda pass through a more or less extensive metamorphosis after leaving the egg. The most complete series of changes occurs among the Penaeidea, some at least of which are hatched as free-swimming nauplii and have a larval history closely parallel to that of the Euphausiacea.

In the Penaeidae the development was first made known by Fritz Müller, and further elucidated by Claus, Brooks, and Kishinouye. The *Nauplius* (Fig. 170, A), which has been hatched from the egg by the last-named of these authors, has a quite typical form. The pear-shaped or oval body is without a shell-fold and has two terminal setae posteriorly. The median eye is present and the three pairs of nauplius-limbs, the third pair of which are without any masticatory process. In the succeeding *Metanauplius*-stage four pairs of limb-rudiments are developed behind those already present, the masticatory process appears on the third pair, the swimming-branches of which begin to diminish, and a pair of papillae on the anterior margin represent the "frontal organs,"

which persist through several of the later stages. The next stage observed is the *Protozoea* (Fig. 170, B), in which the seven pairs of limbs already indicated are well developed; the carapace covers the anterior part of the body; the abdomen, which has a furcate termination, is still unsegmented, but the six posterior thoracic somites are defined, though very short. The mandibular palp has quite disappeared (to reappear at a later stage), and the first and second thoracic appendages are biramous swimming-limbs. At this stage the rudiments of the paired eyes begin to appear beneath the

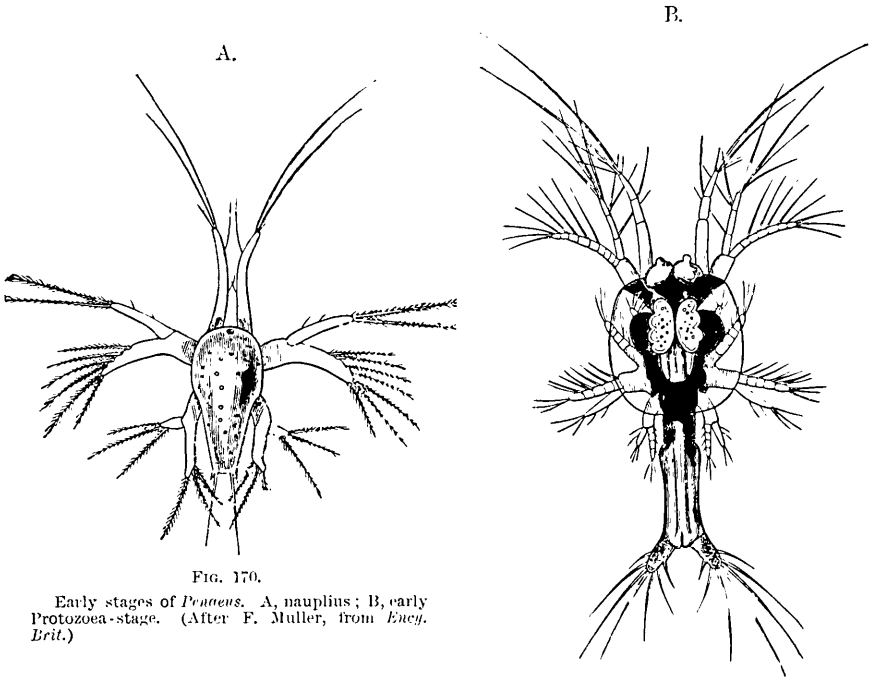

FIG. 170.

Early stages of *Penaeus*. A, nauplius; B, early Protozoea-stage. (After F. Muller, from *Ency. Brit.*)

carapace, there are three pairs of hepatic caeca, and the heart is developed, though as yet with only one pair of ostia. In a later Protozoea-stage (Fig. 171, A) the five anterior abdominal somites are indicated, the sixth being not yet marked off from the telson, and the rudiments of the third pair of thoracic limbs appear. In the following stage, to which the name of *Zoea* is given, the paired eyes become free from the carapace and are movable, the carapace begins to grow out into a median rostral spine, the third pair of thoracic limbs are biramous, and rudiments of the remaining five pairs are present. The first five pairs of abdominal appendages (Fig. 171, B) are present as very small buds, but the sixth pair

have already begun to outstrip these in order of development and are larger and bilobed. In a later Zoea-stage (Fig. 171, C) the sixth pair form with the furcate telson a well-marked tail-fan, but the first five pairs of abdominal limbs are stated to be temporarily suppressed, to reappear again at a later stage; a retrograde change is also observed in the peduncle of the antennule, which in the later Protozoea was divided into five segments but now becomes

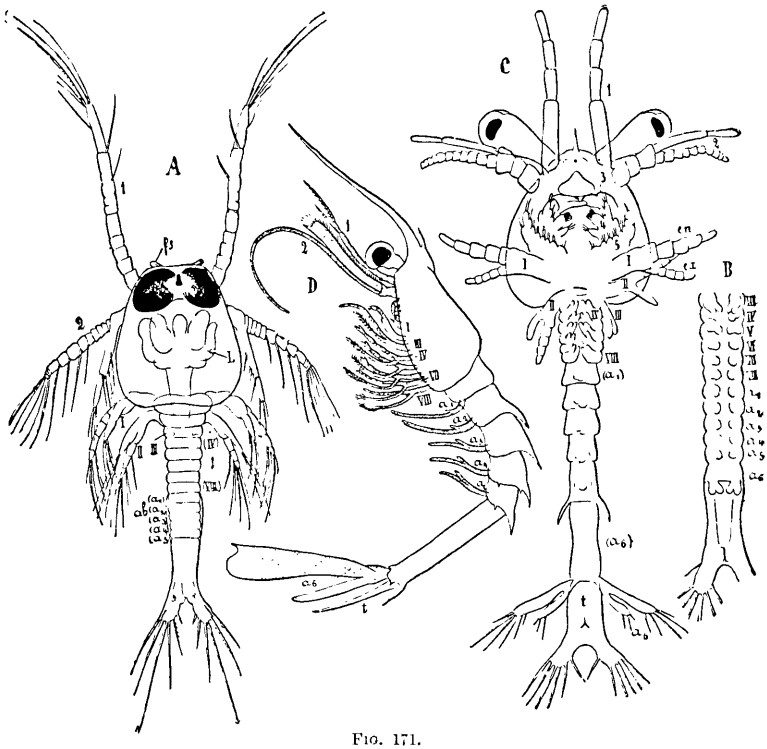

FIG. 171.

Later stages of *Penaeus*. A, older Protozoea-stage. B, under-surface of thorax and abdomen of somewhat later stage with rudiments of limbs. C, Zoea-stage. D, Schizopod-stage. 1, antennule; 2, antenna; 3, mandible; 4, maxillula; 5, maxilla; I-VIII, thoracic appendages; (IV-VIII), the posterior thoracic somites; a_1-a_5, pleopods; a_6, uropods; *ab*, abdomen; *en*, endopodite; *ex*, exopodite; *fr*, frontal sense-organ; *L*, hepatic caeca; *t*, telson. (After Claus, from Korschelt and Heider's *Embryology*.)

once more unsegmented. The five posterior pairs of thoracic limbs (legs), which in this stage are bilobed rudiments, develop in the succeeding *Schizopod*-stage (Fig. 171, D) (usually called the *Mysis*-stage) into biramous natatory limbs and take up the function of locomotion hitherto fulfilled chiefly by the antennae. The abdomen has now increased greatly in size as compared with the cephalothorax, and the first five pairs of abdominal appendages

begin to reappear. The various appendages now begin to assume the form which they have in the adult. The antennules have a three-segmented peduncle, with two flagella as yet unsegmented. The endopodite and exopodite of the antenna become respectively flagellum and scale. The palp of the mandible begins to redevelop. In a later stage, which may be called *post-larval*, the exopodites of the thoracic limbs become reduced and the abdominal appendages, now well developed, take on the function of swimming-organs.

While it is tolerably certain that the general course of development in the Penaeidae is as described above, it is to be observed that as yet the complete series of larval forms has not been traced out in the case of any one species, and it is just possible that some of the changes stated to occur, *e.g.* the alleged temporary disappear-

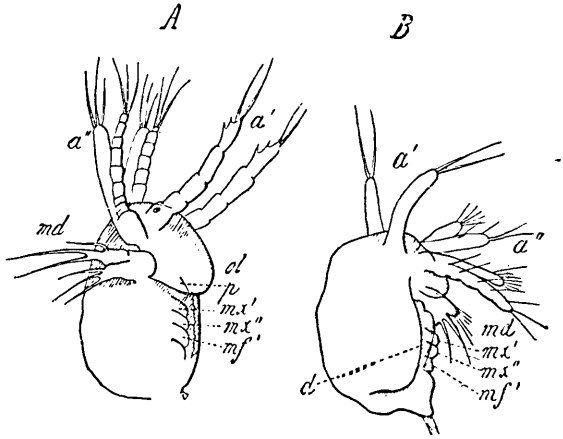

FIG. 172.

Metanauplius-stages of *Leucifer*. A, just hatched; B, later stage. *a'*, antennule; *a''*, antenna; *cl*, shell-fold; *md*, mandible; *mf'*, first maxilliped; *mx'*, maxillula; *mx''*, maxilla; *cl*, labrum; *p*, paragnatha. (After Brooks, from Korschelt and Heider's *Embryology*.)

ance of the first five abdominal appendages in the later Zoea-stage, may be due to confusing together in one series the larvae of different species. In the closely related family of the Sergestidae, however, Brooks has been able to trace out in considerable detail the life-history of a single species, *Leucifer typus*. In this case the animal leaves the egg as a metanauplius (Fig. 172, A) with four pairs of limb-buds already visible behind the three pairs of nauplius-limbs. This is followed by a later metanauplius (Fig. 172, B) in which the shell-fold and the masticatory process of the mandible appear. The Protozoea (Fig. 173, A), with seven pairs of functional limbs, differs from that of *Penaeus* chiefly in the different shape of the carapace, which has already the beginning of a rostrum, and in having only four of the six posterior thoracic

somites defined. The rudiments of the paired eyes appear in the later Protozoea-stage (Fig. 173, D), when also the seventh thoracic

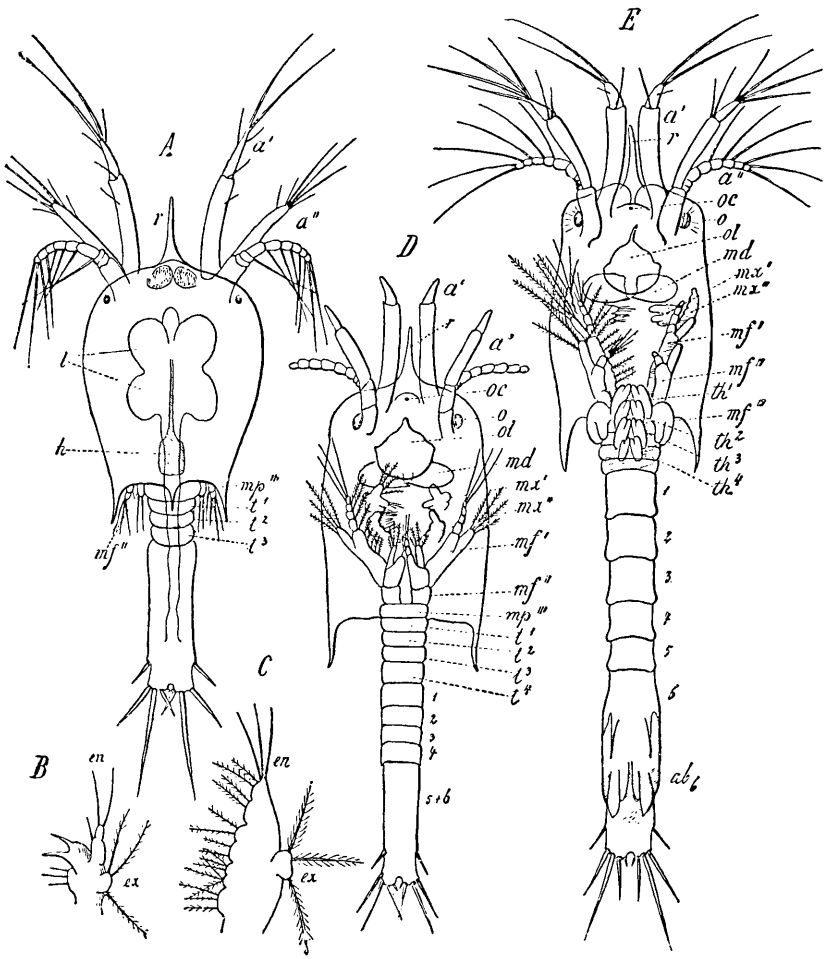

FIG. 173.

Protozoea and Zoea stages of *Leucifer*. A, first Protozoea-stage. B, maxillula of same. C, maxilla of same. D, later Protozoea-stage (*Erichthina*, Dana). E, Zoea-stage. *a'*, antennule; *a''*, antenna; *ab6*, uropods; *en*, endopodite; *ex*, exite; *h*, heart; *l*, hepatic diverticula; *md*, mandible; *mf'-mf'''*, the three pairs of maxillipeds; *mp'''*, somite of third maxillipeds; *mx'*, maxillula; *mx''*, maxilla; *o*, paired eye; *oc*, nauplius-eye; *ol*, labrum; *r*, rostrum; *th⁴-th⁴*, rudiments of fourth to seventh thoracic limbs (first four legs); *t¹-t⁴*, fourth to seventh thoracic somites; 1-6, abdominal somites. (After Brooks, from Korschelt and Heider's *Embryology*.)

somite (the eighth remains undeveloped in the adult *Leucifer*) and the first four abdominal somites appear. The Zoea-stage (Fig. 173, E) differs from that of *Penaeus* in the fact that the eyes are not

yet free from the carapace, and that the third thoracic limbs, like the four following pairs, only appear as bilobed rudiments. The uropods are present as rudiments, but the pleopods are not yet indicated. A Schizopod-stage (Fig. 174, A) follows, with movable paired eyes, with seven pairs of biramous thoracic appendages functioning as swimming-feet, and with well-developed tail-fan. Later stages (Fig. 174, B) show rudiments of the first five pleopods. A *Mastigopus*-stage (Fig. 174, C) intervenes before the assumption of the adult form.

The larvae of *Sergestes*, though differing remarkably in appearance from those of *Leucifer*, conform closely to the same type of development. The youngest known larvae are Protozoeae (Fig. 175, A), which differ from those of *Leucifer* in their compact form and in the possession of stalked eyes and of biramous third maxillipeds. The most characteristic feature, however, is the armature of the carapace. A rostrum, a median dorsal, and a pair of lateral spines are present as in *Leucifer*, but much stronger, and each bearing a double row of secondary spines. The Zoea (*Elaphocaris* of Dana) has this spine armature still more developed, and an additional pair of compound spines appear on either side of the rostrum. In the Schizopod-stage (known as *Acanthosoma*) (Fig. 175, B) the armature of the carapace is very much reduced. Before the adult stage is reached a *Mastigopus*-stage intervenes, characterised by the temporary disappearance of the last two pairs of thoracic limbs, which are present alike in the *Acanthosoma* and in the adult animal. It is interesting to notice that in this character *Leucifer* represents a permanent *Mastigopus*-form.

In the remaining groups of Decapoda no case is known where the larva is hatched at a stage preceding the Zoea, though in some instances a larval cuticle, moulted soon after hatching, has been supposed to present characters of the Protozoea.

Among the Caridea the earliest larval form is a Zoea in which the third thoracic appendages are already well developed. The posterior thoracic region is undeveloped, though the abdominal somites, with the exception of the last, are defined. The carapace has a rostrum and supra-orbital and antennal spines, but no further armature. In many cases the stage at hatching is still farther advanced, the paired eyes are stalked and movable, and one or more pairs of the posterior thoracic appendages are present as rudiments. In spite of the retarded development of the last five thoracic somites, it is noteworthy that the appendages appear in regular order from before backwards, with the exception of the uropods, which generally develop precociously. In the Schizopod-stage it is a very general but not universal character of the Caridean larva that it is without exopodites on the last thoracic feet. In many Caridea there is still further abbreviation, leading to complete suppression of the

larval stages, more especially among Arctic, abyssal, and freshwater forms. A specially interesting case is that of *Palaemonetes varians*,

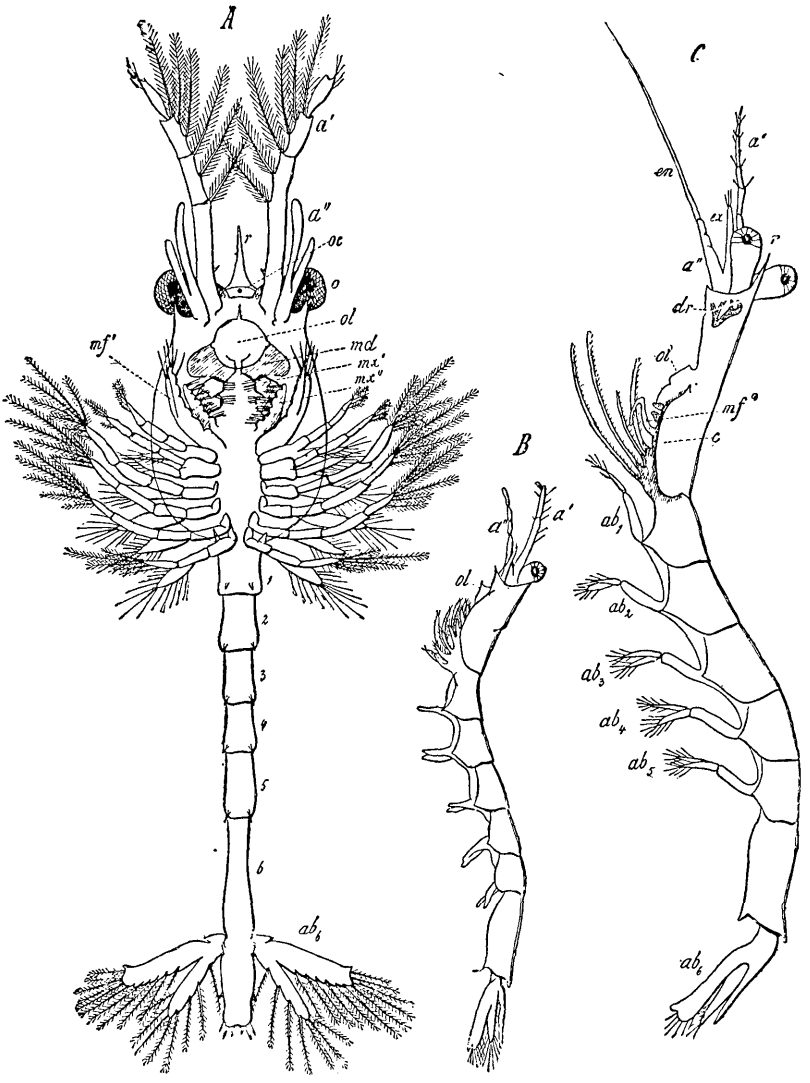

FIG. 174.

Later stages of *Leucifer*. A, younger Schizopod-stage. B, later Schizopod-stage (less magnified). C, Mastigopus-stage. *a'*, antennule; *a''*, antenna; ab_1-ab_5, pleopods; ab_6, uropods; *c*, carapace; *dr*, antennal gland; *en*, flagellum, *ex*, scale, of antenna; *md*, mandible; *mf*, *mf''*, first and second maxilliped; *mx'*, maxillula; *mx''*, maxilla; *o*, paired eye; *oc*, nauplius-eye; *ol*, labrum; *r*, rostrum; 1-6, abdominal somites. (After Brooks, from Korschelt and Heider's *Embryology*.)

of which two races are known, the one found in Southern Europe being exclusively freshwater in habitat; the other, found in Britain and Northern Europe, inhabiting brackish or salt water. The former hatches at a stage when all the limbs except the uropods are present, and the first two pairs of legs have exopodites. In

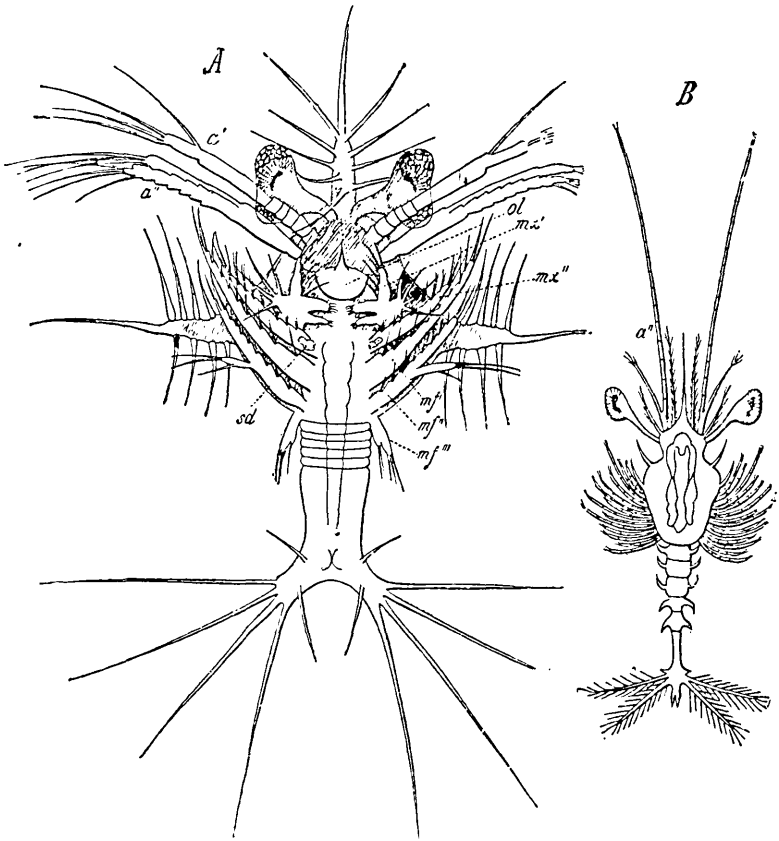

FIG. 175.

Larval stages of *Sergestes*. A, Protozoea-, B, Schizopod-stage (*Acanthosoma*). *a'*, antennule; *a''*, antenna; *mf'*-*mf'''*, the three pairs of maxillipeds; *mx'*, maxillula; *mx''*, maxilla; *ol*, labrum; *sd*, maxillary gland. (After Claus, from Korschelt and Heider's *Embryology*.)

the northern race all the ambulatory legs are rudimentary on hatching, and there are no abdominal limbs.

None of the Astacura are known to possess a Zoea-stage. The Lobster (*Homarus*) is hatched in the Schizopod-stage (Fig. 176), with natatory exopodites on all the thoracic limbs, but without any abdominal appendages. In the further course of development

the uropods are the last to appear. In *Nephrops* (Fig. 177) the course of development is very similar, but the larvae are distinguished by the long spines of the abdominal somites and telson. The freshwater Crayfishes have a direct development, the young on hatching resembling the adult in most points, but lacking the first and the last pairs of abdominal appendages.

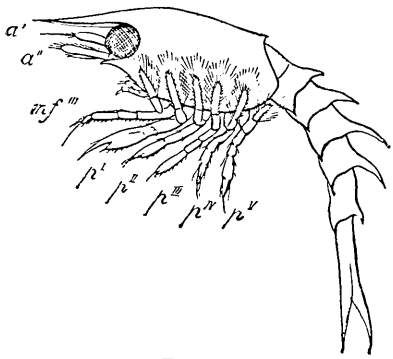

FIG. 176.

Larva of American Lobster (*Homarus americanus*), in Schizopod-stage. *a'*, antennule; *a''*, antenna; *mf'''*, third maxilliped; *p*¹-*p*⁵, the five pairs of legs. (After S. I. Smith, from Korschelt and Heider's *Embryology*.)

The Scyllaridea have a very peculiar and characteristic series of larval forms, which were long described as adults under the generic name *Phyllosoma* (Fig. 178). These larvae are remarkable for the large size to which some attain, and for their extremely flattened and leaf-like form and glassy transparency. The body is sharply divided into three regions. The first, which is covered by the oval carapace, includes the head and the first two thoracic somites. The remainder of the thorax forms a discoidal plate and

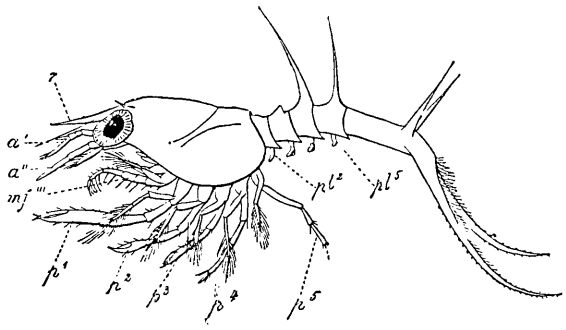

FIG. 177.

Late Schizopod-stage of *Nephrops norvegicus*. *a'*, antennule; *a''*, antenna; *mf'''*, third maxilliped; *p*¹-*p*⁵, the five pairs of legs; *pl*², *pl*⁵, pleopods; *r*, rostrum. (After Sars, from Korschelt and Heider's *Embryology*.)

is followed by the narrow and indistinctly segmented abdomen. The last two thoracic appendages are not developed in the newly hatched larva, but the four pairs in front of them are long and slender, with natatory exopodites. The first thoracic limbs are rudimentary (*Palinurus*) or absent (*Scyllarus*), and the second pair

are uniramous. It will thus be seen that the *Phyllosoma* represents a modification of an early Schizopod-stage.

A point of some interest in these forms is the occurrence of retrogressive changes in the course of development. Thus the antenna and the maxilla undergo a certain degree of degeneration before hatching, and the seventh and eighth thoracic and the abdominal somites, which are well defined in the embryo, become indistinct in the larva.

The development of Thalassinidea is interesting on account of the points of resemblance which it shows with the Caridea. The earliest larva is a Zoea, which in some cases (*Callianassa* and *Calocaris*) resembles that of Caridea in having the three maxillipeds

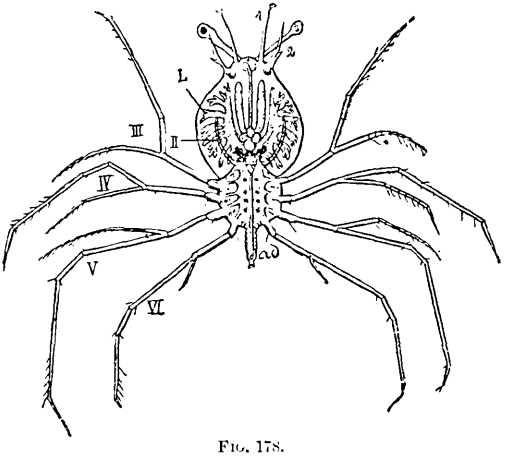

FIG. 178.

Phyllosoma-larva of *Palinurus*, just before hatching. *ad*, abdomen; *L*, hepatic caeca; II-VI, thoracic appendages (second and third maxillipeds and first three pairs of legs); 1, antennule; 2, antenna. (After Claus, from Korschelt and Heider's *Embryology*.)

biramous and natatory; but in others (*Upogebia* and *Jaxea*) only the first and second are present on hatching, the third becoming natatory only in the following Schizopod-stage, while the endopodite is still rudimentary, as in other Anomura. The existence of a Schizopod-stage, in which only the last two thoracic limbs are rudimentary and the uropods and rudiments of the pleopods are present, constitutes an important distinction from the other Anomura. The larvae of *Jaxea* (= *Calliaxis*) are of exceedingly peculiar form, having the cephalic region produced into a long "neck" resembling at first sight that of *Leucifer*. To this larval type the name of *Trachelifer* has been given. The remaining groups of the Anomura and the Brachyura differ from those just described in the suppression of the Schizopod-stage, the legs developing without exopodites in a *Metazoea*-stage which follows the Zoea. In the Anomura the Zoea

(Fig. 179, A) possesses two pairs of maxillipeds, the third pair (Fig. 179, C) being present as rudiments. The carapace has its posterior border produced into two lateral spines (greatly elongated in *Porcellana*, Fig. 180), and a long rostrum is present. In the next succeeding stage, the Metazoea (Fig. 179, B), the third maxilliped becomes biramous and natatory (a point of distinction from the Brachyuran type), and the uniramous ambulatory limbs and the pleopods are developed as rudiments.

The Brachyura, as a rule, are stated to hatch in the Zoea-stage (Fig. 181), but since rudiments of the posterior thoracic limbs are

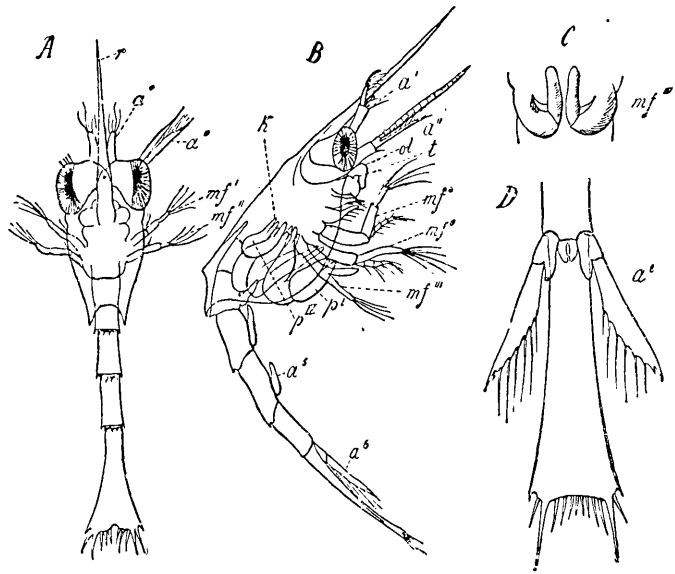

FIG. 179.

Larval stages of *Eupagurus bernhardus* (Paguridea). A, Zoea. B, Metazoea. C, rudiments of third maxillipeds in Zoea-stage. D, caudal fan of Metazoea. a', antennule; a'', antenna; a^5, fifth pleopod; a^6, uropod; k, rudiments of gills; mf'-mf''', the three pairs of maxillipeds; ol, labrum; p^1-p^{iv}, first four legs; r, rostrum; t, mandibular palp. (After Sars, from Korschelt and Heider's *Embryology*.)

frequently present, it might be more correct to call the larva a Metazoea. Throughout the group a very characteristic form is given to the Zoea by the development of long spines on the carapace. As a rule, a rostrum, a median dorsal, and a pair of lateral spines are present. Of these, the dorsal spine (*d.s*) is the most constant; great importance was formerly attached to it as a characteristic of the Zoea-stage. In many Brachyura the larva when hatched is enclosed in a cuticle which is moulted shortly after hatching, and this cuticle in many cases presents characters differing from those of the larva which escapes from it. In

Carcinus maenas, for instance, the first larval skin lacks the spines of the carapace, the antennae are larger and differently formed, the shape of the caudal fork and its spine armature are different from those of the succeeding stage, and the abdominal portion is not distinctly segmented. These characters have been supposed to indicate that we have here the last traces of a Protozoea-stage like that of the Penaeidea.

The Metazoeal stages, which differ from those of the Anomura in the fact that the third maxilliped does not assume a natatory function, are succeeded in nearly all cases by a *Megalopa*-stage (Fig. 182, A, B), in which all the appendages have assumed very much the form which they have in the adult, but the abdomen is large and usually carried extended, and the five pairs of pleopods are used for swimming. In some cases the Megalopa-stage is suppressed, the Metazoea being succeeded by a stage in which the animal has assumed the chief characters of the adult.

Complete suppression of the metamorphosis occurs in some (perhaps all) Potamonidae, and probably in some other freshwater and terrestrial Brachyura. In those Anomura which have become most completely terrestrial (*Birgus* and *Coenobita*) Borradaile has shown that the young are marine, and that hatching takes place at the Zoea-stage.

FIG. 180.

Metazoea of *Porcellana longicornis* (Galatheidea). *mf*-*mf'''*, the three pairs of maxillipeds; *p*, rudiments of legs and gills. (After Sars, from Korschelt and Heider's *Embryology*.)

REMARKS ON HABITS, ETC.

The habits and habitats of the Decapoda are more varied, and have been much more studied, than in the case of any other group of Crustacea. Space will not permit of allusion to more than one or two of the more salient points.

Truly freshwater Decapods (apart from estuarine or brackish-water species which may penetrate into fresh water) are found among the Natantia in the family Atyidae and in several genera of Palaemonidae; of the Reptantia, the Crayfishes of the families Astacidae and Parastacidae, the monotypic Aegleidae among the Anomura, and the Potamonidae (Thelphusidae) and numerous species of Grapsidae among the Brachyura, are also dwellers in fresh water. Some of these are more or less amphibious in their habits, like many Potamonidae, and some Crayfishes are found burrowing in the earth far from streams or ponds, their burrows reaching down to the ground-water. The same is reported of the marine or brackish-water *Thalassina*.

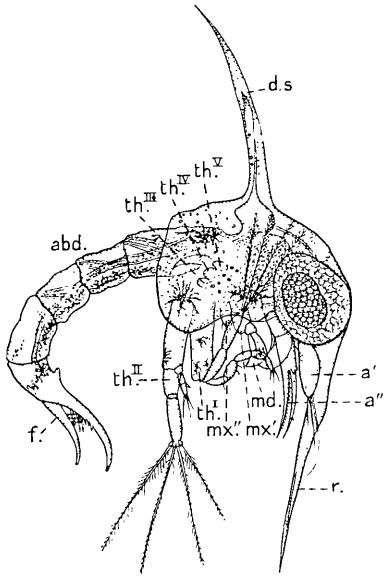

FIG. 181.

First Zoea-stage (after the first moult) of *Carcinus maenas*. *a'*, antennule; *a''*, antenna; *abd*, abdomen; *d.s*, dorsal spine of carapace (the so-called "Zoea"-spine); *f*, furcate telson; *md*, mandible; *mx'*, maxillula; *mx''*, maxilla; *r*, rostrum; th^{i}, th^{ii}, first and second maxillipeds, biramous and natatory; th^{iii}-th^{v}, rudiments of three following thoracic appendages. (After Faxon.)

Truly terrestrial species are found among Paguridae (*Birgus* and *Coenobita*) and Brachyura (Gecarcinidae), and it is interesting to note that these are derived not from freshwater but from marine types, and all (except, possibly, some Gecarcinidae) pass their early stages in the sea.

The Sergestidae belong to the plankton, occurring at the surface and descending to great depths. A few Brachyura (*Planes* and some other Grapsidae) lead a pelagic life, clinging to driftweed, floating timber, and the like.

It is worthy of note that the deep-sea Decapods include the more primitive members of each of the chief subdivisions: the Aristeinae among the Penaeidea, the Hoplophoridae among the Caridea, the Eryonidea among the Palinura, the Pylochelidae among the Paguridea, and the Homolodromiidae among the Brachyura.

Parasitism and commensalism in varying degrees are common. The Paguridae alone, which live in the empty shells of Gasteropod molluscs, present a whole series of cases of commensal association with Sponges, Coelentera (Fig. 183), and Polychaete worms;

Spongicola, *Typton*, and *Eiconaxius* live in sponges, many Pontoniinae and Pinnotheridae (as Aristotle knew) in the mantle-cavity of bivalve molluses; members of the first-named family inhabit the pharyngeal cavity of Tunicates, and some Pinnotheridae are found in the "respiratory trees" of Holothurians and the rectum of sea-urchins. Many Decapods are constantly found among living corals, and the Hapalocarcinidae live in "galls" on the branches of corals. A very peculiar habit is that of some crabs of the genus *Melia*, which carry in each cheliped a living Actinian and use it as a weapon.

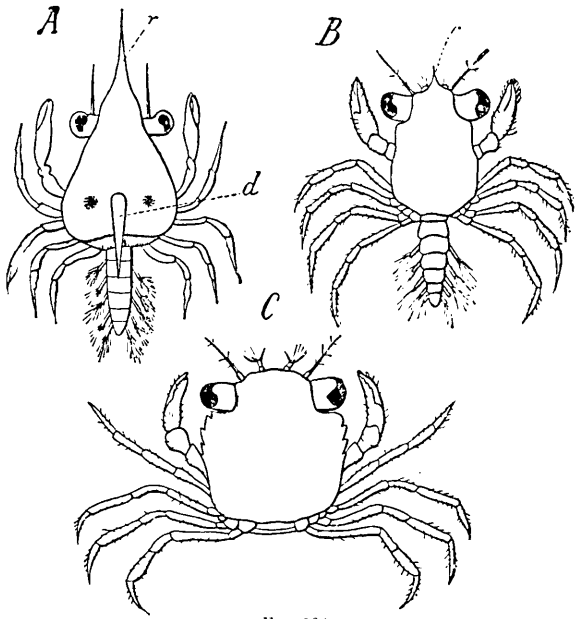

FIG. 182.

Later stages of *Carcinus maenas*. A, young Megalopa. B, older Megalopa. C, post-larval stage. *d*, dorsal spine of carapace; *r*, rostrum (A after Spence Bate; B and C after Brook. From Korschelt and Heider's *Embryology*.)

Special interest attaches to the stridulating organs, found in many Decapoda, since their possession is presumptive evidence that the animals do have some power of hearing. A few Penaeidae, some Palinuridae, and a considerable number of Brachyura are now known to have stridulating organs in various parts of the body. That of *Orypoda*, shown in Fig. 184, is one of the few of which the sound-producing function has been demonstrated by observation of the living animals. It consists of a file-like series of ridges (*a*) on the inner surface of the propodite of one of the chelipeds, which can be rubbed up and down upon a sharp ridge (*b*) on the ischiopodite of the same appendage, producing a hissing sound, which probably

serves to warn intruders from entering the burrows of these shore-living crabs. In the case of purely aquatic species, the function of these organs is less easy to understand.

The range of size in Decapoda is greater than in any other group of Crustacea. Some Natantia do not exceed half an inch in length, one Pagurid is adult when 8 mm. long, a species of Porcellanid has a carapace measuring 3 mm. by 5 mm., and some Brachyura are no larger. The largest forms are found among the

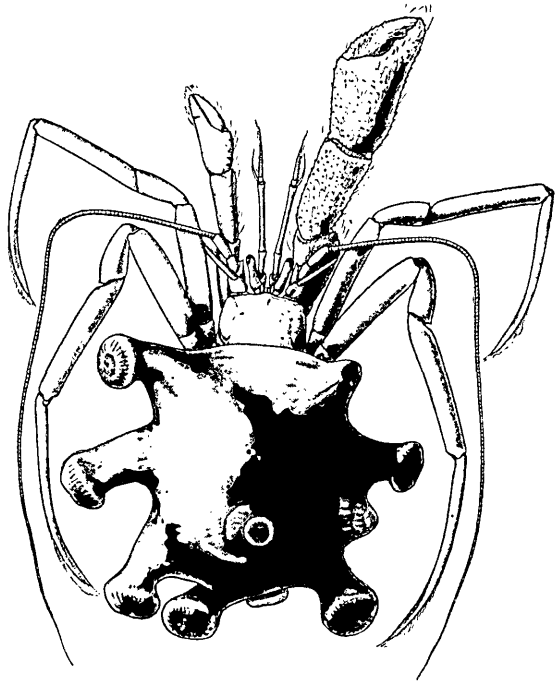

FIG. 183.

Paropagurus pilosimanus (Paguridae), lodged in a colony of zoantharian polypes. (From Alcock, *Naturalist in Indian Seas.*)

Reptantia; some Palinuridae and Astacura reach one or even two feet in length and are bulky in proportion. The largest living Arthropod is the Japanese crab *Macrocheira* (or *Kaempferia*) *Kaempferi*, of which the carapace may measure 15 inches in length, and the extended chelipeds of the male may span more than 10 feet.

PALAEONTOLOGY.

Fossil remains of Decapods are not known with certainty from any Palaeozoic deposits. Many genera from the Devonian upwards

have indeed been described as belonging to this group, but in no case is enough known of their characters to enable more to be said than that they agree with the "caridoid" groups of the Malacostraca in the possession of a carapace and of a tail-fan.

In the Mesozoic rocks many undoubted Decapods occur, including representatives of all the chief groups now living. Many genera of Penaeidea are found from the Jurassic, perhaps from the Triassic period onwards, some of the earliest even resembling closely the existing genus *Penaeus*, to which they have been referred. *Aeger*, from Triassic and Jurassic rocks, presents characters which suggest an affinity with the Stenopidea. True Caridea appear later, in the Upper Jurassic, some at least presenting primitive characters in the retention of exopodites on the ambulatory limbs. Fresh-water Caridea of doubtful affinities occur in the Miocene. The Eryonidea are especially interesting since the few existing deep-

FIG. 184.

Larger cheliped of *Oxypoda macrocera*, from the inner side, showing the stridulating mechanism. *a*, file-like series of ridges on propodite; *b*, ridge or scraper on ischiopodite against which the ridges of the propodite can be rubbed when the limb is flexed. (From Alcock, *Naturalist in Indian Seas.*)

sea forms appear to be only the surviving remnants of what was in the Mesozoic period a dominant group. The genus *Eryon* (Fig. 185) appears in the Trias and persists until the earlier Cretaceous. The Glyphaeidae, a wholly extinct group having much the same range in time as have the fossil Eryonidae, have been supposed to stand in the direct line of descent of the Scyllaridea. True Scyllaridea occur probably in the Jurassic, certainly in the Cretaceous period. The existing genus *Linuparus*, or a very close ally, dates back to the upper Chalk. Astacura are known from Jurassic and later deposits in considerable numbers. *Eryma*, from the Lias, and *Hoploparia* (Cretaceous and Tertiary) are well-known forms.

The Anomura are almost unknown as fossils, except for some Thalassinidea referred to the existing genus *Callianassa* occurring from the Upper Jurassic onwards. The Brachyura, on the other hand, are well represented. The earliest forms present characters of the Dromiacea, and are referred, for the most part, to the extinct family Prosoponidae, which Bouvier has shown to have close relations with the most primitive of existing Brachyura, the Homolo-

dromiidae. One of the oldest, and at the same time one of the most completely known, is *Palaeinachus* (Woodward) from the Forest Marble (Lower Oolite), which has many generalised characters. Later forms belonging to *Prosopon* (v. Meyer) and other genera give evidence, according to Bouvier, of the divergence of a Homoline and of a Dynomeno-Dromiine line of descent leading to such forms as

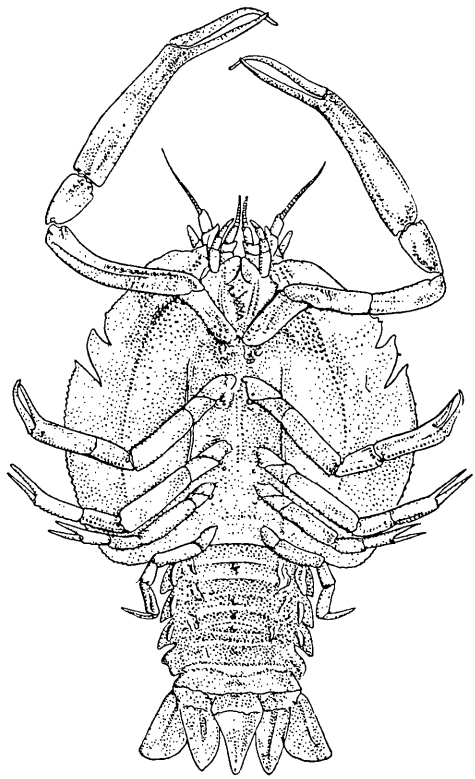

FIG. 185.

Eryon propinquus (from the Jurassic rocks of Solenhofen), under-side. (After Oppel.)

Homolopsis (Bell) and *Dromiopsis* (Reuss) from the Upper Cretaceous, and to the existing Homolidae, Dynomenidae, and Dromiidae. The remaining Brachyura have not yet yielded results of so much phylogenetic interest. The Oxystomata appear about the middle of the Cretaceous system and the Brachygnatha about the same time. In the Tertiary many Brachyura are found, representing the chief existing types of the group.

Affinities and Classification.

The resemblances between the lower Decapoda, especially the Penaeidea, and the Euphausiacea have been mentioned in dealing with the latter Order, and justify the alliance of the two Orders in the Division Eucarida. It may be mentioned that the exopodites of the thoracic legs, the absence of which still survives in text-books as distinguishing the Decapoda from the "Schizopoda," are at least as strongly developed in many Caridea (Hoplophoridae, etc.) (Fig. 160, p. 270) as in Euphausiacea or Mysidacea. Contière has recently called attention to some curious resemblances between certain primitive Caridea and the Lophogastrid Mysidacea. These resemblances, however, by no means outweigh the important differences between the two groups, and may be either primitive characters derived from the common caridoid stock or convergences due to similarity of habits.

The classification of the Decapoda is a very difficult problem, and none of the schemes hitherto proposed can be regarded as entirely satisfactory. The traditional classification of the group into the long-tailed Macrura and short-tailed Brachyura was established by Latreille in 1806; but the difficulty of defining these groups is shown by the varying limits which have been assigned to the intermediate group of Anomura established by Milne-Edwards in 1834. Boas, in 1880, was the first to make a radical departure from this system. He pointed out that the Brachyura and Anomura were only single branches of the Decapod stock, and by no means equal in systematic value to the Macrura, which included several other branches not more closely connected with each other. In other words, just as in the classification of the Malacostraca as a whole, so within the Order Decapoda, the retention of the primitive "caridoid facies" does not necessarily imply close affinity between the groups exhibiting it. Boas proposed a division of the Order into the two primary groups of Natantia and Reptantia as defined below. This division is undoubtedly a more natural one than those formerly employed, although it is hardly more easy to find constant and exclusive structural characters by which to define the sub-orders than it was in the case of the Macrura, Anomura, and Brachyura. A further difficulty is presented by the small group of Stenopidea, which combine, to some extent, the characters of Natantia and Reptantia, and may perhaps deserve separation as a third sub-order. Important modifications of Boas's scheme have been introduced by Ortmann and by Borradaile, and the classification of the last-named author has been adopted here, with some alterations, chiefly of a formal kind, as, on the whole, the most satisfactory yet proposed. Borradaile's chief innovations are the inclusion of the Thalassinidea,

formerly ranked with the Macrura, among the Anomura, the establishment of a group Brachygnatha, opposed to the Dromiacea and Oxystomata among the Brachyura, and the abandonment of the old divisions Cyclometopa and Catometopa among the families which he unites as Brachyrhyncha. These changes appear to be quite justified on morphological grounds, and to conduce to clearness in the delimitation of the groups. Much work remains to be done, however, in readjusting the subdivisions of the smaller groups, and, in particular, the classification of the Caridea is still in a very unsatisfactory condition.

Although abandoned as a systematic category, the name Macrura may still be used (as it has been above) as a convenient descriptive term for those Decapoda which retain more or less the caridoid facies, that is to say, the Natantia with the Palinura and Astacura among the Reptantia.

With regard to many of the generic names mentioned below, it is necessary to warn the student that recent "reforms" of nomenclature have resulted in lamentable confusion, more especially in the naming of long-known and familiar Decapoda, and it is not safe to assume that when an author mentions "*Astacus*" or "*Crangon*" he is referring to the genera including the common Crayfish and the edible Shrimp.

Order **Decapoda**, Latreille (1802).

Sub-Order 1. **Natantia**, Boas (1880).

Body almost always laterally compressed; rostrum usually compressed and serrated; first abdominal somite not much smaller than the rest; antennules generally with stylocerite; antennal scale generally large and lamellar; legs usually slender, except sometimes a stout chelate limb or pair, which may be any one of the first three pairs, with basipodite and ischiopodite very rarely coalesced and with only one fixed point in the carpo-propodal articulation (with some doubtful exceptions), sometimes with exopodites, podobranchiae hardly ever present on the first three and never on the last two pairs; male genital apertures in articular membrane; pleopods always present in full number, well developed, used for swimming.

Tribe 1. Penaeidea.

Pleura of second abdominal somite not overlapping those in front; antennae generally with stylocerite; mandibular palps straight; first maxillipeds without expansion at base of exopodite, endopodite long; second maxillipeds with terminal segments normal; third maxillipeds with seven segments; third legs chelate (except when legs are much reduced), not stouter than first pair; first pleopods of male with petasma; gills dendrobranchiate.

Family Penaeidae. Sub-Family Cerataspinae. *Cerataspis*, Gray.

Sub-Family ARISTEINAE. *Aristeus*, Duvernoy (Fig. 168, p. 289); *Benthesicymus*, Spence Bate. Sub-Family SICYONINAE. *Sicyonia*, H. Milne-Edwards. Sub-Family PENAEINAE. *Penaeus*, Fabricius; *Solenocera*, Lucas. Family SERGESTIDAE. Sub-Family SERGESTINAE. *Sergestes*, H. Milne-Edwards. Sub-Family LEUCIFERINAE. *Leucifer*, H. Milne-Edwards (= *Lucifer*, J. V. Thompson). [Sub-Family AMPHIONINAE. *Amphion*, H. Milne-Edwards. (The validity and the systematic place of this genus are still doubtful.)]

TRIBE 2. CARIDEA.

Pleura of second abdominal somite overlapping those in front; antennae generally with stylocerite; mandibular palp, if present, straight; first maxillipeds with expansion at base of exopodite, endopodite short; second maxillipeds usually with last segment articulating laterally with preceding; third maxillipeds with four to six segments; third legs never chelate; first pleopods of male without petasma; gills phyllobranchiate.

Family PASIPHAEIDAE. *Pasiphaea*, Savigny; *Psathyrocaris*, Wood-Mason (Fig. 160, p. 270). Family BRESILIIDAE. *Bresilia*, Calman. Family HOPLOPHORIDAE (ACANTHEPHYRIDAE). *Hoplophorus*, H. Milne-Edwards; *Acanthephyra*, A. Milne-Edwards. Family NEMATOCARCINIDAE. *Nematocarcinus*, A. Milne-Edwards. Family ATYIDAE. *Atya*, Leach; *Caridina*, H. Milne-Edwards; *Limnocaridina*, Calman. Family STYLODACTYLIDAE. *Stylodactylus*, A. Milne-Edwards. Family PSALIDOPODIDAE. *Psalidopus*, Wood-Mason and Alcock (Fig. 163, p. 272). Family PANDALIDAE. Sub-Family PANDALINAE. *Pandalus*, Leach; *Heterocarpus*, A. Milne-Edwards (Fig. 148, p. 259); *Pandalina*, Calman. Sub-Family THALASSOCARINAE. *Thalassocaris*, Stimpson. Family ALPHEIDAE. *Alpheus*, Fabricius; *Athanas*, Leach. Family HIPPOLYTIDAE. *Hippolyte*, Leach (= *Virbius*, Stimpson); *Spirontocaris*, Spence Bate; *Latreutes*, Stimpson. Family RHYNCHOCINETIDAE. *Rhynchocinetes*, H. Milne-Edwards. Family PALAEMONIDAE. Sub-Family PALAEMONINAE. *Palaemon*, Fabricius; *Palaemonetes*, Heller; *Leander*, Desmarest. Sub-Family PONTONIINAE. *Pontonia*, Latreille; *Typton*, Costa. Sub-Family HYMENOCERINAE. *Hymenocera*, Latreille. Family GNATHOPHYLLIDAE. *Gnathophyllum*, Latreille. Family PROCESSIDAE. *Processa*, Leach (*Nika*, Risso). Family GLYPHOCRANGONIDAE. *Glyphocrangon*, A. Milne-Edwards. Family CRANGONIDAE. *Crangon*, Fabricius; *Paracrangon*, Dana.

TRIBE 3. STENOPIDEA.

Pleura of second abdominal somite not overlapping those in front; antennae without stylocerite; mandibular palp curved inwards; first maxillipeds without expansion at base of exopodite, endopodite short; second maxillipeds with terminal segments normal; third maxillipeds with seven segments; third legs chelate, one or both much longer and stouter than first two pairs: first pleopods of male without petasma; gills trichobranchiate.

Family STENOPIDAE. *Stenopus*, Latreille; *Spongicola*, de Haan.

Sub-Order 2. **Reptantia**, Boas (1880).

Body not compressed, often depressed; rostrum often absent, depressed if present; first abdominal somite distinctly smaller than the rest; antennules without stylocerite; antennal scale generally small or absent; legs strong, the first pair usually, the others never, stouter than their fellows, basipodite and ischiopodite almost always coalesced in the first pair, generally also in the others, two fixed points in the carpo-propodal articulation, exopodites never present, podobranchiae often on some of the first four pairs; male genital apertures on coxopodites or on sternum; pleopods often reduced or absent, not used for swimming.

Section 1. Palinura.

Abdomen extended, well-armoured, with well-developed pleura and broad tail-fan; carapace fused at sides with epistome; rostrum generally small or absent; exopodites of maxillipeds with flagella directed forwards; third legs like the first, chelate or simple; appendix interna present on some pleopods, at least in female; exopodites of uropods not distinctly segmented; branchiae numerous.

Tribe 1. Eryonidea.

Antennae with exopodite, first segment not fused with epistome; first four pairs or all the legs chelate; first pleopods present.

Family Eryonidae. *Polycheles*, Heller; *Pentacheles*, Spence Bate (Fig. 162, p. 271); *Eryon*, Desmarest (Fossil) (Fig. 185, p. 308).

Tribe 2. Scyllaridea.

Antennae without exopodite, first segment fused with epistome; none of the legs chelate except sometimes the last pair in the female; first pleopods absent.

Family Palinuridae. *Palinurus*, Fabricius; *Linuparus*, White; *Palinurellus*, von Martens. Family Scyllaridae. *Scyllarus*, Fabricius; *Ibacus*, Leach; *Thenus*, Leach.

Section 2. Astacura.

Abdomen as in Palinura; carapace not fused at sides with epistome; rostrum well developed; exopodites of maxillipeds as in Palinura; first three pairs of legs chelate; no appendix interna on pleopods; exopodites of uropods divided by a suture; branchiae numerous.

Tribe Nephropsidea.

Family Nephropsidae. *Nephrops*, Leach; *Nephropsis*, Wood-Mason (Fig. 161, p. 270); *Homarus*, H. Milne-Edwards. Family Parastacidae. *Parastacus*, Huxley; *Paranephrops*, White. Family Astacidae. *Astacus*, Fabricius (*Potamobius*, Samouelle); *Cambarus*, Erichson.

Section 3. Anomura.

Abdomen rarely as in Palinura, generally soft, or bent upon itself, pleura generally small or absent, tail-fan often reduced; carapace not fused with epistome; exopodites of maxillipeds with flagella, when present, bent inwards; third legs unlike the first, never chelate; appendix interna sometimes present; uropods rarely absent; exopodites sometimes segmented; branchiae few.

Tribe 1. Galatheidea.

Abdomen bent upon itself, symmetrical; body depressed; rostrum often well developed; first legs chelate; tail-fan well developed.

Family Aegleidae. *Aegla*, Leach. Family Uroptychidae. *Uroptychus*, Henderson; *Chirostylus*, Ortmann. Family Galatheidae. Sub-Family Galatheinae. *Galathea*, Fabricius; *Munida*, Leach (Fig. 150, p. 260). Sub-Family Munidopsinae. *Munidopsis*, Whiteaves. Family Porcellanidae. *Porcellana*, Leach; *Petrolisthes*, Stimpson.

Tribe 2. Thalassinidea.

Abdomen extended, symmetrical; body compressed; rostrum sometimes well developed; first legs chelate, rarely sub-chelate; tail-fan well developed.

Family Axiidae. *Axius*, Leach (including *Eiconaxius*, Spence Bate, and *Iconaxiopsis*, Alcock (Fig. 149, p. 260), as subgenera); *Calocaris*, Bell. Family Laomediidae. *Laomedia*, de Haan; *Jaxea*, Nardo. Family Callianassidae. Sub-Family Callianassinae. *Callianassa*, Leach; *Callianidea*, H. Milne-Edwards. Sub-Family Upogebiinae. *Upogebia*, Leach (= *Gebia*, Leach). Family Thalassinidae. *Thalassina*, Latreille.

Tribe 3. Paguridea.

Abdomen nearly always asymmetrical, either soft and twisted or bent under thorax; rostrum generally small or absent; first legs chelate; tail-fan not typical, uropods (when present) adapted for holding the body into hollow objects.

Family Pylochelidae. *Pylocheles*, A. Milne-Edwards (Fig. 151, p. 261). Family Paguridae. Sub-Family Paguринae. *Pagurus*, Fabricius; *Clibanarius*, Dana. Sub-Family Eupagurinae. *Eupagurus*, Brandt; *Spiropagurus*, Stimpson; *Parapagurus*, S. I. Smith (Fig. 183, p. 306). Family Coenobitidae. *Coenobita*, Latreille; *Birgus*, Leach (Fig. 152, p. 262). Family Lithodidae. Sub-Family Lithodinae. *Lithodes*, Latreille; *Neolithodes*, Milne-Edwards and Bouvier (Fig. 153, p. 262). Sub-Family Hapalogastrinae. *Hapalogaster*, Brandt.

Tribe 4. Hippidea.

Abdomen bent under thorax, symmetrical; rostrum small or absent; first legs styliform or sub-chelate; tail-fan not adapted for swimming.

Family ALBUNEIDAE. *Albunea*, Fabricius. Family HIPPIDAE. *Hippa*, Fabricius ; *Remipes*, Latreille.

SECTION 4. BRACHYURA.

Abdomen small, symmetrical, bent under thorax, tail-fan not developed ; carapace fused with epistome at sides and nearly always in the middle ; exopodites of maxillipeds with flagella, when present, bent inwards ; first legs always, third legs never, chelate ; no appendix interna on pleopods ; uropods rarely present, never biramous ; branchiae generally few.

TRIBE 1. DROMIACEA.

Last pair of legs modified, dorsal in position ; female openings on coxopodites ; first pleopods present in female ; branchiae sometimes numerous ; mouth-frame quadrate.

SUB-TRIBE 1. DROMIIDEA.

Sternum of female with longitudinal grooves ; vestiges of uropods usually present ; branchiae 14-20 on each side ; eyes completely sheltered by orbits ; no linea homolica on carapace.

Family HOMOLODROMIIDAE. *Homolodromia*, A. Milne-Edwards. Family DROMIIDAE. *Dromia*, Fabricius. Family DYNOMENIDAE. *Dynomene*, Latreille.

SUB-TRIBE 2. HOMOLIDEA.

Sternum of female without longitudinal grooves ; no uropods ; branchiae 8-14 on each side ; eyes not completely sheltered by orbits ; linea homolica usually present on carapace.

Family HOMOLIDAE. *Homola*, Leach. Family LATREILLIIDAE. *Latreillia*, Roux.

TRIBE 2. OXYSTOMATA.

Last pair of legs normal or modified ; female openings generally on sternum ; first pleopods wanting in female ; branchiae few ; mouth-frame triangular, produced forwards over epistome.

Family DORIPPIDAE. *Dorippe*, Fabricius ; *Ethusa*, Roux ; *Cyclodorippe*, A. Milne-Edwards. Family RANINIDAE. *Ranina*, Lamarck. Family CALAPPIDAE. Sub-Family CALAPPINAE. *Calappa*, Fabricius. Sub-Family ORITHYINAE. *Orithya*, Fabricius. Sub-Family MATUTINAE. *Matuta*, Fabricius. Family LEUCOSIIDAE. Sub-Family LEUCOSIINAE. *Leucosia*, Fabricius ; *Ebalia*, Leach. Sub-Family ILIINAE. *Ilia*, Leach.

TRIBE 3. BRACHYGNATHA.

Last pair of legs normal, rarely reduced or dorsal in position ; female openings on sternum ; first pleopods wanting in female ; branchiae few ; mouth-frame quadrate.

Sub-Tribe 1. Brachyrhyncha.

Body not narrowed in front; rostrum reduced or wanting; orbits well formed.

Family Corystidae. *Corystes*, Latreille. Family Portunidae. Sub-Family Carcininae. *Carcinus*, Leach (*Carcinides*, Rathbun). Sub-Family Portumninae. *Portumnus*, Leach. Sub-Family Catoptrinae. *Catoptrus*, A. Milne-Edwards. Sub-Family Carupinae. *Carupa*, Dana. Sub-Family Portuninae. *Portunus*, Fabricius. Sub-Family Caphyrinae. *Caphyra*, Guérin. Sub-Family Thalamitinae. *Thalamita*, Latreille. Sub-Family Podophthalminae. *Podophthalmus*, Lamarck. Family Potamonidae. Sub-Family Deckeniinae. *Deckenia*, Hilgendorf. Sub-Family Pseudothelphusinae. *Pseudothelphusa*, Saussure. Sub-Family Potamoninae. *Potamon*, Savigny (= *Thelphusa*, Latreille). Sub-Family Trichodactylinae. *Trichodactylus*, Latreille. Family Atelecyclidae. Sub-Family Acanthocyclinae. *Acanthocyclus*, Milne-Edwards and Lucas. Sub-Family Thiinae. *Thia*, Leach. Sub-Family Atelecyclinae. *Atelecyclus*, H. Milne-Edwards. Family Cancridae. Sub-Family Cancrinae. *Cancer*, Linnaeus. Sub-Family Pirimelinae. *Pirimela*, Leach. Family Xanthidae. Sub-Family Xanthinae. *Xantho*, Leach. Sub-Family Carpiliinae. *Carpilius*, Leach. Sub-Family Etisinae. *Etisus*, H. Milne-Edwards. Sub-Family Menippinae. *Menippe*, de Haan. Sub-Family Oziinae. *Ozius*, H. Milne-Edwards. Sub-Family Eriphiinae. *Eriphia*, Latreille. Sub-Family Trapeziinae. *Trapezia*, Latreille. Family Gonoplacidae. Sub-Family Rhizopinae. *Rhizopa*, Stimpson. Sub-Family Prionoplacinae. *Prionoplax*, H. Milne-Edwards. Sub-Family Gonoplacinae. *Gonoplax*, Leach. Sub-Family Carcinoplacinae. *Carcinoplax*, H. Milne-Edwards. Sub-Family Hexapodinae. *Hexapus*, de Haan. Family Pinnotheridae. Sub-Family Pinnotherinae. *Pinnotheres*, Latreille. Sub-Family Pinnotherelliinae. *Pinnotherelia*, Milne-Edwards and Lucas. Sub-Family Xenophthalminae. *Xenophthalmus*, White. Sub-Family Asthenognathinae. *Asthenognathus*, Stimpson. Family Ptenoplacidae. *Ptenoplax*, Alcock and Anderson. Family Palicidae. *Palicus*, Philippi (= *Cymopolia*, Roux). Family Grapsidae. Sub-Family Plagusiinae. *Plagusia*, Latreille. Sub-Family Sesarminae. *Sesarma*, Say. Sub-Family Grapsinae. *Grapsus*, Lamarck; *Planes*, Bowdich (= *Nautilograpsus*, H. Milne-Edwards). Sub-Family Varuninae. *Varuna*, H. Milne-Edwards. Family Gecarcinidae. *Gecarcinus*, Leach; *Cardisoma*, Latreille. Family Ocypodidae. Sub-Family Macrophthalminae. *Macrophthalmus*, Latreille. Sub-Family Ocypodinae. *Ocypoda*, Fabricius (Fig. 155, p. 264); *Gelasimus*, Latreille. Sub-Family Myctirinae. *Myctiris*, Latreille. Family Hapalocarcinidae. *Hapalocarcinus*, Stimpson.

Sub-Tribe 2. Oxyrhyncha.

Body narrowed in front; rostrum usually distinct; orbits generally incomplete.

Family HYMENOSOMIDAE. *Hymenosoma*, Desmarest. Family MAIIDAE. Sub-Family INACHINAE. *Inachus*, Fabricius; *Macrocheira*, de Haan; *Macropodia*, Leach. Sub-Family ACANTHONYCHINAE. *Acanthonyx*, Latreille. Sub-Family PISINAE. *Pisa*, Leach; *Hyas*, Leach. Sub-Family MAIINAE. *Maia*, Lamarck (= *Mamaia*, Stebbing); *Pericera*, Latreille; *Mithrax*, Leach. Family PARTHENOPIDAE. Sub-Family PARTHENOPINAE. *Parthenope*, Fabricius; *Lambrus*, Leach. Sub-Family EUMEDONINAE. *Eumedonus*, H. Milne-Edwards.

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CHAPTER XVI

THE STOMATOPODA

Division Hoplocarida.

Order **Stomatopoda**, Latreille (1817).

For a definition of the Division Hoplocarida, see p. 149.

Historical.—The common and conspicuous *Squilla mantis* of the Mediterranean can hardly have escaped notice in antiquity, and it is surprising that it cannot be identified with certainty among the Crustacea mentioned by Aristotle. It was described by Rondelet (1555) under the generic name which it still bears. The group Stomatopoda, as defined by Latreille in 1817, had practically the limits now assigned to it, though some larvae were admitted to generic rank along with the adults. By H. Milne-Edwards the group was extended to include not only the "Schizopoda," but also some larval and adult Decapods (*Phyllosoma*, *Leucifer*, etc.). Restricted by subsequent writers to the single family Squillidae, the Order has generally been ranked along with "Schizopoda" and Decapoda in the group Podophthalma, though Huxley and, later, Grobben have pointed out the great differences separating the Stomatopoda from the other stalk-eyed groups.

The first details as to the larval metamorphosis of the Order were given by F. Müller (1862-64). Claus, in a remarkable memoir (1871), traced out several developmental series. Later workers, especially Brooks (1886) and Hansen (1895), have succeeded in referring many larvae to the various genera and species of adults. It is to be noted, however, as Hansen has pointed out, that the number of specific forms among the larvae exceeds that of the known adult species.

Morphology.

The general appearance of the Stomatopoda is highly characteristic and very constant throughout the group. Its most striking features are due to the great development of the abdominal region and its appendages, the small size of the carapace, and the large and peculiarly formed raptorial limbs.

The body (Fig. 186) is more or less flattened dorso-ventrally. The carapace is fused dorsally with at least two of the thoracic somites, two others are represented by indistinct vestiges overlapped by its hinder edge, while the last four are free and completely developed. The lateral wings of the carapace project more or less horizontally, roofing over on each side a widely open channel

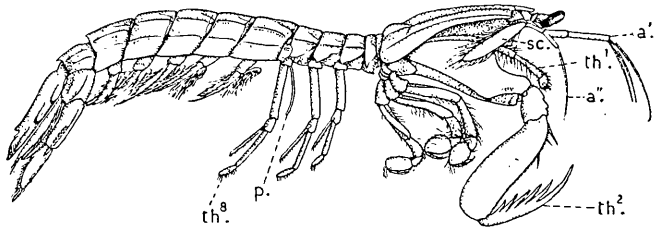

FIG. 186.

Squilla mantis, male, from the side. *a'*, antennule; *a"*, antenna; *p*, penis; *sc*, scale or exopodite of antenna; *th*¹, *th*², *th*⁸, first, second, and last thoracic appendages.

within which lie the epipodites of the anterior thoracic appendages, and which corresponds to the branchial cavity of other forms. Anteriorly the carapace does not extend to the front of the head (Fig. 187), leaving uncovered two movably articulated segments,

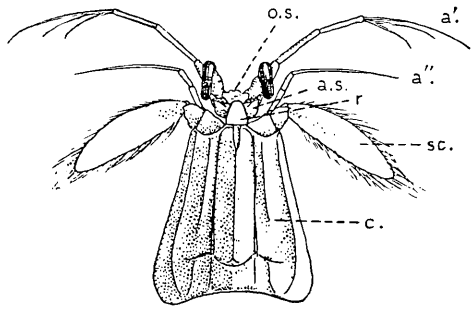

FIG. 187.

Anterior part of body of *Squilla mantis*, from above. *a'*, antennule; *a"*, antenna; *a.s*, antennular segment of head; *c*, carapace; *o.s*, ophthalmic segment of head; *r*, rostral plate; *sc*, scale or exopodite of antenna.

which carry respectively the eyes and the antennules, and which are commonly regarded as representing the ocular (*o.s*) and antennular (*a.s*) somites. A small rostral plate (*r*), movably articulated with the front edge of the carapace, overlies the antennular segment.

That part of the head lying between the point of attachment of the antennae and that of the mandibles is much elongated, forming

a narrow "neck," which, except for the lateral wings of the carapace projecting on either side, recalls the similarly formed "neck" of *Leucifer* and of the *Trachelifer*-larva of *Juxea*. The anterior thoracic somites are much abbreviated and crowded together. The first and second are apparently not distinct from the carapace in the adult. The third and fourth are at most represented dorsally by small sclerites overlapped by the hinder part of the carapace. The fifth and succeeding thoracic somites are complete, and movably articulated. The abdominal somites often increase in width posteriorly, and their horizontally extended pleural plates may become greatly expanded in certain species.

The telson (Fig. 188, *t*) is very broad and its posterior margin is generally cut into sharp teeth; it is firmly united to the preceding somite in certain species of *Gonodactylus* (*Protosquilla*, Brooks).

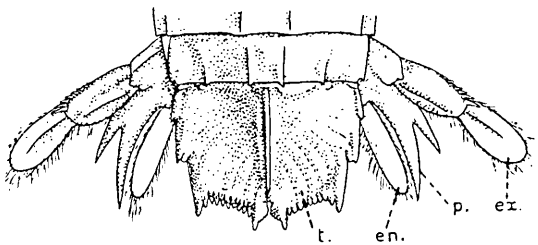

FIG. 188.

Caudal fan of *Squilla mantis*, upper surface. *en*, endopodite; *ex*, exopodite; *p*, process from peduncle of uropod; *t*, telson.

The surface of the carapace and of the body-somites is often ornamented with longitudinal keels, and the telson is always more or less elaborately sculptured.

Appendages.—The *antennules* (Fig. 187, *a'*) have an elongated peduncle of three segments, which bears three comparatively short flagella. Of these, the two on the outer side spring from a common stalk which is unsegmented; the inner flagellum is also unsegmented for a short distance from its base.

The *antennae* (Fig. 187, *a''*) have a protopodite of two segments, a large exopodite, and a comparatively feeble endopodite. The exopodite consists of a small basal segment and an oval membranous scale (*sc*) with setose margins; the endopodite has two elongated proximal segments and a short flagellum.

The *mandibles* (Fig. 189, A) carry a slender palp of three segments. The oral edge is crescentic and strongly serrate, its two cornua corresponding respectively to the incisor and molar processes of other Malacostraca. The proximal cornu projects upwards into the cavity of the mouth.

The *maxillulae* (Fig. 189, B) have two endites, the distal

one terminating in a strong curved spine. A vestigial palp is present (*p*).

The *maxillae* (Fig. 189, C) have a peculiar and characteristic form which cannot be closely compared with that of the corresponding appendage in other Malacostraca. They appear to consist of four segments, of which the first and second are indistinctly separated.

The first five pairs of *thoracic appendages* are similar in structure and are commonly called maxillipeds, though, as they possess no endites or other adaptations for mastication, the name is hardly appropriate. Each consists of only six segments (there is no evidence to show how these are related to the seven segments commonly recognised in other Malacostraca) and terminates in a

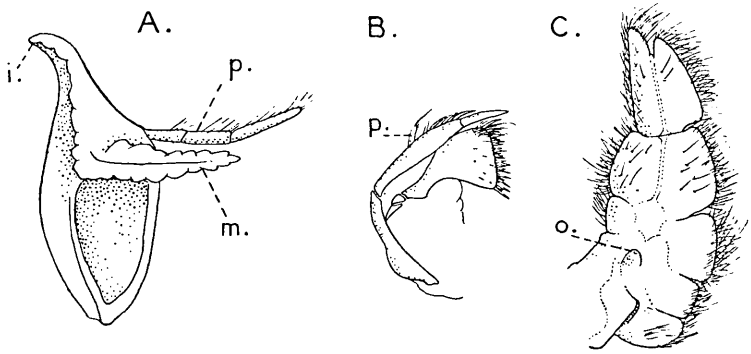

FIG. 189.

Mouth-parts of *Squilla mantis*. A, mandible, seen from the inner, or oral, side; B, maxillula; C, maxilla. *i*, incisor process; *m*, molar process; *o*, papilla bearing opening (of maxillary gland?); *p*, palp.

prehensile "hand" or sub-chela; there are no exopodites, but epipodites (Fig. 190, A, *ep*) are present on all five pairs in the form of discoid membranous plates or vesicles attached to the basal segment by a narrow neck. The first pair of limbs (Fig. 190, A) are long and slender and the terminal segment is minute; the second pair are very massive, forming powerful weapons (Fig. 186, th^2); the third, fourth, and fifth pairs resemble each other and are less powerful. In each case the terminal segment is flexed upon the preceding one in such a way that its point is directed forwards, an arrangement which recalls the peculiar inverted chela of the Amphipod *Trischizostoma*. The last three pairs of thoracic limbs (Fig. 186, th^8) are slender, biramous, and without epipodites. The protopodite is very distinctly composed of three segments, of which the second is elongated. The inner (and anterior) of the two rami is the stouter and consists of two segments; the outer is slender and unjointed. According to Claus, the development of

the limb shows the outer branch to be the endopodite and the inner the exopodite, the relative positions of the two being reversed in the course of development.

The *pleopods* (Fig. 190, B, C) are remarkable in carrying the branchial apparatus. The broad and flattened protopodite has articulated with it at some distance from each other the endopodite and exopodite, each of which is lamellar and membranous and is obscurely divided into two segments. From the inner edge of the endopodite springs a short appendix interna (*i*), bearing a group of coupling-hooks. The branchiae (*br*) consist of a main stem springing from the anterior face of the exopodite near its base, extending horizontally inwards, and carrying on its lower edge a

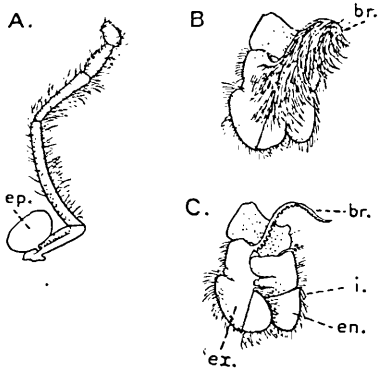

FIG. 190.

A, first thoracic appendage of *Squilla mantis*. B, second pleopod, showing the branchial appendage. C, the same, after removal of the branchial filaments. *br*, branchial appendage; *en*, endopodite; *ep*, epipodite; *ex*, exopodite; *i*, appendix interna.

series of tufts of ramified branchial filaments. In the female all the pleopods are similar, but in the male the first pair have the endopodite modified.

The *uropods* form, with the telson, a broad tail-fan (Fig. 188). The short protopodite runs out into a flattened plate (*p*) lying between and below the rami, divided distally into two sharp teeth. The exopodite is distinctly divided into two segments.

Alimentary System.—The stomach is large and thin-walled and is divided into two chambers. Its armature is slightly developed as compared with that of most Decapods. The anterior or cardiac chamber is large and extends in front of the mouth as far as the base of the rostrum. In its posterior wall lie two pairs of rod-like sclerites, the upper pair articulating with an unpaired plate which forms the floor of the smaller pyloric chamber and projects as a median keel into its cavity. The intestine is very narrow, but expands somewhat at about the fifth abdominal somite to form the

rectum. A pair of glandular sacs lying in the telson on either side of the anus have been observed in the larva and perhaps open into the rectum. It is not known whether they persist in the adult.

The digestive gland is very voluminous. It forms a compact mass of glandular tissue closely investing the intestine throughout the whole of its length and sending out on each side a series of diverticula segmentally arranged corresponding to the last three thoracic and the abdominal somites, and it finally terminates in a series of ramifying processes, which radiate throughout the telson and even penetrate into the peduncles of the uropods. It was formerly stated that this gland originated as a series of segmentally arranged diverticula from the alimentary canal, and that it communicated with the intestine by a series of apertures on each side throughout its whole length. It appears, however, that this is not the case, but that the gland-follicles open into a pair of longitudinal ducts which unite to enter the dorsal part of the pyloric chamber of the stomach.

Circulatory System.—The Stomatopoda are unique among the Eumalacostraca in possessing an elongated tubular heart extending through nearly the whole length of the thoracic and abdominal regions, and provided with numerous segmentally arranged pairs of ostia.

The details of the circulatory system have been most fully made out in the later larval stages by Claus, but the older accounts of the adult by Audouin and Milne-Edwards and by Duvernoy, though incomplete, show that no very profound changes occur in the adult. The anterior part of the tubular heart, lying in the maxillary region, is dilated, and its dorsal wall is perforated by a pair of large ostia. Anteriorly, it gives off a median aorta which sends branches to brain, eyes, antennules, and antennae, and a pair of antero-lateral arteries to the carapace and viscera. Behind the region of the first thoracic appendages the heart is of uniform diameter, and bears twelve pairs of ostia and fourteen pairs of lateral arteries arranged for the most part in correspondence with the segmentation of the body. Posteriorly the heart is continued into a short caudal aorta running into the telson.

From one of the lateral arteries of the first pair there originates an unpaired arteria descendens, which pierces the ventral ganglionic mass between the first and second thoracic ganglia, to communicate with a subneural artery which underlies the nerve-cord throughout its whole length. This subneural artery further communicates with the heart by means of its lateral branches, which anastomose in the various somites, sometimes on one side, sometimes on both, with branches of the lateral arteries. Capillary networks of great complexity are formed in the brain and in the ventral ganglia. A point of some interest is the unsymmetrical origin of the arteries

which supply the rostrum and the dorsal "Zoea"-spine of the larval carapace.

The blood from the respiratory appendages of the pleopods passes to the pericardium by a series of afferent canals in the abdomen.

Excretory System.—It is stated by Kowalevsky that the maxillary gland is well developed in the Stomatopoda, but no details as to its structure appear to have been published. A papilla on the posterior surface of the maxilla in *Squilla mantis* (Fig. 189, C, *o*) bears a minute terminal pore which may be the aperture of the duct of this gland.

Nervous System.—The oesophageal connectives are elongated, and a postoral antennal commissure is present. The first eight pairs of ganglia in the ventral chain are coalesced, but the remaining nine are widely separated.

Sense-Organs.—The paired eyes are always set on movable peduncles and vary greatly in size in the different species. The nauplius-eye, often present in the larvae, does not appear to have been found in the adult. Sensory filaments are developed on the outer branch of the external flagellum of the antennules.

Reproductive System.—The *testes* lie in the abdomen and have the form of fine convoluted tubes uniting posteriorly in an unpaired piece which lies in the telson and passing anteriorly into the vasa deferentia. Each vas deferens opens to the exterior at the end of a long penis springing from the inner side of the proximal segment of the last thoracic appendage, and differing from the corresponding organs of other Malacostraca not only in its great length but also in the fact that it is more or less strongly chitinised and is divided by a movable articulation about the middle of its length. In the posterior thoracic somites lie a pair of convoluted tubular glands which in their form and disposition have a remarkable similarity to the testes, being united anteriorly by a short unpaired piece and continued posteriorly into ducts which traverse the penes alongside of the vasa deferentia and open beside them at the tip. These glands and their ducts never contain spermatozoa and their function is unknown. The spermatozoa are spherical in form, without processes of any kind, and appear to be simple nucleated cells.

The *ovaries* are, in the mature female, very voluminous and closely approximated, so that they appear to form a single-lobed mass which extends through the abdomen and as far forward as the hinder limit of the carapace. In reality the two ovaries are only united, as is the case with the testes, by an unpaired portion lying in the telson. The oviducts open near the middle line on the sternal surface of the sixth thoracic somite, together with a small pocket-like invagination of the integument which functions as a receptaculum seminis. On the ventral surface of each of the three

last thoracic somites of the female lies a glandular mass, sending numerous fine ducts to the exterior. This is in all probability to be regarded as a cement-gland.

The eggs are of very small size, and are agglutinated together into a cake-like mass which either lies free in the burrow inhabited by the female or is carried by means of the last three pairs of chelate feet.

Development.

Little is known of the embryonic development of the Stomatopoda, but their later history is extremely remarkable, on account of the prolonged larval life, the complicated metamorphosis, and the fact that the larval forms of the various species differ from each other more widely than do the adults. The later stages, which may reach a great size, form a conspicuous element of the pelagic fauna in the warmer seas, and many species were described by the older observers as adult animals under several generic names. It is very probable, as Hansen points out, that several forms of larvae belong to species and even genera which in their adult state are still to be discovered.

Two main types of larvae can be distinguished, corresponding to the old genera *Erichthus*, Latreille, and *Alima*, Leach, and the former can be further subdivided into a number of larval genera, *Gonerichthus*, *Lysioerichthus*, etc.

Though the earlier stages of all these are still very imperfectly known, it is certain that great differences exist between them as to the degree of development at the time of hatching. The longest series of larval stages appears to be passed through by certain *Erichthus*-forms, especially by those to which the names *Lysioerichthus* and *Coronideríchthus* have been given (larvae of *Lysiosquilla* and *Coronida*). In the youngest known stage of this series (Fig. 191, A) three regions of the body can be distinguished: (1) An unsegmented cephalic region bearing the median and paired eyes, antennules, antennae, mandibles, maxillulae, and maxillae, and giving rise to the great carapace which envelops the greater part of the body; (2) a thoracic region of eight somites, all of which are free from the carapace, the first five bearing biramous swimming-feet, while the last three are without appendages; (3) a broad tail-plate representing the still unsegmented abdomen. In the following stages the abdominal somites are successively segmented off in front of the tail-plate, which remains as the telson, and their appendages at the same time develop in regular order from before backwards, the uropods at first not differing from the appendages in front of them and not preceding them in order of development. The first and second thoracic limbs early lose their exopodites, and the second pair become greatly enlarged and assume their characteristic

form. The third, fourth, and fifth pairs undergo retrograde changes, losing their exopodites and remaining for some time as shapeless stumps, only later to resume their course of development into chelate limbs. It does not seem to be the case, however, as is sometimes stated, that they actually disappear. The last three

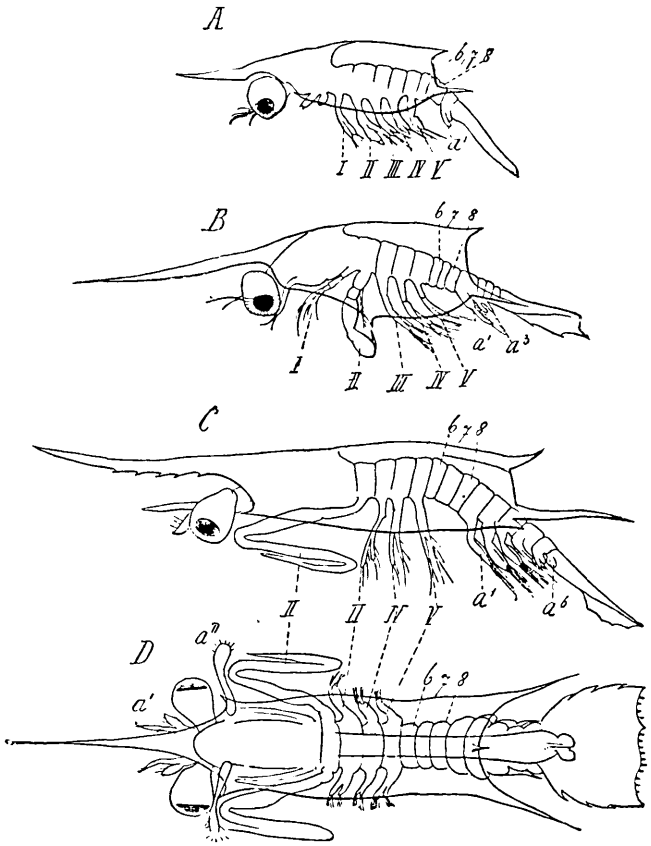

FIG. 191.

Consecutive stages of a larva of the first *Erichthus*-type. (According to Hansen, the larva represented in C and D belongs to a different species from those shown in A and B.) a', antennule; a'', antenna; a^1, first pleopod; a^6, uropod; I-V, first five thoracic appendages; 6-8, last three thoracic somites. (After Claus, from Korschelt and Heider's *Embryology*.)

thoracic somites remain for a long time devoid of appendages, and it is only at a late stage, when the appendages in front and behind are well developed, that rudiments of appendages begin to appear on them (Fig. 192). The adult form is only assumed after a considerable size has been reached, the carapace diminishing in size, becoming coalesced with the anterior thoracic somites, and

losing its spines, and the appendages gradually assuming their definitive characters. The development of the antennae appears to be peculiar in that the endopodite develops as a lateral branch, the distal portion of the larval appendage becoming the large exopod.

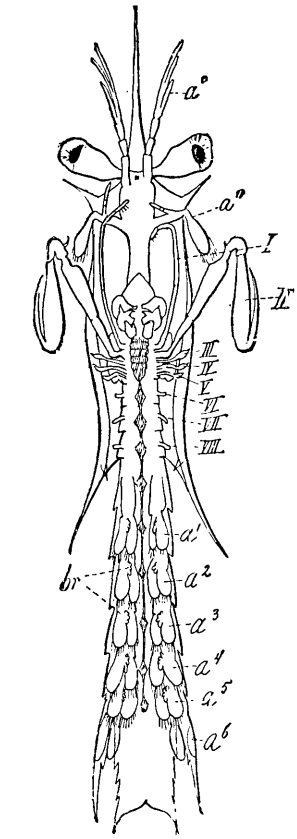

FIG. 192.

Later larva of the first *Erichthus*-type. *a'*, antennule; *a''*, antenna; *a1*-*a5*, pleopods; *a6*, uropods; *br*, rudiments of gills; I-VIII, thoracic appendages. (After Claus, from Korschelt and Heider's *Embryology*.)

In a second series of larval forms of the *Erichthus*-type (Fig. 193), belonging to the genera *Pseuderichthus*, *Gonerichthus*, etc. (*Pseudosquilla* and *Gonodactylus*), the youngest stage known possesses already four or five pairs of pleopods, and the last six thoracic somites are without any trace of appendages.

The larvae of the *Alima*-type (Fig. 194), belonging to the genus *Squilla*, are known to leave the egg at a stage corresponding with that last described. They are distinguished from all the preceding forms by the generally more slender body and short and broad carapace, and more constantly by differences in the armature of the telson and raptorial limbs.

Lister has described a very remarkable larva, which appears to correspond to a metanauplius-stage. The form of the carapace makes it very probable that it belongs to the Stomatopoda, and, if so, it shows that some members of the order leave the egg at a much earlier stage than has hitherto been supposed.

The great size attained by some of these larvae, especially by those of the *Alima*-type, which may exceed two and a half inches in length, has given rise to the suggestion that they are abnormally hypertrophied forms which, by being swept out to sea, have been prevented from completing their metamorphosis. As in the similar cases of the *Phyllosoma*-larvae among Decapods and the *Leptocephalus*-larvae of eels, however, there appear to be no grounds for accepting this view, and it is definitely rejected by Hansen as a result of his extensive studies on the group.

The metamorphosis of the Stomatopoda is of great importance in helping to interpret the larval forms of the Decapoda. While

the regular order of differentiation of the somites from before backwards is preserved, the retarded appearance of the posterior thoracic appendages shows the beginning of the process which has led to the suppression of these somites and appendages in the typical Zoea.

Notes on Habits, etc.

The Stomatopoda are exclusively marine, the adults generally inhabiting burrows in the sand or mud of the sea-bottom in shallow

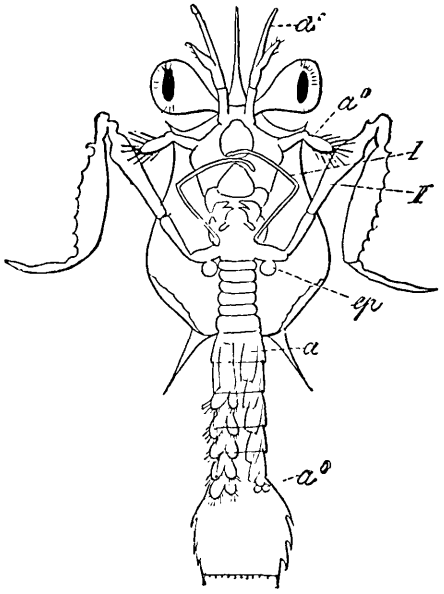

Fig. 193.

Larva of the second *Erichthus*-type (the *Pseuderichthus* group). *a'*, antennule; *a''*, antenna; *a*, first pleopod; *a6*, uropod; *ep*, epipodite; 1, 11, first two pairs of thoracic appendages. (After Claus, from Korschelt and Heider's *Embryology*.)

water (up to 180 fathoms), chiefly in the tropics, but extending north to Britain and Japan, and south as far as Auckland. Many species seem never to wander far from their burrows, into which they retreat with great rapidity when alarmed, and are thus seldom obtained by the ordinary methods of collecting. The larval stages, on the other hand, are exclusively pelagic, of glass-like transparency, and occur in great numbers in the plankton of the warmer seas. All the Stomatopoda appear to be of active, predatory habits. The range in size within the group is about from 38 to 340 mm.

Palaeontology.

The oldest undoubted Stomatopods are found in the Jurassic rocks of Solenhofen, and are referred to the genus *Sculda*, Münster, differing in many details from the living forms. Species referred to the genus *Squilla* occur in the Cretaceous deposits of Westphalia

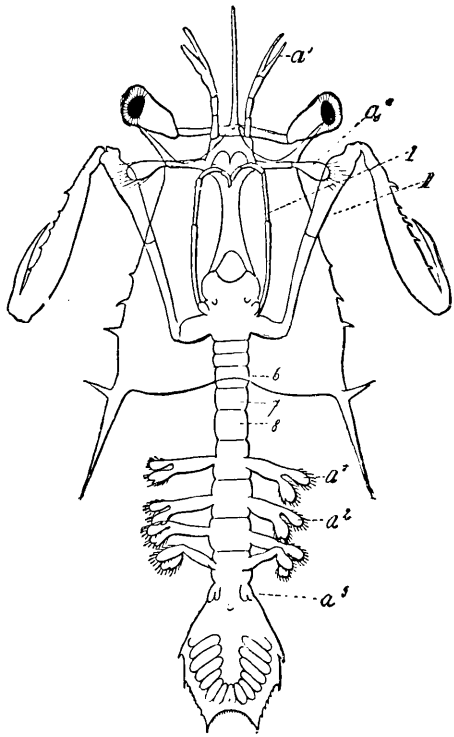

Fig. 194.

Young larva of the *Alima*-type. a', antennule; a'', antenna; a^1-a^5, pleopods; I, II, first and second thoracic limbs; 6-8, last three thoracic somites. (After Brooks, from Korschelt and Heider's *Embryology*.)

and the Lebanon, in which latter larvae of the *Erichthus*-type have also been recognised. Species of *Squilla* also occur in the London Clay and other Tertiary deposits.

Affinities and Classification.

Perhaps the most aberrant character of the Stomatopoda, and one which separates them not only from the other Malacostraca but from all other Crustacea, is the presence of distinct and

movable ophthalmic and antennular "somites." Whatever be the morphological value of these segments of the head, there can be no doubt that their separation in the Stomatopoda is a secondary and not a primitive character.

The movable rostral plate is a character of some interest from its resemblance to that of the Leptostraca; but it is to be noted that the spiniform rostrum of the larval Stomatopod is not articulated, while, on the other hand, the Decapod *Rhynchocinetes* shows the possibility of the ordinary rostrum becoming divided off by a movable joint from the carapace.

The lamellar epipodites of the first five pairs of thoracic limbs recall those of the Syncarida; the bifurcation of the outer flagellum of the antennules is only paralleled among the Caridean Decapods; the modification of the first pair of pleopods in the male may be compared with that found in the Euphausiacea and the Penaeid Decapods; the possession of an appendix interna on the pleopods is shared by the Leptostraca and the lower Eucarida. Other characters, such as the structure of the maxilla and the segmentation of the thoracic limbs, cannot be closely compared with those of any other Malacostraca. It seems most probable that the Stomatopoda are a lateral offshoot from the main stem of the Malacostraca, of which, in the absence of connecting links, it is as yet impossible to determine the exact relations.

The existing Stomatopoda form a very homogeneous group, within which only one family can be recognised, while many of the genera are separated by comparatively slight differences.

Order **Stomatopoda**, Latreille (1817).

Family Squillidae. *Squilla*, Fabricius (Fig. 186); *Lysiosquilla*, Dana; *Pseudosquilla*, Dana; *Gonodactylus*, Latreille; *Coronida*, Brooks.

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