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COMPARATIVE STUDIES ON THE JAWS  
OF MANDIBULATE ARTHROPODS

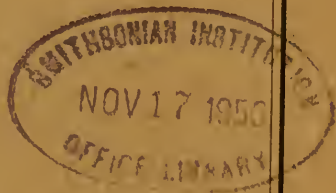
BY

R. E. SNODGRASS

Collaborator, Bureau of Entomology and Plant Quarantine  
U. S. Department of Agriculture



(PUBLICATION 4018)



CITY OF WASHINGTON  
PUBLISHED BY THE SMITHSONIAN INSTITUTION  
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## INTRODUCTION

The organs of feeding associated with the mouth that may be called the *jaws* of an arthropod are usually mandibles, but not always, since in some species one pair or both pairs of the maxillae may take over the biting if not the chewing function. The mandibles, moreover,

are sometimes highly developed for purposes other than feeding, or, on the other hand, they may be so reduced as to have little use of any kind, and finally they may be suppressed entirely. However, the principal subject of the following discussion will be the mandibles.

It may be taken for granted that the arthropod mandibles have been evolved from a pair of legs, since all the postoral appendages of the trilobites were fully developed as ambulatory limbs. There is some difference of opinion, however, as to what part or parts of a generalized limb the mandible represents, though a reasonable answer should be obtained by comparing a mandible of primitive type with an ordinary ambulatory appendage of modern arthropods.

A typical arthropod leg (fig. 1 A) consists of a basal segment known as the *coxa*, or *coxopodite* (*Cx*), and of a segmented distal shaft called the *telopodite* (*Tlpd*). The usual movement of a locomotor appendage on the body, whether for walking or swimming, is anterior and posterior. Generally the coxa is specifically articulated dorsally and ventrally on the body, or if not articulated, it is so attached that the axis of rotation is essentially dorsoventral, though actually it may be oblique at various angles. The dorsal articulation (*a*), when present, is on the tergum of the body segment, or on a laterodorsal plate termed the pleuron (*Pl*); the primary ventral articulation (*b*) is on the sternum. Departures from this type of structure are clearly secondary and need not be considered here.

The body musculature of an appendage is appropriate to the movements of the appendage on the body. If the limb turns anteriorly and posteriorly, or approximately so, it is provided with *promotor* and *remotor* muscles. The legs of most arthropods have both dorsal and ventral muscles, though some have only dorsal muscles, and others only ventral muscles. The dorsal muscles arise on the tergum of the body segment; the ventral muscles usually have their origins on an endosternal support of some kind, but since such structures are secondary formations it is reasonable to suppose that the ventral limb muscles were first attached on the sternal surface of the segment. The number of individual muscles for each appendage is variable, but when dorsal and ventral muscles are both present, the functional groups of fibers are four. In their action on the limb as a whole they were probably in the first place *dorsal* and *ventral promotors* (fig. 1 A, *dpm*, *vpm*), and *dorsal* and *ventral remotors* (*drm*, *vrn*); in their action specifically on the coxa, they are *anterior* and *posterior rotators*. With changes in the coxal articulation, or in the points of origin of the muscles relative to the coxa, however, the same muscles may take on quite different functions.

An arthropod mandible that most closely resembles the coxa of a leg both in structure and musculature may be regarded as a generalized mandible. Such a mandible occurs in many of the entomostracan and in some of the malacostracan Crustacea, and in the Machilidae among the insects. A mandible of this type (fig. 1 B, *Md*) is suspended approximately vertically from a single dorsal point of articulation (*a*) on the tergum of its segment or on the head; its lower end is produced into a strong, usually toothed endite, or *gnathal lobe* (*gnL*); the telopodite may be represented by a palpus (*Plp*), or it may be suppressed. Inasmuch as a mandible of this kind, in order to be a functional jaw, must be able to swing toward its fellow, the pendent mandible has no ventral point of articulation. Furthermore, since the mouth (*Mth*) for practical purposes lies between the jaws, the mandibular sternum itself has been obliterated or reduced and displaced posteriorly.

The musculature of a pair of primitive mandibles includes individual anterior and posterior dorsal muscles for each jaw (fig. 1 B), but in Crustacea with this type of mandible all the ventral fibers from each jaw are attached medially on a transverse sheet or cylinder of fibrous tissue suspended between the mandibles and forming a common ligament uniting the fibers from the opposite jaws. Since the mandibular musculature becomes thus reduced to *three* functional groups of fibers, it will be convenient to designate the groups simply *A*, *P*, and *V*. The *A* and *P* muscles very clearly are the dorsal promotor and dorsal remotor of the leg (*A*), but in their action on a pendent mandible they become an *anterior rotator* (*B, A*) and a *posterior rotator* (*P*). The single large mass of ventral fibers of the mandible (*V*), representing the combined ventral muscles of the leg coxa (*A*), constitute a particularly effective *ventral adductor*. The mandibles being suspended on single dorsal points of articulation (*a*), the adductor muscles, pulling against each other on the median ligament, bring the gnathal lobes of the jaws strongly together beneath the mouth. In mandibles of this type there is no apparent muscular mechanism of abduction, the opening of the jaws evidently depends on the elasticity of their basal connections.

With the further evolution of the mandibles the fibers of the three primary muscles may become dissociated into distinct secondary muscles, with diversified functions correlated with changes in the mandibular mechanism. Functional names for the muscles, therefore, cannot be consistently carried over from one type of mandible to another. In a species of Collembola as many as 17 distinct muscles



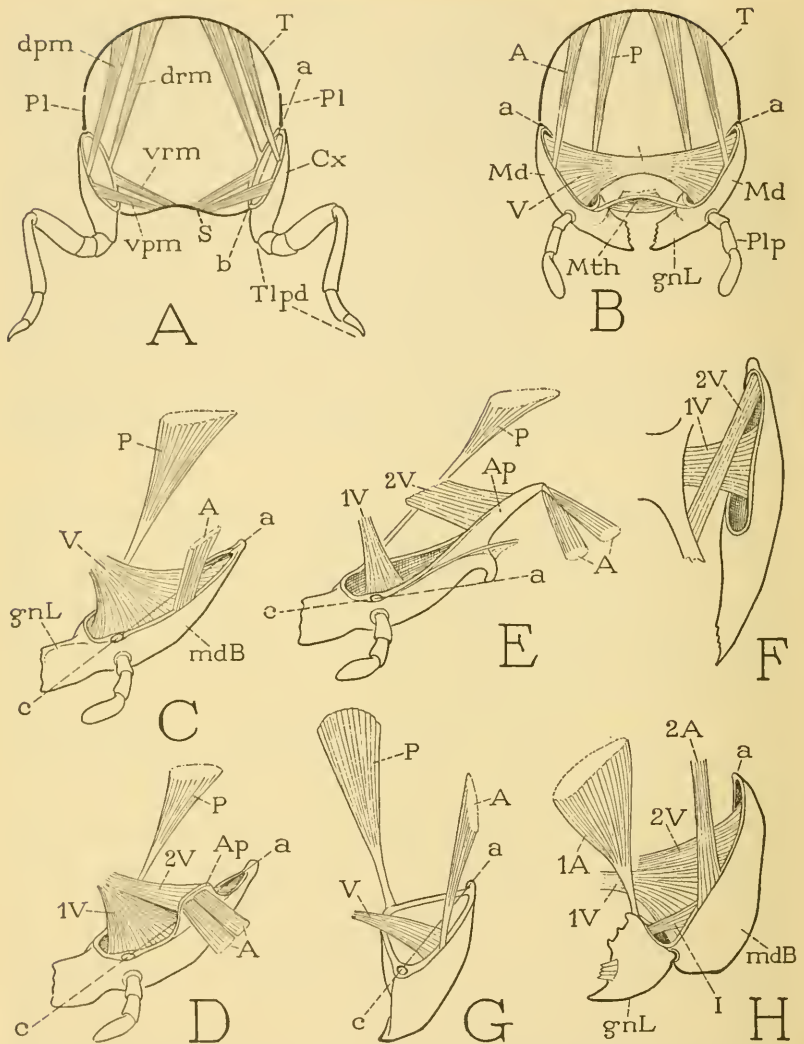


FIG. 1.—Diagrams of the various types of arthropod mandibles, and their apparent derivation from the coxae of a pair of leglike appendages.

A, section of a body segment bearing a pair of legs with generalized dorsal and ventral musculature. B, a pair of mandibles of generalized structure, pendent from single dorsal articulations, adducted by the united ventral muscles. C, a generalized decapod mandible, with gnathal lobe in line with the length of the jaw, doubly articulated, and rotating on a horizontal axis. D, the astacuran mandible, same as the last but with a lateral apodemal lobe (*Ap*). E, the anomuran-brachyuran type of mandible, the apodeme extended in line with the body of the jaw. F, a protractile mandible. G, a doubly articulated mandible with horizontal axis of rotation and gnathal lobe perpendicular to axis (Isopoda, Amphipoda, Lepismatidae, most Pterygota). H, the diplopod-symphylan type of mandible, gnathal lobe freely movable on the mandibular base, and independently muscled.



with varied functions have been described attached on a single mandible, yet they can all be referred to the three original fiber groups.

It is, of course, not literally correct to say that a muscle changes its function, since the only physical activity of muscle tissue is that of contraction. What the muscle accomplishes usually depends on the mechanism of its skeletal connections; so, speaking of the mandibles, the idea would be better expressed if we might say that the arthropods have shown a great versatility in adapting their mandibles by mechanical alterations to different kinds of movement operated by the same muscles. Yet also, shifts in the muscle attachments may bring about radical changes in the action of the muscles on the mandibles.

The intermandibular ligament on which the adductor muscles of the jaws are attached is not a structure limited to Crustacea. In the Diplopoda a large group of the adductor fibers from each mandible merges into a common, transverse, cylindrical ligament (fig. 20 F), and in the thysanuran insect *Machilis*, groups of fibers from opposite jaws are similarly connected by a ligament through the base of the hypopharynx (fig. 22 A, *IV*). The intermandibular ligament of Crustacea is usually connected with a similar though smaller ligament between the first maxillae and another between the second maxillae, or the three ligaments may be united in a single sheet of tissue. A composite structure of this kind is strongly developed in the gnathal region of *Anaspides* (fig. 5 F), and is supported from the dorsum by three pairs of suspensory branches (*sl*). An even more complex structure of the intergnathal ligament is shown by Manton (1934, fig. 17) to be present in *Nebalia* (E) and several other crustaceans. On the other hand, in the copepod *Calanus* the large bundles of ventral fibers of the mandibles (fig. 4 F, *V*) and also the maxillary muscles are attached on an extremely slender median ligament running lengthwise over the nerve cord, and dividing anteriorly into a pair of finely branched suspensory ligaments.

The term "ligament," or "tendon," seems hardly appropriate for the intergnathal muscle-supporting structure when the latter takes the form of a broad, elaborately developed, composite plate, which very much resembles the so-called "endosternum" of *Limulus* and the arachnids, from which the ventral muscles of the prosomatic appendages arise. Both structures are composed of a nonchitinous cellular and fibrillated tissue, and the fibrillae appear to be directly continued into those of the striated muscle fibers (figs. 2 H, 5 A, 6 H). The suspensory branches in Crustacea (figs. 2 E, H; 8 D, E, *sl*) are attached either directly on the dorsal body wall, or by groups of short muscle fibers, as are those of *Limulus*.

It has been shown by Manton (1928, 1934) that in the development of *Hemimysis* and *Nebalia* a transverse ligament is formed from the ectoderm of each ventral intersegmental fold throughout the length of the trunk. On each fold there first appears a median ingrowth between the nerve cords, and at each side a lateral ingrowth. The lateral rudiments then extend mesally and unite with the median rudiment, thus forming an arch or bar over the nerve cords. The lateral connections with the ectoderm are later severed, and the bar sinks backward into the segment behind. The antenno-mandibular bar comes into contact with the mandibular mesoderm, which grows along it from each side and becomes differentiated into the fibers of the adductor muscles, while the bar itself transforms into the supporting tendon. In the same manner are formed the maxillulary and maxillary tendons, and, according to Manton, from the last is developed in *Nebalia* the tendon of the adductor muscle of the shell. The mandibular, maxillulary, and maxillary tendons finally become interconnected, resulting in the formation of the complex intergnathal ligament of the adult (fig. 5 E).

Embryonic phenomena can seldom be translated literally into evolutionary history. According to the above account by Manton, the embryonic adductor muscles of the gnathal appendages wait for the formation of the ligament before they become functional; in evolutionary development the muscles must have been functional from the beginning. We may suppose, therefore, that the ventral muscles of the appendages were first attached on the ventral body wall laterad of the nerve cords, and that the ectoderm then formed a bridge over the nerve cords in the manner described, carrying the muscles with it. In the Arachnida, according to Purcell (1909), the segmental groups of embryonic muscle cells are at first attached on the ventral intersegmental folds, but the areas of contact soon become marked by the appearance of the intermuscular tendons that will form the endosterna ("entochondrites"). The tendons, however, are said by Purcell to be a product of the fusion and metamorphosis of the muscle cells themselves where the latter come into contact with one another and with the epidermis. Purcell thus agrees with Schimkewitsch (1895), who traces the development of the endosternum in spiders from transformed muscle tissue.

Finally, it may be noted that in the Scutigermorpha among the chilopods the adductor muscles of the mandibles and both pairs of maxillae arise from a plate of tissue (fig. 18 D) much like that of the intergnathal ligament of Crustacea and the endosternum of *Limulus* and Arachnida, which Fahlander (1938) claims to be a non-

chitinous endoskeletal substance derived from the inner surface of the epidermis. Furthermore, in each body segment of the Scutigero-morpha the ventral muscles are attached on a cross bar in the posterior part of the segment, which structures are suggestive of the segmental endosternal plates in the opisthosoma of *Limulus*.

All these "ligamentous" or "endosternal," nonchitinous muscle-bearing tissues of the arthropods appear to be related or analogous formations, but their origins and finer structure should be more exactly studied, and their chemical composition determined by modern technique. For the present we can simply accept them as anatomical facts.

In the higher Crustacea the intergnathal ligaments become supported on ventral cuticular apodemes, and are reduced to thin, fascia-like membranes, or they practically disappear, while the muscles are taken over directly by the apodemes. The same transfer of the ventral muscles to apodemes is seen in the chilopods; in *Scutigera* the ligamentous muscle-bearing plate of the head is supported on a pair of apodemes, in other groups the ligament is reduced or absent and the muscles in part or entirety go over to the apodemes. In the diplopods and the insect *Machilis* the ligament persists between one group of mandibular adductor fibers, but the other fibers take their origins directly from head apodemes, and in the rest of the insects all the ventral muscles of the gnathal appendages are attached on the apodemal tentorium of the head. That the transfer of the muscles to cuticular apodemes is secondary is shown by the fact that in the different arthropod groups the apodemes may have quite different origins, and are certainly not homologous structures. It is only among the holometabolous insects that the original ventral muscles of the mandibles are themselves suppressed.

The body of a generalized mandible (corpus mandibulae) is broadly attached by its mesal surface to the membranous lateral wall of the mandibular segment or the head, and the gnathal lobe projects freely from its distal end (fig. 1 B). Inasmuch as the basal muscles of the mandible evidently correspond with the coxal muscles of a leg (A), it is most reasonable to assume that the body of the mandible represents the basal segment of an ordinary limb, which is that commonly called the *coxa*, or *coxopodite*, and that the gnathal lobe is a *coxal endite*. That the basipodite of the mandibular appendage is the first segment of the palpus is shown in crustaceans having a biramous palpus, in which the two rami are carried by the basal segment of the palpus (figs. 2 D, 4 F). Some writers contend, however, that the primitive arthropod limb had a "precoxal," or "subcoxal," segment

proximal to the coxa, and from this idea the mandible has been interpreted as being either the "precoxa," or the "precoxa and coxa combined." The evidence of a subcoxal limb segment is based principally on the occasional presence of small sclerites at the root of the limb, or on ringlike thickenings at the base of the coxa. Störmer (1944), for example, interprets a short ring supporting the coxa in the leg of a trilobite as a "precoxa," but it is difficult to believe that such a structure observed in a fossil can be regarded with any assurance as a limb segment. There is no specific evidence in any case that a so-called "precoxa" or "subcoxa" was ever an individually muscled and independently movable part of the appendage.

Discussions concerning the nature of the arthropod jaw have centered largely around the mandible of the copepod *Calanus*. It happens that the mandibular palpus of *Calanus* is distinctly biramous (fig. 4 F), so that the segment supporting the two rami can be identified as the basipodite (*Bspd*). The jaw part of the appendage is transverse and ends with a broad, toothed gnathal lobe (*gnL*). The basipodite is attached to the jaw segment by a small ring (*bspd*). Some writers, therefore, as Borradaile (1917) and Hansen (1925), have regarded the intercalated ring as the coxa, and interpret the basal segment as a "precoxa." If this interpretation is true for *Calanus* it would have to be carried over to all the other arthropods. An examination of the mandible of *Calanus*, however, gives no support to the idea that the ring supporting the basipodite is a true segment; no muscles arise within it, one small muscle is attached by a tendon on its base, and the other muscles traverse the ring to be attached on the basipodite. More definite evidence as to the nature of the ring may be deduced from the study of Campbell (1934) on the development of the mandible in *Calanus tonsus* Brady; from her figures it appears that the basipodite ring is not present in the appendage until the first copepodid stage. From this fact, therefore, Heegaard (1947, p. 197) convincingly argues that the alleged "coxa" of the *Calanus* mandible "is merely a later sclerite ring separated from the basis, so as to give the mandibular palp a greater mobility," and cannot be regarded as a primary segment. In the following descriptions it will be assumed that the arthropod mandible is in all cases the *coxa* of the mandibular appendage, since on it are attached the muscles that clearly correspond with the coxal muscles of a leg.

The gnathal lobe of the mandible, often called the "gnathobase," being the functional part of the jaw, takes on various forms according to the nature of the food or the manner of feeding of the animal. Very commonly the lobe is differentiated into a toothed incisor process,



and a proximal molar process or masticatory surface (figs. 5 B, C, D; 8 B, I; 17 F; 22 B). Crampton (1921) has followed the relative development of these processes in the various mandibulate groups of arthropods, but he has probably attributed too much phylogenetic significance to them, since the structure of the gnathal lobe may be quite different in related forms with different feeding habits. On the incisor process of the mandible there may be present a small group of loose teeth, or a small, flexibly attached dentate plate. This structure occurs among the peracaridan Crustacea, in the Symphyla, the Diplopoda, and in some insects; it is known as the "lacinia mobilis" (figs. 6 C; 17 G; 20 G, *lm*). The name might be appropriate if the term "lacinia" is taken in its literal meaning of a "fringe," but the structure cannot be supposed to have any relation to the *lacinia* of an insect maxilla, as Crampton (1921) has sufficiently emphasized, the maxillary lacinia being itself a muscled endite equivalent to the entire gnathal lobe of the mandible.

The most leglike mandibular appendage to be found among the mandibulate arthropods occurs in the ostracod family Cypridinidae. The mandible of *Philomedes*, for example (fig. 2 F, G), has the form of a simple, biramous limb consisting of a basal coxopodite (*Cx*) and a 3-segmented telopodite, the exopodite being represented by a small external lobe (*F*, *Expd*) of the basipodite. A gnathal lobe is usually absent, but in some species of the family, as in the male of *Philomedes globosus* (*G*), the coxa bears distally on its mesal surface a small, weak, bidentate process (*gnL*) that evidently represents the gnathal lobe of other forms, though certainly it can have little function as a feeding organ. Though the leglike mandible of *Philomedes* is not to be regarded as a primitive mandibular appendage, but rather as a simplified jaw, which, armed with strong apical spines, has been transformed into a grasping organ for securing food particles, it does, however, give a clear suggestion of how a simple limb might be converted into a jaw by the development of a gnathal endite on the coxa, and the reduction of the telopodite. The functional jaws of the cypridinids are the first maxillae, which in most forms are armed with strong spines for tearing the food.

That the mandibles are appendages of the same segment in all the mandibulate arthropods is generally unquestioned. Silvestri (1933) alone has contended that the jaws of the chilopods, diplopods, and insects represent the first maxillae of Crustacea, and that the crustacean mandibles are the appendages of a segment that corresponds with the so-called intercalary, or premandibular, segment in the embryo of the other forms, in which this segment lacks appendages in

the adult stage. The segment in question, however, is commonly regarded as representing the second antennal segment of Crustacea, the antennae of the chilopods, diplopods, and insects being identified with the antennules of the Crustacea. The essential likeness in the structure and musculature of the mandibles in all the mandibulate arthropods, and their innervation from corresponding ganglia make it difficult to believe that the arthropod mandible is not a common inheritance from a common ancestor; differences in the mandibles are easily seen to be structural modifications correlated with changes in the jaw mechanism.

The principal structural changes of the mandibles and the functional changes of the muscles that take place in the higher arthropods result from the acquisition by the mandible of a second articulation with the head on the anterior margin of its base (fig. 1 C, *c*) at the end opposite from that bearing the primary dorsal articulation (*a*). This secondary articulation is ventral, dorsal, mesal, or anterior in relation to the primary articulation, according to the position assumed by the mandible, and it is not always with the same part of the head, but it gives the jaw a fixed axis of rotation (*a-c*) between the two articular points. The distal articulation does not represent the primary sternal articulation of the appendage; it is never on a true sternal part of the head, and it lies anterior to the ventral muscles. The newly established axis (*a-c*) thus runs close along the anterior, or outer, side of the mandible, but just within the attachment of the anterior dorsal muscle (*A*). The doubly articulated mandible, therefore, is closely hinged to the head by its anterior margin, and its movements resemble those of a door on its hinges; but the mandible differs from a door in that the motor power is applied on both sides of the axis. According to Schmidt (1915), Berkeley (1928), and Cochran (1935), the doubly articulated mandible can no longer "rotate." Actually, however, it is to be seen that its movements *are* the rotary motions of a pendent jaw with one articulation, but on a doubly articulated axis; the rotary movements are now called *abduction* and *adduction*.

With the altered mechanism of the mandible resulting from the articular innovation, the anterior dorsal muscle (fig. 1 C, *A*), if it retains its origin dorsal to the mandible, becomes an abductor, and the directly opposed posterior dorsal muscle (*P*) becomes an adductor. The ventral muscles (*V*) are still adductors as in a singly articulated mandible. Schmidt (1915) and Berkeley (1928) contend that it is impossible to determine the homologies of the muscles of a doubly articulated mandible with those of an ambulatory limb, but Cochran



(1935) has shown that the relation is very simple, and her explanation is that given here.

If the gnathal lobe of the doubly articulated mandible retains its primitive position in line with the axis of the mandibular base (fig. 1 C, *gnL*), as it does in most of the malacostracan Crustacea and in the Chilopoda, the opposing lobes cannot now swing toward each other, they simply work in the manner of a pair of valves opening and closing from below with the rotation of the mandibles. Mandibles having this kind of mechanism are not efficient biting and chewing organs, and must depend on having the food passed to them by some of the following appendages, which are particularly modified to serve as accessory feeding organs.

An improvement in the mechanism of the jaws for increasing the adductor power of the gnathal lobes, however, has been evolved in the decapod Crustacea. By the development of an apodemal lobe on the marginal part of the mandible (fig. 1 D, *Ap*) that carries the anterior muscle, which here consists usually of two or three bundles of fibers (*A*), the insertion of the muscles is brought above the hinge line (*a-c*), and is accompanied by a lowering of the points of origin of the muscles on the carapace, so that these primarily abductor fibers (*C, A*) now become adductors (*D*). Opposed to them is a differentiated group of the ventral fibers (*D, zV*) attached on the inner face of the apodeme above the hinge line; these fibers thus lose their original adductor action and become a ventral abductor muscle. This structure and mechanism of the mandible is characteristic of the natantian and astacuran decapods. The Anomura and Brachyura have still further improved on it by carrying the apodeme out proximally as an arm projecting in line with the body of the jaw beyond the lateral articulation (*E, Ap*). The apodeme, with its opposing muscles, by this alteration becomes an efficient lever for operating the gnathal lobe. This type of mechanism reaches its highest development in the crabs. A mandible rotating on its long axis, however, is still not the most effective kind of jaw, since it has little power of grasping and in general serves only as a masticatory organ for food passed on to it by the following appendages.

The mandibles of the chilopods and the entognathous apterygote insects resemble those of the decapods in that they lie horizontally against the under surface of the head, and the gnathal lobes project in line with the mandibular axes. In these terrestrial groups the mandibles may also be doubly articulated for rotary movement, but the articulations are not fixed points of attachment, and the jaws are more or less protractile. The protractor muscle is generally a differ-

entiated group of the ventral fibers (fig. 1 F,  $\alpha V$ ) attached on an apodemal support.

By a simple modification of form the doubly articulated mandible has acquired its greatest efficiency as a biting and chewing jaw. The change involves merely a shift of the gnathal lobe from a position in line with the mandibular axis (fig. 1 C) to one approximately perpendicular to the axis (G). The mandible thus again swings transversely, but now on a firmly hinged axis ( $a-c$ ) instead of on a single point of articulation as in the primitive mandible (B), so that the two jaws are able to close strongly against each other. Mandibles of this type are largely relieved of dependence on other appendages for the securing of food; by elongation they may become fangs for grasping living prey, and they are particularly amenable to modifications by which they become piercing organs. The anterior, or outer, dorsal muscle of the mandible (fig. 1 G,  $A$ ) retains the abductor function, the posterior dorsal ( $P$ ) becomes the chief or only adductor; the ventral muscles ( $V$ ) lose their importance as adductors, and are reduced or eliminated. Mandibles of this kind have been evolved, apparently independently, in the amphipods and isopods among the Crustacea, and in the Lepismatidae and Pterygota among the insects. The winged insects have the most efficient jaws of all the arthropods for direct mandibular feeding.

Finally, we encounter the curious condition in which the gnathal lobe, ordinarily a solid outgrowth of the mandibular base, becomes either flexible or movably articulated on the base, and independently muscled. The first condition occurs in the Chilopoda, the second (fig. 1 H) is characteristic of the Diplopoda and Symphyla. In the diplopods and symphylids the gnathal lobe ( $gnL$ ), which is the functional jaw of the animal, is supported on a large basal plate ( $mdB$ ) on the side of the head (fig. 20 A, B). That this plate, though relatively immovable, is the true base of the mandible is shown by the fact that most of the usual mandibular muscles are inserted on it (fig. 1 H). Attached on the gnathal lobe, however, is a huge cranial flexor of the lobe ( $IA$ ), and a smaller muscle ( $I$ ) arising within the basal plate. The cranial muscle, since it is attached on the margin of the lobe and goes anterior to the ventral muscles ( $IV$ ,  $\alpha V$ ), may be regarded as an anterior dorsal muscle. More difficult to explain is the presence of the intramandibular muscle ( $I$ ). It can hardly be doubted that the gnathal lobe of the diplopod and symphylid mandibles is the homologue of the immovable lobe in other arthropods, and that it does not represent a segment of the telopodite. It may be supposed to be derived from a flexible lobe with a similar musculature such as

that of most of the chilopods. The movable gnathal lobe of the mandible is identical in its essential structure and its musculature with the lacinial lobe of an insect maxilla, and it is to be noted that endites of the maxillary appendages in general are movable and independently muscled from the limb segment on which they arise.

The distribution of the types of mandibular structure among the arthropods does not show any evolution of the types from one major group to another. Among the Crustacea, for example, are found all the different kinds of mandibles having an immovable gnathal lobe, including mandibles with a single point of articulation, doubly articulated mandibles, some with a horizontal valvelike action, others with a transverse swinging movement, and also piercing mandibles. In the Chilopoda the mandibles are of the horizontal valve type, rocking on a lengthwise axis, though without fixed articulations. The mandibles of the entognathous apterygote insects somewhat resemble the chilopod jaws, but they may be modified for piercing. Among the other insects, mandibles of the generalized type with a single point of articulation recur in the thysanuran Machilidae, and in modified form in larval Ephemeroptera. The characteristic insect mandible, however, is a doubly articulated jaw with a free transverse movement, though the piercing type is of frequent recurrence among the Pterygota. Mandibles with a movable, independently muscled gnathal lobe are characteristic of the Symphyla and Diplopoda, but the jaws of the crustacean Branchiura and Cirripedia, *if* they are mandibles, are to be included in the same category. There is good reason for believing that the pendent, singly articulated mandible represents the primitive arthropod jaw, because it shows the least departure from the coxa of a leg, but it is evident that the other types of mandibular structure and mechanism have been independently evolved in the various arthropod groups.

### I. CRUSTACEA

The principal types of mandibular structure that occur in the Crustacea have been sufficiently outlined in the Introduction. A review of the subject, therefore, need not be repeated here, and the following descriptions will simply give examples of the jaw structure and mechanism developed in the various crustacean groups.

**Branchiopoda and Ostracoda.**—The jaws of the branchiopods well illustrate the structure of the pendent type of mandible with a single dorsal point of articulation (fig. 1 B). In the Anostraca (fig. 2 A, B) the mandibles (*Md*) are articulated on the tergum of the mandibular segment (*II*), which is a small but distinct plate between

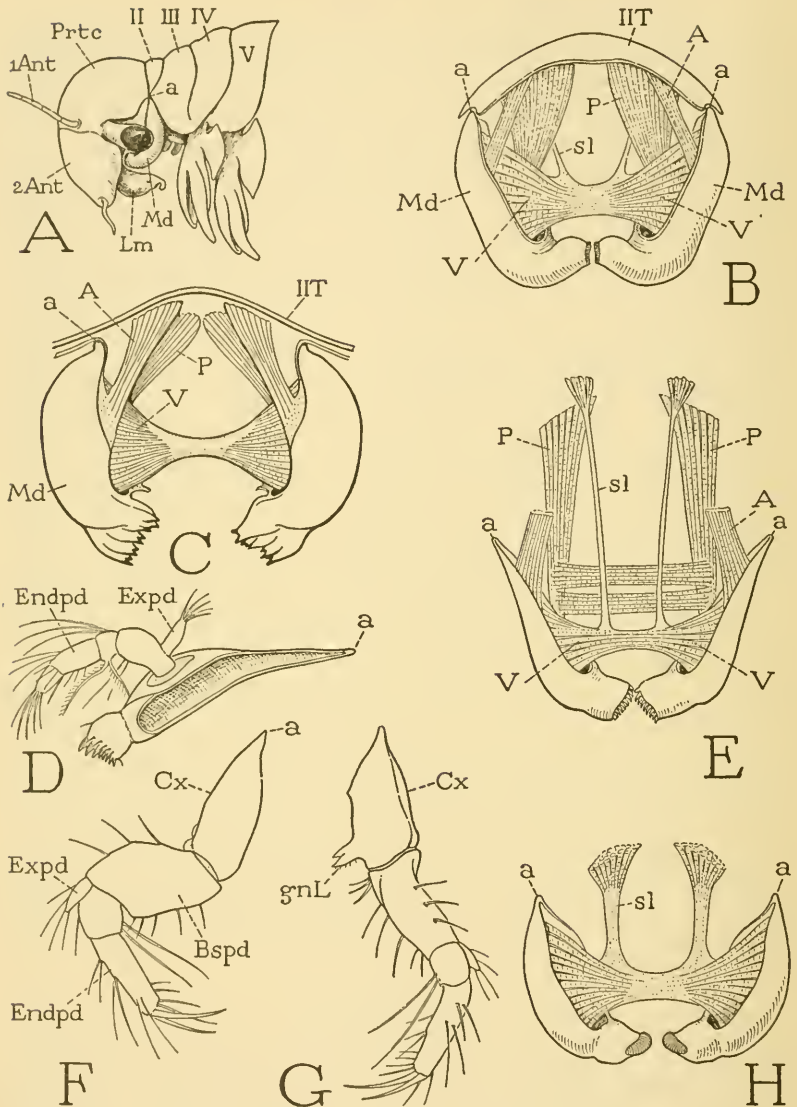


FIG. 2.—Crustacea—Branchiopoda and Ostracoda.

A, *Eubranchipus vernalis* Hay, female (Branchiopoda: Anostraca), head and anterior part of body, lateral. B, same, mandibles and muscles, anterior. C, *Apus longicaudatus* Leconte (Branchiopoda: Notostraca), mandibles and muscles, anterior. D, *Cypris testudinaria* Sharpe (Ostracoda), right mandible, mesal. E, *Daphnia pulex* Degeer (Branchiopoda: Cladocera), mandibles and muscles, anterior. F, *Philomedes globosa* (Lillj.) (Ostracoda), left mandible, lateral. G, same, left mandible, anterior. H, *Estheria clarkii* Packard (Branchiopoda: Conchostraca), mandibles and intergnathal muscles, anterior.



the protocephalic head (A, *Prtc*) and the large tergal plate of the maxillary segments (*III*, *IV*). In the notostracan *Apus* (C) the mandibles are suspended from the under lamellae of the lateral folds of the mandibular part of the shell. The mandibles in each case have large gnathal lobes, but the lobes are not differentiated into incisor and molar processes. Palpi are absent. The same type of mandible is seen in the conchostracan *Estheria* (H), and in the cladoceran *Daphnia* (E). Each mandible is equipped with strong anterior and posterior dorsal muscles (B, C, E, *A*, *P*), and the whole inner cavity of the jaw is occupied by the spreading fibers of the ventral adductor muscle (*V*), the convergent ends of which are united in a thick median ligament with those from the opposite mandible. The strong development of the dorsal muscles leaves no doubt that these muscles are functionally important; probably they give a rotary motion to the jaws, or perhaps some degree of anterior and posterior movement, but, acting together, they might also be adductors. A muscular mechanism of abduction, however, is not evident.

The apparent strength of the mandibles and their musculature in some of these small or minute crustaceans is surprising considering the nature of the food, which, for the most part, consists of organic detritus or micro-organisms filtered from the water, only a few species being predaceous. Elaborate studies have been made by Cannon and others on the feeding mechanism that brings the food to the mouth, but little is said about the specific action of the jaws.

The Branchiopoda in general, except Notostraca, as described by Cannon (1928; 1933b), obtain their food from water currents driven forward to the mouth in a median channel of the ventral body wall by movements of the trunk limbs. The water enters the food channel through the interlimb spaces, and the contained particles are either filtered off on setal fringes of the basal endites of the limbs, or are carried directly in the forward current to the mouth region. The particles lodged on the filters are scraped off, as the latter move forward and backward, by combs of setae on the walls of the food channel, and are then caught in the water current. On reaching the mouth region the accumulated food may be introduced at once between the mandibles by the maxillules, or in some species it is first agglutinated into a mass by a secretion of glands in the labrum. A special description of the labral glands of cladocerans is given by Cannon (1922). The Notostraca lack a median food channel, and with them there is no perceptible forward-flowing water stream. Food particles entering between the limbs are caught on the spiny basal endites, and, with the forward and backward movement of the limbs, are successively

scraped off upon the preceding endites, and so eventually reach the mouth. Both *Apus* and *Lepidurus*, Cannon says, feed also on large food masses grasped with the anterior trunk limbs and held against the mouth.

Among the Ostracoda the mandibles take on various forms, but they are more generalized than those of the branchiopods in the retention of a segmented palpus, which is biramous. In most species, as in *Cypris* (fig. 2 D), the long basal part of the mandible has the structure typical of the branchiopod jaw with a simple, strongly toothed gnathal lobe. In certain species, however, the lobe is armed with strong spines, and in some of the Cytheridae it is produced into a piercing stylet. The simplified, leglike mandible of *Philomedes* (F, G) has been noted in the Introduction.

The Ostracoda feed in various ways. According to Schmitt (1931) fresh-water forms, so far as observed, seem to be omnivorous, but marine species feed largely on diatoms and other plants of the ocean. Some, however, feed on copepods, which they ensnare with a sticky secretion spread over the prey. Species with piercing mouth parts suck the juices of marine plants, and a few are predaceous on other animals. Among the marine ostracods, *Asterope* and *Cytherella* are said by Cannon (1933a) to be purely filtratory feeders. By the activity of the maxillary epipodites currents of water are drawn through the chambers within the shell valves. The filters of *Asterope* are combs of long setae on the maxillules, the particles lodged on them are scraped off by setae of the maxillae and spinous lobes of the mandibles, and passed to long setae on the maxillularly endites, which deliver the food mass to the mouth, from which finally it is introduced into the esophagus by curved processes of the mandibles. Members of the Cypridininae, Cannon says, may feed on detritus from currents driven through the shell chamber by the same mechanism as in *Asterope*, but they are not true filter feeders, and some are raptatory. The food particles from water currents are collected on setae of the basal parts of the maxillules, the maxillae, and the first trunk limbs, and the food is entangled in a secretion from glands in the large labrum. *Cypridina* feeds on large food masses, which, Cannon suggests, are held by the mandibular palps directly under the mouth and here torn to pieces by the strongly armed maxillulae. *Philomedes*, on the other hand, feeds on small particles dislodged by means of its spiny mandibular palps (fig. 2 F, G) from the mud over which it swims, and it has only a relatively weak maxillularly armature. *Gigantocypris*, Cannon notes, "must be an efficient hunter of living prey," since its



stomach was found to be full of large copepods; *Cypridina castanea* "feeds on comparatively large Crustacea."

**Branchiura.**—The functional jaws of adult branchiurans are small, toothed plates or hooks mostly or entirely concealed within a preoral "buccal cavity" in the end of a proboscis. In *Argulus* the proboscis is an elongate tubular organ (fig. 3 A) projecting posteriorly on the under side of the head; in *Dolops* it is a mere hexagonal mound (I) between the bases of the maxillary hooks. The preoral cavity of the proboscis is enclosed between an anterior *upper lip* (*Lm*) and a posterior *lower lip* (*Mst*); the jaws, commonly called "the mandibles," project mesally from the lateral walls of the cavity. Rodlike thickenings of the proboscis wall strengthen the latter and serve as supports for the jaws.

In a young stage of the embryo the apparent mandibles are fully exposed appendages on the under side of the head; as shown by Martin (1932) in *Argulus "viridis"* (fig. 3 C), each mandible of a 26-day embryo consists of a basal segment (*mdB*) bearing a large, lateral, 3-segmented palpus (*Plp*), and a small, toothed gnathal lobe (*gnL*) projecting from its mesal end. At a later embryonic stage (D), according to Martin, the basal segments of the mandibles have increased greatly in size and appear to have formed the principal part of the proboscis, their distal parts uniting with lobes of the head that become the upper and lower lips of the preoral cavity. The apical lobes of the mandibles now appear as a pair of hooks (D, *gnL*) in the end of the proboscis. The same structure found by Martin in the 35-day embryo of *Argulus "viridis"* (D) is carried over into the first larval stage, as shown here in *Argulus americanus* (E), except that the proboscis spine (*Sp*) is now present. At this stage the mandibular palps (*mdPlp*) still arise from the base of the proboscis, and are widely separated from the hooklike gnathal lobes (*gnL*) in the end of the proboscis. Martin's statement, therefore, that the principal part of the proboscis is derived from the mandibular bases seems to be well substantiated. If so, the mouth hooks are not themselves "the mandibles," but are the displaced gnathal lobes. The labrum and paragnaths, Martin believes, are represented by three small processes that form a filter apparatus at the mouth entrance within the preoral cavity. In no other crustacean, however, do these structures occur in any such place; it would seem much more probable that the upper lip is the labrum (A, B, I, *Lm*), and that the lower lip (A, I, *Mst*) is a metastomal lobe formed of the paragnaths. These elements would be readily available in any crustacean for the construction of a proboscis. The mandibular palps, Martin says, are lost at the first larval moult.

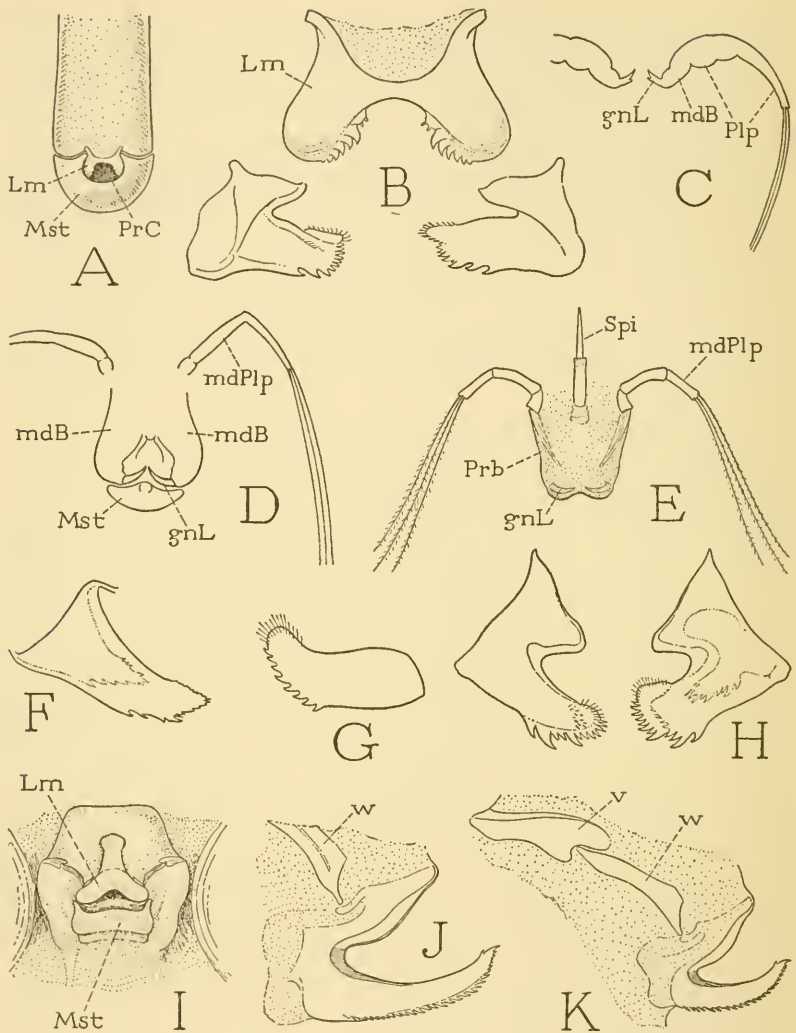


FIG. 3.—Crustacea—Branchiura.

A, *Argulus americanus* Wilson, end of proboscis, ventral. B, same, labrum and jaws, ventral. C, *Argulus viridis* Nettovitch (*foliaceus* L.), mandibles of 26-day embryo (from Martin, 1932). D, same, proboscis of 35-day embryo (from Martin, 1932). E, *Argulus americanus* Wilson, proboscis of newly hatched larva. F, *Argulus viridis* Nettovitch (*foliaceus* L.), gnathal lobe of mandible (from Martin, 1932). G, *Argulus laticauda* Smith, gnathal lobe of mandible. H, *Argulus pugettensis* Dana, gnathal lobes of mandibles. I, *Dolops doradis* Cornalia, proboscis, ventral. J, same, gnathal lobe of mandible. K, same, gnathal lobe of mandible, and supporting plates in wall of proboscis.

The adult jaws of *Argulus* vary in shape and dentition in different species, as shown at B, F, G, and H of figure 3. The jaws of *Dolops doradis* are strong serrated hooks (J, K) projecting mesally from the lateral walls of the moundlike proboscis, and are partly exposed in the preoral cavity between the labrum and the metastome (I). Each hook arises from the posterior end of an elongate base (J, K), which is merely a local sclerotization in the otherwise membranous lateral wall of the proboscis. At about its middle the hook base is pivoted on the tapering end of a slender transverse sclerite (J, K, *w*) in the ventral wall of the proboscis, the outer end of which is held in a notch of a second more lateral sclerite (K, *v*). On each side of the fulcral point muscles are attached on the hook base that evidently rock the latter and thus produce adduction and abduction of the hooks, the jaw hooks being movable by reason of the flexibility of the proboscis integument in which their bases are implanted.

Inasmuch as the observations above cited, if true, seem to show that the functional jaws of adult branchiurans represent the apical hooks of the embryonic mandibles, and thus evidently correspond with the immovable gnathal lobes of the mandibles of most other Crustacea, it is surprising that the structures in question are individually movable and independently muscled. Though the musculature of the branchiuran proboscis needs to be more carefully studied, there is no question that the jaw muscles arise within the proboscis itself; but this condition is one characteristic of maxillary endites, and becomes so pronounced in the case of the first pair of jaws in the Cirripedia that the latter have been interpreted as maxillary endites, and not as mandibles. The musculature of the branchiuran jaw lobes might be justified if we could suppose that the lobe of the embryonic mandible (fig. 3 C, *gnL*) represents the endopodite of the appendage and that the palp (*Plp*) is the exopodite, but there is little in the structure of the organ to support such an interpretation. The interpretation of the branchiuran jaws, as given in figure 3, therefore, must be held subject to further investigation, but the same anomalous condition seems to be even more pronounced in the Cirripedia.

**Cirripedia.**—The mouth parts of the ordinary nonparasitic barnacles, or Thoracica, are so closely associated with one another around the mouth that together they form a thick, proboscislike lobe with a somewhat constricted base (fig. 4 A) projecting from the ventral side of the head. The large, swollen, strongly sclerotized anterior part of the lobe is the labrum (*Lm*). Closely adnate on each side of the labrum is the wide base of an appendage that supports ventrally an elongate, hairy palpus (*Plp*) projecting forward beneath

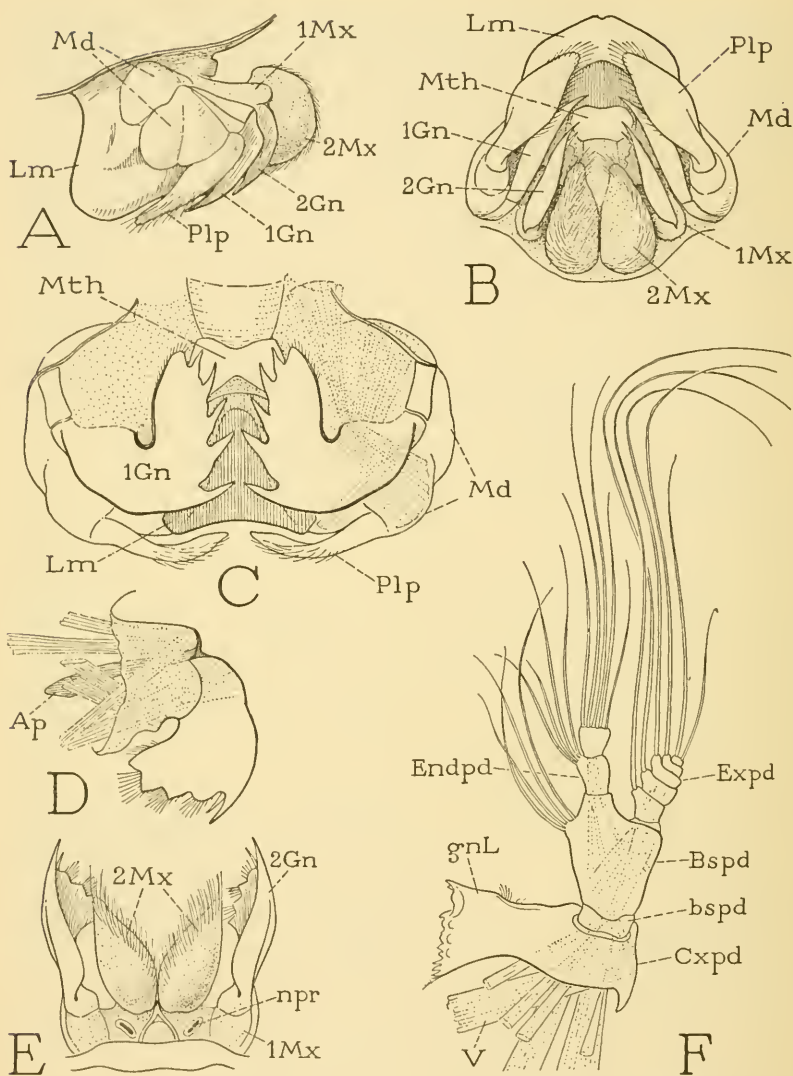


FIG. 4.—Crustacea—Cirripedia (*Lepas*) and Copepoda (*Calanus*).

A, *Lepas anserifera* L., mouth parts, left side. B, same, mouth parts and mouth, ventral. C, same, labrum and first gnathal appendages, posterior, showing first pair of jaws (1Gn). D, same, second jaw of right side, mesal. E, same, second and third gnathal appendages, posterior, showing position of nephropores. F, *Calanus cristatus* Kröyer, left mandible of fifth copepodid stage, ventral.



the labrum, and bears behind the palpus a large, free, flat, strongly toothed jaw lobe, or gnathos (*1Gn*), which is independently movable on the base. The jaw is turned mesally behind the labrum (B, C, *1Gn*), so that only its outer edge is visible in side view (A). Above and behind this first lateral appendage on each side is the base of a second, smaller appendage (A, *1Mx*), which bears a second platelike jaw (*2Gn*) similar to the first though smaller and not so strongly toothed (D). Finally, projecting ventrally behind the other mouth parts is a pair of large, thick, soft, rounded, hairy lobes (A, B, *2Mx*), with a deep groove between them that runs forward to the mouth.

The cirriped mouth parts were first well described by Darwin (1851, 1854), who regarded the first pair of appendages and their jaw lobes as the mandibles, the second pair as the first ("inner") maxillae, and the two postoral lobes as the second ("outer") maxillae. Darwin's interpretation and nomenclature have been followed by most subsequent students of the cirripeds.

An examination of the so-called mandible will show at once that its structure is quite unlike that of any ordinary crustacean mandible. The effective jaw lobe of *Lepas anserifera* (fig. 4 C, *1Gn*) is freely articulated on a small sclerite of the posterior edge of the base of the appendage, and has a strong individual musculature consisting of abductor and adductor muscles arising in the base. The base itself is immovably attached to the side of the labrum, and its outer wall is divided by a groove into an upper and a lower part (A) suggestive of a segmentation, but the division appears to be merely a surface differentiation. The entire body of the appendage is filled with muscle fibers inserted on the palpus and the jaw lobe; the lower part contains an external layer of longitudinal fibers. From their structure, these appendages might well pass for maxillae with a highly developed biting endite. In fact, it has already been said by Hansen (1925, p. 51) that the appendages of the cirripeds called "mandibles" differ "so strongly from the mandibles in other Arthropoda while agreeing much more with the maxillulae or maxillae, that I prefer to name them maxillulae; consequently mandibles are absent." It should be noted, however, that the mandibles of the Diplopoda and the Symphyla have independently movable and individually muscled gnathal lobes quite comparable to the jaw lobes of cirripeds. Borradaile (1917, 1926) suggests that the jaw lobes of the cirriped mandibles may be endites of the second segments of the appendages and not those of the first, but it is not clear how this interpretation makes the matter any easier to understand. In the cypris stage of cirriped ontogeny the second antennae and the mandibles of the nauplius are suppressed;

Darwin (1851) says the mouth parts of the adult are all present in the cypris stage in an undeveloped condition, but apparently it has not been shown that the first pair of mouth appendages of the adult are derived from the naupliar mandibles.

The second pair of mouth-part appendages of *Lepas* (fig. 4 D) are much simpler than the first. The basal part of each is membranous (A, *IMx*); the jaw lobes are smaller and simpler than those of the first pair, and lie behind the latter (B, *2Gn*). From the base of each second jaw projects a large apodemal arm (D, *Ap*), but the relation of the muscles to the apodeme was not determined. If the first appendages are the mandibles, the second are the first maxillae.

The postoral lobes of the cirriped group of mouth parts (fig. 4 A, B, E, *2Mx*), as Hansen (1925) notes, in no way suggest by their form or position that they represent the second maxillae; the deep groove between them runs forward to the mouth. In short, these lobes have the position and character of a pair of thick paragnaths. Hansen remarks that only a single circumstance makes it doubtful that the postoral lobes are the paragnaths, which is that the excretory glands are said to open on their bases. In *Lepas anserifera* the nephropores (E, *npr*) are not on the bases of the lobes, but lie behind them plainly exposed in the membrane between the second and third appendages. The apertures are shown in the same position by Darwin, who regarded them as "olfactory organs." On the other hand, in the lepadid *Conchoderma* Dehner (1910) plainly shows the gland ducts opening on the bases of the postoral lobes, as he says they do also in *Balanus*, and Batham (1945) shows the nephropores on the bases of the lobes in *Pollicipes*. The position of the gland openings must be given priority over all other considerations as evidence that the postoral lobes of the cirripeds are the second maxillae, for, as Borradaile (1926) says, the assumption that the gland apertures have migrated from the maxillae to the paragnaths "will probably not commend itself to carcinologists." The usual interpretation of the mouth parts of *Lepas* is implied in the lettering given here on the figures, but the homology of the parts of the mandibles with those of the jaws of other crustaceans must be left undetermined. The cirriped "mandibles," however, appear to have something in common with the branchiuran "mandibles."

**Copepoda.**—The copepod mandibles show an extreme degree of variation from the generalized calanoid type of jaw to that of parasitic forms in which the mandible takes the form of a long arm or slender stylet armed with teeth on its distal part. The mandible of *Calanus cristatus* (fig. 4 F) has been sufficiently discussed in the Introduc-



tion, but we may note again that its basal segment is produced mesally in a large, flat, toothed gnathal lobe (*gnL*), and bears a biramous palp. Between the basal segment, or coxopodite (*Cxpd*), and the basipodite (*Bspd*), which supports the two rami, is an intermediate ring (*bspd*) that has been interpreted by Borradaile (1917) and by Hansen (1925) as the "coxa" of the appendage, making the basal segment a "precoxa." There is nothing in the nature of the ring, however, to give it the status of a true segment; in appearance it is merely a secondary subdivision of the basipodite. Many examples might be cited among the arthropods of subdivision of primary limb segments, producing parts that may have the appearance externally of segments, but which have no musculature of their own; the ring supporting the basipodite in the *Calanus* mandible is evidently a structure of this kind. Before any limb section devoid of muscles can be held to be a true segment it must be shown by evidence from some source that it was once an individually muscled and therefore independently movable part of the appendage. The basal segment of the *Calanus* mandible certainly is the coxopodite of an ordinary limb; its ventral muscles (*V*) consist of eight or nine slender bundles of fibers, and those from the opposite jaws come together medially, where they are attached on a narrow intergnathal ligament above the nerve cord, which expands anteriorly and branches into a pair of suspensory ligaments attached on the back.

Numerous examples of the elongate or styletlike mandibles of parasitic copepods have been well illustrated by Heegaard (1947), who shows that while some are simple rods, most of them are divided by joints into several segmentlike parts. From comparative studies on different forms Heegaard argues that the divisions represent true segments in course of fusion. From this interpretation it would appear that the styletlike mandible of the copepods is formed of the main shaft of the appendage. The usual mandibular stylet of other arthropods, however, is the elongated gnathal lobe, the telopodite being absent.

**Leptostraca.**—The mandibles of *Nebalia* (fig. 5 A) are of the suspended type of structure; they hang from dorsal articulations (*a*) on the head, with the large, 3-segmented palpi projecting from their lower ends. The long gnathal lobes turn mesally at right angles from the bases of the jaws, and come together behind the edge of the labrum. From the base of each lobe there arises anteriorly a small, thin, bidentate incisor process (*C, inc*). The main part of the lobe, therefore, constitutes a molar process (*mol*). The incisor process of the mandible, first met with in the Leptostraca, as seen in *Nebalia*

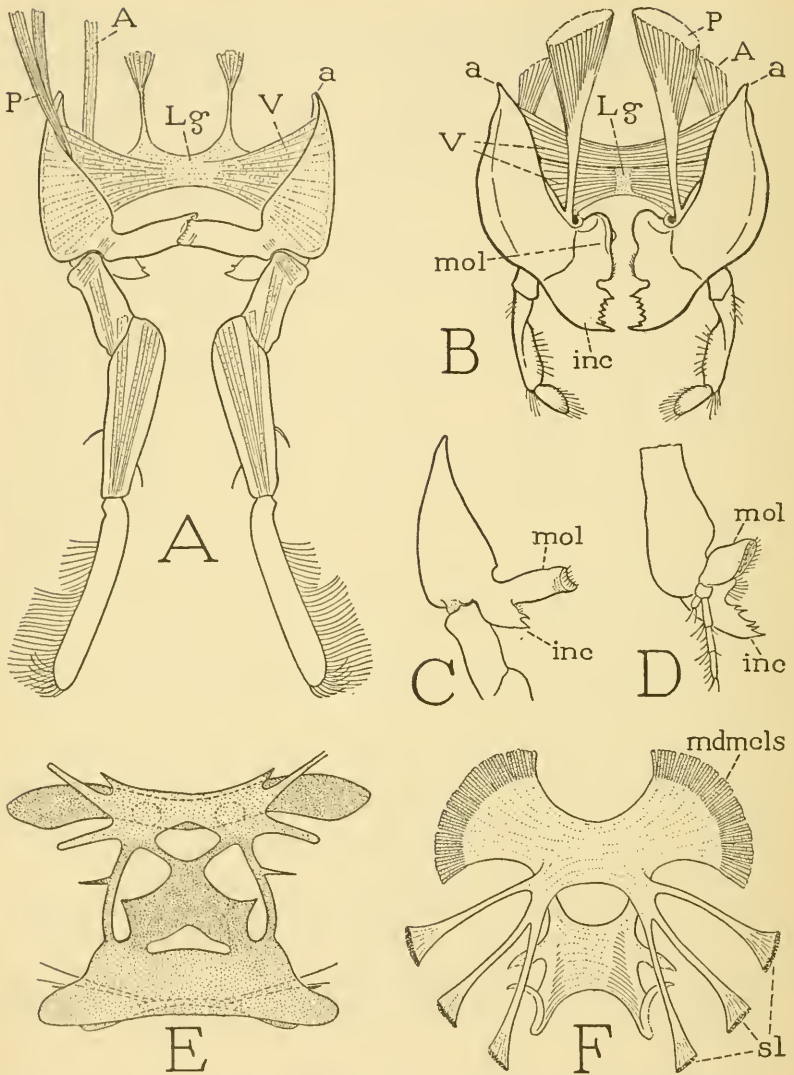


FIG. 5.—Crustacea—Leptostraca (*Nebalia*) and Anaspidea (*Anaspides* and *Paranaspides*).

A, *Nebalia bipes* (Fabr.), mandibles and muscles, posterior. B, *Anaspides tasmaniae* Thomson, mandibles and muscles, posterior. C, *Nebalia bipes* (Fabr.), right mandible, anterior. D, *Paranaspides lacustris* (Smith), right mandible, anterior (from Smith, 1908). E, *Nebalia bipes* (Fabr.), intergnathal ligament (from Manton, 1934). F, *Anaspides tasmaniae* Thomson, intergnathal ligament and suspensory branches, dorsal, flattened under cover glass.

appears to be a secondary outgrowth of the gnathal lobe rather than a result of the division of the lobe into two parts; but, on the other hand, if *Nebalia*, as Cannon (1927) contends, has been evolved from a mysidlike malacostracan, its small incisors may be remnants of once large and functional processes. The musculature of the *Nebalia* mandibles includes two relatively weak dorsal muscles for each jaw (*A*, *A*, *P*), and large ventral adductors (*V*) attached medially on the mandibular expansions of an elaborate intergnathal ligament (*E*).

*Nebalia* lives in shallow water along the shore and in soft mud where there is much organic decay, and feeds largely on particles filtered out of water currents produced by movements of the trunk appendages. The filter chamber, as described by Cannon (1927), is an enclosure beneath the thorax shut in laterally by the appendages, below by a mat of setae on the ends of the endopodites, and closed behind by setae on the last pair of limbs. The chamber is thus open anteriorly, and the water currents enter *in front* and flow posteriorly. The contained particles are filtered out on fringes of long setae on the endopodites of the trunk limbs, which overlap mesally from behind forward. By the forward and backward movement of the appendages, therefore, the particles lodged on the setae are automatically transferred to those of the limb in front, and so on until they reach the maxillary region. Here they are taken over first by the maxillae and transferred to the maxillules, which give the food a preliminary mastication, and then finally pass it forward between the paragnaths to the molar processes of the mandibles. The small, widely separated incisor processes, Cannon notes, do not act as biting parts. Particles that are too large to pass the filters are stopped in the maxillary region and utilized directly.

**Anaspidacea.**—Though the anaspidaceans, or syncarids, are true Malacostraca, they still retain the primitive type of mandible (fig. 5 B) supported by a single point of articulation (*a*) on the tergum of the mandibular segment. The large gnathal lobes are differentiated into broad molar processes (*B*, *D*, *mol*) and toothed incisor processes (*inc*). The mandibular palps of *Anaspides* (*B*) are 3-segmented, but in *Paranaspides* (*D*) the palps of the adult are shown by Smith (1908) to have four apparent segments, and the first segment bears a small lateral lobe suggestive of being a palpal exopodite. In young specimens, however, Smith (1909) finds that the palp may have only three segments and that the basal lobe is less conspicuous, from which fact he doubts that the palp of *Paranaspides* shows a true biramous structure.

The musculature of the *Anaspides* mandibles (fig. 5 B) is the same

as that of the branchiopod mandibles (fig. 2 B, C) in that each jaw has an anterior and a posterior dorsal muscle (*A*, *P*) and a large bundle of ventral adductor fibers (*V*). In *Anaspides*, however, the posterior dorsal muscle (*P*) is attached, as in the Malacostraca generally, by a thick tendon on the posterior mandibular margin close to the base of the gnathal lobe. In the higher Malacostraca having a doubly articulated jaw, this muscle becomes a powerful dorsal adductor (fig. 9 D, E, *P*). The ventral adductor fibers of *Anaspides* (fig. 5 B, *V*) all arise on the surface and margins of the mandibular part of a large, strongly developed intergnathal ligament (*F*) but in the natural condition only a small median area of the ligament is exposed (B, *Lg*).

Concerning the feeding habits of *Anaspides tasmaniae*, Smith (1909) says these fresh-water crustaceans "appear to be omnivorous, as they will feed upon the dead bodies of insect larvae or even upon one another, but their chief food is the algal slime covering the rocks among which they live, and they also browse upon the submerged shoots of mosses and liverworts." Manton (1930) notes that in addition to feeding on algae and detritus covering weeds and stones, the adults of *Anaspides* eat also tadpoles and worms.

The large size of the jaws of *Anaspides*, their strong musculature, and their well-developed incisor and molar processes indicate that these crustaceans are well equipped for direct feeding on the bodies of dead animals, and Cannon and Manton (1929) observe that "an external view of the mouth parts suggests a raptatory function rather than a filtratory type of feeding mechanism." However, these writers show that *Anaspides* and *Paranaspides* are both filtratory and raptatory feeders, though the related *Koonunga*, judging from its mouth parts, apparently is entirely raptatory. (By "raptatory" is meant grasping or scraping, but not necessarily predatory habits.) The filter apparatus of *Anaspides* and *Paranaspides* as described by Cannon and Manton is formed of the broad maxillae and their dense fringes of marginal setae, which lie close against the maxillules. The maxillary filter plates enclose between them a filter chamber through which water is driven from behind by the action of the trunk limbs. Food particles in the water caught on the setal fringes of the maxillae are scraped off by the basal endites of the maxillulae and passed forward to the mouth. The animals are thus equipped for feeding on detritus dislodged from submerged plants and stones.

**Euphausiacea, Cumacea, Mysidacea.**—In these three malacostracan groups the mandibles begin to take on the structure and mechanism that become characteristically developed in the doubly articulated jaws of the decapods, resulting first from a close association of the mandi-



bles with lateral expansions of the epistome. The calcification of the epistomal region spreads to the sides between the bases of the second antennae and the mandibles, usually uniting with the inner lamellae of the carapace folds, and thus establishes a firm support for the anterior margins of the mandibles, which take a more or less horizontal position. The movement of the mandibles is thereby limited to a lengthwise rocking or rotary motion on the epistomal wings, and abduction and adduction now consist of a valvelike opening and closing of the gnathal lobes from below. In the stomatopods and decapods the mandibles further acquire specific articulations on the epistome at the sides of the labrum. Characteristic of mandibles of this type is the attachment of the posterior dorsal muscle by a strong tendon on the mandibular margin at the base of the gnathal lobe (fig. 6 A, D, F, *P* or *Pt*), a condition already noted in *Anaspides* (fig. 5 B), so that this muscle becomes an effective dorsal adductor.

The mandibles of *Thysanopoda tricuspidata* (fig. 6 D), taken as an example of the Euphausiacea, are strongly developed, with broad gnathal lobes differentiated into thick molar processes and toothed incisor processes. The molar process of the left jaw is a blunt projection, that of the right is cup-shaped; when the jaws are closed the left molar fits into the cavity of the right as a pestle into a mortar, and the incisor teeth interlock with each other. The mandibles are closely attached by their anterior margins on the weakly calcified post-antennal expansions of the epistome, but they have no specific epistomal articulations or hinges. The fibers of the ventral adductor muscles arise from a broad, membranous median ligament (*Lg*), which is supported by two pairs of suspensory branches (*sl*) attached directly on the dorsal epidermis of the carapace by their expanded but non-muscular ends.

The elongate mandibles of Cumacea (fig. 6 E, F) lie almost in a horizontal plane, directed convergently forward from their articulations on the carapace, with the gnathal lobes lying against the labrum. The well-sclerotized epistome (*G*, *Epst*) has broad lateral extensions reflected back along the sides of the labrum, and the mandibles are hinged (*h*) on the epistomal margins, so that their movement is definitely restricted to a lengthwise rotation on their dorsal anterior margins. The mandibles of *Diastylis glabra* (fig. 6 E) are more slender than those of *D. rathkei* (F) figured by Hansen (1930), but in both species the molar lobes and the incisor lobes are widely divergent, giving the jaw a branched appearance. The mandibular musculature (E) includes the usual anterior and posterior dorsal muscles (*A*, *P*) and large ventral muscles. The anterior dorsal

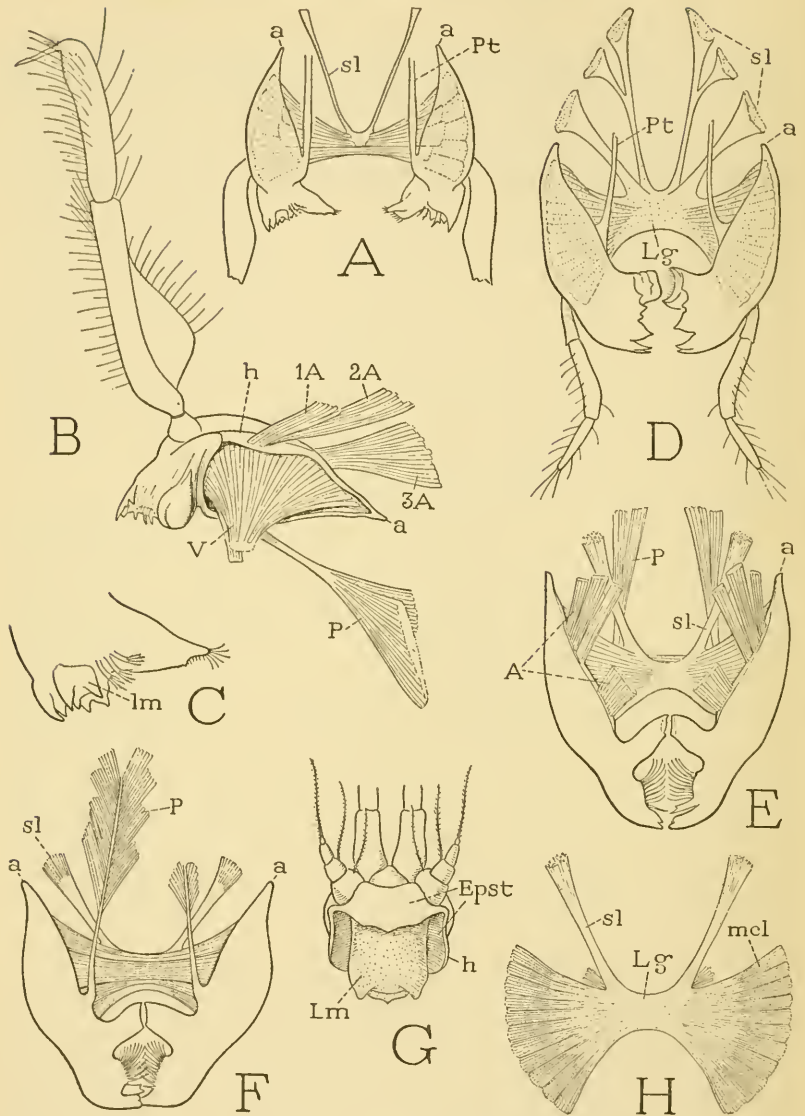


FIG. 6.—Crustacea—Mysidacea (*Neomysis*), Euphausiacea (*Thysanopoda*), and Cumacea (*Diastylis*).

A, *Neomysis franciscorum* Holmes, mandibles and intergnathal muscles, posterior. B, same, right mandible and muscles, mesal. C, same, gnathal lobe of left mandible, posterior. D, *Thysanopoda tricuspidata* M. Edw., mandibles and intergnathal muscles, posterior. E, *Diastylis glabra* (Zimmer), mandibles and muscles, anterior. F, *Diastylis rathkei* Kr., mandibles and muscles, posterior (from Hansen, 1930). G, *Diastylis glabra* (Zimmer), female, epistome and labrum. H, same, intergnathal ligament and its mandibular muscles.



(*A*) is differentiated into several fiber groups, but they all appear to be abductors opposed to the posterior adductor (*P*). The ventral adductors are composed mostly of bundles of striated fibers (*H*, *Mcl*) within the cavities of the mandibles that are continuous from non-striated fibers radiating from the median ligament (*Lg*). Some of the posterior muscle fibers, however, as shown by Hansen (*F*), run without interruption from one mandible to the other, though they are attached on the ligament. The intermandibular ligament is supported by a pair of thick suspensory branches (*E*, *F*, *H*, *sl*) with muscular attachments on the carapace.

The cumaceans are said to feed on detritus from the mud in which they bury themselves, and the dense setal fringes on the incisor processes of the mandibles (fig. 6 *E*, *F*), which cover the mouth entrance, appear to make a retaining sieve when the jaws are closed. The strong incisor and molar lobes and the elaborate musculature of the jaws, however, suggest that these crustaceans are capable of handling tougher kinds of food.

In the Mysidacea the mandibles (fig. 6 *A*, *B*) in their structure and mechanism closely approach those of the decapods. They are hinged by their dorsal anterior margins on lateral wings of the epistome, though there are no specific points of articulation. The anterior dorsal muscles include three groups of fibers (*B*, *1A*, *2A*, *3A*). The first two (*1A*, *2A*), being attached on a flange mesad of the hinge line (*h*), appear to have thus become dorsal adductors, as are the corresponding muscles in the decapods, but the large third muscle (*3A*) evidently retains its original abductor function. The posterior muscle (*P*), attached by a strong tendon (*A*, *Pt*) near the base of the gnathal lobe, is a dorsal adductor. The fibers of the ventral muscles (*V*) occupy the entire cavities of the mandibles (*A*, *B*), and were not observed to be differentiated into abductor and adductor groups as in the decapods. The mysid mandible gives a good example of the so-called "lacinia mobilis," a small toothed plate (*C*, *lm*) flexibly attached on the incisor area of the gnathal lobe.

It is shown by Manton (1928) that in the development of *Hemimysis lamornae* the ligament of the ventral adductor muscles of the mandibles becomes attached on the apex of a V-shaped apodemal plate arising from sternal invaginations in the maxillary region. This condition foreshadows that in the decapods, in which the ventral adductor fibers of the mandibles arise directly on the cuticular "head apodeme" formed of sternal invaginations between the first and second maxillary segments.

*Hemimysis* is said by Cannon and Manton (1927) to exhibit "two

distinct types of feeding, one on large food masses and the other on minute particles filtered from a water current." The filtratory mechanism is that common to all the less-specialized Malacostraca, the maxillae and the adjacent appendages forming the filter apparatus; the thoracic limbs furnish the motor power for producing currents of water. In *Hemimysis*, according to Cannon and Manton, centripetal streams of water are generated by the rotary movements of the exopodites of the thoracic limbs, which currents pass between the limb bases into the food channel below the body, where the water is drawn forward principally by vibrations of the maxillae. In feeding on large food masses, these writers say, the food is held by the thoracic endopodites and consumed as the mysid swims. Such food includes particles too large for filter feeding, and small animals, even *Sagitta* worms longer than the mysid itself. The food is held beneath the mouth parts by the third to eighth endopodites, properly oriented by the long mandibular palps and the first and second endopodites, and is bitten into by the incisor processes of the mandibles and the spinous distal endites of the first maxillae.

**Stomatopoda.**—The stomatopod is a taxonomic misfit; it is introduced here because its mandibles are doubly articulated, though in other respects they do not much resemble the doubly articulated jaws of the decapods.

The mandibles of *Squilla* (fig. 7 D, *Md*) hang vertically behind the epistome and labrum from weak dorsal articulations (*A, a*) on the doublure of the carapace, but they have strong ventral articulations (*c*) with small condyles on the posterior margins of the long lateral wings of the epistome (*D, Epst*) that embrace the labrum (*Lm*). The lower end of each mandible is produced downward into a large, tapering, toothed incisor process (*A, B, inc*), and from the base of the latter, just below the epistomal articulation (*c*), there extends forward a long molar process (*mol*) with a double row of teeth. In the natural position of the jaws the ends of the incisor processes come together with their teeth interlocked behind the mouth, and the molar processes project straight forward into the large mouth cavity above the labrum.

The mandibular musculature of *Squilla* consists of two anterior muscles (fig. 7 B, *1A, 2A*), a single posterior dorsal muscle (*P*), and a large ventral muscle (*C, V*), the spreading fibers of which fill the cavity of the mandible. The fibers of the ventral muscles of the jaws do not arise from a supporting ligament, but are attached separately on large lateral expansions of an apodemal arch arising from premandibular invaginations between the epistome and the doublure

of the carapace (D, *inv*). A corresponding apodeme has not been observed in any other crustacean.

Manipulation of the mandibles of a preserved specimen shows that the only movement the jaws can make is a partial rotation on their vertical epistomal hinges between the two points of articulation (fig. 7 B, *a, c*). Since the molar processes project forward at right angles

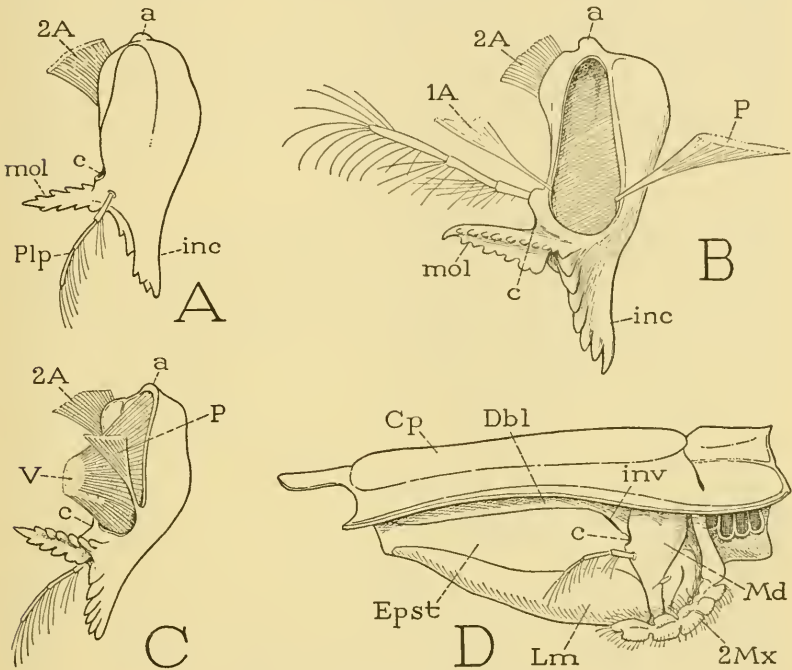


FIG. 7.—Crustacea—Stomatopoda.

A, *Squilla affinis* Berthold, left mandible, lateral. B, *Squilla panamensis* Bigelow, right mandible, mesal. C, *Squilla affinis* Berthold, right mandible and muscles, mesal. D, same, anterior part of body, showing left mandible in place.

to the axes of the mandibles, a rotary movement that corresponds with adduction in a doubly articulated horizontal mandible separates the molar processes, and the opposite movement brings them together. The movements have little effect on the incisor processes other than that of rotation. The stomatopods are predaceous, and are said to feed on small crustaceans, mollusks, and worms.

**Decapoda—Stenopidea.**—The mandibles of *Stenopus hispidus* (fig. 8 E), as those of *Penaeus*, hang from dorsal articulations (*a*) on the carapace, and are articulated ventrally on the lateral wings of

the epistome. The two jaws are connected by the large ventral adductors (*V*) united on a median ligament which is supported anteriorly by a pair of suspensory branches (*sl*) attached on the dorsum of the carapace (*Cp*). From the adductor ligament there extends posteriorly a broad sheet of membranous tissue on which are attached the ventral muscles of the maxillae, and which is itself supported by two pairs of suspensory ligaments. This maxillary "fascia" is common to other natantian decapods. On the anterior margin of the mandible are inserted three dorsal muscles (*C, A*), all of which appear to be abductors. The posterior adductor (*P*) arises by a broad base on the carapace (*E*) and is attached by a long tendon on the posterior margin of the jaw at the base of the gnathal lobe. The fibers of the ventral muscles (*V*) are apparently all adductors, since they show no evident differentiation into adductor and abductor groups.

**Decapoda—Penaeidea.**—Inasmuch as the mandibles of the decapods differ very much in the several suborders, they will be described separately in each group. There is no characteristic difference, however, in the structure and mechanism of the jaws as between those forms classed as Natantia and those included in the Reptantia.

The mandibles of *Penaeus* (fig. 8 A) lie almost in a transverse vertical plane, but they are slanted somewhat forward, and hang obliquely inward, so that the gnathal lobes come together below the mouth. Each jaw is articulated dorsally (*a*) on the base of the inner lamella of the carapace fold, and ventrally by a small process on its anterior margin (*A, B, c*) with the narrow postantennal wing of the epistome. The *Penaeus* mandibles are thus doubly articulated, and rock lengthwise on the axes between the two articular points. The base of each mandible is broadly oval and deeply concave (*B*); the gnathal lobe is split into a flat, toothed incisor process (*inc*) and a thick molar process (*mol*), both of which are turned mesally from the end of the mandibular base (*A*). On the anterior margin of the base of the jaw are attached three anterior dorsal muscles (*B, 1A, 2A, 3A*), which, since they arise on the carapace dorsal to the mandible, and are inserted laterad of the mandibular axis, appear to be all abductors. The opposed dorsal adductor (*P*) arises dorsomedially on the carapace (*A*). The ventral muscles of the two mandibles (*A, V*) are united by a strong median ligament, and most of their fibers (*1V*) are adductors. An anterior group of the ventral fibers (*2V*), however, evidently functions as a ventral abductor, since it is attached on the mandibular margin above the line of rotation. This differentiation of the primarily adductor ventral fibers of the mandible into adductor fibers and abductor fibers is an essential



feature of the jaw mechanism in the Reptantia, and is seen also in such natantian forms as *Lebbeus* (D) and *Macrobrachium* (F), in which the opposed anterior dorsal muscles (*1A*, *2A*) take on an adductor action.

**Decapoda—Caridea.**—The mandibles and the mandibular musculature of the caridean *Pandalus danae* Stimpson have been described by Berkeley (1928), who shows that the mandibles and their mechanism in this representative of the natantian decapods are the same as in the Reptantia, and she follows the muscle nomenclature used by Schmidt (1915) for *Astacus*. In the Caridea the mandibles take a more horizontal position than in *Penaeus* and *Stenopus*, and in their structure and mechanism they more closely resemble the jaws of the Astacura.

The mandible of *Macrobrachium latimanus* (fig. 8 I) is a large, strongly calcified boat-shaped structure, doubly articulated (*a-c*) between the carapace and the epistome. The gnathal lobe is divided into a broad, thick, bluntly toothed incisor process (*inc*), and a long, expanding molar process (*mol*) strongly toothed on its truncate end. The anterior margin of the base of the mandible, proximal to the epistomal articulation (*c*), is somewhat elevated and bears a low, flangelike apodemal ridge (*Ap*).

The musculature of the *Macrobrachium* mandible (fig. 8 F) includes four anterior muscles separated into a distal pair (*1A*, *2A*) and a proximal pair (*3A*). The two distal muscles are inserted on the apodemal flange of the mandibular margin (*I*, *Ap*), laterad of the hinge line of the jaw, and take their origins somewhat ventrally (*F*) on the side of the carapace. These muscles in *Macrobrachium*, therefore, are *anterior adductors* of the mandible, as they are in *Pandalus* and in the Astacura (fig. 9 D, E, *1A*, *2A*), though they belong to the original group of dorsal abductors. The double proximal anterior muscle (fig. 8 F, *3A*) arises dorsally on the carapace and is an *anterior abductor*; it is not given by Berkeley (1928) in *Pandalus*, but is represented in Astacura (fig. 9 D, E, *3A*). The posterior dorsal muscle (fig. 8 F, *P*), attached distally on the mandible by a long thick tendon, is the usual posterior adductor. The ventral muscles from the opposite jaws are united by a thick, cylindrical median ligament (*H*, *Lg*). On each side the ligament gives off dorsally three short branches from which spreading groups of muscle fibers go to the carapace (*Cp*). The ligament itself has a horizontally lamellate structure. The lamellae, which are separated by interlamellar spaces, are distinctly fibrillated and break up at their ends into bundles of fibers that soon become striated muscle tissue. In *Pandalus* Berkeley (1928) notes



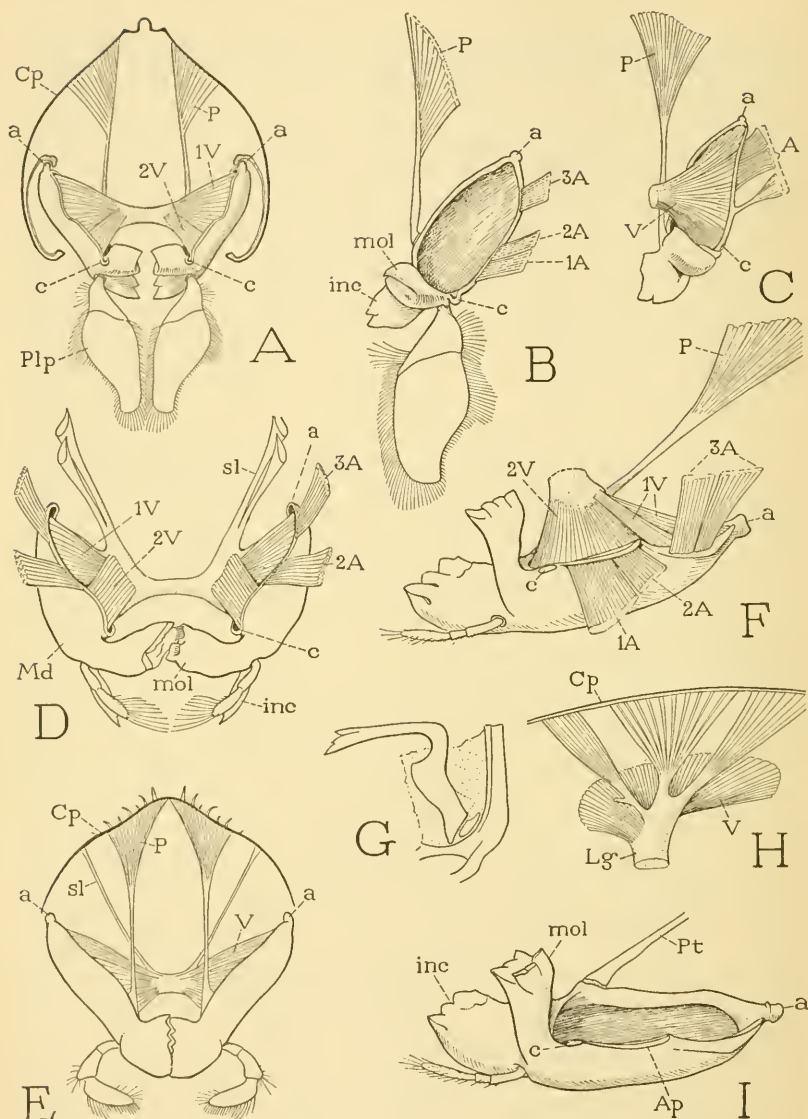


FIG. 8.—Crustacea—Decapoda: Natantia.

A, *Penaeus duorarum* Burkenroad, section of carapace, and suspended mandibles, anterior. B, same, right mandible and marginal muscles, mesal. C, *Stenopus hispidus* (Olivier), left mandible and muscles, anteromesal. D, *Lebbeus groenlandicus* (Fabr.), mandibles and muscles, anterior. E, *Stenopus hispidus* (Olivier), section of carapace, and suspended mandibles, posterior. F, *Macrobrachium latimanus* von Martens, left mandible and muscles, lateral (anterior). G, *Sclerocrangon boreas* (Phipps), left mandible, ventral. H, *Macrobrachium latimanus* von Martens, right half of intergnathal ligament of mandibles, with its suspensory muscles and mandibular adductor (V). I, same, left mandible, dorsolateral.

that the ligament, or "fascia," is supported on sternal apodemes. Most of the ventral muscle fibers are attached within the cavities of the mandibles and have an adductor function. On each side, however, a broad sheet of dorsal fibers (F,  $2V$ ) is inserted on the marginal flange of the mandible opposite the lateral adductors ( $1A$ ,  $2A$ ), and these fibers, therefore, constitute a *ventral abductor* muscle of the mandible, as in *Pandalus* and *Astacura*, opposed to the lateral adductors.

The mandibular musculature of *Macrobrachium* illustrates very clearly how the primitive three muscles of the crustacean jaw ( $A$ ,  $P$ ,  $V$ ) may become differentiated into five groups of fibers with diversified functions; only the posterior dorsal muscle ( $P$ ) preserves its integrity and its original function. It will later be seen that these same muscles persist in the reptantian decapods and become adapted to further changes in the mandibular mechanism.

The mandibles of *Lebbeus* (fig. 8 D) resemble those of *Macrobrachium* except in that the incisor processes (*inc*) are relatively small and slender. The large molar processes (*mol*), as in *Macrobrachium*, are turned toward each other at right angles to the axes of the mandibles, so that with the rocking of the jaws on their axes the opposed surfaces of the molars work upon each other, and, it should be noted, they are turned outward by the adductor movement of the mandible, and inward with the abductor movement. Each mandible has at least two anterior dorsal muscles ( $D$ ,  $2A$ ,  $3A$ ); it is probable that a first muscle of the series was lost in dissection, since a well-differentiated abductor set of ventral fibers ( $2V$ ) is inserted on the inner surface of an elevated part of the mandibular margin that in *Macrobrachium* (F) gives insertion to two lateral adductor muscles ( $1A$ ,  $2A$ ). The relatively slender ligament of the ventral adductors in *Lebbeus* is supported by a pair of dorsal branches attached directly on the carapace.

In the caridean family Crangonidae the mandibles take on a highly aberrant form, and evidently function in a manner quite different from that of the ordinary decapod jaw. The mandible of *Sclerocrangon boreas* (fig. 8 G) is attached by its basal part in a wide membranous area between the mouth and the carapace, but it has no direct connection with either the carapace or the epistome. Its anterior end is turned abruptly mesally as a long, slender gnathal lobe that ends with a toothed expansion. The lobes of the opposing mandibles project directly toward each other into the sides of a capacious preoral cavity enclosed between the huge, 3-lobed labrum in front, and the long, divergent paragnaths behind, which arise from a thick, semicircular

metastomal base (see Snodgrass, in press, fig. 11 F). Mandibles such as these evidently can have no biting or chewing function; they must be used for jabbing into a mouthful of food. The musculature of the *Sclerocrangon* mandibles could not be determined from the material studied.

**Decapoda—Astacura.**—The astacuran mandibles lie transversely between the carapace and the mouth (fig. 9 A, *Md*), but they are somewhat inclined downward and strongly slanted forward, so that the gnathal lobes come together beneath and behind the labrum with their toothed margins in apposition. Laterally each mandible is articulated by a condyle (*a*) on the base of the inner lamella (*Dbl*) of the carapace fold in the angle between the latter and the broad pleural bridge of the maxillary segment (*mxB*) that limits the branchial chamber anteriorly (*brC*). Mesally the mandible is articulated in a socket (*c*) of the epistome at the side of the labrum, and furthermore, it has a strong linear hinge (*h*) on the epistomal margin laterad of the articular socket.

The mandible of *Cambarus*, or of other cambarine species, is somewhat quadrate in shape as seen from below (fig. 9 B). Projecting beyond the palpus as a direct continuation from the body of the mandible is the broad gnathal lobe (*gnL*), and in front of the palpus rises a large process that bears the epistomal articulation (*c*). On the lateral angle of the base of the jaw is a cup-shaped knob (*a*) that articulates with the carapace. The axis of rotation (*a-c*), therefore, is strongly oblique between the two articular points; the long epistomal hinge (*h*) falls in the plane of the axis. The movements of the mandible are thus strictly limited to movements of rotation, but the obliquity of the axis line gives the gnathal lobe (*gnL*) a wide swing on the perpendicular (*d*) from the axis (*a-c*); in adduction the toothed margins of the opposing lobes come directly together.

The operation of the astacuran mandible depends largely on the fact that the anterior margin of the jaw is produced into a wide, triangular apodemal lobe (fig. 9 B, C, *Ap*) between the epistomal hinge (*h*) and the lateral articulation (*a*). The apodeme is smaller in *Homarus* (D) than in *Cambarus* or *Astacus*, but it is characteristically more developed in the Astacura than in the natantian decapods, in which, as in *Macrobrachium* (fig. 8 I, *Ap*) it is represented at best only by a slight elevation of the mandibular margin. The apodeme attains its highest development in the Anomura and Brachyura.

The musculature of the astacuran mandibles presents the same functional fiber groups seen in *Macrobrachium*, but in the reptantian

decapods the ventral fibers no longer form an intermandibular muscle, since they have become attached on the intermaxillary apodemes of the ventral endoskeleton. The mandibular muscles of *Astacus* have

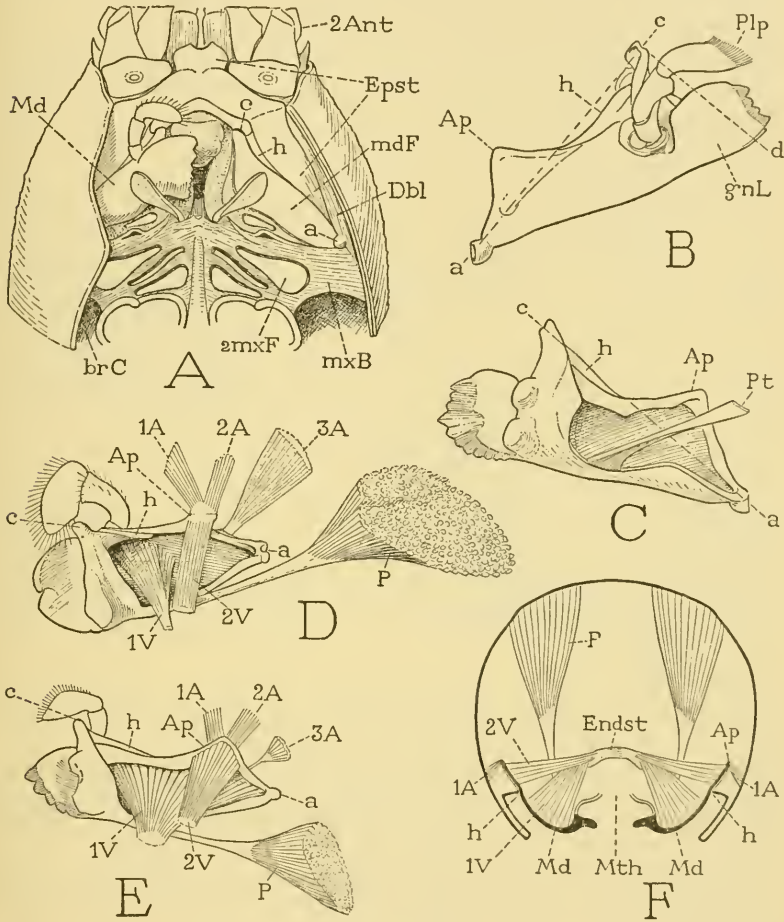


FIG. 9.—Crustacea—Decapoda: Astacura.

A, *Cambarus longulus* Girard, ventral surface of anterior part of body, with left mandible removed. B, *Cambarus* sp., right mandible, lateral. C, same, right mandible, dorsomesal. D, *Homarus americanus* M. Edw., right mandible and muscles, mesal. E, *Cambarus* sp., right mandible and muscles, mesal. F, sectional diagram of astacuran mandibular mechanism.

been fully described by Schmidt (1915); those of *Cambarus* and related genera (fig. 9 E) are the same as in *Astacus*, but in *Homarus* (D) the relative size of some of the muscles is different.

The first two anterior dorsal muscles of the mandible in both



*Homarus* and *Cambarus* (fig. 9 D, E, 1A, 2A), as in *Astacus*, are attached on the outer face of the mandibular apodeme (*Ap*) and pull laterally from their origins on the carapace. These two muscles together, therefore, are termed by Schmidt the *adductor lateralis* of the mandible. The third muscle of the anterior series (3A), inserted laterad of the apodeme, arises dorsally on the carapace and preserves its original abductor function. It is the *abductor minor* of Schmidt, and is also very small in *Cambarus* (E), but in *Homarus* it is a muscle of large size (D, 3A). The *adductor posterior* (*P*) is a huge, conical muscle arising by a broad base on the dorsum of the carapace anterior to the "cervical" groove, with its fibers converging to a long, thick tendon attached on the posterior margin of the mandible at the base of the gnathal lobe (C, *Pt*). The principal group of ventral fibers in *Astacus* and *Cambarus* (E, 1V) spreads into the entire cavity of the mandible, but in *Homarus* (D) the fibers form a relatively small muscle in the anterior part of the mandibular cavity. These fibers retain the primitive adductor function of the ventral muscles, and constitute the *adductor anterior* of Schmidt. A second and quite distinct group of ventral fibers (D, E, 2V) is attached on the inner face of the mandibular apodeme, and thus forms a muscle antagonistic to the lateral adductors (1A, 2A) attached on the outer face of the apodeme. This muscle (2V) is termed by Schmidt in *Astacus* the *abductor maior*, but in *Homarus* it is exceeded in size by the "abductor minor" (D, 3A).

The mechanism of the astacuran mandibles will be readily understood from the diagram, figure 9 F. Each mandible is hinged on the lateral wing of the epistome at *h*. The mandibular apodeme (*Ap*) is inflected above the line of the hinge, so that the muscles (1A, 2V) inserted on its opposite surfaces become respectively adductors and abductors. The principal adductor power of the mandibles, however, must reside in the great posterior dorsal muscles (*P*), and in the ventral muscles (1V) attached within each mandible below the hinge line.

**Decapoda—Palinura.**—The mandibles in this group (fig. 10) are variable in their form and structure, and at one extreme they take on special features of the anomuran and brachyuran mandibles. The palinuran mandibles, however, have one distinctive character, which is the presence of a long, tapering articular process arising mesad of the palpus, which fits into a deep notch between the labrum and the epistome (see Snodgrass, in press, fig. 15 C). On the outer edge of the articular process is the epistomal hinge of the mandible (fig. 10 A, D, *h*), and at its apex the epistomal articulation (*c*). The gnathal lobe



is simple, its margin may be even (A) or toothed (D), but there is no differentiated molar process. The mandibular musculature is the same as in *Astacura*.

The mandible of *Panulirus* (fig. 10 A) has the general features of the astacuran mandible, but the apodemal lobe (*Ap*) is greatly enlarged and produced proximally so that it not only rises far above the axis of the mandible (*a-c*), but projects somewhat beyond the lateral articulation (*a*). The apodeme thus becomes a very effective

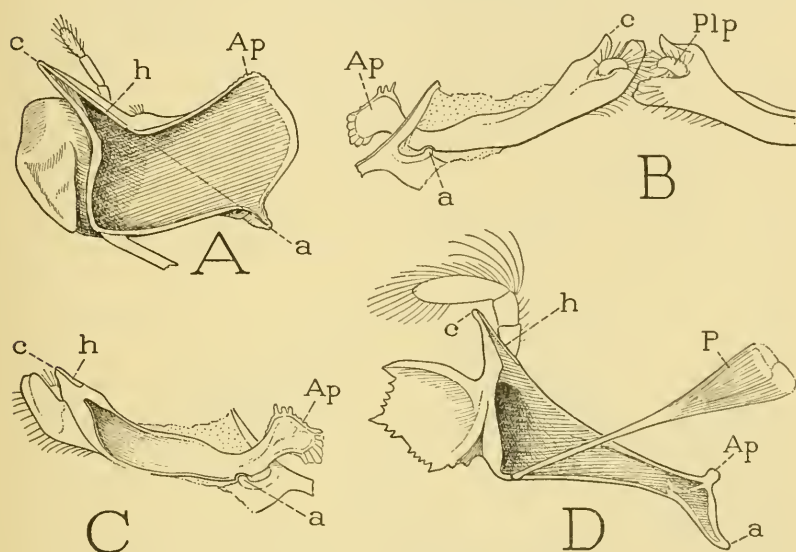


FIG. 10.—Crustacea—Decapoda: Palinura.

A, *Panulirus argus* (Latr.), right mandible, dorsal. B, *Scyllarus americanus* (Smith), mandibles, ventral. C, same, right mandible, dorsal. D, *Polycheles tanneri* Faxon, right mandible, dorsal.

lever for the abductor and adductor muscles attached on its opposite sides.

In *Polycheles* (fig. 10 D) the mandible is more slender and elongate; its apodeme (*Ap*) is a small knob near the proximal end of the anterior margin of the mandible, but the articular process (*a*) is turned posteriorly to give leverage to the short apodeme.

The mandibles of *Scyllarus* (fig. 10 B, C) are still more slender than those of *Polycheles*. The apodeme (*Ap*) is a large, expanded lobe extended into the body cavity so far beyond the lateral articulation (*a*) that it appears to be the outer end of the mandible itself, with the articulation transposed to the posterior margin. The true

relation of the parts, however, is evident on referring back to *Polycheles* (D), *Panulirus* (A), and the *Astacura* (fig. 9 B). On the other hand it will be seen that the scyllarid type of mandibles is still more elaborated in the *Anomura* and the *Brachyura*.

**Decapoda—Anomura and Brachyura.**—The structure and mechanism of the mandibles are so much alike in the anomuran and brachyuran decapods that the mandibles of the two groups may be treated together. Before taking up the mandibles, however, attention must be given to the ventral skeleton on which the jaws are supported. In the *Astacura*, as already noted, the mandibles are articulated laterally on the inner walls of the carapace folds (fig. 9 A, *a*), and behind them are the broad, horizontal pleural bridges (*mxB*) that connect the sternal region of the second maxillary segment with the carapace. In the *Anomura*, as seen in *Aegla* and *Galathea* (fig. 11), the maxillary bridges are reduced to narrow bars (*mxB*), and the mandibles (*Md*), instead of being articulated on the carapace, as in *Astacura* and most other Crustacea, have their lateral articulations (*a*) on the mesal ends of the pleural bars close to the second maxillary foramina (*2Mx*). As a consequence, the mandibles are much shortened. In *Petrolisthes eriomerus* (fig. 12 A, B) the sclerotic bridges themselves (*mxb*) do not reach to the carapace and appear as small lateral extensions from the rims of the maxillary foramina carrying the mandibular articulations (*a*). In the *Brachyura* the maxillary bridges are still more reduced; in *Callinectes* (fig. 14) for example, the only sclerotic connection of the rim of the second maxillary foramen (*2Mx*) with the carapace is a slender, tapering rod on the anterior margin of the branchial chamber (*brC*), and the mandibles have become articulated laterally on the anterior rims of the maxillary foramina (fig. 14; fig. 15 D, H, *a*). Between the mandible and the carapace there is now a wide space (fig. 14) occupied by a thin, semi-membranous extension of the doublure of the carapace that extends forward to the epistome (*Epst*) and forms the dorsal wall of the pump chamber of the respiratory passage. In both the *Anomura* and the *Brachyura* the mandibles retain the usual epistomal connections (figs. 12 A; 15 C, F, G) including the mesal articulations (*c*) and the marginal hinges (*h*).

Another character apparently peculiar to the anomurans and brachyurans is the presence of a pair of arms arising from the metastomal plate of the ventral skeleton (figs. 11 A, B; 16 D, H, *t*) that extend forward along the folds at the sides of the mouth and support the mandibles mesally at the base of the gnathal lobe (fig. 16 H). In *Uca pugilator* these mandibular props are wide sclerites at the sides

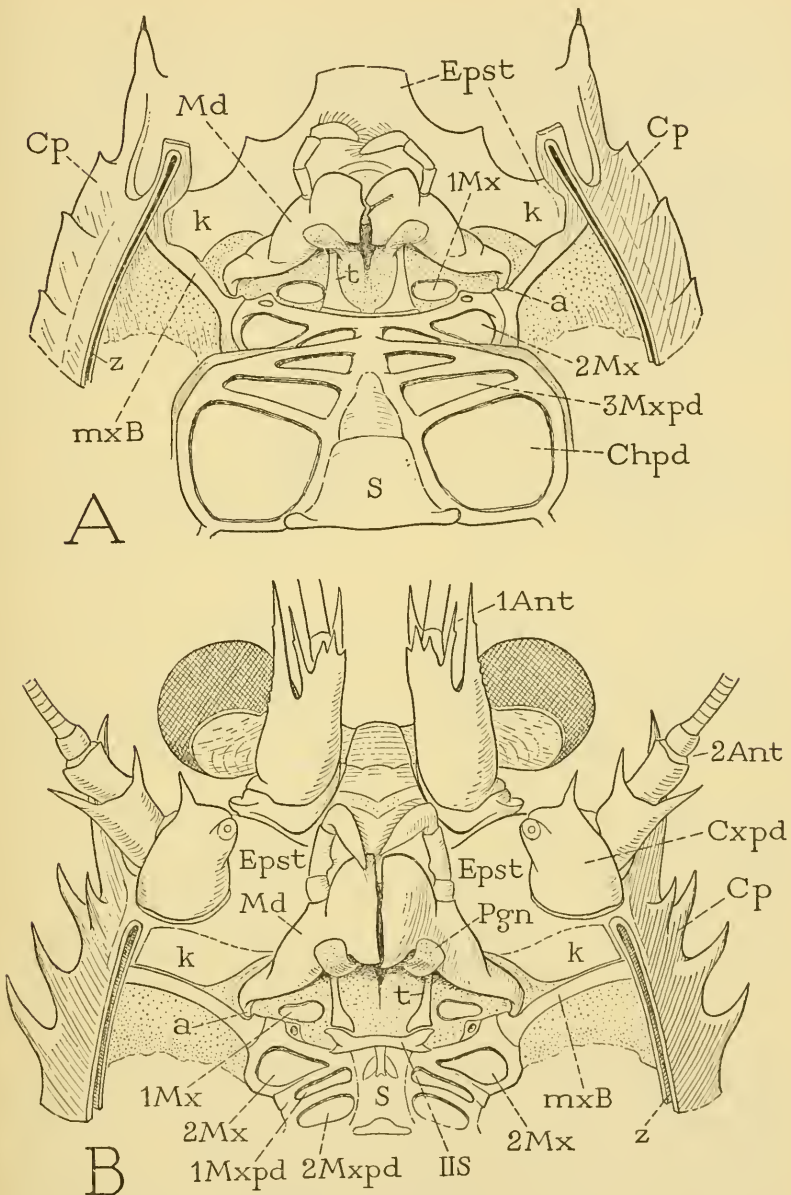


FIG. 11.—Crustacea—Decapoda: Anomura

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*).

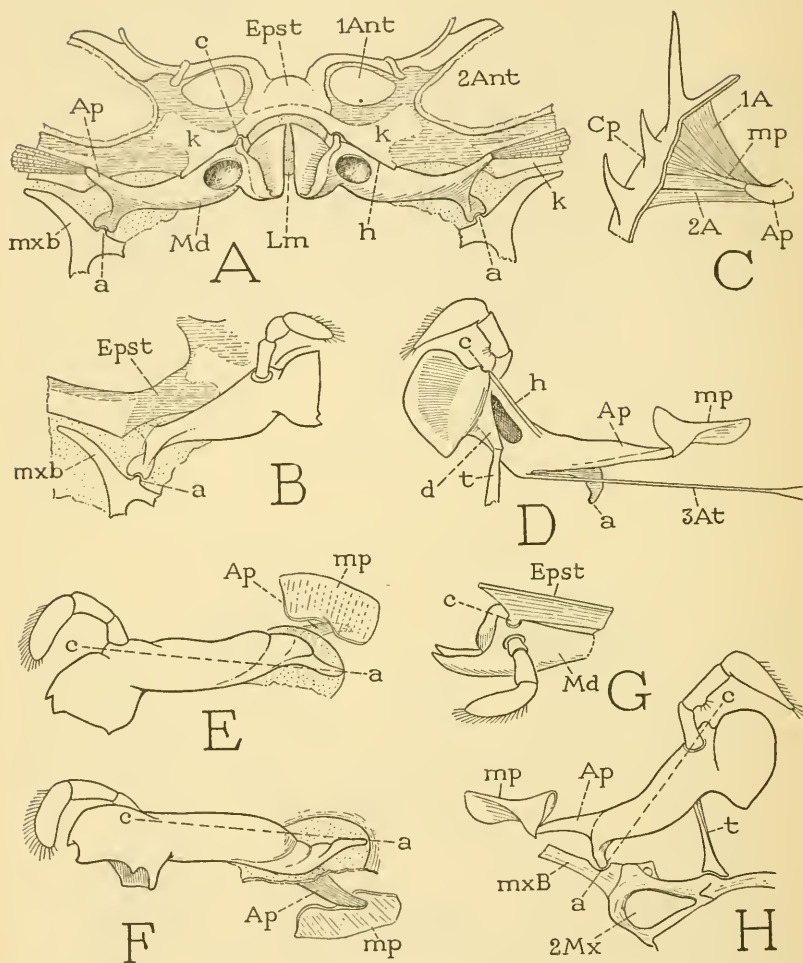


FIG. 12.—Crustacea—Decapoda: Anomura.

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. 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

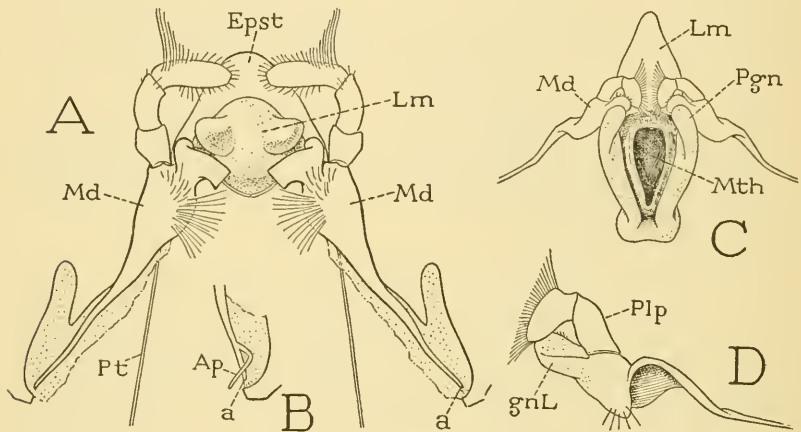


FIG. 13.—Crustacea—Decapoda: Anomura.

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,

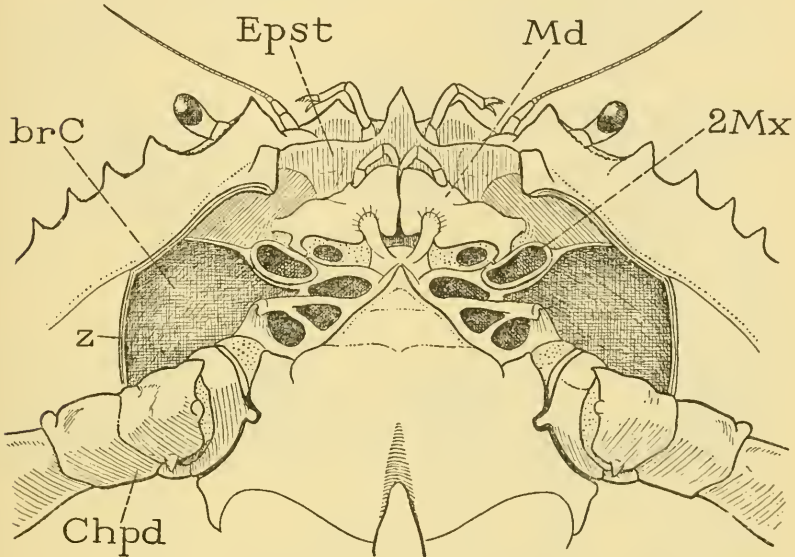


FIG. 14.—Crustacea—Decapoda: Brachyura. *Callinectes sapidus* Rathbun.

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, *IV*). The musculature and mechanism of the crab mandible is well shown in *Callinectes* (fig. 16 A, C) and *Cancer* (B). The great

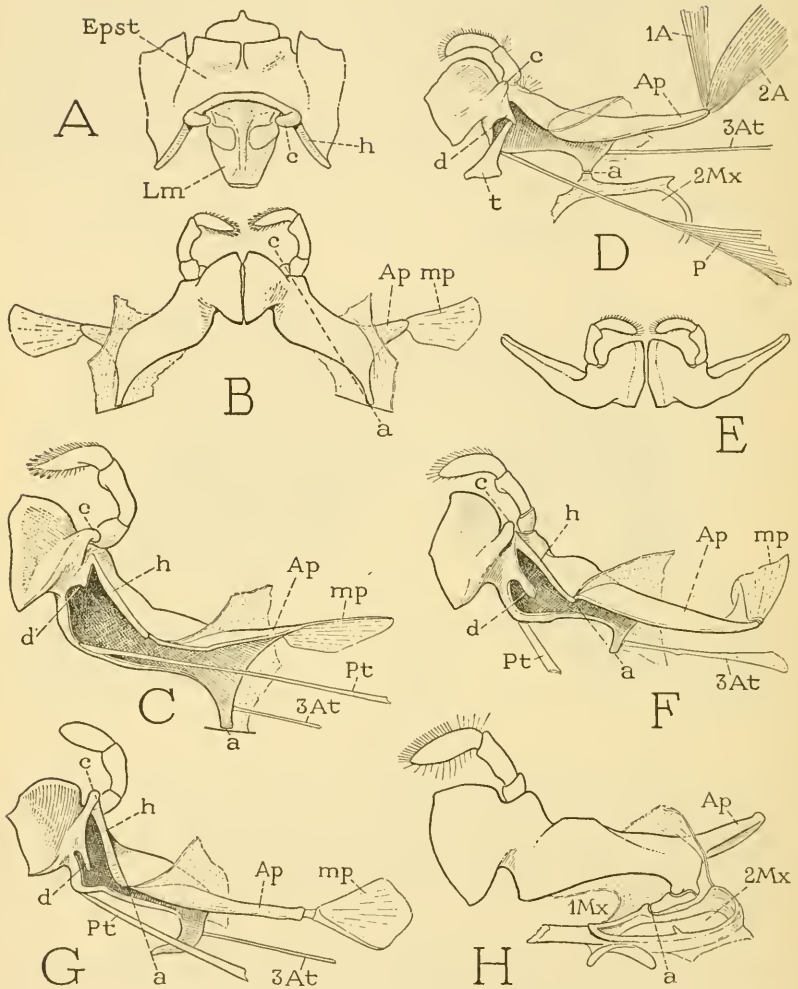


FIG. 15.—Crustacea—Decapoda: Brachyura.

A, *Dromidia antillensis* Stimpson, epistome and labrum, ventral. B, same, mandibles, ventral. C, same, right mandible, mesal. D, *Calappa flaminca* (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.

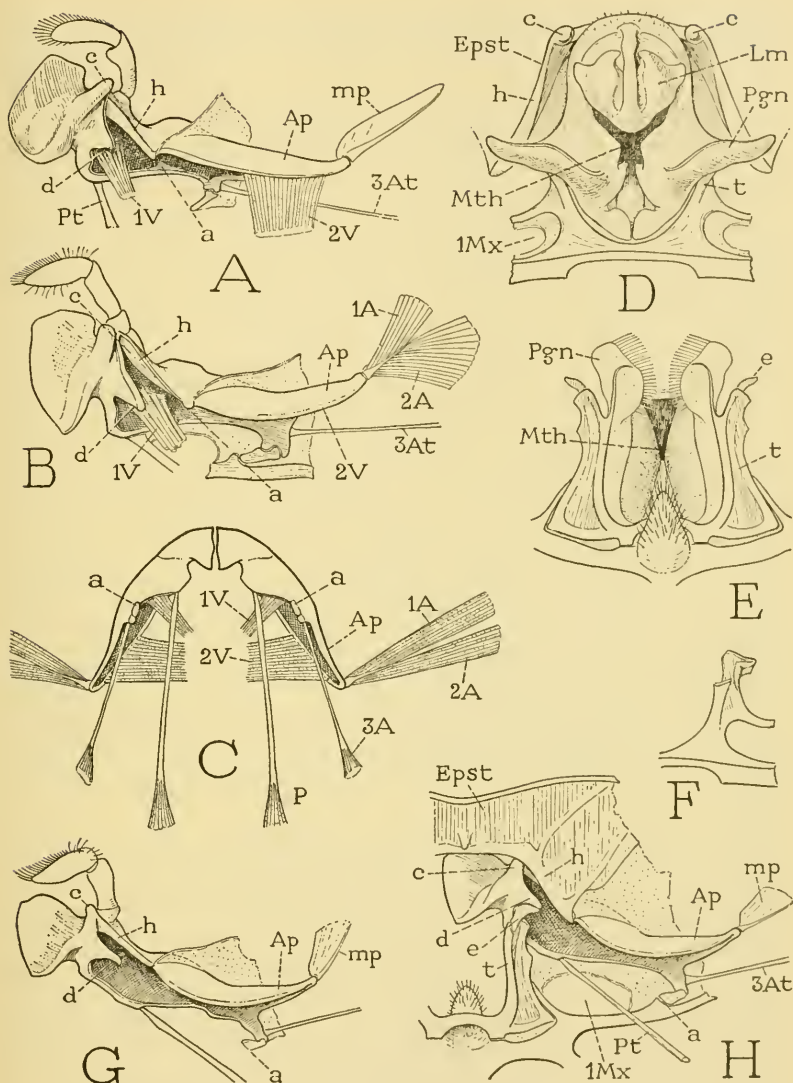


FIG. 16.—Crustacea—Decapoda: Brachyura.

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), mouth region, 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

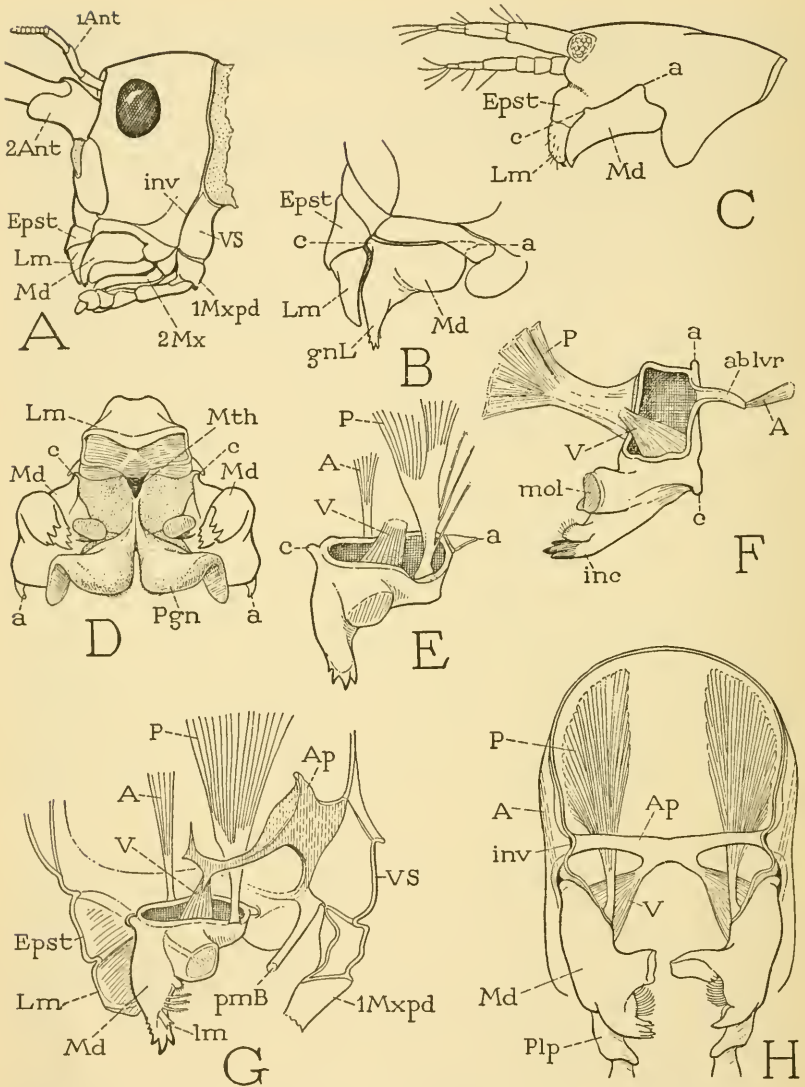


FIG. 17.—Crustacea—Tanaidacea (*Tanais*), Amphipoda (*Orchestoidea*, *Talorchestia*, *Gammarus*), and Isopoda (*Ligyda*).

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 right side 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



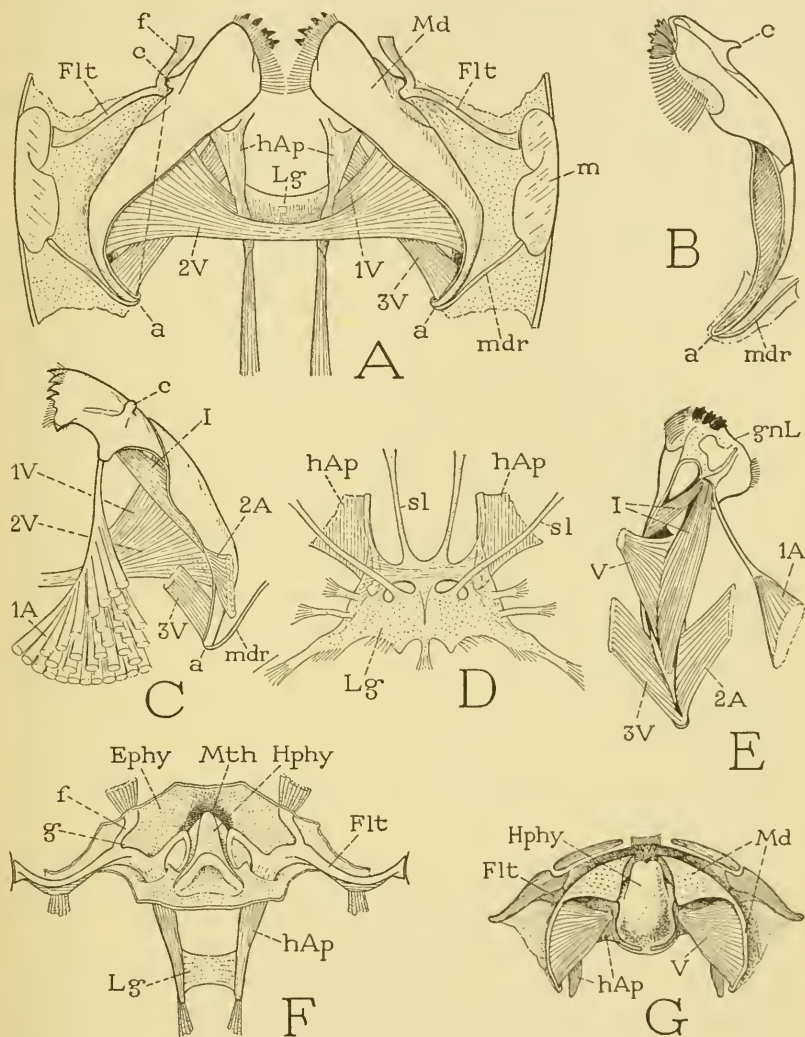


FIG. 18.—Chilopoda.

A, *Lithobius* sp., mandibles and muscles, furlular 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, furlular 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 lacinea 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 futurae*. 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

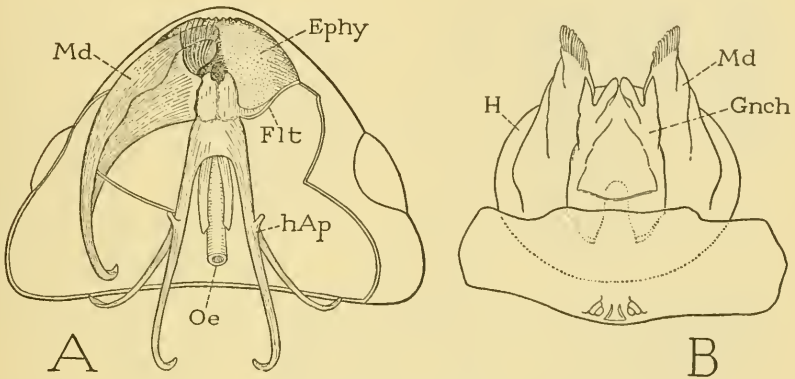


FIG. 19.—Pauropoda.

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

that there are no special muscles of the gnathal lobe, such as are present in those myriapods that have a flexible or articulated gnathal lobe, and which appear to be absent also in the geophilids.

#### IV. SYMPHYLA AND DIPLOPODA

The symphyliids and the diplopods are two groups of progoneate myriapods that have little likeness in their body structure, but in the structure of the head and particularly in that of the mandible they have features in common that set them off from all the other arthropods, and would seem to link them with each other. The mandible in each group consists of a basal plate implanted on the side of the head (fig. 20 A, B, *mdB*), where it is but little movable, and of a gnathal lobe (*gnL*) articulated on the base, and freely movable by its own muscles. The musculature of the lobe is the same as that of the flexible gnathal lobe of a chilopod mandible. It might be supposed, therefore, that the symphyliid-diplopod jaw has been evolved from the more simple jaw of the chilopods; but, aside from the musculature, the mandibles of the two groups are widely different. The gnathal lobe of the symphyliid-diplopod mandible and its musculature have a curious resemblance to the lacinial lobe and musculature of an insect maxilla, but since the symphyliids have both first and second maxillae in addition to the mandibles, there can be no question of the identity of their jaws with the mandibles of other arthropods.

The mandibles of Symphyla are somewhat simpler than those of the diplopods. The elongate basal plates (fig. 20 B, *mdB*) lie longitudinally on the sides of the head, separated from the deeply angulated cranial margins above them by wide membranous spaces containing the head spiracles (*Sp*). The flattened gnathal lobes (*G*, *gnL*) project forward, and are flexible in a horizontal plane. Each lobe is articulated by the outer angle of its base on the end of the supporting plate. On the dorsal side is a small process (*c*) that bears against a sclerotic ridge of the epipharyngeal surface above it, but does not form a true articulation, and is suggestive of the similar structure in the chilopods. The biting edge of the gnathal lobe is strongly toothed, and bears a small dentate plate (*lm*), or so-called "lacinia mobilis," flexibly inserted between the fixed teeth on both sides of it. Attached on the mesal angle of the gnathal lobe is the tendon of the flexor, or adductor, muscle, a huge bundle of convergent fibers (*1A*) from the posterior part of the cranium. The musculature of the basal plate includes a second dorsal (primitively anterior) muscle (*2A*), arising on the cranium, and two ventral adductors (*1V*, *2V*), both of which arise on

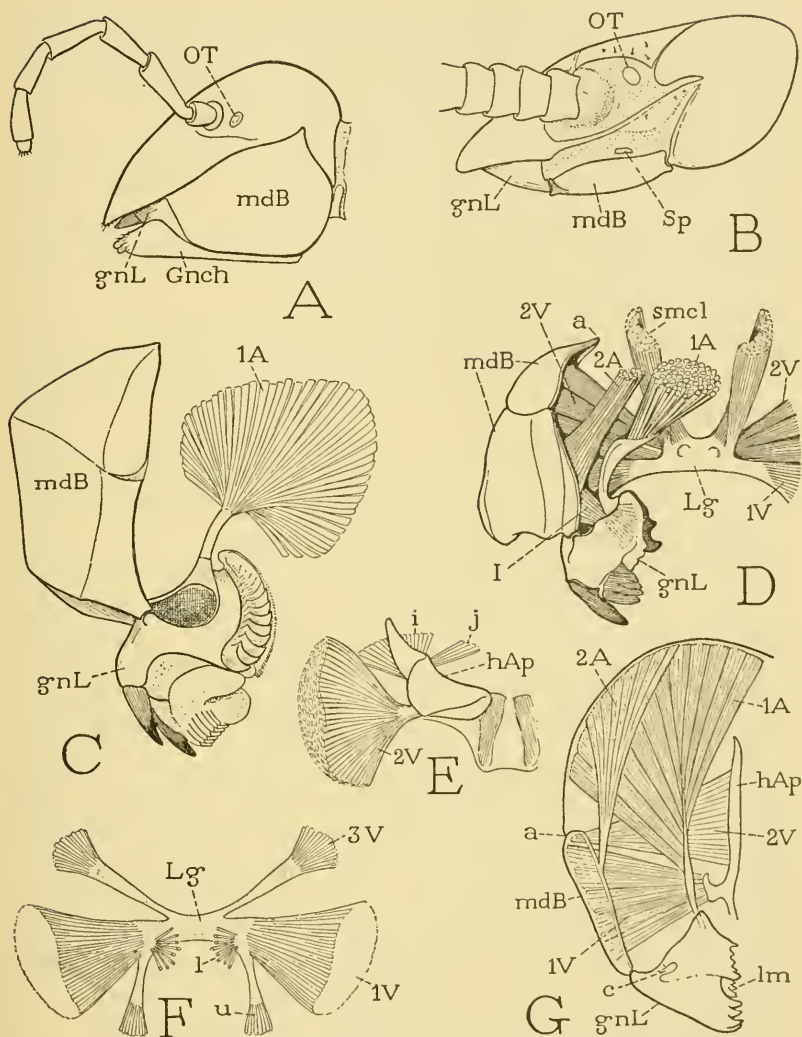


FIG. 20.—Symphyla (*Scutigrella*) and Diplopoda (*Fontaria*, *Thyropygus*).

A, *Fontaria virginiensis* (Drury), head, lateral. B, *Scutigrella immaculata* (Newp.), head, lateral. C, *Fontaria virginiensis* (Drury), left mandible, with cranial flexor muscle of gnathal lobe, ventral. D, *Thyropygus* sp., right mandible and muscles, dorsal. E, *Fontaria virginiensis* (Drury), head apodeme (hypopharyngeal apophysis) of left side, and attached muscles, ventral. F, same, intergnathal ligament and its muscles, dorsal. G, *Scutigrella immaculata* (Newp.), outline of right half of head, and right mandible with muscles, dorsal.

the corresponding head apodeme (*hAp*), there being no intermandibular fibers in the symphylids or any connecting ligament between the apodemes. The head apodemes, or hypopharyngeal apophyses, are invaginated at the side of the hypopharynx, but supporting plates, such as the premandibular fultural sclerites of the chilopods, pauropods, and some diplopods are absent in the Symphyla. Since the symphylids are exceptional among the myriapodous groups in lacking fultural sclerites, and have no intermandibular muscle fibers, they are probably to be regarded as specialized by the loss of these features, though in other respects they are fairly generalized.

In *Scutigera immaculata* (fig. 20 G) the anterior fibers of the adductor musculature of the mandible form a large, fan-shaped muscle (*1V*) arising on a small lateral lobe of the base of the apodeme and spreading to most of the length of the basal plate of the mandible. The fibers of the second muscle (*2V*) arise by a wide base on the apodeme, and converge to a narrow insertion on the posterior part of the mandibular plate. The same musculature is given by Tiegs (1940) for the mandible of *Hanseniella agilis*.

It is in the Diplopoda that the arthropod mandible attains its most remarkable development. The base of the organ in this group is a large plate on the side of the head (fig. 20 A, *mdB*) occupying the entire space between the emarginate edge of the cranium and the gnathochilarium, and is usually divided by a groove into a proximal and a distal part. The plate, in fact, is virtually a part of the head wall, but the attachment on it of the usual mandibular muscles shows that it is truly the base of the mandible. The basal plate of a dead specimen appears to be but little movable, and a live specimen, when handled, keeps its jaws so tightly closed that no evidence of their action can be obtained. The great size of the muscles inserted on the mandibular plates (fig. 20 D), however, attests that these muscles must have some important function. The large gnathal lobe of the mandible, being freely movable on the basal plate and strongly muscled (C, D, *gnL*), becomes the functional jaw of the animal. It is armed at the apex with large teeth flexible at their bases, and on the mesal side is a variously developed molar surface. The principal muscle of the lobe is a huge cranial flexor (*1A*) composed of spreading fibers arising on the dorsal wall of the head and inserted on the mesal angle of the base of the gnathal lobe by a thick tendon. A smaller intramandibular flexor, present at least in some forms (D, *I*), has its origin within the basal plate of the mandible.

The musculature of the basal plate, as above noted, includes the usual dorsal and ventral muscles of a typical mandible. Inserted on



the dorsal (anterior) margin is a thick muscle (fig. 20 D, *2A*) from the dorsal wall of the head, corresponding with the anterior rotator of a primitive mandible; a ventral (posterior) rotator, however, appears to be absent in the Diplopoda, as also in the Chilopoda and Symphyla. The true ventral muscles include an anterior adductor (*1V*) arising on a thick intergnathal ligament (*Lg*), and a posterior group of adductor fibers (*2V*) arising on the head apodeme. In *Fontaria virginensis* the intergnathal ligament (F, *Lg*) gives off on each side a large conical mass of fibers (*1V*) into the anterior part of the mandibular base, and branches posteriorly into two slender arms from which arise smaller groups of fibers (*3V*) inserted in the posterior parts of the mandibular bases, while a pair of short anterior branches support small fiber groups (*u*) inserted within the gnathal lobes. From the bases of the anterior branches groups of slender fibers (*l*) go to the under surface of the stomodaeum. The second large bundle of adductor fiber in *Fontaria* (E, *2V*) arises on the head apodeme (*hAp*) and spreads into the middle part of the basal mandibular plate. The intergnathal ligament of the diplopods is free from the head apodemes below it, but the muscle fibers arising from it are evidently the first groups of adductor fibers in Symphyla (G, *1V*), which have become attached on the apodemes.

Fully developed premandibular ventral sclerites attached laterally on the cranial margins are present in some diplopods as in the chilopods and pauropods, but in most forms the sclerites are reduced to small plate at the sides of the hypopharynx, from which the head apodemes arise. The apodemes of *Fontaria* (fig. 20 E, *hAp*) taper posteriorly and dorsally in the head, and their apices are attached to the central discs of the organs of Tömösvary (A, *OT*). Two small muscles from the dorsal head wall are inserted on each apodeme (E, *i, j*), so that the apodemes appear to act as levers possibly effecting an elevation of the hypopharynx.

#### V. THE ENTOGNATHOUS APTERYGOTE HEXAPODS

The wingless, 6-legged arthropods included under this heading are the Protura, the Collembola, and the Diplura (or Dicellura). They are usually classed as insects along with the Thysanura and Pterygota but are here treated as a separate group of hexapods because, in addition to being entognathous, they have head characters that set them apart from all the other insects, while their mandibles have no counterparts among the Thysanura or Pterygota, either in structure or mechanism, and show certain features suggestive of the mandibles of the

chilopods. The mandibles together with the maxillae lie horizontally on the under side of the head, where their basal parts are enclosed in gnathal pouches formed by union of the labium beneath them with the lateral edges of the cranium. Because of the horizontal position of the mouth parts, the primitive anterior surfaces become dorsal, the posterior surfaces ventral.

A characteristic feature of the entognathous apterygotes, not found in any of the other insects, is the presence of a pair of rodlike sclerotizations extending posteriorly from the hypopharynx in the inner walls of the gnathal pouches between the bases of the maxillae and the labium (fig. 21 D, *imB*), which diverge posteriorly and support the maxillary cardines. As seen in specimens cleared and mounted whole, these rods appear to be apodemes, and have been regarded as "tentorial arms," but it has been shown by Folsom (1900) that, in their origin in Collembola, they are linear sclerotizations of the ventral head wall. In their position between the maxillae and the labium, or second maxillae, the rods are quite comparable to the intermaxillary sternal brachia of Crustacea, which in the isopods and amphipods similarly support the first maxillae (see Snodgrass, in press). In the Protura the anterior parts of the rods are united with each other forming a Y-shaped structure. In the Diplura the two rods are connected inside the head by an arched ligamentous bridge (fig. 21 D, *Lg*), on which are attached muscles of the mandibles and maxillae; in Collembola the bridge is elaborated into a highly developed platform for muscle attachments, which is known as a "tentorium," though it can have no relation to the tentorium of Thysanura and Pterygota.

The mandibles of the entognathous hexapods are elongate, with the gnathal lobes extended in line with the bases of the appendages, sometimes drawn out into piercing stylets, but never flexible or independently movable as in the myriapods. In Protura and Collembola each mandible is connected posteriorly with the cranial margin, as in Chilopoda, by a slender rod in the lateral wall of the gnathal pouch. According to Hoffmann (1908) the mandibles of Collembola have also an anterior articulation on the head. In Diplura there is neither an anterior nor a posterior articulation. Regardless of the type of articulation, however, the mandibles are protractile and retractile, and in addition apparently have a strong rotary movement on their long axes. The mandibular musculature is similar in the three entognathous groups; it becomes unusually complex in the Collembola, probably no other arthropod having so many muscles attached on its jaw, but the musculature is merely an elaboration of the usual anterior and

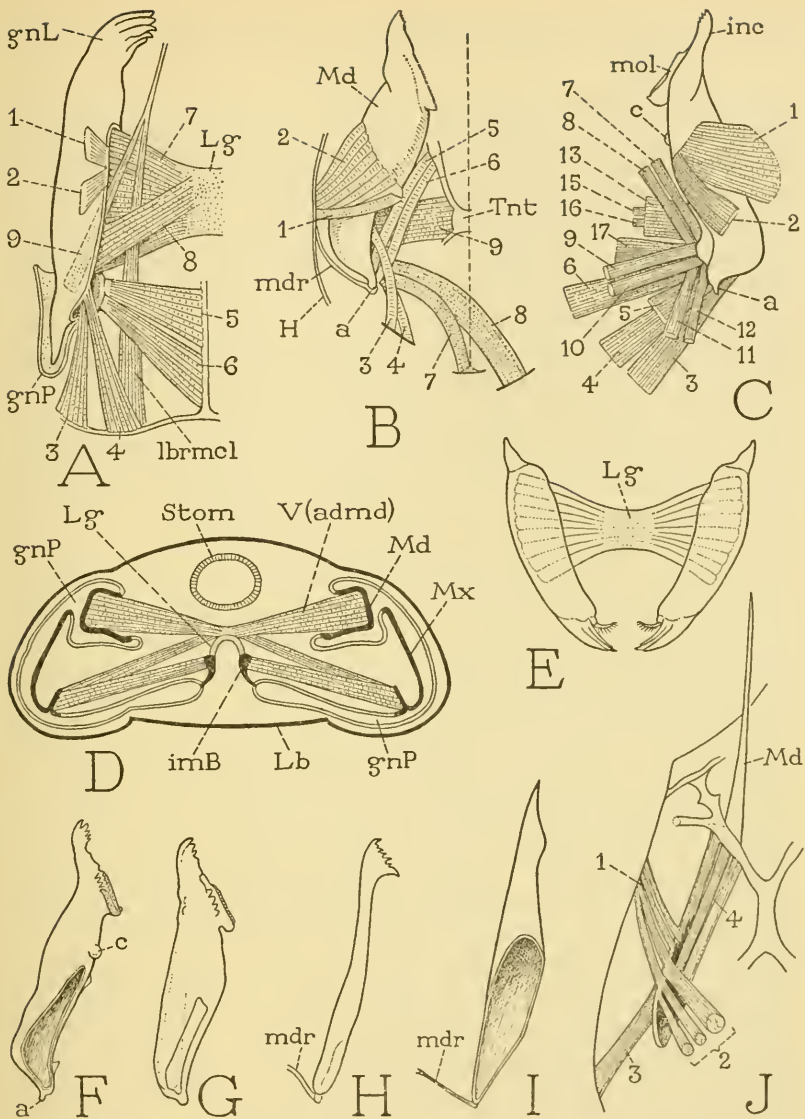


FIG. 21.—Hexapoda—Entagnathous apterygotes: Diplura, Collembola, and Protura.

A, *Heterojapyx gallardi* Tillyard, left mandible and muscles, dorsal. B, *Orchesella cincta* L., left mandible and muscles, dorsal (from Folsom, 1899). C, *Tomocerus plumbeus* L., right mandible and muscles, dorsal (adapted from Hoffmann, 1908). D, *Heterojapyx gallardi* Tillyard, cross section of head. E, *Campodea* sp., mandibles and adductor muscles. F, *Tomocerus plumbeus* L., right mandible, ventral (from Hoffmann, 1908). G, *Entomobrya lanugenosa* (Nicolet), mandible (from von Stummer-Traunfels, 1891). H, *Anurida maritima* Guér., left mandible, dorsal (from Folsom, 1900). I, *Eosentomon germanicum* Prell, right mandible, ventral (from Prell, 1913). J, *Acerentomon doderoi* Silvestri, left mandible and muscles, dorsal (from Berlese, 1910, part of fig. 121, pl. 12).

posterior dorsal muscles and the ventral muscles of a more primitive mandible.

**Diplura (Dicellura).**—The simple, elongate mandible in this entognathous order (fig. 21 A) has a long mesal attachment on the membranous inner wall of the gnathal pouch (D, *Md*), but it has no articulation with the cranium either anteriorly or posteriorly. The elongate, toothed gnathal lobe is blunt in Japygidae (A); in *Campodea* (E) it is more acute and bears mesally a small setose appendage. The proximal end of the mandible is extended into a tapering process (A) that lies free in the containing gnathal pouch (*gnP*).

The mandibular musculature, as seen in *Heterojapyx gallardi* (fig. 21 A), consists of six dorsal muscles (1-6) arising on the cranium, and two ventral muscles (7, 8) attached on the ligamentous bridge (*Lg*) that connects the two intermaxillary sternal brachia (D, *Lg*) of the inner walls of the gnathal pouches. The cranial muscles attached dorsally on the mandible (representing the *A* fibers of a more generalized mandible) include two distal lateral rotators (A, 1, 2) and two proximal retractors (3, 4); those attached ventrally (the *P* fibers) are two large mesal rotators (5, 6) from the median ridge of the cranium. The ventral muscles include a wide sheet of transverse adductor fibers (7), and a smaller band of oblique fibers (8), which is evidently a protractor. All the ventral fibers of the mandibles, as above noted, arise from the ligamentous bridge between the intermaxillary sternal brachia (D, *Lg*). Superficially the fibers from the opposite mandibles united on the bridge give the appearance of an intermandibular muscle, as seen in *Campodea* (E), and were formerly described as such by the writer (1928). The association of the mandibular muscles with the sternal brachia (D, *Lg*), however, is certainly secondary, since these rods support the first maxillae and can have no relation to the mandibular segment. The mandibular adductors of the Diplura represent the ventral muscles of the mandibles that are attached on an intergnathal ligament in more generalized arthropods.

Within the mandible of *Heterojapyx* there arises posteriorly a slender muscle (fig. 21 A, 9) that anteriorly joins the tendon of a long labral muscle (*lbrmcl*) arising posteriorly on the cranium, and inserted by its tendon on the base of the under wall of the labrum. No such muscle has been observed in any other insect.

**Collembola.**—The collembolan mandibles in general resemble the mandibles of Diplura, but in vegetable-feeding species the gnathal lobe is more or less differentiated into an incisor process and a molar surface (fig. 21 B, C, F, G); in *Anurida*, however, which is said by



Folsom (1900) to feed on the soft tissues of the mollusk *Littorina*, the slender mandible (H) simply expands distally in a sharply toothed lobe.

The mandibles of Collembola, being protractile and retractile within the gnathal pouches, have no fixed articulations, but each mandible is supported posteriorly on the end of a slender, rodlike thickening of the lateral pouch wall (fig. 21 B, *mdr*), which is attached anteriorly on the margin of the cranium (*H*). This suspensory structure of the collembolan mandible, found also in Protura (*I*), exactly duplicates the attachment mechanism of the jaw in the Chilopoda (fig. 18 A, *mdr*) and Pauropoda. The mandibular rod is called the "stirrup" by Folsom (1899); Denis (1928) refers to it as a "ligament." Folsom believed that in protraction the mandible left the socketlike end of the "stirrup," but Denis points out that the rod, or "ligament," is attached to the mandible and is itself a part of the wall of the gnathal pouch, so that it simply bends forward or backward with the movement of the jaw. According to Hoffmann (1908) the collembolan mandible has an anterior process (fig. 21 F, *c*) that bears against an articular surface of the head at the base of the "anterior tentorial arm." Evidently a disarticulation must take place here when the mandible is protracted. Other writers have not recorded the existence of an anterior articulation in Collembola.

Descriptions of the collembolan mandibles have been given by several writers, including von Stummer-Traunfels (1891), Folsom (1899, 1900), Hoffmann (1908), Denis (1928), Hansen (1930). Folsom, Hoffmann, and Denis include also a full account of the mandibular musculature. The number of muscles attached on each mandible differs in different genera, but the fiber bundles all fall into the usual three major groups attached on a generalized mandible, namely, anterior dorsal muscles and posterior dorsal muscles arising on the cranial wall, and ventral muscles, which in the Collembola arise on the "tentorium." Because of the horizontal position of the collembolan jaws, the primitively anterior muscles become dorsal, and the posterior ventral. By diversification of their points of origin on the head, the dorsal muscles are differentiated functionally into rotators and retractors of the jaw, and similarly the fibers of the primary ventral adductor are differentiated into adductors and protractors.

Folsom (1899) finds in *Orchesella cincta* 10 muscles attached on each mandible (fig. 21 B), 7 arising on the cranial wall, and 3 on the "tentorium." Of the cranial muscles, four are attached dorsally on the mandible and three ventrally. As named and numbered by Folsom,

the dorsal muscles include a *lateral rotator* (1), an *abductor* (2), a *retractor and rotator* (3), and a *retractor* (4); the ventral muscles include two long rotators (7, 8) and another not shown in the figure lying beneath 7. The "tentorial" fibers are differentiated into a broad transverse *adductor* (9), and into two *protractors* (5, 6) extending from the posterior end of the mandible to the anterior arm of the "tentorium."

It will be observed that the musculature of the mandible in *Orchesella* (fig. 21 B) is essentially identical with that of the dipluran *Heterojapyx* (A). A much simpler mandibular musculature is found by Denis (1928) in *Anurida maritima*, consisting of three rotators arising on the head wall, adductors from the body of the "tentorium," and protractors arising at the base of the lingua. In *Onychiurus fimentarius* Denis shows the musculature to be more complex than that of *Anurida*, since it includes the same muscles and some others in addition. In *Tomocerus catalanus* he finds an elaborate mandibular musculature essentially the same as that described by Hoffmann for *Tomocerus plumbeus*.

The mandibles of *Tomocerus plumbeus* have the greatest number of muscles attached on them yet recorded for any collembolan. As given by Hoffmann (1908) there are 17 distinct fiber bundles inserted on each mandible of this species (fig. 21 C). To eight of these muscles (1-6, 9, 10) arising dorsally on the head wall, Hoffmann ascribes a rotary function, while two others (11, 12) with posterior origins are retractors. Opposed to the last are two muscles (7, 8) arising anteriorly on the "tentorial" arm, which are protractors. The rest of the muscles, five in number (13-17), are adductors with their origins on the body of the "tentorium" (14, being ventral, is not seen in the figure). Clearly, the mandible of this collembolan is equipped for hard work.

It should be noted here that the so-called "tentorium" of the Collembola appears to be a structure of the nature of the intergnathal ligament of the crustaceans and myriapods, supported on the intermaxillary sternal brachia, and clearly has no homology with the cuticular tentorium of Thysanura and Pterygota (see Snodgrass, in press).

**Protura.**—The mouth parts of Protura have been described by Berlese (1910), Prell (1913), Hansen (1930), and Tuxen (1931). The mandibles are slender and sharp-pointed (fig. 21 I), in some forms drawn out into long, tapering stylets (J, *Md*). The base of each mandible is attached mesally to the membranous inner wall of the gnathal pouch and opens by an elongate foramen into the head cavity (I); the narrowed posterior end is shown by Prell to be con-

nected with the cranium by a slender rod (I, *mdr*). Tuxen interpreted the mandibular rod as a "pleural apodeme" of the head, but there can be little doubt that it is a mere thickening of the wall of the gnathal pouch, as is the similar rod in Collembola and Chilopoda.

The mandibular musculature in the Protura is simplified because its chief function is that of protraction and retraction. The musculature of the mandible of *Acerentomon doderoi* (fig. 21 J), as described and figured by Berlese (1910), consists of anterior and posterior fiber bundles disposed in the form of an X, so that the two opposing sets appear to be protractors and retractors. The lateral anterior muscles (1) and the mesal posterior muscles (2), however, both arising on the cranium, are diagonal with respect to the axis of the mandible and are attached on its upper margin. These muscles, therefore, must have a rotary action on the mandible accompanying protraction and retraction. The other muscles (3, 4) are approximately parallel with the mandibular axis, and undoubtedly are protractors and a retractor. The single retractor (3) arises posteriorly on the cranium; the three protractors (4) take their origins anteriorly on the anterior arm of the Y-shaped sternal sclerite of the head (the so-called "tentorium" of Berlese and Prell). These ventral protractors of the proturan mandible, as noted by Tuxen, are derivatives of the primitive ventral adductors of the appendage; as are the corresponding protractors of the mandible in Collembola, Diplura, and Chilopoda; functionally adductor fibers appear to be absent in Protura.

## VI. THYSANURA

There can be little question that the ectognathous thysanuran and pterygote insects are more closely related to each other than either group is to the entognathous apterygotes, and yet their likenesses and differences are so inconsistently distributed that it is difficult to discover the nature of their interrelationships. The mandibles of the Thysanura differ conspicuously between the two principal families of the order, the Machilidae and the Lepismatidae, but not in a way that would preclude the evolution of the lepismatid type of jaw from that of the machilid. The machilid mandible is a pendent jaw with a single dorsal articulation, and is quite comparable in its form, musculature, and mechanism to the mandibles of lower Crustacea. The lepismatid mandible has a horizontally elongate base, is doubly articulated on the head, and the gnathal lobe projects downward from the axis of rotation, in which features it closely resembles, on the one hand, the mandibles of the isopods and amphipods among the

Crustacea, and, on the other, the biting and chewing type of jaw of the Pterygota, except larval Ephemeroptera. The ephemeropterid mandible more resembles the mandible of *Machilis* than that of the other pterygotes. The machilid jaw is simply a mandible of generalized type from which the doubly articulated jaw has been evolved independently in the Crustacea, Thysanura, and Pterygota.

The mandibles of Machilidae (fig. 22 A, B) are elongate and hang downward from the cranial margins behind the antennae on single points of articulation (*a*). The long oval base of each jaw is attached to the membranous lateral wall of the head below the cranial support, so that the jaw swings freely in a transverse plane; the free gnathal lobe is divided into an elongate, apical incisor process, and a thick molar process directed mesally. The musculature of the machilid mandible is typical of a jaw of its kind. Each mandible has an anterior and a posterior dorsal muscle (*A, A, P*), apparently rotary in function, and a large mass of ventral adductor fibers. The adductor fibers, however, are differentiated into a distal adductor (*1V*) and a proximal adductor (*2V*). The fibers of the first spread into the cavity of the mandible (*A, B, 1V*) and converge to a median ligament (*Lg*) by which they are united with the corresponding fibers of the opposite mandible. The ligament passes through the base of the hypopharynx behind the roots of the anterior tentorial arms (*A, AT*). The other ventral fibers form a wide, flat muscle (*A, 2V*) for each mandible arising on the tentorial arm and inserted on the posterior edge of the mandibular base. This muscle would appear to have a rotary as well as an adductor action on the jaw. The ventral musculature of the machilid mandible is thus seen to be the same as that of *Lithobius* (fig. 18 A) or a diplopod (fig. 20 D) in that the adductor fibers of each jaw are separated into a distal group united with the corresponding fibers from the opposite jaw, and into a posterior group attached individually on a head apodeme. The entire musculature of the machilid mandible is carried over into the Lepismatidae and the Pterygota, but in these groups the anterior fibers of the ventral adductors from each jaw become separately attached on the base of the hypopharynx.

The mandibles of Lepismatidae (fig. 22 D, *Md*) are attached to the lower margins of the head by their elongate bases, with anterior and posterior articulations, so that the gnathal lobes swing transversely on horizontal axes of rotation. The posterior articulation (*a*) is in a notch of the cranial margin. The anterior articulation (*c*) is not with the clypeus, as it is in the pterygote insects, but with a small condyle (*F, c*) on the ventrally inflected anterior angle of the gena (*Ge*) behind the clypeus, just outside the invagination (*at*) of the



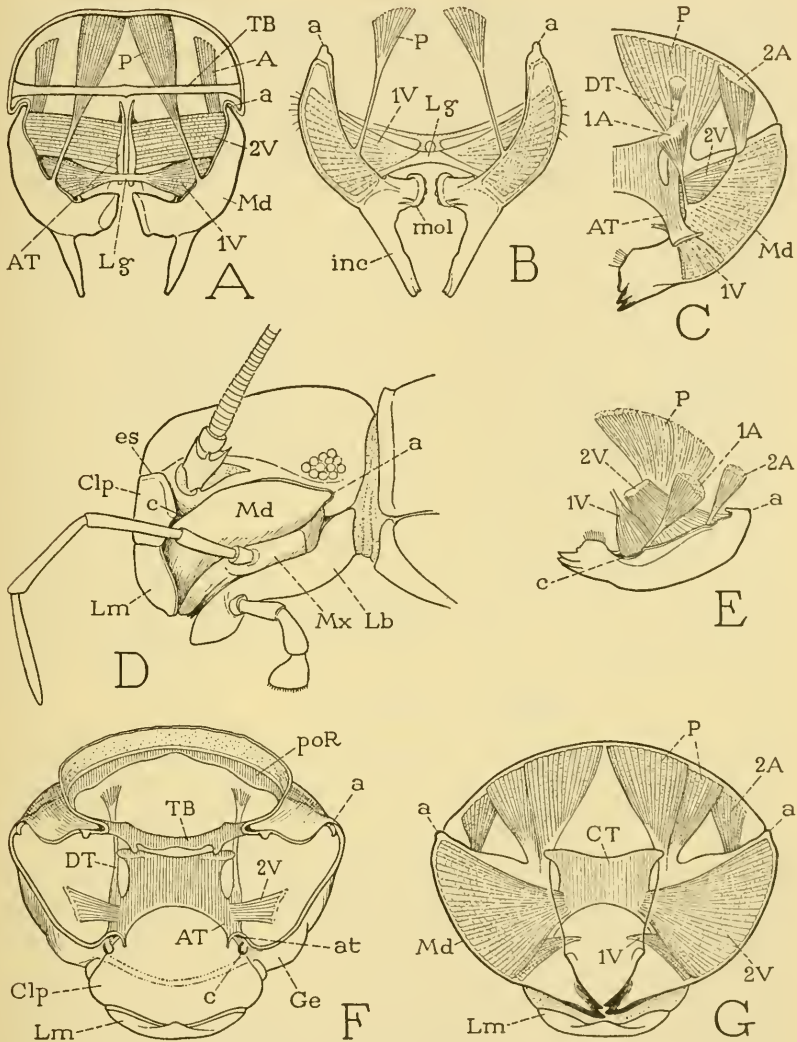


FIG. 22.—Hexapoda—Thysanura.

A, *Nesomachilis maoricus* Tillyard, vertical cross section through back of head, with suspended mandibles and their muscles, posterior. B, *Machilis* sp., mandibles, with intergnathal adductor and posterior cranial muscles, posterior. C, *Ctenolepisma urbana* Slabaugh, left mandible and muscles, with part of tentorium, dorsal. D, same, head, lateral. E, same, left mandible and muscles, lateral. F, same, horizontal section of head below tentorium, ventral. G, same, section of head and mandibles, showing distribution of mandibular muscles, ventral.

anterior arm of the tentorium (*AT*). It is evident that this anterior articulation of the mandible has been independently acquired in the Lepismatidae, since it is not the same as that in the Pterygota. The musculature of the lepismatid mandible corresponds with that of the machilid mandible in that it consists of anterior and posterior dorsal muscles and two ventral muscles (fig. 22 C, E); but, because of the horizontal axis of rotation of the lepismatid jaw (E, *a-c*), the anterior muscles, of which there are two in *Ctenolepisma* (*1A*, *2A*), become lateral abductors, and the single, greatly enlarged posterior muscle (*P*) a mesal cranial adductor. Of the two ventral muscles (C, E, *1V*, *2V*), both of which evidently are adductors, the second (*2V*) is much the larger and is attached on the anterior arm of the tentorium (C, F, G); the first (*1V*) is a relatively small muscle clearly corresponding with the intermandibular muscle of *Machilis* (A, B, *1V*), but the fibers from each mandible are attached separately on the suspensory arms of the hypopharynx, just as they are in the lower pterygote insects (fig. 24 B, C, *1V*). It is of interest to note again here that the lepismatid hypopharynx, as the writer has elsewhere shown (in press), has the structure typical of the orthopteroid hypopharynx, and in no way resembles the primitive 3-lobed hypopharynx of Machilidae and larval Ephemeroptera.

## VII. PTERYGOTA

The winged insects in their fundamental adult structure are well standardized, probably because the function of flight does not permit any great degree of diversification in body form. The flightless young, however, being free from the restrictions placed on the adults, have had liberty to adapt themselves to various special environments, and many of them have taken advantage of their freedom to the extent of assuming bodily forms that in most cases have no relation to the ancestral adult form, though, for the most part, the larval feeding organs have retained a fairly generalized structure. On the other hand, since the manner of feeding has little effect on the function of flight, adult insects have been free to develop highly specialized kinds of mouth parts. Hence, in a study of the mandibles, the jaws of the larva are likely to be more representative of the primitive mandibles of the species than are those of the adult.

Among the winged insects the Ephemeroptera stand apart from the other orders by various features that give them a relatively primitive status, as the wing venation and the paired genital openings of the adult, but other primitive characters, less commonly considered,

are found in the head and the mouth parts of the larva. The larval tentorium, for example, has its anterior roots in the ventrally inflected lower margins of the genae *mesad* of the mandibles (fig. 23 C, *at*) between the base of the clypeus and the posterior articulations of the mandibles, while in all other pterygote insects the anterior tentorial invaginations are *laterad* of the mandibles on the sides or the facial aspect of the head. The mayfly larva has a well-developed 3-lobed

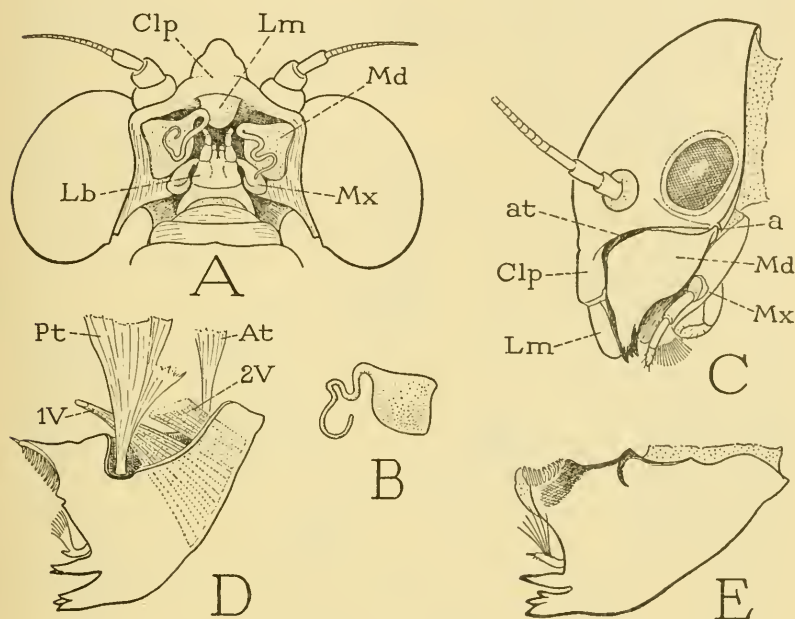


FIG. 23.—Hexapoda—Pterygota: Ephemeroptera.

A, *Hexagenia* sp., adult, ventral view of head and mouth parts. B, same, left mandible, ventral. C, *Leptophlebia* sp., larva, head, lateral. D, same, right mandible and muscles, mesal. E, same, left mandible, dorsolateral.

hypopharynx, such as occurs in Machilidae, the entognathous apterygote hexapods, the symphylids, and various crustaceans, but is found in no other pterygote insects, nor even in the Lepismatidae among the apterygotes. The large jaws of the ephemeropterid larva (fig. 23 C, *Md*) resemble those of other pterygote insects in general appearance and in their position on the head, but most surprising it is to find that they have no anterior articulations and no connection whatever with the clypeus. Each mandible has a posterior articulation, and is membranously attached to the subgenal margin of the cranium by only its posterior part, leaving a long, concave space on the ventrally

inflected area of the gena between it and the clypeus, in which the anterior part of the jaw rests and turns. Though the ephemerid larval jaw resembles in form and position the mandible of an orthopteroid insect (fig. 24 A), its actual structure is that of the singly articulated, pendent mandible of the Machilidae. Its musculature (fig. 23 D) is that typical of Lepismatidae and the lower Pterygota, there being a huge dorsal adductor inserted on a broad tendon (*Pt*), a slender dorsal abductor attached on a smaller tendon (*At*), and two ventral muscles, one of the latter (*IV*) being attached on the base of the hypopharynx, the other (*zV*) on the tentorium. Murphy (1922) erroneously ascribes all the muscle fibers inserted within the mandible, termed "flexors," to the tentorium.

In the adult mayfly (fig. 23 A) the mouth parts are greatly reduced. Sternfeld (1907) says the mandibles have vanished entirely, but in the species of *Hexagenia* here figured mandibles (A, *Md*) are distinctly present, though each mandible (B) is merely a small, soft, somewhat quadrate, flattened lobe with a long vermiform flagellum arising from its anterior mesal angle. Mandibles of similar form are shown by Murphy (1922) in the subimago of *Hexagenia recurvata*. Sternfeld notes that the reduction of the mayfly mouth parts begins in the nymphal stage, but that the alimentary canal, on the contrary, is not reduced at any stage. In the imago, Sternfeld says the alimentary canal is filled with air and serves for facilitating flight and particularly the act of hovering; the digestive tract thus gives up its original function, but it takes on a new one. From Sternfeld's sectional view of the anterior part of an adult mayfly it would appear that the pharyngeal muscles and the sucking apparatus are well preserved.

The typical pterygote mandible, as seen in the cockroach (fig. 24 A), is a doubly articulated jaw with an approximately horizontal axis of movement (*a-c*) on the lower, lateral margin of the cranium, so that it swings transversely toward its opponent. The mandibles close between the clypeus and labrum in front and the hypopharynx behind (D); in the cockroach the left mandible overlaps the right. The mandible is membranously attached to the head and the articular surfaces are external points of contact with the head wall (A). The primary articulation (*a*) is posterior on the subgenal margin of the cranium, the secondary articulation (*c*) is anterior on the base of the clypeus (*Clp*), which latter in the cockroach is not separated from the frons (*Fr*). If the insect is prognathous, the axis of the jaw becomes vertical instead of horizontal, but the relation of the mandible to the head is not changed. In biting-and-chewing insects a molar surface of the mandible is differentiated from a toothed incisor



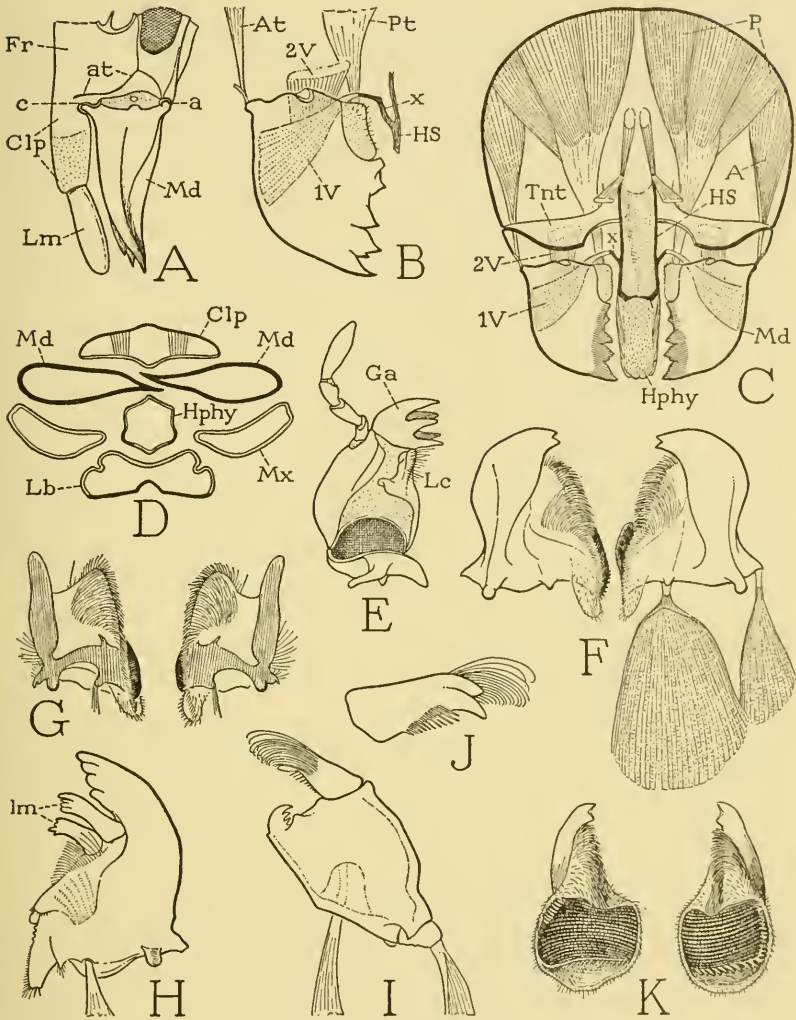


FIG. 24.—Hexapoda—Miscellaneous Pterygota.

A, *Blatta orientalis* L. (Blattidae), left mandible and adjoining parts of head, lateral. B, same, right mandible and muscles, anterior. C, same, section of head showing mandibles with muscles, hypopharynx, and tentorium, anterior. D, *Periplaneta americana* (L.) (Blattidae), section of mouth parts showing relative positions. E, *Popillia japonica* Newm. (Scarabaeidae), left maxilla, dorsal. F, same, mandibles, ventral. G, *Cotinis nitida* (L.) (Scarabaeidae), mandibles, ventral. H, *Berosus pugnax* LeConte (Hydrophilidae), left mandible, ventral. I, *Mycetobia* sp. (Mycetophilidae), left mandible of larva, lateral. J, same, incisor lobe of mandible, mesal. K, *Popillia japonica* Newm. (Scarabaeidae), left and right mandibles turned dorsally, showing masticatory surfaces on mesal sides.

process. The ordinary mandible of the winged insects is practically identical in its structure and mechanism with the mandibles of the isopods and amphipods among the Crustacea, but since the mandibles of the apterygote insects and the ephemeropterid larva are not of this type, it is clear that the doubly articulated mandible having the gnathal lobe perpendicular to the axis of rotation has been independently developed in both the crustaceans and the insects.

The mandibular musculature of the cockroach and of most other orthopteroid insects except Acrididae is the same as that of the lepis-matid mandibles (fig. 22 E) in that each jaw has *four* distinct muscles (fig. 24 B), though the corresponding muscles differ in relative size in the two groups. The principal motors of the pterygote mandible, however, are the dorsal muscles (C), including a slender lateral abductor (A) and a huge mesal adductor (P). The ventral muscles of the cockroach mandible (B, C, V) are inserted within the cavity of the jaw and consist of two distinct fiber groups, one being a fan-shaped muscle (IV) inserted laterally in the mandible, with its convergent fibers attached on a small arm (*x*) of the hypopharyngeal suspensorium (HS), the other (zV) a short, thick muscle inserted posteriorly in the mandible and attached on the anterior arm of the tentorium (C, Tnt). The musculature of the pterygote mandible is thus seen to be fundamentally the same as in the Thysanura and other arthropods. In most of the holometabolous insects, however, the ventral muscles have been lost, and the dorsal muscles become the only muscles of the jaw (F), though in some of the mandibulate Diptera, as in Tabanidae, a small tentorial muscle of the mandible may be retained.

In no other group of arthropods do the mandibles undergo such diverse and numerous modifications in adaptation to different ways of feeding as they do in the insects. Though the typical biting and chewing mandible has a well-differentiated toothed incisor process and a grinding molar surface, either part may be reduced or eliminated. Among the beetles the mandibles of species that practice extra-oral digestion of the food have no molar surfaces; in the leaf-feeding Scarabaeidae on the other hand, in which strongly toothed lobes of the maxillae serve as jaws for biting off the leaf surface (fig. 24 E), the mandibles have become specialized as masticatory organs by a great development of the molar surfaces and a reduction of the incisor processes (F, G, K). In various orders the mandibles are drawn out into piercing stylets, in the worker bees they are modified for purposes other than that of feeding, and finally the mandibles may be greatly reduced in size or entirely suppressed. Weber (1939) has

given a classified account of various atypical kinds of insect mandibles, among which may be mentioned the mandibles of certain leaf-mining lepidopterous larvae in which the molar lobes have been converted into saws, and others in which the usual action of the jaws and the relative size of the muscles have been reversed, so that the jaws work outward instead of inward, as in the elephant louse, *Haematomyzus*, and in the larvae of the tenthrudinid *Phyllotoma aceris*.

The mandibles of some of the Hydrophilidae, as in *Berosus* (fig. 24 H), are armed each with a pair of large dentate processes (*lm*), flexibly attached on the inner margin of the jaw, which have been cited by Hansen (1930) as examples of the occurrence of a "lacinia mobilis" among the insects; similar processes he says are present in *Hydrobius*, but not in *Hydrophilus*. A small, flexible appendage bearing a brush of hairs is seen also on the larval mandibles of Ephemeroptera (fig. 23 D, E), and is termed a "lacinia mobilis" by Murphy (1922). Though such structures are widely distributed among the arthropods, as already pointed out, there is no reasonable basis for regarding them as homologues of the lacinia of an insect maxilla.

In the larvae of lower nematoceros Diptera the entire incisor process of the mandible may be separated by membrane from the sclerotized base of the jaw, and thus becomes freely flexible on the latter. An example is here given in a species of *Mycetobia* (fig. 24 I, J). The mandibles of such species are so articulated on the head that they work in longitudinal planes parallel with each other and not in opposition. In a comparative study of families having this type of larval jaw Anthon (1943a, 1943b) finds that the distal lobe, or "segment," of the mandible is most freely movable in the Sylvicolidae (Rhyphidae), in which it is doubly articulated on the base. In the Melusinidae (Trichoceridae) the lobe is united with the base by a sclerotic bridge on the dorsal side. Among the Psychodidae the lobe in some species is freely movable, while in others it has an extensive union with the base. In the Liriopeidae (Ptychopteridae) the incisor lobe is apparently immovable, since it is set off from the base only by a groove. The apical lobes of the jaws in Sylvicolidae (Rhyphidae) bear large brushes of long hairs, which Anthon says serve as brooms for sweeping into the mouth particles of detritus, algae, and diatoms on which the larva feeds. Other forms, in which the lobes are armed with strong teeth and are not so freely movable, feed on vegetable fragments less easily removed from their source. The purely aquatic rhyphid larvae, Anthon observes, use the mandibles also for locomotion, creeping by means of the jaws on the bottom, while the rear end of the body with the spiracles is held at the surface of the water.

Insect mandibles of the type just described have a certain resemblance to the diplopod jaw, but the flexible incisor lobe of the dipterous larval mandible is entirely devoid of muscles, and is movable merely by a desclerotization of the mandibular wall around its base. Considering the evidence that the entire arthropod jaw represents only the coxa of the mandibular appendage, and that the true distal segments, when present, form a palpus, it is impossible to accept Anthon's conclusion that the divided mandible of the sylvicolid (rhyphid) larval type is a primitive, segmented mandible, from which the solid type of jaw has been derived by union of the two "segments." The dipterous larva certainly does not represent a primitive arthropod.

The most specialized mandibular mechanism among the insects is that of the muscularly protractile and retractile styletlike or bristlelike mandibles of Hemiptera. In the Homoptera the enlarged base of each mandibular stylet (fig. 25 E), where it is attached to the wall of the containing pouch, is produced into a slender retractor arm (*ra*) and a broad protractor arm (*pa*). The retractor muscles (*F*, *A*, *P*) are attached on the retractor arm and in the notch between the bases of the two arms; these muscles evidently represent the dorsal muscles of a generalized mandible. The protractor muscles (*IV*), inserted on the upper end of the protractor arm, arise on the lower end of a plate of the head wall (*A*, *Lor*), inserted between the clypeus and the maxillary lobe, termed the *lorum* by taxonomists. The identity of the protractor muscles of the mandibles, therefore, depends on the homology of the loral plates.

By some students of Homoptera the loral plates of the head have been thought to be detached parts of the clypeus, while others have regarded them as extensions of the genae. The writer (1938) suggested that the lora belong to the hypopharynx, since their lower ends are confluent with the hypopharyngeal floor of the sucking pump (fig. 25 C). The independence of the loral plates from the clypeus, and their direct continuity with the sides of the hypopharynx in the cicada has been fully demonstrated by Butt (1943, fig. 2), and in a sectional view of the head of *Typhlocyba ulmi*, Willis (1949, fig. 4) shows clearly that the inflected lateral edges of the clypeus are continued into the epipharyngeal roof of the sucking pump.

A horizontal section of the head of a cicada through the lower part of the postclypeus (fig. 25 B) shows that the contiguous edges of the postclypeus (*Pclp*) and the lora (*Lor*) are inflected individually clear through the head. The clypeal lamellae become the epipharyngeal wall (*Ephy*) of the sucking pump (*CbP*) with the plunger on which the dilator muscles (*dlec*) are attached; the loral lamellae (*n*) become



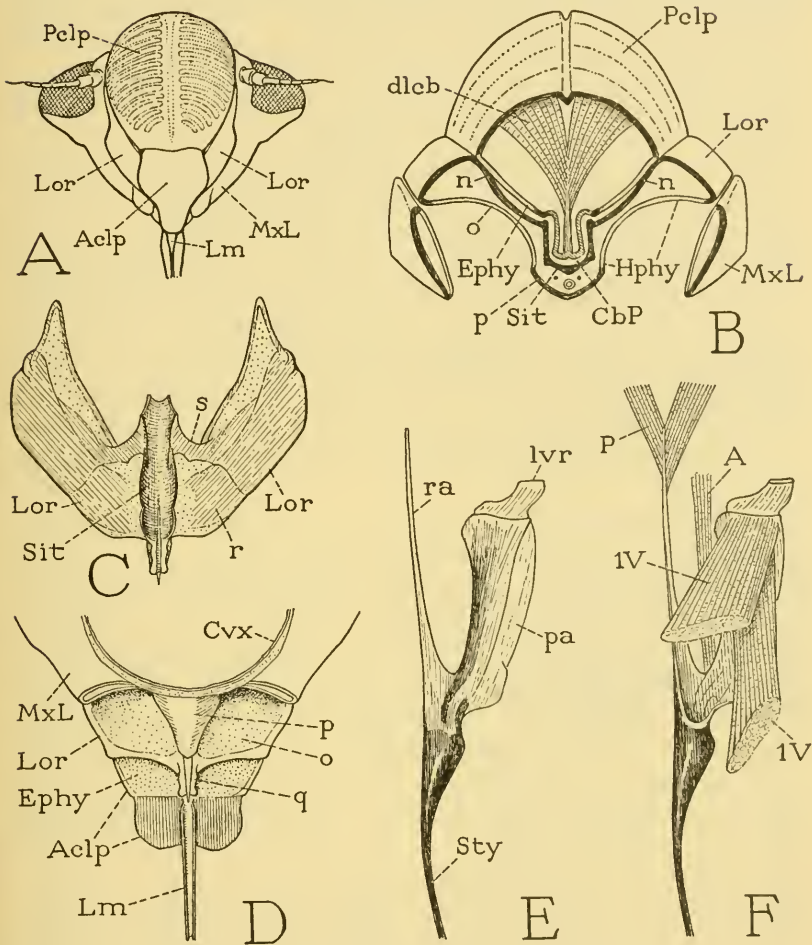


FIG. 25.—Hexapoda—Pterygota: Homoptera.

A, *Cephisus siccifolia* Walker, head, anterior. B, *Magicicada septemdecim* (L.), horizontal section of head through lower part of postclypeus. C, same, anterior surfaces of loral plates connected with hypopharyngeal trough (*Sit*) of sucking pump. D, *Tibicen* sp., posterior view of lower part of head after removal of labium, lower ends of maxillary lobes and stylets, showing posterior median lobe of hypopharynx (*p*) membranously connected (*o*) with loral plates (*Lor*). E, *Magicicada septemdecim* (L.), basal part of right mandible, posterior. F, same, basal part of left mandible with muscles, anterior; anterior branch of protractor muscle (*IV*) attached below *r* on C, posterior branch at *s*.

the hypopharyngeal floor of the pump with the deep, median, trough-like sitophore (*Sit*). Likewise, the posterior edges of the loral plates are inflected, but become thin membranes (*o*) continuous medially with the ventral wall of the posterior lobe (*p*) of the hypopharynx. The hypopharynx and the lora, therefore, constitute an anatomically integral structure; the loral plates are merely the exposed outer surfaces of lateral expansions of the hypopharynx (*Hphy*). The same relations can be demonstrated by dissection. On lifting or removing the anteclypeus (*A*, *Aclp*), it is seen that the lower ends of the loral plates (*C*, *Lor*) converge behind the anteclypeus and that their broad, sclerotized anterior lamellae are united with the sitophore trough (*Sit*) of the hypopharynx. Working from the back of the head (*D*), by removal of the labium and cutting off the lower parts of the maxillary lobes (*MxL*), the median posterior lobe of the hypopharynx (*p*) is exposed, and is seen to be continuous with the membranous areas (*o*) on each side inflected from the posterior margins of the loral plates (*Lor*).

From these facts it is clear that the loral plates of Homoptera are literally parts of a complex hypopharyngeal structure. It then follows that the protractor muscles of the mandibles arising on the lora can be no other than the hypopharyngeal muscles of the orthopteroid mandibles (fig. 24 B, *IV*), the altered relative position of which results from the retraction of the mandibles and the lateral expansion of the loral wings of the hypopharynx. In some Fulgoridae the upper ends of the loral plates appear to be united with the clypeus. In the Heteroptera (Hemiptera) it is shown by Butt (1943) that the sclerites corresponding with the lora of Homoptera are concealed within the head.

In the cicada, either *Tibicen* or *Magiccicada*, there are two large branches of the protractor muscle inserted on the upper end of the protractor arm of each mandible (fig. 25 F, *IV*), one lying anterior to the other. The anterior branch arises ventrally on the inner surface of the lower part of the inflected dorsal lamella of the lorum behind the point *r* on C of the figure; the posterior branch arises on the same loral lamella at the base of the sitophore (*s*). The protractor arm of the mandible is not an apodeme; it is a sclerotic extension of the mandibular base in the membranous anterior wall of the gnathal pouch. The muscle-bearing haemocoelic surface, therefore, corresponds with the inner lateral wall of the orthopteroid mandible on which the hypopharyngeal muscle of the jaw is inserted. The homopterous head, the mandibles and their muscles can thus be inter-

preted in terms of orthopteroid structure; they show merely the extreme degree to which modifications of a basic anatomical complex may be carried in the evolution of a new mechanism.

## EXPLANATION OF LETTERING ON THE FIGURES

## ABBREVIATIONS

- A*, anterior dorsal muscle of a primitive mandible (*1A*, *2A*, *3A*, subdivisions of same).  
*ablvr*, abductor lever.  
*Aclp*, anteclypeus.  
*admd*, adductor muscle of mandible.  
*1Ant*, first antenna (antennule), or its head foramen.  
*2Ant*, second antenna, or its head foramen.  
*Ap*, apodeme.  
*at*, anterior tentorial invagination.  
*At*, tendon of muscle *A*.  
*AT*, anterior tentorial arm.  
  
*brC*, branchial chamber.  
*bspd*, subdivision of basipodite.  
*Bspd*, basipodite.  
  
*CbP*, cibarial sucking pump.  
*Chpd*, cheliped, or its foramen.  
*Cp*, carapace.  
*CT*, central plate of tentorium (corpulentorium).  
*Cvx*, neck, cervix.  
*Cx*, *Cxpd*, coxa, or coxopodite.  
  
*Dbl*, doublure (inner wall) of carapace fold.  
*dpm*, dorsal promotor muscle of coxa.  
*drm*, dorsal remotor muscle of coxa.  
*DT*, dorsal tentorial arm.  
  
*Endst*, endosternum.  
*Ephy*, epipharyngeal surface.  
*Epst*, epistome.  
*es*, epistomal sulcus.  
*Expd*, exopodite.  
  
*Flt*, futura (premandibular sternal sclerite supporting hypopharynx).  
  
*Fr*, frons.
- Ga*, galea.  
*Ge*, gena.  
*Gn*, jaw (gnathal endite).  
*Gnch*, gnathochilarium.  
*gnL*, gnathal lobe of mandible.  
*gnP*, gnathal pouch.  
  
*H*, head.  
*hAp*, head apodeme, "hypopharyngeal apophysis" of myriapods.  
*Hphy*, hypopharynx.  
*HS*, hypopharyngeal suspensorium.  
  
*I*, intramandibular muscle of gnathal lobe.  
*II*, *III*, *IV*, etc., somatic segments (*I*, segments of second antennae).  
  
*imB*, intermaxillary sternal brachium.  
*inc*, incisor process of mandible.  
*inv*, site of an endoskeletal invagination.  
  
*Lb*, labium.  
*Lc*, lacinia.  
*Lg*, intergnathal ligament.  
*lm*, "lacinia mobilis."  
*Lm*, labrum.  
*Lor*, lorum.  
*lvr*, leverlike sclerite.  
  
*mcl*, striated muscle tissue.  
*Md*, mandible.  
*mdB*, base of mandible (corpus mandibulae).  
*mdF*, mandibular foramen.  
*mdmcls*, mandibular muscles.  
*mdr*, articular rod of mandible.  
*mol*, molar process or surface of mandible.  
*mp*, muscle plate.  
*Mst*, metastome.

- Mth*, mouth.  
*1Mx*, first maxilla (maxillula), or its foramen.  
*2Mx*, second maxilla, or its foramen.  
*mx<sub>b</sub>*, remnant of maxillary bridge.  
*mx<sub>B</sub>*, maxillary bridge (pleuron of maxillary segment).  
*2MxF*, foramen of second maxilla.  
*MxL*, maxillary lobe.  
*Mxpd*, maxilliped (*1Mxpd*, *2Mxpd*, *3Mxpd*, first, second, and third maxillipeds, or their foramina).  
  
*npr*, nephropore.  
  
*Oe*, oesophagus.  
  
*P*, posterior dorsal muscle of a primitive mandible.  
*pa*, protractor arm of mandible.  
*Pclp*, postclypeus.  
*Pgn*, paragnath.  
*Pl*, pleuron.  
*Plp*, palpus (telopodite or a part of it).  
  
*pmB*, postmaxillary sternal brachium.  
*Prtc*, protocephalon.  
*Pt*, tendon of muscle *P*.  
  
*ra*, retractor arm of mandible.  
  
*S*, sternum.  
*Sit*, sitophore (troughlike floor of cibarial pump).  
*sl*, suspensory ligament.  
*smcl*, suspensory muscle.  
*Sp*, spiracle.  
*Stom*, stomodaeum.  
*Sty*, mandibular stylet.  
  
*T*, tergum.  
*Tlpd*, telopodite.  
*Tnt*, tentorium.  
  
*V*, ventral muscle, or muscles (*1V*, *2V*, *3V*), of mandible.  
*vpm*, ventral promotor muscle of coxa.  
*vrm*, ventral remotor muscle of coxa.  
*VS*, sternum of first maxilliped segment.

## ALPHABETICAL LETTERING

- a*, primary dorsal articulation of coxa or mandible.  
*a-c*, axis of rotation of doubly articulated mandible.  
*b*, primary ventral articulation of coxa.  
*c*, secondary ventral or anterior articulation of mandible.  
*d*, process of mandible supported on metastomal prop (*t*).  
*e*, small sclerite between *d* and *t*.  
*f*, epipharyngeal arm of fultura.  
*g*, angle of mandibular articulation on fultura.  
*h*, epistomal hinge of mandible.  
*i, j*, cranial muscles of head apodeme.  
*k*, lateral, postantennal expansion of epistome.  
*l*, stomodaeal fibers of intergnathal ligament.  
*m*, marginal sclerite of cranium in *Lithobius*.  
*n*, sclerotic anterior wall of loral lobe of hypopharynx.  
*o*, membranous posterior wall of loral lobe of hypopharynx.  
*p*, median ventral lobe of hypopharynx.  
*q*, apical lobe of hypopharynx.  
*r*, origin on lorum of anterior protractor of mandible.  
*s*, origin on lorum of posterior protractor of mandible.  
*t*, arm of metastomal plate supporting mandible.  
*u*, branch of intergnathal ligament to gnathal lobe of mandible.  
*v, w*, sclerites of proboscis wall in *Dolops*.



- x*, loral arm of hypopharyngeal suspensorium.  
*y*, oral arm of hypopharyngeal suspensorium.  
*z*, cut edge of carapace.

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