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The Structure and Function of the Mouth Parts of Adult Caddis Flies (Trichoptera)

M. I. Crichton

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THE STRUCTURE AND FUNCTION OF THE MOUTH PARTS OF ADULT CADDIS FLIES (TRICHOPTERA)

By M. I. CRICHTON, Ph.D.
Zoology Department, University of Reading

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CONTENTS

The paper gives a detailed account of the structure and function of the mouth parts of *Phryganea striata* L., followed by a comparative study of these structures throughout the order Trichoptera. Observations on the feeding of caddis flies are reviewed. Consideration is given to homologies and phylogeny.

In *Phryganea* the head is produced ventrally into a proboscis to which all parts of the mouth complex contribute. A detailed account is given of external and internal structure, musculature, and nervous system of the head and mouth parts. The central area of the anterior surface of the head capsule is interpreted as a frontoclypeus because of the origin of muscles to the foregut. The elongate labrum covers a sclerotized groove or sitophore. Mandibles are reduced to small lobes. The cardines and stipites of the maxillae contribute to the base of the proboscis. The single maxillary lobe is interpreted as a lacinia on grounds of musculature.

The distinctive protrusible haustellum is regarded as derived from the hypopharynx. It is traversed by a common salivary duct, provided with a muscular valve. The anterior surface of the haustellum is covered with a system of channels which converge to the sitophore. These channels are formed by cuticular outgrowths arranged in lines and drawn out into filaments which roof the channels thus formed. These outgrowths, which are named pectinate hairs, differ in form according to their position on the haustellum.

The labium forms part of the base of the proboscis. There is no ligula.

Extension of the proboscis is brought about both by muscle action on sclerites and increased blood pressure affecting the flexible areas of cuticle. Relaxation results from reduction in blood pressure, and contraction of retractor muscles. The haustellum functions as an organ for taking up liquids. A direct drinking and a lapping attitude are described.

The comparative study includes observations on fifty-three species, which are representative of each of the thirteen families found in Britain. All species examined have a protrusible haustellum, and are capable of drinking. The most highly developed condition is seen in the Phryganeidae and Limnephilidae. A channelled haustellum is also found in the Sericostomatidae, Beraeidae, Molannidae, Odontoceridae, Leptoceridae and Polycentropidae. A simple granulose haustellar surface, devoid of channels, is present in the Hydropsychidae, Psychomyidae, Philopotamidae, Rhyacophilidae and Hydroptilidae.

The mandibles are of doubtful function. They are largest in the Hydropsychidae and Rhyacophilidae, and most reduced in Limnephilidae. Small lobes, which are thought to represent the ligula of the labium, are seen in the Philopotamidae, Hydropsychidae, Psychomyidae and Polycentropidae. These differing conditions of the mouth parts are shown to accord with views on the phylogeny of the Trichoptera, which are derived from other data.

An account is given of published descriptions of modified mouth parts in some exotic species. The nature of these modifications is discussed.

Published observations on the feeding of caddis flies are reviewed. It is concluded that using the haustellum to drink nectar and water is a normal activity of caddis flies.

Introduction

The present investigation was undertaken to provide both a comprehensive account of the mouth parts of an adult caddis fly, and a review of these structures throughout the order. Without such information textbook accounts must remain inadequate.

Although it is known that some caddis flies are capable of drinking, their mouth parts are frequently described as reduced or vestigial. For example, Brues (1946), in his study of insect dietary, referred to 'a number of insects belonging to several orders which do not feed at all after maturity.... This condition known as aphagia prevails among the may-flies, proverbial for their ephemeral period of sexual life, but is encountered generally among the caddis flies,....' The mouth parts may appear to be vestigial in preserved specimens because the tongue-like organ used in drinking is normally retracted out of sight. This organ, known as the haustellum, is in fact characteristically developed in the Trichoptera, but living specimens must be available for its proper study.

The first part of this investigation is a detailed study of the structure and function of the mouth parts of *Phryganea striata* L. This species was chosen because of its large size and the full development of its mouth parts. The second part is a comparative study of the mouth parts throughout the order with notes on some modifications. This is followed by a review of observations on the feeding of caddis flies. Homologies and phylogeny are considered in the discussion and conclusions.

The only detailed account available is that of Lucas (1893). He described the general external features of the mouth parts of *Anabolia furcata* (Limnephilidae), but not their detailed structure or internal anatomy. Most of his paper, however, is concerned with the mouth parts and head glands of the larva; the pupal mouth parts are also briefly described. This work is the source of most descriptions and figures in textbooks.

Kellogg (1895) gave some information on Trichoptera in a study of the mouth parts of the Lepidoptera. In *Halesus* (Limnephilidae) he observed the rudiments of mandibles, which Lucas had failed to find in *Anabolia*. He saw the haustellum in some species, but gave no further details of any value.

Genthe (1897), in a paper on the mouth parts of Lepidoptera, recorded notes on the mouth parts of fifteen species of caddis flies. While he was concerned mainly with the structure of the maxillary palps, Genthe was apparently the first worker to describe well-developed mandibles in an adult caddis fly, *Hydropsyche pellucidula*. Unfortunately, he was working mainly with dry material and there is no evidence that he studied the living insects or had a true conception of the mobility and function of the haustellum.

Cummings (1913, 1914*a* and *b*) gave brief details of the unusual condition of the mouth parts in certain species. He declared that he had found the haustellum present in every family of the Trichoptera. While he must have made observations on a number of species, he seems to have published no other work on the mouth parts of Trichoptera. His interpretation of the haustellum will be referred to later.

Deoras (1943, 1944) described and figured the head and mouth parts of eight species of caddis flies, representing six families. His paper is an example of the unfortunate result of working on preserved material, without proper study of the living insect. Because the haustellum was retracted in some of his specimens, he described it as reduced or nearly absent.

In a few exotic genera, some modifications of the mouth parts have been recorded by Ulmer (1904), Cummings (1913, 1914*b*) and Döhler (1914, 1915). They were mentioned briefly by Betten (1934).

From the published work reviewed above, it is apparent that these earlier investigators paid little attention to living insects. It is thus understandable that textbook accounts are unsatisfactory. In addition, the mouth parts are usually neglected in systematic works, except for the segmentation and structure of the maxillary palps.

Material and methods

Adult *Phryganea striata* were collected in a Robinson-pattern mercury-vapour light trap, which was set up at Millbarn Pond, Wokefield, Berkshire. This trap was operated regularly in 1953, 1954 and 1955, in order to study the seasonal occurrence of caddis flies. In each year, *P. striata* had a flight period of about 1 month, with the main emergence in the last week of May. Nearly all the specimens collected were males. The only sexual difference in the head is found in the maxillary palps, which have five segments in the female, and only four in the male. Confirmatory observations were made on *P. grandis*, the main emergence of which was about 1 month later.

Most of the species studied in the comparative review of the order were captured at the same site, others were collected elsewhere in the Reading area. A few species, which were not obtainable locally, were collected in Gloucestershire.

The insects were first studied individually, under a dissecting microscope, while in the act of drinking. For this purpose, they were confined in a Petrie dish with a small drop of water. The smaller species were found to cling to the glass and continue drinking while inverted. For the larger species, which could not remain clinging to the glass, a circle of filter paper, with a central hole of about $\frac{1}{2}$ in. diameter, was fitted in the dish. The drop of water was then put in the window thus provided, and the fly was able to grip the filter paper while feeding in the inverted position. Thus it was possible to watch the movements of the proboscis and to confirm the intake of water. In most species, flies of both sexes were examined.

For the detailed study of the external structure and movements of the mouth parts, the caddis fly was held in an insect compressor which was developed for this work (Crichton 1955). The fly was lightly anaesthetized with ether before being placed between the two slides of the compressor, leaving the head free. The slides were then brought together by a fine screw adjustment, so that gentle pressure thus applied to the thorax and abdomen caused the protrusion of the haustellum in the head. In this way it was possible to make drawings from the living insect. It was unharmed by the small pressure necessary, and could be repeatedly subjected to this treatment.

Specimens for dissection were fixed in Pampel's fluid, with the haustellum protruded during fixation by light pressure on the body. The head was cut into two parts with a small scalpel, and each part then dissected with fine needles. While the initial cut was made in various planes, it was found that a sagittal cut produced most information. Dissection was carried out under a dissecting miscroscope, using magnifications of up to ×150.

Serial transverse and longitudinal sections of the head, cut at $10\,\mu$, were stained in Mallory's triple stain, from material fixed in alcoholic Bouin's fixative, and embedded in paraffin wax. These sections confirmed details seen in dissection, and were necessary for the study of the structure of the collecting channels of the haustellum. A phase contrast microscope, with $\frac{1}{12}$ in. oil immersion, was used for investigating the pectinate hairs on the haustellum. The technique of using polaroid disks in the microscope (Imms 1939) was employed for the study of the muscles in the palps.

THE HEAD AND MOUTH PARTS OF *PHRYGANEA STRIATA* L.

External anatomy

The head is hypognathous. The strongly sclerotized head capsule is produced ventrally into a flexible proboscis to which all parts of the mouth complex contribute. In the following account, the facial surface of the head (figure 1) will be referred to as anterior, and the opposite surface (figure 3), where the head is joined to the body, as posterior.

Head capsule (figures 1 to 3)

The strongly sclerotized head capsule appears broad because of the well-developed compound eyes which project laterally from it. These eyes are composed of a large number of ommatidia. There are three prominent dorsal ocelli, one between the antennae facing forwards, and one above each compound eye facing laterally. Each antenna arises from an area of flexible unpigmented cuticle on the antero-dorsal surface of the head capsule, between the eye and the median ocellus. The scape pivots on an antennifer (*antf.* in figure 1), and bears a short pedicel which is followed by a long multiarticulate flagellum.

The flattened anterior surface of the head capsule, which is strongly setose, bears on each side a shallow vertical groove, in which is seen the anterior tentorial pit (*a.tent.p.* in figure 1). The central undivided area between these grooves is interpreted as a fronto-clypeus (*frclp.*) on the basis of muscle origins, which will be described later. Thus the vertical groove is regarded as a frontogenal suture, where it lies above the anterior tentorial pit, continuing below this point as a clypeogenal suture (see figure 1).

Ventral to the eye, the gena is produced into a prominent process (figure 2). Posterior to the eye, the gena is followed by a postgena, which is continuous dorsally with the occiput (*pge.* and *occ.* in figure 2). On both the postgena and occiput there are strongly setose areas (figures 2 and 3). Otherwise the posterior surface of the head capsule is devoid of setae.

Close to the dorsal and lateral margins of the occipital foramen there is a pigmented line (*pocc.s.* in figure 3) which leads to the posterior tentorial pit on each side. Along this line, the cuticle is produced internally into a thin apodeme which tapers off laterally. This serves for the origin of muscles which extend back into the neck of the insect. This line appears to be a postoccipital suture, delimiting a narrow postocciput (*pocc.* in figure 3). Slightly dorsal to the posterior tentorial pit, the postocciput is produced into an occipital condyle (*occ.c.* in figures 2 and 3) which articulates with a sclerite on each side of the neck.

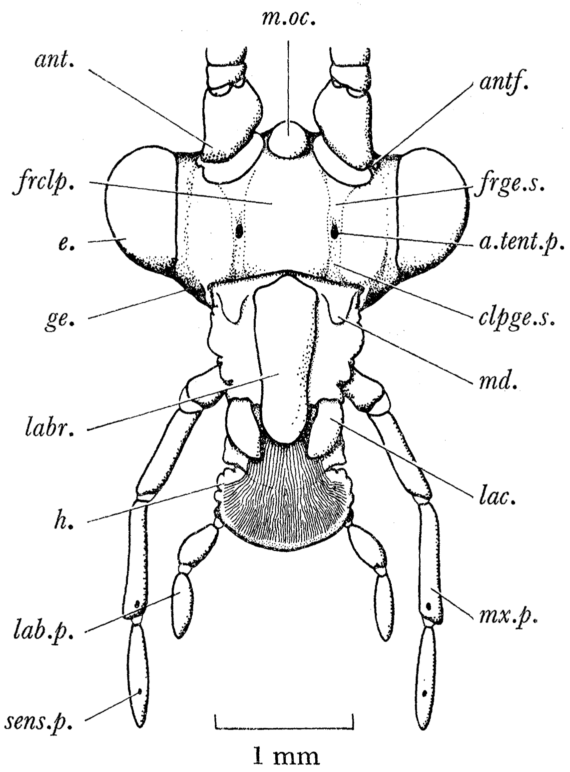


FIGURE 1. *Phryganea striata* ♂. Anterior view of head with haustellum protruded. Outline drawing with setae omitted. For list of abbreviations used in the figures see p. 91.

Proboscis (figures 1, 2, 3 and 5)

Ventral to the head capsule is a flexible proboscis, held at right angles to the main axis of the body when the insect is feeding. It is figured protruded in the feeding position (figures 1 to 3), but with the maxillary and labial palps extended conventionally, and not in the natural feeding position.

The basal part of the proboscis is formed from hypopharynx, maxillae, and labium. It bears on its anterior surface the much-reduced mandibles and the elongate labrum which covers the sclerotized groove or sitophore leading to the mouth (*sit.* in figure 5). The terminal part of the proboscis, which is protrusible, functions as a tongue in feeding. Lucas (1893) named this organ a haustellum (Latin *haustus*, a drinking). As this name is appropriate to its function, I propose to use it in this account, without implying homology with the part of the dipterous proboscis bearing the same name.

The terminal haustellum and that part of the anterior surface of the proboscis which includes the sitophore are regarded here as derived from hypopharynx.

Labrum (figures 4 and 6)

The elongate labrum arises from an area of flexible cuticle at the base of the proboscis, directly ventral to the frontoclypeus. While the whole of the convex anterior surface is

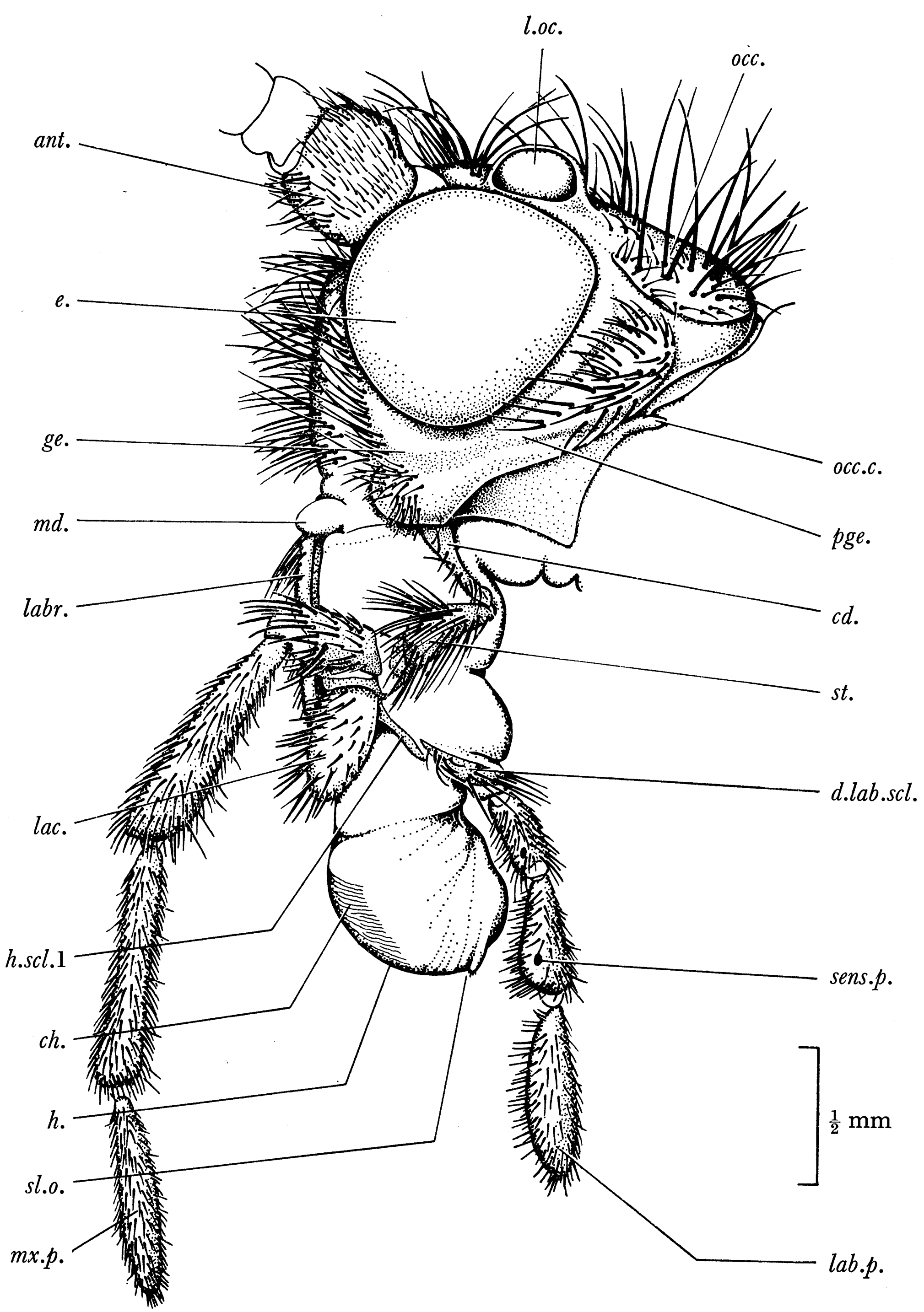


Figure 2. *Phryganea striat a* ♂. Lateral view of head with haustellum protruded.

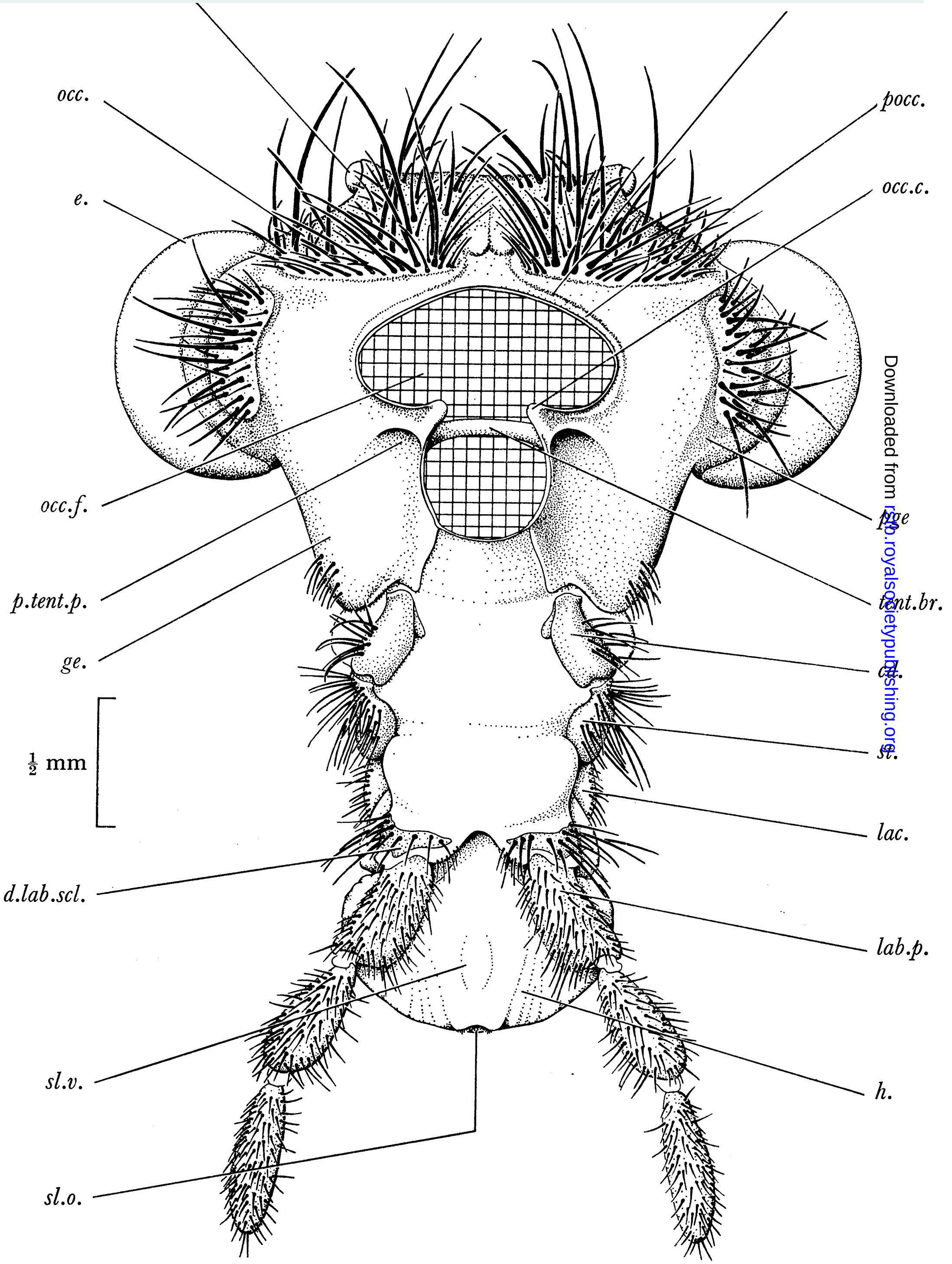


Figure 3. *Phryganea striata* ♂. Posterior view of head with haustellum protruded.

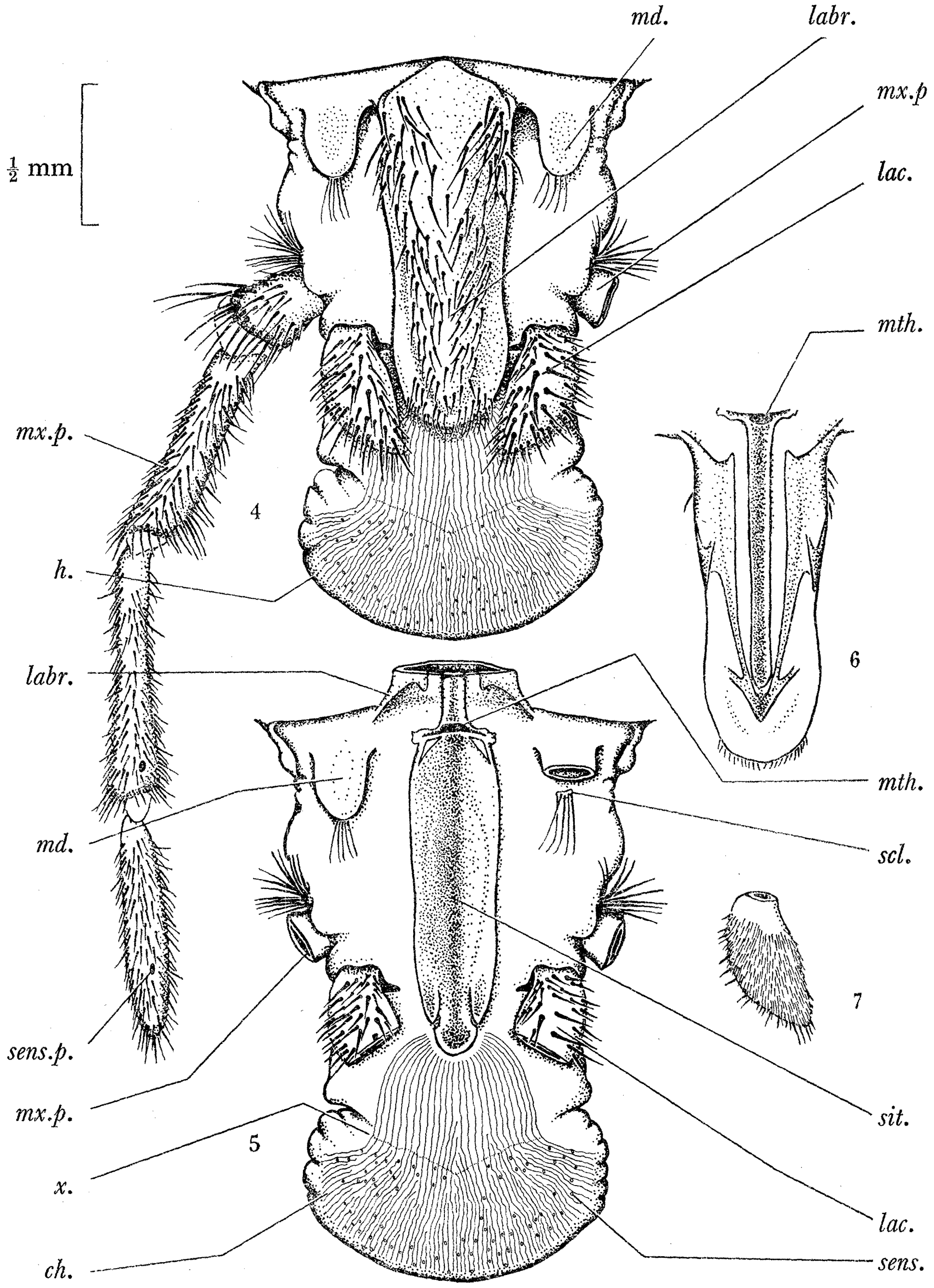


Figure 4. *Phryganea striata* ♂. Anterior view of proboscis with haustellum protruded. The left maxillary palp has been cut off, and the labial palps are not shown.

Figure 5. *Phryganea striata* ♂. Anterior view of proboscis with haustellum protruded. The labrum has been lifted up and cut off at its base so as to display the sitophore. The maxillary palps have been removed, and the laciniae cut back to display the channels on the haustellum. The left mandible has been cut back to display the small sclerite posterior to it.

Figure 6. *Phryganea striata* ♂. Posterior surface of labrum.

Figure 7. *Phryganea striata* ♂. Posterior surface of left lacinia.

clothed with setae, only the basal half is pigmented and strongly sclerotized. The tip can be raised independently by muscle action.

On the posterior surface of the labrum (figure 6), a narrow sclerotized groove in the centre is flanked by sclerotized areas, which converge to form a V near the apex. These lateral sclerotized areas fit closely against the edges of the sitophore, forming a channel from the base of the haustellum to the mouth.

Mandibles (figures 4 and 5)

The mandibles, which are devoid of setae, are small lobes lying one on each side of the base of the labrum. Their cuticle is soft and flexible, with a small pigmented patch on the anterior surface. From their small size and position it is assumed that the mandibles have no function.

On the proboscis, behind the mandible, is a tiny sclerite (*scl.* in figure 5) which bears a group of long slender setae, which project a little way beyond the tip of the mandible.

Maxillae (figures 2 to 4)

The basal part of each maxilla is composed of a cardo and stipes which are clearly defined from the rest of the proboscis by their dark sclerotized cuticle and well-developed setae. The basal cardo (*cd.* in figures 2 and 3) is an elongate sclerite, with a small condyle which articulates in a depression on the ventral margin of the postgena. The cardo widens out distally, and bears a few short setae.

The main body of the stipes is shorter and broader than the cardo, and is thickly set with long setae. In the extended condition of the proboscis, the cardo and stipes form approximately a right angle, with the stipes directed obliquely forwards and ventrally (see figure 2). In the retracted condition they are flexed and come to lie almost parallel to each other as do the blade and handle of a pocket knife (see figure 31).

Distally, the stipes is drawn out into a slender curved sclerite. This bifurcates into an anterior branch which partly encircles the base of the maxillary palp, and a posterior branch which curves behind the single maxillary lobe. This latter branch is closely associated with the proximal end of the basal haustellar sclerite (*h.scl.*1 in figure 2).

The single maxillary lobe is interpreted as a lacinia, on the grounds of musculature, as will be explained later. It is a prominent ovate lobe only lightly sclerotized, with short stout setae covering the convex anterior surface (*lac.* in figure 4). The concave posterior surface (figure 7), which is thickly clothed with fine short setae, is closely applied to the base of the haustellum. The laciniae lie on each side of the tip of the labrum. They come closer together and hide the end of the haustellum when this organ is retracted (see figure 32).

The maxillary palp consists of four segments in the male, and five in the female. These are strongly sclerotized, and thickly covered with setae. The basal segment is appreciably shorter than the others, which are approximately equal in length in both sexes. There is a sensory pit near the distal end of the third and fourth segments in both male and female (*sens.p.* in figure 4).

Haustellum (figures 1 to 5)

This distinctive tongue-like organ can be completely retracted within the basal part of the proboscis (see figures 31 and 32). Apart from three pairs of small haustellar sclerites the entire cuticle is soft and flexible. The common salivary duct traverses the organ and opens just posterior to its apex. For reasons given later, the haustellum is considered to be derived from the hypopharynx, with possibly a labial element incorporated posteriorly.

On the anterior surface of the haustellum, the flexible laminated endocuticle is thicker than elsewhere, as shown in transverse sections (figures 18 to 20). The cuticle is here formed into longitudinal ridges, with separate channels of semicircular section between them; these cover the whole anterior surface. In the specimen from which figure 5 was drawn there were seventy-eight smaller peripheral channels. These united and converged into twenty-five main channels, which opened into the sitophore. The diameter of these channels ranged from 13 to 22 μ.

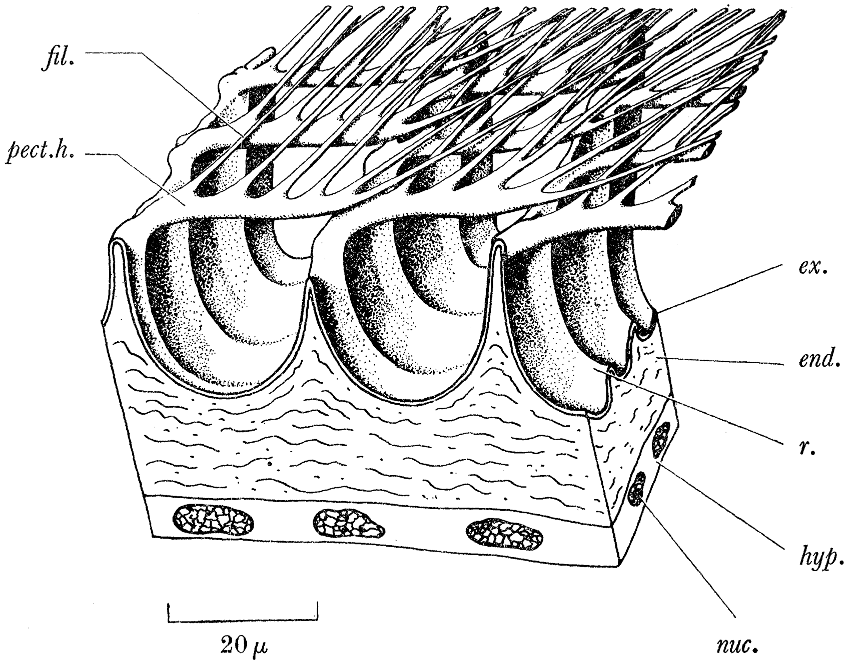
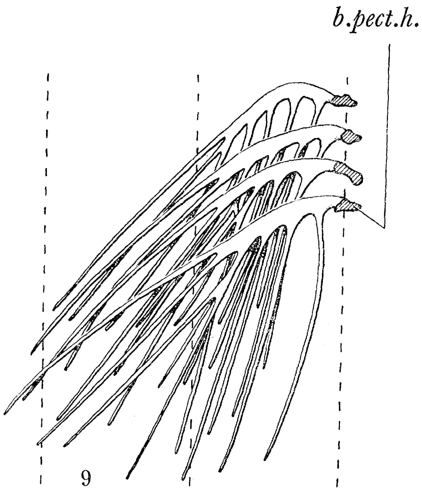
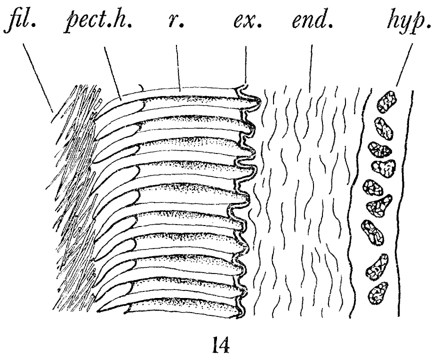


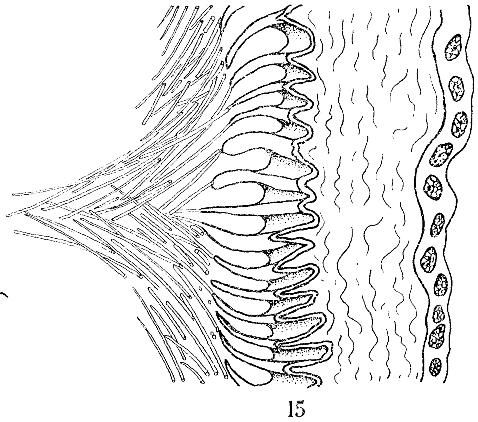
FIGURE 8. *Phryganea striata*. Stereogram to show structure of the channels near the base of the haustellum on the left side. The main axis of each pectinate hair is directed towards the mid-line, while the filaments point towards the apex of the haustellum.

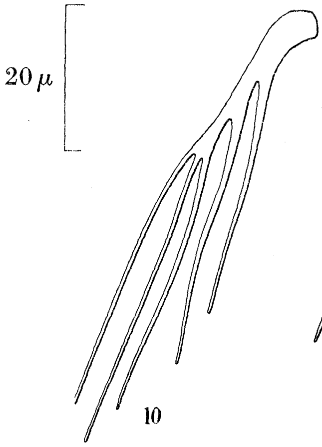
In addition to the longitudinal ridging which forms the channels, the endocuticle is transversely ribbed. Along the longitudinal ridges the exocuticle from each transverse rib is drawn out into a compound hair. Each of these hairs has a main axis which bears five to seven slender filaments on one side only (figure 10). I propose to call these distinctive structures *pectinate hairs*. They lie obliquely across the channels which are thus roofed by a fine felting. Reference to figure 8 should help to explain the complicated structure of the surface of the haustellum. This figure illustrates portions of some main channels near the base of the haustellum, with the distances between transverse ribs exaggerated for the sake of clarity. The actual disposition of four pectinate hairs, seen from the inside in a surface section, is shown in figure 9. The broken lines in this drawing mark the edges of two channels, thus showing how the pectinate hairs lie obliquely across them.

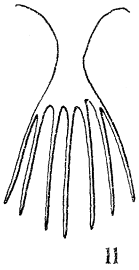
The pectinate hairs with their filaments are directed obliquely across the channels from each side towards the mid-line of the haustellum. This results in a line of convergence

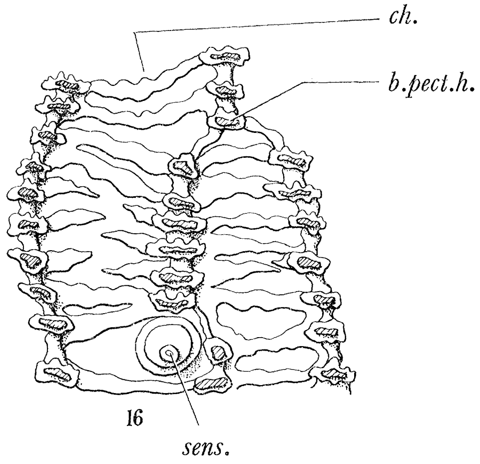


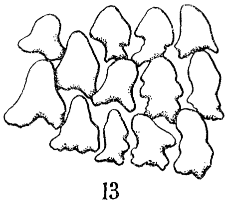












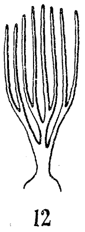


FIGURE 9. *Phryganea grandis* ♂. An inner surface view of four pectinate hairs from the basal part of the haustellum. The broken lines mark the edges of two channels.

FIGURE 10. *Phryganea striata* ♂. A pectinate hair from the basal part of the haustellum.

FIGURE 11. *Phryganea striata* ♂. A pectinate hair from the mid-line in the basal part of the haustellum.

FIGURE 12. *Phryganea striata* ♂. A pectinate hair from the apex of the haustellum, distal to the channelled area.

FIGURE 13. *Phryganea striata* ♂. Tubercles from the apex of the haustellum close to the opening of the salivary duct.

FIGURE 14. *Phryganea grandis* ♂. Longitudinal section through a channel at the base of the haustellum.

FIGURE 15. *Phryganea grandis* ♂. Longitudinal section through a channel in the middle region of the haustellum at the level of the transverse line of convergence of pectinate hairs.

FIGURE 16. *Phryganea grandis* ♂. Surface view of the junction of two channels near the apex of the haustellum. A sensillum is shown in one of the channels.

below which there are short symmetrical pectinate hairs (see figure 11) in place of the asymmetric hairs already described.

In addition to this line of convergence down the mid-line of the haustellum, there is a transverse line of convergence, which is seen as a shallow V (*x.* in figure 5). While proximal to this line, the filaments of the pectinate hairs are directed towards the apex of the haustellum, distally they are directed towards the base of the organ. The appearance of this transverse line of convergence, in a longitudinal section of a channel, is shown in figure 15. Only fragments of individual filaments are shown, since they are mostly running obliquely to the plane of section. Under the low power of a dissecting microscope both longitudinal and transverse lines of convergence are clearly seen as raised lines of filaments.

The peripheral channels are smaller with irregular transverse ribs, as shown in a surface section of the confluence of two channels (figure 16). Round the apex of the haustellum, beyond these channels, is an area of scattered tubercles. Each of these is drawn out into a small symmetrical pectinate hair of the type illustrated in figure 12. The filaments of these hairs are directed proximally. Near the orifice of the common salivary duct the tubercles are simple, without pectinate hairs (see figure 13).

The succession of these cuticular structures can now be considered briefly in the reverse order, i.e. from apex to base of the haustellum. The simple tubercles at the apex are succeeded by those with small symmetrical pectinate hairs directed proximally. These are then arranged in lines and joined by their bases in longitudinal ridges, thus forming the channels between them. The pectinate hairs are next seen to be asymmetric, and directed obliquely proximally and towards the mid-line. There is then the transverse line of convergence, proximal to which the filaments of the well-developed pectinate hairs are directly obliquely towards the apex and the mid-line of the haustellum. The succession of these structures is conveyed in figure 28.

About 100 basiconic sensilla are distributed in the apical channels of the haustellum, distal to the transverse line of convergence (see figure 5). These sensilla are described and figured later (see figure 30).

The posterior surface of the haustellum is devoid of channels. It bears, at the sides, a number of longitudinal folds which become deeper when the haustellum is retracted. The projecting central area does not become folded, because of the presence internally of the salivary valve. The posterior surface is soft and flexible except for the three pairs of haustellar sclerites which have been numbered for ease of reference (*h.scl.* 1 to 3 in figure 22). Here the sclerotized exocuticle is much thicker, as shown in transverse sections (figures 19 to 21).

The slender curved haustellar sclerites 1 encircle the narrowed base of the haustellum, and are closely associated with the extensions of the stipites posterior to the laciniae. These sclerites control the form of the base of the haustellum.

The crescentic haustellar sclerites 2 which lie longitudinally (figure 22) are important areas for muscle attachments. The slender distal ends of sclerites 3 lie close to the tapered proximal ends of sclerites 2, forming a flexible joint. Sclerites 3 curve round through 180° to the anterior surface of the prementum of the labium. Thus, in a transverse section through the base of the haustellum and the prementum (figure 21), these sclerites are seen to be cut twice.

Labium (figures 2 and 3)

The unsclerotized posterior surface of the proboscis, between the laterally placed cardines and stipites of the maxillae, is presumably derived from the labium. This surface is continued into a terminal region, which projects a little way beyond the base of the haustellum, and bears the well-developed labial palps. Between the bases of these palps there is a deep cleft but there are no lobes representing a ligula.

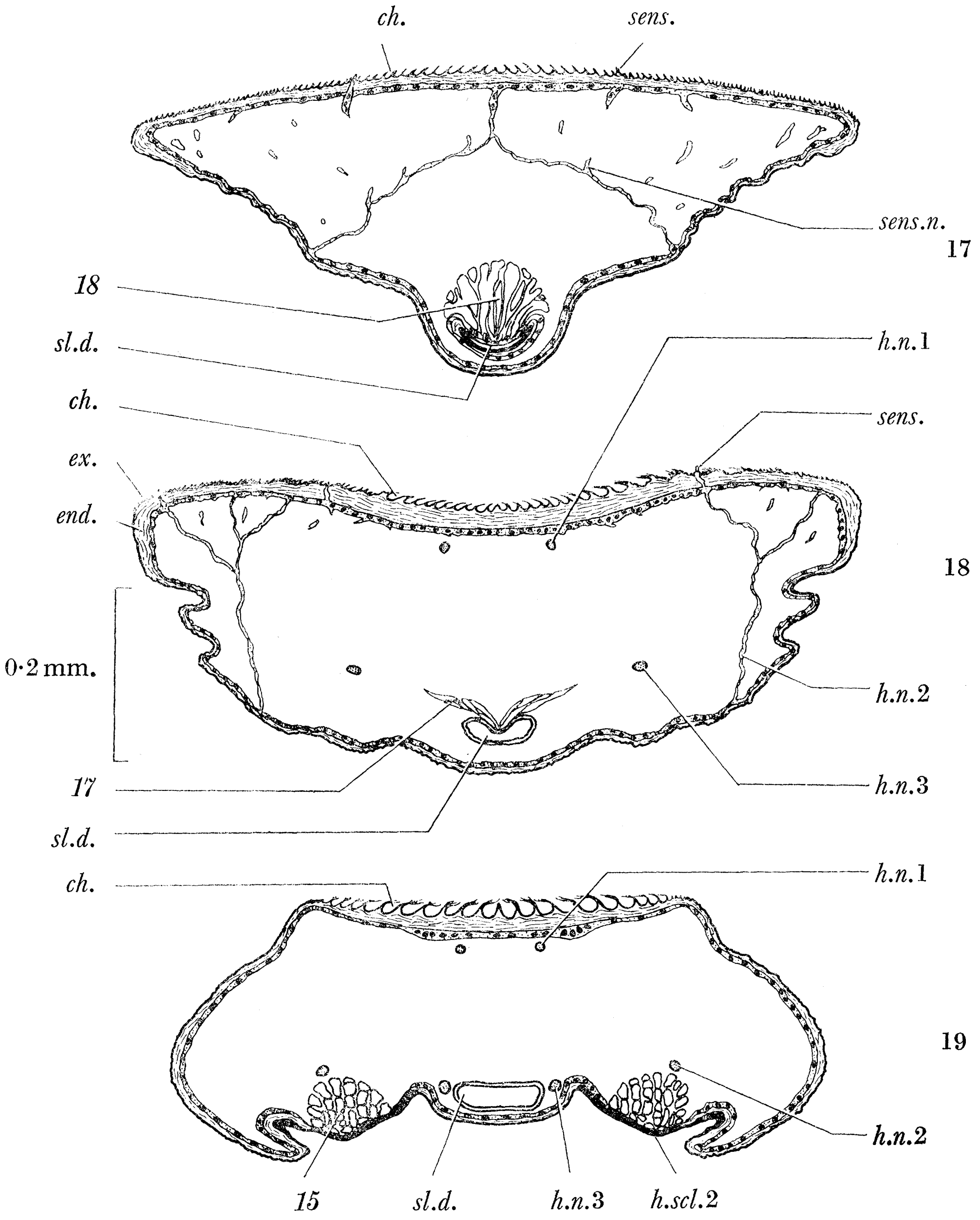


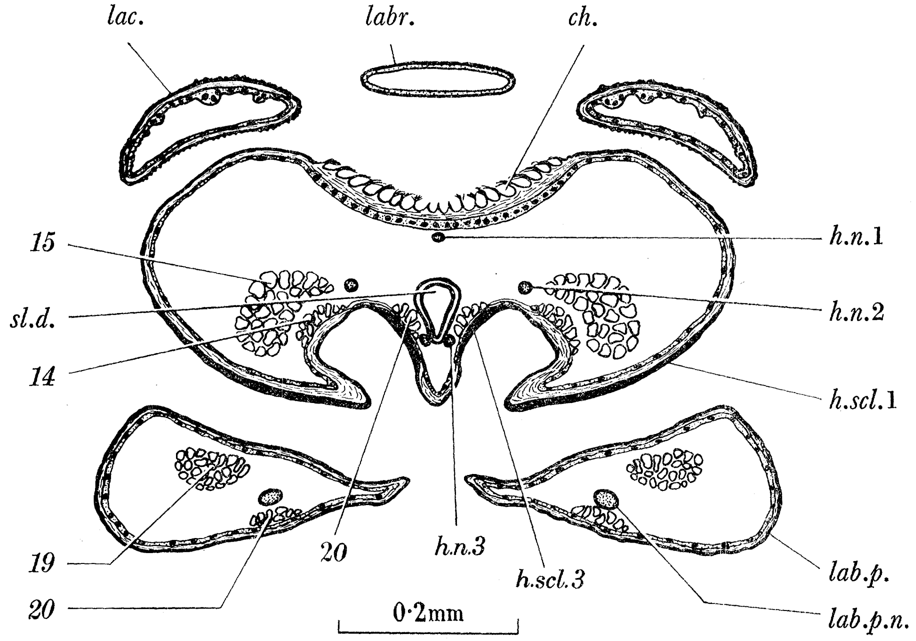
Figure 17. *Phryganea striata* ♂. Transverse section through apical part of haustellum at the level of the salivary valve.

Figure 18. *Phryganea striata* ♂. Transverse section through middle region of haustellum, proximal to the salivary valve.

Figure 19. *Phryganea striata* ♂. Transverse section through base of haustellum.

In *Phryganea*, this region bears a pair of small transverse sclerites which extend round the sides towards the haustellum, and carry a few long setae. These sclerites are here named distal labial sclerites (*d.lab.scl.* in figures 2 and 3), because in some other species of caddis fly there is also a proximal sclerite. It will be shown later that the labial retractor muscles are inserted just proximal to these distal labial sclerites. Thus, this terminal region of the labium is here interpreted as a prementum.

The well-developed labial palps are approximately half the length of the maxillary palps. Each palp is composed of three similar elongate segments, which are thickly



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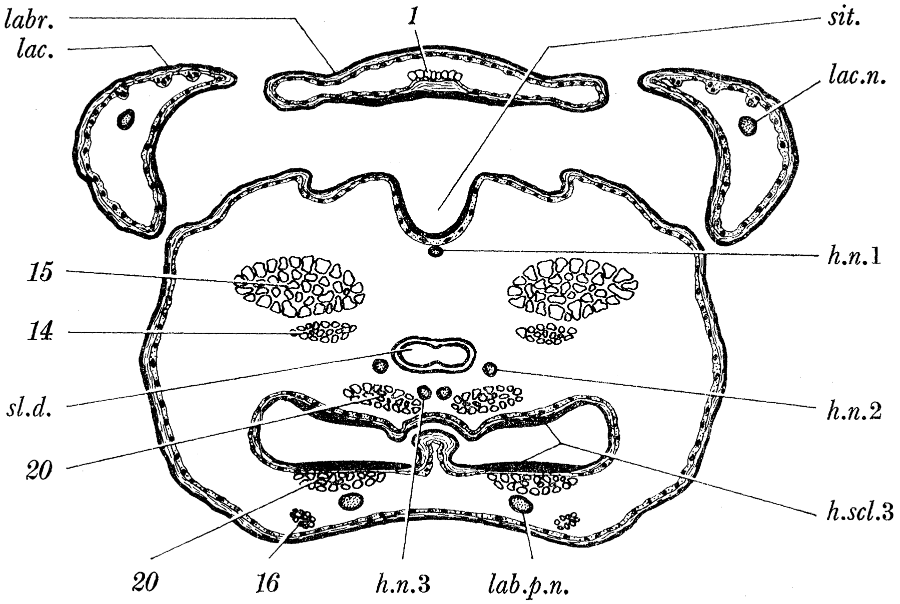

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FIGURE 20. *Phryganea striata* ♂. Transverse section through the base of haustellum and labial palps and the extremities of labrum and laciniae.

FIGURE 21. *Phryganea striata* ♂. Transverse section through proboscis just proximal to base of haustellum.

clothed with setae and sclerotized. Near the apex of both the first and second segments is a sensory pit containing trichoid sensilla. The medial surface of the terminal segment bears a large number of trichoid and basiconic sensilla.

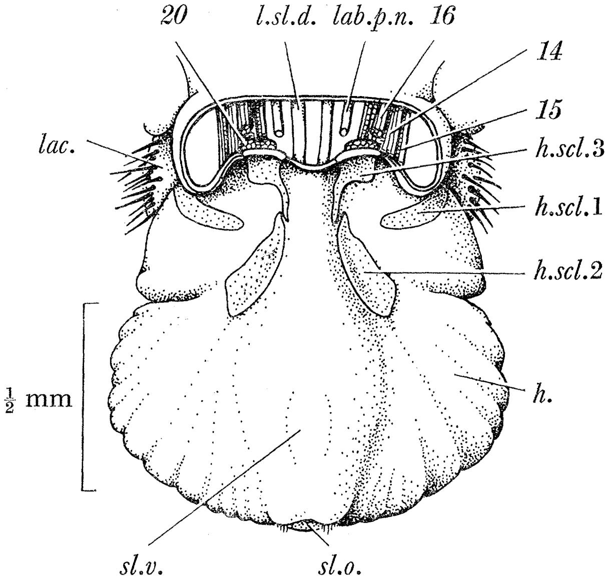


FIGURE 22. *Phryganea striata* ♂. Posterior view of haustellum after removal of terminal region of labium with labial palps.

Tentorium (figures 23, 24 and 27)

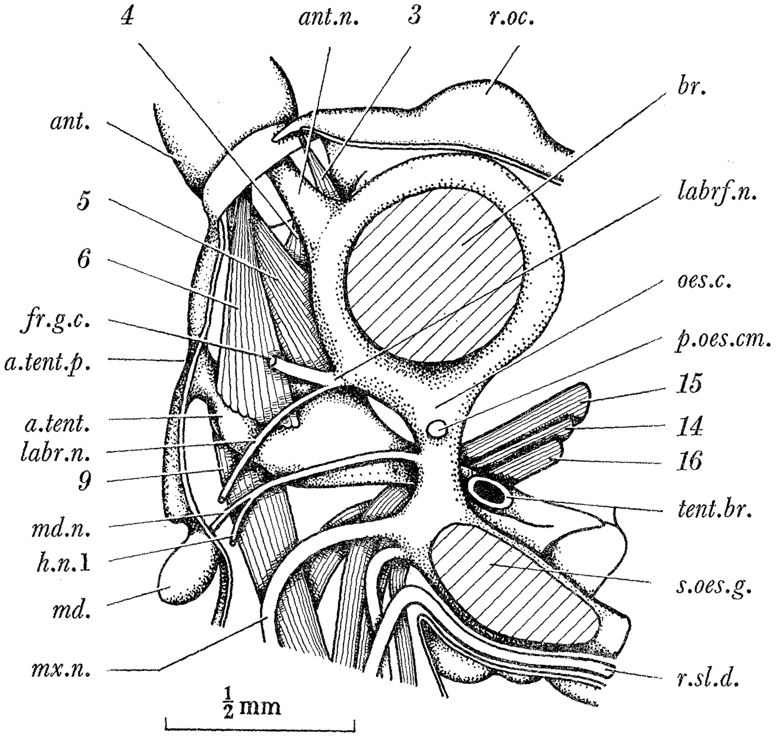
The tentorium consists of a pair of anterior arms each produced into a dorsal arm, and a pair of very short posterior arms connected by a tentorial bridge.

On the anterior surface of the head capsule the anterior arms originate from prominent pits, the position of which has already been described. These strongly developed arms are deep in section and taper gradually posteriorly. The ventral margin of each arm is produced laterally into a lamina. The slender dorsal arm, which arises halfway along the anterior arm, runs vertically to its point of fusion with the head capsule immediately posterior to the antennal socket (see figure 24). The tentorial bridge is a stout tubular structure which lies transversely at the level of the posterior tentorial pits. It is seen cut in section in figures 23 and 24, and in posterior view in figure 27. The posterior arms are thus very short.

The tentorium gives origin to muscles to the antennae, the cardines of the maxillae and the foregut.

Musculature

For ease of reference, the muscles in the head of *Phryganea* have here been numbered. The numbering system employed by Snodgrass (1928) for the head muscles of *Dissosteira* (Orthoptera) has been used elsewhere in attempts to homologize the head muscles of different insects. Thus, Albrecht (1953) used the same numbers for homologous muscles in the head of the locust, *Locusta migratoria*. While such a procedure is justified for insects which are closely related, Snodgrass (1952) did not extend this numbering system to the cockroach, *Periplaneta americana*, which has more head muscles than *Dissosteira*. As Snodgrass has informed me (1955, *in litt.*), 'In order to give the numbers a homology status we should have to know first the maximal number of muscles that insects may have, and this we do not know.' For this reason, the numbers here adopted for the muscles of *Phryganea* have no homology status, although many of them do, of course, have their homologues in insects belonging to such a generalized order as the Orthoptera.



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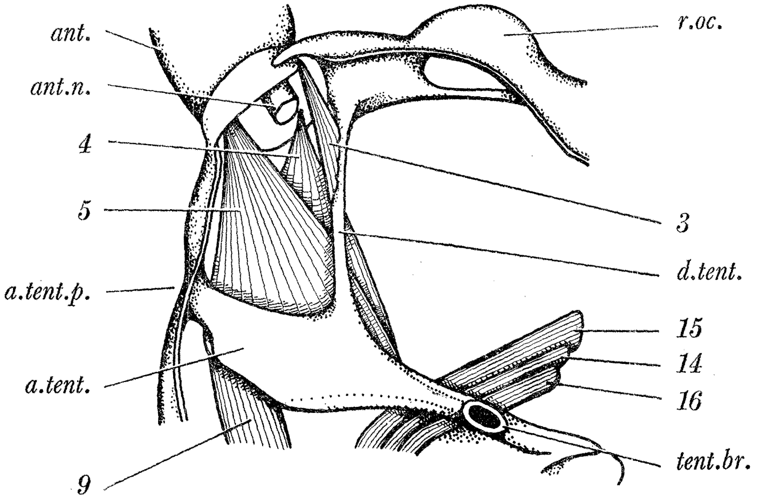

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FIGURE 23. *Phryganea striata* ♂. Nervous system and tentorium with associated muscles, as seen after vertical section of the head capsule in the sagittal plane.

FIGURE 24. *Phryganea striata* ♂. A later stage in the dissection shown in figure 23, after removal of the nervous system and antennal depressor muscle *6*, showing the medial surface of the right half of the tentorium.

Muscles of the antennae (figures 23 to 25)

The scape of the antenna is moved by two levator and two depressor muscles, all of which have their origin on the tentorium.

The main levator muscle (*4* in figures 24 and 25) has its origin on the lamina of the anterior arm of the tentorium. The other levator muscle (*3* in figure 24) which is much smaller and shorter, arises from the dorsal arm close to the base of the antenna.

The main depressor muscle (*5* in figures 23 to 25) has its origin on the lateral surface, and on the lamina of the anterior arm. It lies medial to the main levator muscle *4*. A smaller depressor muscle (*6* in figure 23) arises from the medial surface of the anterior arm.

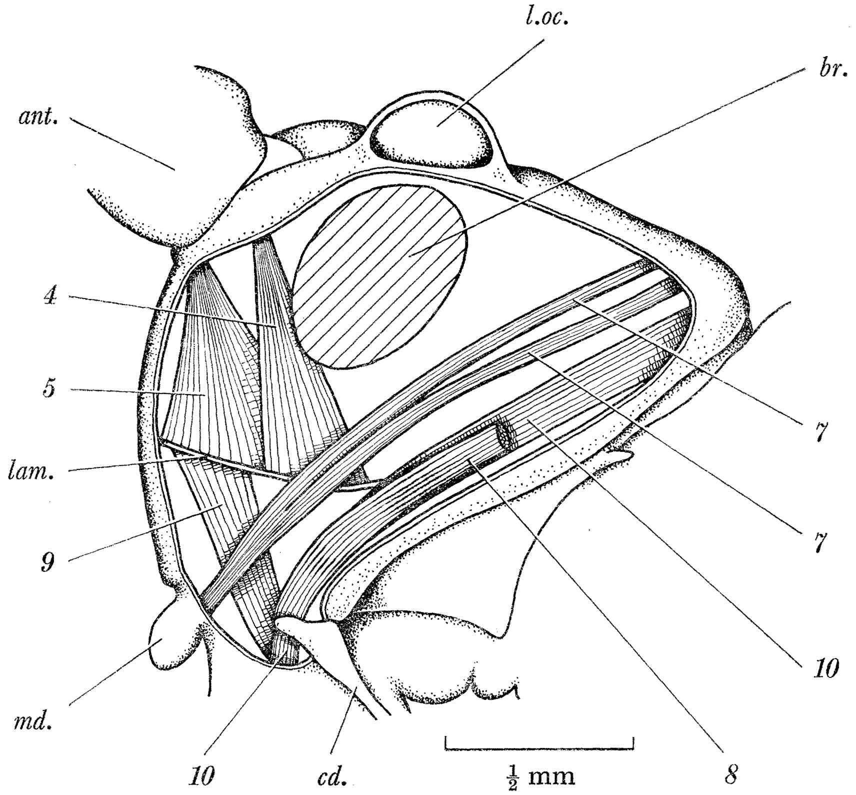

FIGURE 25. *Phryganea striata* ♂. Dissection from the left side of certain muscles in the lateral part of the head capsule.

Muscles of the foregut (figure 26)

The part of the foregut which lies in the head is well provided with muscles, and appears to function as a sucking pump. The muscles are displayed here in a lateral dissection (figure 26).

The first part of the foregut receives anterior (*21*) and lateral (*22*) dilator muscles from the head capsule, and a pair of posterior dilator muscles (*23*) from the tentorial bridge. Since these anterior and lateral dilator muscles lie anterior to the frontal ganglion and its connectives (see figure 26), this region of the foregut represents a cibarium (Snodgrass 1947). The relation of this interpretation to the homology of parts of the head capsule will be dealt with in the discussion.

The succeeding part of the foregut is regarded as a pharynx, because it receives six pairs of dilator muscles (*24* to *28* in figure 26) which have their origin posterior to the frontal ganglion and its connectives.

Both cibarium and pharynx are encircled by constrictor muscles (*29* in figure 26).

Muscles of the labrum (figure 26)

At the tip of the labrum a small apical muscle (*1* in figure 26) runs obliquely from the anterior to the posterior surface. Fibres of a compressor muscle (*2* in figure 26) converge from the anterior surface to the narrow sclerotized groove which extends down the middle of the posterior surface. This muscle occupies most of the length of the labrum.

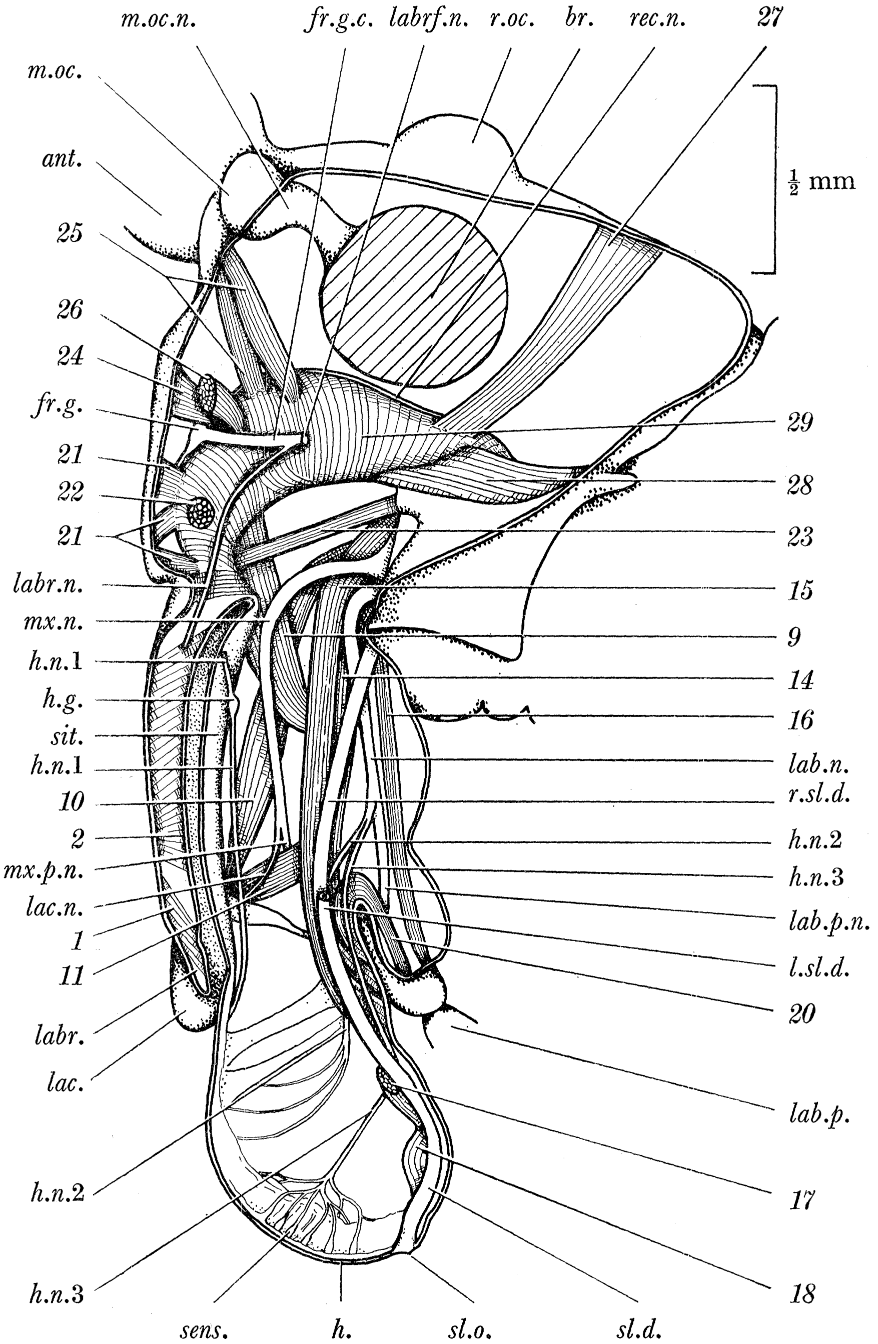

FIGURE 26. *Phryganea striata* ♂. Dissection of the head, with haustellum protruded, after vertical section to the left of the sagittal plane.

Muscles of the mandibles (figure 25)

Two poorly developed muscles (*7* in figure 25) have their origin in the occipital region of the head capsule, anterior to the muscles leading to the other mouth parts. They run obliquely downwards and converge shortly before reaching the mandible. These two muscles apparently represent a much reduced adductor and abductor of the mandible.

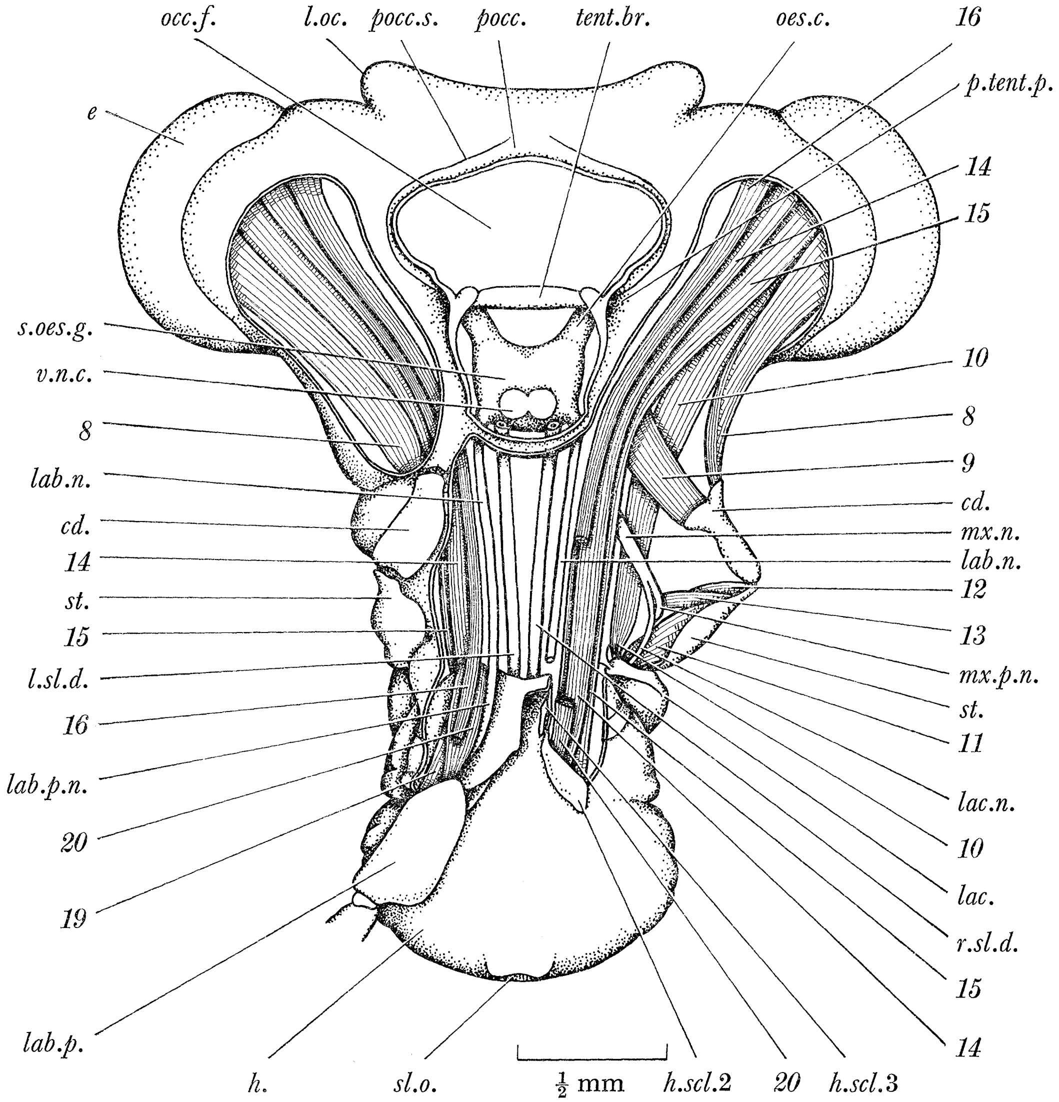

FIGURE 27. *Phryganea striata* ♂. Posterior dissection of head with haustellum protruded. On the right side the labial palp has been removed so that the dissection has been carried deeper, and cardo and stipes have been reflexed outwards. No detail is shown in the dorsal part of the occipital foramen through which the oesophagus passes.

Muscles of the maxillae (figures 23 to 27)

The cardo articulates with the head capsule, as already described, and is moved by a flexor and extensor muscle. The flexor muscle (*8* in figures 25 and 27) originates in the occipital region of the head capsule, ventral to the other muscles shown in figure 27, and is inserted on a projection at the proximal end of the cardo. The extensor muscle (*9* in figures 23, 25, 26 and 27) has its origin anteriorly on the lamina of the anterior arm of the tentorium and passes directly down to the proximal end of the cardo.

The cardo and stipes flex on each other at an elbow joint, but there are no muscles between the two sclerites.

The single maxillary lobe is provided with two muscles. One of these, the stipital extensor (*11* in figures 26 and 27), originates on the inner surface of the stipes and is inserted laterally in the base of the lobe. The other muscle, the cranial flexor (*10* in figures 26 and 27), has its origin in the occipital region of the head capsule, and is inserted medially in the base of the maxillary lobe. Because of the presence of this cranial flexor muscle, the maxillary lobe is interpreted as a lacinia. This will be considered in more detail in the discussion.

The maxillary palp is moved by a levator muscle (*12*) and a depressor (*13* in figure 27), both of which originate on the stipes proximal to the origin of the extensor of the lacinia. They are inserted on the basal segment of the palp. The second and third palpal segments are each moved by separate flexor and extensor muscles. The fourth segment is moved by a single flexor muscle. Likewise, the additional fifth segment of the female is moved by a single flexor muscle.

Muscles of the haustellum (figures 22, 26 and 27)

Two muscles from the occipital region of the head capsule are inserted on haustellar sclerite 2. The larger of these muscles (*15* in figures 26 and 27), which is anterior, is inserted on the distal part of the sclerite. The smaller muscle (*14*) is inserted on the middle part. Transverse sections (figures 20 and 21) illustrate the size and position of these muscles. The section in figure 19 shows the insertion of the larger muscle (*15*) which is distal to that of the other. In the discussion on function, it will be explained why the larger muscle (*15*) is regarded as a protractor, and the smaller (*14*) as a retractor, of the haustellum.

The right and left salivary ducts unite in the base of the haustellum to form a common duct. The salivary valve, with its muscles (figure 28), is a prominent structure on this common salivary duct a short distance from its external opening at the apex of the haustellum. The proximal muscles (*17* in figures 18, 26 and 28) originate at the distal end of haustellar sclerite 2 on each side, and converge on the anterior surface of the salivary valve. The distal muscle (*18* in figures 17, 26 and 28) is composed of a mass of fibres running longitudinally within the concavity here formed on the anterior surface of the salivary duct. While there are a few fibres running with those of the proximal muscles (see figure 28), the main mass of this distal muscle has no connexion with any part of the external cuticle.

Muscles of the labium (figures 22, 26 and 27)

The two retractor muscles of the labium (*16* in figures 26 and 27) have their origin one on each side in the occipital region of the head capsule, posterior to the other mouth-part muscles. They remain posterior to the other muscles (see figures 26 and 27) on their course to the posterior surface of the labium, just proximal to the distal labial sclerites. This apical part of the labium is interpreted as a prementum.

The levator muscle of the labial palp (*19* in figure 27) originates on that part of haustellar sclerite 3 which extends into the labium. Thus it has a short course, and is inserted laterally on the basal segment of the labial palp. The depressor muscle (*20* in figures 22, 26 and 27) originates at the proximal end of haustellar sclerite 2, and runs over the bearing surface of sclerite 3 to its insertion towards the medial side of the basal segment of the palp. As this muscle thus reverses its direction, it can be seen cut twice in transverse section in figures 20 and 21. The second segment of the palp is moved by a flexor and extensor muscle from the basal segment. A single flexor muscle runs from the second to the terminal segment.

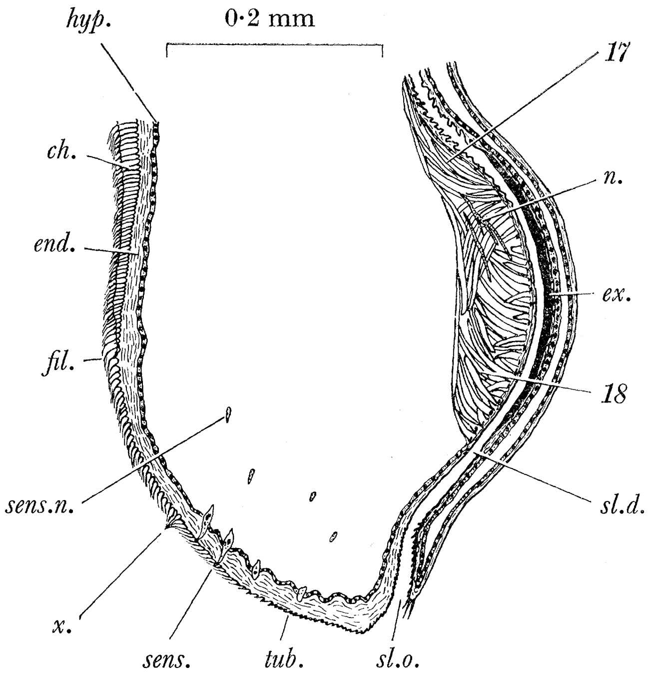

FIGURE 28. *Phryganea grandis* ♂. Sagittal section through the protruded haustellum, showing the salivary valve.

Nervous system (figures 23, 26, 27 and 29)

That part of the nervous system in the head which was investigated is shown in figure 29. The brain gives rise to three ocellar nerves, a pair of large optic nerves, and a pair of antennal nerves. In addition, there is a pair of labrofrontal nerves from the base of the brain. These branch immediately into labral nerves and connectives to the median frontal ganglion (*fr.g.* in figures 26 and 29). This ganglion, which lies on the anterior surface of the pharynx, gives origin to a small anterior nerve, and a recurrent nerve which runs back along the dorsal surface of the pharynx.

The short circumoesophageal connectives are linked by a postoesophageal commissure (*p.oes.cm.* in figure 29). While the pharynx passes dorsal to this commissure, the posterior dilators of the cibarium (*23* in figure 26), which originate on the tentorial bridge, pass ventral to it. The small mandibular nerve which arises from the circumoesophageal connective, travels forwards to the mandible, giving off ventrally the slender haustellar nerve 1 (*h.n.*1 in figures 23 and 29). The pair of these haustellar nerves 1 unite in a small haustellar ganglion (*h.g.* in figure 26) from which a median nerve continues posterior to the sitophore. This nerve divides into two nerves again in the base of the haustellum. These haustellar nerves 1 are seen at different levels in transverse section in figures 18 to 21.

The suboesophageal ganglion gives origin to paired maxillary and labial nerves. The maxillary nerve gives off a branch to the lacinia, while the main trunk continues to the palp (see figures 26 and 27). The labial nerve supplies the labial palp and also gives rise to two nerves to the haustellum. These nerves (*h.n.*2 and 3 in figure 26) are distributed as many fine branches to the sensilla on the haustellum. Haustellar nerve 2 runs directly to the sensilla placed laterally and proximally. Haustellar nerve 3 loops round the proximal salivary muscle (*17* in figure 26) and is distributed to the apical sensilla.

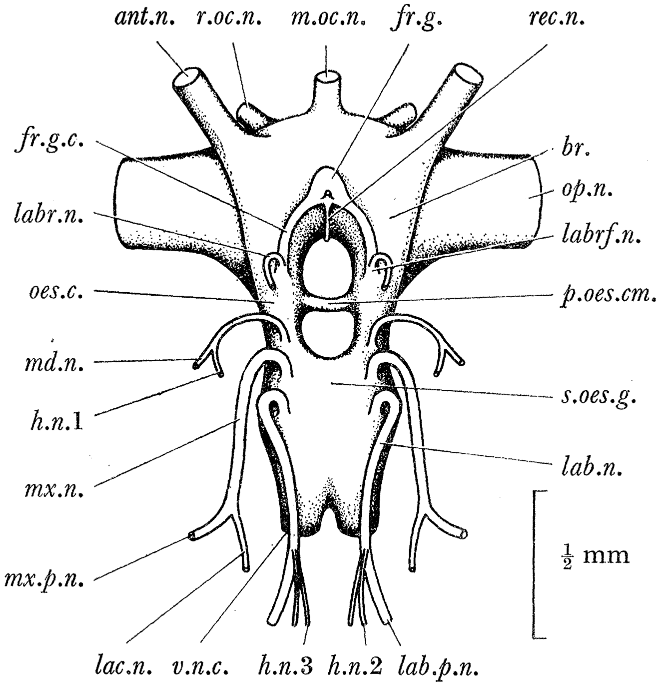

FIGURE 29. *Phryganea striata* ♂. Anterior view of nervous system in head.

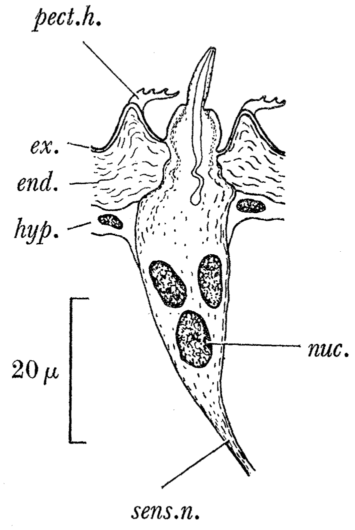

FIGURE 30. *Phryganea striata* ♂. Sensillum as seen in a transverse section of the apical part of the haustellum.

In the apical channels of the haustellum there are about 100 sensilla distributed as shown in figure 5. Each sensillum (figure 30) consists of a tapering terminal cone, on a swollen base. There is a central canal ending in a small ampulla. The internal part of the sensillum, containing several nuclei, tapers off into the nerve.

Function of the mouth parts

In the preceding account, the proboscis has been described in the feeding position with the haustellum protruded (see figures 1 to 3). When resting, the haustellum is retracted out of sight, while the whole proboscis is swung back beneath the head and shortened (see figures 31 and 32). These figures illustrate also the characteristic attitude of the maxillary palps directed forwards, and the labial palps flexed round the laciniae and the tip of the labrum.

Observations were made on specimens in the act of feeding. Both sexes were found to drink from a drop of water or dilute sucrose solution. They drank more readily, and for longer, after being kept for some time without access to water.

When the insect was about to drink, the proboscis was swung forwards, and the haustellum quickly protruded. Two drinking attitudes were observed. In the direct drinking attitude, the haustellum was flattened backwards and the tip of the labrum lifted. Water was seen to stream directly into the passage between labrum and sitophore, without apparently passing through the channels on the haustellum. In the lapping attitude, the haustellum was moved quickly in and out, and approximately the apical third of the channelled area was applied to the liquid. A repeated withdrawal of the central region gave a surface concavity. The tip of the labrum was seen to be held closely against the base of the haustellum while water was drawn up through the channels. When a small drop of liquid had been absorbed, the fly often continued to lick the dried area, moving the haustellum quickly in and out.

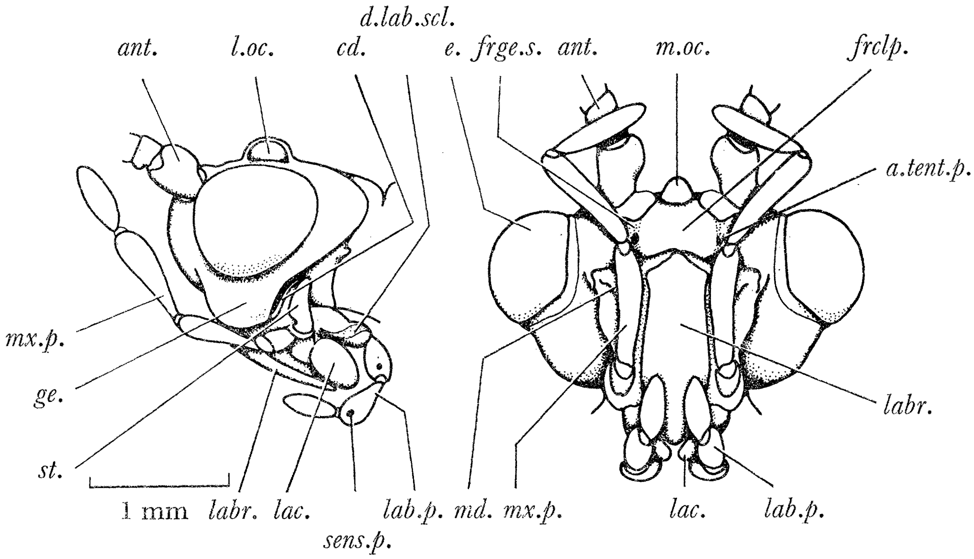

FIGURE 31 FIGURE 32

FIGURES 31 and 32. *Phryganea striata* ♂. Lateral and ventral views of living specimen with proboscis swung back and haustellum retracted in the resting attitude.

By holding the living insect in the compressor, the channels on the haustellum could be studied under the dissecting microscope. A tiny drop of water applied anywhere on the anterior surface of the haustellum was seen to spread rapidly over the whole channelled area. This surface is thus of a nature which is easily wetted. Within a short time the channels were seen to dry out again. There was always a distinct curved meniscus at the end of the water column in a channel.

These channels on the haustellum are thus apparently filled by capillarity. The sucking pump in the head would then maintain the flow of liquid into the gut. The pectinate hairs may function as a filtering device over the channels. There is some evidence that the reversal in the direction of their filaments may be a rejection mechanism, as small foreign particles were sometimes seen along the transverse line of convergence.

There is a parallel between the two drinking attitudes described here for *Phryganea*, and two of those described for the fly *Calliphora* by Graham-Smith (1930). It should be remembered, however, that the muscid proboscis is not homologous to that of the caddis fly, although they both serve for the uptake of fluid. In the direct drinking attitude of *Calliphora*, the labella are folded back out of the way, and water streams directly in under the labrum-epipharynx. This is comparable to the direct drinking attitude of *Phryganea*. In the filtering attitude of *Calliphora*, the labella are outspread so that the interbifid spaces, giving access to the pseudotracheae, are in contact with the food, and larger particles are filtered out from the fluid which is ingested. Presumably the pseudotracheae of *Calliphora* are filled by capillarity in the same way as the channels on the haustellum of *Phryganea*. This filtering attitude of *Calliphora* would, therefore, correspond to the lapping attitude of *Phryganea*.

Protrusion of the haustellum appears to be brought about by increased blood pressure. Thus, compression of the body of the insect, or gentle pressure on the frontoclypeus causes protrusion of the organ. The cavity of the haustellum communicates directly with that of the rest of the proboscis and head capsule. No valvular mechanism was found. Puncture of any part of the proboscis results in collapse of the haustellum, indicating that the maintenance of an internal pressure is necessary for protrusion.

The cuticle covering the haustellum is flexible as it is unsclerotized, except for the three pairs of small sclerites on the posterior surface. The elongate sclerites 1 encircle the base, and act as a restraining collar, while allowing swelling of the rest of the haustellum. The changes in shape of the haustellum are most prominent on the anterior surface, which becomes convex in protrusion and concave in retraction. To this end, the cuticle of the anterior surface consists of a horizontally laminated endocuticle, which is thicker than elsewhere (see transverse sections in figures 17 to 20). There is a natural tendency for folding in the lateral posterior walls to accommodate some of the changes in internal pressure (see figure 22). The projecting middle region of the posterior surface tends to retain its form because of the internal mass of the salivary valve.

There are two muscles from the head capsule to haustellar sclerite 2. The smaller of these (*14* in figures 26 and 27), which is posterior, is inserted on the proximal part of the sclerite, while the larger muscle (*15*) is inserted distally. This sclerite, in the living insect, is seen to move backwards and forwards about the flexible joint between it and sclerite 3 (see figures 22 and 27). Because of its insertion relative to this joint, it is suggested that muscle *15* brings about the forward movement of the haustellum, and so can be called a protractor. As muscle *14* appears to have an antagonistic function it is interpreted as a retractor of the haustellum. Posterior to these haustellar muscles are two muscles which are inserted on the prementum of the labium (*16* in figures 26 and 27). As they must act as retractors of this part of the proboscis complex, they are named retractors of the labium.

Two muscles are inserted on the cardo, one (*9* in figures 26 and 27) from the tentorium, and the other (*8* in figure 27) from the head capsule. Comparison of figures 2 and 31 shows how the cardo moves in relation to the head capsule and also at the elbow joint between it and the stipes. From the insertion and course of these two muscles to the cardo it appears that muscle *8* is a flexor and muscle *9* an extensor of this sclerite. They will thus play a part in bringing about the backward and forward movement of the proboscis as a whole.

There remains the mechanism of the salivary valve. Transverse section of this organ (figure 17) shows that the lumen of the salivary duct is crescentic because the anterior wall is invaginated within the posterior wall. Furthermore, the cuticle of the anterior wall is thin and flexible, whereas that of the posterior wall is thick, sclerotized and rigid. Contraction of both proximal and distal salivary muscles (*17* and *18* in figures 17, 18 and 28) must open the lumen of the valve. Closure of the valve will result from relaxation of these muscles, allowing the elastic return of the anterior wall.

A similar salivary valve has been described by Heddergott (1938) in *Panorpa* (Mecoptera), where, however, there are no muscles linking the valve with any sclerite. In *Panorpa* also a thin flexible anterior wall is invaginated within a thickened sclerotized posterior wall, and the muscles lie within the invagination.

When the caddis fly is taking in water in the direct drinking attitude, the tip of the labrum is lifted. This movement is brought about by contraction of the apical muscle of the labrum (*1* in figure 26). The main compressor muscle (*2* in figure 26) must approximate the flexible posterior surface of the labrum to the more rigid domed anterior surface, and thus hold the labrum closely over the sitophore completing the channel to the mouth. This muscle may also exert a suction effect on the liquid travelling up the sitophore to the mouth.

Frings & Frings (1949), in their review of the loci of chemoreceptors in insects, recorded no published morphological or experimental work on Trichoptera. They showed how, in insects from various orders, chemoreceptors may be located on antennae, hypopharynx, maxillary and labial palps, ligula and tarsi. Recently Frings & Frings (1956) have carried out experiments on chemoreceptors in four species of Trichoptera, from the families Phryganeidae and Limnephilidae. They demonstrated extension of the proboscis in the presence of sugar solution and retraction from salt solution. Chemoreceptors were shown to be present on maxillary and labial palps, and tarsi. From a preliminary examination of these organs, they suggested that the chemoreceptors on the tarsi and terminal palpal segments were trichoid sensilla, while those on the haustellum were both trichoid and basiconic sensilla. No details of structure or innervation were given.

A COMPARATIVE STUDY OF THE MOUTH PARTS OF CADDIS FLIES

Of the 191 species of caddis flies recorded in Britain, observations were made on 53 species, representing all 13 families. Living specimens were studied to find out if they were capable of protruding the haustellum and drinking water.

Outline drawings of the anterior surface of the head show the haustellum protruded as in living specimens, but because of the small scale, the channels are omitted. For the sake of clarity, the labial palps are not shown here, but they are included in drawings of the posterior surface of the apex of the labium. In all these outline drawings setae are omitted. The mandibles are drawn separately if they are partially hidden by the labrum.

Observations are grouped under families. The nomenclature and order of classification adopted are based on Mosely (1939), with the alterations and additions proposed by Kimmins (1949*a*, *b*, 1952, 1956).

In every species studied, there was found to be a protrusible haustellum, which as a rule exhibited fewer channels in the smaller species. In certain families, however, the anterior surface of the haustellum lacked these channels and appeared granulose. Although a few species were not observed in the act of drinking, I have no doubt that they were all capable of doing so.

Phryganeidae

Phryganea grandis L., *P. varia* F., *Trichostegia minor* (Curt.)

The above three species exhibit no essential differences from *Phryganea striata* in the structure of the proboscis. Many of the details of structure and function already described in the account of *P. striata* were confirmed in *P. grandis*. A minor point of difference is that *P. grandis* lacks the small setose sclerite posterior to the mandible. This sclerite is also absent in *P. varia* and *T. minor*. The latter two species, however, possess a sclerite with four prominent white setae, ventral to the mandible on the anterior surface of the proboscis. This appears to be the same as the anterior sclerite described in Limnephilidae (*a.scl.* in figure 33*A*).

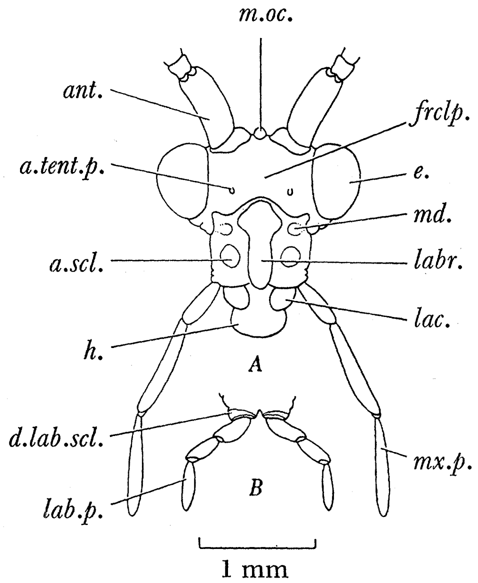

Figure 33. *Limnephilus lunatus* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

Limnephilidae—Limnephilinae

Limnephilus lunatus Curt. (figure 33), *L. flavicornis* (F.), *L. marmoratus* Curt., *L. sparsus* Curt., *L. auricula* Curt., *L. vittatus* F., *Grammotaulius atomarius* (F.), *Glyphotaelius pellucidus* (Retz.), *Anabolia nervosa* (Curt.), *Halesus radiatus* (Schr.), *H. digitatus* (Curt.), *Stenophylax permistus* McL., *S. lateralis* (Steph.), *S. sequax* (McL.).

Limnephilidae—Apataniinae

Apatania muliebris McL.

Limnephilidae—Drusinae

Drusus annulatus Steph.

The head and mouth parts of *Limnephilus lunatus* (figure 33) are closely similar to those of *Phryganea striata*. The basal part of the proboscis is well developed as in *Phryganea*, but it bears two additional setose anterior sclerites (*a.scl.* in figure 33*A*). Dorsal to these sclerites, the mandibles are slight rounded swellings, seen clearly only on the fully protruded proboscis of a living specimen. The male has only three segments in the maxillary palp, a character common to all species of the family Limnephilidae. There is a rounded channelled haustellum.

The structure of the mouth parts of the other fifteen species of Limnephilidae listed above resembles closely that already described for *Limnephilus lunatus*. All fifteen species have slight mandibular swellings, which are difficult to see in preserved specimens. It is understandable, therefore, that mandibles are usually described as absent in the family Limnephilidae.

Limnephilidae—Dicosmoecinae

Kimmins (1956) lists *Ironoquia dubia* (Steph.) as the only British representative of this sub-family. Formerly this species was included, as *Caborius dubius* (Steph.), in the Limnephilinae. Specimens were not available for examination. It is unlikely that this species would depart from the naturally uniform condition of mouth parts already described for sixteen species of Limnephilidae.

Sericostomatidae

The maxillary palps of male sericostomatids are modified in various ways, and are thought to function as scent-producing organs.

Sericostomatidae—Sericostomatinae

Sericostoma personatum (Spence) (figure 34)

The extraordinary specialization of the maxillary palps in the male of *S. personatum* has been described by Cummings (1914*a*), from preserved material. These palps, which are held vertically touching each other, are closely applied to the anterior surface of the head capsule (figure 34*A*). Their sclerotized convex outer surfaces are covered with short setae. The soft orange-yellow lips, which meet in the mid-line, are subject in the living insect to pulsating movements. The concave inner surfaces of the palps are filled with a mass of fine orange-yellow setae. Two clefts (*cl.* in figure 34*B*) lead into separate cavities inside the palp, as has been shown by Cummings. Near the base of the palp is a tiny lobe beset with long black setae (*l.* in figure 34*B*). At the apex of the palp is a rounded lobe which fits into a recess, bounded behind by a median lobe (*ant.l.*) from the scape of the antenna.

When the maxillary palps are reflexed it can be seen that a large part of the anterior surface of the head capsule is unsclerotized. The central sclerotized area, which bears the anterior tentorial pits, is continued dorsally into a transverse ridge which serves to hold the lips of the maxillary palps in position. All this anterior surface of the head capsule is devoid of setae.

The tapering mandibles (*md.* in figure 34*B*), which are soft and unpigmented, were overlooked by Cummings. The lacinia possesses a leaf-like internal lobe (*lac.l.* in figure 34*A*), only visible when the haustellum is protruded. The elongate haustellum bears a system of channels.

The female differs from the male in having a sclerotized and strongly setose head capsule, normal five-segmented maxillary palps, and labial palps which are somewhat shorter than those of the male.

Notidobia ciliaris (L.) (figure 35)

The head capsule and maxillary palps of the male of this species are specialized, although not to the extreme degree seen in *Sericostoma personatum*. The maxillary palps, which appear to be formed of only one segment, cover the anterior surface of the head capsule, but their unsclerotized inner surfaces bear only a few scattered setae. As shown in figure 35*A*, there is an unsclerotized area (*unscl.*) extending up each side of the head capsule lateral to the anterior tentorial pits.

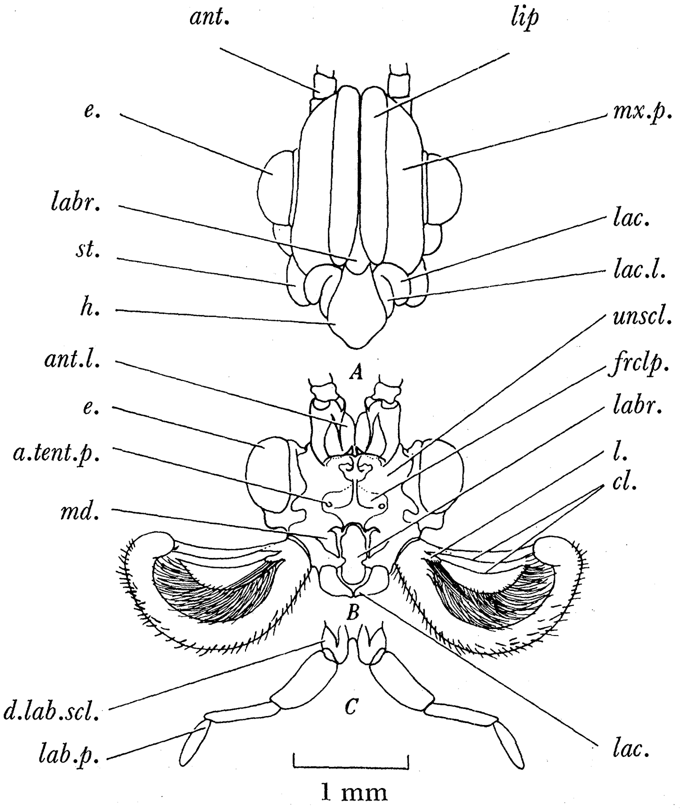

FIGURE 34. *Sericostoma personatum* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Anterior view of head with haustellum retracted and with the maxillary palps reflexed outwards. *C*. Posterior view of labium.

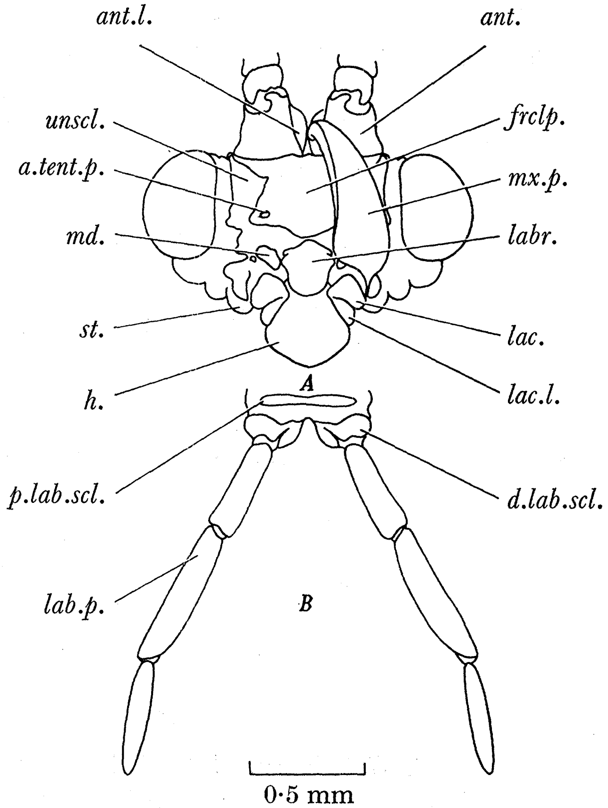

FIGURE 35. *Notidobia ciliaris* ♂. *A*. Anterior view of head with haustellum protruded, and with the right maxillary palp removed. *B*. Posterioe view of labium.

The mandible, which is too short to reach under the labrum, is a small finger-like structure bearing a few short setae. Immediately lateral to the mandible is a tiny sclerite bearing a bundle of long setae, which are, in fact, the only setae present on the anterior surface of the head capsule. As in *Sericostoma* there is an internal flattened lobe to the lacinia. There are channels on the rounded haustellum. In addition to the distal labial sclerites, there is a narrow transverse proximal sclerite (*p.lab.scl.* in figure 35*B*). The labial palps are unusually long and covered thickly with setae.

The female has a fully sclerotized head capsule and normal elongate 5-segmented maxillary palps.

SERICOSTOMATIDAE—GOËRINAE

Goëra pilosa (F.) (figure 36)

The male exhibits a unique specialization of the maxillary palps which, in the resting postition, are held together vertically in front of the head capsule (figure 36*A*). While the two basal segments are sclerotized and covered with setae, the third segment is unsclerotized. When the insect is subjected to pressure, the palps separate and the third segment swells to about four times its original length, unfolding a terminal finger-like process from its inner surface. This surface, which is now exposed, is covered with small black scales. These are leaf-like in form, with 12 to 16 closely set longitudinal striations. The dark line along the middle of the third segment in figure 36*B* represents the intucking from which the terminal process is unfolded. The fact that these scales are only exposed when the palp is protruded suggests that this is a scent organ.

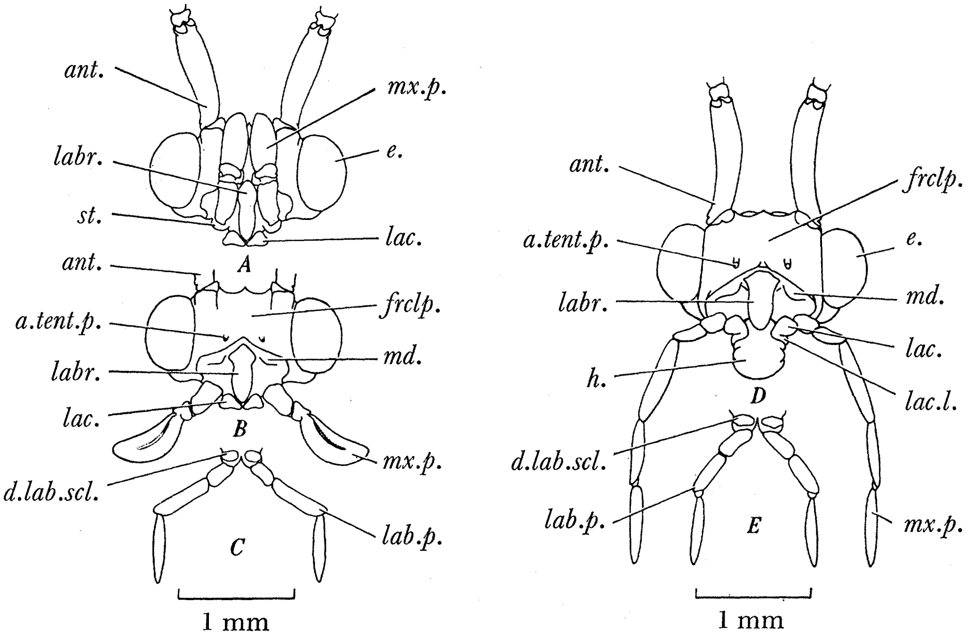

FIGURE 36. *Goëra pilosa*. *A*. Anterior view of head of male with haustellum retracted. *B*. Anterior view of head of male with haustellum retracted and maxillary palps reflexed outwards. *C*. Posterior view of labium of male. *D*. Anterior view of head of female with haustellum protruded. *E*. Posterior view of labium of female.

The anterior surface of the head capsule is fully sclerotized, but is hollowed out for the reception of the maxillary palps. The mandibles are represented by slight swellings. The lacinia bears an internal lobe which is not visible when the haustellum is retracted as in figure 36*A* and *B*. The maxillary palps and head capsule of the female are not specialized (see figures 36*D* and *E*). Both sexes possess a normal elongate haustellum which bears channels.

SERICOSTOMATIDAE—BRACHYCENTRINAE

Brachycentrus subnubilus Curt. (figure 37)

In this species only the maxillary palps exhibit sexual dimorphism. In the male they are carried vertically in front of the head (see figure 37*A*). Each of the three segments is sclerotized, and closely set with long setae. The mandibles are reduced to small lobes (see figure 37*C*). The labial palps of the female are only about two-thirds the length of those of the male. Both sexes possess the same elongate form of haustellum bearing a system of channels.

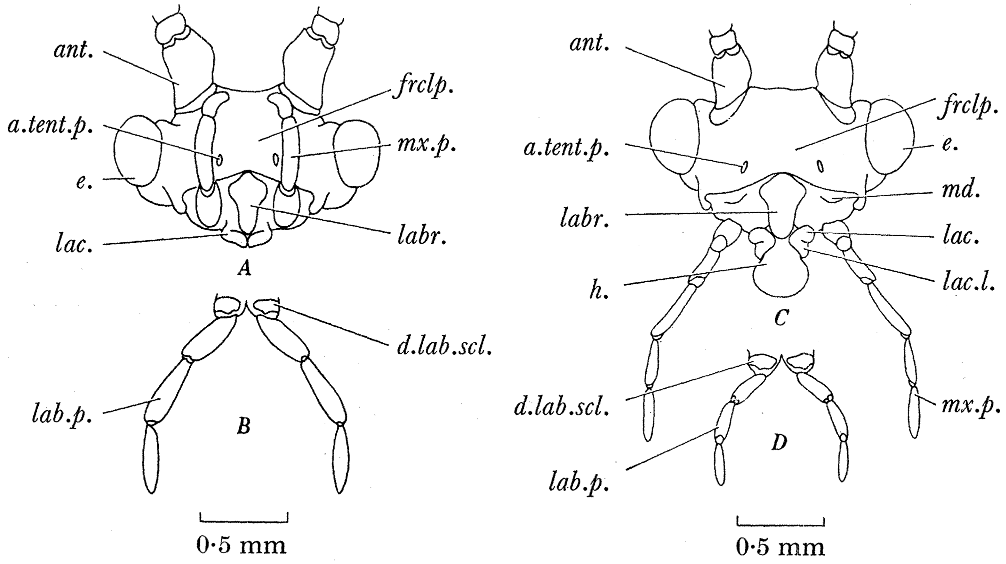

FIGURE 37. *Brachycentrus subnubilus*. *A*. Anterior view of head of male with haustellum retracted. *B*. Posterior view of labium of male. *C*. Anterior view of head of female with haustellum protruded. *D*. Posterior view of labium of female.

SERICOSTOMATIDAE—LEPIDOSTOMATINAE

Crunoecia irrorata (Curt.) (figure 38)

In the male each maxillary palp is composed of a single elongate sclerotized segment which is covered thickly with long setae. These palps are carried vertically in front of the head capsule. The mandibles are represented by slight swellings. There is a rounded haustellum bearing channels. The female has normal 5-segmented maxillary palps, and labial palps which are only about two-thirds the length of those in the male.

BERAEIDAE

Beraea maurus (Curt.) (figure 39)

This small species has slender, lightly sclerotized mandibles, which almost meet between labrum and sitophore. The elongate haustellum bears a system of channels. The only sexual difference lies in the greater development of setae on the antennal scape and first maxillary palp segment of the male.

MOLANNIDAE

Molanna angustata Curt. (figure 40)

The delicate flattened mandibles reach only as far as the sides of the labrum. The rounded haustellum bears a system of channels.

The male exhibits an unusual development of the maxillary palp. When this is bent ventrally, in a living specimen, a lobe (*p.l.* in figure 40*A*) appears at the distal end of the first segment. This lobe bears a number of short stout setae which are mainly black, with a few white ones distally. This structure, which does not appear to have been noted previously, is probably a scent organ.

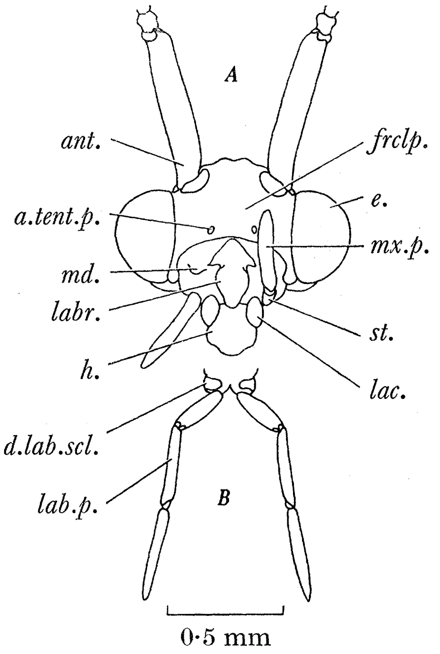

FIGURE 38. *Crunoecia irrorata* ♂. *A*. Anterior view of head with haustellum protruded and the right maxillary palp reflexed downwards. *B*. Posterior view of labium.

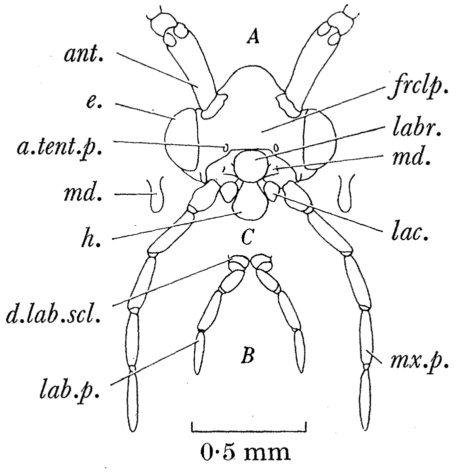

FIGURE 39. *Beraea maurus* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

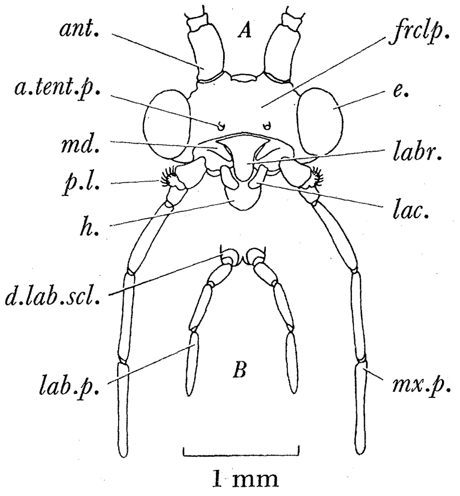

FIGURE 40. *Molanna angustata* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

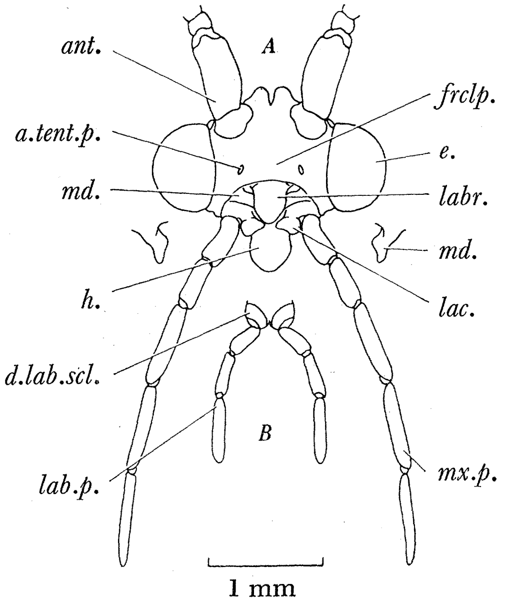

FIGURE 41. *Odontocerum albicorne* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

ODONTOCERIDAE

Odontocerum albicorne (Scop.) (figure 41)

The lightly sclerotized mandibles are not long enough to meet between the labrum and sitophore. There is a system of channels on the elongate haustellum.

LEPTOCERIDAE

Athripsodes cinerea (Curt.) (figure 42), *A. aterrima* (Steph.), *A. senilis* (Burm.), *Mystacides nigra* (L.), *M. azurea* (L.), *M. longicornis* (L.), *Triaenodes bicolor* (Curt.), *Oecetis ochracea* (Curt.), *Leptocerus tineiformis* Curt.

The head and mouth parts of *Athripsodes cinerea* are illustrated in figure 42. The slender unsclerotized mandibles extend a short way beneath the labrum, without meeting in the mid-line. There are channels on the rounded haustellum.

The other species of Leptoceridae listed above all possess small mandibles and a channelled haustellum of the same form as in *A. cinerea*.

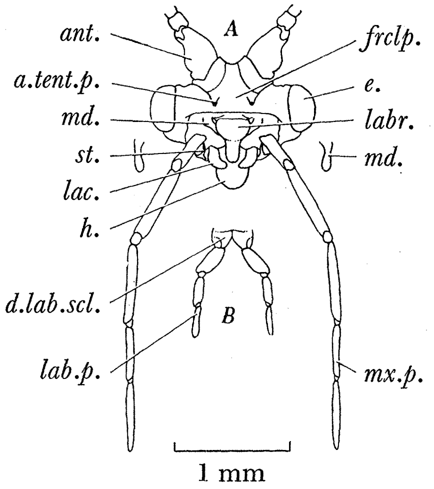

FIGURE 42. *Athripsodes cinerea* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

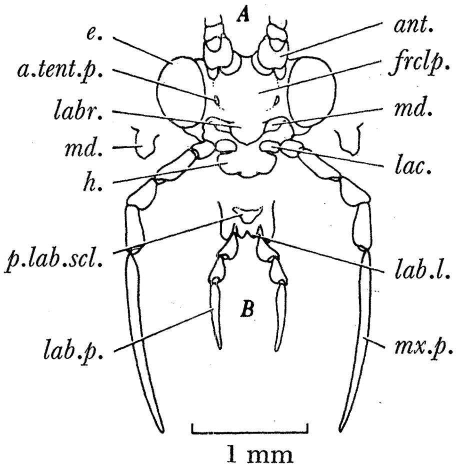

FIGURE 43. *Hydropsyche angustipennis* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

HYDROPSYCHIDAE

Hydropsyche angustipennis (Curt.) (figure 43), *H. instabilis* (Curt.), *H. ornatula* (Curt.), *Diplectrona felix* McL.

The head and mouth parts of *Hydropsyche angustipennis* are illustrated in figure 43. In contrast to the species so far described here, the mandibles are sclerotized and fairly well developed. They have thin oblique edges which meet in their natural position between labrum and sitophore.

The haustellum consists of a wide, slightly domed central region, with a flattened lobe on each side. It is thus distinctive in being transverse rather than elongate in form. A further significant feature is that there is no system of converging channels on its surface. This is covered with small tubercles and so appears granulose under the dissecting microscope. On the periphery these are simple tubercles pointing inwards towards the central area of the haustellum. Over the main central area, these tubercles are drawn out into symmetrical pectinate hairs. On the basal part of the haustellum, next to the sitophore, the pectinate hairs are larger and also directed towards the central area. Thus, between the periphery and base of the haustellum, there is a reversal in the direction of tubercles and pectinate hairs, resulting in a central area of convergence. These hairs are not arranged in lines to form channels, and there are no lines of convergence, as described in *Phryganea*. Except for a small area near the sitophore, elongate basiconic sensilla are scattered over the whole anterior surface of the haustellum.

Both maxillary and labial palps bear terminal segments which are longer than the combined basal segments. As their cuticle is sclerotized in small irregular areas, these terminal segments are flexible. A distinctive feature of the labium is the presence of a pair of small lobes between the bases of the labial palps (*lab.l.* in figure 43*B*). These lobes, which are lightly sclerotized and bear short setae, are visible in both anterior and posterior views.

The mouth parts are the same in the other three species of the family listed above.

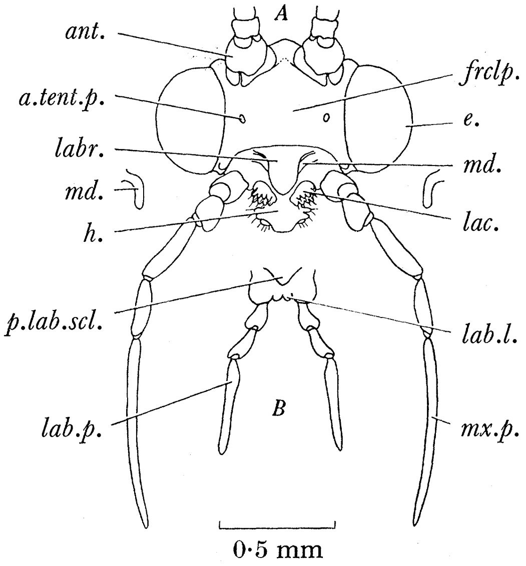

FIGURE 44. *Polycentropus flavomaculatus* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

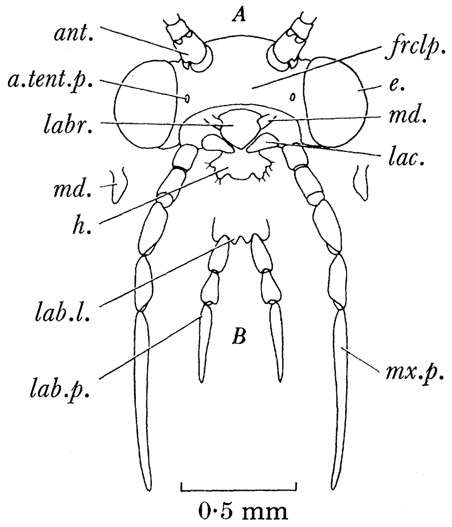

FIGURE 45. *Ecnomus tenellus* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

POLYCENTROPIDAE

Polycentropus flavomaculatus (Pict.) (figure 44), *Neureclipsis bimaculata* (L.), *Cyrnus trimaculatus* (Curt.)

In *Polycentropus* the slender mandibles are partly hidden by the labrum. Unlike the species so far described from other families where cardo and stipes are distinct, there is here a single maxillary sclerite. The laciniae are of unusual form in being covered with papillae, each bearing a short seta.

The distinctive haustellum is drawn out into papillose lateral lobes, bearing a small number of short setae. There is a system of channels on its anterior surface. Between the bases of the labial palps there are two small, lightly sclerotized labial lobes (*lab.l.* in figure 44*B*).

Because of their irregular sclerotization the long terminal segments of both maxillary and labial palps are flexible.

The mouth parts of *Neureclipsis bimaculata* and *Cyrnus trimaculatus* are similar to those of *Polycentropus*.

Psychomyidae

Ecnomus tenellus (Ramb.) (figure 45), *Tinodes waeneri* (L.) (figure 46), *Psychomyia pusilla* (F.).

In *Ecnomus* (figure 45) the small, lightly sclerotized mandibles do not meet beneath the labrum. The haustellum is produced into papillose lateral lobes which bear a few short setae and resemble those described in *Polycentropus*. The surface of the haustellum, however, is granulose with no evidence of channels. The long terminal segments of maxillary and labial palps are flexible, and there is a pair of small labial lobes between the bases of the labial palps.

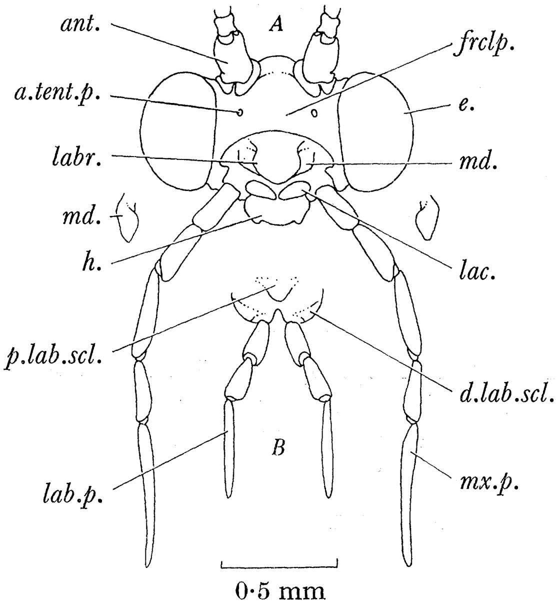

Figure 46. *Tinodes waeneri* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

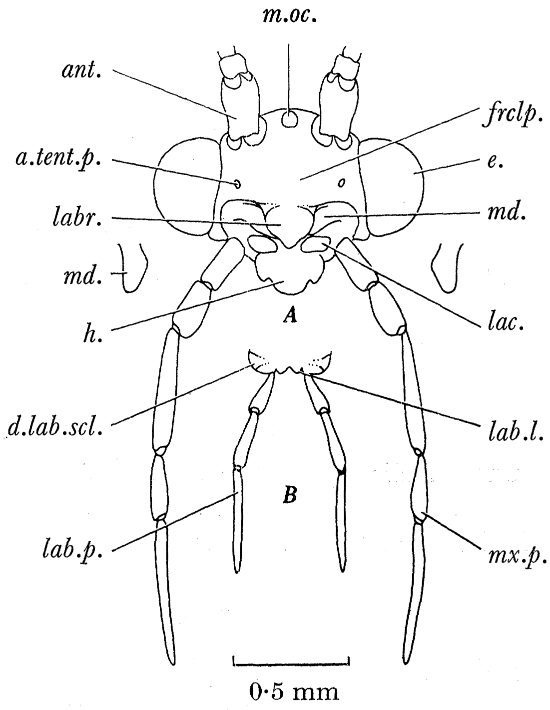

Figure 47. *Wormaldia occipitalis* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

In *Tinodes* (figure 46) the mandibles are fairly well developed and their oblique inner edges can meet between labrum and sitophore. The stipes is not clearly separated from the more strongly sclerotized cardo. With its broad transverse lobes, the haustellum appears transverse. Its granulose surface bears no evidence of channels. The tubercles are simple on the periphery, but nearer the centre they are drawn out into cuticular processes, but not into pectinate hairs. The general arrangement of these structures resembles that described in *Hydropsyche*. Basiconic sensilla are present near the periphery of the haustellum. The labium (figure 46*B*) is unusually long and deeply cleft, with no trace of labial lobes. The long terminal segments of maxillary and labial palps are flexible.

Psychomyia pusilla resembles *Tinodes waeneri* in the structure of the mouth parts.

PHILOPOTAMIDAE

Wormaldia occipitalis (Pict.) (figure 47), *Philopotamus montanus* (Don.)

The well-developed mandibles of *Wormaldia* meet in the mid-line between labrum and sitophore. The haustellum bears rounded lateral lobes and is thus transverse. There are no channels, and it appears granulose, with simple tubercles covering the whole anterior surface. Basiconic sensilla are present near the periphery. The labium bears a pair of small lobes (*lab.l.* in figure 47*B*) between the bases of the labial palps.

Philopotamus montanus is closely similar to *Wormaldia occipitalis* in the structure of its mouth parts.

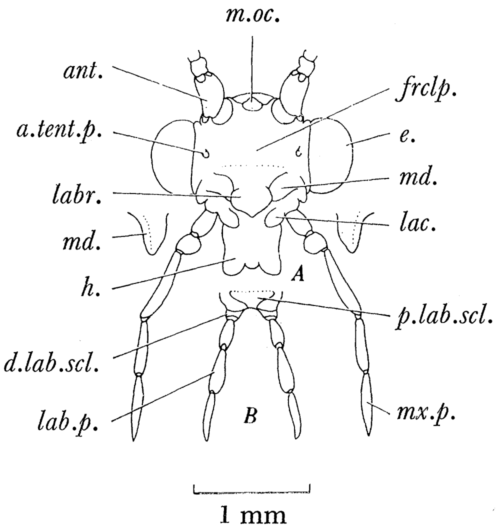

FIGURE 48. *Rhyacophila dorsalis* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

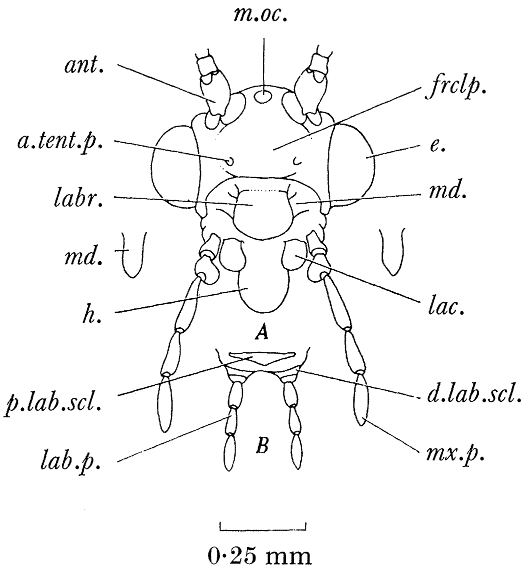

FIGURE 49. *Agapetus fuscipes* ♀. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

RHYACOPHILIDAE—RHYACOPHILINAE

Rhyacophila dorsalis (Curt.) (figure 48)

The sclerotized mandibles bear a distinct ridge near the lateral margin. Their oblique inner edges meet in the mid-line between labrum and sitophore. The elongate haustellum projects into a pair of terminal lobes. The anterior surface is granulose, with no evidence of channels. The tubercles on the periphery are simple; elsewhere they are produced into pectinate hairs which are better developed basally, near the sitophore. The arrangement of these hairs and tubercles is similar to that described for *Hydropsyche*. The distal part of the organ bears a number of basiconic sensilla. There are no lobes between the bases of the labial palps.

RHYACOPHILIDAE—GLOSSOSOMATINAE

Agapetus fuscipes Curt. (figure 49)

The mandibles are sclerotized and large enough to meet between labrum and sitophore. The elongate haustellum has a smoothly rounded apex. The surface is granulose with no sign of channels. There are no lobes between the labial palps.

HYDROPTILIDAE

Agraylea multipunctata Curt. (figure 50), *Oxyethira costalis* (Curt.)

The insects belonging to this family are all very small. In *Agraylea* the head capsule is not fully sclerotized (see figure 50*A*). The delicate mandibles can meet in the mid-line between labrum and sitophore. The short rounded haustellum has a granulose surface, with no channels. There are no lobes between the bases of the labial palps.

The minute species *Oxyethira costalis* has head capsule and mouth parts similar to those of *Agraylea*.

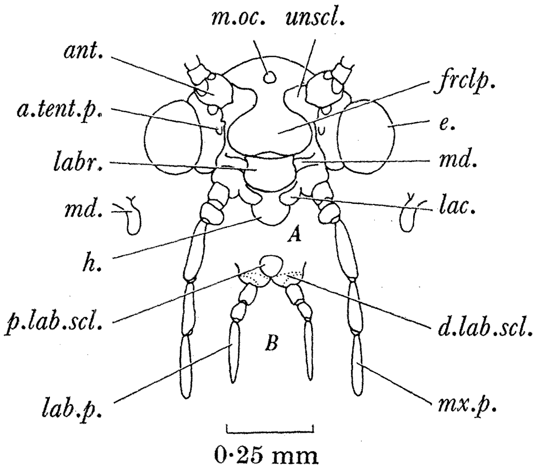

FIGURE 50. *Agraylea multipunctata* ♂. *A*. Anterior view of head with haustellum protruded. *B*. Posterior view of labium.

SOME MODIFICATIONS OF THE MOUTH PARTS

In the introduction, reference was made to modifications of the mouth parts which have been described in some exotic genera. In these cases, the proboscis has been variously elongated, presumably to make it suitable for entering flowers. The information available is fragmentary, and there seem to have been no observations on living insects.

A copy of a drawing of *Plectrotarsus gravenhorstii* (Plectrotarsidae) by Cummings (1914*b*) is reproduced in figure 51. If this is compared with the drawing of *Phryganea* (figure 1), it can be seen that *Plectrotarsus* possesses a more elongate proboscis of the same type. The labrum is long and narrow, while the sitophore is correspondingly elongate. The haustellum is unusual in having a deep median furrow, bordered on each side by what Cummings described as 'short comparatively broad chitin plates, arranged transversely and end to end'. He assumed that the two small processes seen at the tip of the haustellum were the openings of the salivary glands.

A similar extension of the proboscis has been noted by Kimmins (1953) in his description of *Mecynostomella fusca*, a species of sericostomatid from New Caledonia. Here there is a long labrum, covering a well-developed sitophore. At the tip of the proboscis, Kimmins describes 'a membranous structure containing two sinuous tubes, composed of incomplete chitinous rings'. This must be the haustellum, only partly protruded, so that the tubes are seen in a sinuous condition.

Another example of an elongate proboscis, which may be of the same type, is that of *Stenopsychodes mjöbergi* (Polycentropidae). Mosely & Kimmins (1953) reproduce a drawing of the head of this species, after one by Ulmer. This outline drawing of the proboscis shows a long tapering labrum, but no laciniae. There is insufficient information for further comment on this species. Of the six species of *Stenopsychodes* recorded from Australia, this is the only one described as possessing an unusual form of proboscis.

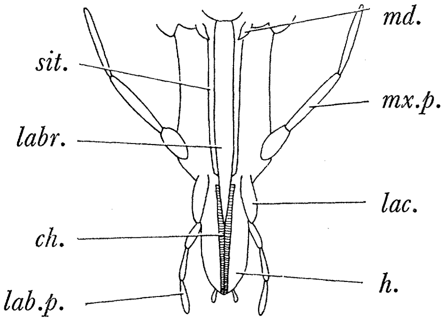

FIGURE 51. *Plectrotarsus gravenhorstii*. Anterior view of proboscis (after Cummings 1914*b*).

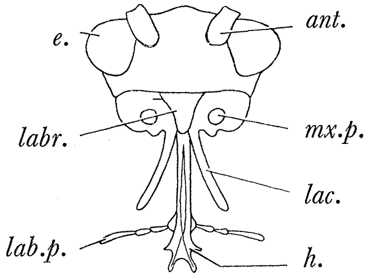

FIGURE 52. *Pseudostenopsyche sugens*. Anterior view of head; bases only of maxillary palps shown (after Döhler 1915).

Döhler (1915) described a new species, *Pseudostenopsyche sugens* (Stenopsychidae) from a single female specimen collected in Chile. This exhibited a different condition of the mouth parts. A copy of his drawing of the head is reproduced in figure 52. The labrum is short, and the maxillary palps arise close to the head capsule. (In Döhler's specimen they had been broken off.) The elongate proboscis, grooved on its anterior surface, appears to be derived from haustellum and labium, with the labial palps carried well out from the base. The tip of the haustellum is produced into four little processes. One detail of particular significance is the elongate condition of the maxillary lobes (laciniae). Döhler described them thus: 'Zu beiden Seiten des Labrums sitzen die Lobi externi an als 2 blattartig dünne, gleichbreite Streifen, ungefähr so lang wie der Stiel bis zum Ansatz der Taster. Ich vermute, dass der Stipes gewöhnlich ganz eingezogen ist und nur beim Saugen derart weit vorgestreckt wird: die Lobi würden sich dann auf die vom Stiel gebildete Rinne darauflegen und auf diese Weise eine geschlossene Saugröhre schaffen.'

In *Dipseudopsis* (Polycentropidae), the maxillary lobes, which are elongate and highly specialized, have been compared with the galeae forming the proboscis of Lepidoptera. Ulmer (1904) gave brief notes on this species, and Cummings (1913) supplied further details. On the inner surface of the maxillary lobe he described a groove, bordered on each side by a line of papillae which he regarded as sense organs. The outer surface of the lobe was covered with closely set transverse ridges. He thought that each lobe could be formed into a tube, so giving a condition comparable to that in Lepidoptera where the galeae did not come together to form a proboscis.

Some details of an African species of *Dipseudopsis* from Lake Victoria are included here, based on the study of three male specimens sent to me by G. Marlier. An adequate description of the mouth parts of this species, however, must wait for a proper study of the living insect in the field and laboratory.

In *Dipseudopsis* (see figure 53), the broad frontoclypeus bears anterior tentorial pits dorsolaterally, and tapers off dorsally into a narrow sclerite between the antennae. The labrum is sclerotized basally, and has a soft distal part, which had collapsed in these preserved specimens. The sclerotized mandible tapers from a broad base into an apex, shaped to fit into a groove on the inner surface of the lacinia. The mandibles are thus directed ventrally and do not meet in the mid-line. The laciniae are covered with close-set transverse ridges and may well be capable of extension in the living insect. There is a short papillose projection from the anterior surface at the base of the lacinia (see figure 53*A*). This appears to be part of the lacinia. In an Indian species of *Dipseudopsis*, Betten (1934) regarded this projection as the 'usual small lobe' of the maxilla, but did not make clear how he interpreted the elongate grooved lobe.

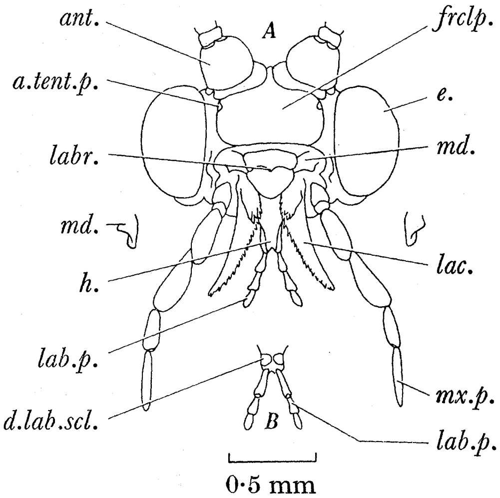

FIGURE 53. *Dipseudopsis* sp. ♂. *A*. Anterior view of head. *B*. Posterior view of labium.

Anterior to the labium is a small bifid structure which presumably represents the haustellum (*h*. in figure 53*A*), and may be capable of protrusion. There is no long grooved sitophore, but only a narrow transverse sclerotized area close to the mouth, hidden by the labrum in figure 53*A*. The elongate labium bears well-defined sclerites (*d.lab.scl*. in figure 53*B*) close to the bases of the slender palps.

OBSERVATIONS ON THE FEEDING OF CADDIS FLIES

Caddis flies, which had access to water, were kept alive by Siltala (1907) for periods up to 20 days. The species concerned were four phryganids, four limnephilids, *Silo pallipes* (Sericostomatidae), and *Lype phaeopa* (Psychomyidae).

Döhler (1914), after reviewing published observations on the feeding of caddis flies, demonstrated that they would live for a longer time in captivity if sugar solution was substituted for water. In his experiments he used the large species, *Limnephilus flavicornis*. When provided with water only, eight males and fifteen females lived for periods from 19 to 40 days, with an average length of life of 29·9 days. On the other hand, nine males and ten females, provided with sugar solution, lived for periods from 45 to 105 days, with an average length of life of 70·6 days.

Descriptions have been published of the general form of the alimentary canal in a number of caddis flies. Döhler (1914) described the alimentary canal of some Limnephilids, and, from experiments, he decided that absorption took place mainly in the midgut. Glasgow (1936) gave an account of the gut of a species of *Hydropsyche*. Deoras (1944) gave descriptions of the gut in a further eight species, from the families Limnephilidae, Sericostomatidae, Leptoceridae, Hydropsychidae, Polycentropidae and Rhyacophilidae. All the species studied by these different investigators were shown to have a normally developed alimentary canal of the same general form.

The above observations are sufficient proof that some caddis flies are capable of imbibing and utilizing a nutrient solution. Most of these observations were made on larger species of the families Phryganeidae and Limnephilidae.

In my study of living specimens from all thirteen families found in Britain, I have shown that they all possess a protrusible haustellum and the ability to drink. It is unlikely that the mandibles have any function in feeding. Even in the Rhyacophilidae and Hydropsychidae, where they are largest, and can meet between labrum and sitophore, they are only lightly sclerotized, and obviously unsuited for the handling or chewing of solid material. In other families the mandibles exhibit different degrees of reduction.

Consideration must now be given to field observations on the feeding of Trichoptera. The sugaring mixtures used to collect nocturnal Lepidoptera are often attractive to caddis flies. All the records I have seen refer to phryganids and limnephilids. There are few records of caddis flies feeding from flowers. Furthermore, they would only be expected to frequent plants with accessible floral or extra-floral nectaries, since the haustellum is not adapted for entering long corolla tubes. The elongate probosces of some exotic species are presumably modified for this purpose, but I have not come across any accounts of their feeding.

Döhler (1914), in his review of this subject, collected only a few definite records of caddis flies feeding on nectar from flowers. He quoted Siltala's note on *Phryganea striata* and *Limnephilus rhombicus* feeding readily at the flowers of *Spiraea salicifolia*, after having had access only to water for several days. He recorded a phryganid on *Tanacetum vulgare* and *Nuphar luteum*, and also a note by Wesenberg-Lund of a limnephilid at an umbelliferous inflorescence. Döhler went on to record that he himself and other trichopterists such as Kolenati, Ulmer, Thienemann and Alfken, had never seen caddis flies on flowers. McLachlan (1865) noted that *Anabolia nervosa* was occasionally found on the flowers of ivy, and he has referred to myriads of caddis flies on coffee trees in Ceylon, which were covered with honey dew from aphids.

Mosely (1939) '...observed in France, a species of *Drusus* moving from floret to floret of a large gentian, applying its mouth to the base of each cup with evident relish'. Nielsen (1943) recorded *Apatidea auricula* flying actively in the sunshine, visiting *Ranunculus glacialis*, which was the only plant in flower. They sat 'with their heads buried between the stamens, no doubt sucking honey'. Wesenberg-Lund (1943) in a general account of Trichoptera noted that the adults took in fluids, particularly water, and continued '...sie werden aber oft auf Blumen angetroffen, von denen sie wohl Honig aus offenliegenden Honiggrübchen auflecken oder aufsaugen; vor allem locken die Blüten von *Spiraea* an Seeufern in der Dammerung oft zahlreiche Individuen an'.

I am indebted to A. F. Peacey for searching in Gloucestershire for caddis flies on flowers at night. He found four species of limnephilids, *Limnephilus lunatus*, *Stenophylax permistus*, *S. sequax* and *Drusus annulatus*, feeding on ivy flowers. I myself have only once seen a caddis fly taking nectar in the field. This was a male of *Anabolia nervosa*, with its haustellum protruded, feeding on an extra-floral nectary on a leaf petiole of *Viburnum opulus*. It was early afternoon, and other specimens of the same species were flying actively round the bush, accompanied by numbers of other insects.

Many species of caddis flies make short fluttering flights close to water, settling frequently on the surface for a few seconds at a time. I have observed this behaviour in both sexes of *Brachycentrus subnubilus* in the day-time, and in species of *Athripsodes* and *Mystacides* in the evening. These are presumably mating flights, and some of the momentary rests on the water surface may well be for the purpose of drinking.

In conclusion, it is clear that caddis flies, in fact, drink both nectar and water under natural conditions, and can be kept alive in the laboratory for several weeks. By experiments with some of the larger limnephilids, I have confirmed this longevity in the field. Marked individuals, released beside Millbarn Pond, were recaptured in a light trap at the same site, after periods of freedom of up to 35 days. Records of these light trap captures over 3 years have also shown that the activity of caddis flies at night is largely dependent on weather conditions. As fewer individuals are active on cold dry nights, there is less chance of finding them feeding on such nights. It is necessary to examine flowers at night, in the vicinity of water, in order to see caddis flies feeding, as they are mainly crepuscular or nocturnal in habit. In view of all this, it is understandable that field observations on this normal activity are so few.

Discussion and conclusions

The head capsule

On the anterior surface of the head capsule of *Phryganea* (figure 1) a central area is marked off from the gena on each side by a shallow vertical groove, in which lies the anterior tentorial pit. From the dissection (figure 26) it is clear that the foregut muscles which originate on this area are separated, by the frontal ganglion and its connectives, into a dorsal group (*24*, *25* and *26*) and a ventral group (*21*).

Snodgrass (1947) regarded the frontal ganglion as a landmark separating dilators of the cibarium, with their origin on the clypeus, from dilators of the pharynx, with their origin on the frons. This central area in *Phryganea* may, therefore, be interpreted as a frontoclypeus. All the caddis flies from other families which I have examined exhibit between the anterior tentorial pits a similar central area with no external sign of subdivision into frons and clypeus.

Cook (1944), in studying larvae of Trichoptera, interpreted this area as a clypeus, and postulated the disappearance of the frons, and the shift of its muscle origins to the clypeus. A different interpretation in larvae and adults, as frons only, was put forward by DuPorte (1946) without evidence from musculature. Snodgrass (1947), however, showed clearly in some caddis larvae that this area is a frontoclypeus, since labral and hypopharyngeal muscles arise dorsally, and cibarial muscles ventrally upon it. The anterior tentorial pits lie at the level of separation between these two groups of muscles.

If the central area is accepted as a frontoclypeus, then the groove on each side can be regarded as a frontogenal suture, where it lies dorsal to the anterior tentorial pit, continuing ventrally as a clypeogenal suture (see figure 1). This would accord with the interpretation of the head of Hymenoptera advanced by DuPorte & Bigelow (1953), and DuPorte (1953). In Hymenoptera, DuPorte postulated a downward growth of the gena, and a strengthening of this part of the head capsule to support the mandible. He considered also that there was a correlation between the size of the eye and the downgrowth of the gena. *Phryganea* has large eyes, and although the adult mandible is much reduced, it was the gena which gave support to the large pupal mandible. Hinton (1946*b*) has shown how the pupal mandibles in Trichoptera are moved by the adult mandibular muscles at the time of escape from the pupal case. *Phryganea* thus appears to exhibit the same downward extension of the gena which DuPorte has suggested for the Hymenoptera. This condition is seen in some other species illustrated here, but there are a number in which the head capsule is less produced and so the anterior tentorial pits lie close to its ventral margin. DuPorte (1956) proposes the name laterofacial suture to include frontogenal and clypeogenal sutures, since he regards them as formed in the same developmental process.

The maxillary lobe

In the absence of any previous study of the head muscles of a caddis fly, the usual interpretation of the single maxillary lobe as a galea appears to be derived from relationship with the Lepidoptera, where the single lobe incorporated in the coiled proboscis is considered to be a galea.

Imms (1944) made use of muscles in his study of the homologies of maxillae and labium in Mecoptera and Diptera. He stated, 'It is noteworthy that no cranial flexor or its counterpart is developed in connection with the insectan galea.' He concluded that the single maxillary lobe in Diptera is a lacinia, because it has inserted on it a cranial flexor muscle. In *Phryganea* the single lobe of the maxilla is likewise moved by a cranial flexor muscle (*10* in figure 27). I propose, therefore, that this lobe should be called a lacinia, and not a galea. Likewise, all the other caddis flies which I have examined have a single maxillary lobe in the same position as in *Phryganea*.

It should be recorded that Das (1937), in his investigation of the mouth parts of insect larvae, described a cranial flexor to the single maxillary lobe of the larva of *Anabolia* (Limnephilidae). He therefore interpreted this lobe as a lacinia.

The haustellum

Lucas (1893) described, on the anterior surface of the haustellum of *Anabolia*, a system of branching grooves, which were separated by ridges drawn out into modified hairs. In a simple drawing of a transverse section he showed these hairs to be directed towards the mid-line. He also noticed the sensilla, but gave no further details of the structure of the haustellum.

Although frequent use has been made of some of Lucas's drawings, little attention has been paid to the information he gave on the structure of the haustellum. Thus Despax (1951) figured a side view of the head of *Anabolia* (after Lucas), with the lines of folding on the posterior surface of the haustellum, but with no channels indicated on the anterior surface. He described the haustellum briefly as traversed by furrows. In Mosely (1939), figure 1 is apparently derived from one of Lucas's drawings, which showed the anterior surface of the head, with the labrum removed. Thus, the sitophore is exposed, and although not labelled, the impression gained is that this structure must be the labrum. No detail at all is shown on the haustellum. A similar outline drawing has been perpetuated by Hickin (1952).

Textbooks such as Comstock (1948), Essig (1942), Handlirsch & Beier (1936) and Imms (1951) omit all mention of the structure of the haustellum. Comstock (1948) went so far as to state that the mouth parts of adult caddis flies, except for the palps, are vestigial.

In addition to this lack of information on structure, there is confusion over homologies. Lucas (1893) described a fold, partly enveloping the base of the haustellum on each side, as the outer lobe (paraglossa) of the labium. He regarded the haustellum itself as formed from the inner lobes (glossae). When the haustellum of *Phryganea* is fully protruded, these outer lobes are not evident, as they are simply the base of the organ and not distinct lobes. Later workers have generally assumed that the main structure is formed from glossae and paraglossae together.

Imms (1951) is not clear, as he describes a median glossa on the labium, and the hypopharynx as prominent and receiving the opening of the salivary glands. In his figure of *Limnephilus*, the structure labelled glossa is the retracted haustellum, which is only just visible. This would suggest that the hypopharynx and glossa are separate structures.

Deoras (1943) stated that the haustellum '...would appear to be the modified glossae and paraglossae of the ligula'. Despax (1951) defined the Trichoptera as possessing a kind of maxillo-labial 'mufle', but he regarded the haustellum as formed from the distal part of the labium. Handlirsch & Beier (1936) likewise considered the haustellum to be derived from the ligula of the labium.

From the above review it can be seen that the consensus of opinion expressed in textbooks and elsewhere is that the haustellum is derived from the ligula of the labium.

The other interpretation of the haustellum must now be considered. Cummings (1914*a*), in a paper on scent organs in Trichoptera, included the following explanatory footnote: 'Haustellum was the name given by Lucas (1893) to what he regarded as an enormously developed fleshy labium projecting from the head as a sort of proboscis by means of which caddis flies obtain their nourishment. In reality the haustellum is a modification of the region of the hypopharynx.' Cummings seems to have been the first to suggest this origin of the haustellum, but he gave no further details. Betten (1934), while including the haustellum as part of the labium, mentioned this interpretation of Cummings, which appears to have been ignored by other workers.

There is, however, the opinion of Tillyard (1923), expressed in his study of the mouth parts of the Micropterygoidea (Lepidoptera). When comparing the Trichoptera and Lepidoptera he wrote: 'In the Trichoptera, the mouth parts are specialized by the absence of functional mandibles—these organs being at the most mere flaps—by the loss of maxillary lacinia and reduction of the galea, and by the reduction of the labium to a small mental plate, without any definite ligula. Maxillary and labial palpi, however, remain primitive and well developed, the former having five and the latter three segments. The labrum is well developed and there is also generally a definite functional hypopharynx, with salivary ducts.'

Tillyard described the hypopharynx of *Micropteryx* as a specialized triturating basket working in conjunction with mandibles and labrum. Its position in relation to the other structures was the same as that of the haustellum in caddis flies. Furthermore, the salivary duct opened on its posterior surface. Tillyard did not quote any work on Trichoptera, nor did he give further details.

The family Micropterygidae, although normally included in the Lepidoptera, was placed in a separate order, the Zeugloptera, by Chapman (1917). Hinton (1946*a*) also recognized the Zeugloptera as a separate order which he considered was more archaic than either Trichoptera or Lepidoptera. It should be possible to derive the mouth parts of caddis flies from an ancestor of *Micropteryx*.

If allowance is made for the extreme reduction of mandibles, the position and relations of the haustellum and sitophore of *Phryganea* are the same as those of the hypopharynx of an insect with generalized biting and chewing mouth parts. In the cockroach, for example, there is a well-developed hypopharynx, with sclerites in its base, which bear a resemblance to those in the haustellum of *Phryganea*. In both insects there is a deep groove separating the labium from the hypopharynx. But, whereas in the cockroach this groove constitutes a salivarium where the salivary duct opens, in *Phryganea* the duct opens close to the tip of the haustellum. There are no muscles or nerves which would have hindered such a forward migration of the salivary aperture. Furthermore, it should be pointed out that in the cockroach the salivary duct does, in fact, open on the base of the hypopharynx. This detail has been emphasized by Snodgrass (1952) in his account of *Periplaneta americana*.

Although in *Phryganea* there is no trace of a ligula between the bases of the labial palps (see figure 3), I have seen two small lobes in this position in Hydropsychidae, Polycentropidae, Psychomyidae and Philopotamidae (figures 43, 44, 45 and 47). I think that these labial lobes, as I have called them, represent the ligula which has been lost in other families.

It is concluded, therefore, that the haustellum and sitophore of *Phryganea* correspond to the hypopharynx of an insect with generalized biting and chewing mouth parts. The hypopharynx is here defined as a median structure lying between mouth and labium. There is uncertainty over its segmental origins, and on embryological grounds it has been derived from one or more segments. It may well not be strictly homologous throughout the insect orders. Henry (1948), supporting the theory of Ferris based on nerve distribution, regards the hypopharynx as the ventral part of a clypeal segment. Young (1953), in a study of the embryology of Anopluran mouth parts, seeks to restrict the term hypopharynx to a ventral lobe anterior to a median maxillary lobe.

It is difficult to accept the suggestion of Ferris that the hypopharynx belongs to a clypeal segment, which he describes as two segments anterior to the mandibular segment. As DuPorte (1953) has argued, there is strong evidence that the '...hypopharyngeal nerve originates from the mandibular neuromere, which would be expected if, as generally claimed, the mandibular segment is the principal source of the hypopharynx'.

It should be noted that the first pair of haustellar nerves in *Phryganea* (*h.n.*1 in figures 23, 26 and 29) branch off from the mandibular nerves. The sensilla of the haustellum are supplied by branches from the labial nerves (*h.n.*2 and 3 in figures 26 and 29), but as tegumentary nerves these need not be restricted to their original segment. In considering the musculature of *Phryganea*, it can be seen that haustellar sclerite 2 gives origin to muscles to the labial palps. Inserted on this sclerite are muscles *14* and *15* (see figures 26 and 27), which originate on the head capsule between muscles to the maxillae and the labium. It appears, therefore, that the posterior surface of the haustellum includes a labial element. There are, however, no muscles originating in the labium and inserted on the haustellum, which would be expected if the main part of the haustellum was derived from glossae and paraglossae of the labium.

Evolution of caddis fly mouth parts

In this study, observations were made on fifty-three species, representative of all thirteen families of Trichoptera found in Britain. Mosely & Kimmins (1953) recognize a world total of eighteen families of Trichoptera, four of which are found only in the Australasian region. Of the fourteen families in the Palaearctic region, all but one, the Calamoceratidae, are represented in Britain. The British species here studied can, therefore, be claimed to be fairly representative of the order as a whole. Allowance must, however, be made for the possibility of modifications of the mouth parts being reported.

In all the species which I have examined, there is a haustellum which can be protruded like a tongue for the purpose of drinking. While in most species the anterior surface of the haustellum is channelled, as in *Phryganea*, in a few families this surface is simply granulose. Differences are also apparent in the shape of the haustellum, the size of the mandibles, and the presence of labial lobes. As will be shown, these different conditions of the mouth parts can be related to views on the phylogeny of the families of Trichoptera.

Of the species examined, the Phryganeidae and Limnephilidae display the most highly developed mouth parts. The channelled haustellum, laciniae and palps, are carried out some way from the head capsule on a flexible basal region, so forming a proboscis. Related to this development of the proboscis is the elongation of cardo and stipes. The mandibles have nearly disappeared.

In other families, the basal part of the proboscis and the labrum being short, the haustellum is not carried far out from the head capsule. Cardo and stipes are short sclerites which have little movement, and in the Polycentropidae they are not even separable. The haustellum bears a system of converging channels in the Sericostomatidae, Beraeidae, Molannidae, Odontoceridae, Leptoceridae and Polycentropidae. In these families the mandibles are not reduced to the same degree as in the Phryganeidae and Limnephilidae.

The haustellum exhibits a more primitive condition in the Hydropsychidae, Psychomyidae, Philopotamidae, Rhyacophilidae and Hydroptilidae. Its anterior surface appears granulose because it is covered with tubercles drawn out into cuticular processes, but not arranged in lines, so that there is no system of channels. Here the mandibles are somewhat larger, and thus more generalized than in the other families. Another significant feature of the Hydropsychidae, Polycentropidae, Philopotamidae and *Ecnomus* in the Psychomyidae, is the possession of a pair of small labial lobes between the bases of the labial palps. These lobes are not seen in the families with more specialized mouth parts.

It is interesting to relate these conditions of the mouth parts to opinions on the phylogeny of the order. The Rhyacophilidae is generally regarded as one of the most primitive families (Ulmer 1907; Betten 1934; Mosely 1939; Nielsen 1948; Despax 1951). Ulmer (1907) regarded the Rhyacophilidae, Philopotamidae, Hydroptilidae, Polycentropidae and Hydropsychidae, as a group of related families. Betten (1934) grouped the Rhyacophilidae, Philopotamidae and Hydroptilidae together.

Ross (1956) considers the Philopotamidae, Rhyacophilidae and Glossosomatidae to be the most primitive families of Trichoptera. (In his classification, the glossosomatids are given family rank; a total of thirty families are recognized.) He bases his conclusions on larval, pupal, and adult characters. The adult characters which he regards as primitive include the possession of five-segmented maxillary and three-segmented labial palps, dorsal ocelli, and certain punctate areas on head and thorax.

The granulose haustellum, which I regard as primitive, is found in those three families, Philopotamidae, Rhyacophilidae and Glossosomatidae, which Ross considers to be the most primitive in the order. The other families with this primitive haustellum, the Hydroptilidae, Hydropsychidae and Psychomyidae, are placed by Ross close to these primitive families. I have already shown that this form of haustellum is associated with mandibles which are larger than those in other families—another primitive feature.

In his phylogenetic diagram of the Trichoptera, Ross derives two lines from an ancestral form. One line includes the families whose larvae make retreats; the other, those whose larvae are free-living, leads to the specialized case-building species. The caddis flies, which I have found to possess labial lobes, all belong to families in Ross's line of retreat builders. Ross agrees with other workers in associating the Limnephilidae and Phryganeidae as highly evolved families. These two families possess the most highly developed mouth parts of any I have studied.

Thus, in considering the evolution and classification of the Trichoptera, my findings on the mouth parts agree closely with those of Ross based on other characters.

In insects, sucking mouth parts, which are not adapted for piercing, have evolved in several different ways. One line of specialization is seen in Diptera, where the labium with the palps transformed into labella, forms the major part of a proboscis. The Lepidoptera have utilized the maxillae, combined to form a long coilable proboscis. In Hymenoptera, the bees possess a specialized labium, which is associated with the other mouth parts, to form a passage to the mouth for nectar. In all these orders the hypopharynx is reduced, while other mouth parts have been enlarged and specialized. In contrast, the Trichoptera are unique in possessing a hypopharynx adapted for taking up fluids. The condition here can be derived from generalized biting and chewing mouth parts, by enlargement and specialization of the hypopharynx, and reduction of the mandibles.

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a.scl. anterior sclerite
a.tent. anterior arm of tentorium
a.tent.p. anterior tentorial pit
ant. antenna
ant.l. lobe on scape of antenna
ant.n. antennal nerve
antf. antennifer
b.pect.h. base of pectinate hair
br. brain
cd. cardo
ch. channel on haustellum
cl. clefts into cavity of maxillary palp
clpge.s. clypeogenal suture
d.lab.scl. distal labial sclerite
d.tent. dorsal arm of tentorium
e. eye
end. endocuticle
ex. exocuticle
fil. filament of pectinate hair
fr.g. frontal ganglion
fr.g.c. frontal ganglion connective
frclp. frontoclypeus
frge.s. frontogenal suture
ge. gena
h. haustellum
h.g. haustellar ganglion
*h.n.*1, 2, *or* 3. haustellar nerve 1, 2 or 3
*h.scl.*1, 2 *or* 3. haustellar sclerite 1, 2 or 3
hyp. hypodermis
l. lobe of maxillary palp
l.oc. left ocellus
l.sl.d. left salivary duct
lab.l. labial lobe
lab.n. labial nerve
lab.p. labial palp
lab.p.n. labial palpal nerve
labr. labrum
labr.n. labral nerve
labrf.n. labrofrontal nerve
lac. lacinia
lac.l. lacinial lobe
lac.n. lacinial nerve
lam. lamina of anterior arm of tentorium
m.oc. median ocellus
m.oc.n. median ocellar nerve
md. mandible
md.n. mandibular nerve
mth. mouth
mx.n. maxillary nerve
mx.p. maxillary palp
mx.p.n. maxillary palpal nerve
n. nerve
nuc. nucleus
occ. occiput
occ.c. occipital condyle
occ.f. occipital foramen
oes.c. circumoesophageal connective
op.n. optic nerve
p.l. palpal lobe
p.lab.scl. proximal labial sclerite
p.oes.cm. postoesophageal commissure
p.tent.p. posterior tentorial pit
pect.h. pectinate hair
pge. postgena
pocc. postocciput
pocc.s. postoccipital suture
r. rib
r.oc. right ocellus
r.oc.n. right ocellar nerve
r.sl.d. right salivary duct
rec.n. recurrent nerve
s.oes.g. suboesophageal ganglion
scl. sclerite posterior to mandible
sens. sensillum
sens.n. nerve to sensillum
sens.p. sensory pit
sit. sitophore
sl.d. common salivary duct
sl.o. orifice of common salivary duct
sl.v. salivary valve
st. stipes
tent.br. tentorial bridge
tub. tubercles on haustellum
unscl. unsclerotized cuticle
v.n.c. ventral nerve cord
x. transverse line of convergence of filaments of pectinate hairs

1 apical muscle of labrum
2 compressor muscle of labrum
3 levator muscle of antenna, from dorsal arm of tentorium
4 levator muscle of antenna, from anterior arm of tentorium
5 depressor muscle of antenna, from lateral surface of anterior arm of tentorium
6 depressor muscle of antenna, from medial surface of anterior arm of tentorium
7 muscles of mandible
8 flexor muscle of cardo
9 extensor muscle of cardo
10 cranial flexor muscle of lacinia
11 stipital extensor muscle of lacinia
12 levator muscle of maxillary palp
13 depressor muscle of maxillary palp
14 retractor muscle of haustellum
15 protractor muscle of haustellum
16 retractor muscle of labium
17 proximal muscle of salivary valve
18 distal muscle of salivary valve
19 levator muscle of labial palp
20 depressor muscle of labial palp
21 anterior dilator muscle of cibarium
22 lateral dilator muscle of cibarium
23 posterior dilator muscle of cibarium
24 anterior dilator muscle of pharynx
25 anterodorsal dilator muscle of pharynx
26 lateral dilator muscle of pharynx
27 posterodorsal dilator muscle of pharynx
28 posterolateral dilator muscle of pharynx
29 constrictor muscle of pharynx