

Trophic analysis of three species of *Marilia* (Trichoptera: Odontoceridae) from the neotropics

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Abstract: The trophic ecology of the aquatic insect fauna has been widely studied for the Northern temperate zone. However, the taxa originally classified within a given particular trophic group in temperate ecosystems, do not necessarily exhibit the same dietary profile beyond its geographic limits. Since, the trophic ecology of caddisfly larvae is largely incomplete in the Neotropical Region, the present work aims to describe feeding habits inferred from quantitative analysis of data taxonomically resolved at the species level. For this, the feeding habits of three Trichoptera species *Marilia cinerea*, *M. elongata* and *M. flexuosa* were recorded in the Yungas forests of Argentina and Bolivia. A total of 15 larvae of each species were sampled from 13 different streams were selected for gut content analysis. The ingested material was extracted from the foregut and midgut by using ventral dissection of thorax. For each species, mandibles were dissected, mounted in glycerin and illustrated in order to highlight morphological differences between these mouth pieces purportedly associated to the dietary behavior of individuals, and their habitats. The niche overlap was estimated through Schoener's method. The diet analysis revealed that *M. cinerea*, *M. elongata* and *M. flexuosa* feed on the same food items, but through different patterns of preferences. Larvae of *M. cinerea* were collected on both emerging surfaces of rocks on which a thin layer of running water flows and streams sliding areas with stony bottoms attached to the rock surfaces. They displayed a gut content consisting predominantly of invertebrate vestiges and have strong mouthparts provided of large molar areas; this allowed us to allocate the species within the functional group of predators. *M. elongata* feeds mainly on fine particulate material, its mouthparts are scoop-shaped and occurs in areas of low flow; this set of features is linked to a collector-gatherer strategy. Finally, larvae of *M. flexuosa* have been primarily assigned to the functional group of shredders and secondarily to the collector-gatherer class. They inhabit sandy bottoms of mountain streams, have strong scoop-shaped mouthparts and show a diet dominated by leaf litter and fine particulate material. We concluded that the functional group assignment to the genus level for *Marilia* is not recommended, and further studies at species level are necessary. Rev. Biol. Trop. 62 (2): 543-550. Epub 2014 June 01.

Key words: functional feeding group, *Marilia cinerea*, *Marilia elongata*, *Marilia flexuosa*, Schoener's index.

The knowledge about the functional feeding groups of aquatic insects that inhabit lotic environments contributes to a right comprehension of the ecology of such ecosystems (Cummins, 1973). This knowledge is critical for understanding both (i) the energy pathways (nutrients cycling) and (ii) the resident entomofauna structure (community composition). In the organismic scale of analysis, the accurate definition of trophic traits is also

important because these traits influences every vital aspect of individuals such as life cycles, habitat choice, agonistic behavior, food search, reproductive fitness, among others. The correct assignment of species to functional feeding groups depends upon evidence taken from three empirical levels of information: 1) the kind of ingested food item; 2) the behavioral strategy oriented to obtain resources; 3) the nature of the morphological structure for



alimentary acquisition. Aquatic insects have been assigned to four different feeding categories, namely collectors (gatherers/filterers), shredders, scrapers and predators. The bulk of work on trophic ecology and functional classification of aquatic insects has been performed in the temperate zone (Merrit & Cummins, 1996). However, direct extensions of those results to other regions such as the Tropics of the New World could be misleading. Several authors have warned about the risks of the free importation of classificatory schema since taxa from temperate ecosystems do not necessarily match their dietary habits with those from the outside (Dobson, Magana, Mathooko & Ndegwa, 2002; Cheshire, Boyero & Pearson, 2005; Tomanova, Goitia & Helešić, 2006; Reynaga, 2009; Chará-Serna, Chará, Zúñiga, Pedraza & Giraldo, 2010).

In the Neotropical Region, the knowledge about ecology, behaviour or life history of caddisfly larvae is largely incomplete (Posada-García & Roldán Pérez, 2003). The available literature based on feeding habits is focused to the genus level (Cummins, Merrit & Andrade, 2005; Rincón & Martínez, 2006; Tomanova et al., 2006; Reynaga, 2009) and a few to the species level (Albariño & Valverde, 1998; Díaz-Villanueva & Trochine, 2005; Reynaga & Rueda-Martín, 2010). In this region, *Marilia* (Trichoptera: Odontoceridae) is the most speciose genus in the family, with about 30 species. As all the Integripalpians larvae, they build transportable cases using silk. Portable cases are well suited to a foraging lifestyle in which the insects move throughout in search of food. Regarding this background, the aim is to study the feeding habits of three species belonging to this genus that occur in the mountain rain forests, or Yungas ecoregion of Argentina and Bolivia (Rueda-Martín, 2008): *Marilia cinerea* Navás 1931, *M. elongata* Martynov 1912 and *M. flexuosa* Ulmer 1905.

This study was carried out in order to analyze the functional feeding group of these species of *Marilia* present in Northwestern Argentina. We considered three different aspects: (1) where the food was obtained, focusing on the

habitat where the larva was found, (2) what kind of material was ingested, animal, vegetal, and other items, and (3) morphological aspects of mouthparts.

The knowledge on the functional feeding groups of aquatic insects constitutes an important tool in biomonitoring programs. Moreover, it provides a basic knowledge for the identification of policies and proposal for conservation and maintenance use of natural resources of a given area.

MATERIAL AND METHODS

Study material: *Marilia cinerea* is distributed in mountain and plane areas from central and Northwestern Argentina and Bolivia (from 400m to upper than 1 500m). The general coloration of the larva is light brown with some muscular scales (Fig. 1A); the head is rounded and bears a semicircular crest and has an average body length of 9.42 ± 0.9 mm. *Marilia elongata* is recorded from Peru and Northwestern Argentina. Some of the larvae have unusual cases in which the posterior portion is made of a case of a larva from another genus (Leptoceridae: *Grumichella*). The larvae are dark colored, with oval head bearing two triangular white spots and white area around the eyes (Fig. 1B) and have an average body length of 10.31 ± 1.5 mm. *Marilia flexuosa* is widely distributed from North America to Northwestern Argentina. The general color of the larval sclerites is dark with a dorsal carina and lateral bridges that cross the ocular area (Fig. 1C). Larvae have an average body length of 6.40 ± 0.7 mm.

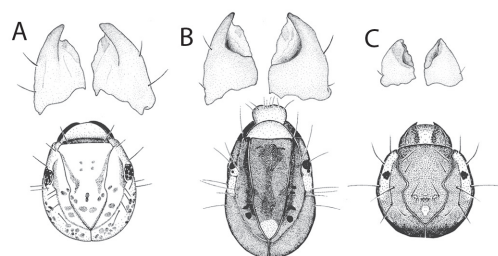


Fig. 1. Dorsal view of head and mandibles. (A) *Marilia cinerea*, (B) *Marilia elongata*, (C) *Marilia flexuosa*.

Diet analysis: Larvae of the three species were collected in 13 streams of Southern Andean Yungas. For each study site and sampling occasion, qualitative samples were taken from riffles and pools using a strainer (Rueda-Martín, 2008). The samples were preserved in 75% ethyl alcohol. In the laboratory, the individuals were identified to species level. A total of 15 larvae of each species were selected for gut content analysis from different sites. The diet was analyzed by removing the foregut and midgut content using ventral dissection of thorax (Peckarsky, 1996). The description and identification of ingested items were made under a microscope (200X). The gut content of each specimen was mounted with glycerin. The scale bar of the microscope eyepiece was used as a transect. A total of 15 transects were randomly selected, where each food category was recorded at each sampling point and its coverage percentage was estimated according to Reynaga & Rueda-Martín (2010). The food categories considered were: sediment particles, fine particulate organic matter (FPOM<1mm), coarse particulate organic matter (CPOM>1mm), microphyte and invertebrate remains. The mandibles of one individual of each species were dissected, mounted in glycerin and illustrated under microscope with a camera lucida to record possible differences

in morphology and possible association with dietary items.

The niche overlap was calculated via Schoener's (1970) method:

$$PS = 1 - 0.5 \sum [p_{ij} - p_{ik}]$$

where p_{ij} and q_{ik} represent the fraction of food item i that is used by species j and k respectively, with regards to the total of food items. The index ranges from 0 which indicates no dietary overlap to a maximum overlap of 1 when all items are found in equal proportions (Jaksic, 2001) across the dietary profile. All statistical analyses and graphics were produced through the R platform (R Core Team, 2012).

RESULTS

The diet analysis shows that *M. cinerea*, *M. elongata* and *M. flexuosa* consume the same food items, but in different proportions (Table 1). In general, invertebrate remains were the dominant item in *M. cinerea*; *M. elongata* feeds on amorphous matter and fine particulate organic matter; the diet of *M. flexuosa* is mainly characterized by particulate organic matter both coarse and fine (Fig. 2). In the latter two species it also should be stressed the occurrence of sediment particles (>15%).

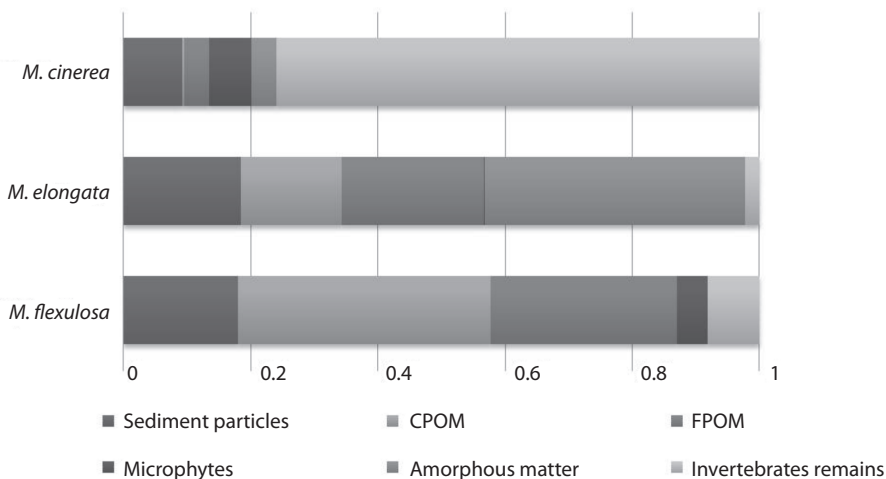


Fig. 2. Barplot showing the average feeding profiles for each species.

TABLE 1
Average diet composition of *Marilia* species found throughout the study area. Relative frequencies for feeding items are in percentage

Species	Sites	Altitude	Date (m/d/yr)	Sediment particles	CPOM	FPOM	Microphytes	Amorphous matter	Invertebrates remains	Code
<i>M. cinerea</i>	26°51'51" S-65°34'12" W	983	9/17/2004						100	cine_2
<i>M. cinerea</i>	26°51'51" S-65°34'12" W	983	9/17/2004						100	cine_3
<i>M. cinerea</i>	25°28'5" S-65°3'0" W	1 027	11/9/2005				34.28		65.71	cine_4
<i>M. cinerea</i>	25°28'5" S-65°3'0" W	1 027	11/9/2005	8.57					91.43	cine_5
<i>M. cinerea</i>	25°28'5" S-65°3'0" W	1 027	11/9/2005	14.28	3.57		14.28	2.38	65.48	cine_6
<i>M. cinerea</i>	26°51'51" S-65°34'12" W	983	9/17/2004	1.25				10	88.75	cine_7
<i>M. cinerea</i>	26°51'51" S-65°34'12" W	983	9/17/2004	7.27				5.45	87.27	cine_8
<i>M. cinerea</i>	26°51'51" S-65°34'12" W	983	9/17/2004	12.9					87.1	cine_9
<i>M. cinerea</i>	25°28'5" S-65°3'0" W	1 027	11/9/2005	2.27			15.87		97.73	cine_10
<i>M. cinerea</i>	26°11'13" S-65°29'52" W	1 220	10/29/1999	17.46				12.7	53.97	cine_11
<i>M. cinerea</i>	30°56'32" S-64°31'7" W	1 065	10/1/1999	50			25		25	cine_12
<i>M. cinerea</i>	27°15'25" S-65°32'60" W	1 065	10/1/1999	6.25			4.17		89.58	cine_13
<i>M. cinerea</i>	27°15'25" S-65°32'60" W	1 065	10/1/1999	3.85					96.15	cine_14
<i>M. elongata</i>	22°22'47" S-64°44'20" W	1 481	11/13/2004	5.55	62.96	11.11			20.37	elong_1
<i>M. elongata</i>	22°29'58" S-64°45'67" W	1 481	11/15/2004	23.37	9.09	2.59		64.93		elong_2
<i>M. elongata</i>	22°29'58" S-64°45'67" W	1 481	11/15/2004	14.28				85.71		elong_3
<i>M. elongata</i>	22°29'58" S-64°45'67" W	1 481	11/15/2004	18.07		7.23	2.41	65.06	7.23	elong_4
<i>M. elongata</i>	22°29'58" S-64°45'67" W	1 481	11/15/2004	9.23	6.15	7.69		75.38	1.54	elong_5
<i>M. elongata</i>	22°29'58" S-64°45'67" W	1 481	11/15/2004	19.29	7.01			73.68		elong_6
<i>M. elongata</i>	22°29'58" S-64°45'67" W	1 481	11/15/2004	47.22	5.55	11.11		33.33	2.78	elong_7
<i>M. elongata</i>	22°29'58" S-64°45'67" W	1 481	11/15/2004	35.89	12.82	2.56		46.15	2.56	elong_8
<i>M. elongata</i>	22°29'58" S-64°45'67" W	1 481	11/15/2004	19.05	11.9	9.52		59.52		elong_9
<i>M. elongata</i>	22°29'58" S-64°45'67" W	1 481	11/15/2004	12.24	55.1	6.12		26.53		elong_10
<i>M. elongata</i>	22°29'58" S-64°45'67" W	1 481	11/15/2004	2.06	14.43	25.77		57.73		elong_11
<i>M. elongata</i>	22°29'58" S-64°45'67" W	1 481	11/15/2004	9.3	51.16	27.91		11.63		elong_12
<i>M. elongata</i>	22°22'47" S-64°44'20" W	1 481	11/13/2004	27.27	1.82	69.09		1.82		elong_13
<i>M. elongata</i>	22°22'47" S-64°44'20" W	1 481	11/13/2004	8.69	80.43			10.87		elong_14
<i>M. elongata</i>	22°22'47" S-64°44'20" W	1 481	11/13/2004	25	75					elong_15
<i>M. cinerea</i>	26°05'34" S-65°32'60" W	1 018	11/14/2005	5.54	54.54			23.64		cine_1
<i>M. flexuosa</i>	26°11'13" S-65°29'52" W	1 220	10/29/1999	35.53	1.31	63.16				flex_1
<i>M. flexuosa</i>	24°40'44" S-65°25'50" W	1 491	3/2/2000	21.27	53.19	2.13	21.27			flex_2



TABLE 1 (Continued)

Species	Sites	Altitude	Date (m/d/yr)	Sediment particles	CPOM	FPOM	Microphytes	Amorphous matter	Invertebrates remains	Code
<i>M. flexuosa</i>	26°25'42" S-65°34'4" W	1 442	10/29/1999	20.51	33.33	35.89	7.69		2.56	flex_3
<i>M. flexuosa</i>	26°25'42" S-65°34'4" W	1 442	10/29/1999	19.51	19.51	39.02	19.51		2.44	flex_4
<i>M. flexuosa</i>	26°25'42" S-65°34'4" W	1 442	10/29/1999	17.65	73.53				8.82	flex_5
<i>M. flexuosa</i>	26°25'42" S-65°34'4" W	1 442	10/29/1999	22.67	43.94	15.15	12.12		6.06	flex_6
<i>M. flexuosa</i>	26°44'34" S-65°34'54" W	1 657	9/12/2006	10.34	25.86	22.41			41.38	flex_7
<i>M. flexuosa</i>	26°44'34" S-65°34'54" W	1 657	9/12/2006	12.24	32.65	42.85	10.2		2.04	flex_8
<i>M. flexuosa</i>	26°44'34" S-65°34'54" W	1 657	9/12/2006	5.88	33.82	57.35	2.94			flex_9
<i>M. flexuosa</i>	26°44'34" S-65°34'54" W	1 657	9/12/2006	17.78	35.55	40			6.67	flex_10
<i>M. flexuosa</i>	25°06'28" S-64°16'9" W	414	10/20/1999	12.5	50	37.5				flex_11
<i>M. flexuosa</i>	25°06'28" S-64°16'9" W	414	10/20/1999	18.6	41.86	30.23			9.3	flex_12
<i>M. flexuosa</i>	25°06'28" S-64°16'9" W	414	10/20/1999		65.12	20.93			13.95	flex_13
<i>M. flexuosa</i>	24°7'0" S- 65°23'58" W	1 441	6/26/1997	38.09	40.48	21.42				flex_14
<i>M. flexuosa</i>	24°7'0" S- 65°23'58" W	1 442	6/26/1997	17.02	46.81	10.63			25.53	flex_15

When analyzing their habitats and shapes of the mandibles differences were found between species. Larvae of *M. cinerea* were associated to the upper surface of rocks in mountain streams, in areas of running waters provided of periphyton or in gravelly bottoms. Their mandibles are stout; they have an apical blade ending in a blunt toothed edge and moderately large inner grinding areas (Fig. 1A). The *M. elongata* and *M. flexuosa* larvae were found in sandy areas of mountain streams with low flow velocity. Their mandibles are stout and the molar area is concave like a basin or scoop (Fig. 1B and 1C).

The complete linkage dendrogram (Fig. 3) obtained from the functional dissimilarity between taxa can be partitioned into three groups. The first group includes individuals of *M. cinerea*, assigned to the predator functional group. The second group comprises individuals of *M. flexuosa*, shredder primarily and collector-gatherers secondarily, and the last group composed by *M. elongata*, collector-gatherers specialized in amorphous matter and fine particulate organic material. This analysis suggests that there is no overlap in diet between the species studied. According to the dietary profile of individuals, species were grouped consistently regardless of the date or site where they were collected.

DISCUSSION

Generally, studies on functional feeding groups of macroinvertebrates focus on the genus level. In this study, we analyzed the diet of the three species of *Marilia* registered for the Yungas region of Argentina and Bolivia, finding that both diet and habitat preferences are different. Larvae of *M. cinerea* were collected on emerging surface of rocks on which a thin layer of water runs or rivers sliding areas with stony bottoms, attached to the rock surfaces. The larvae displayed a diet of predominantly invertebrate remains; their mouthparts are strong with large molar areas, features which allow us to allocate this species within the functional group of predators. *M. elongata* feeds mainly on fine material, their mouthparts

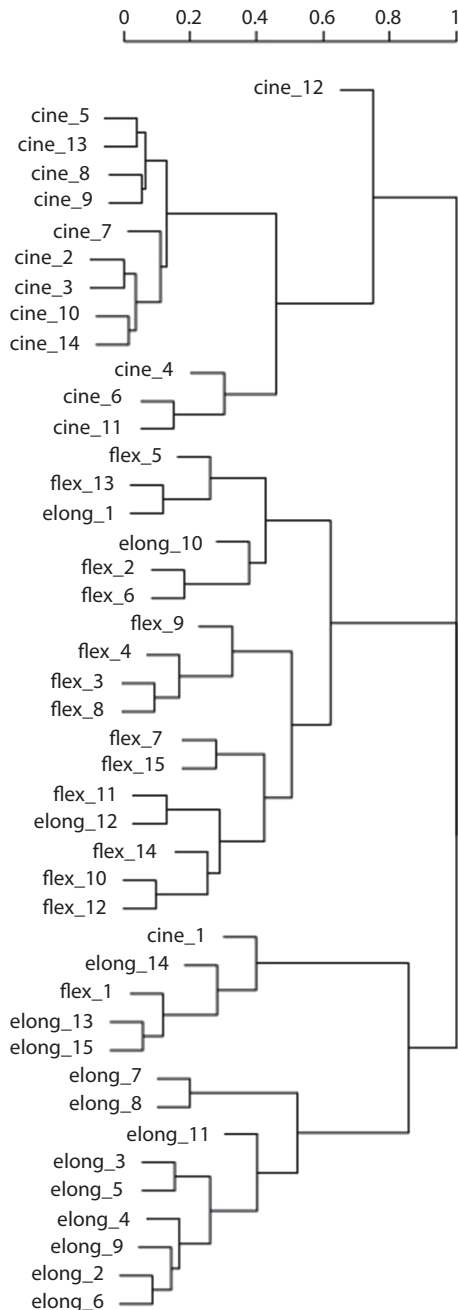


Fig. 3. Groups derived from the dendrogram based on absolute differences between dietary profiles of individuals. The Schoener's Index and complete linkage were used as similarity measure and clustering method, respectively. Codes in table 1.

have scoop shape and their location in low flow area is associated with a collector-gatherer strategy. Larvae of *M. flexuosa* are associated to sandy bottoms in mountain streams. They have a diet composed of leaf litter and fine particulate material, their mouthparts are strong and scoop-shaped. The functional group assignment for this species corresponds to a shredder, mainly, and collector-gatherer, secondarily.

Wiggins (2004) suggests that the Odonocerid larvae in North America are primarily detritivores. Analysis of gut contents suggest that the larvae are omnivorous, feeding on detritus, algae, and animal materials, although the presence of insect parts in the gut contents could reflect predation. Oliveira & Froehlich (1997) and Henriques-Oliveira & Nessimian (2010) determined the functional group of *Marilia* of southeastern Brazil as predator and collector-gatherer. Spies, Froehlich & Kotzian (2006) analyzed larvae in Rio Grande do Sul and Chará-Serna et al. (2010) studied larvae of Colombia, both studies described the genus as shredder. Reynaga (2009), analyzing individuals in a basin of Yungas classified the genus *Marilia* within the collector-gatherer functional group, while Tomanova et al. (2006) classified it as scraper and collector-gatherer.

The fact that functional assignments are so different in the literature would be associated to the analysis of different species of *Marilia*, with morphological characteristics of their mouthparts and dissimilar habitat preference. These strategies would allow coexistence of different species without overlapping of their trophic niche.

In this paper, it is suggested that the functional group assignment to the genus level is not recommended for *Marilia*, and further studies at species level are necessary.

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RESUMEN

Análisis trófico de tres especies de *Marilia* (Trichoptera: Odontoceridae) del neotrópico. La ecología trófica de insectos acuáticos ha sido desarrollada en zonas templadas. Sin embargo, la asignación de un taxón a un grupo trófico no representa necesariamente el mismo en otras regiones. En la Región Neotropical, el conocimiento sobre la ecología trófica de larvas de tricópteros es incompleta y la literatura sobre este tema rara vez se ocupa del análisis de los hábitos alimentarios de larvas con datos cuantitativos a nivel de especie. Este trabajo aporta al conocimiento de las características tróficas de la trichoptero fauna del Neotrópico. Se describen los hábitos alimentarios de tres especies de Trichoptera registrados en arroyos de Yungas de Argentina y Bolivia: *Marilia cinerea*, *M. elongata* y *M. flexuosa*. Se seleccionaron 15 larvas de cada especie en 13 arroyos de Yungas surandinas para analizar las piezas bucales y el contenido estomacal. El solapamiento de nicho trófico se estimó mediante el índice de Schoener. El análisis de la dieta reveló que las especies difieren en la preferencia de los ítems registrados, hábitat y forma de sus mandíbulas. Las larvas de *M. cinerea* habitan en superficies de rocas emergentes. Poseen mandíbulas fuertes con grandes zonas molares y consumen principalmente invertebrados. Esta evidencia permite asignarle el grupo funcional depredador. *M. elongata* consume material fino, sus mandíbulas tienen forma de cuchara y su ubicación en zonas de bajo flujo permite asignarle una estrategia colectora-recolectora. Las larvas de *M. flexuosa* habitan en fondos arenosos de arroyos de montaña, tienen fuertes piezas bucales en forma de cuchara y una dieta dominada por hojarasca y material fino. Pertenecen al grupo funcional triturador, secundariamente colector-recolector. Sugerimos que la asignación de grupo funcional a nivel de género no es recomendable para *Marilia*. Se recomiendan mayores estudios a nivel de especie.

Palabras clave: grupo funcional alimentario, *Marilia cinerea*, *Marilia elongata*, *Marilia flexuosa*, índice de Schoener.

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