

THE MORPHOLOGY AND FUNCTIONING OF THE MOUTHPARTS OF
CHLOEON DIPTERUM L. AND *BAETIS RHODANI* PICTET
 (INSECTA, EPHEMEROPTERA)*

BY

D. SEYMOUR BROWN†

Zoology Department, University of Leicester

[Communicated by Professor H. P. Moon—Accepted 10th May, 1960]

(With 8 figures in the text)

The morphology of the mouthparts of *Chloeon dipterum* L. and *Baetis rhodani* Pictet is described and the manner of functioning of the mouthparts is interpreted on the basis of their morphology and direct observations of feeding larvae. In *C. dipterum* the way in which the mouthparts were used depended upon the nature of the food material. The ways in which the mouthparts of *B. rhodani* differ from those of *C. dipterum* are shown to be consistent with the overall adaptation of the former species to flowing water.

CONTENTS

	Page
Introduction	147
Methods	148
The morphology of the mouthparts of <i>C. dipterum</i>	149
The functioning of the mouthparts of <i>C. dipterum</i>	159
When feeding upon fine detritus	159
When feeding upon other food materials	162
The rate of movement of the mouthparts	162
The part played by the limbs in feeding	162
The morphology of the mouthparts of <i>B. rhodani</i>	163
The functioning of the mouthparts of <i>B. rhodani</i>	169
The relationship of the differences in the mouthparts between <i>C. dipterum</i> and <i>B. rhodani</i> with their habitats	170
Discussion	173
Acknowledgments	174
References	174
Key to the lettering to figures	175

INTRODUCTION

Many descriptions of the anatomy of larval Ephemeroptera contain accounts of the mouthparts (Lestage 1921, Murphy 1922, Schoenemund 1930, Uéno 1954), and although these are frequently incomplete and the identity of the species described is rarely known with certainty it is clear that there is a great diversity in the external morphology of the mouthparts within the Order. This diversity extends to the intrageneric level and Macan (1950) has demonstrated the value of detailed study of the mouthparts for taxonomic purposes.

The existing accounts of the musculature of the mouthparts (Murphy *loc. cit.*, Strenger 1953) show that intergeneric differences exist, and the disagreement between the accounts by these two authors of the anatomy of *Ecdyonurus*

* Part of a thesis accepted for the degree of Doctor of Philosophy in the University of London.

† Present address: c/o British Medical Research Council, 38 Old Queen Street, London, S.W.1.

suggests the presence of specific characteristics in the internal as well as the external morphology of the mouthparts.

It is likely that these characters form an important part of the adaptation whereby a species is enabled to occupy its particle niche in the aquatic macro-habitat. Hitherto the ecological adaptation of mayfly larvae has been considered almost exclusively in terms of general body shape and the structure of the limbs, and the effect of specialisation in these characters on the feeding mechanism has been neglected. For an understanding of the adaptive radiation of the feeding mechanism in ephemeropteran larvae detailed studies of the food and feeding mechanism in a large number of species are necessary.

The results are given below of a study of the pond-dwelling species *Chloeon dipterum* L., and *Baetis rhodani* Pictet which occurs abundantly in rapidly flowing streams. Both species belong to the "freeswimming" group of ephemeropteran larvae in contrast to the extremely flattened forms *Ecdyonurus* sp. and *Rhithrogena* sp. described by Strenger (*loc. cit.*). In addition *Chloeon* and *Baetis* were of interest in providing an opportunity for determining the ways in which a similar feeding apparatus was adapted to function successfully in habitats as different as a pond and a rapidly flowing stream.

Both Murphy, Strenger, and Dunn (1954) attempted to deduce the way in which the mouthparts functioned from their morphology alone. That this may be a misleading approach is shown by the erroneous conclusion arrived at by early workers (Pictet, 1943, Lampert 1899), from a study of morphology alone, that the diet of ephemeropteran larvae was of a carnivorous nature. Morgan (1913) investigated the feeding mechanism of *Iron fragilis* by direct observation of living animals as well as by dissection, and the same method was used in the case of *C. dipterum* and *B. rhodani* which, being hypognathous, can be observed more successfully than a flattened form such as *Iron*.

MATERIALS AND METHODS

The external morphology of the mouthparts was investigated in whole animals and ecdysed skins, permanent preparations being mounted upon large cover slips so that they could be examined under high magnification from both sides. Musculature was studied by dissection of the heads of specimens fixed in Bouin's fluid (alcoholic).

Observation of larvae was carried out in small aquaria and plane sided jars, furnished with material gathered from the natural habitat, by means of a binocular microscope on a travelling arm. The relatively low magnification necessary allowed a wide depth of focus that enabled the larvae to be followed fairly easily in the large containers. In the case of *B. rhodani*, the natural conditions of the habitat were simulated as far as possible by causing the water to circulate over the substratum by blowing compressed air through one end of the container.

In the anatomical descriptions the terms posterior and anterior are used in relation to the posterior and anterior poles of the longitudinal axis of the animal, i.e., the surfaces on the caudal side of an appendage are referred to as posterior. When muscles are described in the text they are accompanied by the numbers with which they are labelled in the figures.

THE MORPHOLOGY OF THE MOUTHPARTS OF *C. DIPTERUM*

Understanding of the spatial relationships of the mouthparts is aided by a preliminary knowledge of the structure of the head capsule to which the mouthparts are attached.

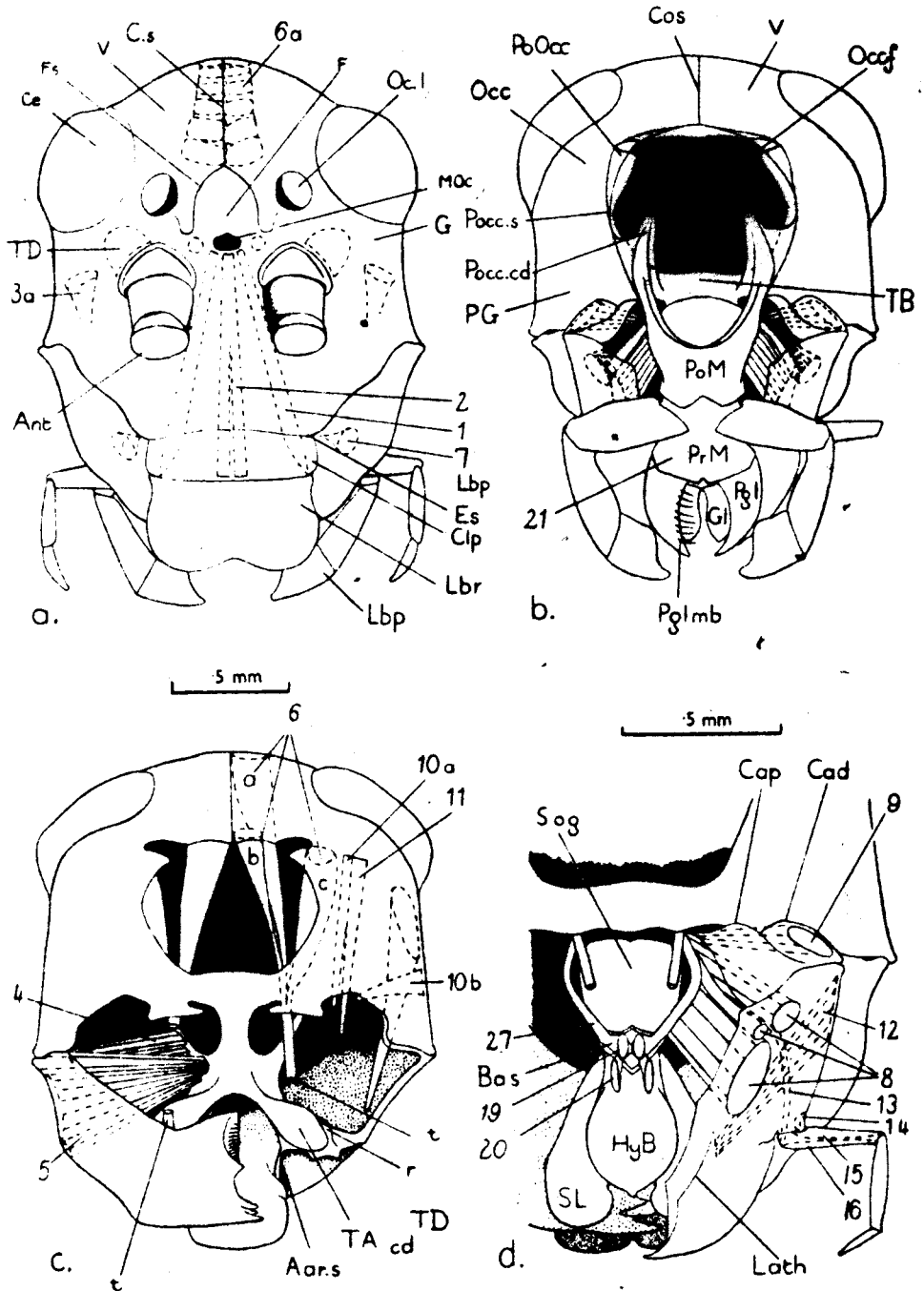
The head capsule

The external features of the head capsule are reminiscent of those of an orthopteroid insect such as *Periplaneta* or *Locusta*. The long axis of the head is held approximately vertically; there is a demarcation into an anterior surface, composed of vertex, frons and genae (Fig. 1a), and a posterior surface composed of vertex, occiput, postocciput, and post genae (Fig. 1b). The coronal suture extends from its point of junction with the postoccipital suture in the rim surrounding the occipital foramen (Fig. 1b) to a point just above the lateral ocelli where it divides into two frontal sutures extending below the lateral ocelli (Fig. 1a). The compound eyes occupy the dorsal corners of the anterior surface of the head capsule, and the median ocellus is situated midway between the top of the vertex and the epistomal suture (Fig. 1a).

It has not been possible to make out ocular and subocular sutures corresponding to those described in *Locusta* by Albrecht (1953), and the posterior sclerites of the head capsule are indistinguishably fused together in *C. dipterum* as is the case in the species of *Ecdyonurus* described by Strenger (1953). The terms post genae and vertex are used to designate parts of the posterior wall of the head capsule in a way that corresponds as closely as possible to the usage of Strenger.

A large part of the posterior wall of the head capsule is pierced by the occipital foramen through which pass the oesophagus and the neck muscles. These muscles are inserted on the thick ridge which forms the dorsal and lateral boundaries of the occipital foramen and which contains the post occipital suture between the occiput and the postocciput. The postocciput is for the most part a delicate membrane that is easily lost in detaching the head from the body. Ventrally and externally the occipital foramen is bounded by the base of the postmentum, while internally the median edges of the post genae are connected by the body of the hypopharynx (Figs. 1b, 1c & 2a). Between the hypopharynx body and the postmentum lies the sub-oesophageal ganglion of the central nervous system.

The tentorium body projects forward from its ventral edge into the head and divides into paired dorsal and anterior tentorial arms (Figs 1c & 2a). A pair of very small posterior arms project backwards from the tentorium body and fuse with the postocciput forming the postoccipital condyles (Fig. 1b). The dorsal tentorial arms are slender and pass antero-dorsally fusing with the vertex dorso-lateral to the insertion of the antennae (Figs. 1a & 2b). Far more strongly developed are the anterior arms which provide places of origin for several large muscles (Fig. 1c), and serve to brace the ventral margin of the head capsule against the stresses developed during the movements of the mouthparts. They pass antero-ventrally as broad bars fusing with the inflected genae dorsal to the ventral edge of the head capsule (Figs. 1c & 2a). As is the case in *Ecdyonurus* there is no definite boundary between the anterior

Fig. 1.—*Chloeon dipterum*

a. Head capsule. Anterior surface, showing origins of muscles; b. Head capsule. Posterior surface, oesophagus and cervical muscles removed; c. Head capsule. Posterior view, mouthparts removed with the exception of the left mandible; d. Head capsule. Posterior view of ventral part, labium removed showing the posterior surfaces of the hypopharynx and the right maxilla. (Key to lettering p. 175.)

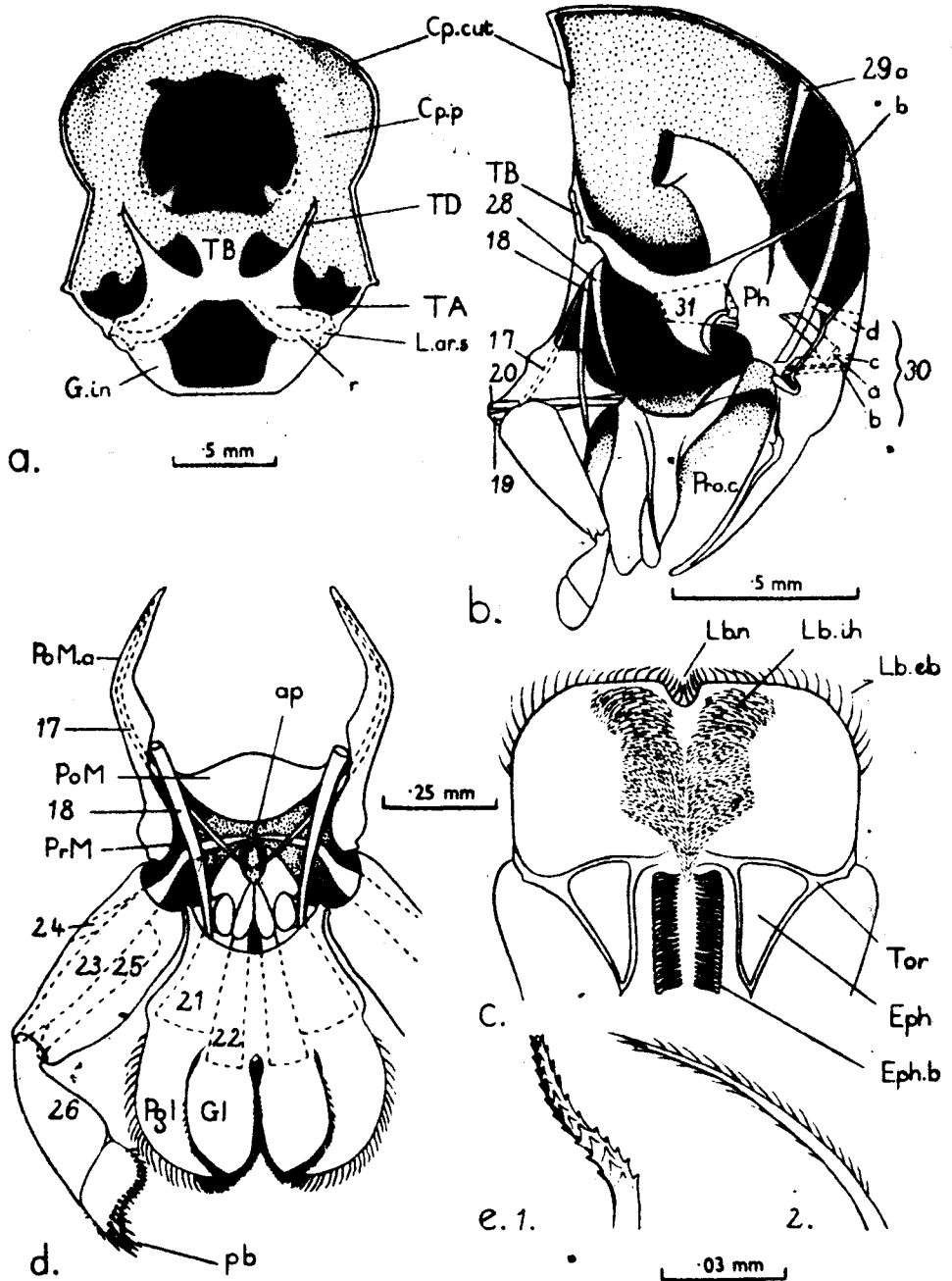


Fig. 2.—*Chloeon dipterum*

a. Tentorium displayed by cutting away the anterior surface of the head capsule; b. Head capsule viewed laterally with the near lateral and posterior wall removed together with the mandibles and maxillae, to show the preoral cavity and pharynx, and the relationship between the labium and the hypopharynx. The anterior arm of the tentorium is cut through just beyond the base of the dorsal arm; c. Clypeo-labral lobe, posterior surface; d. Labium, anterior surface; e. (i) bristle from notch of labrum; (ii) bristle from lateral edge of labrum. (Key to lettering p. 175.)

tentorial arm and the inflected margin of the head capsule; it is probably marked by a thickened ridge (Figs. 1c & 2a, r) that surrounds the posteriorly bulging surface of the anterior tentorial arm. Laterally the ridge bears a narrow grooved projection (ed), that contributes to the lateral articulation between the mandible and the head capsule and may be seen projecting below the gena when the head is viewed laterally (Fig. 7b). The ventral inflection of the capsule edge extends from the anterior tentorial arm to the base of the clypeus, at which point it fuses with an inflection from each end of the epistomal suture forming a heavily sclerotised slot (Figs. 1c & 3a, A.ar s) that receives the anterior articular facet of the mandible.

The clypeo-labral lobe

The mouthparts are enclosed anteriorly by the clypeo-labral lobe, the cuticle of the outer surface of which is fairly strongly sclerotised and is divided into clypeus and labrum (Fig. 1a).

The posterior surface of the clypeo-labral lobe (Fig. 2c) is soft and membranous; it forms the anterior wall of the preoral cavity and there is no sharp division between the epipharynx and the inner surface of the labrum. The epipharyngeal surface bears a double row of strong medianly directed bristles that extend as far as the mouth opening and is supported by strips of heavily sclerotised cuticle, the tormae, that arise from the basal corners of the labrum. A field of fine orally directed hairs clothes the inner surface of the labrum as far as the beginning of the bristle rows on the epipharynx. Strong bristles project from the edge of the labrum, those situated latero-ventrally have sharp bifid tips and a fringe (Fig. 2e, 2), while those within the median notch are shorter and stouter with blunt tips and several rows of spines (Fig. 2e, 1), and between these two forms there are bristles of intermediate structure.

Two pairs of muscles govern the tightness with which the clypeo-labral lobe is applied to the anterior surfaces of the mandibles. Labrum retractor muscles (1) arise on the frons just lateral to the median ocellus (Fig. 1a) and are inserted by fine tendons on the proximal arms of the tormae. Labrum extensor muscles (2) arise on the frons between them and are inserted on the distal edge of the clypeus (Fig. 1a).

The mandibles

The body of each mandible (Figs. 3 & 4e) is elongated and twisted so that the outer surface of the proximal portion lies in a vertical plane parallel to the longitudinal axis of the head, while the distal portion is inflected so that its anterior surface lies in a plane transverse to the longitudinal axis of the head.

Each mandible terminates in two groups of sharp teeth, the outer and inner canines, consisting of four and two or three teeth respectively. At the base of the inner canine is articulated the prosthema that is freely movable but is provided with no muscles; that of the left mandible is stouter than that of the right and bears five teeth (Fig. 4e). Between the prosthema and molar surface of each mandible there is a thick cluster of fine hairs.

There are three positions of articulation between the mandible and the head capsule which correspond to those present in *Ecdyonurus* and *Rhithrogena*

(Strenger, *loc. cit.*). Apart from the molar surfaces and the canines, the articulatory surfaces are the most heavily sclerotised parts of the mandible.

Posterior articulation is between the ventro-lateral surface of the post gena and a strongly sclerotised surface developed on the extreme proximal end of the body of the mandible (Figs. 3d & 4e); both articulatory surfaces are long and narrow. Anterior to the articulation the base of the mandible is joined to the head capsule by an arthro-dial membrane.

A thickening at a point midway along the mandible base forms the lateral articulatory surface (Figs. 3d & 4e), that fits into a grooved projection (cd) arising from the point of fusion of the anterior tentorial arm and the gena already described in the account of the head capsule.

The anterior articulatory surface is situated on the body of the mandible in the form of a blunt peg (Fig. 4e), that projects from the anterior surface so that its lateral edge rests in a slot formed by the inflected gena (Fig. 3a).

Three dorsal adductor muscles (6) (Fig. 1c) are inserted upon a tendon (t) which is attached to the dorsal anterior edge of the mandible base at the point of inflection of the distal part of the body of the mandible. The two smaller of these muscles have their origin on the vertex (6b) and the occiput (6c), while the largest, that is composed of several groups of fibres (6a), is inserted on the frons (Figs. 1a & 1c). Three bundles of tentorial adductor muscle fibres (5) originating on the body of the tentorium and the lateral surface of the base of the dorsal tentorial arm are inserted on the proximal lateral wall of the mandible body (Figs. 1c & 3d).

Abduction of the mandible is produced by two groups of muscles inserted on the base of the mandible. Two cranial abductors (3a & b) arising on the gena (Fig. 1a) and post gena (Fig. 1c) respectively, are inserted just proximal to the lateral articulatory surface (Fig. 3d). Four bundles of tentorial abductor fibres (4) lie close to those of the tentorial adductor muscles from which they may be distinguished by the position of their insertion on the basal rim and not in the body of the mandible, one bundle being anterior and the remainder posterior to the posterior articulation (Fig. 3d).

In an actively feeding larva the posterior articulatory surface of the mandible performs small movements, in a horizontal plane transverse to the long axis of the head, mainly directed to and away from the midline. The lateral articulation acts as a pivot, and as it is situated nearer to the proximal than to the distal end of the mandible, movements at the anterior articulation are of a far greater amplitude. They also take place in a different direction to those at the posterior articulation because of the twisted shape of the mandible. The anterior articulatory process slides against the thickened edge of the inflected gena in a direction approximately parallel to the long axis of the head, so that the tip of the mandible traces a complex path in which the movement of adduction includes ventral and anterior components. This movement is of great importance in feeding as the canines are made to dig against the substratum and then sweep up into the preoral cavity. The movement of the anterior articulatory process against the gena probably guides and limits the movement of the mandible to the precise direction necessary for the successful operation of the feeding mechanism.

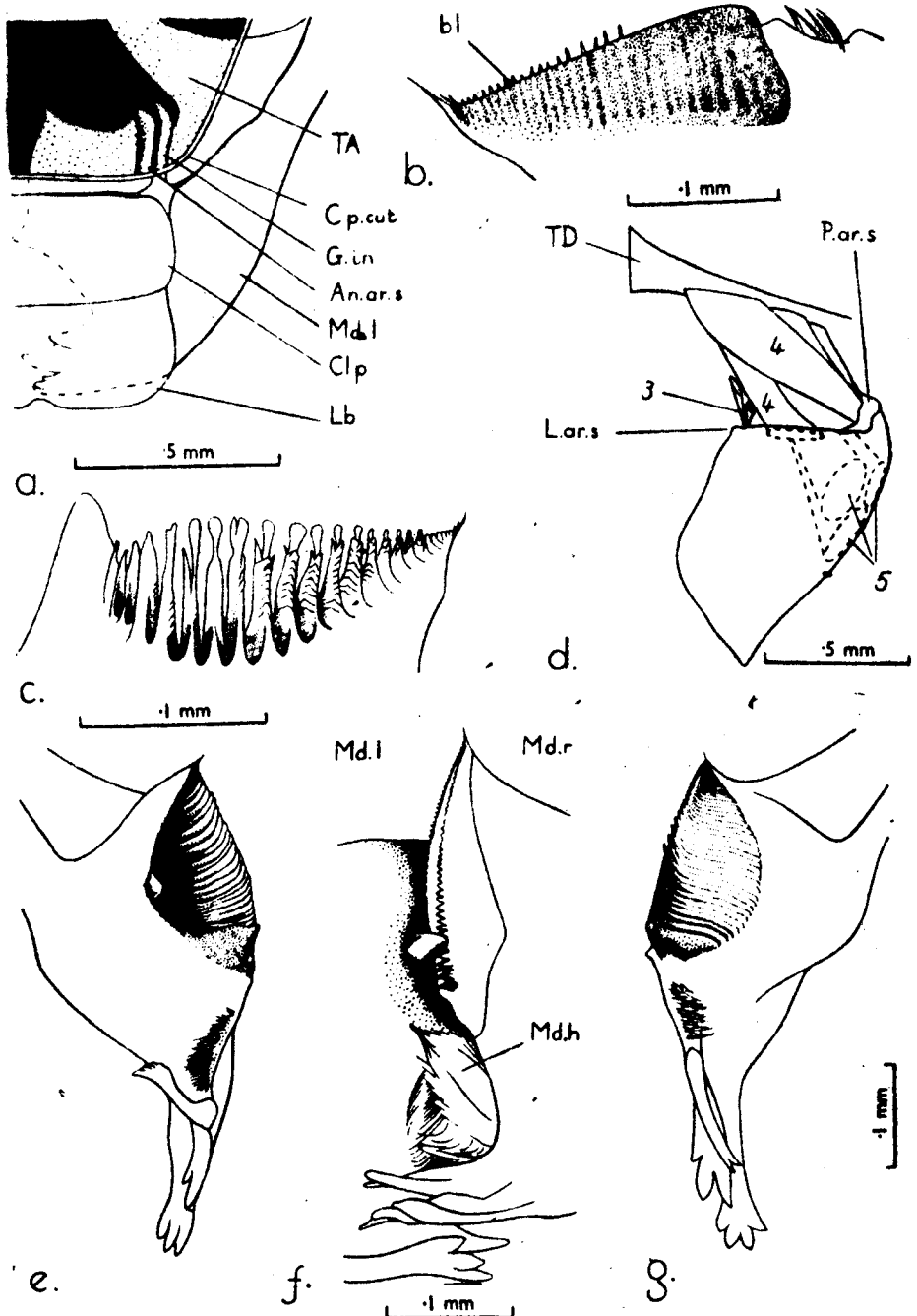


Fig. 3.—*Chloeon dipterum*

a. Head capsule. Anterior view of ventral part with wall dorsal to the epistomal suture cut away to show the anterior articulation of the mandible; b. Molar surface of right mandible, anterior edge; c. Molar surface of left mandible, anterior edge; d. Left mandible. Lateral view of tentorial abductor muscles (4); e. Left mandible, median view; f. Posterior view of the distal part of the mandibles in the closed position. g. Right mandible, median view. (Key to lettering, p. 175.)

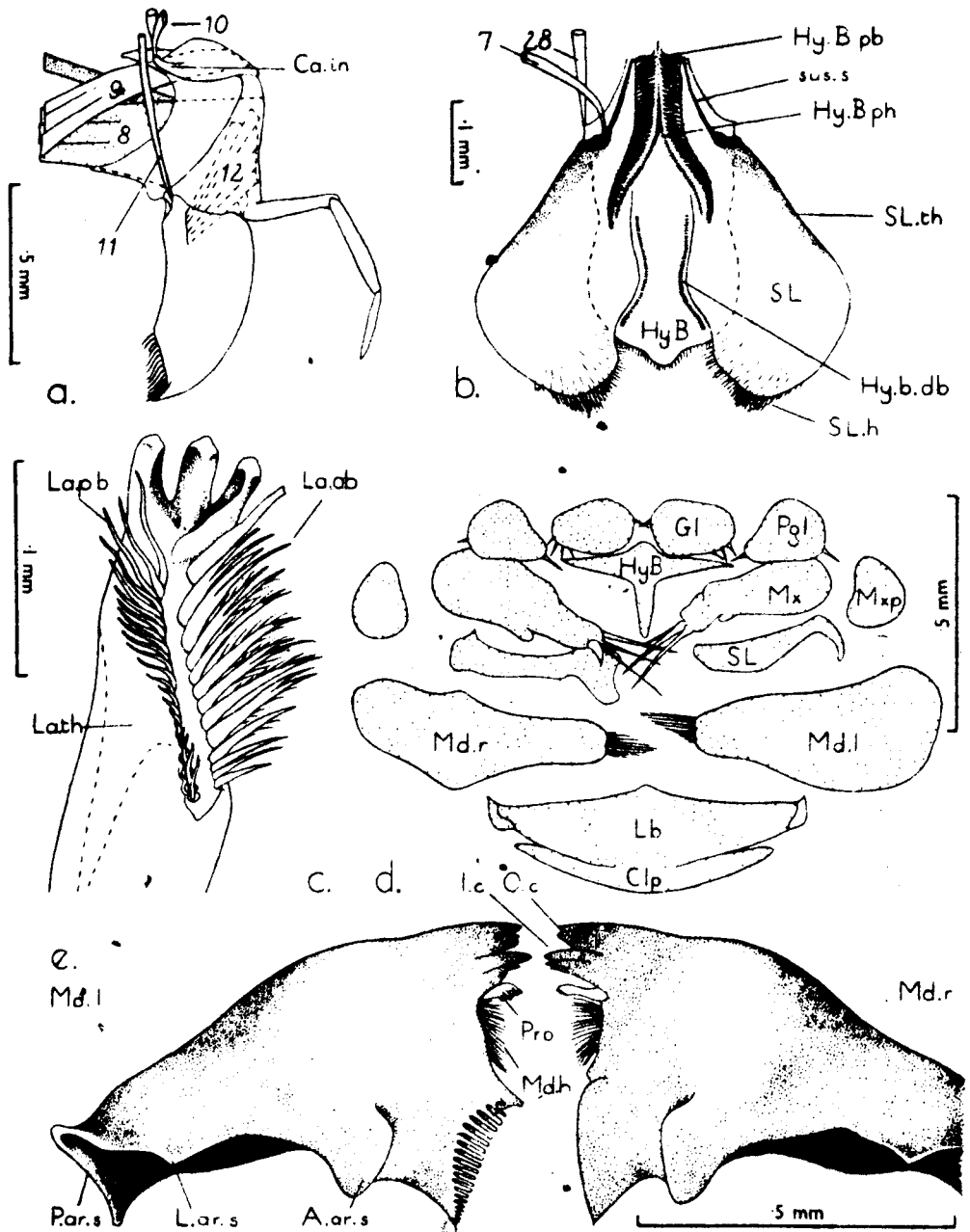


Fig. 4. - *Chloeon dipterum*

a. Left maxilla, anterior view ; b. Hypopharynx, anterior surface ; c. Tip of lacina, median edge ; d. Diagram of the mouthparts in a horizontal transverse section of the head at the level of junction between the clypeus and the labrum ; e. Left and right mandibles, anterior surfaces. (Key to lettering, p. 175.)

Asymmetry in the structure of the mandibles, that has already been noted in the prosthecae, is very marked in the structure of the molar surfaces (Fig. 3), which are conspicuous as a result of their heavily sclerotised cuticle and which project into the proximal part of the preoral cavity. The right molar surface is covered anteriorly by a smooth edged blade of cuticle (Fig. 3b, bl). From this there run a large number of ridges that lie across the preoral cavity and are perpendicular to the anterior surface of the mandible (Fig. 3g). The ridges decrease in size towards the mouth and are toothed; fine spines project from many of them where they join the blade and at the posterior ends of the biggest are larger spines. The spines and teeth on the ridges are sharpest and most numerous on mandibles from freshly ecdysed larvae. On mandibles from larvae approaching ecdysis the ridges of the right molar surface are often worn smooth and spines may be absent (Fig. 3g).

The molar surface of the left mandible (Fig. 3c & e) differs greatly from that of the right and when the anterior surface of the mandible is examined appears to consist of a row of stout blunt tipped prongs. Under a magnification of $\times 1450$ these prongs are seen to have a complex structure, the majority of them bearing rows of V-shaped ridges and tips that are relatively thin and spatulate (Fig. 3c). On the posterior surface of the mandible the bases of the prongs are drawn out as ridges arising from the floor of a hollow surface of heavily sclerotised cuticle (Fig. 3e).

When the mandibles are closed the canines of the left lie anterior to those of the right and the prongs of the left molar surface overlap the blade of the right molar surface, the ridges of which fit fairly closely into the hollowed surface of the left (Fig. 3f). At the posterior edge of the left molar surface is a stout conical projection that bears against the right mandible and probably serves to limit the closeness with which the mandibles can be brought together.

The maxilla

The stipes and lacinia form the elongate and antero-posteriorly flattened body of the maxilla (Figs. 1d & 4a) which is articulated to the head capsule by means of the cardo.

Great mobility of the maxilla results from the large size and structure of the cardo which is divided by a groove into two portions (Fig. 1d, Cap & Cad), between which there is considerable freedom of movement due to the flexibility of the cuticle. The median end of the proximal portion bears a small condyle that articulates with the body of the tentorium close to its junction with the post gena. A narrow projection from the anterior edge of the distal portion (Fig. 4a, Ca. in) curves under the post gena and provides the point of insertion for two cardinal-cranial muscles (10), the dorsal of which originates on the post gena lateral to the post occipital foramen (10a), and the ventral (10b) on the post gena laterally below the cranial abductor (3b) of the mandible (Fig. 1c).

While the attachment of the cardo to the stipes allows free movement between these parts there is very little freedom of movement between the stipes and lacinia. It is possible that a slight anterior movement of the lacinia tip in relation to the stipes may be produced by the contraction of the stipital-lacinal muscle (12) that passes from the postero-lateral surface of the stipes to the anterior surface of the lacinia.

From the ventral surface of the tentorium body there arise three groups of stipes adductor muscle fibres (8) that are inserted on the postero-lateral surface of the stipes, and the single cardo adductor muscle (9) inserted in the distal portion of the cardo (Fig. 1d). A single cranial lacinial muscle (11) whose origin overlies that of the dorsal cardo cranial muscle (10a) on the post gena (Fig. 1c) is inserted on the median edge of the base of the lacinia (Fig. 4a).

Movement of the first segment of the maxillary palp is brought about by a long thin protractor muscle (13) that passes from the base of the segment to the stipes, and its antagonist (14) which is short and inserted upon the lateral wall of the stipes (Fig. 1d). Protractor (15) and retractor (16) muscles pass from the base of the first to the base of the second palp segment. The terminal segment is without muscles.

The tip of the lacinia plays an important part in the gathering of food and bears a group of three prongs (Figs. 4a & 3b), two of which are movable, which are described more fully in conjunction with similar structures present in *B. rhodani*. Proximal to these the median edge of the lacinia is strongly sclerotised to support the insertions of two rows of large bristles. Those of the anterior row curve towards the labrum and are finely fringed with bifid tips (Fig. 4c, La. ab). Those of the posterior row curve towards the anterior surface of the labium and are finer and simple with sharp tips (Fig. 4c, La. pb.). The heavy sclerotisation of the bristle insertions is continued as a strengthening strip almost to the base of the lacinia (Figs. 1d & 4c) where the stipes lacinial muscle is inserted.

The movement of the maxilla is not a simple adduction and abduction in a plane transverse to the longitudinal axis of the head, but includes components in the anterior-posterior and dorsal-ventral directions so that the tip traces a complex path. Of the muscles producing adduction the strongest is the stipes adductor (8) whose origin on the tentorium lies anteriorly in relation to its insertion in the maxilla so that there is an anterior component in the movement it produces which is enhanced by the contraction of the dorsal cardinal-cranial muscle (10a). The contraction of the cardo adductor muscle (9) besides producing an anterior movement of the maxilla as a result of the anterior position of its origin relative to its insertion, brings about a straightening of the maxilla and hence a strong ventrally directed movement of the tip. This elongation of the maxilla is a consequence of the looseness of the connection between the cardo and the head capsule and the cardo and the stipes.

Abduction is produced by the contraction of the cranial-lacinial muscle (11) and the ventral cardinal-cranial muscle (10b), there being a strong dorsal component in the movement as a result of the dorsal position of the origins of these muscles in relation to the maxilla.

The labium

Cuticular attachment of the labium to the head capsule occurs by the fusion of the proximal arms of the postmentum with the post-occipital condyles on either side of the occipital foramen (Fig. 1b). A prementum is set at an angle of approximately 90 degrees to the postmentum and bears well-developed glossae and paraglossae that enclose the other mouthparts posteriorly.

The paraglossae are larger than the glossae and curve around them, their bases overlapping those of the glossae posteriorly (Fig. 1 b). A row of short, stout, anteriorly curved bristles extends along the median edge and around the tip of each glossa (Fig. 2d), and the median edges bear a row of 7-8 long straight bristles (Fig. 1b, Pgl. mb) that project over the posterior surfaces of the glossae. Long, fine hairs that presumably serve a sensory function are present on the posterior surface of both glossae and paraglossae. The glossal and paraglossal muscles arise on the distal end of an apodeme (ap) that projects from the posterior wall of the prementum; the glossal protractors (22) being inserted on the anterior edge of the bases of the glossae, and the paraglossal extensors (21) on the lateral edge of the bases of the paraglossae (Fig. 2d).

The labial palps articulate with the postero-lateral surface of the prementum and consist of three segments, the first two being subequal and about twice as long as the third (Fig. 2d). On the dorsal surface of the tip there is a row of stout bristles that increase in length towards the tip and are interspersed with many smaller bristles and hairs; over the rest of the surface of the palp chaetae are very sparsely distributed. No abductor muscle passes to the first segment of the palp, which is provided only with a very small adductor muscle (24) inserted on its lateral wall and arising on the posterior wall of the prementum near the median apodeme. Nearby is the origin of the large abductor muscle (23) of the second segment which is inserted on the lateral edge of the base of this segment. The adductor muscle (25) of the second segment is well developed and arises upon the posterior surface of the first segment. An adductor muscle (26) inserted on the median edge of the base of the third segment arises on the proximal lateral surface of the second segment. It was deduced from the distribution of the muscles, and directly observed in feeding animals, that movement of the labial palp is confined almost entirely to the second and third segments.

Connection between the labium and the hypopharynx in *C. dipterum* is not so close as that described by Strenger in *Ecdyonurus*; two pairs of muscles, the posterior hypopharynx retractor muscles (19 & 20), arise on either side of the apodeme on the floor of the prementum (Fig. 2b) and are inserted on the basal sclerite of the hypopharynx body (Fig. 1d). These are probably homologous with the very large muscles that in *Ecdyonurus* extend from the hypopharynx body to the base of the labial palps (see below). They probably produce retraction of the hypopharynx because during observation of feeding larvae no movement of the base of the labium was seen. Their antagonist is the hypopharyngeal-mandibular muscle (7), which is described in the account of the hypopharynx.

Two pairs of retractor muscles of the prementum (Figs. 2b & d) originate beneath the body of the tentorium on a membrane inflected from the arms of the postmentum; the posterior retractors (17) are inserted on the apodeme and are enclosed within the arms of the postmentum, the anterior retractors (18) are inserted on the anterior edge of the prementum near the base of the palps.

The hypopharynx

In *C. dipterum* the hypopharynx forms the posterior as well as the dorsal wall of the preoral cavity (Fig. 2b). The tip of the thick, median, tongue-like

hypopharynx body (Fig. 4b) is fringed with short fine hairs, and on the anterior surface following the median edge of each superlingua is a row of fine short bristles. A conspicuous row of much larger bristles which are curved towards the median line begins near the base of each superlingua, and the two rows converge and extend, running parallel on the base of the hypopharynx body, as far as the mouth opening. Parallel and median to each of these rows of bristles is a row of hairs that are elevated on a ridge on the hypopharynx base.

The superlinguae (Fig. 4b) are flattened lobes inserted obliquely on the hypopharynx body, their lateral edges being attached at the posterior end of the suspensorial sclerite (sus. s) that supports the base of the hypopharynx body on each side. Each is capable of being pressed closely into a depression on the posterior surface of the mandible body where this is bent towards the preoral cavity, and the cuticle of the lateral edge is thickened at the point of contact (Sl. th). The lacinia fits into the space between the superlinguae and the labium on either side of the head (Fig. 2b)—the relative positions of the mouthparts as they appear in a horizontal transverse section of the head is shown in Fig. 4b. A field of relatively long fine hairs clothes the median surface of the tips of the superlinguae.

Three pairs of muscles are inserted upon the basal sclerite which is present on the posterior surface of the base of the hypopharynx body (Fig. 1d). Of these, two pairs of posterior retractor muscles (19 & 20) that arise on the posterior surface of the prementum have already been described. In addition dorsal retractor muscles (28) are inserted on the lateral basal corners of the sclerite and arise on the membrane inflected beneath the tentorium body from the arms of the postmentum (Figs. 1d & 2b). A hypopharyngeal-mandibular muscle (7) arising on the antero-lateral surface of the mandible (Fig. 1a) is inserted by means of a fine tendon on the lateral edge of the base of the hypopharynx body (Fig. 4b).

It is notable that there are three pairs of muscles (19, 20 & 28) capable of producing retraction of the hypopharynx and only one small pair (7) capable of producing protraction. This disparity indicates that when the muscles are relaxed the hypopharynx lies closely pressed forwards against the mandibles and that after contraction of the retractor muscles it returns to this position as a result of the elasticity of its cuticle and perhaps also the pressure of the internal fluids of the head capsule within the lobes. It is likely that the hypopharyngeal-mandibular muscle is responsible for drawing the hypopharynx tightly against the posterior surface of the mandibles while swallowing takes place.

THE FUNCTIONING OF THE MOUTHPARTS OF CHLOEON DIPTERUM

When feeding upon fine detritus

Both the rate of activity of the mouthparts as a whole and the rate and direction of movement of particular parts in relation to the others varied according to the kind of food being ingested. The mechanism employed when the larvae were feeding upon a fine loose detritus was that most frequently observed in captivity and is described in detail below. A brief account follows

of the ways in which this mechanism is modified to deal with a more aggregated detritus, rotted higher plant tissue, and filamentous algae.

When the head is viewed from the ventral or anterior aspects, it is seen that there is a regular alternation between the mandibles and maxillae in their inward and outward movements. Fig. 7a, 1 shows these mouthparts in the resting position. At the commencement of feeding the laciniae move inwards and the mandible tips move outwards to the position shown in Fig. 7a, 2. The mandibles are then closed and their tips brush against those of the laciniae at position X in Fig. 7a, 3. The mandibles are brought more closely together than in the resting position so that the tip of the left lies anterior to and overlapping that of the right (Fig. 7a, 3). As the mandibles now move apart the laciniae are brought together so that they occupy the position shown in Fig. 7a, 2, and from this position the sequence of movements is repeated at a rate varying from 10 to about 250 times per minute, for periods of up to four minutes.

Food is collected by the activity of the labial palps, laciniae and mandible tips. When fine detritus is provided as food, the labial palps move more quickly than the mandibles and maxillae and perform rapid flicking movements by which food particles caught in the bristles are brushed towards the preoral cavity. They are swept further into the preoral cavity by the laciniae which gather particles directly from the substratum both by means of bristles on the median edge and the terminal claw. The laciniae play the most important part in food collection, the mandibles rarely being used for this purpose when the detritus is fine and loose.

It is impossible to observe directly the mechanism by which fine detritus swept into the preoral cavity by the laciniae is held there and swallowed, and the following account of this process is deduced from the structure of the mouthparts and their known movements. While for descriptive purposes it is assumed that the head is held with its long axis approximately vertical so that the force of gravity is opposing the passage of the food to the mouth opening, this is not the only position in which the larva feeds; larvae have in fact been observed feeding in a great variety of positions and it is probable that the orientation of the head has no effect on the successful functioning of the feeding mechanism.

Each inswinging lacinia passes between the superlingua and the hypopharynx body and food is deposited between the tips of the hypopharynx lobes and the edge of the labrum, (position X Fig. 7b). It is retained in this position when the laciniae withdraw by the bristles of the glossae and the paraglossae, the edge of the labrum, and the fine hairs on the tips of the hypopharynx lobes. As the laciniae withdraw they must pass once more between the superlinguae and the hypopharynx body and any food particles adhering to the bristles are removed, probably mainly by the lateral rows of bristles on the hypopharynx body (Fig. 4b, Hy. b. db.). The hypopharynx is probably retracted when the laciniae move inwards thus enabling them to pass more easily between the lobes and enlarging the preoral cavity to receive the food.

As the mandibles are closed the superlinguae press tightly into the grooves on their posterior surfaces and the hypopharynx as a whole is probably drawn

forwards by the contraction of the hypopharyngeal-mandibular muscles (7). In this way the volume of the ventral part of the preoral cavity would be reduced and the food, being unable to pass ventrally out of the preoral cavity because of the tips of the hypopharynx lobes and the canines of the mandibles, would be forced towards the mouth. Further, the direction of movement of the mandibles as they close is such that the food within the preoral cavity tends to be swept towards the mouth by the canines, hairs, and prosthecae. The fine hairs on the posterior surface of the labrum, being dorsally directed, serve to prevent food particles from falling ventrally. A dark mass of food appears to fill completely the preoral cavity of an actively feeding larva when food is abundant, and it would seem that an important factor tending to force food towards the mouth under these conditions is the pressure of the new food that is continually being introduced into the preoral cavity. Swallowing is probably aided by the closing of the molar surfaces which occupy the dorsal part of the preoral cavity, that of the right mandible projecting slightly into the mouth. The shape of the molar surfaces is such that as they close the intervening space between them is reduced progressively in a ventral-dorsal direction, so that any food lying between them is displaced to the mouth.

It is to be expected, in view of the disturbance of the osmotic properties of the body fluids and the dilution of the digestive enzymes that would result from the ingestion of large quantities of water, that the food is swallowed in a relatively dry condition. This view is supported by the tightness into which food is found to be packed into the foregut of an actively feeding larva. From a consideration of the structure of the molar surfaces it may be concluded that they are adapted to performing a straining as well as the grinding function usually attributed to them. As the mandibles close, water is free to pass between the large bristles of the hypopharynx body and those on the epipharynx, and between the prongs of the left molar surface, but food particles will be retained by these structures. Only when the prongs of the left molar surface have completely overlapped the blade of the right molar surface (Fig. 3f), and no more water can be expelled between them, will the food be subjected to the crushing action of the molar surfaces.

The passage of food consisting of fine detritus to the mouth may be summarised as follows—

1. Food collected by the labial palps, laciniae, and occasionally the tips of the mandibles.
2. Food swept into the preoral cavity by the laciniae, the hypopharynx being retracted.
3. Food retained in the ventral part of the preoral cavity by the bristles or hairs situated on
 - i. the labrum edge.
 - ii. the inner surface of the labrum.
 - iii. the glossae and paraglossae.
 - iv. the tips of the hypopharyngeal lobes.
4. Food forced towards the mouth by the mandibles as they close and the pressure produced by the protraction of the hypopharynx.

5. Food prepared for swallowing by the straining and crushing action of the molar surfaces, being held in position between them by the bristles of the epipharynx and the hypopharynx body.

When feeding upon other food materials

When larvae were feeding upon filamentous algae, aggregated detritus or vascular plant tissue, the mandibles played a more important part in the collection of food than when this was fine detritus. Larvae were observed to bring the tips of the mandibles to bear upon the food by lowering the head, and the small fragments broken off by the canines were brushed into the preoral cavity by the other food collecting appendages. Filaments of algae were drawn continuously into the preoral cavity by deliberate chewing movements of the mandible. On one occasion the mandible tips were seen to actually bite short pieces from a stout filament of *Spirogyra*.

The movements of the other mouthparts in relation to the mandibles during the ingestion of these food materials were the same as those described for the ingestion of fine detritus. It was the rate of movement of the mouthparts as a whole, and the extent to which the mandible tips were used as food collecting organs, that varied with the type of food.

The rate of movement of the mouthparts

The number of complete cycles of inward and outward movements made by the mandibles and maxillae in 30 second periods was counted in several large larvae. Three distinct rates of movement occurred that were correlated with the nature of the food.

In the case of larva feeding upon a coarsely aggregated detritus the deviation from a mean rate of 68 movements/30 secs. was slight, i.e., for five individuals the extreme values observed were 65 and 70 movements/30 secs. Larvae brushing up fine detritus from the surface of the filaments of algae or vascular plants showed a far higher rate of movement that was difficult to count because of its rapidity. It was approximately four times as great as that observed in larvae feeding upon aggregated detritus.

The slowest rates of mouthpart movement, 10-30/30 secs., were recorded when larvae were ingesting filaments of algae.

The part played by the limbs

Larvae climbing amid vegetation or loose detritus were occasionally seen to draw material towards the head with the forelimbs but it is probable that this occurred by chance in the normal process of locomotion. On several occasions larvae were observed to remove material adhering to the bristles of the legs by drawing the leg through the mouthparts in a manner that was reminiscent of the behaviour described in *Habrophlebia lauta* McLach. and *Habroleptoides modesta* Hagen by Pleskot (1953). In *H. modesta* the forelimbs performed sweeping movements, and pieces of detritus caught in the thick field of serrated bristles on the tibiae were passed forwards to the mouthparts by a deliberate movement of the limbs, or held fast by retracting the tibia closely against the femur. Pleskot suggests that the resemblance between the long

hairs upon the fore tarsus and those on the labial palps is the result of parallel adaptation to food collection. None of the limbs of *Chloeon dipterum* bear thick fields of bristles that would be obviously suitable for food collection, and although food may be taken by the mouthparts from the limbs as described above, this is not a regular part of feeding behaviour and appears to be an accidental means of food collection in this species. The prime purpose of the action observed in *C. dipterum* appeared to be to free the limb of encumbering material and the origin of the kind of behaviour described by Pleskot may lie in cleaning actions of this kind.

Autocoprophagy, a phenomenon rarely recorded in insects, was observed in both *Habrophlebia lauta* and *Habroleptoides modesta* by Pleskot. In the former species, faecal pellets were deliberately caught by passing the posterior end of the abdomen through the crook between the tibia and femur of the foreleg and conveyed to the mouthparts. In *H. modesta* pellets were collected by the hind leg and passed forwards to the tibial bristles of the middle leg and thence to the bristles of the fore tibia and the mouthparts. In *C. dipterum* this was not observed but occasionally a larva, irritated by the presence of a particle of detritus on the cerci, would bend the abdomen forwards and quickly brush the cerci against the mouthparts so that the particle was removed. Again, in *C. dipterum* there appeared to be a possible origin of behaviour far more highly developed in other species of ephemeropteran larvae.

THE MORPHOLOGY OF THE MOUTHPARTS OF *BAETIS RHODANI*

The head capsule

In general appearance the head capsule of *B. rhodani* resembles that of *C. dipterum*, differing from it mainly in the relative proportions of various parts and in the generally greater sclerotisation of the cuticle. The ocelli and antennae are situated more ventrally so that the upper part of the head capsule consists of a large expanse of smoothly curved vertex and is well adapted to present only slight resistance to flowing water (Fig. 5a). Adaptation to the same end is seen in the posterior wall of the capsule which is hollowed so that the margins slightly overlap the prothorax and the head and thorax together present a streamlined shape to the water.

As in *C. dipterum* only coronal, frontal, and epistomal sutures are visible and there is no definite boundary between the frons and the lower part of the gena and between the posterior part of the vertex and the occiput (Figs. 5a & 6b). Muscles inserted on the mouthparts are attached to the head capsule in similar positions in the two species. The dorsal arm of the tentorium is attached to the cranium in a more ventral position in *B. rhodani*.

The clypeo-labral lobe

The labrum is relatively narrower than that of *C. dipterum* but it forms an effective anterior wall to the preoral cavity because of the elongated and tapered shape of the distal parts of the mandibles and maxillae. The posterior surface of the labrum is strongly concave and as a result of the thickening of the cuticle of the outer wall, particularly at the edges, it is difficult to bend the labrum away from the preoral cavity.

Well-developed tormae (Fig. 6e) support an epipharyngeal surface that bears long bristles arranged in two asymmetrical rows. The longer arms of the tormae are asymmetrical in correlation with these bristle rows which merge into fields of short fine bristles that extend to cover a median raised area on the surface of the labrum. On either side of the apex of the posterior surface of the labrum is a field of medianly directed hairs.

The bristles of the labrum edge are distributed in three rows (Fig. 8f); a row of simple bristles on the lateral edges extends on to the anterior surface, basally the bristles of this row are interspersed with fringed bristles which are confined to the edge and are situated nearer the posterior surface, apically these are succeeded by stouter fringed bristles that are set close together beneath a flange of cuticle.

The labrum protractor muscles (2) arise on the frons ventral to the median ocellus and are inserted basally on the outer wall of the labrum. Retractor muscles (1) arise on the frons on either side of the protractors and are inserted by fine tendons on the shorter arms of the tormae.

The mandibles

The tip of the mandible is more tapered than in *C. dipterum*, and the straight canines project towards the substratum rather than into the preoral cavity (Fig. 5d). The inner canine is composed of several blunt teeth but the outer shows only traces of subdivision. Asymmetrical prosthecae are present, that of the left mandible bearing four blunt teeth and three long bristles while that of the right is comparatively slender and terminates in a cluster of fine hairs (Fig. 5d).

Three groups of muscle fibres, originating on the frons (6a), the vertex (6b) and the occiput (6c), form the dorsal adductor muscle (Figs. 5a & 6b). Three groups of tentorial adductor muscle fibres (5) originate on the body and base of the dorsal arm of the tentorium and are inserted on the lateral surface of the mandible. Two cranial abductor muscles (3a & 3b) arising on the gena and post gena respectively (Figs. 5a & 6b), are inserted on the mandible base just posterior to the lateral articulation, and two tentorial abductors (4) that arise on the base of the anterior tentorial arms are inserted on the mandible anterior to the posterior articulation.

On examination of the anterior surface of the right mandible, the edge of the molar surface is seen to consist of a blade of heavily sclerotised cuticle similar to that of *C. dipterum*, beyond which project the tips of blunt tubercles (Fig. 7c). These are the biggest of the large number of tubercles of cuticle that cover the whole of the molar surface, increasing in size towards the posterior edge where they are arranged in rows (Fig. 7d). A few sharp spines are present at the end of some of the rows in the same position as they occur in *C. dipterum*.

The anterior edge of the left molar surface consists of a row of curved prongs (Fig. 7e), resembling those of *C. dipterum* but lacking ridges and spatulate tips. Large numbers of tubercles of cuticle cover the adoral part of the surface, and there is a row of sharp bristles on the posterior edge (Fig. 7f). A large blunt peg occupies a similar position as in *C. dipterum*,

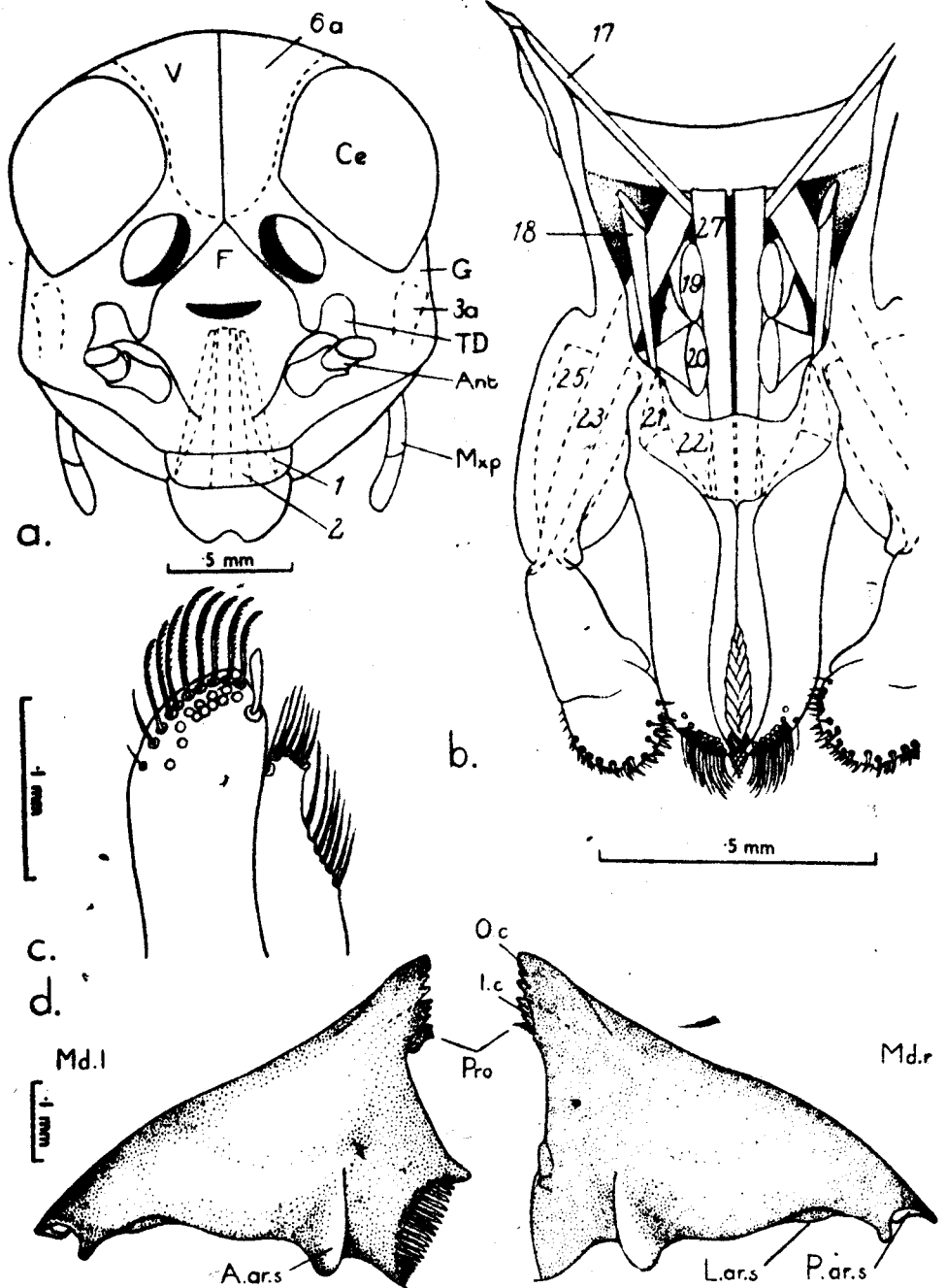


Fig. 5.—*Baetis rhodani*

a. Head capsule, anterior surface ; b. Labium, anterior surface ; c. Tips of glossae and paraglossae. Anterior surface (only the distal row of paraglossal bristles shown) ; d. Left and right mandibles, anterior surfaces. (Key to lettering, p. 175.)

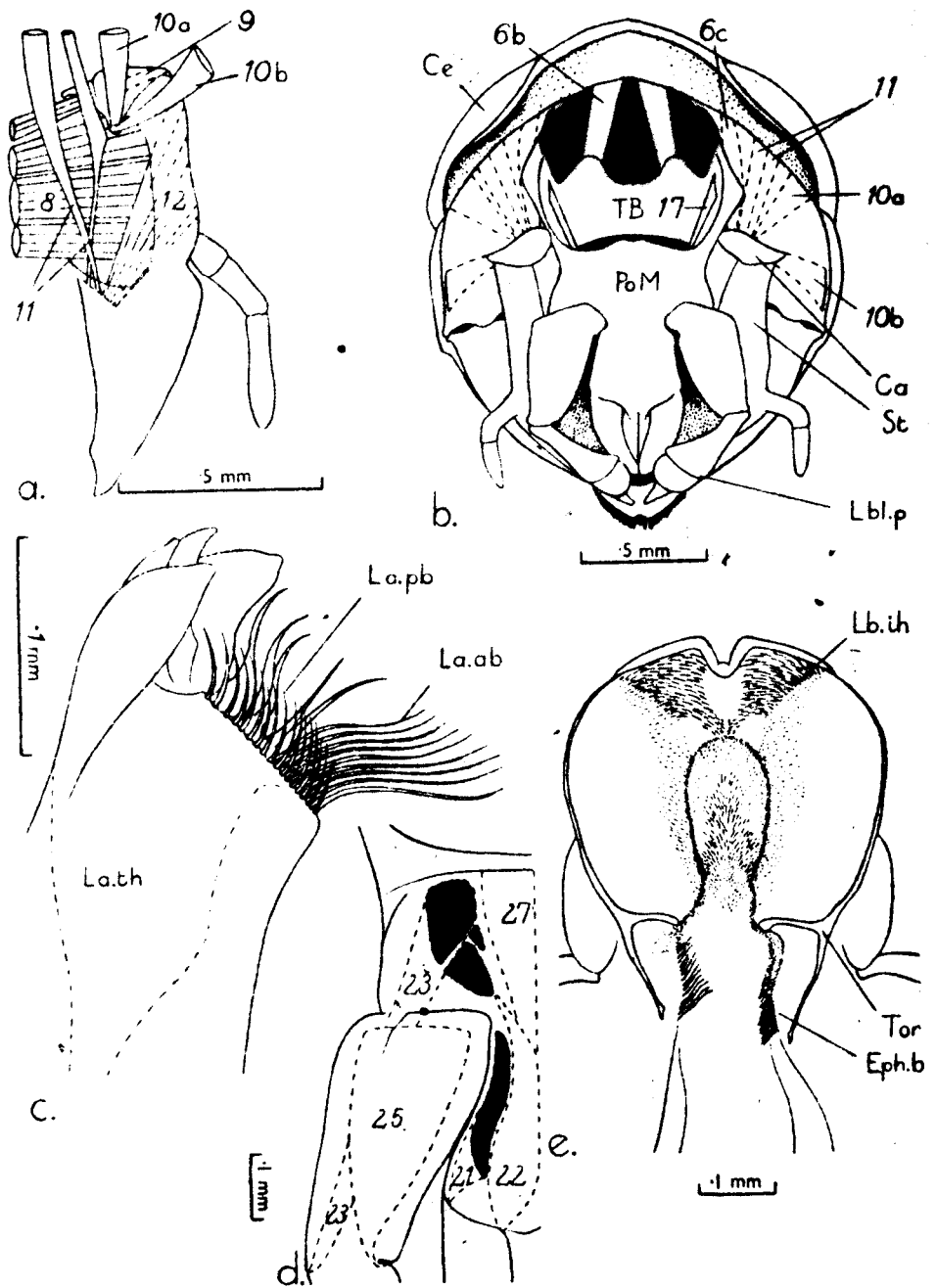


Fig. 6.—*Baetis rhodani*

a. Left maxilla, anterior surface; b. Head capsule. Posterior surface, oesophagus and cervical muscles removed; c. Tip of lacinia. Oblique view of posterior surface; d. Labium. Posterior view, including the basal segment of the palp showing the distribution of the muscles; e. Clypeo-labral lobe, posterior surface. (Key to lettering, p. 175.)

and when the mandibles are closed projects over the edge of the right molar surface, probably serving the purpose of limiting the tightness with which the mandibles are closed and preventing damage to the molar surfaces by their being ground together.

The maxillae

The body of the maxilla (Fig. 6a), which is more compact and tapered than that of *C. dipterum* is articulated to the head capsule in a similar manner by the proximal part of the subdivided cardo.

Two rows of bristles are present on the lacinia tip (Fig. 6c). Those of the posterior row are simple, but of the anterior row only the three large distal bristles are bifid and fringed as in *C. dipterum*, the remainder being slender and relatively far longer.

In *B. rhodani* each lacinia terminates in four claw-like prongs (Figs. 8a & c) resembling the three that occur in *C. dipterum*, of which that arising from the posterior surface (1) is immovable, its heavily sclerotised cuticle being continuous with the thick strip in the posterior wall of the lacinia (Fig. 6c, La. th. Fig. 8a, P.th). Of the movable prongs, that on the anterior surface of the lacinia tip (4) is the largest and its rounded base articulates with a slight thickening in the anterior wall of the lacinia (Fig. 8a, a.th). The two lateral prongs (2 & 3) are smaller with less heavily sclerotised cuticle which is continuous with that of the lacinia so that there is no definite articulation at their bases. When the claw of the lacinia is closed the two lateral prongs fit closely together between the anterior and posterior prongs so that the tip of the lacinia is scoop shaped (Fig. 8e).

The functioning of the tip of the lacinia, which in appearance resembles certain types of mechanical grab, depends on the elasticity of the cuticle at the bases of the prongs, as there are no muscles present in the distal part of the lacinia. While the maxilla is inactive the prongs are closed but as the lacinia is brought to bear on the substratum the pressure causes them to splay open. When the lacinia is retracted they close again and tend to grip any material that has been dislodged from the substratum which is then conveyed towards the preoral cavity. In *C. dipterum*, while the cuticle of the posterior immovable prong (1) is continuous with the thickening in the posterior wall of lacinia as in *B. rhodani* (Fig. 8b), the two other prongs (2 & 3) can move and a similar scoop-like structure can be formed. There is, however, no clearly demarcated articulation between the bases of either of these movable prongs and the lacinia as is present at the base of the anterior prong in *B. rhodani*. It is possible that the three prongs of *C. dipterum* are homologous with the posterior and lateral prongs of *B. rhodani* and that the anterior prong in this species should be regarded as a greatly enlarged bristle of the anterior row on the lacinia tip. This bristle (Figs. 4a & 8b, 4) is very large in *C. dipterum* and closely associated with the terminal prongs.

The arrangement of the muscles in the maxilla closely resembles that in *C. dipterum* and produces a similarly complex movement. Stipes and cardo adductor muscles (8 & 9) arise on the lateral surface of the tentorium body and base of the anterior tentorial arm and are inserted on the postero-lateral surface

of the maxilla (Fig. 6a). Two parts of the cardinal-cranial muscle, arising on the dorsal (10a) and the lateral (10b) parts of the post gena (Fig. 6b), are inserted on the inflected distal part of the cardo (Fig. 6a). The cranial-lacinal muscle (11) is relatively more strongly developed than in *C. dipterum*, it is divided into two parts arising on the dorsal wall of the post gena (Fig. 6b) and inserted by fine tendons on the anterior edge of the base of the lacinia (Fig. 6a). A well developed stipital-lacinal muscle (12) is present although the possible movement between the stipes and lacinia appears to be very slight.

When fully extended the maxillary palp does not extend to the tip of the lacinia, being relatively shorter than that of *C. dipterum*, which it resembles in bearing a few short hairs only. The first and second segments are provided with protractor and retractor muscles that are uncrossed as in *C. dipterum*.

The labium

The glossae, paraglossae, and the prementum (Fig. 6b) are relatively longer than in *C. dipterum*, and, as a result of the posterior inclination of the mouth-parts, the angle between the postmentum and the prementum is not so acute. There is close contact between the narrow glossae and the hollowed median edges of the paraglossae (Figs. 5b & c). The median edges and tips of the glossae bear long bristles, and stouter medianly curved bristles are distributed on the anterior surface of the tips of the paraglossae in three rows (Fig. 5c). A magnification of $\times 950$ reveals a fine fringe on these bristles. One bristle situated on the median edge of the tip of the paraglossa is sharply differentiated from the others being short and stout with a blunt tip (Fig. 5c). No such structure is present in *C. dipterum* and the significance of its occurrence in *B. rhodani* is at the present time obscure. Well developed muscles (Fig. 6d) pass from the prementum to the glossae (22) and paraglossae (21). As a result of the lateral position and small area of their insertions these muscles must produce a movement of extension rather than protraction which appears to be their function in *C. dipterum*. No antagonistic muscles are present and the elasticity of the cuticle must be presumed to play an important part in the functioning of the glossae and paraglossae.

The labial palps are articulated to the lateral posterior surface of the prementum (Figs. 6b & d). Their bases are stouter than those of *C. dipterum*. The third segment is rounded, and its articulation with the second segment is incomplete; distally it bears many fine hairs and curved bristles (Fig. 5b). There is no trace of either the small adductor muscle (24) of *C. dipterum* or of a muscle passing from segment two to segment three. The movement of the palp is brought about entirely by the abductor (23) and adductor (25) muscles, inserted on the base of the second segment and arising on the posterior wall of the prementum and the posterior base of the first segment of the palp respectively (Fig. 6d).

Two posterior hypopharynx retractor muscles (19 & 20), inserted on the basal sclerite of the hypopharynx body, arise on the posterior wall of the prementum as in *C. dipterum* (Fig. 5b).

Posterior (17) and anterior (18) prementum retractor muscles are inserted on the prementum in similar positions as in *C. dipterum* but the former arises

on the posterior surface of the tentorium body (Fig. 6) and does not pass beneath it.

A pair of muscles (27) which is absent in *C. dipterum* arises on the basal posterior surface of the prementum and is inserted close to the bases of the glossae (Fig. 5b). The cuticle of the prementum is not strongly sclerotised and the contraction of these large muscles probably produces an anterior movement of the distal part of the labium relative to the base which presses it closely against the other mouthparts.

The hypopharynx

A well developed hypopharynx is present consisting of a tongue like body and lateral superlinguae, which are elongated in comparison with those of *C. dipterum* and are more densely covered with chaetae (Fig. 8d).

Almost the entire anterior surface of the distal part of the hypopharynx body is occupied by fields of hairs, of greatest length and density near the tip, that converge upon the mid-line and are directed towards the mouth. Proximally there are two rows of stout medianly curved bristles, with parallel rows of fine hairs, that are very similar to those of *C. dipterum*.

The cuticle of the lateral edges of the superlinguae is relatively heavily sclerotised proximally where the superlinguae fit closely against the posterior surfaces of the mandibles as in *C. dipterum*. Their tips bear a dense field of fine hairs.

Two posterior retractor muscles (19 & 20), that have already been described, are inserted on the basal sclerite of the hypopharynx body on the corners of which are inserted a pair of dorsal retractor muscles (28) arising beneath the body of the tentorium. As in *C. dipterum* a hypopharyngeal-mandibular muscle (7) passes from the suspensorial sclerite in the lateral edge of the hypopharynx body to the lateral wall of each mandible.

THE FUNCTIONING OF THE MOUTHPARTS OF *BAETIS RHODANI*

The movements of the mouthparts closely resembled those of *C. dipterum* in that the mandibles and maxillae performed regular alternating movements and food was collected by the labial palps, laciniae, and mandible tips.

In general the rate of movements was slower than in *C. dipterum* and at all times the mandibles were brought to bear upon the food. Larvae of *B. rhodani* were observed feeding upon detritus and a mixture detritus and diatoms adhering to the surfaces of stones, but could not be induced to feed upon filamentous algae. On no occasion did larvae brush up fine detritus solely by means of the labial palps and the laciniae as frequently occurred in *C. dipterum*.

The greater importance assumed by the mandibles in food collection in *B. rhodani* is probably necessitated by the difficulty of dislodging particles of detritus and diatoms from the surface of stones in streams. The crouching stance assumed by larvae of *B. rhodani* when feeding serves to thrust the mouthparts close against the substratum, as well as preventing the animal being swept away by the current.

THE RELATIONSHIP OF THE DIFFERENCES IN THE MOUTHPARTS BETWEEN
C. DIPTERUM AND *B. RHODANI* WITH THEIR HABITATS

There are a few differences between the mouthparts of *C. dipterum* and *B. rhodani* of which the functional significance is not clear, but the majority of the morphological characteristics of *B. rhodani* are consistent with the overall adaptation of this species to flowing water.

Larvae of the genus *Baetis* are among the most active of the insect larvae occurring in flowing water, they are frequently seen on the tops of stones, swim rapidly when disturbed, and rely on their stream-lined shape to keep them from being swept away down stream. The effects of streamlining on the head capsule are seen in the ventral positions of the antennae and ocelli, the large expanse of smoothly curved vertex, and the indentation of the posterior wall of the capsule so that the edges overlap the prothorax.

Three different effects of streamlining appear in the structure of the mouthparts. Firstly, the surface area of the distal parts of the mandibles and maxillae is reduced by their tapered shape; the glossae, paraglossae, and the hypopharynx body being correspondingly elongated to form an effective posterior wall to the preoral cavity. Secondly, a reduction of bristles and hairs in places where they are not essential for retaining food particles is seen in the glossae and paraglossae which, apart from their tips, are devoid of chaetae. Reduction of the length and mobility of the appendages so that they do not move outside the area sheltered by the front margin of the head is a third means whereby the resistance offered to the water by the mouthparts is reduced, and is characteristic of the extremely flattened forms of mayfly larvae; such adaptation is present in *B. rhodani* in the shortness of the labial and maxillary palps and the absence of a muscle in the third segment of the former.

The body of an animal living in flowing water is exposed for most of its life to physical stresses that are absent in a pond, and the general appearance of the head capsule of *B. rhodani* is more robust than that of *C. dipterum*, the sclerotisation of the cuticle, particularly of anterior surface and edges of the labrum, being relatively greater. The glossae and paraglossae fit far more closely together than in *C. dipterum* and are supported by wide bases, those of the paraglossae overlapping those of the glossae posteriorly, so that they are not easily forced away from the preoral cavity. It is likely that the pair of muscles (27), present in the prementum of *B. rhodani* and absent in *C. dipterum*, is a further adaptation to strengthen the labium and brace it against the preoral cavity.

Besides the direct effect described above, flowing water exerts an indirect influence on mouthpart morphology through the effect it has in the food both before and after this is collected. Encrusting organisms are firmly attached to the substratum in a stream and detritus is confined to small crevices where the flow is at all rapid. The mechanical difficulties of food collection are thus greater than in a still water habitat and even when material has been dislodged it may be swept away by the current before reaching the mouth. Several of the details in which the mouthparts of the two species differ appear to be correlated with these difficulties. The blade-like outer canine of *B. rhodani* is better fitted to dislodge epilithic algae and encrusting particles than the sharp

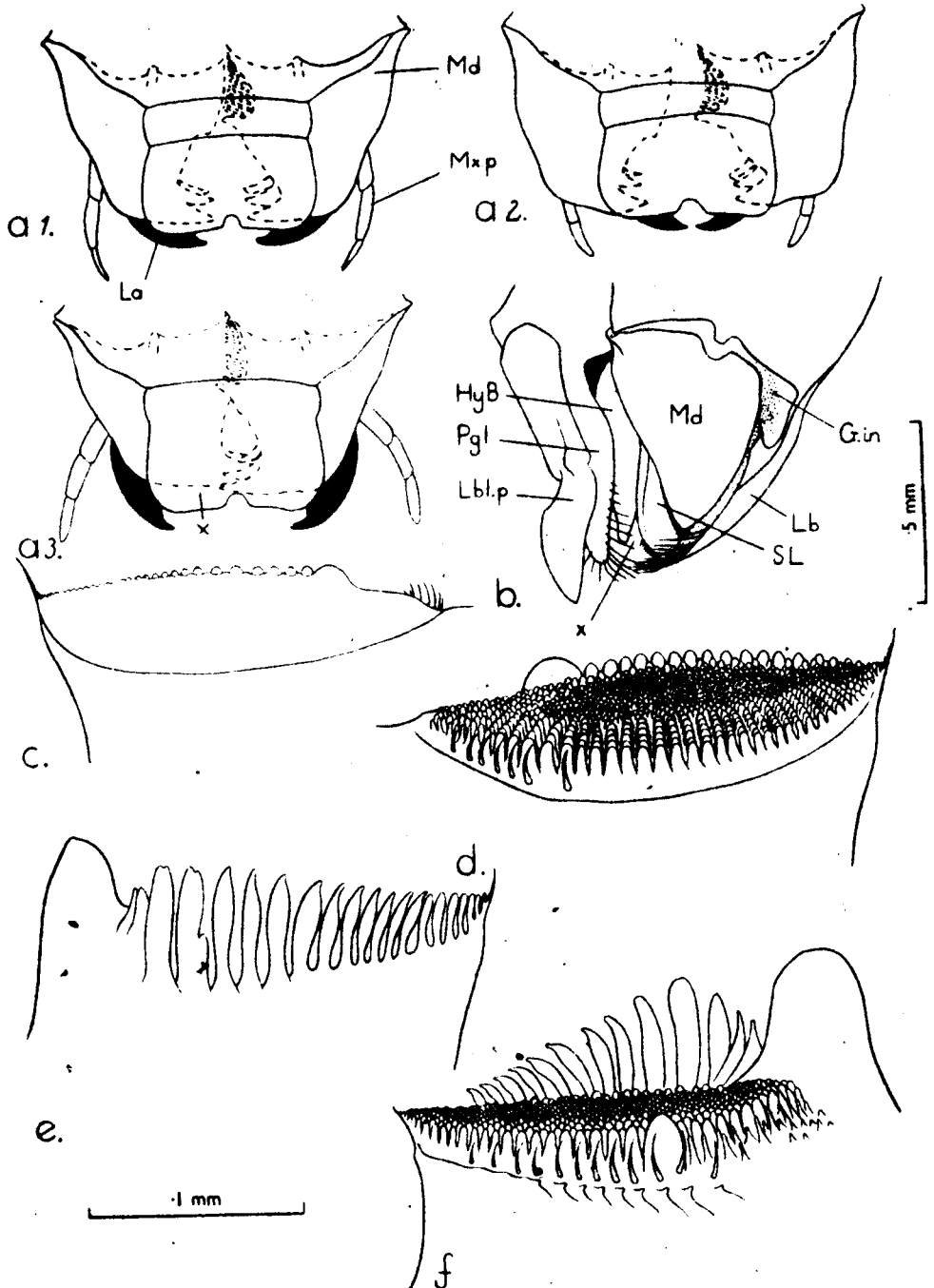


Fig. 7.—*Chloeon dipterum* and *Baetis rhodani*
 a. 1-3. *C. dipterum*. Diagrams of the movements of the mandibles and maxillae. The outline of the mandibles is shown through the clypeo-labral lobe and the ventral part of the anterior surface of the head capsule; b. *C. dipterum*. Lateral view of the mouthparts, right maxilla removed; c. *B. rhodani*. Right molar surface, anterior edge; d. *B. rhodani*. Right molar surface viewed obliquely from the posterior surface of the mandible; e. *B. rhodani*. Left molar surface, anterior edge; f. *B. rhodani*. Left molar surface, viewed obliquely from the posterior surface of the mandible. (Key to lettering, p. 175.)

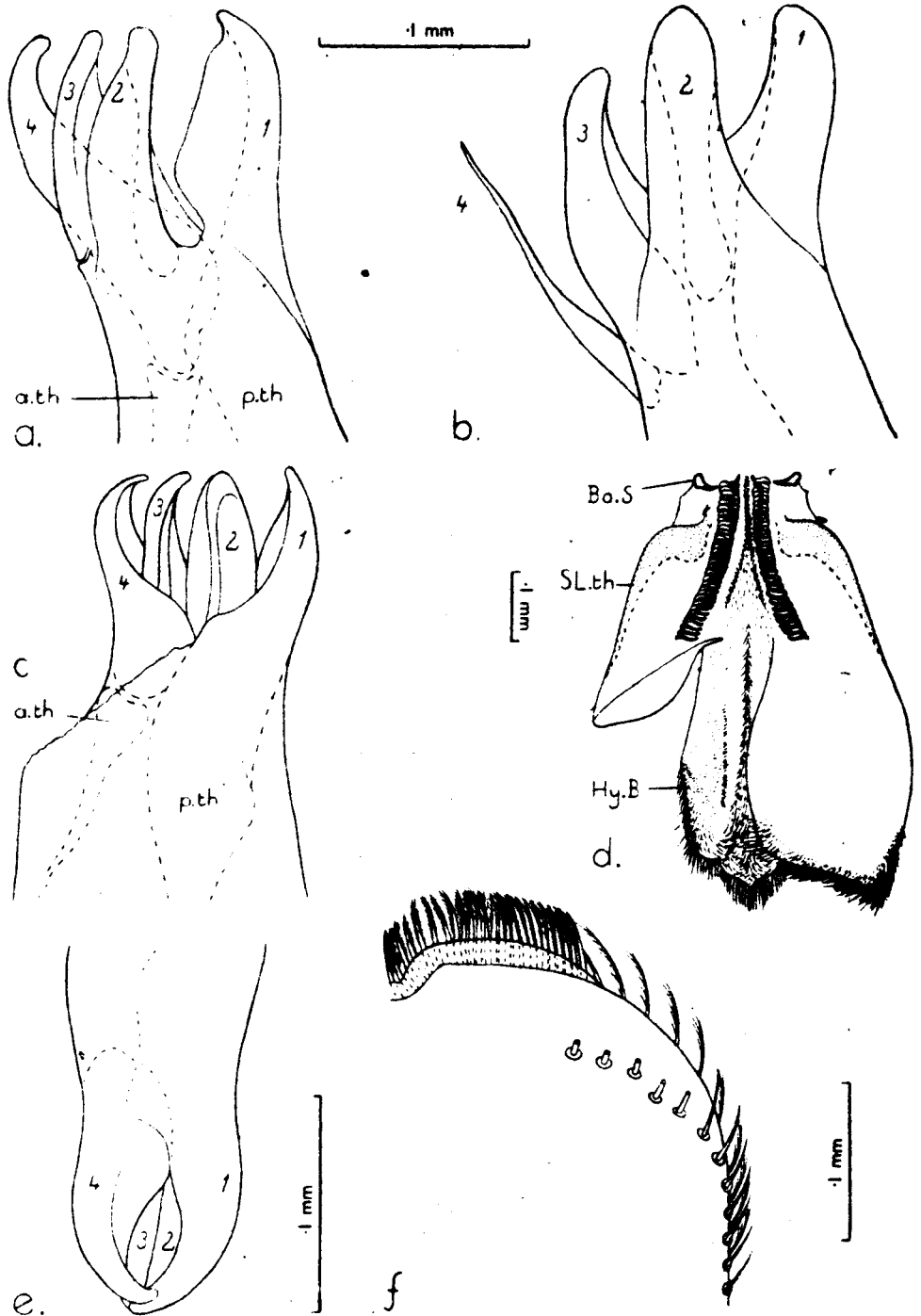


Fig. 8.—(a, c, e, f) *Bactis rhodani*; (b) *Chloeon dipterum*

a. Lacinia tip. Lateral view, prongs open; b. *C. dipterum*. Lacinia tip. Lateral view, prongs open; c. Lacinia tip. Median view, prongs open (bristles omitted); d. Hypopharynx. Anterior surface, right superlingua removed; e. Lacinia tip. Median view, prongs closed; f. Labrum. Posterior view of edge. 1. Posterior prong of lacinia tip; 2 & 3. Lateral prongs of lacinia tip; 4. Anterior prong of lacinia tip (*B. rhodani*). Distal bristle of anterior row (*C. dipterum*). (Key to lettering, p. 175.)

points of the subdivided outer canine of *C. dipterum*. A lacinia with a greater number of more mobile prongs and longer bristles would also serve as a more efficient food collecting organ under these conditions. Greater complexity and strength in the molar surfaces, particularly the presence of large numbers of tubercles of cuticle, may be regarded as adaptation to the more gritty and finely particulate food that is deposited by flowing water. Adaptation to the function of retaining food within the preoral cavity is present in *B. rhodani* in the form of the thick chaetation in the anterior surfaces and tips of the hypopharynx lobes and the inner surface of the labial-epipharyngeal lobe. Similarly the bristles of the labrum edge, glossae, and paraglossae of *B. rhodani* are well adapted to prevent the loss of food particles from the preoral cavity, being relatively longer and more closely set together than in *C. dipterum*. Further, the fringing of the labral bristles is thicker and a fringe is present on the paraglossal bristles that are simple in *C. dipterum*.

DISCUSSION

The feeding mechanisms described provide several examples of the importance of the elasticity of the cuticle in the relationship between the skeleton and the muscles in insects. This is seen particularly in the labium and hypopharynx where several muscles act singly with no antagonists, and in the functioning of the movable prongs on the tip of the lacinia in which no muscles at all are present. Structures similar to the prongs described on the lacinia of *C. dipterum* and *B. rhodani* are also present in the closely related genus *Centroptilum* and are obviously a suitable adaptation of mayfly larvae in which the tips of the mouthparts are used to collect food. However, the only other genera, of which figures of the lacinia have been examined, in which similar structures occur are *Epeorus* (Lestage 1921, after Eaton) and *Iron* (Morgan, 1911) of the family Heptageniidae. These are both flattened forms and their mouthparts resemble those of *Ecdyonurus*, the surfaces of the maxillary and labial palps being greatly enlarged as food collecting organs. The lacinial prongs of *Epeorus* and *Iron* differ from those of *Chloeon* and *Baetis* in being borne on a separate process apparently articulated to the tip of the lacinia, and it is probable that they have been acquired independently in the Baetidae and the Heptageniidae, functioning in different ways in the two families.

Many specimens of *C. dipterum* and *B. rhodani* approaching ecdysis showed marked signs of wear in the molar surfaces. Very few other examples of mechanical deterioration of the hard parts have been recorded in invertebrates. Those occurring in mature animals, where they are an aspect of senescence, have been reviewed by Comfort (1954). It is probable that the efficiency of the feeding apparatus in *C. dipterum* and *B. rhodani* is impaired in aged larvae of each instar.

Murphy (1922) attempted to group the molar surfaces of larval Ephemeroptera into three types, and describes rounded and knobbed transverse ridges as the prevailing type among the Baetinae that inhabit streams with sand or gravel bottoms. The molar surfaces of *B. rhodani* differ from this description in the presence of a multitude of tubercles and conspicuous processes on the anterior edge of the left surface. It is probable that future work will show

Murphy's classification to be far too simple. The molar surfaces of *B. rhodani* and *C. dipterum* show constant differences in the details of their structure, which can be partly explained by reference to the composition of the diet, and further study may reveal precise specific correlation between the morphology of the molar surfaces and the diet in many species of ephemeropteran larvae. Such specialisation will be most obvious in those forms in which the food is relatively homogeneous. For example, the laciniae of several flattened rapid water genera are equipped with stout comblike bristles that are adapted to rake up the diatoms that form the major part of the food, e.g., *Ameletus* (Schoenemund 1930), *Stenonema pulchellum* (Trama, 1957) and *Rhithrogena* (Strenger, 1953). The feeding mechanism of *C. dipterum* and *B. rhodani* is adapted to allow the ingestion of a heterogeneous diet in a wide variety of habitats, and hence structures that can be related to the ingestion of a particular food component are absent.

The study of the feeding mechanism of *C. dipterum* and *B. rhodani* has added to the already great diversity of mouthpart morphology described in larval Ephemeroptera, and, as a result of combining dissection with direct observation of the feeding mechanism, it has been possible to establish or suggest the functional significance of many anatomical features. In view of this it seems likely that similar studies of more species will result in a general understanding of the morphology and functioning of the feeding apparatus within the Order, and of the ways in which the various mechanisms have been evolved from each other. When such an understanding is possible it will probably provide useful evidence concerning the phylogeny of recent mayflies. It is reasonable to suppose that the feeding apparatus of *C. dipterum* and *B. rhodani* most closely resembles that from which other mechanisms developed, because the orthopteroid appearance of the head and mouthparts in these genera is that which would be expected in the ancestral mayfly stock, and occurs in *Pthartus*, a larva described from the Permian by Handlirsch (1918) that closely resembles a modern baetine larva.

ACKNOWLEDGMENTS

This work was carried out while I held a Department of Scientific and Industrial Research Studentship in the University of Leicester under the supervision of Professor H. P. Moon to whom I am grateful for much stimulating discussion. I am grateful to Dr D. S. Guthrie for his criticism of the text.

REFERENCES

- MEYER, F. (1953). *The anatomy of the migratory locust*. London.
- BROWN, D. SEYMOUR (1959). The food and feeding mechanism of *Chloeon dipterum* L. and *Baetis rhodani* Pictet. Ph.D. Thesis, University of London, 1959.
- COMFORT, A. (1954). Biological aspects of senescence. *Biol. Rev.* **29** : 284-329.
- DENN, D. B. (1954). The feeding habits of some fish and other members of the bottom fauna of Llyn Tegid (Bala Lake) Merioneth. *J. Anim. Ecol.* **23** : 233-242.
- HANDLIRSCH, A. (1918). Fossile Ephemeridenlarven aus dem Bundsandstein der Vogesen. *Verh. Zool. Bot. Ges.* **78** : 112-114.
- LAMPERT, K. (1899). *Das Leben der Süßwasser*. Leipzig.

- LESTAGE, J. A. (1921). Ephemeroptera. *Les larves et nymphes aquatiques des insectes d'Europe*, ed. E. Rousseau. Brussels.
- MACAN, T. T. (1950). Descriptions of some nymphs of the British species of the genus *Baetis* (Ephem.). *Trans. Soc. Brit. Ent.* 10 : 143-166.
- MORGAN, A. H. (1911). Mayflies of Fall Creek. *Ann. ent. Soc. Amer.* 4 : 93-114.
- MORGAN, A. H. (1913). A contribution to the biology of mayflies. *Ann. ent. Soc. Amer.* 6 : 371-413.
- MURPHY, H. (1922). Notes on the biology of some of our N. American species of mayflies. *Bull. Lloyd Lib. (Ent.)* 22 : 1-46.
- NEEDHAM, J., TRAYER, J. & HSU, Y. (1935). *The biology of mayflies*. New York.
- PICTET, E. I. (1843). *Histoire naturelle des insectes Neuroptères. Ephémérides*. Paris.
- PLESKOT, G. (1953). Zur Ökologie der Leptophlebiiden. *Öst. zool. Z.* 4 : 45-107.
- SCHOENEMUND, E. (1930). Eintagsfleigen. *Tierwelt Dtsch.* 19.
- SNODGRASS, R. E. (1935). *Principles of insect morphology*. New York.
- SNODGRASS, R. E. (1951). *Comparative studies on the head of mandibulate arthropods*. New York.
- STRENGER, A. (1953). Zur Kopfmorphologie der Ephemeridenlarven 1. *Ecdyonurus & Rithrogena*. *Öst. zool. Z.* 4 : 191-228.
- TRAMA, F. B. (1957). The transformation of energy by an aquatic herbivore *Stenonema pulchellum* (Ephem.). Ph.D. thesis. University of Michigan.
- UENO, M. (1954). Mayfly nymphs. *Scientific results of the Japanese Expeditions to Nepal Himalaya 1952-1953*. Kyoto.

KEY TO THE LETTERING TO FIGURES

A.ar.s	Anterior articular surface of mandible.	La	Lacinia.
Ant	Antennal base.	La.ab	Anterior bristles of lacinia.
Ap	Apodeme of posterior wall of postmentum.	La.pb	Posterior bristles of lacinia.
Ba.S	Basal sclerite.	Lb.eb	Bristles on edge of labrum.
bl.	Blade of right molar surface.	Lb.ih	Hairs on inner surface of labrum.
Ca.	Cardo.	Lb.n	Median notch in edge of labrum.
Cad	Distal part of cardo.	Lb.p	Labial palp.
Ce	Compound eye.	Lbr.	Labrum.
Ca. in	Inflected portion of distal part of cardo.	M.Oc	Median ocellus.
Clp	Clypeus.	Md.h	Mandibular hairs.
Cp.p	Posterior wall of head capsule.	Md.l	Left mandible.
Cp. cut.	Cut edge of head capsule.	Md.r	Right mandible.
Ca	Coronal suture.	Mx.	Maxilla.
Cap	Proximal part of cardo.	Mxp	Maxillary palp.
Eph	Epipharyngeal surface.	O.c	Outer canine.
Eph.b	Epipharyngeal bristles.	Oc.l	Left ocellus.
Es	Epistomal suture.	Occ	Occiput.
F	Frons.	Occ.f	Occipital foramen.
Fs	Frontal suture.	P.ar.s.	Posterior articular surface.
G	Gena.	pb.	Bristles on the terminal segment of the labial palp.
G.in	Inflected edge of gena.	PG.	Post gena.
Gl	Glossa.	Pgl.	Paraglossa.
HyB	Hypopharynx body.	Pgl.mb.	Paraglossal bristles.
Hy.B.db.	Lateral bristles of hypopharynx body.	Ph	Pharynx.
Hy.B.pb.	Proximal bristles of hypopharynx body.	Pocc.ed	Postoccipital condyles.
I.o	Inner canine of mandible.	Pocc.s	Postoccipital suture.
L.ar.s	Lateral articular surface.	PoM	Postmentum.
		PoM.a.	Posterior arm of postmentum.
		PoOcc.	Postocciput.
		Pr.M.	Prementum.
		Pro	Prostheca.

Pro.c	Preoral cavity.	t	Tendon of dorsal adductor muscle (6) of mandible.
r	Ridge at distal end of anterior tentorial arin.	TA	Anterior arm of tentorium.
SL	Superlingua.	TB	Body " "
SL.h	Fine bristles on tips of superlinguae.	TD	Dorsal arms " "
SL.th	Thickened edge of superlingua.	TP	Posterior " "
Sog	Suboesophageal ganglion.	Tor	Torma.
St	Stipes.	V.	Vertex.

KEY TO THE NUMBERS USED TO DENOTE MUSCLES IN THE FIGURES AND TEXT

1. Labrum retractor.
2. Labrum protractor.
3. Cranial abductor of mandible.
4. Tentorial abductor of mandible.
5. Tentorial adductors of mandible.
6. Dorsal adductors of mandible.
7. Hypopharyngeal-mandibular.
8. Stipes adductor.
9. Cardo adductor.
10. Cardinal-cranial.
11. Cranial-lacinal.
12. Stipital-lacinal.
13. Adductor of 1st segment of maxillary palp.
14. Abductor of 1st segment of maxillary palp.
15. Adductor of 2nd segment of maxillary palp.
16. Abductor of 2nd segment of maxillary pulp.
17. Posterior retractor of prementum.
18. Anterior " " "
19. Dorsal posterior retractor of hypopharynx.
20. Ventral posterior retractor of hypopharynx.
21. Extensor of paraglossa.
22. Protractor of glossa.
23. Abductor of 2nd segment of labial palp.
24. Abductor of 1st segment of labial palp.
25. Adductor of 2nd " " " "
26. Adductor of 3rd " " " "
27. Protractor of the prementum.
28. Dorsal retractor of hypopharynx.