# Functional morphology of the feeding apparatus of the nymph of *Farrodes* sp. (Ephemeroptera: Leptophlebiidae)

C. M. Polegatto and C. G. Froehlich

Department of Biology, FFCLRP, University of São Paulo, 14040–901, Ribeirão Preto, SP, Brazil

#### **Keywords:**

functional morphology, mouth parts, insect muscles, Ephemeroptera nymphs

Accepted for publication: 3 October 2000

#### **Abstract**

Polegatto, C. M. and Froehlich, C. G. 2001 Functional morphology of the feeding apparatus of the nymph of *Farrodes* sp. (Ephemeroptera: Leptophlebiidae). — *Acta Zoologica* (Stockholm) **82**: 165–176

Farrodes nymphs are specialized periphyton/biofilm scrapers. Their maxillae are the most specialized mouthparts, but other elements, with their systems of variously modified setae, are designed to obtain and transport food particles to the pharynx with a minimum of loss. The morphology and adaptations of these mouthparts and related head areas, as well as associated musculature, are described.

Cleber M. Polegatto and Claudio G. Froehlich. Department of Biology, FFCLRP, University of São Paulo, 14040–901, Ribeirão Preto, SP, Brazil. E-mail: cgfroeh@usp.br

# Introduction

The majority of ephemeropteran nymphs inhabit lotic waters and are either collectors or scrapers in feeding strategy, although some are predators and a few are shredders (Edmunds *et al.* 1976; Merritt and Cummins 1996). The family Leptophlebiidae is cosmopolitan in distribution, but in the Neotropics they are represented by the Gondwanian subfamily Atalophlebiinae (Savage 1987).

The mouthparts of Ephemeroptera, as well as those of other insects, are commonly illustrated in taxonomical descriptions, but discussions on their functional morphology are scarce. Here an analysis of the morphology of ephemeropteran nymphal mouthparts, their associated muscles and relationship to the head as a whole are presented for a species of *Farrodes*, an atalophlebiine leptobhlebiid. This genus may serve as a model for understanding the feeding of other Atalophlebiinae nymphs and our study may help to understand the evolution of the family, in addition to complementing studies on functional morphology made by earlier authors (Snodgrass 1935, 1952; Grandi 1940; Strenger 1954; Brown 1961; Froehlich 1964; McShaffrey and McCafferty 1988; Arens 1989, 1990, 1994; Elpers and Tomka 1992).

#### **Materials and Methods**

Nymphs were collected mainly in Jardinópolis and Cajuru in south-eastern Brazil, but material from Campos do Jordão, Intervales State Park, and the Museum of Zoology, University of São Paulo (several localities) were also examined. All localities are in São Paulo State. Only full-grown nymphs were used, corresponding to the instar preceding the sub-imago stage. For live observations, some nymphs were kept in small aquaria ventilated by air pumps and kept in an air conditioned room.

Nymphs were fixed in 80% ethyl alcohol or a mixture of 80% alcohol and glycerol. Nymphs or relevant anatomical parts were mounted in Canada balsam or, for semipermanent slides, in glycerol jelly (Pantin 1969). Serial sections of heads in transverse, sagittal and horizontal planes were made. Dissections were made with sharp-pointed tweezers and 'minuten' insect pins. For ascertaining feeding habits, extracted guts were opened and their contents mounted on slides in glycerol. Illustrations were facilitated with the help of a stereomicroscope camera lucida and on observations and interpretations from sections, dissections and live material.

Presently it is not possible to identify Brazilian *Farrodes* to species. Reference material is being deposited in the Museum of Zoology of the University of São Paulo.

#### Results and Discussion

The head

As in other Leptophlebiidae, the head of nymphs of *Farrodes* is flattened and bears prognathous mouthparts (Fig. 1A–C),

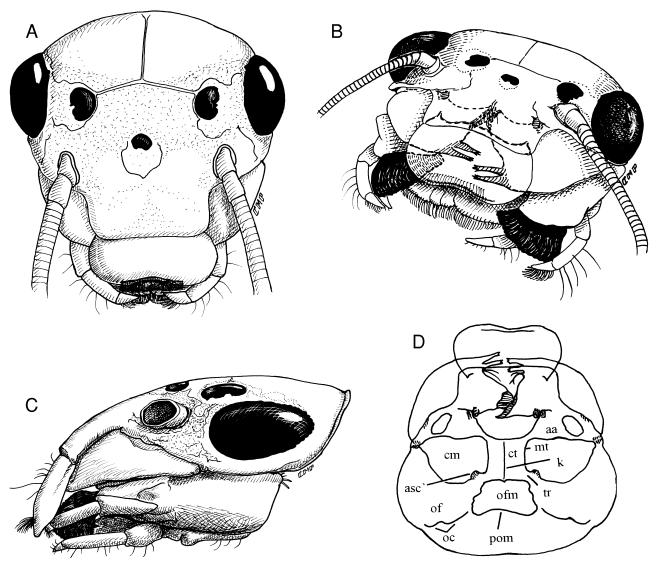


Fig. 1—Farrodes sp., head —A, Dorsal view —B, Oblique antero-lateral view —C, Lateral view —D, Cephalic capsule.

although the medial plane of the head is kept at an angle of  $\approx\!45^\circ$  in relation to the substrate. This inclination is similar in confamilial scrapers and filterers, and even in other families, such as Heptageniidae. The broad anterior part of the head is almost completely occupied by mouthparts. Posteriorly, the distance between the posterior margin (pmc) and the postoccipital one (pom) is large, allowing ample head movements, different from those ephemeropteran nymphs with hypognathous heads, such as Baetidae. The tips of the mouthparts are far from the head–thorax articulation, giving them a wide reach over the substrate. The postoccipital margin (pom) of the head capsule (cc) is strongly connected to the tentorium (tn) and postmentum (psm). On each half of the occipital region an internal crest (oc) and an accompanying trough (of) are found; a median elevation (emo)

separates both (Figs 1D, 2 and 3). These crests are important as points of origin for muscles.

The shape of the tentorium varies considerably among insect orders (Snodgrass 1935), and this structure is important for points of origin of muscles responsible for mouthpart movements.

The tentorium of *Farrodes* is robust (Fig. 1D); the corpus (ct) is squarish with a median carina (k), strengthened posteriorly, and the bases are broad. The entire structure forms a reinforcement of the cephalic capsule.

# Labrum

The labrum (Fig. 4A,B), about twice as broad as long, presents apically two rows of close-set hairs (b1lbr) and five

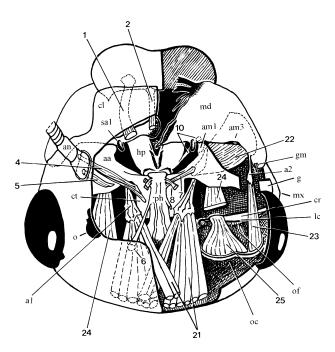


Fig. 2—Farrodes sp., head muscles, dorsal view.

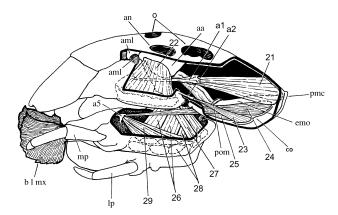


Fig. 3—Farrodes sp., head muscles, lateral view.

denticles (dl) along a shallow anterior emargination. The epipharynx is minimally sclerotized and possesses several fields of hairs or bristles mostly directed mesially (Fig. 4B).

The labrum is moved by two pairs of muscles, a pair of flexors (depressors, 1) and a pair of extensors (levators, 2) (Figs 2, 3 and 5A,B). In addition to these, a set of small muscles (3), not yet referred to in the Ephemeroptera, are inserted in the posterior epipharynx, of which some are restricted to the same side (3') but others cross from one side to the other (3") (Fig. 5). Labrum compressor muscles were not found. These muscles were described by Snodgrass (1935) for several groups of insects and for *Arthroplea congener* (Heptageniidae) by Froehlich (1964), but were not

referred to by Strenger (1954) for *Rhithrogena* sp. and *Ecdyonurus* sp. (Heptageniidae) and by Brown (1961) for *Cloeon dipterum* and *Baetis rhodani* (Baetidae).

The movements of the labrum are chiefly dorsoventral; pendular movements or retraction also would be possible, but were not observed in live nymphs. Muscles 3 would act as elevators-retractors of the epipharynx, dilating the preoral cavity.

The labrum shields the other mouthparts from the water current, reducing the loss of food particles. Food particles accumulating among the epipharynx hairs are periodically removed by galealacinial bristles. The dorsal hairs of the labrum could retain substrate food particles, but these could be used only if removed naturally. The denticles could have limited use in the scraping of irregular surfaces.

#### Mandibles

The mandibles (md, Fig. 6A,B) are approximately crescentic with two incisors (in) and a mola (m). The molae (Fig. 6A,B,E,F) are asymmetrical and provided with a system of meshing crests. Situated basally to the incisors is a prostheca (pr). A set of bristles (b3md) occurs basally to each mola. An L-shaped row of bristles (b1md, Figs 6A and 7) is found on the ventral surface of the mandibles; these bristles are directed outwards.

The anterior articular surface (am1) is strong and bears most of the load of the mandibular action. The posterior one (am2) is much smaller and works as an auxiliary support. An axis (e) through both shows the movements to be very oblique (Fig. 8), an important adaptation in prognathous forms, especially those with dorso-ventrally flattened heads, allowing for a wide gape. A third articular surface (am3) is seen in an intermediate position. Some authors (Grandi 1940; Arens 1989) have considered the anterior articulation as a 'pseudo-articulation', having appeared secondarily, and the median articulation to be the true articulation that has shifted laterally. This topic needs more studies for its elucidation. Two apodemes serve as insertion points for the muscles (Fig. 6B).

The mandibles are responsible principally for taking up food from the maxillae. They exhibit alternate movements during the grinding of food by the molae. The progressive closing of the molae during adduction allows a precise grinding of the food particles, which are pressed against the pharynx. The bristles basal to the molae help to retain the food, and those of the left mola remove food adhering to the right one. The incisors help to comminute food lumps and, on irregular surfaces, they may have a scraping role. The L-shaped row of bristles on the ventral surface captures many food particles, preventing their loss during mouthpart movement. The outward orientation of these bristles may be explained because they are occasionally cleaned by maxillary bristles.

The strong cranial adductors of the mandible (21, Figs 2, 3 and 9) have their inner muscles bundles originating on the

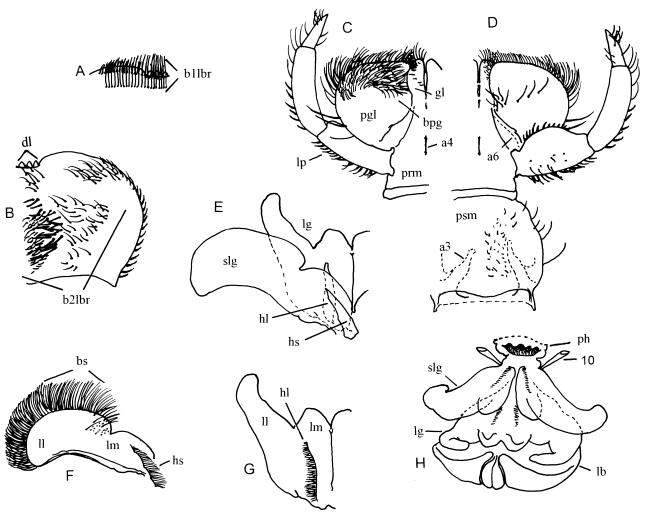


Fig. 4—Farrodes sp., labrum, labium and hypopharynx
A, Denticles and bristle rows of labrum, left half, dorsal view

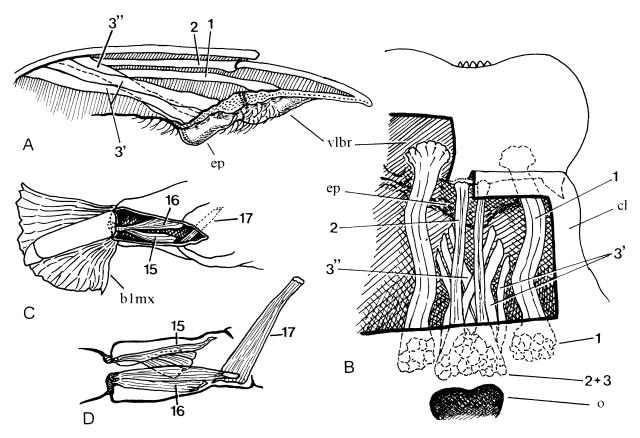
-B, Labrum, left half, ventral view -C, Labium, left half, dorsal

view — **D**, Labium, left half, ventral view — **E**, Hypopharynx — **F**, Left superlingua, dorsal view — **G**, Lingua, left half, dorsal view — **H**, Hypopharynx, oblique anterior view.

opposite side of the head capsule with respect to the midline. The crossing of these muscles was illustrated for Hexagenia (Ephemeridae) by Needham et al. (1935), for Ecdyonurus and Rhithrogena (Heptageniidae) by Strenger (1954) and for Arthroplea congener (Heptageniidae) by Froehlich (1964). In Baetidae such as Cloeon dipterum and Baetis rhodani (Brown 1961), these muscles do not cross to the other side, which is probably a plesiomorphic state. This crossing is important in prognathous heads such as those of Leptophlebiidae and Heptageniidae, where the internal head space is reduced both dorso-ventrally and longitudinally. The tentorial adductors (22, Figs 2 and 3) are inserted deep and slanting into the mandible. The mandibular abductor (23, Figs 2, 3 and 9) is considerably smaller than the adductors. Between gena and mandible there is a thickened region, the geno-mandibular ligament (gm, Fig. 2).

# Maxillae

The maxillae (mx, Fig. 6C,D) are the most complex of mouthparts in the Leptophlebiidae. In Farrodes sp. maxillae are flattened and approximately rectangular. Their extensive membranous connection with the head capsule allows for extensive abduction movement, as in other mayflies (Brown 1961; Froehlich 1964). Distally on the galealaciniae there is a dense brush of bristles (b1mx) that is obliquely orientated ventrally. The bristles are longer laterally, forming a morphological gradient, a term used by Arens (1989) for similar maxillary structures in many insect species. On the medial edge there is distally a tuft of setae (b4mx), followed basally by a row of progressively longer setae (b2mx). On the mediodistal angle, three pectinate bristles (pb, Fig. 6C) are found. The maxillary palpi (mp) have fused second and third



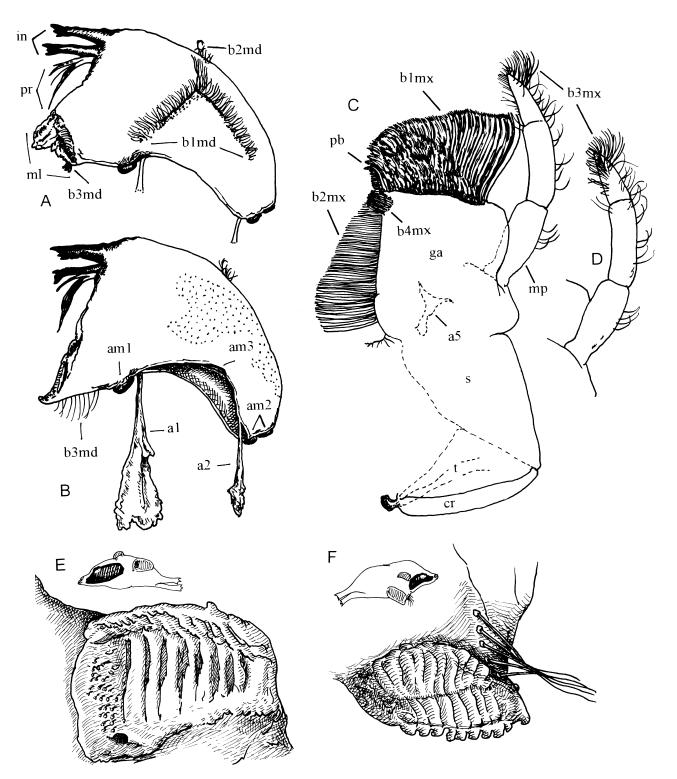
**Fig. 5**—*Farrodes* sp., muscles of labrum-epipharynx and of maxillary palpi — **A**, **B**, Labrum-epipharynx muscles — **A**, Lateral view of sagittal section — **B**, Dorsal view — **C**, **D**, Muscles of the left maxillary palpus — **C**, Lateral view — **D**, Dorsal view.

segments and a group of ventral setae on the third one. In repose the maxillae rest between the superlinguae and mandibles dorsally and the labium and lingua ventrally (Fig. 7).

The bristles of the apical brush scrape and remove food particles from the substrate. The median setae retain these particles. The apical tuft and the pectinate bristles remove particles accumulated on the epipharynx. The pectinate bristles are also used to remove particles from the glossae and paraglossae and to scrape the substratum. The alternation of movements of the maxillae and mandibles is the main mechanism in particle acquisition and transportation.

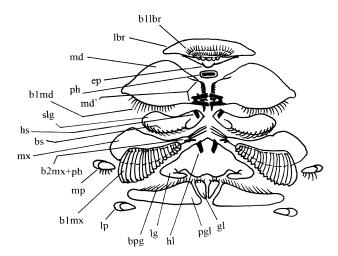
The complexity of maxillary movements has been demonstrated for *Arthroplea congener* (Heptageniidae) (Froehlich 1964), *Rhithrogena pellucida* (Heptageniidae) (McShaffrey and McCafferty 1988), and for the Dictyoptera (Snodgrass 1935, 1952). Based on the single articulation and a complex synergetic interaction of the muscles, the maxillae present broad and diverse movements. Adduction and abduction are always coordinated with protraction and retraction, respectively. In addition, rotation (Froehlich 1964; l.c.), elevation and depression, arcing and a movement here termed 'lateromedian shift' also take place. Generally the tentorio-stipital (26), tentorio-cardinal (27) and labio-stipital muscles (28)

(Figs 3, 9 and 10) are responsible for adduction and protraction and also for the latero-median shift, while the cranio-lacinial (24) and cranio-cardinal muscles (25) (Figs 2, 3, 9 and 10) are responsible for abduction and protraction. The labiostipital muscles work in an antagonistic way to the other adductors; although a reference to this muscle has not been found in the literature. A good example of synergetic action is the combination of the cranio-lacinial muscle with the cranio-cardinal muscle which cause elevation with a slight retraction. Rotation, as described by other authors, are caused by 'rotators' or cranio-cardinal muscles (25, Figs 2, 3, 9 and 10). In Farrodes sp. that do not have a dorsal craniocardinal muscle, a slight rotation is possible by the antagonistic action of the labio-stipital with other muscles and to the synergetic action of others that block adduction. Arcing is easier than rotation, having been observed in living nymphs. The labio-stipital muscle corresponds to bundles of the tentorio-stipital muscle that shifted their origins to the postmentum. Part of the origin of the tentorio-stipital muscle is a tendon common to both sides. The maxillae have few intrinsic muscles, as the palps are simple and the stipites are fused to the galeae. A single oblique muscle is inserted in the base of the palp, the levator of the palp (17) and the first segment



**Fig. 6**—*Farrodes* sp., mandibles and maxillae — A, Left mandible, ventral view — B, Right mandible, dorsal; view — C, Right maxilla, ventral view — D, Left maxillary palpus, ventral view — E, Left

molar surface —  $\mathbf{F}$ , Right molar surface. In  $\mathbf{E}$  and  $\mathbf{F}$  the small figures show the position of the molae in the mandibles.



**Fig. 7**—*Farrodes* sp., comprehensive schematic topography of mouth parts in an idealized transverse section.

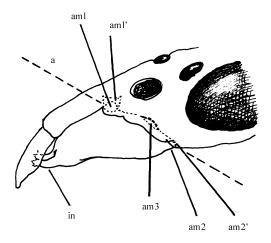


Fig. 8—Farrodes sp., mandible articulations and axis of movement.

contains a flexor (15) and an extensor (16) of the distal palp (Fig. 5C,D). Some of the muscles have been observed to lack specific antagonists.

#### Labium

The postmentum (psm, Fig. 4D) of *Farrodes* sp. is approximately trapezoidal and the obliquely orientated lateral margins (Fig. 11) allow the passage of the important labiostipital muscle (28, Fig. 10). The glossae (gl) and paraglossae (pgl) are the main ventral structures of the head. The 3-segmented labial palps (lp) are similar to the maxillary ones, including in the fusion of the second and third segments.

The glossae and paraglossae hold the food taken up by the maxillae, but on irregular substrata they may assume a scraping role, which also occurs with the labrum and incisors. As the paraglossae move, food may be held between them and

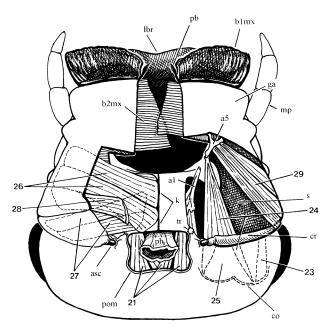


Fig. 9—Farrodes sp., head muscles, ventral view; labrum removed.

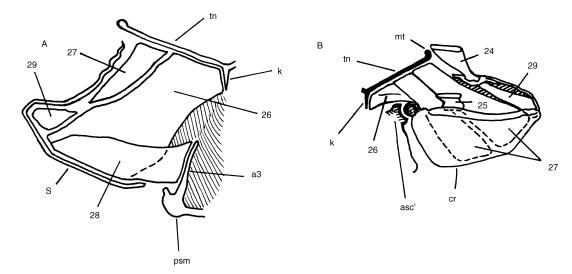
the glossae. The labial palps, when vibrating rapidly, produce a flow of water directed towards the mouthparts and is an important mechanism for feeding on suspended particles.

The labium as a whole is capable of only restricted movements; the glossae and paraglossae move more freely. The prementum retractor (18) is the only unpaired muscle of the head. There are short muscles (20) between the prementum and the paraglossae that apparently cause their flexion and extension. Flexors (11) and extensors (12) of the labial palpi (Figs 3 and 12A) originate on the hypopharynx, that serves as their support. They are oblique and their origins have migrated from the primitive positions on the preor postmentum, a condition not referred to in the literature. The second and third palpal segments are moved by a flexor (13) and an extensor (14) (Fig. 12A), responsible for rapid palpal movements.

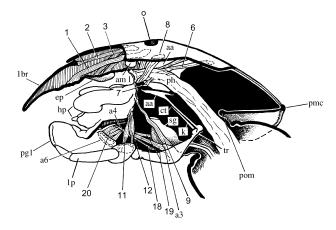
# Hypopharynx

The hypopharynx (hp) of Farrodes sp. (Fig. 4E–H) fills up a large space among the other mouthparts (Fig. 7). The lingua (lg) is robust and the lateral superlinguae (slg) are flattened. Medially both the lingua and superlinguae slope upwards towards the pharynx, directing food transport to the latter. Posteriorly and dorsally to the lingua there is a gap between the two superlingual lobes. The general positioning conforms to the type described for other Ephemeroptera (Brown 1961; Arens 1989). Obvious suspensoria were not seen, but a well-delimited border forms the base of the hypopharynx.

Basically the lingua holds food taken up by the maxillae preventing their loss to outer areas between the labium and



**Fig. 10**—*Farrodes* sp., maxillary and mandibular muscles, schematic transverse sections —**A**, **B**, Maxillary muscles —**C**, Tentorial adductor of the mandible and geno-mandibular ligament.



**Fig. 11**—*Farrodes* sp., head muscles, lateral view; mandibles and maxillae removed.

the other mouthparts. The hypopharynx, especially its posterior portion, takes the food towards the pharynx directed by its shape and the arrangement of hairs. The gap between the superlinguae serves as a food channel.

The action of the hypopharynx is restricted and depends on the action of the other mouthparts. It is moved by retractors-depressors (9) and by mandibulo-hypopharyngeals or levators of the hypopharynx (10) (Figs 2 and 11); the latter were also observed in *Arthroplea congener* by Froehlich (1964).

# Pharynx

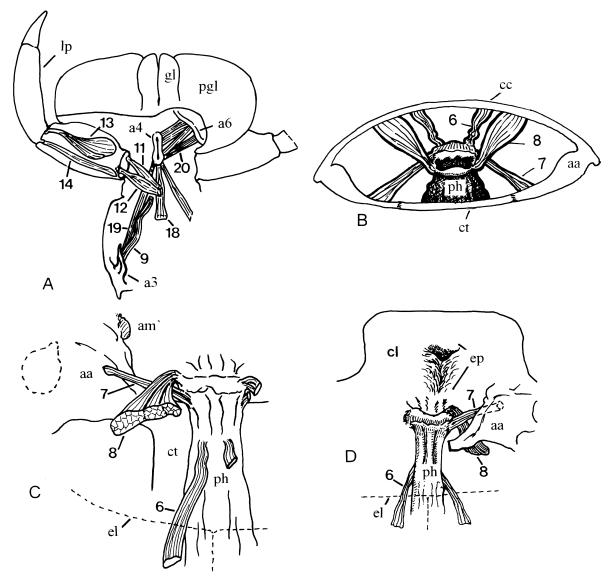
The pharynx (Figs 2, 3, 9, 11 and 12B–D), as the head, is flattened dorso-ventrally. It has simple movements, caused by simpler and fewer muscles than those described by

Snodgrass (1935) for other insects. The retractors-levators (6) could open the pharyngeal lumen; the depressors (7) and levators (8) seem to act at the pharyngeal entrance. All are important in maintaining the position of the pharynx.

# **Conclusions**

The nymphs of Farrodes sp., as those of many Leptophlebiidae, are specialized scrapers or brushers of the biofilm, which consists mainly of diatoms and other algae, including colonial algae, fungi, minute animals, unidentifiable detritus, all items referred as FPOM and UPOM (fine and ultrafine particulate organic matter), differently from some species of the subfamily Leptophlebiinae, opportunistic feeders that deals with CPOM (coarse particulate organic matter) too (Williams and Feltmate 1992; Mattingly 1987). Each of the mouthparts presents very specific adaptations to obtain and transport food particles. The distal brushes of bristles and hairs on the distal border of the maxillae are used to obtain food from the substrate. The maxillary palpi remove the food particles from the brushes taking them towards the mandibles and hypopharynx. The labrum and labium assist in retaining food. The labial palpi are important in producing a water current towards the prebuccal cavity. The mandibles, besides fragmenting lumps of food with the incisors and molae, are important, in alternating movements with the maxillae, to press the food towards the pharynx. The prosthecae help in retaining particles.

Most setae on the mouthparts are directed medially and/ or posteriorly, channeling food towards the pharynx. The principal setal fields are those of the epipharynx and labrum, the dorsal ones of the paraglossae, those of the median border of the galealacinia, and those of the hypopharynx.



**Fig. 12**—*Farrodes* sp., muscles of labium, hypopharynx and pharynx —**A**, Muscles of labium, dorsal view —**B**, **D**, Muscles of pharynx —**B**, Schematic anterior view —**C**, Dorsal view —**D**, ventral view.

The pectinate bristles of the medio-distal galealacinia help in scraping the substrate and removing particles from the epipharynx and paraglosssae. The L-shaped row of setae occurring on the mandibles, with bristles directed outwards, are cleaned periodically by the maxillae. As the pharyngeal opening is significantly dorsal in position, the medial parts of the maxillae and hypopharynx are orientated obliquely upwards for more efficient transport of food.

# Abbreviations used in the figures

a1 medial apodeme of mandible a2 lateral apodeme of mandible

a5 dorsal apodeme of maxilla
a6 apodeme of paraglossa
a axis of mandible movements
aa anterior tentorial arm
am 1 anterior articulation of mandible
am 2 posterior articulation of mandible
am 3 middle articulation of mandible
am 1' anterior articular surface for mandible
am 2' posterior articular surface for mandible
am 2' posterior articular surface for mandible and antenna
asc articular surface of cardo
asc' articular surface for cardo

a3 apodeme of postmentum a4 apodeme of prementum

b1lbr dorsal bristles of labrum

b2lbr ventral bristles of labrum (epipharynx)

b1md mandibular ventral bristles in L-shaped row

b2md marginal bristles of mandible

b3md molar bristles

b1mx bristle brush of galealacinia

b2mx median bristle row of maxilla

b3mx bristles of maxillary palpus

b4mx dorsal bristles of the median row of maxilla

bpg dorsal bristles of paraglossa

bs marginal bristles of superlingua

cc cephalic capsule

cl clypeus cm cavity for the maxilla

co occipital crest of occipital fossa

cr cardo

ct corpus tentorium

dl denticle

el ecdysial line

emo median occipital ridge

ep epipharynx

g gena

ga galealacinia

gl glossa

gm geno-mandibular ligament

hl dorsal hair row of lingua

hp hypopharynx

hs dorsal hair row of superlingua in incisors

k tentorial keel

lb labium

lbr labrum

lc limit of cavity for maxilla

lg lingua

ll lateral lobe

lm median lobe

lp labial palpus

md mandible

md' incisors, mola and prostheca

ml mola

mp maxillary palpus

mt lateral margin of tentorium

mx maxilla

o ocellus

oc occipital crest of occipital fossa

ofm occipital foramen

pb pectinate bristles of maxilla

pgl paraglossa

ph pharynx

pmc posterior margin of cephalic capsule

pom postoccipital margin

pr prostheca

prm prementum

psm postmentum

s stipes

sal anterior articulation of mandible

sg suboesophageal ganglion

slg superlingua

t ventral thickening of cardo

tn tentorium

tr posterior tentorium root

vlbr ventral portion of labrum

#### Muscles

1 flexor of labrum

2 extensor of labrum

3 levators-retractors of epipharynx

3' simple

3" crossed

4 flexor of antenna

5 extensor of antenna

6 levators-retractors of pharynx

7 depressors of pharynx

8 levators of pharynx

9 retractors-depressors of hypopharynx

10 mandibulo-hypopharyngean; levator of hypopharynx

11 flexor of labial palpus

12 extensor of labial palpus

13 flexor of middle and distal segments of labial palpus

14 extensor of middle and distal segments of labial palpus

15 flexor of middle and distal segments of maxillary palpus

16 extensor of middle and distal segments of maxillary palpus

17 depressor of maxillary palpus

18 retractor of prementum

19 levator-retractor of prementum

20 muscles of paraglossa

21 cranial adductors of mandible

22 tentorial adductor of mandible

23 abductor of mandible

24 cranio-lacinial muscle

25 cranio-cardinal muscle 26 tentorio-stipital muscles

27 tentorio-cardinal muscles

28 labio-stipital muscle

29 stipito-lacinial muscle

# Acknowledgements

C.M.P. is grateful to CAPES for a Master Fellowship. C.G.F. is grateful to CNPq (Brazilian Council for Scientific and Technological Development) for a Research Fellowship (No. 301247/1996–0). Both authors are grateful to Conrad Labandeira and to an anonymous reviewer for the comments and improvements to the manuscript.

#### References

Arens, W. 1989. Comparative functional morphology of the mouthparts of stream animals feeding on epilithic algae. (Monographische Beiträge). – Archiv für Hydrobiologie (Suppl.) Band 83(3): 253–534.

- Arens, W. 1990. Wear and tear of mouthparts: a critical problem in stream animals feeding on epilithic algae. *Canadian Journal of Zoology* **68**: 1896–1914.
- Arens, W. 1994. Striking convergence in the mouthpart evolution of stream-living algae grazers. Journal of Zoological Systematics and Evolutionary Research 32: 319–343.
- Brown, D. S. 1961. The morphology and functioning of the mouthparts of *Chloeon dipterum L. & Baetis rhodani* (Pictet), (Insecta, Ephemeroptera). – *Proceedings of the Zoological Society of London* 136(2): 147–176.
- Edmunds, G. F., Jensen, S. L. and Berner, L. 1976. *The Mayflies of North and Central America*. University of Minnesota Press, Minneapolis.
- Elpers, C. and Tomka, I. 1992. Struktur der Mundwerkzeuge und Nahrungsaufnahme bei den Larven von Oligoneuriella rhenana Imhoff (Ephemeroptera: Oligoneuriidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 65: 119–139.
- Froehlich, C. G. 1964. The feeding apparatus of the nymph of *Arthroplea congener* Bengtsson (Ephemeroptera). *Opuscula Entomologica* **29**(3): 188–208.
- Grandi, M. 1940. Contributi allo studio degli efemerotteri italiani.
  I. Note di morfologia e di etologia comparate su alcune specie di Betidi, Efemerelledi ed Eptagenidi. Bollettino di Entomologia Bologna 12: 1–62.
- Mattingly, R. L. 1987. Handling of coarse and fine particulate

- organic matter by the aquatic insects *Paraleptophlebia gregalis* and *P. Temporalis* (Ephemeroptera: Leptophlebiidae). *Freshwater Biology* 18: 255–265.
- McShaffrey, D. and McCafferty, W. P. 1988. Feeding behavior of *Rhithrogena pellucida* (Ephememeroptera, Heptageniidae). *Journal of the North American Benthological Society* 7(2): 87–99.
- Merritt, R.W. and Cummins, K.W. 1996. An Introduction to the Aquatic Insects of North America, 3rd edn. Kendal/Hunt Publishers, Dubuque, Iowa.
- Pantin, C. F. A. 1969. *Notes on Microscopical Technique for Zoologists*. University of Cambridge, Cambridge.
- Savage, H. M. 1987. Biogeographic classification of the neotropical Leptophlebiidae (Ephemeroptera) based upon geological centers of ancestral origin and ecology. – Studies on Neotropical Fauna and Environment 22(4): 199–222.
- Snodgrass, R. E. 1935. *Principles of Insect Morphology*. McGraw-Hill Book Company, New York..
- Snodgrass, R. E. 1952. Arthropod Anatomy. Comstock Publishing Associates, Cornell University Press, Ithaca, New York.
- Strenger, A. 1954. Zur Kopfmorphologie der Ephemeridenlarven.
   I, Ecdyonurus und Rhithrogena. Österreichische Zoologische Zeitschrift 4: 191–228.
- Williams, D. D. and Feltmate, B.W. 1992. Aquatic Insects. University of Toronto, Toronto.