

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 *Koomunga*, 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 Euphausiaceae, 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

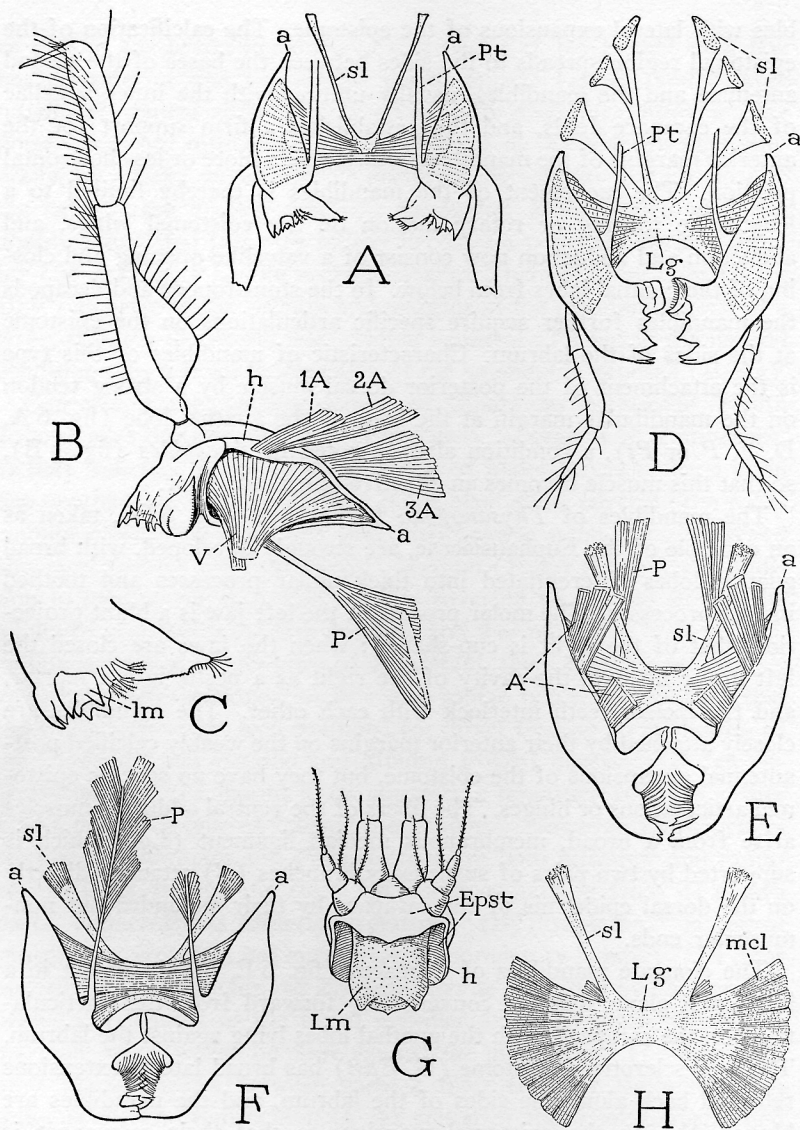


FIG. 6.—Crustacea—Mysidacea (*Neomysis*), Euphausiacea (*Thysanopoda*), and Cumacea (*Diastylis*).

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 intergnathal muscles, anterior. F, *Diastylis rathkei* Kr., mandibles and intergnathal 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

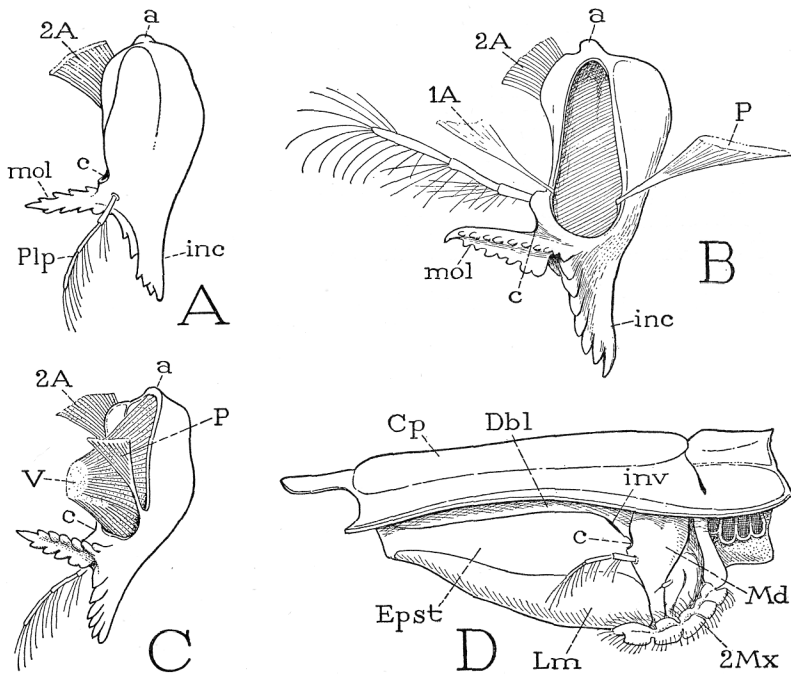


FIG. 7.—Crustacea—Stomatopoda.

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

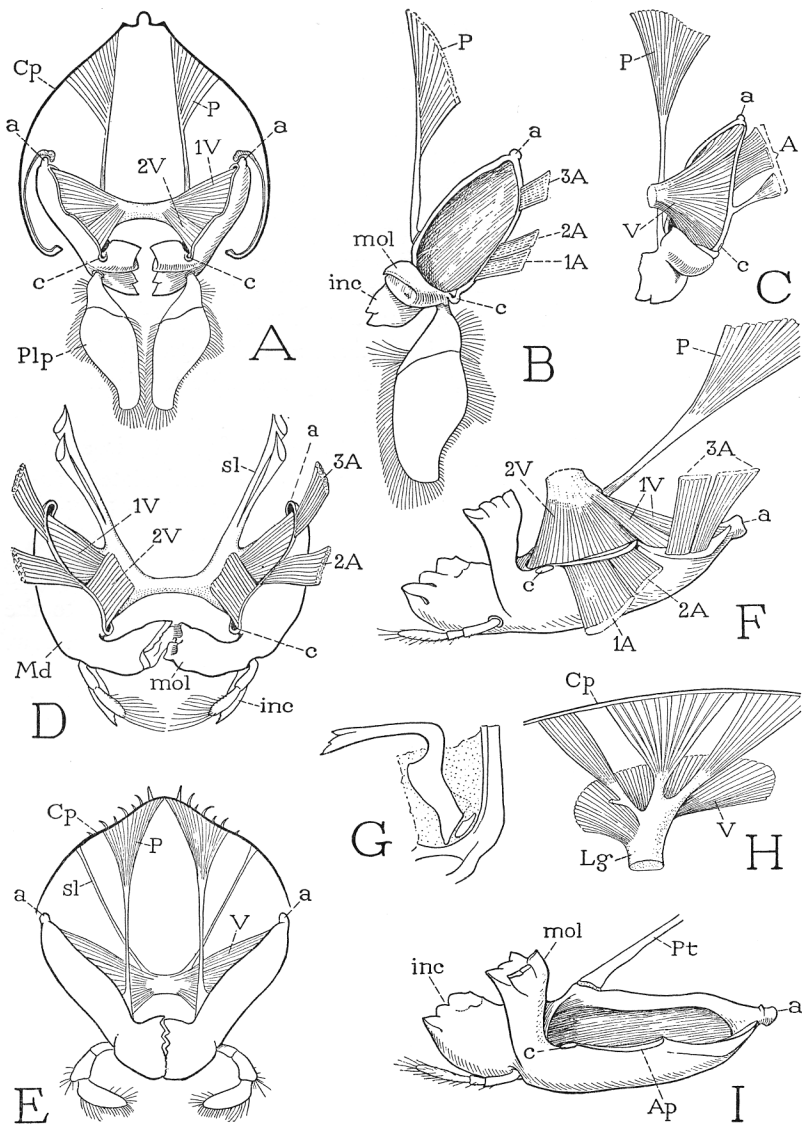


FIG. 8.—Crustacea—Decapoda: Natantia.

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

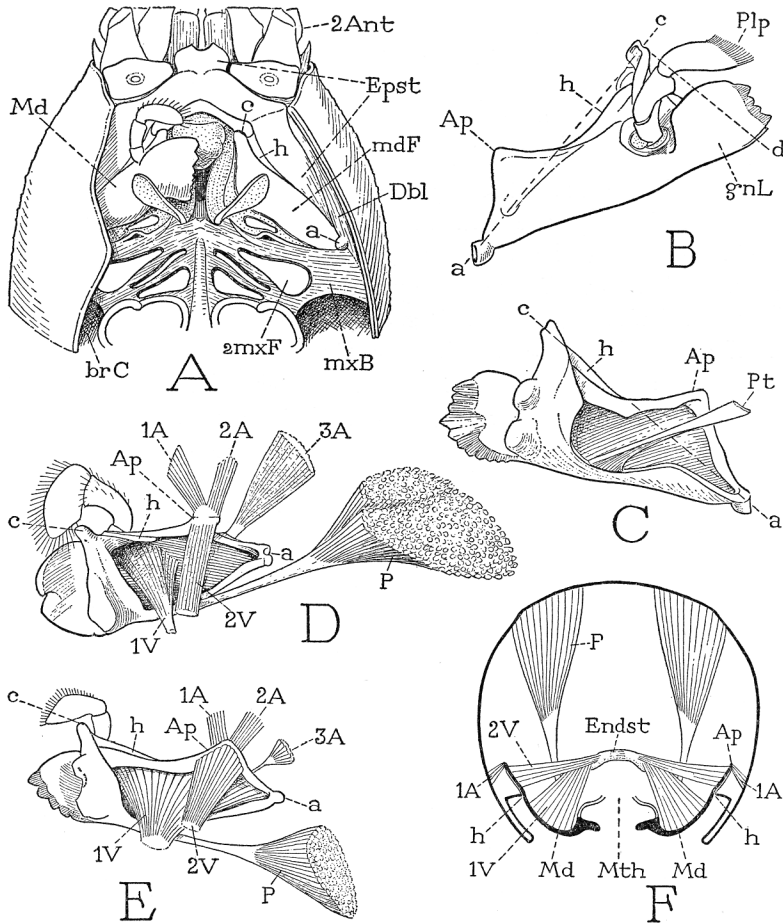


FIG. 9.—Crustacea—Decapoda: *Astacura*.

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

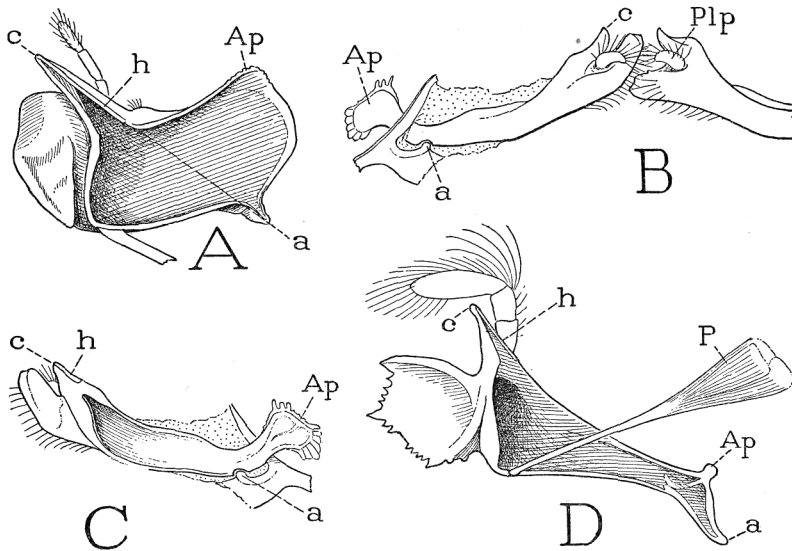


FIG. 10.—Crustacea—Decapoda: *Palinura*.

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