Feeding strategies in Atalophlebiinae (Ephemeroptera: Leptophlebiidae), with considerations on scraping and filtering

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Abstract

The largest neotropical group of mayflies are the Atalophlebiinae; their nymphs are commonly considered as scrapers, feeding on the biofilm. Images obtained with a VHS camera coupled to a stereomicroscope were used for a better understanding of their feeding. Some genera scrape, e.g. *Massartella*, *Thraulodes* and *Farrodes*, others filter, in spite of their lack of specialized structures, e.g. *Ulmeritoides* and *Farrodes*. In *Hermanella*, filtering was the only mechanism observed. A good part of the time is used to remove particles from the bristles; that retention-removal process we also call filtering. To consider the Atalophlebiinae as scrapers is vague, for they may present two types of filtering, one occasional, as in *Farrodes* and *Ulmeritus*, the other obligatory, as in *Hermanella*. The morphological differences of the strategies lie chiefly in the bristles, long and loose in filterers, close-packed and rigid in scrapers. Feeding strategies of other species are suggested.

Keywords: feeding strategies, mayflies diet, Atalophlebiinae.

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Introduction

The nymphs of Atalophlebiinae, Leptophlebiidae, feed on the biofilm (mostly algae, bacteria, fungi and detritus) and are often referred to as scrapers (cf. Merritt and Cummins, 1996). They are well diversified and ecologically important as detritivores-herbivores. They have their counterparts in the holarctic Heptageniidae. Feeding and diet of the latter and also of the Baetidae are relatively well-studied (Brown, 1959; Froehlich, 1964; McShaffrey and McCafferty, 1988; Strenger, 1954), in contrast to the neotropical Atalophlebiinae.

Material and Methods

VHS images were used, obtained from a portable video camera coupled to a stereomicroscope. Nymphs were collected in streams of São Paulo State, Brazil and reared in rearing aquaria and Petri dishes. Most of the nymphs studied were full-grown.

Results

Species of *Massartella*, *Ulmeritoides*, *Thraulodes* and *Farrodes* obtain food by scraping the surfaces of leaves or stones with their galealacinial brushes. However, some filtering processes were often used by all the species, except mature *Massartella* sp. Flocculated particles are easily collected in some processes, e.g. two-abduction-scraping in *Farrodes* sp. (see below).

Hermanella sp., on the other hand, filters suspended particles with the maxillae serving as a "basket", and removes the food by sweeping the galeolacinial brushes with the maxillary palps and labrum.

Differences in behavior details among *Massartella*, *Thraulodes*, *Ulmeritoides* and *Farrodes*, as well as within the same species of all genera, were observed.

The main mouth parts used are the maxillae, which have highly specialized galealacinial brushes. The mandibles often work alternately with the maxillae, and the labial and maxillary palps are variously used, according to the strategy. The non-*Hermanella*-group genera have firm galealacinial brushes with short and strong bristles, whereas the *Hermanella*-group has soft and long bristles. In the latter, the maxillae are wide and laminar with an antero-median tooth, present also in *Ulmeritoides*.

Table 1 - *Massartella* sp.

Mature nymph

Strategy	Mouth parts action
I- SIMPLE SCRAPING	0,83 maxillary adductions/s, reaching 1,3/s
II- SPECIAL SCRAPING, TWO-ABDUCTION-SCRAPING	IIA- Scraping of the substrate; IIB- Removal of food from the mouth parts=ingesting; IIA and IIB alternate in similar speed; 0,6 cycle(A+B)/s

Small nymph

Strategy	Mouth parts action
III- FILTERING, SIMPLE	0,7 maxillary adductions/s

Table 2 - *Ulmeritoides* sp. - Mature nymph

Strategy	Mouth parts action
I- SPECIAL FILTERING, TWO-ACTION-FILTERING	IA- Maxillary palp: 1 strong abduction, labial palps: 4-5 adductions (falling to 3-4)=gathering; IB- Maxillary palp adduction, followed by mandible adduction=ingesting; 0,9 cycles (IA+IB)/s; Also low movements: ca. 30% of those

Table 3 - *Thraulodes* sp. - Mature nymph

Strategy	Mouth parts action
I- SCRAPING	3,5 maxillary adductions/s
II- FILTERING 1, SIMPLE	1 maxillary adduction/s
III- FILTERING 2, ESPECIAL	IIIA- Maxillary adduction+labial palp alternate=gathering; IIIB- Maxillary adductions+participation of the mandible=ingesting; 0,7 cycles(IIIA+IIIB)/s

Table 4 - *Farrodes* sp. - Mature nymph

Strategy	Mouth parts action
I-SPECIAL SCRAPING, TWO-ABDUCTION-SCRAPING, SUCH AS IN *MASSARTELLA* (LIGHTLY ON SUBSTRATE=FILTERING?)	IA- maxillae strongly abducted= gathering; each 8-10 of 'B' IB- maxillae moderately abducted+labial palps actions+strong mandible adduction= ingestion; 2,4 maxillary adductions/s, reaching 2,8; 4-5 labial palp adductions/1 maxillary adduction; Cycle(IA+IB): 0,3/s
II- SIMPLE REMOVAL (FILTERING)	Galeolacinial brush/labrum-paraglossae: Cycle: 2-3 maxillary adductions=>mandibular adduction=>pause; Super maxillary Abduction, stopping for 10s

Table 5 - *Hermanella* sp. - Mature nymph

Strategy	Mouth parts action
I- FILTERING 1, SPECIAL PROCESS, TWO-ACTION-FILTERING	IA-"Basket": maxillary abductions, stopping for ca. 25s; 5 labial palps adductions/s=gathering; IB- 3 maxillary adductions/40s=ingesting, removal of food from the mouth parts
II- VARIATION OF FILTERING 1	IIA- "Basket": maxillary abductions, stopping for ca. 15s, without labial palps actions=gathering; IIB- Quick and strong maxillary adduction=ingesting
III- FILTERING 2, SIMPLE	Without "*basket*": quick and strong maxillary adduction: 2-3/s, for 5-6s; labial palps alternate with maxillae: 1 adduction/1 maxillary adduction; in each maxillary abduction, mandibles adduces slowly but abduces quickly

Table 6 - Feeding strategies of genera of neotropical Atalophlebiinae; suggestion for a Functional Feeding Groups table.

Species-Genera	Feeding Strategy	Processes described here
Non-*Hermanella*-Group		
Massartella sp.	Scraper→Filterer (juvenile)	Simple Scraping Two-abduction-Scraping Filtering, Simple
Ulmeritoides sp.	Scraper*=Filterer	2-action-Filtering
Thraulodes sp.	Scraper→Filterer	Scraping Filtering 1, Simple Filtering 2, Special
Farrodes sp.	Scraper**→Filterer**	Two-abduction-Scraping Removal (Filtering)
***Hermanella*-Group**		
Hermanella sp.	Filterer→Scraper*→Shredder*	Filtering 1, Special Process, two-abduction-filtering Filtering 1, Variation Filtering 2, Simple
Expected		
Non-*Hermanella*-Group		
Ulmeritus	Scraper=Filterer	
Askola	Scraper→Filterer	
Hagenulopsis	Scraper→Filterer	
Miroculitus	Scraper→Filterer	
Miroculis	Scraper→Filterer	
Ecuaphlebia	Scraper→Filterer	
Homothraulus	Scraper→Filterer	
Perissophlebiodes	Scraper→Filterer	
Meridialaris	Scraper→Filterer	
Hagenulus	Scraper=Filterer→Shredder	
***Hermanella*-Group**		
Hylister	Filterer→Scraper→ Shredder	
Hydrosmilodon	Filterer→Scraper→ Shredder	
Leentvaaria	Filterer→Scraper→ Shredder	
Traverella	Filterer→Scraper→ Shredder	
Needhamella	Filterer→Scraper→ Shredder	

→ from more to less used
= balanced
*expected, but not observed
**reported previously (cf. Polegatto and Froehlich, 1998)

Feeding strategies and its mechanisms

We separate the scraping and filtering into 'simple', when the mouth parts maintain a regular cycle without additional or special movements, e.g. mandible-maxilla alternation with similar speeds, and, on the other hand, 'special processes', when the mouth parts work in different ways in a delimited cycle, i.e., a cycle with more than one distinct action of the mouth parts, e.g. two-abductions-scraping or filtering (see also schemes in the figures 1-3).

Massartella sp.

Massartella (Table 1, Fig. 1A) presented (I) a simple scraping and (II) a scraping that we call two-abduction-scraping, or special, in which (IIA) the scraping of the substrate, with a strong abduction, is distinct and alternate to (IIB) the removal of food obtained in 'A', with a smaller abduction. Small nymphs presented (III) simple filtering, with the maxillae removing suspended food from the water. In this strategy, there was sometimes a strong mandibular adduction coupled with a strong maxillary abduction.

Ulmeritoides sp.

Ulmeritoides nymphs (Table 2, Fig. 2) were observed to filter, with (IA) movements of the labial palps gathering food from the water, with the maxillary palps strongly abducted, and (IB) the adduction of the maxillary palps, followed by mandibular adduction, in the ingestion. Sometimes, filtering movements are made slowly. This strategy was treated as two-action-filtering.

Thraulodes sp.

Thraulodes (Table 3, Fig. 1 A, B) presented (I) scraping, (II) basic and (III) special filtering. In the latter, there is (IIIA) a main action of the maxillae, gathering food with the use of the labial palps, and (IIIB) small maxillary actions, with help from the mandibles, ingesting food. Sometimes, the mandibles are abducted, while the other mouth parts stay resting.

Farrodes sp.

Farrodes (Table 4, Fig. 1A) presented (I) the so called two-abduction-scraping, or special, but with a light touch on the surfaces, similar to a filtering, or an intermediate stage. In one of the abductions (IA), the maxillae abduct strongly and gathers food; in another (IB), the maxillae abduct moderately, the labial palps move, and the mandibles adduct strongly, removing food from the mouth parts and ingesting it. After the end of this strategy, the labial palps can continue to move. There was also (II) simple removal, as a filtering, with the galealacinial brushes taking food from the labrum and paraglossae, followed by unique mandibular adduction, or ingestion, and a pause. In this strategy, a very strong maxillary abduction, stopping for a long time, was also observed in filtering.

Hermanella sp.

Observed in *Hermanella* (Table 5, Fig. 3) were (I) filtering 1, two-action-filtering, a special process, with the maxillae opening as "baskets", held this position for a long time, while the labial palps move, gathering food (IA), and then the maxillae adduct, removing of obtained food (IB). In a variation (II), they open without action of the labial palps, gathering food (IIA), and then there is a strong and quick maxillary adduction, ingesting food (IIB). In the filtering 2 (III), or simple, no basket is formed; there are quick maxillary adductions working alternately with the labial palps. Here, the mandibles have unequal movements, adducting slowly but abducting rapidly. Simple filtering can alternate with baskets, with the labrum extended. Sometimes, independently of the strategies, the pre-mentum and the paraglossae move considerably. The galeolacinial bristles are loosed in the basket positions.

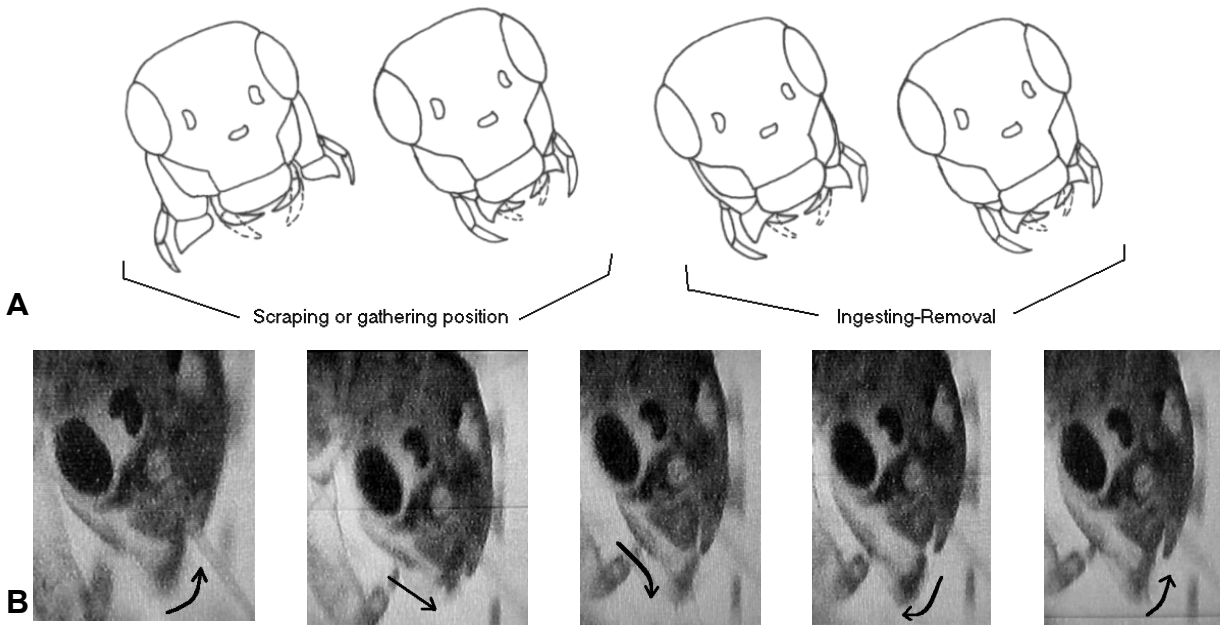

Fig. 1 - A, Schematic action for *Massartella* sp., *Thraulodes* sp. and *Farrodes* sp.: in the scraping/gathering position the abduction of the maxillae is strong, while in the ingesting-removal their abduction is limited, but the mandible movements are similar in both. B, cycle of abduction and adduction of the maxillae of *Thraulodes* sp.: see that the maxillae are moved for anterior and then for lateral direction, as the arrows show.

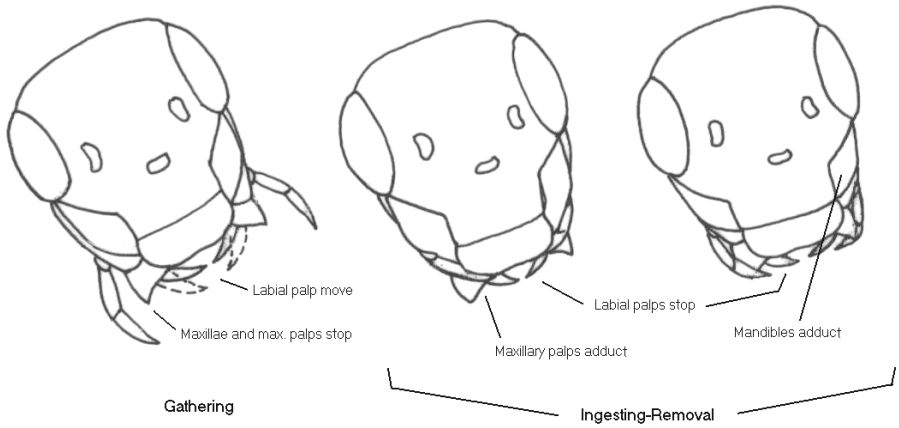

Fig. 2 - *Ulmeritoides* sp., schematic action: in the gathering position the labial palps move with the maxillae abducted, but in the ingesting-removal the mandibles and maxillary palps work.

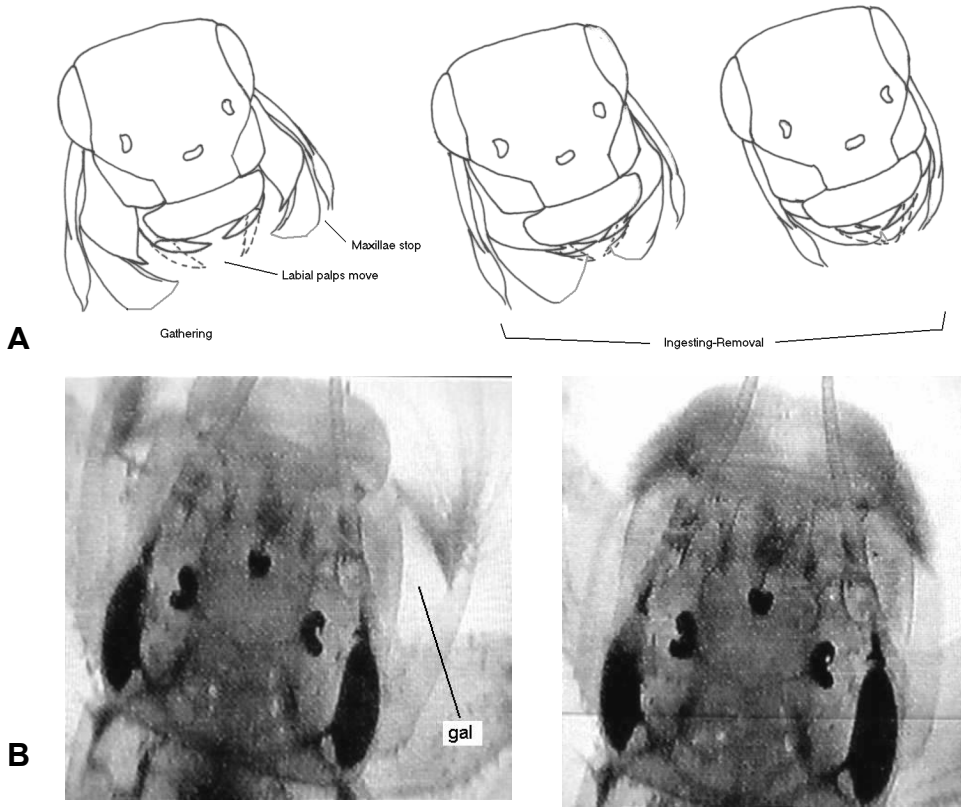

Fig. 3 - A, *Hermanella* sp., schematic action: in the gathering the maxillae and their palps form a basket with labial palps obtain particles, but in the ingest-removal the mouth parts work altogether. B, abduction, "basket", and adduction of the maxillae; see the bristles well separated in the abduction. Gal=galealacinia.

Many of the processes are preceded by little movements of some mouth parts.

The fore legs are used in the feeding behavior to obtain particles from the galeolacinial brushes and other distal regions of the mouth parts, and they can push food towards the ventral face of the head, e.g. *Massartella* and *Farrodes*.

A difference in the frequency and duration of the feeding behavior was observed, in the following order: "high frequency and duration=>low":
"*Farrodes*=>*Massartella*=>*Thraulodes*/*Ulmeritus*=>*Hermanella*".

All movements are highly stereotyped, being regular in the strategies and in its variations, i.e. each combination is associated to its stereotypy; intermediate or irregular processes were not observed.

Discussion

Most Leptophlebiidae are often referred as scrapers (Merritt and Cummins, 1996). However, *Massartella*, *Ulmeritoides*, *Thraulodes* and *Farrodes*, are not only efficient scrapers but also filterers, while members of the *Hermanella*-group are filterers. The derived morphology of the latter is comparable to genera of other regions, e.g. Oceania and South Asia (cf. figures in Campbell and Peters, 1993; Hubbard *et al*., 1992), that should be filterers too. Little or nothing was understood about the behavior of neotropical groups. In most Atalophlebiinae, such as the neotropical non-*Hermanella*-group, there are no specialized structures for filtering, such as long and soft bristles, but only structures for scraping, such as short and stiff bristles. But they use filtering processes that do not require long bristles; instead they use complex motions of the mouth parts, sometimes at high speed (Polegatto and Froehlich, 1998), and specialized associations and alternations of the mouth parts. Therefore, the Atalophlebiinae present specializations in the actions of the mouth parts and in the musculature (Polegatto and Froehlich, 2001), as well as in external morphology. The observation of several modes of scraping and filtering, including more than one for each species, shows that such variation optimize the feeding processes. Simple scraping and simple filtering were previously reported for *Farrodes* sp. (Polegatto and Froehlich, 1998) as well as different ways of scraping. It is possible that *Farrodes* scraping and filtering-like strategy could be done alternately in short distance of time. A similar condition about the use of scraping and filtering is found in *Rhithrogena pellucida*, Heptageniidae (cf. McShaffrey and McCafferty, 1988). The behavioral and morphological variation, that do not occur in Baetidae, Leptohyphidae and other generalist collectors, is needed to compensate for the relatively limited diet of scrapers and filterers, specially in particle size. A great variation is found also in Heptageniidae (Froehlich, 1964; McShaffrey and McCafferty, 1988; Strenger, 1954).

As Arens (1990) states, the mayflies with many molts during the nymphal stage have advantages because the damaged mouth parts of scrapers are replaced. Independently of the number of molts, it would be reasonable to state that filtering, that causes less wear of the mouth parts, would be advantageous.

Other processes such as scraping and some shredding could be expected for the *Hermanella*-group because the galealacinial tooth is big in *Hydrosmilodon* and *Leentvaaria* (cf. Demoulin, 1966; Hubbard *et al*., 1992). Filtering is a subdivision of the group of the collectors (Merritt and Cummins, 1996), but here filtering is treated as an independent strategy, because it forms a separate and complex manner of obtaining food and there is no similarity between filterers and collectors, the latter presenting strong action of the mandibles on detritus.

Observed strategies of Atalophlebiinae genera and inferences are presented in the Table 6. Inferences were also based on illustrations from works on taxonomy by Hubbard *et al.,* (1992), Demoulin (1966) and Kluge (1993).

Utilization of the fore legs (see also McShaffrey and McCafferty, 1988), and frequency and duration of the feeding process, could have also adaptative variations, but it is difficult to investigate.

McShaffrey and McCafferty (1988) and Polegatto and Froehlich (1998) showed that the movements of the mouth parts are highly stereotyped. They are as specific as the strategies, but a low plasticity in Ephemeroptera is only apparent, as demonstrated here. In fact, the several stereotypies form the feeding behavior, which do not occur in lower animal taxons, and this wide behavioral repertory, being highly plastic, allows "choices" (Silvio Morato de Carvalho, personal communication).

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