The feeding apparatus of the nymph of *Arthroplea congener* Bengtsson (Ephemeroptera)

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During the summer of 1959, at the request of Svenska Naturskyddsföreningen, Stockholm, a team composed of Prof. Per Brinck, Lund, Prof. and Mrs. K. G. Wingstrand, Copenhagen, and Mr. and Mrs. L. Cederholm, Lund, made a zoological survey in the western parts of Lule Lappmark in Swedish Lapland. Among the Ephemeroptera, the very interesting nymphs of *Arthroplea congener* Bengtsson were collected. These nymphs live typically among sedges in standing or very slowly flowing waters, and they present uniquely modified mouth parts for straining detritus and small organisms from the environment. The collection data of the material studied are as follows:

1. Lake Jäkaure, western part, in small basins at the lake margin with sedges and detritus-covered bottom, July 9th, 1959: 3 nymphs.
2. Lake Jäkaure, near Tjåmotis, at the bottom among sedges, near the beach, July 9th, 1959: 3 nymphs.
3. Lake Rittak, sandy beach, July 10th, 1959: 1 nymph.

The material was fixed in alcoholic Bouin and preserved in 70 % alcohol.

The genus *Arthroplea* is at present generally classified in the family Heptageniidae (Ecdyonuridae). Ecologically it differs from the remaining Heptageniids because it lives in quiet waters but, nevertheless, it still retains the flat and broad head characteristic of the family. Both adults and nymphs, besides the nymphal mouth parts, differ also in some morphological details from the remaining Heptageniids, as is discussed in length by Balthasar, 1937, who created a new family for the genus. The differences may well justify its being kept in a distinct subfamily—Arthropleinae Balthasar—of the Heptageniidae. This arrangement is found, e.g., in recent papers by Demoulin (1956, pp. 98–99; 1958, p. 9; including also the fossil *Electrogenia*) and Edmunds (1962, p. 11).

Arthroplea comprises only two species, *A. congener* Bengtsson and *A. bipunctata* (McDunnough). The known distribution of *A. congener* is Central (Bengtsson, 1908, 1909) and Northern Sweden (present paper), Finland (Tiensuu, 1939), Czechoslovakia (Balthasar, 1937; Landa, 1962), and Pommerania and Poznania (Keffermüller, 1960). The occurrence in Britain is doubtful (Macan, 1962); even more so is that in Switzerland (Tiensuu, l.c., p.

99, footnote). *A. bipunctata* is known from localities in New England, Ontario and Quebec (cf. Burks, 1953, p. 201).

The nymph of *A. congener* was described for the first time by Bengtsson (1909, p. 18), who in a later paper figured also some of the mouth parts (1930, p. 24, figs. 45–46; p. 26, fig. 49). The nymph of *A. bipunctata* was described by Ide, 1930, who also figured some of the mouth parts. Both these authors' figures are good. Bengtsson's figure of the labium (l.c., fig. 46) is seen from the dorsal aspect, that of the hypopharynx (l.c., fig. 49), from the ventral aspect, despite the indication "von oben gesehen". Ide's figures are all from the ventral aspect. *A. congener* (imago and nymph) was also described (in Finnish) and figured by Aro, 1910 and 1928, under the name *Cinygma mirabilis* Aro. He made, moreover, observations on the feeding of nymphs kept in aquaria. His observations were translated into English by Tiensuu, 1939.

A more extensive study was made by Balthasar, 1937, on *A. frankenbergeri,* a form he described from Czechoslovakia, and now considered to be conspecific with *A. congener* (cf. Landa, 1962, p. 249). Balthasar studied the nymphal mouth parts in detail and figured them all, except the labrum. He also studied the muscles of some of the mouth parts, chiefly of the labium, and the distribution of the tracheae in the maxillae, labium, and hypopharynx. His treatment of the musculature is rather superficial and, in some points, inaccurate. He put a great emphasis on the rich tracheation of some of the mouth parts, particularly that of the maxillae and labium. He stated that the tracheae of these mouth parts send numerous branches to the surface, where they form a dense net of capillaries. He supposed the mouth parts to be important accessory respiratory organs, the movements of the palpi producing currents to renew water at the mouth cavity. He stated also he believed the grown nymphs to be mainly raptorial, resorting to particle-feeding only if pressed by food-shortage.

My observations on *A. congener* confirm Balthasar's description and figures of the tracheation of the mouth parts, except in that only the muscles are richly supplied with tracheae, there being no superficial network. Clearly the hard-working muscles of both pairs of palpi need an ample tracheal supply for their gas exchange. The most important respiratory organs are surely the gills, the gas exchange with the environment occurring through other body surfaces being probably slight. As regards the feeding habits, I have examined the gut contents of four well-grown nymphs. In all of them, among unrecognizable detritus and some sand grains, I observed many algae (both unicellular and colonial, including desmids and diatoms), fungal hyphae, spores, and debris of testaceous wood or of other tissues of higher plants. Of animal matter, I found decays of rhizopods, occasionally of rotifers, and remains of a few copepods and cladocerans. These contents point out clearly that *A. congener* is a particle-feeder, using its highly specialized feeding apparatus for this purpose.

In the present paper, through a kind request of Prof. Per Brinck, to whom I am deeply indebted for a general orientation and for valuable information on living nymphs observed in the field, I make a redescription of the morphology of the mouth parts of *A. congener* and an analysis of the related musculature. For these purposes I have studied whole heads both in alcohol and cleared and mounted on slides, I have made dissections, and I have also mounted isolated mouth parts on slides. Two important papers on the head morphology of Ephemeropteran nymphs, recently published, have been of great value to me in this study. The first is a paper by Strenger, 1953, on the head morphology of *Ecdyonurus* and *Rhithrogena,* two genera of the Heptageniidae, the second, a paper by Brown, 1961, on the mouth parts of *Cloeon dipterum* and *Baetis rhodani,* two baetid mayflies. I have named structures, especially muscles, as possible in accordance with these authors and with Snodgrass, 1935. A description of the basic working of the feeding apparatus follows the morphological part. Careful observations on living nymphs are, of course, necessary to a more detailed (and, I should say, truer) description of the working of the mouth parts, including also the precise role of many of the muscles.

The head capsule and labrum

The head of *Arthroplea* (Fig. 1), as that of other Heptageniids, is prognathous, flattened dorso-ventrally, and broad. It is kept at an angle of ca. 45° with the horizontal plane of the animal.

The head capsule presents the same general structure as those of *Ecdyonurus* and *Rhithrogena,* as described by Strenger, 1953. Anteriorly it is broadly emarginate, exposing part of the labrum when viewed from above. The labrum (Figs. 3, 5, L; Fig. 6) is much larger than in the two genera studied by Strenger, and presents extensive lateral lobes. The upper and anterior surfaces of the labrum are provided with numerous long hairs gently bent mesially and downwards. The median hairs are much shorter and bent downwards. The hairs of the under surfaces of the lateral lobes (Fig. 6) are strongly bent mesially; the most mesial of these hairs are almost straight and are stronger than the rest. From near the place of origin of these stronger hairs there proceeds to the epipharynx, on each side, a band of short hairs directed mesially. These rows are continuous with two epipharyngeal ones, which converge to the mouth and are formed of short fringed bristles directed toward the mouth. These rows are supported by sclerotized bars connected to the tormae. The epipharynx is not delimited from the labrum. Besides the rows of bristles, the epipharyngeal surface is clothed with numerous minute hairs directed in accordance with the larger hairs or bristles. The two rows of bristles are located just anteriorly to the molar surfaces of the mandibles, and are likewise asymmetrical, its oral ends curving to the left (Fig. 6).

The labrum is moved by two pairs of muscles, a pair of dorsal muscles (1)

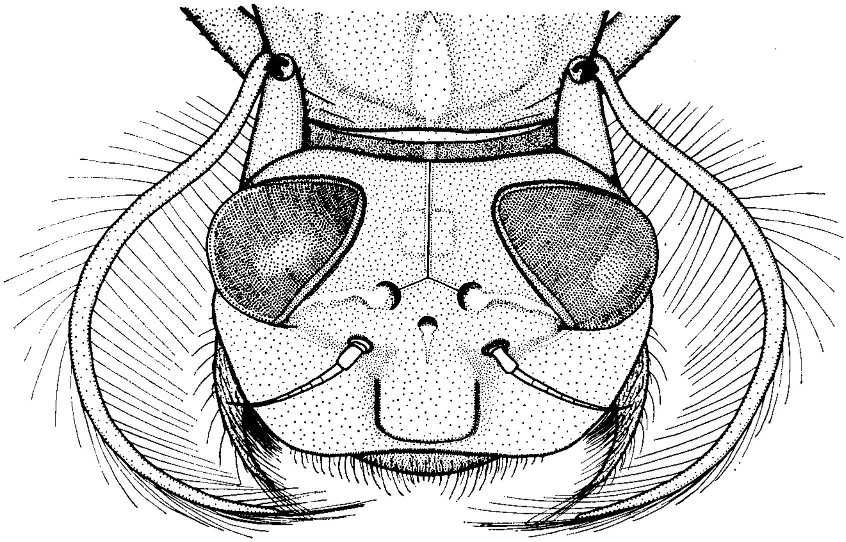


Fig. 1. Head of the nymph of *Arthroplea congener* BENGTSSON seen from the dorsal aspect.

which take origin on the frons anteriorly to the median ocellus (Fig. 3) and are inserted, close to the median line, at the clypeo-labral suture; and a pair of ventral muscles (2), the origins of which lie laterally or latero-anteriorly to those of the dorsal ones, and which are inserted on the epipharyngeal extensions of the tormae. By the action of these muscles, the labrum is capable of making up-and-down and lateral movements. Besides those two pairs, the labrum presents a compressor muscle (3), the fibres of which are attached ventrally to a small median button-like apodeme of the epipharyngeal surface, and from that point they fan out to attach themselves to the dorsal surface at the clypeo-labral suture.

Mandibles

The mandibles (Fig. 7) present a general resemblance to those of *Ecdyonurus*. As in the latter genus, from the elongate basal part, the body of the mandibles broadens considerably toward the molar surfaces and end apically in two canines. The apical canines have three teeth, the basal ones two teeth, or they may have a small third tooth between the two. The apical part of the mandibles, including the canines, is bent ventrally (Fig. 8). The mandibles articulate with the cranium at three points, as is the case with the genera studied by both Strenger and Brown. As in these genera, the posterior articulation is approximately transverse, the heavily sclerotized extreme proximal end of the base

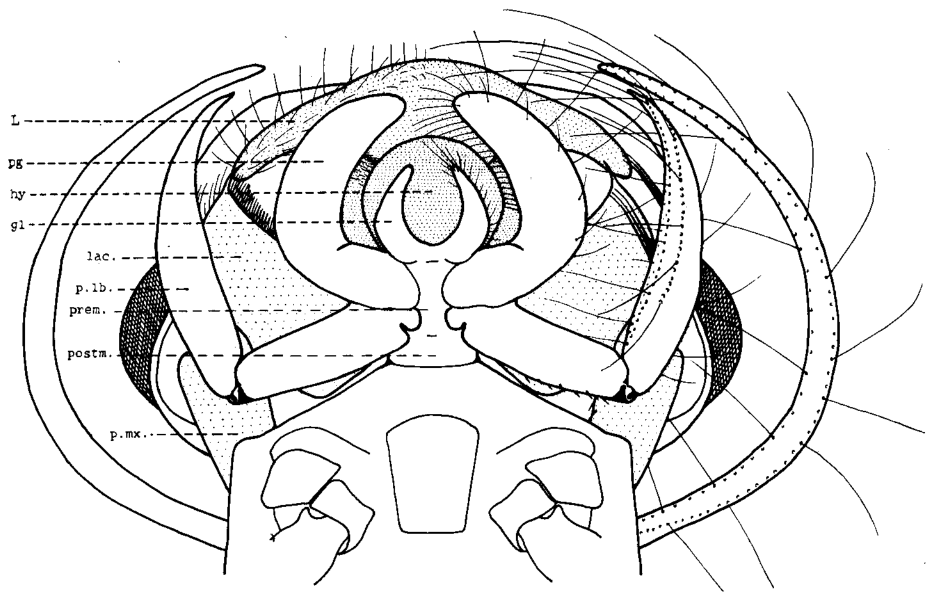


Fig. 2. Head, ventral aspect. Of each set, only some of the hairs and bristles have been drawn, and in only one of the halves. The ventral hairs of the blade of the maxilla have not been drawn, cf. Fig. 10.

of the mandible fitting into a corresponding sclerotized depression at the margin of the subgena (Fig. 5, left side). The middle articulation takes place between a sclerotized area of the dorsal margin of the mandible base and an articulatory process formed by the anterior tentorial arm at the limit with the gena. The middle articulation is nearer to the anterior than to the posterior one. The anterior articulatory process is a rather large, ridge-like sclerotized elevation of the dorsal surface of the body of the mandible (Fig. 8). The lateral surface of this elevation forms the articulatory facet which slides against a corresponding thickened portion of the posterior arms of the epistomal ridge.

The molar areas of the two mandibles are strongly asymmetrical (Fig. 9). Both comprise a series of ventral serrated ridges that project mesially as prongs (Figs. 7 and 9). The mesial contour of the left molar area is a simple curve, that of the right one, a sinuous curve. The prongs of the left molar area are short, and its ends are irregularly spiny. The more anterior prongs of the right molar area are flattened and spatulate, those that follow posteriorly are serrate, and the more posterior ones are spiny. The lengths of the ridges and prongs increase to about a third of their number, then decrease progressively toward the posterior ones. Laterally to the ridges, both molar areas are covered with numerous fringed hairs and some bristles. A strongly sclerotized, tooth-like process occurs on this hairy area of the right mandible. On each canine, both on its ventral as on its dorsal side, there occurs a row of spinules.

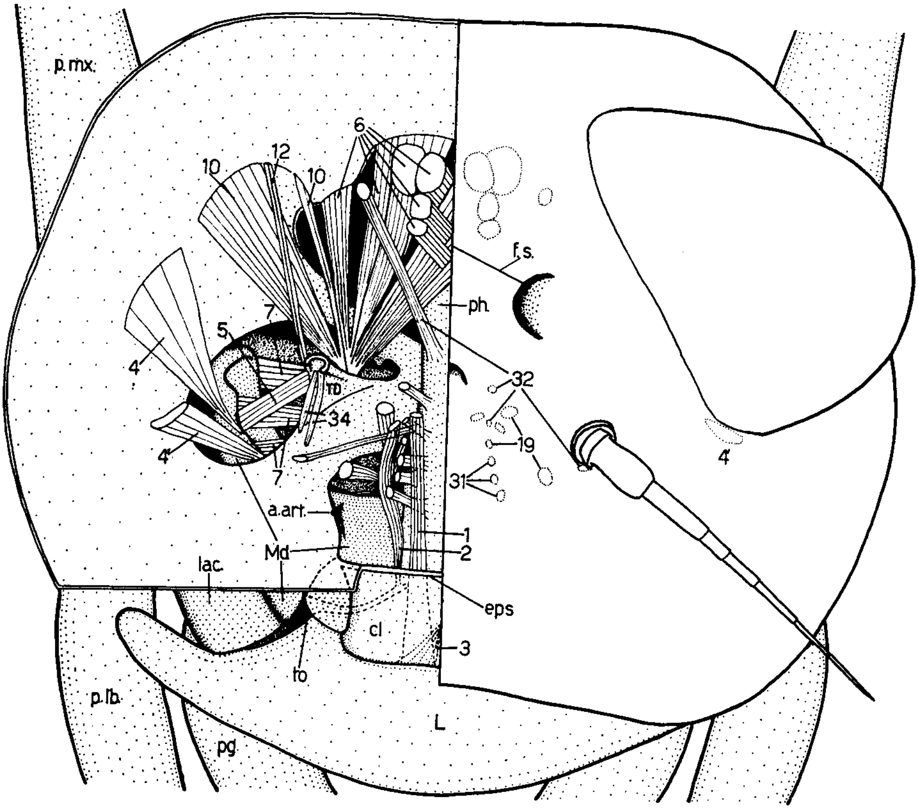


Fig. 3. Head, dorsal aspect, hairs and bristles not drawn. On the right half of the drawing the origins of the muscles are outlined. On the left half, the dorsal wall of the head capsule has been removed exposing the muscles.

A prostheca is absent. On its place is found a bundle of bristles. A few isolated bristles occur at the posterior margin of the left mandible close to the molar area. On the same region of the right mandible, a long isolated bristle is found (Figs. 7 and 9).

The mandibles are moved by cranial and tentorial adductors and abductors. The adductors are much more developed than the abductors. The cranial adductor (6) is inserted on the ventral rim of the base of each mandible through a long tendon (Fig. 5, t). One bundle of fibres of this muscle originates on the postoccipital lateral apodeme. Still other bundles originate on the vertex, between the eyes, some of them contralaterally (Fig. 3). The tentorial adductors (7) are composed of several bundles, most of which are inserted inside the base of the mandibles and originate on the anterior arms of the tentorium. Two bundles are inserted on the ventral rim; one of these originate on the dorsal arm, the other, on the body of the tentorium. The tentorial abductor (5) runs

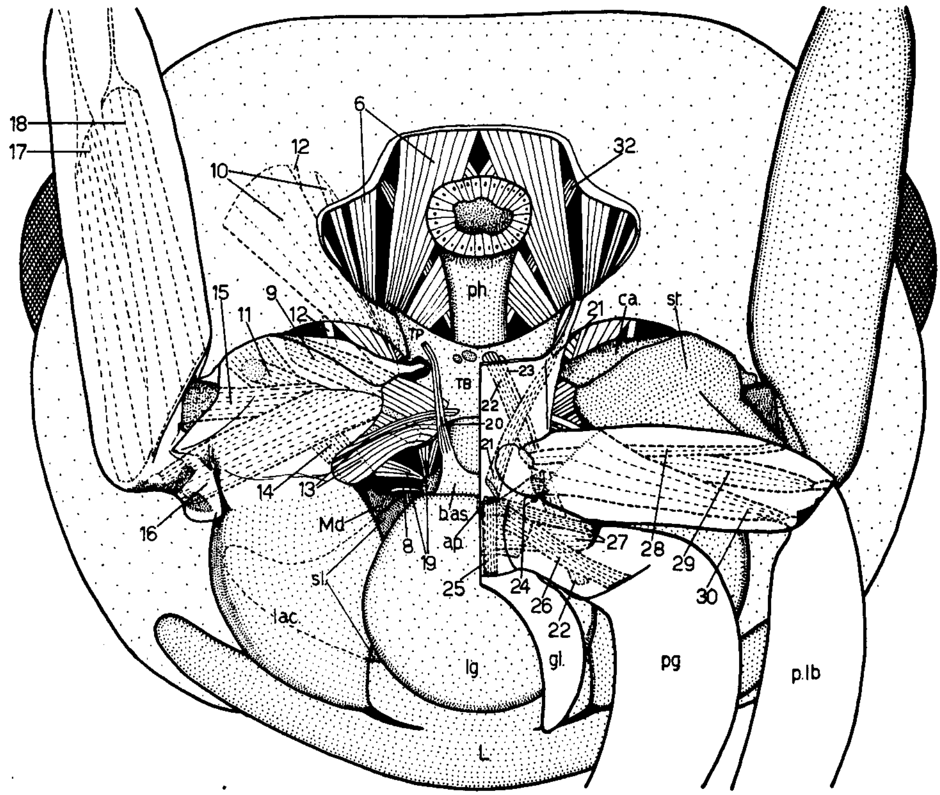


Fig. 4. Head, ventral aspect, hairs and bristles not drawn. On the right half of the drawing the labium has been left unstippled. On the left side it has been removed.

from an elevated, more sclerotized part of the dorsal rim of the base of the mandible (Fig. 8, ab.ins) to the dorsal arm of the tentorium. The cranial abductors (4, 4') are represented by two muscles inserted on the dorsal rim close to the tentorial abductor. One of them (4) originates on the postgena under each eye, the other (4') originates on the gena at the antero-mesial corner of each eye. Originating fanwise inside the dorsal surface of the mandible close to the middle articulation are seen the fibres of the weak mandibular-hypopharyngeal muscle (8). It is connected through a thin flat tendon to the hypopharynx near the angles of the mouth.

The three articulations restrict almost completely transverse movements of the whole mandibles. Abduction and abduction are chiefly rolling movements, the axis of which passes through posterior and middle articulations. The molar surfaces thus roll against each other with a grinding action. The tooth lateral to the molar surface of the right mandible seemingly serves as a stop to the adduction movement of the mandibles. The mechanical load on the molar surface, as has been pointed out in *Ecdyonurus* by Strenger, is borne by the anterior articulations. The canines, being bent ventrally, perform the usual, although restricted, movements of adduction and abduction during working of the mandibles. Whereas the adductor muscles are very strong, making up the largest muscle mass within the cranium, the abductors are rather weak. The tentorial (5) act clearly as abductors. The cranial ones (4, 4'), while having their insertions close to that of the tentorial abductor, have their origins postero-laterally to the insertions. It seems, therefore, that they would really act as adductors, but their precise role could not be ascertained.

Maxillae

The cardo (Figs. 4, 5, 10, 11, ca) articulates basally with a projection of the tentorium at the limit with the postgena. To its dorso-basal edge (Fig. 11) is inserted, through a short tendon, the cranial-cardinal (rotator of the cardo) muscle (10), which consists of two bundles, a weaker one that originates at the occipital region close to the postoccipital apodeme, and a stronger one which originates on the postgena ventrally to the eye. This muscle, besides rotating the cardo, what would result in a rising of the blade (lac) of the maxilla, seems to function chiefly as the abductor of the maxilla. To the distal part of the cardo, at its junction with the stipes, is inserted the cardo adductor muscle (9), which originates on the anterior arm close to the body of the tentorium. As the junction of cardo to stipes is quite firm, this muscle must work jointly with the adductor of the stipes (11).

The stipes (Figs. 4, 10, 11, st) bears anteriorly the single blade (lac) and laterally the maxillary palpus (p.mx). The stipes itself is smaller than either of these appendages. The blade is much flattened; its lateral outline is a regular convex curve, its mesial one, a gently sinuous curve. It ends apically in a strong spine. Along its mesial edge there occurs, from base to apex, first a short bare portion, then a longer row of rather long fringed hairs, and then a long double comb (Fig. 10, l.cb) made up of two rows of closely-set, strong, fringed hairs set at an angle to each other (Fig. 12). While the ventral row is composed of typical hairs (Fig. 12, b), those of the dorsal row appear as extensions of the free edge of the blade and lack the basal articulation (Fig. 12, a). The basal hairs of the comb are short but they get progressively longer apically. The comb ends at the apical spine of the blade. The dorsal surface of the blade is devoid of hairs. On the ventral surface one finds mesio-basally a cluster of fine fringed hairs and, apically to the cluster, an irregular loose row of similar but on the whole smaller hairs. Near the lateral margin, beginning at a distance from the base, one finds a series of closely-set hairs that continue apically along the edge as a row of much longer and thicker ones that ends at the apical spine. The more basal hairs of the marginal row are the longest.

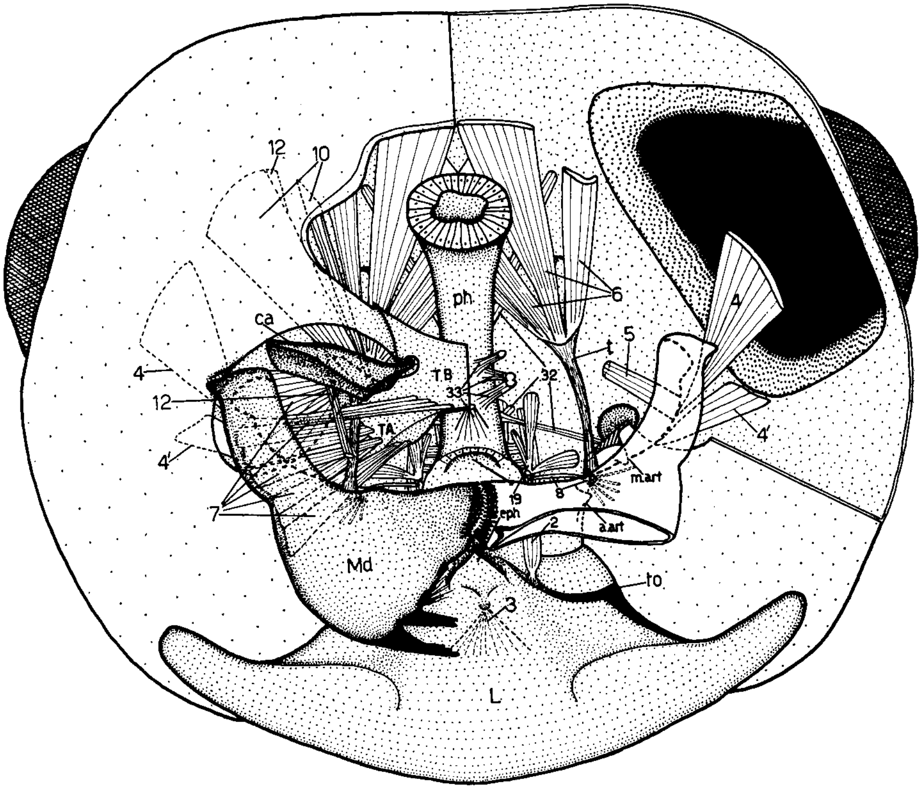


Fig. 5. Head, ventral aspect, hairs and bristles mostly not drawn, labium and hypopharynx removed. On the left half, the maxilla has been removed except the cardo. On the right half, the maxilla, most of the ventral wall, part of the tentorium, and the distal portion of the mandible have been removed; the basal portion of the mandible has been left unstippled.

The tentorial-stipital (adductor of stipes) muscle is divided into two, one of which originates antero-laterally to the tentorial-cardinal (9) on a ventrally bent, rounded process of the anterior arm of the tentorium, is inserted on the ventro-posterior part of the stipes, and forms the tentorial-stipital proper (11); while the other originates on the body of the tentorium, is inserted on the ventro-mesio-basal limit of the blade, and is here called the tentorial of the lacinia (13). The latter (13) is stronger than the former (11) and comprises two chief bundles (Fig. 10). Besides the tentorial-lacinial, two more muscles are inserted at the mesio-basal limit of the blade, but at its dorsal portion: the cranial-lacinial (12) and the stipital-lacinial (14). The cranial-lacinial, which is inserted mesially to the stipital one, originates on the postgena mesially to the larger bundle of the cranial-cardinal (10).

The blade presents ventro-laterally at the base a sclerotized bar which meets a similar sclerotized portion of the stipes; the rest of the connection between stipes and blade is made up of softer cuticle. This arrangement allows flexing movements of the blade against the stipes accompanied by a strong dorsal component. The extent of these movements is, however, restricted. As there are no antagonists to the lacinial muscles, the return movements must be due to elasticity of the cuticle and to pressure of fluids inside the parts concerned. On the whole, the muscles that produce adduction of the blade constitute a relatively strong set.

The two-segmented maxillary palpus is very large (Figs. 1, 2, p.mx). The basal segment is broad and flattened; it is directed backward and in nymphs seen from above, each of them appears from behind the posterior edge of the head and extends to above the antero-lateral part of the mesonotum. Its mesial edge is armed with short bristles. The distal segment, much longer and thinner than the basal one, curves forward and mesially. It is provided with two rows of very long hairs. The hairs of one of the rows are directed mainly mesially, those of the other, mainly ventrally. Each of these hairs is finely fringed along one side. Between the rows of long hairs and close to each of them, there is a row of much thinner and shorter hairs (not drawn).

The basal segment of the maxillary palpus is capable of restricted movements of flexion (adduction) and extension (abduction) brought about by corresponding flexor (15) and extensor (16) muscles, assisted, however, by movements of the stipes. Both (15) and (16) originate ventro-mesially inside the stipes on a sclerotized bar which extends from the junction with the cardo to the base of the blade, and on the ventral surface itself. The movements of the distal segment, which are of great amplitude, are produced by two strong muscles, a flexor (17) and an extensor (18), both of which originate at the base of the first segment and are inserted to the base of the distal one through long tendons (Fig. 10).

Hypopharynx

The large hypopharynx (Figs 13, 14) comprises a rounded, rather flattened, cushion-like lingua and a pair of wing-like superlinguae that extend dorsolaterally to the lingua. The connection of the ventro-basal portion of the lingua with the dorsal surface of the prementum is rather rigid, but apparently less so than in *Ecdyonurus*. In any case, the hypopharynx is capable of only small movements, in particular raising and depressing ones, in relation to the labium. The hypopharynx is supported ventro-basally by the basal sclerite (Fig. 14, bas). To posterior extensions of the basal sclerite are inserted the rather weak posterior muscles of the hypopharynx (retractors of hypopharynx, 20), which originate ventro-laterally on the postoccipital region. From the basal sclerite a bar extends dorsally on each side, following the junction of superlingua and lingua.

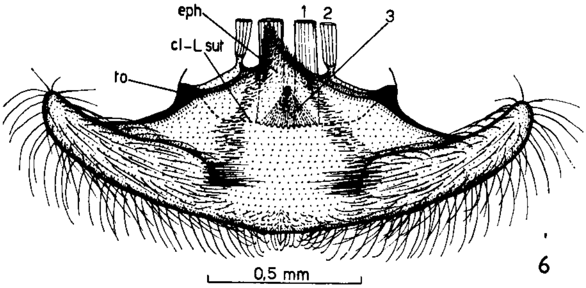
The ventral surface of the lingua is flat, membranous and devoid of hairs. The margin is more sclerotized, especially at the apex. The dorsal surface is also mostly soft, but on each side, beginning at the apex and ending near the limit with the superlingua, there occurs a more sclerotized stripe densely clothed with hairs and bristles directed mesio-basally. Most of the rest of the dorsal surface is provided with numerous small spine-like microtrichia directed along lines that converge to the mouth. Medio-basally the dorsal surface rises steeply toward the mouth. On the median line, about level with the mesial ends of the superlinguae, there is a shallow depression. From the mesial end of each superlingua, a row of closely-set short strong bristles converge to the mouth. These rows are supported basally by the mesial ends of the suspensoria, which form the mesial walls of a U-shaped depression at the mouth. From the lateral walls of this depression spring also bristles similar to those just mentioned above. The area from the median depression and the mesial ends of the superlinguae backward is densely covered with minute hairs directed along lines converging to the mouth.

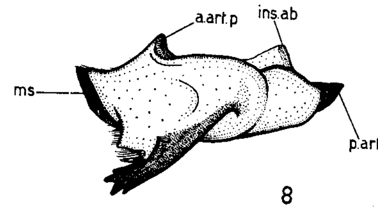
The superlinguae are more heavily sclerotized only in a ventro-posterior area beginning at the mesial bar connected to the basal sclerite and extending laterally to about the bending point of their posterior edge. Laterally to this place, the sclerotization becomes progressively reduced. On the lateral half of each superlingua hairs occur only on a band that extends from the anterior edge to about half of the ventral side. These hairs are thin and simple. The band of hairs broadens at the lingual edge, extends also to the dorsal side and, besides hairs, comprises also numerous bristles, the tips of which may be simple, forked or even present several points. Toward the base, along the mesial edge, the hairs diminish in size as well as in numbers. All the hairs and bristles of the superlinguae are directed mesially.

To the dorsalmost part of the hypopharynx, i.e., to the angles of the mouth, is inserted on each side a muscle composed of three bundles that originate on the frons. This muscle is the dorsal of the hypopharynx (19) or levator of the angles of the mouth. Its function is probably to raise the hypopharynx as a whole. Nearby is inserted the tendon of the mandibular-hypopharyngeal (8). Each dorsal muscle is also connected by means of a tendon-like strip to the lateral portion of the suspensorial sclerites.

Labium

The postmentum and prementum together are small in relation to the appendages (Figs. 2, 4). The labial suture is not well marked. Both post- and prementum are, on the whole, little sclerotized. The lateral, ascending portions of the postmentum, from the bases of the palpi to the postocciput, are its most sclerotized areas. Besides, both post- and prementum have each, on the ventral





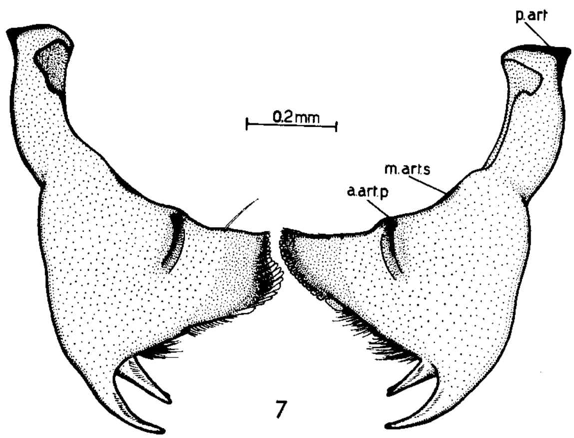


Fig. 6. Labrum and epipharynx, ventral view, showing the distribution of hairs and bristles. The asymmetry of the epipharynx, related to that of the mandibles, may be noted. – Fig. 7. Right and left mandibles, dorsal view, drawn from a pair mounted on a slide. They are in a position of extreme abduction, not possible *in situ*. – Fig. 8. Left mandible, oblique anterior view, showing the twist of the canines.

surface, a median more sclerotized, lightly pigmented area. From the dorsal wall of the prementum, at the limit with the hypopharynx, arises a tendon-like median apodeme (Fig. 4, ap).

The glossae (Fig. 2, gl) arise from the anterior part of the prementum and are situated just under the lingua. Each glossa is a soft, approximately crescentic lobe, provided with a row of rather short hairs along the lateral margin and with an apical tuft (Figs. 2, 15). The paraglossae (Fig. 2, pg), also soft, cushion-like and roughly crescentic, arise from the sides of the prementum posteriorly of the glossae. They are much larger than the glossae and are provided with much more numerous hairs. Each paraglossa is more sclerotized at its antero-basal margin and, latero-ventrally to this margin, at the slope where the paraglossal muscle (26) is inserted. The ventral surface of each paraglossa (Fig. 2) is mostly devoid of hairs, but at the ventro-lateral margin a set of long hairs occur. The more marginal of these hairs radiate outward, while the more ventral are directed forward. The dorsal surface (Fig. 15) is bare at its basalmost portion and along a lateral area; the rest, including the mesial margin, is covered by close-set long hairs that curve mesially. The ends of the more mesial of these hairs rest on the dorsal surface of the lingua (Fig. 2, right half).

The large, two-segmented labial palpi arise from the prementum immediately behind the paraglossae (Fig. 2). The basal segment of each palpus is approximately transverse at rest and articulates antero-ventrally with the prementum at the base of the paraglossa. It is bare except for a row of short bristles along the posterior edge. The distal segment is falciform, almost twice as long as the basal one and, in a resting position, directed forward. The distribution of hairs on this segment is quite complex. On the ventral surface (Fig. 2), there begins basally at the mesial edge a row of long hairs that shortly on separates from the edge, proceeding on a parallel to the latter toward the apex. Between this row and the edge, on the basal half of the segment, smaller hairs occur. Beginning at a distance from the base, a second row, made up of very long hairs, runs along the middle of the segment but, toward the apex, moves to the lateral edge. Near the apex it meets the first row; the apex itself lack hairs. The basal hairs of the second row are directed ventro-posteriorly, but toward the apex they are more and more inclined anteriorly. The more apical ventral hairs, together with some dorsal ones, form a dense brush. On the lateral edge, along the two basal thirds, there are a series of long hairs directed outwards. On the dorsal surface (Fig. 15), there spring up, near the base, a set of very long hairs bent, on the whole, forward. The more mesio-basal of them are directed more mesially, while the more lateral are directed more laterally. Anteriorly to this set, the dorsal surface is covered with very numerous, mostly long hairs that slant mesially. Approximately along the third quarter of the segment, a row of finely fringed, close-set bristles occur along the mesial edge. These bristles curve antero-mesially. Both basally and apically to this row, along the same edge, thinner hairs with the same orientation occur. Besides the bristles, many of the hairs of the distal segment are also fringed.

The musculature of the labium is complex (Fig. 4). The retractors of the prementum (21) originate at the postoccipital region close to the origins of the retractors of the hypopharynx (20), and are inserted ventrally between the bases of the palpi. Two pairs of muscles originate near the posterior margin of the body of the tentorium, those of a pair close to each other. The more mesial pair is inserted dorso-anteriorly in the base of the paraglossa (tentorial muscle of the paraglossa, 22). The more lateral, a pair of very slender muscles, is inserted at the base of the first segment of the palpi, just dorsally to the articulation (muscle from tentorium to base of labial palpus, dorsally to articulation, 23). Muscle (22) is apparently homologous to muscle 14 (dorsal of mentum) of *Ecdyonurus* (Strenger, 1953) and to muscle 18 (anterior retractor of prementum) of *Cloeon* (Brown, 1961). The homologies of muscle (23) I could

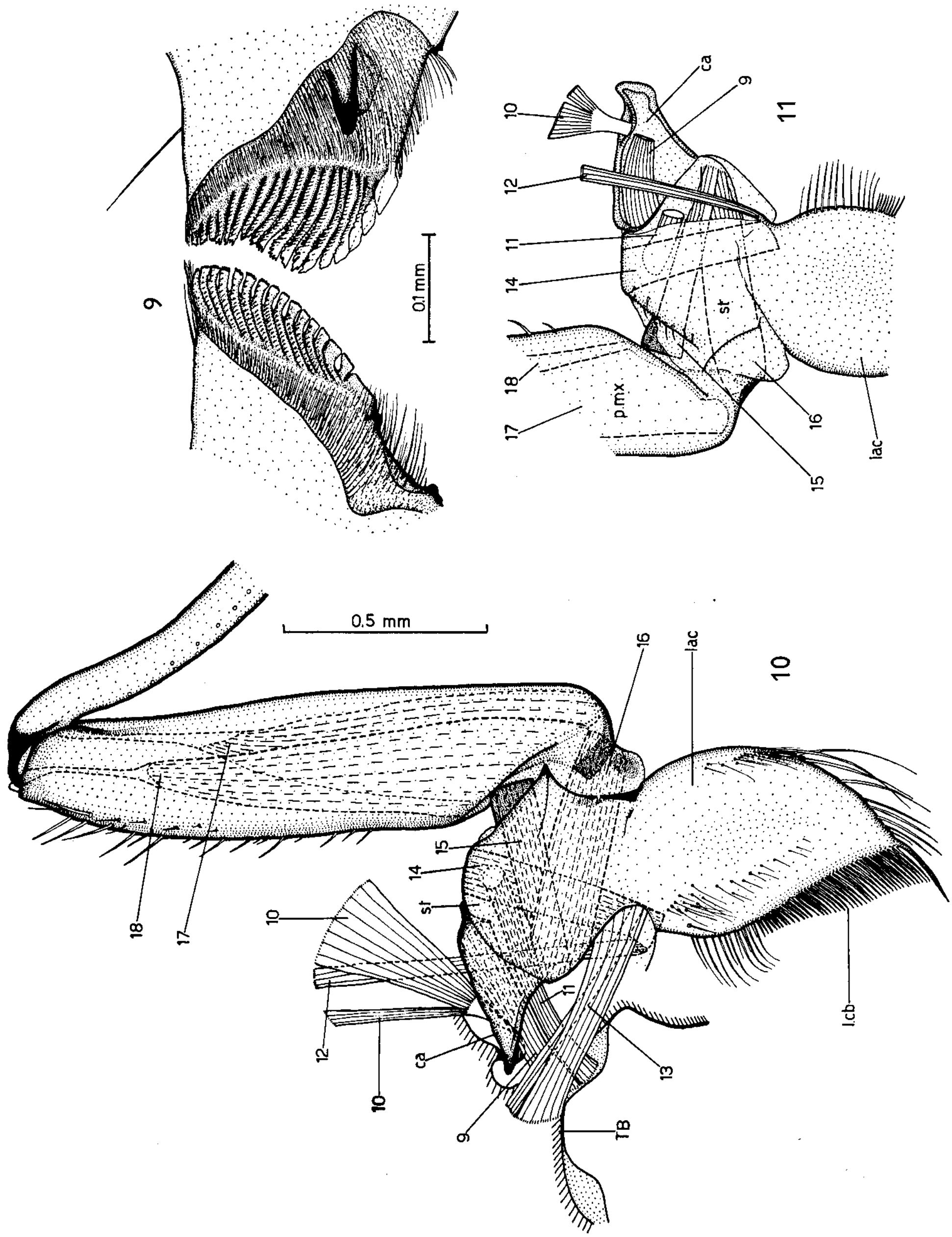


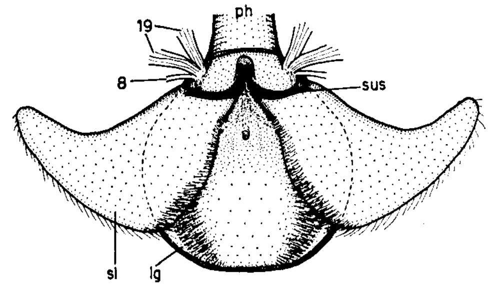
Fig. 9. Molar surfaces of the mandibles of fig. 7, ventral view. – Fig. 10. Right maxilla, ventral view. Most of the distal segment of the palpus has been cut away. – Fig. 11. Right maxilla, dorsal view. The distal part of the blade and most of the palpus have been cut away; muscle (13) has not been drawn.

not make out. From the ventral wall of the prementum, near the median apodeme, originate the flexors (adductors, but with a ventral component) of the glossae (25), which are inserted ventrally at the base of the glossae. Laterally to the origins of (25), on a ventral elevation of the prementum at the base of the paraglossa, originate on each side the flexors (adductors, as 25) of the paraglossae (26), which are inserted on the ventral wall of the paraglossae, on the more sclerotized slope already referred to. A short muscle (24) extends from about the ventral base of the hypopharynx to the dorsal margin of the labial palpus close to the insertion of muscle (23). Muscle (24) corresponds to, but is much weaker than muscle 17 of *Ecdyonurus*. The corresponding muscle of *Cloeon* is probably muscle 19. The basal segment of the labial palpus is moved by two muscles, a flexor (promotor, 27), inserted on a process that projects inside the paraglossa at the limit between the latter and the palpus, and originating in part on the median apodeme and in part contralaterally on a strong internal ridge formed by the dorsal wall of the prementum at the limit with the paraglossa; and an extensor (remotor, 28) situated inside the segment proper. It originates on a strengthened infolding of the surface of the postmentum at the base of the palpus, and is inserted on the posterior margin of the first segment near the apex. This segment contains, besides its remotor, the flexor (30) and the extensor (29) of the second segment. The flexor originates on the cuticle at the base of the first segment along a line that begins dorsally, passes at the articulation with the prementum and crosses the ventral surface, slanting laterally, to end at the posterior edge. The extensor originates on the infolding of the postmentum, together with the extensor of the first segment (28). Both the flexor (30) and the extensor (29) are inserted on the base of the second segment through short tendons. Of all the labial muscles, only the flexors (30) and extensors (29) of the second segment of the palpi and the promotors of the palpi (27) are strong. The strongest of them are the flexors (30).

Feeding Mechanism

Regarding it illuminating, I present in the first place a transcription of Tiensuu's (1939, p. 106) translation of the observations made by Aro on living nymphs. Follow some comments and a further analysis of the working of the mouth parts as could be inferred from their morphology.

Tiensuu's translation follows: "Aro, who reared nymphs in an aquarium, relates about its mode of living as follows (Aro, 1910, p. 22–23) 'The nymph, that is thickly covered with rust, living in water containing rust, loses this protecting coloration in the aquarium and becomes pitch black, shining, and it is then difficult to distinguish it from the black twig, on which it is sitting. It collects food in its mouth in a very remarkable way. Its maxillary palpi are 2-jointed and uncommonly long, and the terminal joint has two thick rows of



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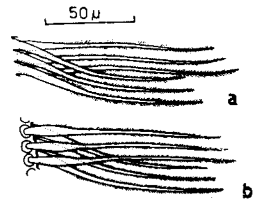

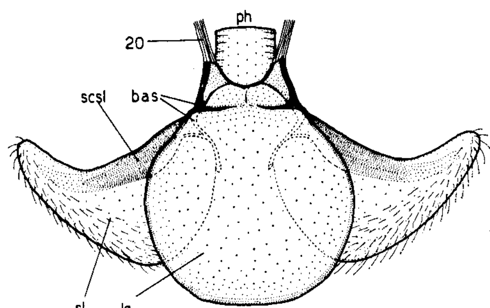

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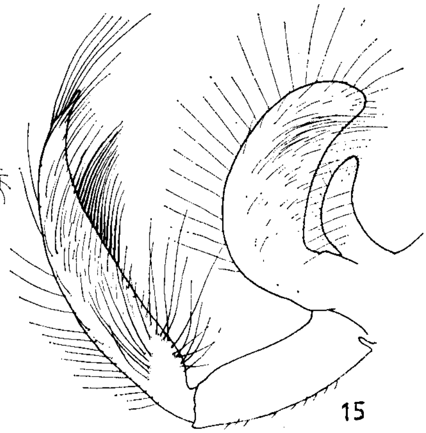

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Fig. 12. Dorsal (a) and ventral (b) views of a small portion of the double comb of the blade of the maxilla. – Fig. 13. Hypopharynx, dorsal view, basal sclerite not drawn. – Fig. 14. Hypopharynx, ventral view. – Fig. 15. Labium: dorsal view of left labial palpus, paraglossa and glossa, showing the distribution of hairs and bristles.

long bristles. These peculiar maxillary palpi the insect uses in the way, that it tosses that bowed joint backwards, over its back and jerks it from there obliquely upwards back to the front of the labial palpi. At the same time, of course, all the water in the way strains through the bristles of the maxillary palpi, while, on the other hand, the algae, etc. catch in them. Then the animal draws the maxillary palpi between the drooping and outspread longhaired labial palpi, whereat the food caught in the former, is now held by the latter, and the maxillary palpi return to their catching trip. The labial palpi are in the same manner cleaned by the outer and inner lobes of the labium, and first by the united action of these and the maxillae the grains of sand and other worthless stuff are removed, while the actual foodstuffs are carried between the mandibles. Sitting under stones, trees, etc. so near the bottom, that the outspread maxillary palpi just touch the bottom lightly, the animal can collect in its mouthparts all the organisms within its reach and make a couple of shallow depressions in the bottom. Then it moves to another place and here continues its catching in the same manner, until it has collected all the food that there is there. Larger *Cladocera, Copepoda,* etc., that are too large, are carefully removed, but the small and soft animals and the algae are utilized for nourishment. And when the bristles of the maxillary palpi for some reason or other have got into disorder, mixed up with one another etc., the nymph cleanses them and sets them right, drawing them slowly through between the palpi and the outer lobes of the labium.' "

The distal segments of the maxillary palpi are, therefore, responsible for straining particles floating in the water and for stirring up particles from the substratum. Besides their role in feeding, the maxillary palpi are also used for a backward jump-swimming, presumably in response to noxious stimuli (Bengtsson, 1909, p. 18; Balthasar, 1937, p. 207). Particles clinging to the long hairs of the maxillary palpi are removed by the dorsal and mesial hairs and bristles and the apical brush of the second segments of the labial palpi as the former are drawn through the outspread labial palpi. To bring this about, the distal segments of the maxillary palpi must stay flexed, while the proximal ones are flexed (adducted) and, at the same time, very probably, the maxillae are abducted, an action that reinforces the adduction of the first segments of the palpi.

Particles not caught by the maxillary palpi but floating about may be strained out by the more crowed hairs of the second segments of the labial palpi on their flexing movement. At the end of the flexing stroke, these segments shove themselves between the paraglossae below, and the blades of the maxillae, the superlinguae and, perhaps, the labrum above. Both above and below the hairs of each distal segment meet sets of hairs directed mesially, viz., the dorsal hairs of the paraglossae, the comb of the blade of the maxilla, and the ventral hairs of the blade, superlinguae and labrum. On extension of the labial palpi, all these hairs comb and hold back the particles brought in by the distal segments. The close-set mesial hairs of the paraglossae, the tips of which lie on the lingua, form a narrow-meshed bridge between these two parts.

Aro states that the labial palpi are cleaned by the outer (paraglossae) and inner lobes (glossae) of the labium. As the glossae are covered by the lingua, I cannot see how they could take such a direct part in the handling of food. Besides, particles clinging to hairs on the dorsal part of the distal segments of the labial palpi cannot be cleaned by the dorsal hairs of the paraglossae, but must instead be cleaned by hairs lying dorsally to them.

On adduction of the blades of the maxillae, the ventral hairs of the double comb rake up first the dorsal hairs of the distal segments of the labial palpi and then the dorsal hairs of the paraglossae, while the dorsal, rigid hairs sweep through the ventral hairs of the superlinguae. Particles clinging to hairs lying outside the range of the double comb may be brought nearer to the middle line by the other sets of hairs of the blade, to be, on the next adduction of the blades, caught by the comb or, perhaps, progressively pushed toward the mandibles by arrival of new food and/or by movements of other mouth parts, e.g., the labrum. As regards the selection of particles by the combined action of the maxillae and the lobes of the labium, observed by Aro, I could not, based on morphology alone, deduce how it works. That, in any case, the selection is not perfect, is shown by the occurrence of sand grains in the gut of all specimens examined.

The food material removed by the comb of the maxillae is held between its two rows of bristles and is, at the end of adduction, pushed in between the superlinguae and the lingua. On abduction of the blades, the dense hairs and bristles on the dorsal surface of the lingua and on the ventro-mesial portions of the superlinguae, aided perhaps by compression due to a rising of the hypopharynx on contraction of its dorsal muscles, retain the food material brought in by the comb. Further movement toward the mandibles is probably due chiefly to pressure caused by new food material being pushed in by successive movements of the blades. The functional parts of the mandibles, as in other Heptageniids, are concealed between the labrum and lingua, and have no direct role in the capture of food (cf. Strenger, 1953, p. 222). The canines may chop up larger particles arriving into their field of action, but even they may have, through the rows of spinules an auxiliary function in conveying particles toward the molar surfaces. The mandibular hairs and bristles serve to drive food toward the molar surfaces, which lie immediately in front of the mouth. As has been already pointed out for *Cloeon* by Brown (1961, p. 161), the molar surfaces, besides crushing the food, have also very probably a straining function, expelling excess water from the food and thus concentrating it. Larger food particles, however, may be not completely crushed, as in the gut relatively large remains of, for instance, copepods and cladocerans were found.

It is important to notice that the labrum, blades of the maxillae, hypopharynx, glossae and paraglossae, and even the labium as a whole, are capable of up and down, and of retraction and protraction movements. These movements, even if small ones (several of the muscles responsible for these or other movements are weak, indicating that movements depending on them are restricted), may be of great significance during feeding. If, as it probably happens, during inswinging of the labial palpi the parts between which they push themselves in are more apart, the action is facilitated, while if, when the extension of the palpi begins, these same parts are approximated, removal of particles from the hairs of the palpi would become more efficient. Some of the muscles of the mouth parts have no antagonist ones, e.g., the lacinial and glossal muscles, in which case the return movement must be due to elasticity of the cuticle and to pressure of fluids inside the parts concerned.

The general pattern of feeding is similar to those of *Ecdyonurus* and *Rhithrogena* (and also to those of *Cloeon* and *Baetis* when feeding on particles), and is of a microphagous type based on successive transfers of particles from one set of hairs to another closer to the mouth. Whereas, however, *Ecdyonurus* and *Rhithrogenea* scrape up particles from a firm bottom in running water, *Arthroplea* strains out particles floating about or stirred up from the bottom in quiet waters. The hairs taking part in the transport of food are directed toward the median line or toward the mouth. Many of these hairs are fringed, an adaptation that increases their working area and so contributes to lessen the loss of particles and, therefore, to increase the efficiency of the feeding appartus. The palpi are the principal organs for the collection of food. The mandibles are hidden and have no direct role in the capture of food.

Abstract

The morphology of the mouth parts and of the related musculature are described. Feeding is based on straining out of particles from the water by long hairs of the palpi and their successive transfers to other sets of hairs closer to the mouth. The distal segments of the maxillary palpi are the chief straining organs. The mandibles have no direct role in capture of food, but are hidden between labrum and hypopharynx.

KEY TO THE LETTERING TO THE FIGURES

a.art	Anterior articulation of mandible.
a.art.p	Articulatory process of mandible for the anterior articulation.
ap	Median apodeme of prementum, originating at base of lingua.
bas	Basal sclerite of hypopharynx.
ca	Cardo.
cl	Clypeus.
cl-Lsut	Clypeolabral suture.
eph	Epipharynx.
eps	Epistomal suture.
f.s	Frontal suture.
gl	Glossa.
hy	Hypopharynx.
ins.ab	Place of insertion of tentorial abductor of mandible (5).
L	Labrum.
lac	Lacinia (blade of maxilla).
l.cb	Double comb of lacinia, formed of two rows of closely-set hairs.
lg	Lingua.
m.art	Middle articulation of mandible.
m.art.s	Articulatory surface of median articulation of mandible.
Md	Mandible.
ms	Molar surface.
p.art	Posterior articulation of mandible.
pg	Paraglossa.
p.lb	Labial palpus.
p.mx	Maxillary palpus.
ph	Pharynx (and oesophagus).

postm	Postmentum.
prem	Prementum.
sc.sl	Sclerotized postero-ventral portion of superlinguae.
sl	Superlingua.
st	Stipes.
sus	Suspensory ligament.
t	Tendon of cranial adductor of mandible (6).
TA	Anterior arm of tentorium.
TB	Body of tentorium.
TD	Dorsal arm of tentorium.
to	Torma.
TP	Posterior arm of tentorium.

Muscles

1 Dorsal of labrum.
2 Ventral of labrum.
3 Compressor of labrum.
4 Ventral cranial abdutor (?) of mandible.
4' Dorsal cranial abductor (?) of mandible.
5 Tentorial abductor of mandible.
6 Cranial adductor of mandible.
7 Tentorial adductor of mandible.
8 Mandibular-hypopharyngeal.
9 Tentorial of cardo.
10 Cranial of cardo.
11 Tentorial of stipes.
12 Cranial of lacinia.
13 Tentorial of lacinia.
14 Stipital of lacinia.
15 Flexor of first segment of maxillary palpus.
16 Extensor of first segment of maxillary palpus.
17 Flexor of second segment of maxillary palpus.
18 Extensor of second segment of maxillary palpus.
19 Dorsal of hypopharynx (Levator of angle of mouth).
20 Posterior of hypopharynx (Retractor of hypopharynx).
21 Retractor of prementum.
22 Tentorial of paraglossa.
23 Tentorium-Base of labial palpus dorsally to articulation with prementum.
24 Prementum at base of hypopharynx – Dorsal margin of base of labial palpus.
25 Flexor of glossa.
26 Flexor of paraglossa.
27 Flexor (promotor) of first segment of labial palpus.
28 Extensor (remotor) of second segment of labial palpus.
29 Extensor of second segment of labial palpus.
30 Flexor of second segment of labial palpus.
31 Anterior dorsal pharyngeal.
32 Posterior dorsal pharyngeal.
33 Ventral pharyngeal.
34 Antennal.

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