

FIG. 11.—Crustacea—Decapoda: Anomura

A, *Aegla prado* Schmitt, ventral skeleton of anterior body region, with mandibles in place, exposed by removal of ventral folds of carapace. B, *Galathea californiensis* Benedict, ventral surface of protocephalon and skeleton of gnathal region, ventral folds of carapace cut off at z.

Note in each species mandibles articulated at a on mesal ends of narrow maxillary pleural bridges (mxB).

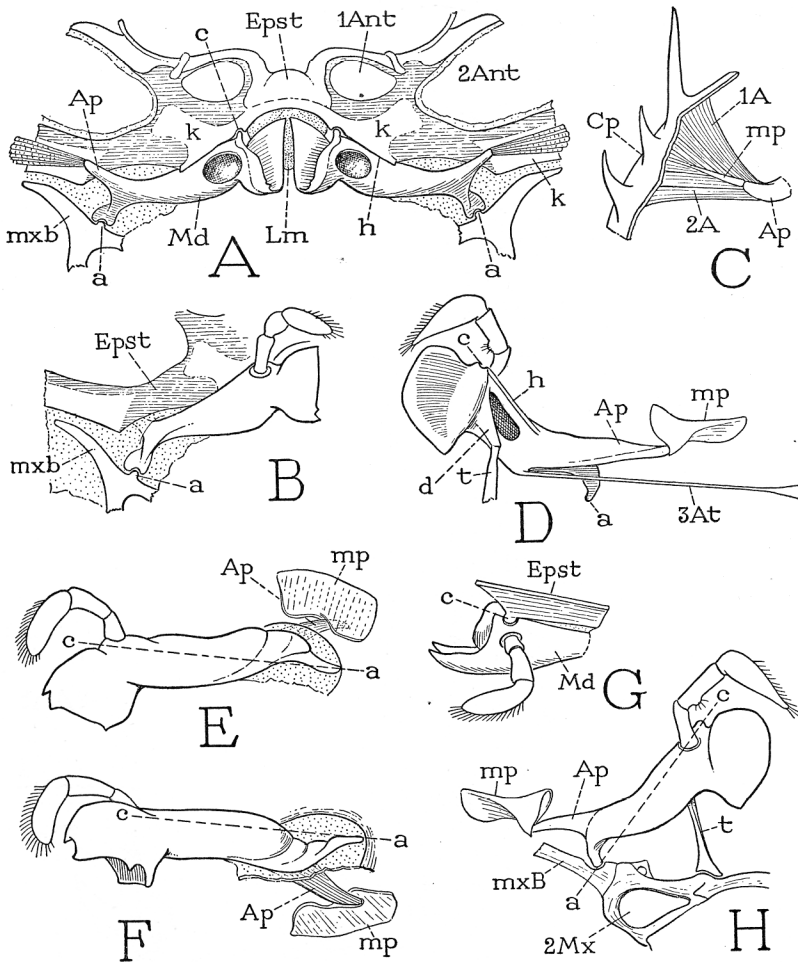


FIG. 12.—Crustacea—Decapoda: Anomura.

A, *Petrolisthes eriomerus* Stimpson, epistomal region and mandibles, dorsal (interior) view, showing mandibles articulated at *a* on remnants of maxillary bridges (*mxb*). B, same, right mandible, ventral. C, *Galathea californiensis* Benedict, muscles of mandibular apodeme arising on carapace. D, same, right mandible, dorsal. E, *Pagurus pollicaris* Say, left mandible in position of adduction, ventral. F, same, same mandible in position of abduction. G, same, distal part of left mandible, showing articulation on epistome. H, *Galathea californiensis* Benedict, right mandible and its skeletal supports, ventral.

of the mouth folds (fig. 16 E, *t*), each of which at its distal end divides into a mesal branch that goes into the paragnath (*Pgn*), and a lateral branch that supports the mandible by means of a small intervening sclerite (E, H, *e*). The connection on the mandible is with a process behind the base of the gnathal lobe (figs. 12 D; 15 C, D, F, G; 16 A, B, G, H, *d*), a feature characteristic of anomuran and brachyuran mandibles; in most cases the metastomal arm makes a direct contact with the mandibular process. Inasmuch as the mandibular attachments on the metastomal arms are not in line with the mandibular axes of rotation, they cannot be regarded as true articulations; the arms merely furnish an extra support for the jaws, and evidently they must be flexible in order to permit the normal movement of the latter.

The most important modification of the mandible in the Anomura and Brachyura is the progressive elongation of the mandibular apodeme in line with the body of the jaw, by which the apodeme becomes an increasingly efficient lever for abduction and adduction of the gnathal lobe.

Among the Anomura, the mandibles of *Petrolisthes* (fig. 12 A, B) and of *Pagurus* (E) resemble those of the palinuran *Polycheles* (fig. 10 D) in that the apodeme (*Ap*) arises from the anterior margin of the mandible a short distance mesad of the lateral articulation (*a*). The apodeme carries loosely attached to its apex a large thin plate (fig. 12 E, *mp*), on the opposite sides of which are inserted the first and second anterior muscles of the mandible (C, 1A, 2A), which arise laterally on the carapace (*Cp*). Antagonistic to these muscles is a large group of ventral fibers attached posteriorly on the apodeme itself, as shown in the brachyuran *Callinectes* (fig. 16 A, C, 2V). The opposing sets of muscles, therefore, alternately pulling in opposite directions on the apodeme, rotate a mandible such as that of *Pagurus* (fig. 12 E, F) on its lengthwise axis (*a-c*), the mandible being articulated mesally on the epistome (G).

By a change in the position of the apodeme relative to the lateral articulation of the mandible, the anomuran mandible may take on the type of structure and mechanism that is particularly developed in the Brachyura. In *Galathea*, for example (fig. 12 D, H), the mandibular apodeme (*Ap*) is produced laterally far beyond the articulation (*a*) so that it appears to be a proximal extension of the body of the mandible itself. The apodeme thus takes a position more nearly perpendicular to the oblique rotation axis of the jaw (H, *a-c*), and hence acquires a mechanical advantage in being almost directly opposed to the gnathal lobe.

Again, among the Anomura, mandibles occur that show a retrogressive type of structure. The weak, fragile mandibles of *Callianassa major*, for example (fig. 13 A), are well developed at their mesal ends, where they are strongly articulated and hinged on the epistome, but proximally they taper out into slender arms that do not quite make contact with the ventral skeleton. The mandibular apodeme is merely a small, angulated rod (B, *Ap*) arising near the end of the slender shaft. In the sand crab, *Emerita talpoida*, the mandibles (D) somewhat resemble those of *Callianassa*, but they are of minute size

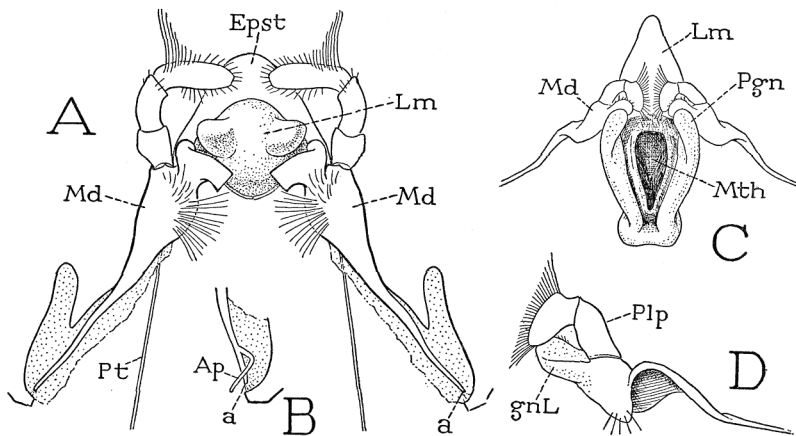


FIG. 13.—Crustacea—Decapoda: Anomura.

A, *Callianassa major* Say, mandibles, labrum and epistome, ventral. B, same, proximal end of mandible, with small apodeme. C, *Emerita talpoida* (Say), mouth region and mandibles, ventral (labrum normally turned forward). D, same, right mandible, dorsal.

and are immovably fixed on the epistome (C). The small, thin gnathal lobes of the opposite jaws are widely separated, and apparently only the palpi can be functional organs. Since the food of *Emerita* consists of particles gathered from the water on the large, feathery antennae, this highly specialized inhabitant of sand beaches evidently has no use for functional jaws.

Among the Brachyura there are forms, such as *Dromidia* (fig. 15 B), in which the mandibular apodeme (*Ap*) projects as a short arm from the anterior margin of the mandible, but it is almost perpendicularly opposed to the axis of rotation. In most of the brachyurans, however, the apodeme is extended beyond the lateral articulation directly in line with the body of the jaw (figs. 15 D-H; 16 A, B, G, H, *Ap*). The lateral point of articulation (*a*) thus comes to lie

behind the base of the apodeme, and the axis of rotation becomes increasingly oblique (fig. 15 F, G, *a-c*) instead of longitudinal. As if to bring the axis as near as possible to a transverse position between the apodemal lever and the gnathal lobe, the articular process becomes elongate and extended mesally (G), and finally it is supplemented by a small articular sclerite, as in *Cancer* (fig. 15 H), *Callinectes* (fig. 16 A), and *Uca* (fig. 16 H). The evolution of the brachyuran jaw,

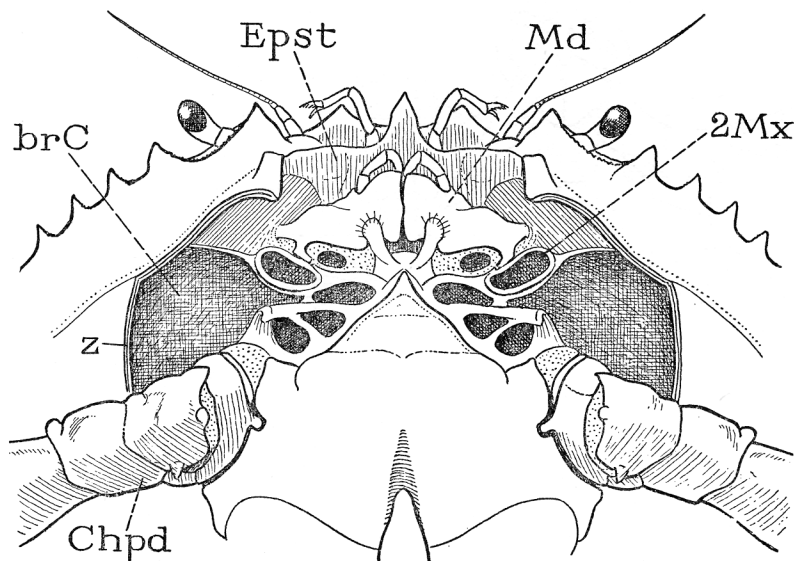


FIG. 14.—Crustacea—Decapoda: Brachyura. *Callinectes sapidus* Rathbun.

Ventral view of anterior part of body with mesal lobes of carapace cut away before bases of chelipeds to expose the ventral skeleton of the maxillary and maxilliped region, after removal of the appendages, showing the mandibles articulated laterally on the anterior rims of the second maxillary foramina (see also fig. 15 D, H).

therefore, is toward a more efficient leverage action of the apodeme on the gnathal lobe. The axis of the jaw, however, can never become completely transverse in position because of the intervention of the first maxilla between the mouth and the articular point of the mandible on the ventral skeleton (figs. 15 H; 16 H, *1Mx*).

The muscles of the brachyuran mandibles have been described by Borradaile (1922) in *Carcinus maenas*, and by Cochran (1935) in *Callinectes sapidus*, but each of these writers overlooked a small group of fibers representing the ventral adductor of *Astacura* (fig. 9 D, E, *1V*). The musculature and mechanism of the crab mandible is well shown in *Callinectes* (fig. 16 A, C) and *Cancer* (B). The great

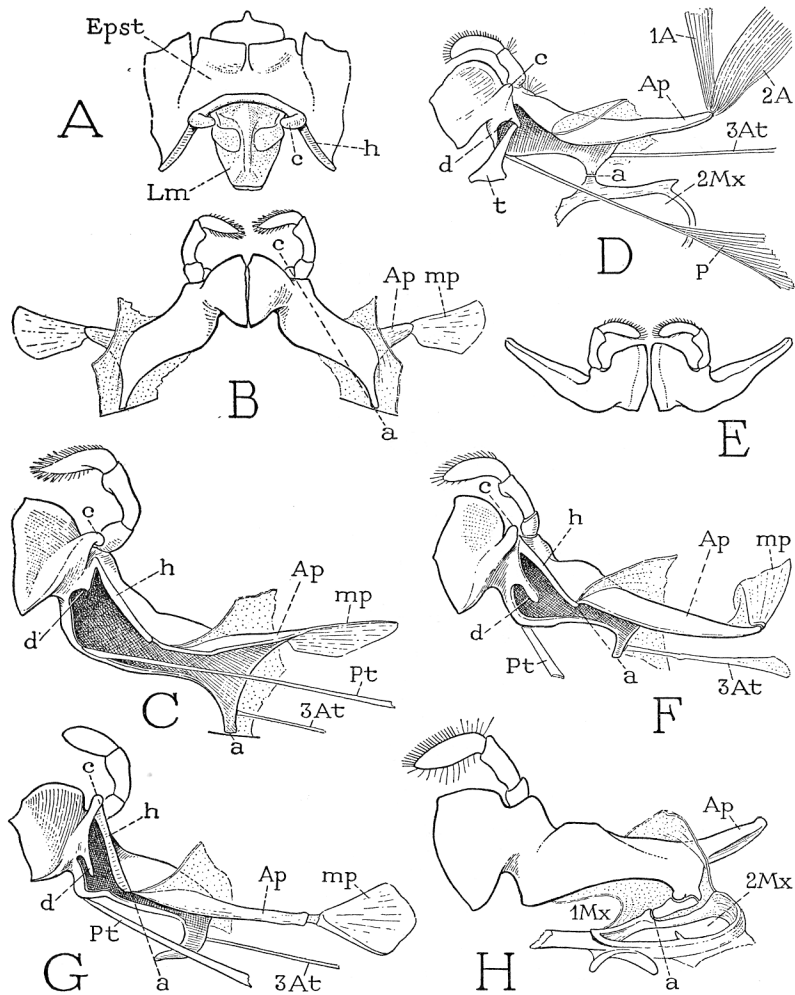


FIG. 15.—Crustacea—Decapoda: Brachyura.

A, *Dromidia antillensis* Stimpson, epistome and labrum, ventral. B, same, mandibles, ventral. C, same, right mandible, mesal. D, *Calappa flaminea* (Herbst), right mandible, mesal. E, *Callinectes sapidus* Rathbun, mandibles, anterior. F, *Ovalipes ocellatus* (Herbst), right mandible, mesal. G, *Ocypoda albicans* Bosc, right mandible, mesal. H, *Cancer borealis* Stimpson, left mandible, ventral.

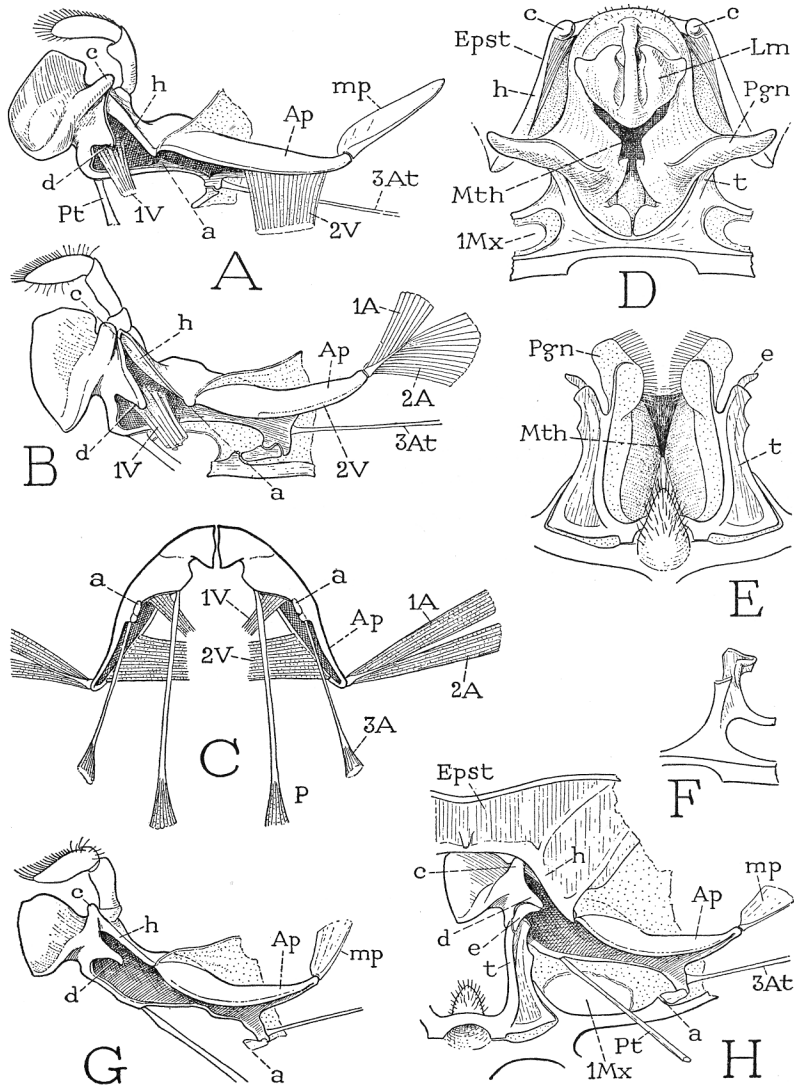


FIG. 16.—Crustacea—Decapoda: Brachyura.

A, *Callinectes sapidus* Rathbun, right mandible, mesal. B, *Cancer borealis* Stimpson, right mandible, mesal. C, diagram of mandibles and their muscles in *Callinectes sapidus* Rathbun, ventral. D, *Libinia emarginata* Leach, mouth region, ventral. E, *Uca pugilator* (Bosc), metastomal prop of left mandible, ventral. F, *Libinia emarginata* Leach, metastomal prop of left mandible, ventral. G, *Uca pugilator* (Bosc), right mandible, mesal. H, same, right mandible and its skeletal connections, dorsal (internal view).

elongation of the mandibular apodeme (*Ap*) in these forms has carried the first and second anterior dorsal muscles (*B*, *C*, *1A*, *2A*) attached on the apodeme far beyond the lateral mandibular articulation (*a*). By the same process, the third muscles of the anterior series (*C*, *3A*) comes to be attached on the mandible (by a long tendon) below the base of the apodeme (*A*, *B*, *3At*). The two apodemal muscles are regarded by Borradaile and by Cochran as a single muscle, as indeed they are functionally, but they clearly represent the two lateral muscles of the apodeme in *Astacura* (fig. 9 *D*, *E*, *1A*, *2A*). The third anterior muscle of the crab (fig. 16 *C*, *3A*) is erroneously grouped by Cochran with the posterior adductor of the jaw. The ventral muscles of the crab mandible arise on the endosternal skeleton, and consist of two groups of fibers. A small mesal group (fig. 16 *A*, *B*, *C*, *1V*), attached within the cavity of the mandible, represents the principal mass of ventral fibers in other forms, but in the crab these fibers form only an unimportant ventral adductor of the jaw. The other, much larger group of ventral fibers (*2V*) is attached mesally on the upper margin of the mandibular apodeme. These fibers, therefore, constitute the principal abductor of the gnathal lobe, and are directly opposed by the lateral muscles (*1A*, *2A*) attached on the apex of the apodeme, which are the principal adductors. In brachyurans such as *Ovalipes* (fig. 15 *F*), *Callinectes* (fig. 16 *A*), and *Cancer* (*B*), in which the axis of the jaw (*a-c*) becomes strongly oblique across the body of the mandible, the decapod type of mandible attains its most efficient mechanism for abduction and adduction of the gnathal lobe.

The crab, in feeding, Borradaile (1922) says, cuts or tears its food into small pieces, which it swallows without chewing. The food is seized by the chelae, and by them placed between the jaws, perhaps assisted by one or more of the legs. If the food is soft, pieces are bitten off by the mandibles; otherwise it is securely held in the grip of the mandibles, while the chelae or the third maxillipeds pull on it until a fragment comes off in the jaws, which is then swallowed without chewing. The "molar" surfaces of the mandibles were not observed to have any grinding action on the food. The mechanics of the crab mandible would indicate that the jaws are merely a pair of very efficient pincers, but, as in the decapods generally, they have little capacity for grasping food directly.

Tanaidacea, Isopoda, Amphipoda.—In these three groups of malacostracan Crustacea we find a new mechanical principle developed in connection with the mandibles, which converts the latter again into a pair of jaws swinging transversely against each other,

but now on a doubly articulated axis instead of on a single dorsal point of suspension. The jaws thus acquire a strong grasping and biting action.

The change in the mandibular mechanism involves three correlated structural modifications. The mandible itself is altered in shape by a shift of the gnathal lobe from a position in line with the length of the jaw, as in the decapods, to one perpendicular to the axis (fig. 17 B, E, G, *Md*). This change in the form of the mandible, to be effective, must be accompanied by a change in the position of the mandible on the head. The mandible still keeps its cranial and epistomal articulations (*a, c*), but, in order to swing transversely, the axis between the two articular points, instead of lying crosswise on the under side of the head, has taken a longitudinal position on the lateral margin of the cranium. Finally, to accommodate the anterior position of the epistomal articulation, it is necessary that the epistome itself should have a frontal position on the head (*A, Epst*). The whole cranial structure in the Tanaidacea, Isopoda, and Amphipoda, therefore, is quite different from that in any other crustaceans, but it is duplicated among the insects with doubly articulated jaws working transversely.

In the Tanaidacea (fig. 17 C) the mandible is hinged on the side of the cranium between the usual articular points (*a, c*), but the line of the hinge is strongly declivous from behind forward, and the gnathal lobe, therefore, is but little deflected from the body of the mandible. Each lobe consists of a long, toothed incisor process, and a large molar process arising at the base of the incisor. Palpi are present in some genera, but are absent in *Tanais*.

In Isopoda and Amphipoda with typical biting and chewing jaws (fig. 17 A, *Md*) the mandibular axis (*B, a-c*) becomes horizontal along the edge of the cranium, and the gnathal lobe (*gnL*) projects downward from the anterior part of the mandible at right angles to the axis. The lobes of the opposing jaws, therefore, open and close directly against each other (*D*) in the space below the mouth between the labrum in front and the paragnaths behind.

The musculature of the amphipod mandible as seen in *Gammarus* (fig. 17 H) has been described by Börner (1909), whose chief interest was in showing that it is carried over into the orthopteroid insects. On the other hand, the mandibular musculature of both the amphipods (*E*) and the isopods (*F*) is directly comparable with that of the Branchiopoda, *Nebalia*, and *Anaspides*. The anterior rotator of the primitive mandible becomes a dorsal abductor (*E, F, G, A*), the posterior rotator a large dorsal adductor (*P*); the ventral muscle (*V*) retains its original adductor function, but the fiber bundles from the

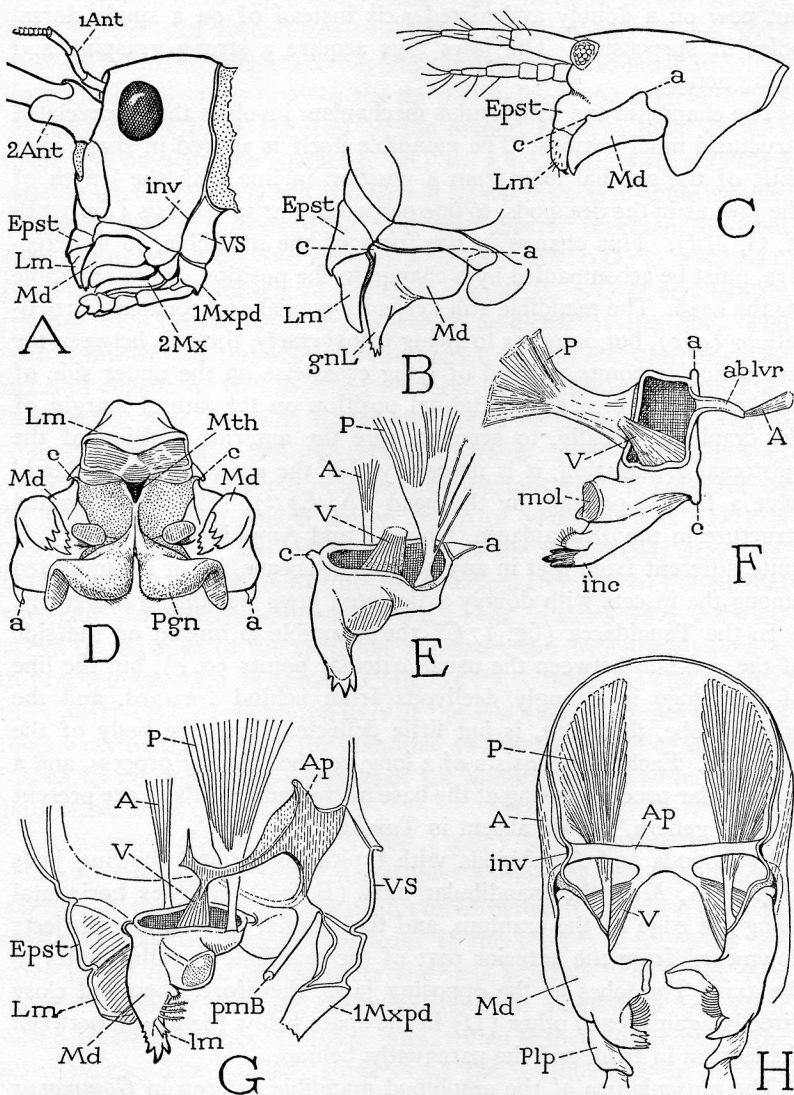


FIG. 17.—Crustacea—Tanaidacea (*Tanais*), Amphipoda (*Orchestoidea*, *Talorchestia*, *Gammarus*), and Isopoda (*Ligyda*).

A, *Orchestoidea californiana* (Brandt), head, lateral. B, *Talorchestia longicornis* (Say), left mandible and adjacent parts of head, lateral. C, *Tanais carolinii* M. Edw., head, lateral. D, *Talorchestia longicornis* (Say), mouth region, ventral, with mandibles in abduction. E, same, right mandible and muscles, mesal. F, *Ligyda exotica* Roux, left mandible and muscles, anterior. G, *Orchestoidea californiana* (Brandt), lower part of inner wall of cranium, with head apodeme of same side, and right mandible in place. H, *Gammarus locusta* (L.), outline of head with mandibles, posterior, showing head apodemes united in a transverse bar (*Ap*).

two jaws are separately attached on head apodemes, and not united by a median ligament. In the isopods the head apodemes arise from the intermaxillary sternal brachia (see Snodgrass, in press), and thus have the same position morphologically as the first sternal apodemes of the decapods, though they take on very different forms.

The head apodemes of the amphipods arise from grooves (fig. 17 A, *inv*) between the lower posterior parts of the cranium and the plate (*VS*) that carries the first maxillipeds. Since this plate can hardly be interpreted otherwise than as the sternum of the first maxilliped segment (or possibly as the base of the maxillipeds themselves), the apodemes appear to be intersegmental inflexions between the second maxillary segment and the first maxilliped segment. Further evidence that the amphipod head apodemes (*G*, *Ap*) are postmaxillary and not intermaxillary is seen in the fact that the postmaxillary arms of the head sternum (*pmB*) are directly continuous with the bases of the apodemes. The apodemes of the amphipod head, therefore, represent the second pair of potential intersegmental apodemes. In the decapod *Cambarus* there are no apodemes between the maxillary and first maxilliped segments, the second developed pair of sternal apodemes being between the first and second maxilliped segments, and the first pleural apodemes between the second and third maxilliped segments.

The postmaxillary apodemes of the amphipod Orchestoidea (fig. 17 G, *Ap*) have broad bases from each of which a slender arm curves forward and downward, and gives attachment to the ventral adductor muscle (*V*) of the corresponding mandible. In *Gammarus* (*H*) the two apodemes are united in a thick bar (*Ap*) that extends through the back of the head, and the mandibular adductors (*V*) are attached on anterior branches of the bar. This structure in *Gammarus* suggests the tentorial bridge of the insect head, and is termed the "tentorium" by Börner (1909), who notes the attachment of the mandibular muscles on it, but does not discuss the nature of the apodeme, except to say that it is invaginated on each side *behind* the maxillary bases. The posterior bridge of the insect tentorium certainly does not arise behind the second maxillae; it represents a pair of intermaxillary apodemes. The amphipods, therefore, furnish another example of the apparent indifference of the ventral mandibular adductors as to what apodemal structures they become attached after severing connections with each other. We have thus far noted their attachment on premandibular apodemes in the stomatopods, on intermaxillary apodemes in the decapods and isopods, and on postmaxil-

lary apodemes in the amphipods; other examples of inconsistency will be seen in the myriapods and insects.

II. CHILOPODA

The mandibles of the chilopods seem to initiate a new line of jaw evolution, since their structure cannot be matched anywhere among the Crustacea, and, on the other hand, it appears to lead into the type of mandible characteristic of the Diplopoda and Symphyla, while some of its lesser features are repeated in the entognathous apterygote hexapods.

The mandibles of a centipede (fig. 18 A) are elongate, widened anteriorly, narrowed posteriorly, and lie horizontally against the under side of the head with their axes convergent toward the mouth lying above the approximated gnathal lobes, which latter are strongly toothed on their opposed margins. In the normal condition the anterior parts of the mandibles are mostly concealed above the edge of the labrum, and are covered below by the broad palps of the first maxillae. The tapering posterior end of the jaws are deeply sunken into pouches of the membranous ventral wall of the head invaginated at the sides of the first maxillae, and extended above the basis of the second maxillae.

Each mandible has an anterior and a posterior point of articulation. The anterior articulation (fig. 18 A, *c*) is by means of a knob or hook on the lateral surface of the jaw, some distance back from the anterior end, which is loosely held in the notch (*F, g*) between the epipharyngeal arm (*f*) and the hypopharyngeal arm of the corresponding premandibular sternal sclerite of the head (*Flt*) that supports the hypopharynx. The posterior articulation (*A, a*) is at the rear extremity of the mandible, where the latter is attached to the end of a slender rod (*mdr*) in the wall of the enclosing pouch, which extends posteriorly and mesally from the cranial margin; in *Lithobius* the rod arises from a small marginal plate of the cranium (*m*). The posterior attachment of the mandible (*a*) on the rod is evidently the primary dorsal articulation of a primitive mandible on the mandibular tergum, which in the chilopods is intermediated by the articular rod as a result of the invagination of the mandible. The anterior articulation, on the other hand, is clearly secondary; it is merely one of contact serving to hold the mandible against the head, and has no relation to the anterior articulation of a doubly articulated crustacean or insect jaw. The different positions of the two articular points relative to the axis of the chilopod mandible brings the hinge line of the

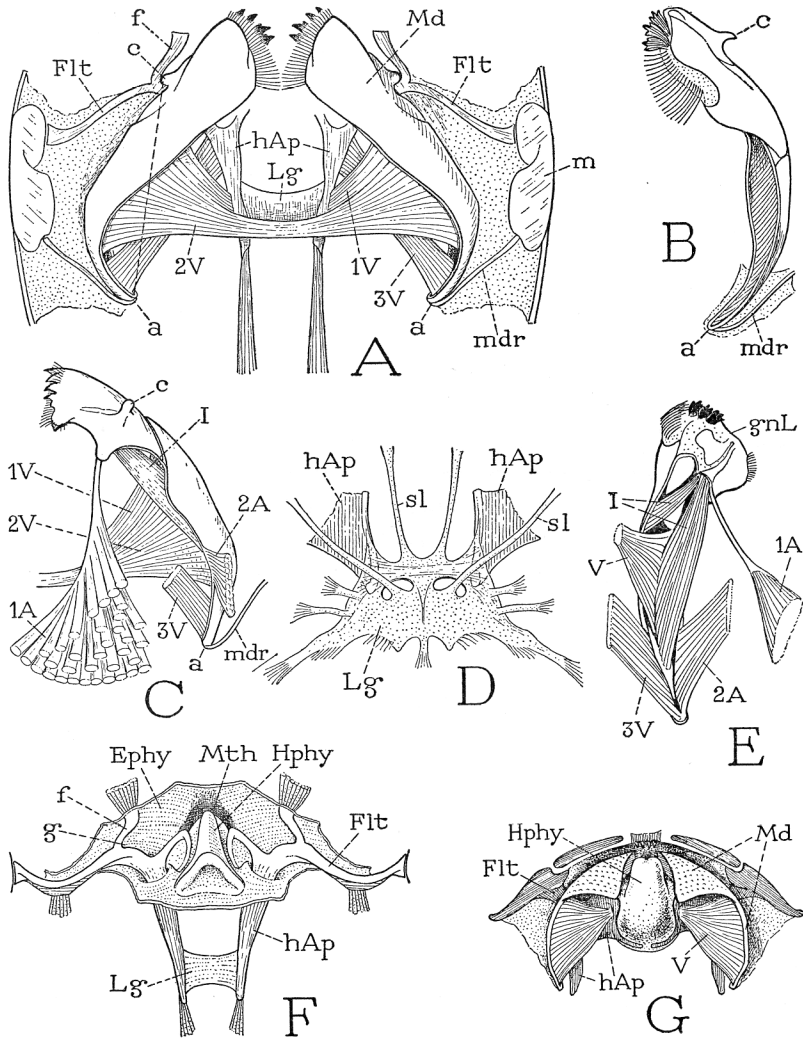


FIG. 18.—Chilopoda.

A, *Lithobius* sp., mandibles and muscles, furler sclerites with cranial connections, and head apodemes, ventral. B, *Scutigera coleoptrata* (L.), right mandible, dorsal. C, *Lithobius* sp., right mandible and muscles, dorsal. D, *Scutigera coleoptrata* (L.), intergnathal ligament supported on ends of head apodemes, dorsal. E, same, right mandible and muscles, mesal. F, *Lithobius* sp., hypopharynx, furler sclerites, and head apodemes, ventral. G, a geophilid, hypopharynx and mandibles, ventral.

jaw (A, *a-c*) almost parallel with the midline of the head. In action, therefore, the mandibles rotate lengthwise, and the toothed edges of the gnathal lobes separate ventrally in abduction and come together in adduction.

In Scutigermorpha, Lithobiomorpha, and Scolopendromorpha the broad anterior part of the mandible bearing the articular process projects forward and mesally as a free gnathal lobe (fig. 18 A, B), armed on its distal margin with strong teeth, and fringed with brushes of hairs. On the dorsal surface of the mandible (C) the sclerotized wall of the lobe is separated from the basal part of the jaw by an oblique line of flexibility proximal to the articular process (*c*). Attached mesally on the base of the lobe are two large muscles (C, E), one (*I*), arising in the base of the mandible, the other (*IA*) by widely spreading fibers on the dorsal wall of the cranium. The gnathal lobe of the jaw in these three chilopod groups, therefore, would appear to have an independent movement of flexion on the base of the organ; the huge cranial muscle (*IA*) otherwise would be merely an abductor or retractor of the mandible as a whole. A live specimen, however, refuses to demonstrate any action whatever of its jaws. The cranial muscle of the gnathal lobe may be supposed to be derived from the anterior dorsal musculature (*A*) of a generalized mandible; the intramandibular muscle (*I*) is comparable to the stipital flexor of the lacinia of an insect maxilla, but it appears to have no antecedent in the mandible. This same musculature of the gnathal lobe, however, is carried over into the Diplopoda and Symphyla, in which the jaw lobe becomes freely movable by a definite articulation on the base of the mandible.

In the Geophilomorpha the mandibles are extremely small and weak, relative to the length of the body, but they have the general shape of the jaws in the other groups. The mandibular base is a slender, curved bar, from the end of which the gnathal lobe expands mesally against the side of the hypopharynx (fig. 18 G, *Md*). In unidentified specimens examined by the writer, however, there is no line of flexibility separating the lobe of the mandible from the base, and no cranial muscle of the lobe could be discovered, such as that so highly developed in the rest of the chilopods, and which is characteristic also of the symphylids and diplopods. On the other hand there is a striking similarity between the geophilid mandible and the mandible of the pauropods (fig. 19 A, *Md*).

The basal musculature of the mandible of *Lithobius* (fig. 18 C) includes a dorsal muscle (*2A*), perhaps a rotator, attached on the posterior end of the mandible, and three groups of ventral fibers (*V*).

The fibers of the first ventral group ($1V$) arise on the head apodeme of the same side (A, hAp), those of the second group ($2V$) appear to be continuous from one jaw to the other, but they are attached on a ligamentous bridge (A, Lg) between the apodemes; these two sets of fibers are adductors of the mandible. The third group of ventral fibers ($3V$) arises on the base of the apodeme, and is attached on the posterior end of the mandible; these fibers constitute a protractor muscle, the cranial muscle of the gnathal lobe ($1A$) being evidently a retractor of the mandible as well as a flexor of the lobe.

In the Scutigermorpha the mandible has the same musculature (fig. 18 E) as in *Lithobius*, but all the adductor fibers of the ventral muscles are attached on a broad sheet of ligamentous tissue (D, Lg) supported from below on the posterior ends of the head apodemes (hAp), and suspended from the dorsal wall of the cranium by suspensory ligaments (sl). The intergnathal ligament of *Thereuonema tuberculata* (Wood) has been described in detail by Fahlander (1938), who shows by its muscle connections that it pertains to the three gnathal segments of the head, and is correspondingly divided into three parts by median foramina. The ligament is a nonchitinous tissue which Fahlander says has a fibrillar structure and contains cell remnants; this and other similar tissues of the chilopods he contends are formed of an "endoskeletal substance" generated from the inner surface of the epidermis. A comparison of the intergnathal ligament of the scutigermorph chilopods (fig. 18 D) with the similar ligament in lower Crustacea (fig. 5 E, F) can scarcely leave any doubt of the identity of the two structures. As in the higher Crustacea, the ligament in the chilopods has become supported from below on ventral head apodemes. In Lithobiomorpha the ligament is reduced to a bridge between the apodemes (fig. 18 A, F, Lg) and some of the ventral fibers of the jaws have become attached on the apodemes themselves; in Scolopendromorpha the bridge is still narrower; in Geophilomorpha it is eliminated, all the ventral muscles of the mandibles (G, V) are attached directly on the head apodemes (hAp).

The head apodemes of the chilopods are cuticular ingrowths from the mesal ends of a pair of premandibular sternal sclerites of the head (fig. 18 A, F, Flt) that extend transversely from the margins of the cranium to the sides of the hypopharynx ($F, Hphy$). They are the "Kommandibulares Gerüst" of German writers, so named because the mandibles loosely articulate on their mesal parts, but since the sclerites appear to support the hypopharynx, the writer (in press) has termed them the *hypopharyngeal fulturae*. It is clear that the head apodemes of the Chilopoda, being premandibular in origin,

can have no homology with the postmandibular head apodemes of Crustacea, though the same muscles come to be attached on them in both groups, showing that the apodemal support of the intergnathal ligament, and finally of the muscles, is secondary. On the other hand, head apodemes clearly homologous with those of chilopods are present in the diplopods, pauropods, and symphylans, and possibly in the insects. Fahlander (1938) calls the interapodemal ligament of the chilopod head the "tentorialkörper," but, being a nonchitinous structure, the ligament can have no homology with the central plate of the insect tentorium, since the latter is entirely a cuticular structure.

III. PAUROPODA

In the general structure of the head, the presence of a single mouthpart appendage, the gnathochilarium, behind the mandibles, and in the anterior position of the genital outlets, the pauropods appear to be closely related to the diplopods. In common with the chilopods and some of the diplopods, the pauropods have premandibular sclerites of the ventral head wall (fig. 19 A, *Flt*) attached laterally on the cranium and mesally on the hypopharynx. These sclerites are described in *Pauropus silvaticus* by Tiegs (1947) as suspensorial sclerites of the head apodemes, or hypopharyngeal apophyses (*hAp*), which arise from their inner ends. The head apodemes of the pauropods, as shown by Silvestri (1902) and by Tiegs (1947), are long slender arms extending posteriorly through the head into the first body segment, each arm giving off a lateral branch attached to the occipital margin of the cranium. The pauropods thus show unquestionably that they belong to the "myriapod" series of arthropods. The pauropod mandibles resemble the chilopod mandibles in that they have a longitudinal position against the under side of the head, and the long tapering bases are invaginated into the head (*A, Md*); the gnathal lobes are direct extensions from the bases of the appendages. As noted by Hansen (1930), therefore, the pauropod mandibles differ strongly from the mandibles of both the Diplopoda and the Symphyla, in which the gnathal lobes are independently movable on the mandibular bases.

The mandibles of *Allopauropus brevisetus*, as shown by Silvestri (1902), are simple elongate organs (fig. 19 B, *Md*), the wide tapering bases of which are sunken into the head, and the free distal parts armed mesally with rows of slender teeth. The mandibles of *Pauropus silvaticus* (*A, Md*), as illustrated by Tiegs (1947), have a striking resemblance to the mandibles of a geophilid centipede (fig. 18 G).

Each mandible of *Pauropus*, Tiegs says, consists "of an unsegmented piece of chitin, whose base is prolonged into an apodeme, a long curved blade of chitin, which extends far back into the cavity of the head." The mandibular "apodeme" is said to be attached medially by a fibrous ligament to the head apodeme, and laterally by a similar ligament (not shown in the figure) "to the wall of the head just to the rear of the pseudoculus." As already noted, the cranial rod supporting the mandible is characteristic of the invaginated jaws of the chilopods; it will be met with again in the Collembola and Protura. In these forms the "ligament" is a sclerotic rod in the membranous wall of the containing pouch, and it seems probable that the mandible

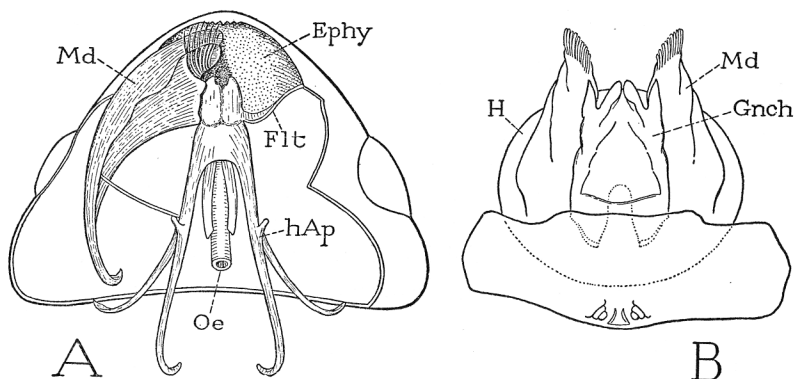


FIG. 19.—Pauropoda.

A, *Pauropus silvaticus* Tiegs, outline of head, ventral, showing right mandible and head apodemes (adapted from Tiegs, 1947). B, *Allopauropus brevisetus* Silvestri, head and first body segment, ventral (from Silvestri, 1902).

of *Pauropus* is likewise simply invaginated and connected in the same way with the cranium. However, it is most surprising to find that the pauropod mandible is so entirely different from the diplopod mandible, and so nearly duplicates the mandible of a geophilid centipede. What significance, if any, this fact may have as to the taxonomic position of the Pauropoda the writer leaves to the phylogenists.

The mandibular musculature of *Pauropus* as described by Tiegs consists of four groups of fibers, two of which are dorsal in origin, and two ventral. The two dorsal muscles arising on the roof of the head are attached anteriorly and posteriorly on the base of the mandible. A group of obliquely transverse adductor fibers arises on the corresponding head apodeme. The fourth muscle, a ventral protractor, has its origin on the suspensory plate (fultura) of the apodeme, and is inserted on the posterior end of the mandible. It is noteworthy