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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
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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 remoters* (*drm*, *vrm*); 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

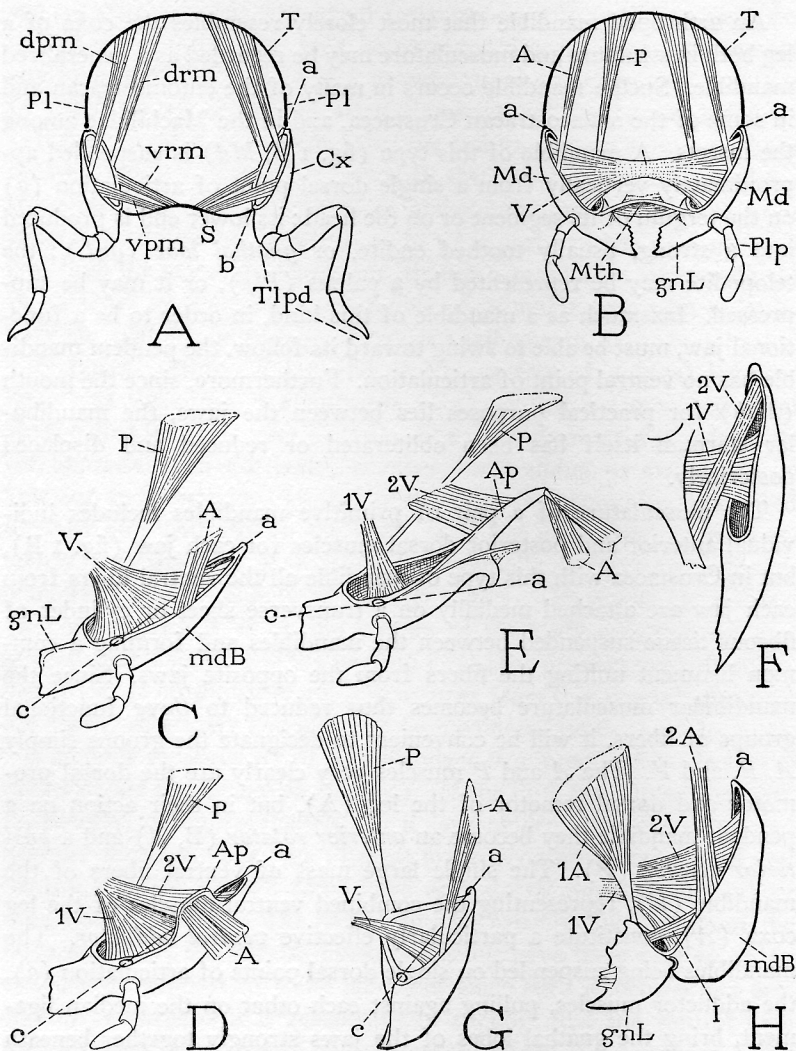


FIG. 1.—Diagrams of the various types of arthropod mandibles, and their apparent derivation from the coxae of a pair of leglike appendages.

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 *Nebatia* (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, v*) 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-