entiated group of the ventral fibers (fig. 1 F, *2V*) 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 musculated. 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 (*1A*), 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 (*1V, 2V*), 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 musculated 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 musculated 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
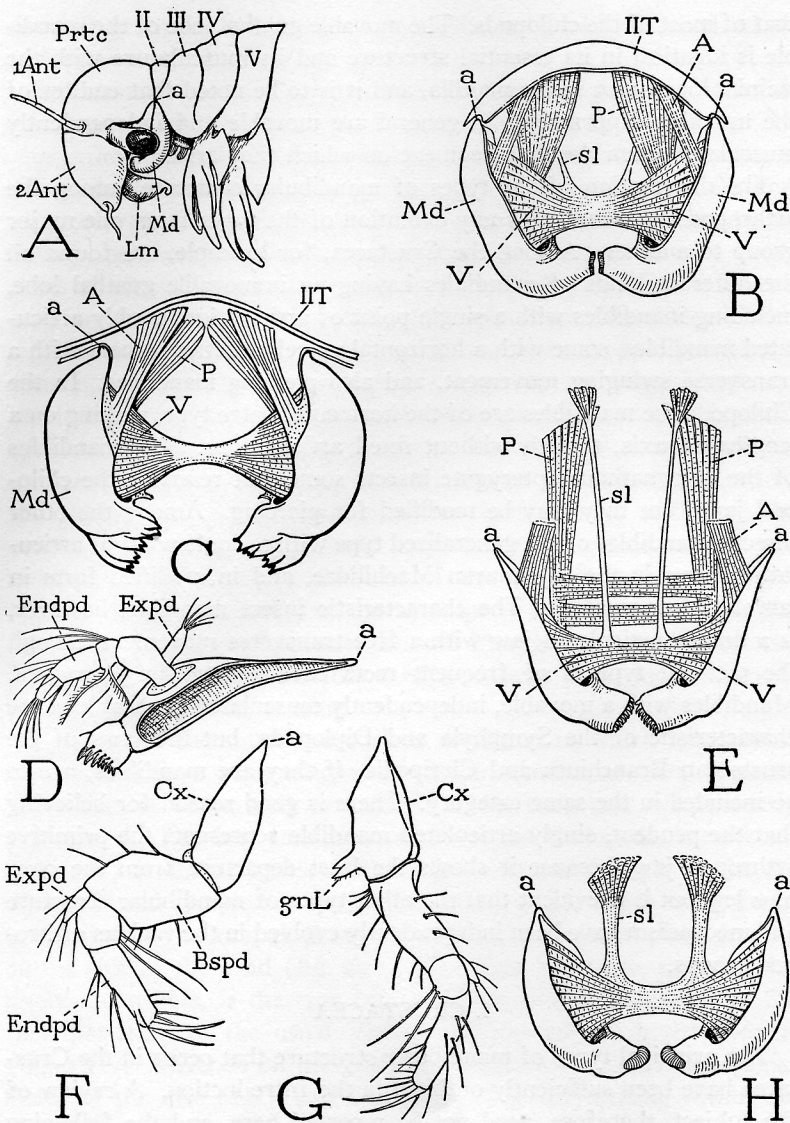
FIG. 2.—Crustacea—Branchiopoda and Ostracoda.

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 or 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 maxillulary 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 maxillulary 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 (*Spi*) 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.
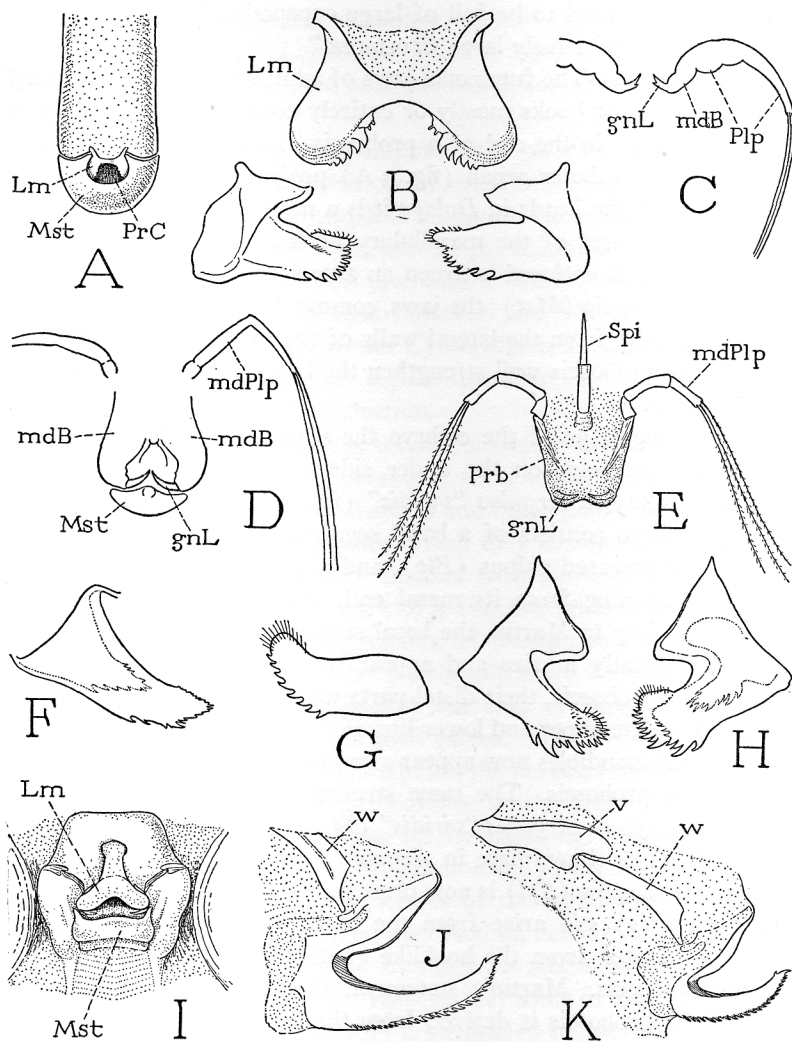
FIG. 3.—Crustacea—Branchiura.

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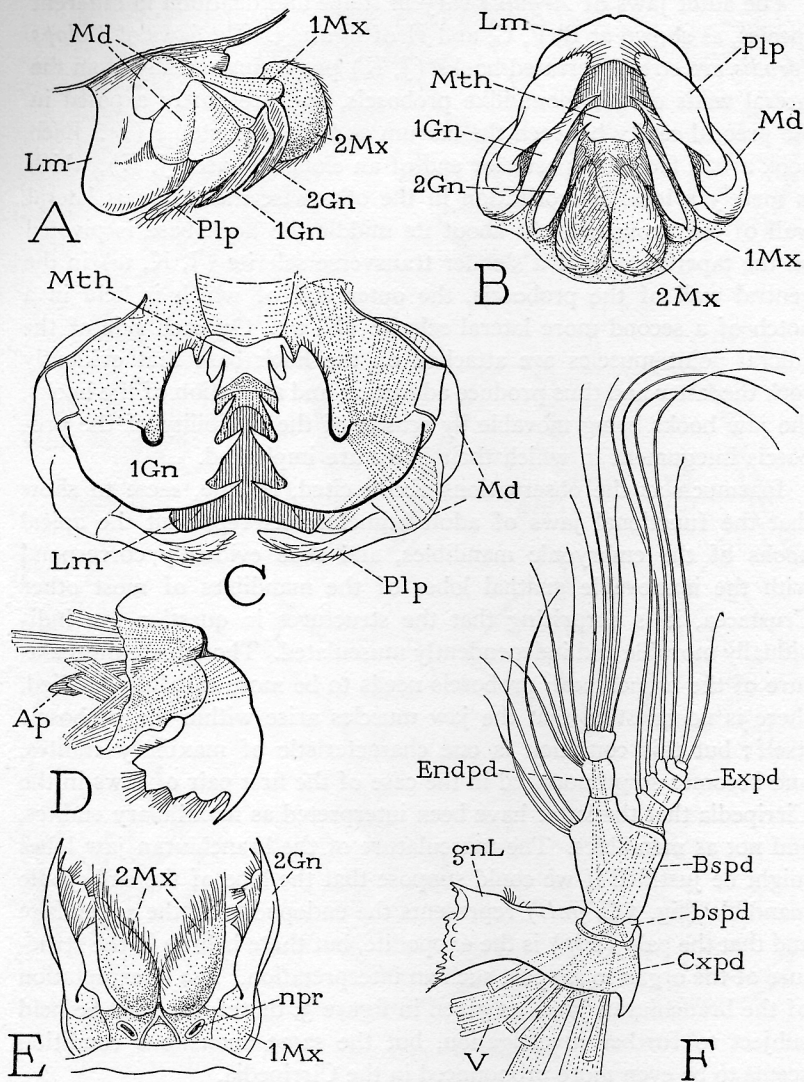
FIG. 4.—Crustacea—Cirripedia (*Lepas*) and Copepoda (*Calanus*).

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 musculated 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, *1Mx*); 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* Dephner (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 musculated 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*
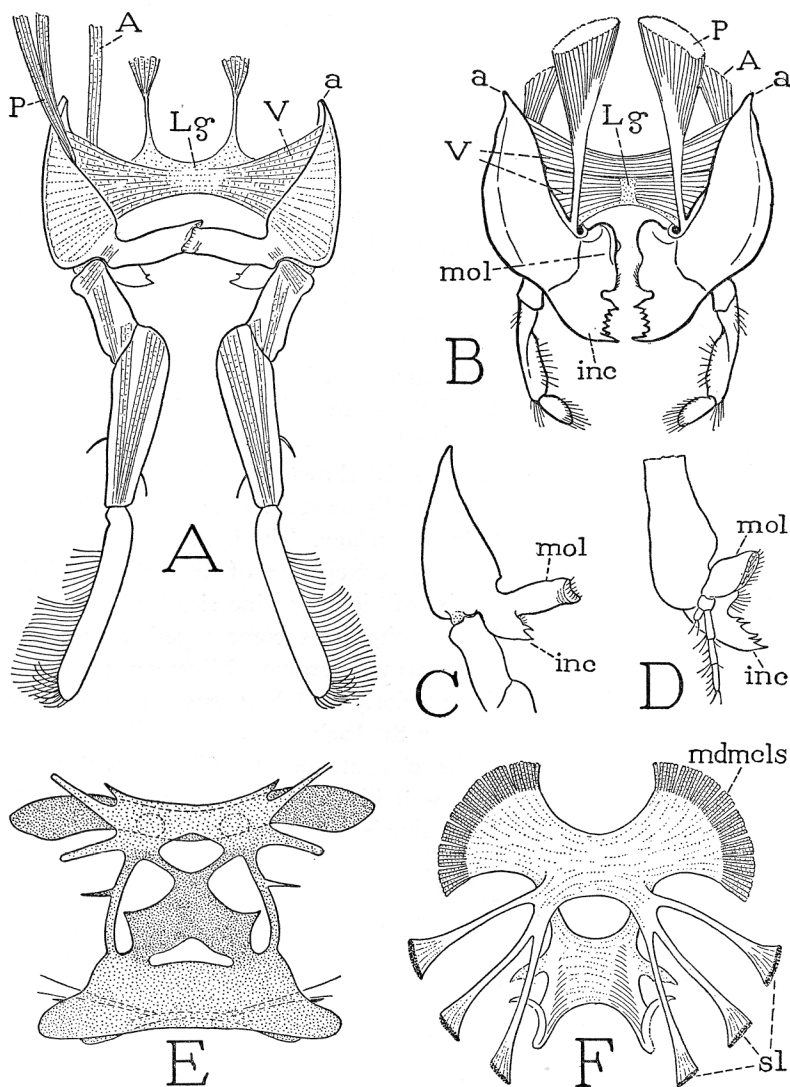
FIG. 5.—Crustacea—Leptostraca (*Nebalia*) and Anaspidacea
(*Anaspides* and *Paranaspides*).

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.