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 symphylids 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 symphylid-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 symphylid-diplopod mandible and its musculature have a curious resemblance to the lacinial lobe and musculature of an insect maxilla, but since the symphylids 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

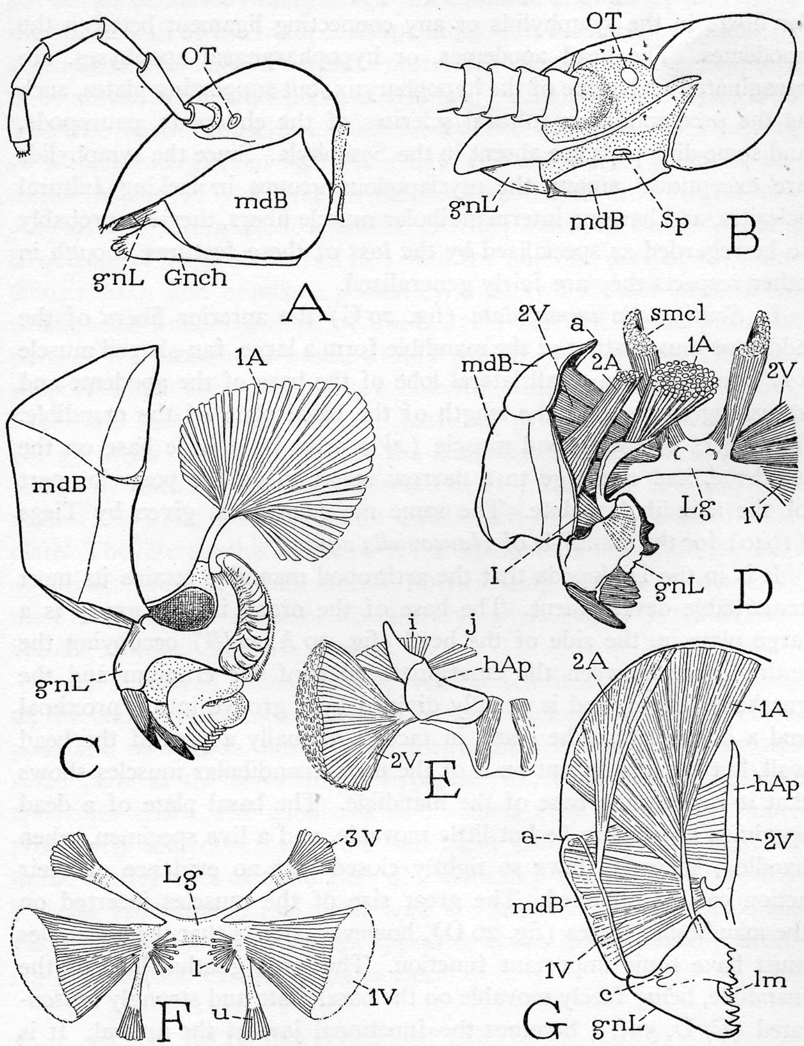

FIG. 20.—Symphyla (*Scutigerella*) and Diplopoda (*Fontaria, Thyropygus*).

A, *Fontaria virginiensis* (Drury), head, lateral. B, *Scutigerella 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, *Scutigerella 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 *Scutigerella 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 musculated (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 virginiensis* 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

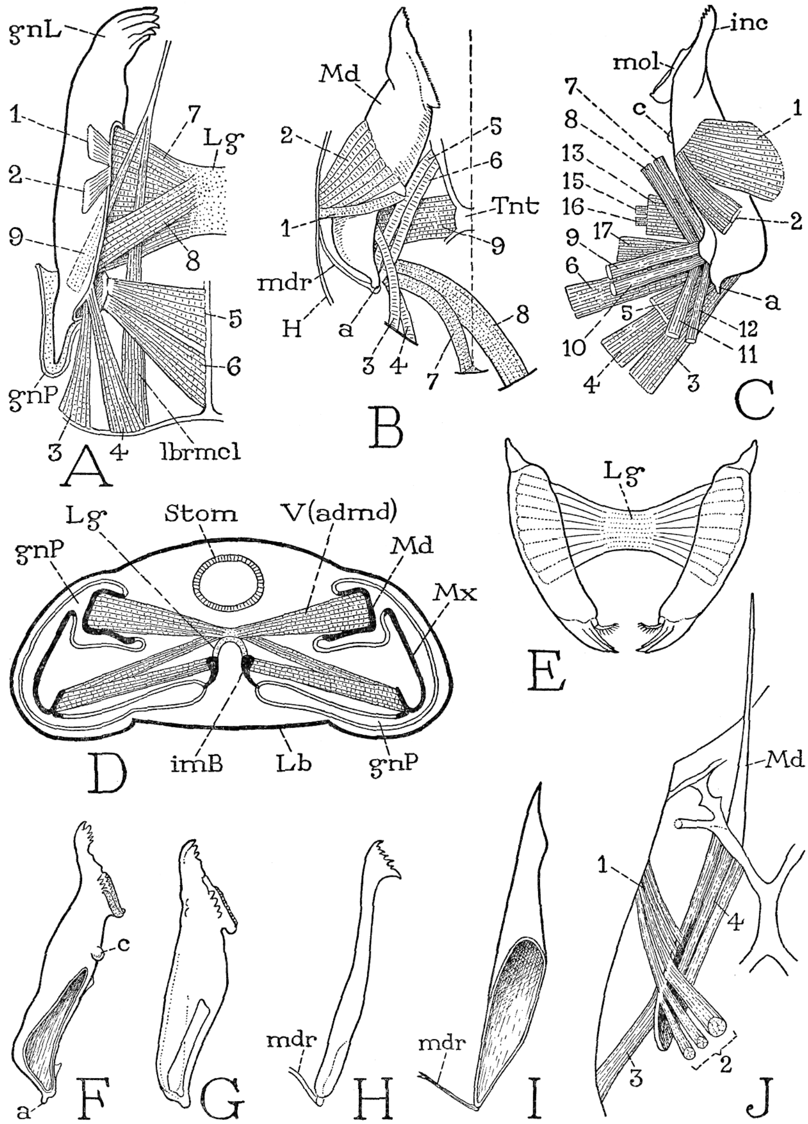

FIG. 21.—Hexapoda—Entagnathous apterygotes: Diplura, Collembola, and Protura.

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 connected with the cranium by a slendor 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

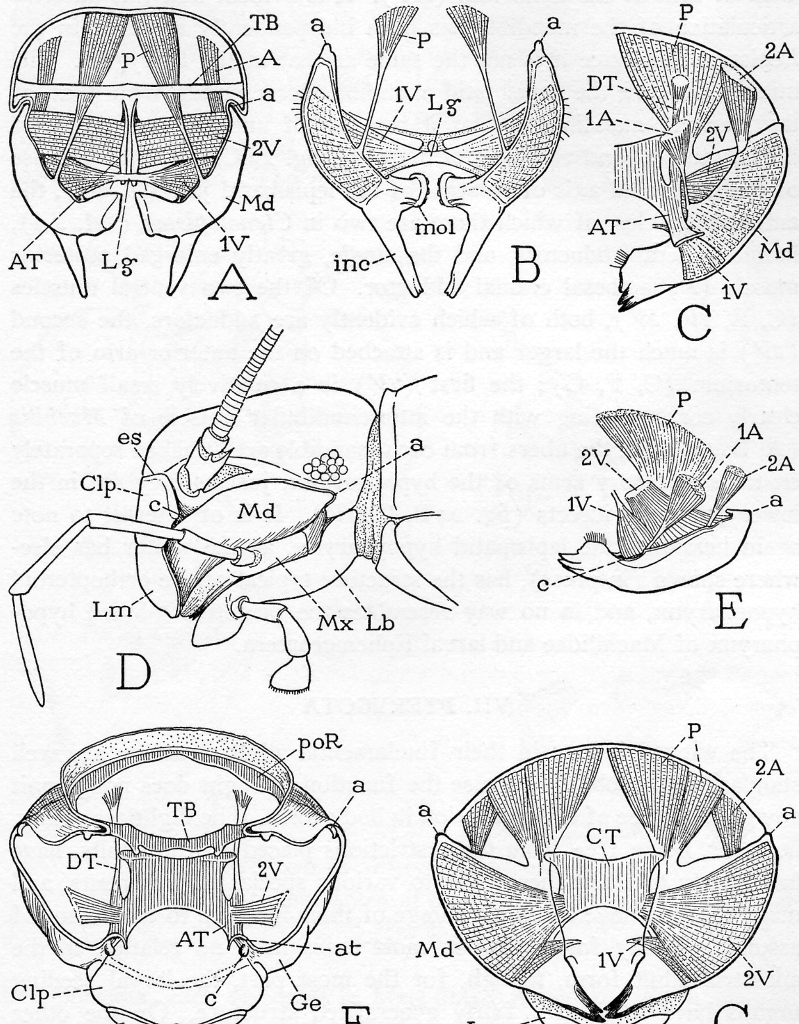

FIG. 22.—Hexapoda—Thysanura.

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

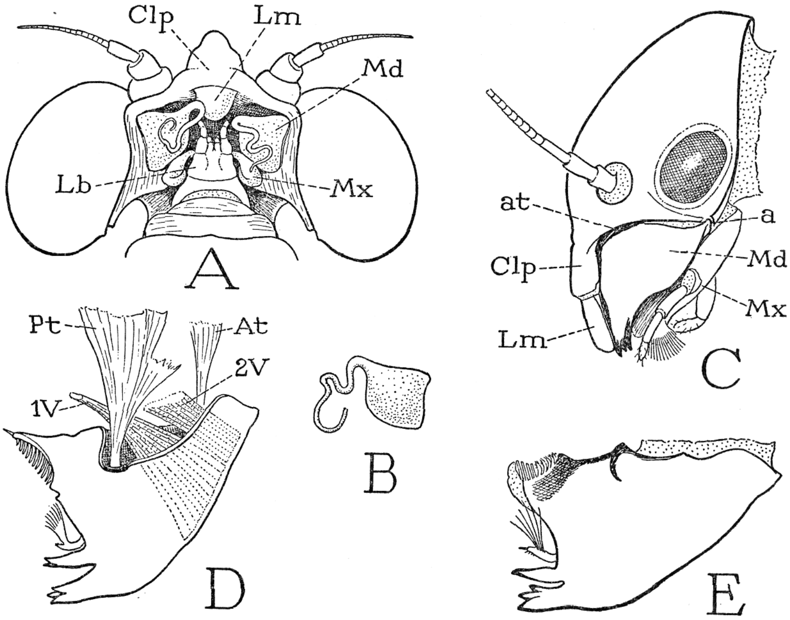

FIG. 23.—Hexapoda—Pterygota: Ephemeroptera.

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