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THE SAND CRAB EMERITA TALPOIDA (SAY) AND SOME OF ITS RELATIVES

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INTRODUCTION

Emerita talpoida (Say) of the Atlantic coast of the United States, and several related species found elsewhere, are small anomuran crabs of the family Hippidae, which are of particular interest because of their total adaptation to a special way of living and to what is probably, among the arthropods, a unique method of feeding. The Emeritas bury themselves with the head end up, "facing" the ocean, in the wet sand of sloping beaches covered by the wash of the waves. Here they extend their long, plumose antennae to collect from the descending water over them whatever food material may be carried in suspension, which is then transferred to the mouth parts by a ventral flexing and folding of the antennae, which in turn are enclosed by the large platelike meropodites of the third maxillipeds. The mandibles are much reduced and are entirely functionless as organs of feeding. The antennal method of food gathering by *Emerita* was first described by Weymouth and Richardson (1912) for the west-coast species *analoga*.

Smith (1877) in his study of *Emerita* (*Hippa*) *talpoida* of the Atlantic coast did not recognize the feeding function of the antennae, which he thought were used for cleaning the legs; finding the stomach full of sand, he concluded that the crabs swallowed sand for whatever nutritive matter it might contain. The essential likeness in structure of the several *Emerita* species, however, can leave no doubt that they all feed in the same manner. Their habits alone would suggest that the antennae are food-collecting organs, and the mouth is so closely shut in by the maxilliped plates that a direct ingestion of sand would hardly be possible.

It is surprising to find that no other members of the hippid family are equipped for antennal feeding, though they are all sand burrowing in their habits. In the two other principal genera of the family, *Hippa* and *Mastigocheirus,* the mandibles are even more reduced than in *Emerita,* but the second antennae have short, simple flagella in no way adapted to food gathering. In both these genera, however, the inner lobes of the first maxillae are developed into a pair of strong, toothed jaws closing beneath the mouth. Evidently, then, the functional loss of the mandibles by the hippids has been compensated in two ways: in *Hippa* and *Mastigocheirus* by the formation of substitute jaws from the maxillulae; in *Emerita* by the development of the antennal flagella into food-gathering organs. One is tempted to wonder why the adult hippids lost their mandibles in the first place, and how they fed while making adjustments to their present structure. The nature of the food and the feeding method of *Hippa* and *Mastigocheirus,* however, are still unknown. The members of the related family Albuneidae, which likewise live in sand, have well-developed, functional mandibles, and strongly chelate first pereiopods.

Both *Emerita talpoida* and *E. analoga* are commonly found in great numbers between tide marks on sandy beaches, where they will be covered by the inflowing waves. As the crabs are exposed by the receding water they quickly back themselves into the wet sand in a slanting position with the ventral surface toward the ocean. Here they await the return wave, and when the downflow begins they spread the antennae out before them against the current. According to the tides, the crabs move up or down the beach. MacGinitie (1938) says of *E. analoga* that a "general migration with the tide takes place in mass movement" and is done so quickly that to an observer "it appears that a portion of the beach comes up, moves either up or down, and then disappears. . . . On a gently sloping beach this migration usually occurs at a time when the sand crab colony is covered with from two to six inches of water." When the movement of the water begins to slacken, the crabs quickly orient themselves facing the ocean and dig into the sand. Wharton (1942) says of *E. talpoida* that the crabs "will follow a shallow wave towards the water and a deep wave up the beach." The usual stimulus for proper orientation, according to MacGinitie, is the water flowing over the crabs from behind, and if a stream of water from a hose is made to flow over them away from the ocean, "they will immediately reverse their position in the sand and face toward the land, even if they must move uphill to do so." Under natural conditions, MacGinitie says, "the stimulus of the current appears to be much stronger than the stimulus of sight," though when the current is at a minimum, if a large black screen is placed between the crabs and the ocean, they will face landward.

The mating of the sexes of *Emerita analoga* on the California coast is said by MacGinitie (1938) to take place late in spring and early in summer. The males, generally several at a time, bury themselves in the sand at the side of a female and attach to her under surface packets of spermatozoa in a thick adhesive mucus. According to Wharton (1942), the very young males of *E. talpoida,* with a carapace length of 3 mm., which appear in August at Beaufort, N. C., are sexually mature, and attach themselves to year-old females for mating, as many as seven of the miniature males having been found on a single large female. The spermatophores are attached between the coxopodites of the fourth legs of the female. From the time of their first appearance in August until the following June, the small males increase in length of the carapace from an average of about 3 mm. to about 7 mm.

I. GENERAL STRUCTURE OF EMERITA TALPOIDA

The material on which the anatomical part of this paper is based has been furnished by the Division of Marine Invertebrates of the United States National Museum.

A specimen of *Emerita talpoida* as ordinarily seen (fig. 1 B), when freshly dug up out of the sand, or in museum collections, has the general appearance of a small, symmetrically egg-shaped object, the largest females being about 30 mm. in length, the males half as long. A pair of short antennules (*1Ant*) and two slender eyestalks project from the anterior end, and on the sides at the posterior end are two paddlelike uropods (*Urpd*). The rest of the appendages are closely folded against the underside of the body, where the legs, except those of the first pair, are further concealed by lateral extensions of the carapace, and by the long telson (*Tel*) bent forward below them. The color is a uniform pale yellowish brown. When buried in soft wet sand the crabs are thus well protected from their granular environment; their only problem is that of respiration, but the antennules projecting into the water above the sand together form a respiratory tube.

When an *Emerita* is stretched out at full length (fig. 1 C) it is seen to be a complete crab. A smooth, rounded, shell-like carapace covers the gnathothoracic region of the body, a 6-segmented abdomen bears an extremely long, pointed telson (*Tel*), at the base of which project the relatively large uropods (*Urpd*). On the under surface, the region of the mouth and the feeding organs, and the flagella of the second antennae, unless the latter are extended, are completely covered by a pair of large valvelike plates, which are the meropodites of the third maxillipeds (fig. 3 A, *Mrpd*). At the sides of the latter are two elongate pterygostomial plates (fig. 1 B, *Ptst*) flexibly attached to the edges of the carapace. The maxilliped plates open ventrally like a pair of trap doors, and if they are lifted the long plumose flagella of the second antennae will be seen looped upon each other immediately above them (fig. 3 B). When the antennae are artificially extended, the flagella project in curves outward and posteriorly (fig. 1 A). Following the maxillipeds are five pairs of legs, the first pair of which are directed forward against the maxilliped plates, the second, third, and fourth pairs usually folded under the carapace, and the slender fifth pair bent upward and forward into the branchial chambers. The abdomen of the female has three pairs of slender pleopods in addition to the uropods.

In its postembryonic development *Emerita talpoida*, according to Smith (1877), goes through four zoea stages and a megalops stage. The first zoea stage was not observed by Smith, but in the other stages the zoea has a long rostral spine and two lateral spines on the carapace, large eyes on short peduncles, and an abdomen of five segments bent forward beneath the thorax. The telson is a broad plate, with a wide, rounded distal margin. The mandibles in all the zoea stages appear to be functional organs. In the second stage the appendages include, besides the mandibles, two pairs of maxillae, two pairs of maxillipeds, and the uropods. The third maxillipeds

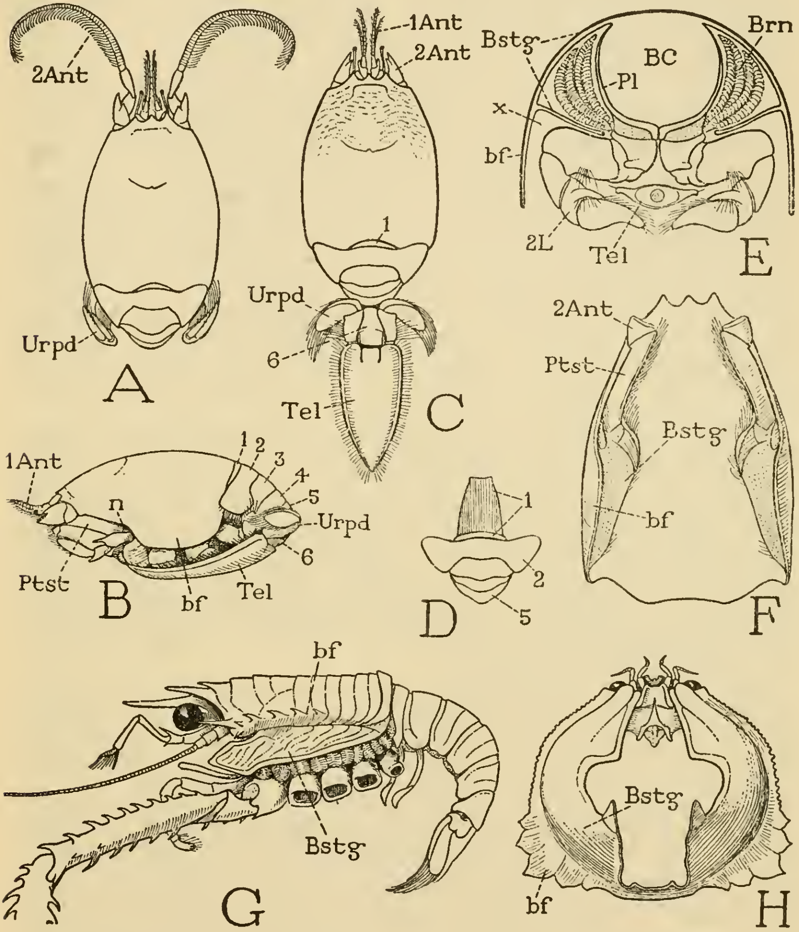

Fig. 1.—External features of *Emerita, Galathea,* and *Calappa.*

A, *Emerita talpoida* (Say), female, with antennae extended, dorsal. B, same with antennae concealed, left side. C, same, abdomen artificially extended, dorsal. D, same, abdomen detached, showing long apodemal plate of first tergum, dorsal. E, same, cross section of body behind second legs. F, same, carapace, pterygostomial plates, and branchiostegites, ventral. G, *Galathea californiensis* Benedict, female. H, *Calappa flammea* (Herbst), carapace, ventral.

and the legs are still unsegmented rudiments. In the third zoea the legs are better developed, and those of the fifth pair appear; the gills are now represented by slender processes above the first four legs. In the fourth stage the full number of gills (nine on each side) is present, the uropods have two apical lamellae, but the telson preserves the broad form of earlier stages. The megalops at once takes on in many ways the form and habits of the adult. The second antennae, Smith says, have assumed all the important features of the adult antennae, including the mechanism for folding beneath the body, but there are still fewer annulations in the flagella. The mandibles have been reduced to the adult condition, the third maxillipeds form large opercular plates, the abdomen and telson resemble these parts in the adult. At Woods Hole the young Emeritas in the megalops stage, according to Smith, may be taken at the surface of the water in the towing net during late August and the early part of September. Specimens in aquaria swim rapidly at the surface, but in a shallow dish of sea water with sand on one side, they at once back themselves into the sand "with an evident satisfaction and with an ease and agility that could not have been excelled by their sand-loving parents after months or years of practice."

The first zoea stage of *Emerita talpoida* is said by Wharton (1942) to lack the lateral spines of the carapace. The megalops, according to Wharton, are amphibious like the adults, being well adapted for both swimming and burrowing. In swimming, the megalops keeps the abdomen extended, while the young adults swim with the abdomen flexed. The ventral pleopods of the megalops are used as swimmerets, there being four pairs in the megalops stage, differing in form from those of the adult.

It is customary to describe the body of a decapod crustacean as divided into two parts, a cephalothorax covered by the carapace, and a free abdomen, or pleon. However, there is a distinct head structure in front of the carapace, or beneath its projecting anterior end, which bears the eyestalks, the two pairs of antennae, and the labrum. It is not intimately united with the body, except in Palinuridae, and should be regarded as the true *head* of the animal. The region covered partly or wholly by the carapace includes the segments of the mandibles, the maxillae, the maxillipeds, and the legs, and is hence really a *gnathothoracic* tagma, or section of the body. The *abdomen,* then, constitutes a third part carrying the pleopods and the telson. This concept of a triple division of the decapod will be followed in the description of *Emerita.*

II. THE HEAD AND ITS APPENDAGES

The head of most of the malacostracan Crustacea represents the simplest type of head structure found among the arthropods, and therefore, in an evolutionary sense, the first known stage of head development. For this reason the writer (1951) has termed it the *protocephalon.* A more complex secondary type of head structure results from the addition of two or more postoral segments to the protocephalon, as in the amphipods, isopods, myriapods, and insects, in which the head bears, in addition to the eyes and antennae, the appendages concerned with feeding.

The head.—The head of *Emerita* is a typical protocephalon; though it is not so well sclerotized or so strongly developed as that of a crayfish or a lobster, it can be separated as a discrete head unit from beneath the anterior end of the carapace (fig. 2 A, C). On the dorsal surface (A) is a V-shaped ocular plate (*e*) supporting the eyestalks (*ES*), and behind it a larger, weakly sclerotized postocular plate (*m*) flexibly connected with the base of the under lamella of the projecting rostral part of the carapace. The small first antennae (*1Ant*) arise anteriorly beneath the edge of the ocular plate, and at the sides are the bases of the large second antennae (*2Ant*). On the ventral surface (C), the head presents a broad calcified region, the epistome (*Epst*), between and behind the bases of the antennules, with lateral extensions to the bases of the antennae and irregular postantennal wings (*k*). Supported on the posterior margin of the epistome is the triangular labrum (*Lm*), which projects forward inverted against the epistomal surface. If the labrum is turned posteriorly (D, *Lm*) it will be seen to have covered a noncalcified area of the epistome from which arise a pair of small setigerous processes. In most decapods the postantennal wings of the epistome (*k, k*) extend laterally to the bases of the inner lamellae of the carapace folds, but in *Emerita* the intervening regions are not calcified. At the basal angles of the labrum are the small mandibles (E, *Md*) solidly united with the adjoining edges of the epistomal wings, and behind the labrum is the mouth (*Mth*) flanked by a pair of small paragnaths (*Pgn*). The mandibles and the paragnaths, however, do not belong to the head.

The crustacean protocephalon is an anatomical fact, but its segmental composition is an uncertainty. The origin of the second antennae of the adult from the protocephalon might suggest that the protocephalon contains the second antennal segment. The second antennae, however, are postoral in their embryonic origin, and acquire their definitive preoral position secondarily. The idea that the mouth has migrated posteriorly from a more anterior position seems hardly tenable if it is implied that it has pushed clear through one or more segments. More probably, the ventral parts of the invaded segments are simply folded forward around the sides of the mouth. That something of this nature has taken place is indicated by the finding of Tiegs (1940, p. 133), in his study of the development of a symphylan, that much of the roof of the preoral cavity of the head is

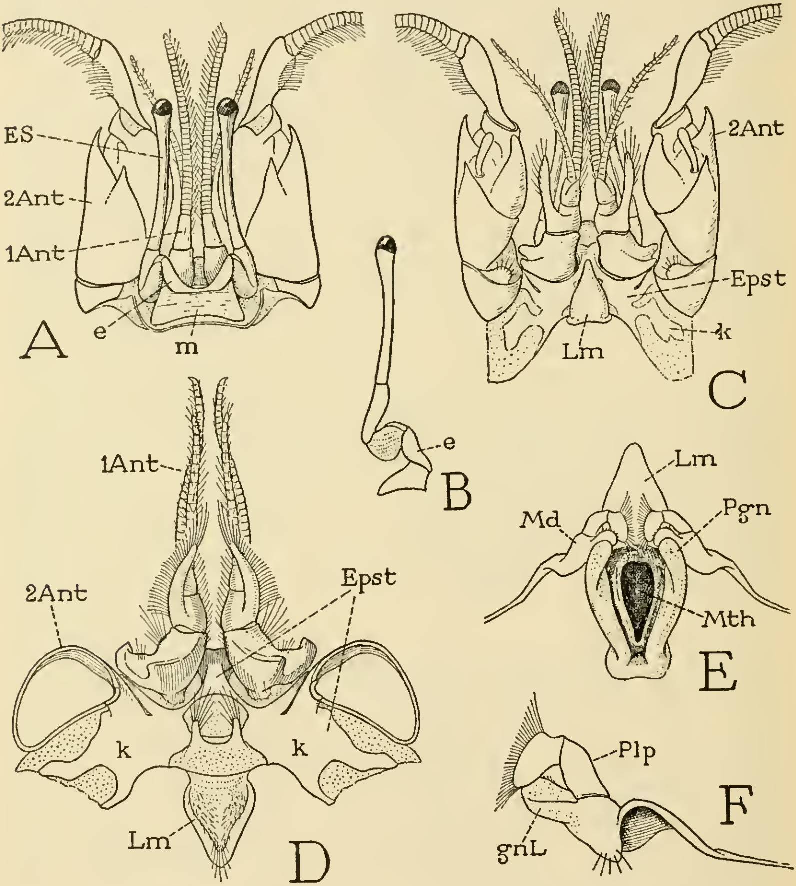

FIG. 2.—*Emerita talpoida* (Say), head, mandibles, and mouth region.

A, head (protocephalon) bearing eyestalks and first and second antennae, dorsal. B, left eyestalk, and supporting plate of head (*e*), dorsal. C, head, ventral, labrum normally turned forward beneath epistome. D, epistome, first antennae, and bases of second antennae, ventral, labrum artificially turned posteriorly. E, mouth region with associated labrum, mandibles, and paragnaths, ventral. F, right mandible, dorsal.

derived from the premandibular (second antennal) segment. However, in the adult arthropod, no remnant of a postoral arc of even the second antennal segment has been anatomically identified as such. The identity of the dorsal arc of this segment is equally elusive in the adult. The origin of dorsal muscles of the second antennae in the decapods on the anterior part of the carapace might suggest that the rostral area of the carapace includes the dorsum of the second antennal segment; yet in the adult anostracan branchiopod there is clearly no segment between the protocephalic head and the mandibular segment. Recently it has been asserted (Henry, 1948) that there is no second antennal segment. It would indeed simplify matters very much to have this segment abolished, but unfortunately there is too much evidence of its existence, at least in works on arthropod embryology.

The eyestalks.—The slender eyestalks of *Emerita* (fig. 2 B) are 3-segmented, with the small eyes on the ends of the long distal segments. The second segments are abruptly and flexibly elbowed on the mostly membranous basal segments, which are borne on the ends of the ocular plate (*e*) of the head, so that the eyestalks can be freely protracted and retracted in a lengthwise direction.

The first antennae.—The relatively small first antennae, or antennules (fig. 2 A, *1Ant*), project forward between the eyestalks. Each antennule consists of a 3-segmented basal stalk, best seen from below (C, D), and a pair of multiarticulate flagella, of which the ventral one is more slender and a little shorter than the dorsal one. The large basal segment of the stalk is of irregular form and articulates below on the epistome; the second segment bears ventrally a large setigerous process. The flagella are fringed with short hairs and when the four of them are held together they enclose a narrow space between them, which is the usual exit canal of the respiratory system, but may become inhalant when the crab is buried in the sand. The antennular canal of *Emerita,* however, is not so well closed by setae as in some other sand-burrowing crabs.

The second antennae.—The second antennae are organs of vital importance to *Emerita* inasmuch as they are the food-collecting instruments of these crabs. Each appendage (fig. 3 F) consists of a 2-segmented basal stalk, of a middle part that contains two segments which constitute the flexing mechanism, and of a distal part including an elongate proximal segment, and the long, plumose terminal flagellum. The two basal segments are evidently the coxopodite (*Cxpd*) and the basipodite (*Bspd*). The second is produced laterally into a pointed lobe, but there is no true exopodite branch. The identity of the other segments is difficult to determine. Schmidt (1915) in his study of the antennal muscles of the crayfish accounts for seven antennal segments, making the flagellum the dactylopodite. There are, however, only five functional segments besides the flagellum in the antenna of *Emerita,* and the third and fourth are of irregular form.

The third antennal segment (fig. 3 F) is largely membranous, but its mesal part contains a strongly calcified convex plate supported on the inner angle of the basipodite. The fourth segment presents dorsally (B) a large, smooth, convex surface, but ventrally (F) it is represented only by a Y-shaped bar that supports the fifth segment, and articulates by each arm on the mesal plate of the third segment. The two articular points lie in an oblique line (*d-e*) extending proximally and laterally between the third and fourth segments, and it is on this line as an axis that the distal part of the antenna is flexed ventrally. The fourth segment, moreover, is braced laterally against the basipodite by a short rod (*f*) in the ventral wall of the third segment, which turns on the basipodite at a point in the axis of flexion. When, therefore, the distal part of the antenna bearing the flagellum is flexed ventrally on the oblique axis (*d-e*) between the third and fourth segments, it not only turns downward and posteriorly, but it goes over to the opposite side of the body, and the bar (*f*) braced against the fourth segment prevents any other movement. The two antennal flagella are thus assured of being symmetrically folded upon each other (B) ; in most specimens the left flagellum is below the right, but in some the right is below the left.

In the folded position of the antennae (fig. 3 B), the parts beyond the lines of flexion are entirely concealed within the large meropodite plates of the third maxillipeds (A, *Mrpd*), and the flagella are looped upon each other. According to Weymouth and Richardson (1912), *Emerita analoga* folds the antennae separately as the water runs off the beach. The flagella are first allowed to trail out with the current, and are then "folded up and withdrawn under cover of the third maxillipeds with such a rapid motion as to escape analysis." So closely are the antennae shut in above the maxilliped plates, however, that it would seem the plates must first open to receive them.

Inasmuch as the antennal flagella are specifically the food-collecting organs of *Emerita,* the details of their structure become a matter of special interest. Each flagellum of *Emerita talpoida* is cut into about 150 small rings by circular joints that impart a flexibility to the shaft as a whole. In cross section the shaft is rounded above and somewhat flattened below (fig. 3 E). The plumose character of the flagellum is due to the presence of eight rows of setae on the under surface, there being duplicate sets of four on each ring, so that in all there are about 1,200 setae on the entire flagellum. The setae of the outermost rows (E, *g*) are long, tapering filaments flaring outward with incurved tips; the concave margins are densely fringed with long slender hairs, giving these setae a featherlike structure. The setae of the second rows (*h*) are somewhat curved outward;

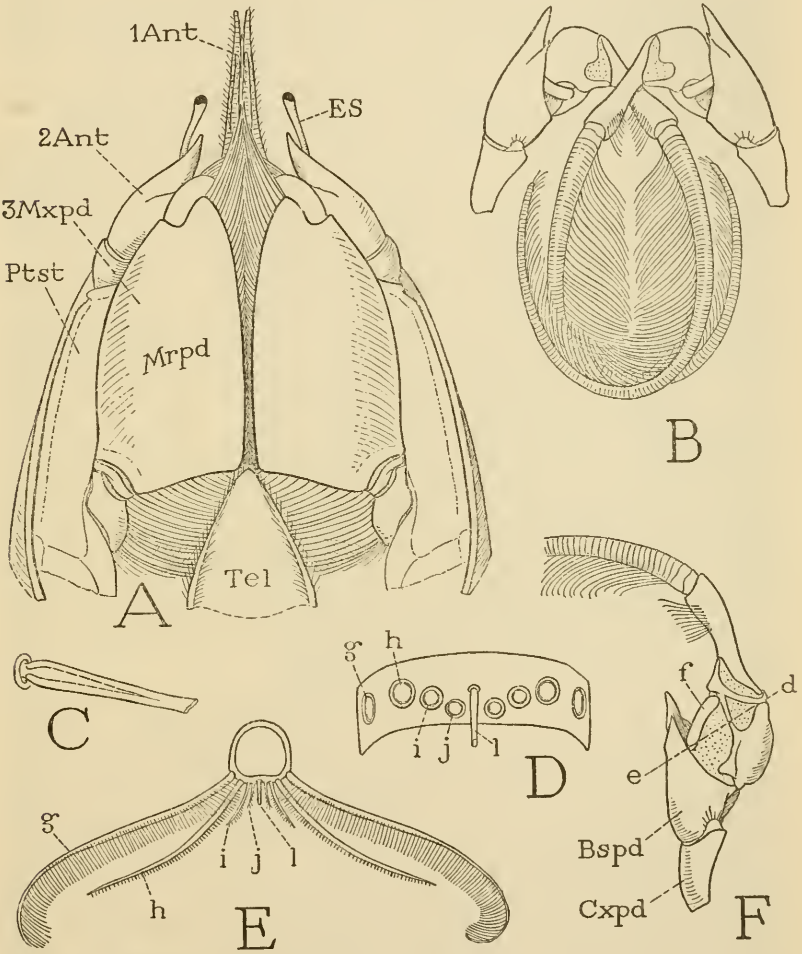

Fig. 3.—*Emerita talpoida* (Say), second antennae and third maxillipeds.

A, ventral surface of anterior part of body, second antennae folded above meropodite plates of third maxillipeds. B, second antennae in folded position, ventral. C, a median process of antennal flagellum (E, *l*). D, under surface of a flagellar ring, showing position of setae. E, cross section of flagellar ring, with setae. F, proximal part of right second antenna, showing folding mechanism, ventral.

their inner surfaces are armed with short, blunt, closely set processes like the teeth of a comb. The setae of the third and fourth rows (*i, j*) are short and simple with fine hairs on their inner margins.

Finally, along the midline of the flagellar shaft, between the innermost setae, is a row of slender, tapering processes (*l*), all slightly inclined toward the base of the flagellum. The tip of each of these median processes (C) is obliquely truncate and appears to contain a slight membranous depression. Weymouth and Richardson suggest that these structures in *E. analoga* may be sensory organs. At D of figure 3 are shown the relative positions of the several rows of setae and the median processes on a single ring of the flagellum.

When the antennae of a dead specimen of *Emerita talpoida* are extended (fig. 1 A) they project forward from the body and the flagella curve outward and posteriorly; in this position the marginal rows of setae are dorsal and ventral, with respect to the body. If, however, the antennae are turned horizontally away from the ventral surface as the crab stands vertically in the sand, or are carried into this position by the downflow of the water on the beach, the antennae will be rotated into a position in which the concave sides of the flagella are away from the ocean, and the setae will now be spread out against the descending current. Living specimens of *E. analoga*, buried in the sand in the feeding position, are said by Weymouth and Richardson to hold the antennae "directed forward" (presumably meaning oceanward) and laterally with the tips curved outward. In this position, these writers note, "the antennae thus present to the water flowing against the concave side a very efficient straining apparatus." In other words, the opposite rows of setae are spread out as a fine-meshed sieve against the downflowing water.

The stomach contents of *Emerita analoga* were found by Weymouth and Richardson to be always of the same kind of material, "chiefly shells of various diatoms, masses of brownish oily matter apparently derived from the diatoms, radiolarians, foraminifera, spicules of unrecognized origin, what were probably one-celled algae, and considerable amounts of sand—about what would be obtained by unselective straining of the water along the shore." From experimental feeding of *E. analoga* on suspensions of bacteria in liter jars of sea water, Zobell and Feltham (1937-38) found that the crabs can be sustained to a certain extent on bacteria alone, but that they do not thrive on a pure bacterial diet as well as does the mussel *Mytilus californianus*, and that they are not as efficient as the mussel in removing bacteria from the water. The antennae of *Emerita* in the folded position above the plates of the third maxillipeds are separated from the mouth by the second and first maxillipeds and the two pairs of maxillae; the method by which food material is transferred from the flagella to the mouth is, therefore, not open to observation.

III. THE GNATHOTHORAX

The gnathothoracic part of the body of *Emerita* is entirely covered above and on the sides by the carapace (fig. 1 A, B). The anterior dorsal margin of the carapace is produced into three small points over the head, the posterior lateral areas are extended downward in broad folds (B, *bf*) over the leg bases. In front of these folds on each side is an elongate plate (*Ptst*) reaching from the base of the second antenna to the base of the first leg, and flexibly attached to the margin of the carapace. This plate is known as the *pterygostomial plate* because it evidently represents the so-called pterygostomial region of the carapace of an astacuran decapod. The posterior end of the plate is not continued into the lateral fold (*bf*) of the carapace behind it, but goes beneath the latter to be continued into a soft, horizontal inner fold (F, *Bstg*) lying above the leg bases and closing the gill chamber from below (E). This soft inner fold is the true lower part of the branchiostegite (*Bstg*), the outer sclerotic fold (*bf*) is a secondary extension of the branchiostegite beyond the base of the inner fold. The branchiostegites themselves are folds of the thoracic walls projecting from the sides of the back; their inner lamellae are continuous dorsally with the mesal walls of the gill chambers, which are the true lateral walls of the thorax on which the legs are articulated (fig. 8 B). In carcinology the inner wall of the gill chamber is called either the epimeron or the pleuron, but for general usage *pleuron* is preferable because the gill-chamber wall of the crustacean evidently corresponds with the skeletal parts called the pleura in other arthropods.

In order to establish a basis for a consistent nomenclature, it will be of interest to follow the various modifications of the sclerotized dorsal part of the body wall that occur among the arthropods. In a simple, soft-bodied animal with ventrolateral rows of legs, such as an onychophoran (fig. 4 A), the circumference of the body is divided by the lines of the leg bases into a dorsum (*D*) above the appendages, and a venter (*V*) between them. A simple sclerotization of the body wall would then produce in each segment a dorsal plate, or *tergum,* and a ventral plate, or *sternum.* If the tergum comes down to the leg bases, the legs will be suspended from, or articulated on, its lower margins, a condition found in some arachnids. More commonly, however, as in the crustacean *Anaspides* (B), the dorsum of a thoracic segment contains a major tergal plate (*T*) covering the back, and on each side a small *pleural plate* (*Pl*) carrying the outer articulation (*a*) of the leg. Usually, however, the contour of the segment

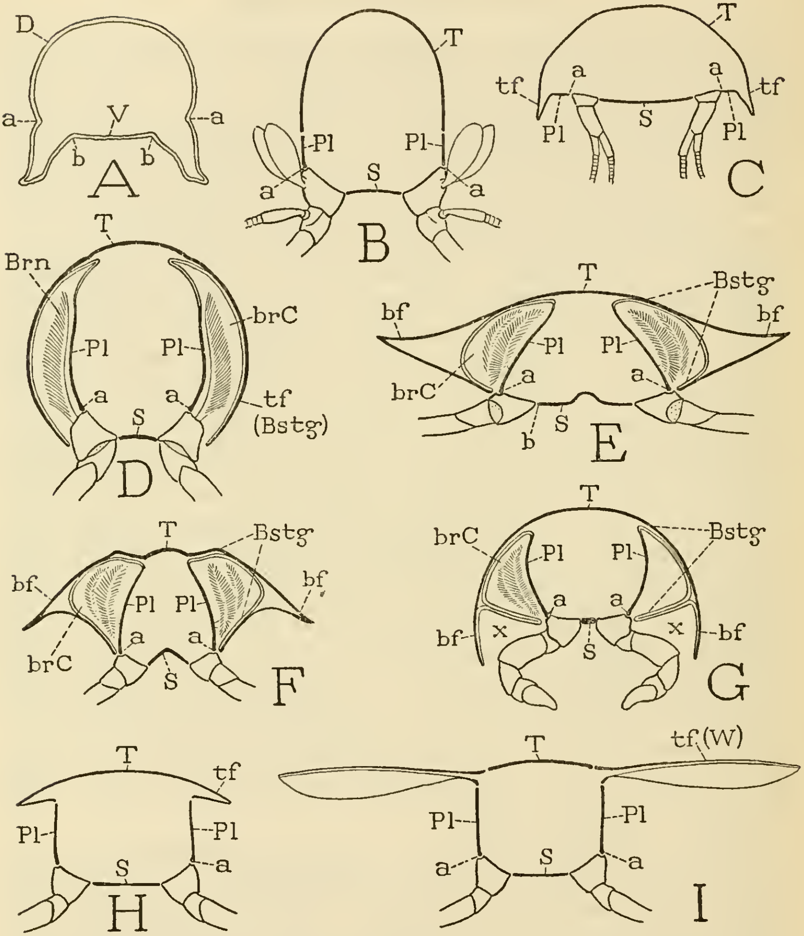

FIG. 4.—Diagrammatic cross sections of arthropods, showing various types of modification of the dorsal sclerotization.

A, dorsum entirely unsclerotized, as in an onychophoran. B, thorax of the crustacean *Anaspides,* dorsal sclerotization differentiated into a principal back plate, or *tergum* (*T*), and small laterotergal plates, or *pleura* (*Pl*), carrying lateral articulations of coxae. C, abdomen of an astacuran decapod, with small tergal folds (*tf*) projecting over pleura. D, thorax of an astacuran decapod, with tergal folds extended downward as gill covers, or branchiostegites. E, thorax of a crab, *Callinectes,* with branchiostegites produced into lateral folds (*bf*). F, thorax of a crab, *Calappa,* with branchiostegite folds depressed. G, thorax of *Emerita,* with branchiostegite folds (*bf*) extended downward over the legs, enclosing subbranchial canals (*x*). H, prothorax of an insect with short lateral folds (paranotal lobes) of tergum. I, alate segment of an insect, with tergal folds greatly extended horizontally and flexible at their bases, forming wings.

is not so simple as in *Anaspides*. In the decapod abdomen (C) the tergum is generally produced into short lateral folds (*tf*) overhanging the pleura (*Pl*). In the thorax (D) the pleura maintain a more or less vertical position as the lateral walls of the body cavity, while the tergal folds (*tf*) arise high up on the sides and descend as long branchiostegites (*Bstg*) over the gills to the bases of the legs. In most of the Brachyura (E, F) the outer walls of the branchiostegites (*Bstg*) are extended laterally into sharp-edged folds, but finally, in *Emerita* (G), the branchiostegite folds (*bf*) become thin ventral extensions of the carapace. A lesser development of branchiostegite folds is seen in the crab *Calappa* (fig. 1 H) in the form of flangelike projections from the sides of the back, and in the anomuran *Galathea* (G) there is a suggestion of the same thing in the presence of spiny ridges (*bf*) above the branchiostegites.

In all the decapod forms above discussed, it will be seen that the pleura form the true lateral walls of the thoracic segments, and carry on their lower margins the lateral articulations of the legs. The same is true for the thoracic segments of insects. In the insect prothorax there are usually short tergal folds (fig. 4 H, *tf*) overhanging the pleura; in the winged segments (I) the tergal folds are greatly extended, flexible at their bases, and become organs of flight. It is interesting to note, therefore, that the wings of an insect (I, *W*) may be regarded as structures topographically homologous with the branchiostegites of an astacuran decapod (D, *Bstg*).

The ventral surface of the gnathothorax of *Emerita* can be fully seen only after removal of the appendages, so, unless specimens are plentiful, it will be well to study first the mouth parts and legs, described in the next section. On the exposed ventral surface (fig. 5) there is to be noted an abrupt change in the sternal structure between the region of the maxillae and maxillipeds (A) and that of the pereiopods (B). The foramina of the legs (B, *1L-5L*) lie in regular rows at the sides of the narrow median sterna (*S*). The third maxillipeds (A, *3Mxpd*) arise lateral of the first legs (*1L*), and the three pairs of maxillipeds lie along oblique lines converging forward toward the mouth; the second maxillae (*2Mx*) again have lateral positions, and the first maxillae (*1Mx*) arise in membranous areas at the sides of the mouth. The sternal sclerotization of the maxillo-maxilliped region (A) is not segmentally divided; from the narrow metastomal area it expands posteriorly into a large, diamond-shaped plate between the bases of the maxillipeds in front of the first legs. The maxillary region is extended on each side in a strong bridge (*mxB*) to the base of the inner lamella, or doublure (*Dbl*), of the pterygostomial plate of the carapace. The maxillary bridges evidently represent the pleura of the second maxillary segment; they form the anterior limits of the branchial chambers. It is to be noted that the slender outer ends of the mandibles reach to the maxillary bridges, on which in the Anomura generally the mandibles have their outer articulations. The second maxillae have a lateral position because of the respiratory function of the scaphognathites, and the first and second maxillipeds are thrust forward between them, so that the second maxillae are immediately followed by the third maxillipeds.

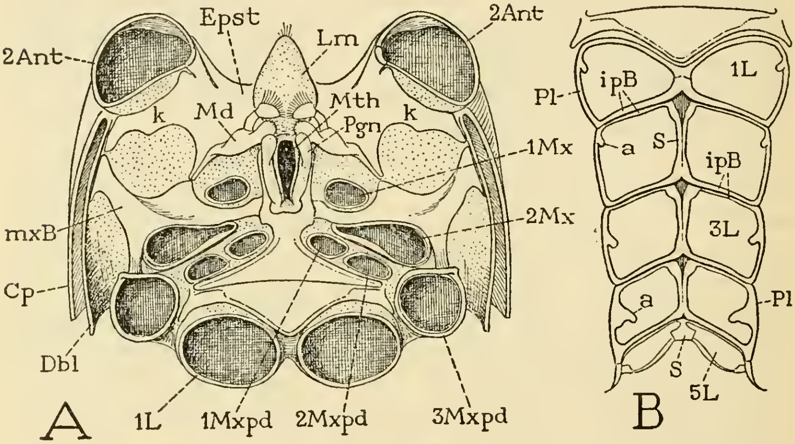

FIG. 5.—*Emerita talpoida* (Say), ventral skeleton of head and gnathothorax, exposed by removal of appendages.

A, ventral surface of head, mouth region, maxillary and maxilliped segments, anterior to first legs (*1L*). B, ventral surface of pereiopod segments.

In the region of the pereiopods (fig. 5 B) the ventral sclerotization at once assumes a regular pattern repeated in each of the five leg-bearing segments. Between each pair of legs is a narrow sternal plate or bar (*S*), which gives off laterally from its anterior end a pair of slender precoxal sternopleural arms, and from its posterior end a pair of similar postcoxal arms, which are continuous at their outer ends with the pleura of the same segment. The adjacent sternopleural arms of consecutive segments, however, are united to form a series of *interpedal brachia* (*ipB*), in which the intersegmental lines are marked by deep grooves.

The internal skeleton of *Emerita* consists of the usual intersegmental pleural and sternal apodemes of decapods. The sternal apodemes of the thorax are four pairs of plates or arms diverging forward and upward from the intersegmental grooves of the interpedal brachia, the fourth pair arising from the brachia between the fourth and fifth legs. The apodemes of the last two pairs are united at their bases, the others are narrowly separated over the sternal plates; in no case are they bridged by expansions of their inner ends as in the Astacura. A pair of divergent ridges in front of the first legs are probably intersegmental between the third maxillipeds and the first pereiopods. A pair of intermaxillary apodemes are united in a transverse bridge, the so-called "head apodeme" behind the mouth. The pleural apodemes are relatively small and are confined to the thorax; they arise on each side from the intersegmental grooves of the pleuron (fig. 8 B), and are Y-shaped, one arm joining the corresponding sternal apodeme, the other going back to the one following.

IV. THE GNATHOTHORACIC APPENDAGES

The segmental appendages of the gnathothorax are the mandibles, the first maxillae (maxillulae), the second maxillae (maxillae), the first, second, and third maxillipeds, and the five pairs of legs, or pereiopods. The mandibles and the two pairs of maxillae may be distinguished as the gnathal appendages; the maxillipeds are commonly regarded as thoracic, though in *Emerita* the first two pairs are entirely concerned with the feeding function.

The mandibles.—The mandibles of *Emerita talpoida* (fig. 2 F) are very small, though larger than in the other genera of Hippidae, and are immovably united with the posterior edges of the epistome. The basal part of each mandible (corpus mandibulae) is produced mesally into a weak gnathal lobe (*gnL*), and bears a relatively large 2-segmented palpus (*Plp*). The two diminutive jaws lie entirely in front of the mouth (E, *Mth*), with the gnathal lobes and the palpi underlapping the base of the labrum (*Lm*). Though the mandibles of *Emerita* clearly can have no use as biting or chewing organs, the palps may have a sensory function, or, together with the gnathal lobes, they perhaps serve to prevent the escape of food material from in front of the mouth. A pair of small paragnaths (*Pgn*) underlie the mandibular lobes.

In the zoea stages of *E. talpoida* the mandibles, as described by Smith (1877), are evidently functional organs, since they have broad, toothed gnathal lobes, though molar areas are absent. In the megalops stage, however, Smith says, "the mandibles have become thin and foliaceous and completely consolidated with the wall of the oral opening." A relatively large, indistinctly 2-segmented palpus is present, but the gnathal lobe is a small thin flap as in the adult.

The first maxillae.—The small, flat first maxillae (fig. 6 A) arise at the sides of the oral region and project mesally beneath the mouth. The body of each appendage contains a small basal plate and, proceeding from the latter, a pair of parallel bars, each of which supports a large free mesal lobe, while at the base of the more distal of these lobes there arises a small anterior lobe. The structure of the first maxilla of *Emerita* is similar to that in other decapods, and the small anterior lobe is commonly regarded as the endopodite, according to which interpretation the other two lobes are coxal and basal endites. It is of interest to note that the flat, weak, proximal mesal lobe of the maxillula of *Emerita* is developed in other hippid genera into a strong, toothed jaw (fig. 10 E).

The second maxillae.—These appendages (fig. 6 B, C) are larger than the first maxillae, but they have essentially the same structure, except for the presence of the huge scaphognathites (*Scpg*) attached laterally on their bases. Three mesal lobes of each maxilla arise from a common base and clearly correspond with the three lobes of the maxillula (A). The maxillary scaphognathite is generally interpreted as the exopodite of the appendage, but its position suggests that it might be a highly developed epipodite. The scaphognathites are the active organs in the maintenance of water currents through the gill chambers, as will be explained in the description of the respiratory system.

The first maxillipeds.—The first maxillipeds (fig. 6 D) are 2-branched appendages borne on a pair of small basal plates situated close to the midline of the body. The maxilliped branches are without doubt true exopodites and endopodites. The endopodites of the first maxillipeds are unsegmented; a sievelike arrangement of hairs on their concave mesal borders lies below the mouth. The exopodites are 2-segmented; the apical segments bear brushes of long hairs and converge against the sides of the labrum.

The second maxillipeds.—The maxillipeds of the second pair (fig. 6 E) resemble those of the first pair in that each consists of an endopodite and an exopodite supported on a small basal segment. Their bases are farther apart than those of the first maxillipeds, which latter in the figure (E) are seen between the basal segments of the outer maxillipeds. The exopodites of the second maxillipeds bear each an apical, brushlike segment similar to that of the first maxillipeds, but the endopodites are 4-segmented, with the two slender distal segments turned posteriorly. The long basal segments of the endopodites are fringed mesally with wide, comblike rows of setae directed

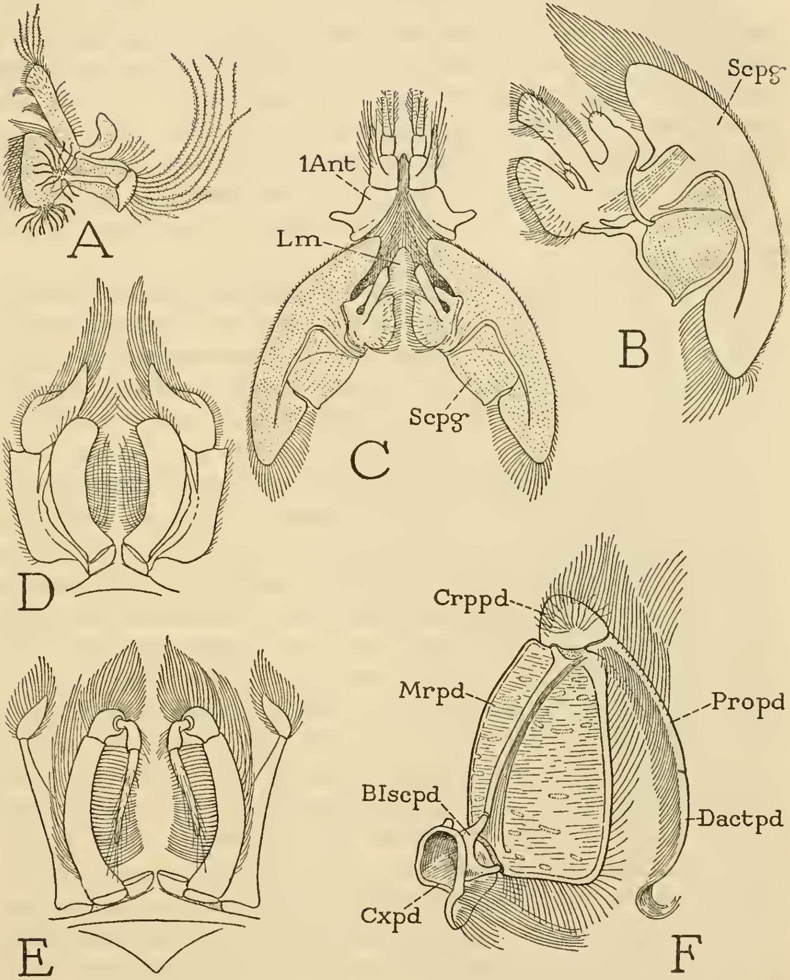

FIG. 6.—*Emerita talpoida* (Say), maxillae and maxillipeds.

A, left first maxilla, ventral (posterior). B, left second maxilla, flattened, ventral. C, second maxillae, with scaphognathites in natural position relative to the labrum and bases of first antennae, ventral. D, first maxillipeds, ventral. E, second maxillipeds, ventral. F, left third maxilliped, dorsal.

toward each other, and laterally with long hairs that blend with large setal brushes on the second segments.

The two pairs of maxillae and the first two pairs of maxillipeds lie horizontally between the mouth and the infolded antennal flagella, and the latter in turn are completely shut in ventrally by the plates of the third maxillipeds. Weymouth and Richardson (1912) say that "the mouth parts are admirably adapted for the manipulation of the minute organisms which the antennae have strained from the waves." Undoubtedly this is true, but it remains for some ingenious investigator to discover just how the various mouth-part appendages perform their function.

The third maxillipeds.—The third maxillipeds (fig. 6 F) have the same segmentation as the legs; each consists of the endopodite alone, there being no exopodite branch. The two appendages are widely separated at their bases (fig. 3 A), but the broad meropodites (*Mrpd*) come together mesally; the distal segments are turned posteriorly (fig. 6 F) and are ordinarily concealed above the meropodites. A short basal stalk of each appendage is formed by the coxopodite and the basi-ischiopodite (fig. 6 F, *Cxpd, BIscpd*). The large meropodite (*Mrpd*) is capped by a small carpopodite (*Crppd*), from which a long slender distal arm of the appendage, composed of the propodite (*Propd*) and the dactylopodite (*Dactpd*), turns posteriorly. The valve-like meropodites are opened and closed by an axial rotation of the appendages on their bases, but the mode of action by which they embrace and enclose the antennae has not been recorded. In the closed position (fig. 3 A), fringes of long hairs on the proximal parts of the appendages shut in the space behind the meropodites, covered medially by the anterior end of the telson (*Tel*), which lodges the posterior parts of the antennal loops (B). The narrow space between the meropodites, and the triangular opening at their divergent anterior ends are covered by overlapping setal fringes of the meropodites and the distal segments (fig. 6 F). The outer edges of the meropodites lie close against the pterygostomial plates (fig. 3 A, *Ptst*), and the large first legs are pressed against their ventral surfaces. Whatever food material the antennal flagella bring with them into the food chamber above the meropodites is thus effectively imprisoned for transference to the mouth.

The legs.—The legs of both the anomuran and the brachyuran crabs have generally only six disinct segments, while the typical decapod limb has seven, there being in the crabs only one apparent segment between the coxopodite and the meropodite. When a crab's leg is broken off, however, it leaves a small ring attached to the coxopodite, which may be supposed to be a much reduced basipodite (fig. 7 B, *Bspd*) detached from the ischiopodite. The functional second segment of the leg, therefore, is termed the basi-ischiopodite (D, *BIscpd*).

The legs of *Emerita,* together with the uropods, are principally organs for burrowing, though they must be used also for emergence from the sand. The uropods serve both for burrowing and for swimming. The burrowing activities of *Emerita* have been described by several writers. Smith (1877) notes merely that *E. talpoida* burrows backward by means of the thoracic legs and the uropods, while the telson is kept appressed to the under surface of the body. Concerning *E. analoga,* Mead (1917) says, "burrowing is accomplished by the combined action of the uropods and pereiopods, the latter being the more serviceable." Animals with clipped uropods could burrow, though more slowly than normally. MacGinitie (1938) gives only the statement that the crabs bury themselves rapidly in the sand by use of the anterior legs and the uropods. Weymouth and Richardson (1912) record more detailed observations on the use of the different appendages by *E. analoga.* The uropods, according to these writers, appear to be the most important digging implements; they strike upward and forward in unison, thus thrusting the body downward and backward if the sand is firm. The pereiopods take part in the burrowing in different ways; the second and third pairs thrust the body backward, those of the fourth pair push outward, and the large first legs are used to scull the body backward. "Under the combined action of all these appendages the animal is carried diagonally downward and backward until the anterior end of the carapace is just covered." According to Wharton (1942) *E. talpoida,* when preparing to burrow, backs up into the wet sand, and the uropods, rotating in unison, throw the sand dorsally, while the body is forced backward. The first legs work alternately pushing the sand laterally and anteriorly. The fourth legs, and also the third and the second legs, Wharton says, "move in unison laterally and posteriorly," but the posterior movement observed must be the relaxing stroke, since the statement follows that these legs "move the sand anteriorly and force the posterior end of the body into the sand."

The first legs of *Emerita* are large, thick, and strong, with broad, flat dactylopodites (fig. 7 A). As already noted, these legs project forward and are closely applied against the meropodite plates of the third maxillipeds, apparently serving to keep the plates tightly shut when they enclose the antennae. The wide, broadly fringed dactylopodites, however, adapt these legs also to their function in burrowing. The other legs take a more transverse position and are ordinarily mostly concealed beneath the branchiostegite folds of the carapace on the sides and by the telson below (fig. 1 B). The second and third legs (fig. 7 C, D) are similar in size and shape to each other. The dactylopodites have the form of short pruning hooks with broad bases and decurved tips. Each dactylopodite is firmly hinged ventrally by a double articulation on the end of the propodite, and when flexed upward its wide base overlaps the posterior surface of the propodite. Anteriorly the dactylopodite is braced against a strong projection from the propodite (G, *Propd*). In either the flexed or the extended position of the dactylopodite, therefore, the propodite and the dactylopodite of the second and third legs present a firm posterior surface for pushing backward against the sand. On the other hand, a forward push would appear to be more effective with the dactylopodites flexed against the propodites. Evidently, then, the second and third legs are constructed both for burrowing into the sand, and for emerging from it. In the female the openings of the oviducts are on the coxae of the third legs.

The smaller fourth legs (fig. 7 E) are turned posteriorly and upward, and furthermore, are twisted in such a manner that the posterior surfaces of the dactylopodites face outward. In *Emerita talpoida* the dactylopodites of these legs are simpler in shape than those of the second and third legs, but they are likewise articulated ventrally on the propodites and overlap the outer surfaces of the latter when flexed. There is no bracing process of the protopodite against the mesal surface of the dactylopodite, but the fourth legs, with the dactylopodites in the flexed position, are clearly constructed to push outward, as they are said to do by Weymouth and Richardson. In *E. talpoida* there is little difference in the structure of the fourth legs between the female (E) and the male (H).

According to MacGinitie (1938) the males of *E. analoga* "attach to the female by the dactyls of their fourth legs, which are equipped with a sort of sucker pad surrounded by stiff hairs. Sometimes they hold on with both dactyls, at other times with only one. As viewed under the microscope the sucking pad with its surrounding hairs does not look very efficient, but the ease with which the males cling to a female is surprising, for they have merely to place the dactyl against any part of the carapace or appendage of the female to attain a hold. However, the clinging is voluntary and not automatic." A similar habit has not been observed in the case of *E. talpoida,* but an examination of the end segments of a fourth leg of the male *analoga* reveals a structure (fig. 7 I) quite different from that of *talpoida* (H). The

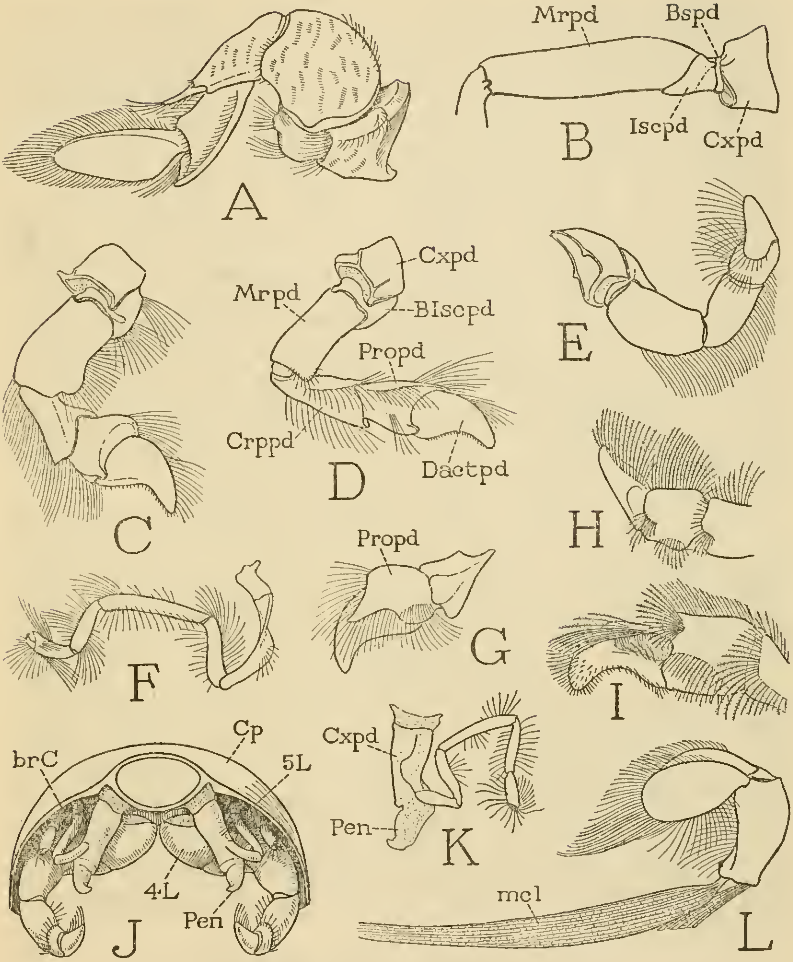

FIG. 7.—*Emerita talpoida* (Say) and *analoga* (Stimpson), pereiopods and uropod.

A, *Emerita talpoida* (Say), left first leg, ventrolateral. B, left leg of a crab, *Callinectes sapidus,* showing narrow basipodite ring (*Bspd*) on which the rest of the leg breaks off. C, *Emerita talpoida,* left second leg, posterior. D, same, left third leg, posterior. E, same, left fourth leg, lateral. F, same, left fifth leg of female, dorsal. G, same, anterior surface of distal segments of left second leg, showing process of propodite against anterior surface of dactylopodite. H, same, mesal surface of distal segments of fourth leg of male. I, *Emerita analoga* (Stimpson), mesal surface of distal segments of fourth leg of male. J, *Emerita talpoida,* posterior end of thorax of male, showing fourth and fifth legs. K, same, right fifth leg of male, posterior. L, same, left uropod and muscles from telson, in natural inverted position.

dactylopodite of the fourth leg in the female of *analoga* is the same as that of *talpoida* (E), but in the male (I) the dactylopodite is broad and hook-shaped as in the preceding legs; on its mesal surface is a large oval depression, which is fully exposed when the dactylopodite is extended, but it is overhung by a large brush of stiff hairs from the propodite, and from its upper margin a brush of long hairs projects beyond the tip of the dactylopodite, while a few delicate hairs arise from its lower margin. Otherwise also the setal arrangement on both the propodite and the dactylopodite is entirely unlike that of *talpoida* (H). It seems clear, therefore, that the fourth legs of the male in *analoga* are made for some special purpose, to which the corresponding legs of *talpoida* evidently are not adapted, but it is difficult to understand from the structure of the dactyls in *analoga* how this special function can be adhesion. The means by which the male of *analoga* holds the female with one or both of his fourth legs, therefore, needs closer observation on the living animals.

The fifth legs are small, slender, 7-segmented appendages (fig. 7 F) that can be seen on an intact specimen only by depressing the telson and straightening the abdomen. The coxopodites (J, *5L*) arise close behind the bases of the fourth legs (*4L*); the telopodites turn dorsally and forward and are usually looped in the branchial or subbranchial chambers (*brC*). These legs have diminutive apical chelae, the dactylopodite being a small hook opposed by a short process from the propodite. The distal segments are armed with long hairs, some of which are directed proximally (F), forming brushes, suggestive that the small fifth legs are used for cleaning the branchial chambers, or for preventing the entrance of sand into their open posterior ends. In the male (J, K) the coxopodites are particularly large and are produced distally into thick, soft papillae (*Pen*) on which open the genital exit ducts.

V. THE RESPIRATORY SYSTEM

The respiratory organs of Crustacea are primarily the gills, or branchiae. When the gills are enclosed in branchial chambers, however, various accessories become necessary for efficient respiration: there must be entrances into the chambers containing the gills, an apparatus for maintaining currents of water through the chambers, and an exit for the discharge of the respired water. In the decapods all these parts together constitute the external respiratory system.

In *Emerita* the gills (fig. 1 E, *Brn*) are very closely shut within the branchial chambers both laterally and ventrally by the branchiostegites (*Bstg*), and the posterior ends of the chambers are effectively closed by the deflexed abdomen. The broad, descending lateral folds of the branchiostegites (*bf*) enclose on each side a subbranchial canal (*x*) between the inner fold of the branchiostegite and the legs. Inasmuch as the inner folds taper in width posteriorly (F, *Bstg*), the subbranchial canals and the branchial chambers become confluent in the posterior part of the thorax. Anteriorly the soft inner folds of the branchiostegites are continuous with the sclerotic pterygostomial plates (F, *Ptst*), which are fully exposed on the sides of the body (fig. 1 B, *Ptst*), except as they are partly overlapped by the first legs. The lower margins of the pterygostomial plates lie close against the bases of the first legs, so that in *Emerita* there are here no apparent openings directly into the branchial chambers, as there are in some crabs. At their posterior ends, however, the pterygostomial plates go mesad of the lateral folds of the branchiostegites, where they become continuous with the inner folds of the latter, and thus create openings (fig. 1 B, *n*) that lead directly into the subbranchial canals. The pterygostomial apertures, therefore, would appear to offer a possible way for the intake of respiratory water, which would have easy access to the branchial chambers from the posterior ends of the subbranchial canals, or, in the case of a reversal of the currents, the same openings would serve as exits. This suggestion has only an anatomical basis, and needs the support of experimental evidence.

Each branchial chamber (fig. 8 A, *brC*) opens anteriorly into a pump chamber (*PC*) of the respiratory system, in which is lodged the scaphognathite (*Scpg*) of the corresponding second maxilla. The pump chambers are closed laterally by the pterygostomial plates. The two scaphognathites converge anteriorly past the sides of the labrum (fig. 6 C, *Lm*) into the triangular space below the bases of the antennules (*1Ant*), which finally runs out into the median respiratory tube formed by the close apposition of the four antennular flagella. If water enters through the antennular tube, it will be split into two streams by the apex of the labrum and thus drawn into the two pump chambers; or, if the current is reversed, the outgoing streams from the pumps will unite at the bases of the antennules to be discharged through the flagellar tube.

The vibratory movement of the scaphognathites is the force that drives the water through the respiratory passages. In the decapods generally the currents usually go from behind forward, but it has been observed in some burrowing crabs and also in certain other species that the currents can be reversed, presumably by a reversal in the action of the scaphognathites, and the same is probably true of *Emerita*. According to Smith (1877), when *E. talpoida* is buried, the excurrent forms a small opening and a slightly boiling motion in the sand. Mead (1917) says that by dropping small quantities of ink into the water over a buried individual of *E. analoga* the current was always found passing from posterior to anterior. On the other hand, Weymouth and Richardson (1912), by the same experiment on *E. analoga,* observed that the water is usually drawn into the antennular tube when the animal is buried, though occasionally it goes in the opposite direction, but that when the crabs are resting on the surface of the sand beneath the water or are swimming, the water is drawn in at the sides and expelled through the antennular tube. Evidently, therefore, *Emerita* when buried adjusts the direction of its respiratory currents according to conditions imposed by the sand.

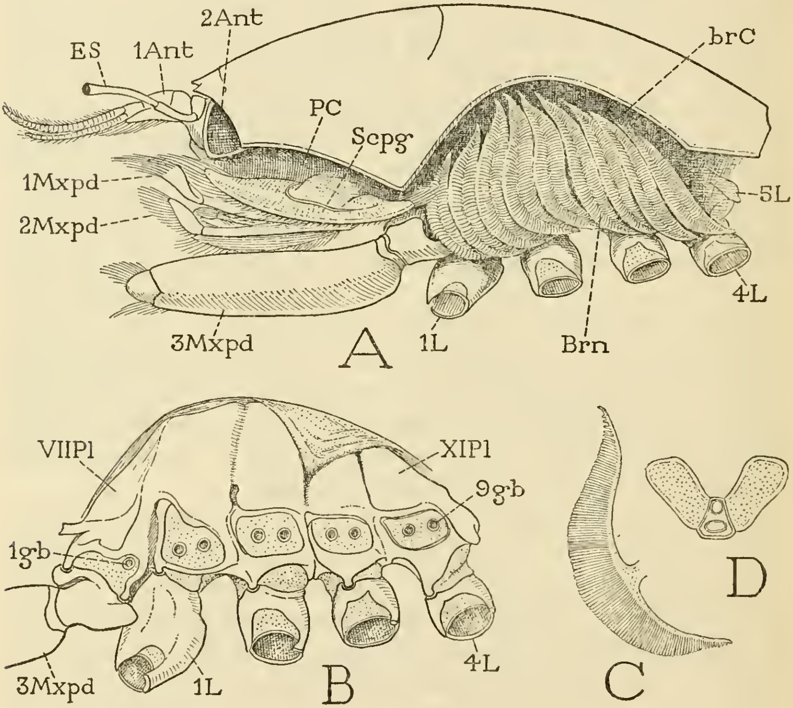

FIG. 8.—*Emerita talpoida* (Say), respiratory organs and thoracic pleuron.

A, lateral view of thorax with pterygostomial plate removed and fold of carapace cut away in the gill region, exposing anteriorly the pump chamber of the respiratory system, with the scaphognathite in place, and posteriorly the nine gills of the branchial chamber. B, left pleuron and leg bases of the gill-bearing segments, gills removed but their positions shown. C, a single gill, posterior. D, section of a gill, with paired lamellae on the axial shaft.

There are nine gills in each gill chamber of *Emerita talpoida* (fig. 8 A, *Brn*). The first gill pertains to the segment of the third maxillipeds (B, *1gb*), the others occur in pairs on the first four leg segments. The gills all arise from large membranous areas above the bases of the appendages. In the leg segments these areas lie within the pleura, since they are closed below by marginal pleural bars bearing the coxal articulations, so that the gills of the leg segments have the position of pleurobranchiae. The membranous area containing the gill base on the maxilliped segment (*1gb*), however, is not separated from the articular membrane of the coxa, which fact gives this gill the status of an arthrobranchia, though in position it falls in line with the other gills, and evidently is serially homologous with them. The coxa of the maxilliped is doubly articulated on the pleuron.

The gills themselves are crescent-shaped (fig. 8 C), and are closely massed in the gill chambers (A, *Brn*) with their upper ends converging to a peak where the pleural wall is highest (B). Each gill consists of two lateral rows of thin, closely set lamellae (D) arising from an axial shaft on the concave inner margin. Below its middle the shaft is connected with the pleuron by a short stalk.

VI. THE ABDOMEN, OR PLEON, AND ITS APPENDAGES

The abdomen of *Emerita* (fig. 1 C) consists of the usual six segments (*1-6*) and the telson (*Tel*) of the decapod abdomen. Dorsally the tergum of the first segment (*1*) appears only as a narrow transverse sclerite wedged between the thoracic carapace and the large tergum of the second abdominal segment, but from its anterior margin there is extended forward a large apodemal plate (D) inflected close beneath the carapace, which gives attachment to numerous muscles. The tergum of the second segment is as wide anteriorly as the carapace, but the next three terga are successively narrower, so that the margins of these four terga complete posteriorly the oval symmetry of the body (A). The sixth tergum (C, *6*) is a larger plate normally having a ventral position (B, *6*) when it is turned forward from the fifth. The sixth segment carries the uropods (*Urpd*) and the telson (*Tel*).

The abdominal appendages of the Crustacea are appropriately called *pleopods,* because the abdomen is known also as the pleon. Some writers limit the term "pleopod" to the appendages of the first five segments, and thus distinguish them from the uropods of the sixth segment, but if the abdomen is the pleon, it is consistent that all its appendages should be pleopods. The pleopods, however, are not necessarily "swimming legs" as the name might seem to imply from its derivation (Gr. *pleo,* sail, or swim), for some of them in the male are usually genital accessories, and in the female egg-carrying organs, the uropods alone being more consistently organs of aquatic locomotion.

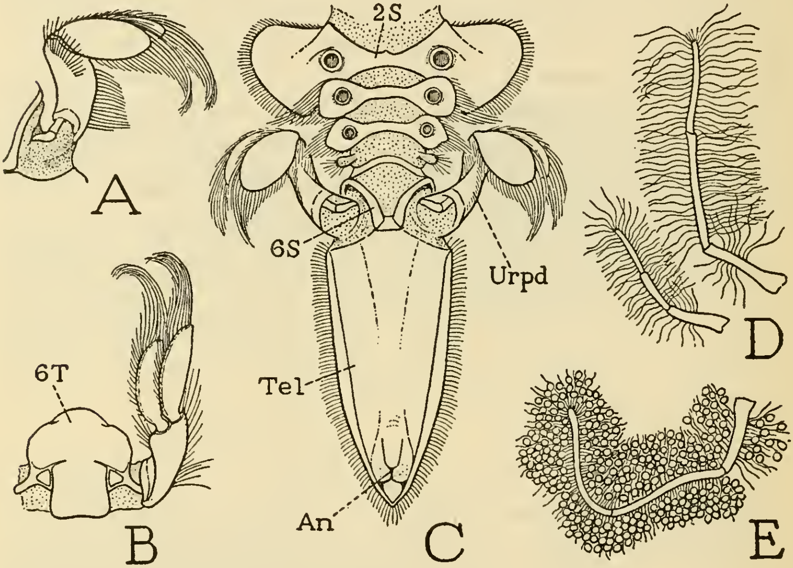

FIG. 9.—*Emerita talpoida* (Say), abdomen and pleopods.

A, left uropod, ventral. B, sixth abdominal tergum and right uropod, dorsal. C, ventral surface of female abdomen and telson, with uropods in place, pleopods of second, third, and fourth segments removed. D, second and third pleopods. E, first pleopod with eggs.

In *Emerita* the adult female has three pairs of slender pleopods pertaining to the second, third, and fourth abdominal segments (the position of their bases is shown at C of figure 9). These pleopods of the female are slender, 3-segmented appendages fringed with long simple hairs (fig. 9 D), and are used as egg-carrying organs (E). The first two pairs are much longer than the third. Corresponding pleopods are absent in the male.

The uropods are present alike in both the female and the male. They are relatively large appendages projecting from the sides of the sixth abdominal segment (fig. 9 C, *Urpd*). Each consists of a long, thick basal segment and of two flat, oval, closely appressed distal lobes with apical brushes of long hairs. The uropods are freely movable appendages, since they have large, membranous basal supports on the body, and are articulated only on pivotlike processes from the sides of the tergum of the sixth segment (B). On the ventral side (A) a rigid leverlike process projects from the base of the uropod into the articular membrane and gives attachment to two small muscles from the sixth tergum, which evidently serve to turn the uropod outward on the tergal pivot. The principal muscles of the uropods, however, arise in the telson. A long outer muscle (fig. 7 L, *mcl*) runs the full length of the telson to be attached on the posterior side of the base of the uropod; a much smaller muscle is attached anteriorly. The long muscles evidently give a strong posterior stroke to the uropods, but when the abdomen is flexed ventrally and the telson turned anteriorly, the direction of the stroke will be forward. *Emerita* is said to swim always backward, and in burrowing the uropods push forward.

VII. COMPARISON OF EMERITA WITH OTHER MEMBERS OF THE HIPPIDAE AND WITH THE ALBUNEIDAE

Inasmuch as *Emerita* appears to stand alone as an antennal feeder, it would be interesting to know the evolutionary steps by which it became structurally adapted to its mode of gathering food, because no halfway stage would seem to be practical. None of its relatives, however, gives any helpful suggestion, since the other hippids have gone their own way in the matter of feeding.

The genus *Hippa* in most respects is very similar to *Emerita*. Its second antennae (fig. 10 B, *2Ant*), however, do not appear to be in any way adapted for food collecting; though the large basal segments are comparable with those of *Emerita*, the flagella are short, and the whole appendages are brushlike by reason of their fringes of long hairs, and are ordinarily folded beneath the bases of the antennules, evidently to protect the respiratory passage between the latter. The third maxillipeds of *Hippa* have broad meropodites similar in shape to those of *Emerita*, but they are relatively smaller and only partly cover the mouth parts. In both *Hippa* and *Mastigocheirus* the mandibles (B, *Md*) are even more reduced than in *Emerita*, but in these two hippid genera substitute jaws have been developed from the mesal lobes of the first maxillae. The first maxilla of *Hippa cubensis* (fig. 10 E) has essentially the same structure as that of *Emerita* (fig. 6 A), but the proximal median lobe is a thick, strongly toothed jaw, those of the two appendages closing together beneath the mouth. Each jaw lobe is articulated on a basal rod of the appendage and has a second articulation on the ventral skeleton by means of an articular arm of its base. From the mesal surface (fig. 10 C) projects a strong process on which is attached the tendon of a large adductor muscle (E, *admcl*). Smith (1877) has described and figured the maxillula of *Hippa* (*Remipes*) *pacificus*, which appears to be the same as that of *H. cubensis*. For some reason, hard to guess, the hippids have all given up their mandibles as feeding organs. *Emerita* has adopted plankton feeding; the food and feeding habits of *Hippa* and *Mastigocheirus* appear to be unknown, but evidently their food is of such a nature that a pair of jawlike organs was found necessary for its proper ingestion.

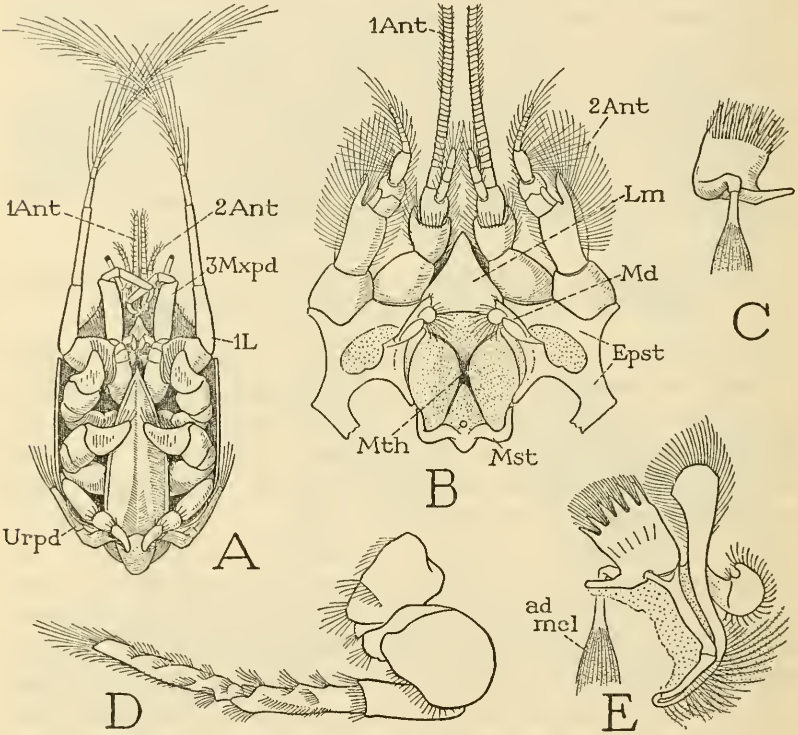

FIG. 10.—*Mastigocheirus* and *Hippa* (Hippidae).

A, *Mastigocheirus gracilis* (Stimpson), ventral surface. B, *Hippa cubensis* Saussure, head and mouth region, ventral. C, same, jaw lobe of first maxilla, mesal. D, same, right first leg, ventral. E, same, left first maxilla, ventral.

The second antennae of *Mastigocheirus* (fig. 10 A, *2Ant*) are relatively smaller than those of *Hippa* (B), but the first legs (A, *1L*) have an extraordinary length, and the long, multiarticulate, brushlike dactylopodites must have some special function when extended into the water over a buried individual; but if the function is food gathering, it is not evident from the structure of these legs that the dactylopodites could be brought back to the mouth. The corresponding legs of *Hippa* (D) are large, but they reach only a little beyond the tips of the antennules.

The antennules of the hippids are not so elaborately fringed as to make a respiratory tube so well enclosed as that of the albuneids (fig. 11 A). In *Emerita* the four antennular rami are of about equal length (fig. 2 A, D), in *Hippa* (fig. 10 B) the ventral rami are short, in *Mastigocheirus* they are minute. The longer rami have fringes of short hairs on their outer margins (fig. 10 B, *1Ant*) and a few very small setae on their mesal margins. The space below and between the antennular bases, however, is completely covered below by the large, flat, brushlike apical segments of the exopodites of the first maxillipeds, which are closely applied against the sides of the labrum, and in turn are shut in below by the infolded second antennae. There is thus formed at the base of the antennules a respiratory chamber which is continuous distally with the interantennular tube, and divides proximally into well-defined passages leading to (or from) the pump chambers.

The members of the family Albuneidae, though clearly related to the Hippidae, differ from the latter in various respects. The antennules have each only a single flagellum, but the two flagella are held securely together by fringes of interdigitating hairs along their dorsal and ventral margins, forming thus an efficient respiratory tube, which in *Albunea* (fig. 11 A) and *Lepidopa* is longer than the body. The second antennae of these two genera are relatively short, but in *Blepharipoda* they are long and the flagella are plumose, resembling those of *Emerita.* A distinctive feature of the albuneids, in contrast to the hippids, however, is the presence of strongly developed mandibles of the typical crab type of structure. The albuneids thus retain their ancestral feeding organs. Benedict (1886) reports that the stomach of a specimen of *Lepidopa* was found to contain setae of annelids, the skin of a very small holothurian, and parts of the flagella of some small crustacean.

The mandibles of *Blepharipoda occidentalis* converge anteriorly and mesally behind the epistome, so that when closed the gnathal lobes come together beneath the mouth. Each mandible (fig. 11 B) has an elongate basal part expanded mesally, where it bears a broad, flat gnathal lobe (*gnL*) and a 3-segmented palpus (*Plp*). The narrowed lateral end is bent posteriorly, and from the point of angulation a strong apodemal arm (*Ap*) projects laterally. The mandible is hinged on the edge of the epistome, but has a specific mesal articulation in front of the palpus, and a lateral articulation (*a*) with the ventral skeleton at its recurved posterior end. The axis of rotation (*a-c*), therefore, is oblique through the body of the jaw, and the apodeme (*Ap*) stands almost at right angles to the axis. The apodeme supports a large plate (*mp*) on which are attached antagonistic masses of muscle fibers, and is thus an effective lever for abduction and adduction of the gnathal lobe.

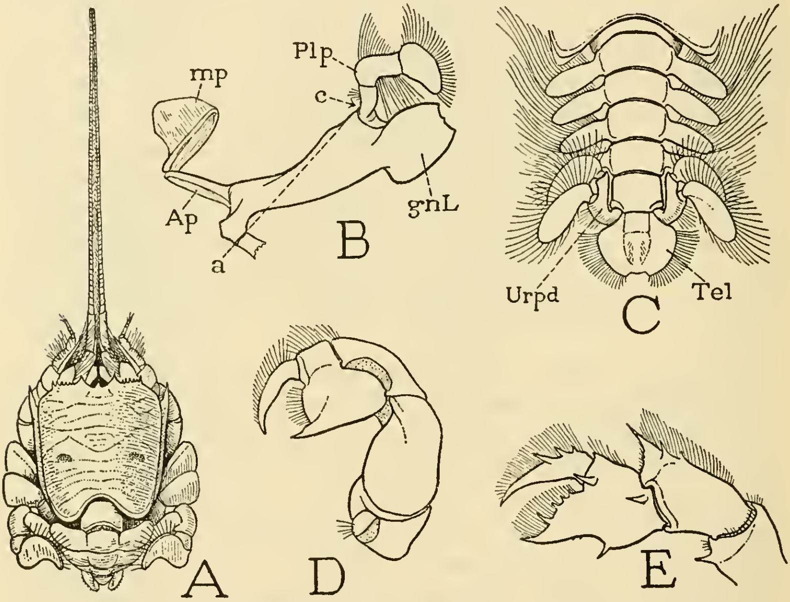

FIG. 11.—*Albunea* and *Blepharipoda* (Albuneidae).

A, *Albunea oxyophthalma* Leach, dorsal. B, *Blepharipoda occidentalis* Randall, right mandible, ventral. C, same, abdomen extended, dorsal. D, *Albunea oxyophthalma,* left first leg, ventral. E, *Blepharipoda occidentalis,* distal segments of left first leg, lateral.

The third maxillipeds of the albuneids have exopodite branches, and the meropodites are not widened. The first legs are strongly chelate (fig. 11 D, E). The pterygostomial plates are continuous posteriorly with the wide, soft branchiostegites, the two together forming on each side of the thorax a broad fold flexibly attached on the edge of the carapace, much the same as in *Galathea* (fig. 1 G). There are no outer folds of the branchiostegites such as are characteristic of the Hippidae. The albuneid telson is a short apical lobe of the abdomen (fig. 11 C, *Tel*), which, when the abdomen is flexed ventrally, covers the bases of only the fourth and fifth legs.

EXPLANATION OF LETTERING ON THE FIGURES

a, pleural articulation of coxopodite (lateral articulation of mandible).
admd, adductor muscle.
An, anus.
1Ant, first antenna, antennule.
2Ant, second antenna, antenna.
b, sternal articulation of coxopodite.
BC, body cavity, haemocoele.
bf, fold of branchiostegite.
BIscpd, basi-ischiopodite.
brC, branchial chamber.
Brn, branchia, gill.
Bspd, basipodite.
Bstg, branchiostegite, gill cover.
c, epistomal articulation of mandible.
Cp, carapace.
Crppd, carpopodite.
Cxpd, coxopodite.
D, dorsum.
Dactpd, dactylopodite.
Dbl, doublure of carapace.
d-e, axis of ventral flexion of antennal flagellum.
e, ocular plate of head.
Epst, epistome.
ES, eyestalk.
gb, gill base.
gnL, gnathal lobe of mandible.
ipB, interpedal brachium.
Iscpd, ischiopodite.
k, postantennal extension of epistome.
L, leg.
Lm, labrum.
m, postocular area of head.
mcl, muscle.
Md, mandible.
Mrpd, meropodite.
Mth, mouth.
1Mx, first maxilla, maxillula.
2Mx, second maxilla, maxilla.
mxB, pleural bridge of maxillary segment.
1Mxpd, first maxilliped.
2Mxpd, second maxilliped.
3Mxpd, third maxilliped.
n, aperture into subbranchial canal.
PC, pump chamber of respiratory system.
Pen, penis.
Pgn, paragnath.
Pl, pleuron.
Plp, palpus.
Propd, propodite.
Ptst, pterygostomial plate.
S, sternum.
Scpg, scaphognathite.
T, tergum.
Tel, telson.
tf, tergal fold.
Urpd, uropod.
V, venter.
W, wing.
x, subbranchial canal.

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