

First description of the larva of *Farrodes roundsi* (Traver) (Ephemeroptera: Leptophlebiidae: Atalophlebiinae) with comments on its phylogenetic relationships

Eduardo Domínguez^{a*} and María del Carmen Zúñiga^b

^aCONICET – Facultad de Ciencias Naturales, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina; ^bDepartamento de Biología-Grupo de Investigaciones Entomológicas, Facultad de Ciencias, Universidad del Valle, Cali, Colombia

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The phylogenetic relationships of the species of *Farrodes* were revised recently (Domínguez 1999). Species of *Simothraulopsis* and *Homothraululus* (components of the *Farrodes* lineage) and three species formerly placed in other genera, *Thraululus caribbeanus* (Traver, 1943), *Thraululus roundsi* (Traver, 1947) and *Homothraululus maculatus* (Needham and Murphy, 1924) were included in the analysis. As a result, these three species (the last two known only from adults) were transferred to *Farrodes*. Due to the unusual genitalia and the unknown larva of *F. roundsi*, some doubts about its position within the *Farrodes* lineage remained. Here, the recently reared larva of *F. roundsi* is described for the first time. Also, the original data matrix is re-analysed with the addition of larval characters of *F. roundsi* and *F. carioca*, recently described. As a result, a more stable phylogeny was obtained, and the position of *F. roundsi* within the *F. caribbeanus* group was reconfirmed.

Keywords: Ephemeroptera; Leptophlebiidae; *Farrodes roundsi*; larvae; Colombia

Introduction

Domínguez (1999) revised the phylogenetic relationships of the species of *Farrodes* (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). In the same paper, he transferred three species formerly placed in other genera to *Farrodes*: *Thraululus caribbeanus* (Traver, 1943), *Thraululus roundsi* (Traver, 1947) and *Homothraululus maculatus* (Needham and Murphy, 1924). After the cladistic analysis, the monophyly of the “*Farrodes* lineage” (Savage 1987), including the genera *Homothraululus*, *Simothraulopsis* and *Farrodes*, was reconfirmed. Within the genus *Farrodes*, two different species groups were separated. The *Farrodes caribbeanus* group included *F. mexicanus*, *F. savagei*, *F. caribbeanus*, *F. maya* and *F. roundsi*. The unusual genitalia and the unknown larva of *F. roundsi* posed some doubts about its position within this lineage. The *Farrodes bimaculatus* group included *F. grenadae*, *F. hyalinus*, *F. tulija*, *F. flavipennis*, *F. maculatus*, *F. texanus*, *F. bimaculatus*, *F. iguazuanus*, *F. yungaensis*, *F. carioca*, *F. xingu*, *F. longispinus*, *F. tepui*, *F. pakitza*, and *F. ochraceous*. Due to the differences between the groups, mainly based on the characteristics of the male genitalia, it was suspected that these two species

*Corresponding author. Email: mayfly@unt.edu.ar

groups could be separated in different genera. Nevertheless, because of the lack of information on the larvae of several species, and that both clades were supported only by homoplasies, they were maintained in the same genus.

Since then, the larva of *F. carioca* was described (Da-Silva 2002), and the larva of *F. roundsi* was reared, providing new information. In this study, the larva of *F. roundsi* is described for the first time, and the new information is included in a new cladistic analysis of the genus.

Materials and methods

The material belonging to *F. roundsi* is deposited half in the entomological collection of the Universidad del Valle, Cali, Colombia, and half in the collection of the Fundación-Instituto Miguel Lillo, Tucumán, Argentina. Mouthparts, larval legs, and male genitalia were mounted in Canada balsam.

The phylogenetic relationships were analysed using WinClada (Nixon 2002) and PeeWee (Goloboff 1993).

Taxonomy

Farrodes roundsi (Traver, 1947)

Thraululus roundsi Traver, 1947: 153; Traver, 1960: 73.

Farrodes roundsi, Domínguez, 1999: 161.

Studied material. Colombia, Pasto, R. N. La Planada, Arroyo El Tejón, 1830 m. 6♂ imagines; 33 larvae; 2♂ subimagines, reared; 2♀ subimagines, reared; 19/VIII/ 1999 E. Domínguez & M.C. Zúñiga coll.

Description of mature larva

In alcohol. Body length, 4.6–5.1 mm. General colouration yellowish brown, abdomen darker. *Head.* Yellowish brown, washed with black at base of antennae. Upper portion of eyes of male orange brown, lower portion black. Eyes of female black. Antennae: scape yellowish brown, pedicel and flagellum whitish.

Mouthparts (Figures 1–3). Yellowish brown, molars and incisors of mandibles, and crown of setae of maxillae orange brown; labium, basal 2/3 of mandibles and outer margin of maxillae washed with black.

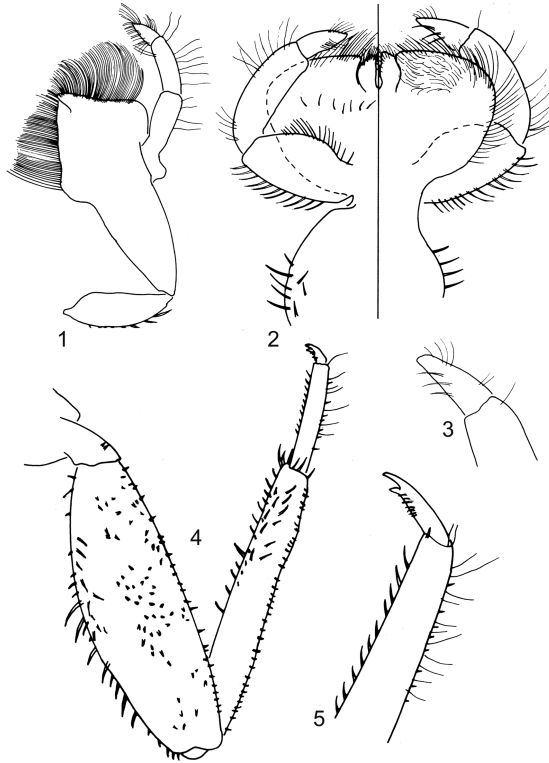
Thorax. Terga light orange brown, with lateral margins of pronotum, mid-lateral spots and anterolateral margin of mesonotum washed with black; pleura yellowish, darker around articulation of legs; sterna yellowish white.

Legs. Yellowish brown, with coxae washed with black; subapical spot on femora I and subapical band on femora III, orange brown. Claws light orange. Spines on dorsum of hind femora blunt (Figure 4); long spines on outer margin of hind tarsi (Figure 5).

Abdomen. Terga yellow orange, with posterior 1/3 of segments II–VIII blackish. Gills blackish. Caudal filaments yellowish, lighter apically.

Distribution

Costa Rica, Panama, Colombia.



Figures 1–5. *Farrodes roundsi*, larva. (1) Left maxilla, ventral view; (2) labium, left half in ventral view; right half in dorsal view; (3) segment III of labial palp; (4) right hind leg, dorsal view; (5) right hind tarsus and tarsal claw.

Discussion

This species was previously recorded from Central America only (Costa Rica and Panamá). With the new record from Colombia, it seems to present a distribution more similar to its sister species, *F. caribbeanus*, which is also distributed in Central America and northern South America. The larvae of *F. roundsi* can be separated from all the other species of the genus by the following combination of characters: (1) spines on dorsum of hind femora blunt (Figure 4); (2) spines on outer margin of tarsi III long (Figure 5); (3) thick setae along outer margin of labial palps II; (4) abdominal terga yellow orange, with posterior 1/3 of segments II–VIII blackish.

Cladistics

Characters and coding

The new data available from the reared larva of *F. roundsi* and from the description of *F. carioca* was added to the original matrix used in Domínguez (1999).

The matrix included 27 characters (17 adult and 10 larval external characters). Fourteen characters are binary, and coded as 0 (plesiomorphic) and 1 (apomorphic).

Multistate characters were treated in two different ways: additive (characters 3, 12, 15, 25–26) or non-additive (characters 1, 6–8, 11, 13, 16–17). Characters with no information available were assigned a missing code (?).

Character list (for explanation of coding, see Domínguez 1999)

Adult characters

♂ *Genitalia*

1. *Lateral projection of styliger plate [nonadditive]*. 0 = Absent; 1 = small, slightly projected; 2 = rounded, base not well defined; 3 = short to long, apex blunt or acute, base well defined; 4 = medium sized, cylindrical, curved medially.
2. *Medial projection of styliger plate*: 0 = absent; 1 = present.
3. *Spines on ventral surface of styliger plate [additive]*. 0 = small, equal sized; 1 = larger on medial area, between sockets; 2 = larger on lateral areas, especially on lateral projections.
4. *inner margin of forceps sockets elevated*. 0 = no; 1 = yes.
5. *Shape of basal part of segment I of forceps*. 0 = quadrangular, forming an internal angulation; 1 = not quadrangular, narrowing evenly toward apex.
6. *Division of penis [nonadditive]*. 0 = lobes totally separated; 1 = apical 1/2–1/3 divided; 2 = apical 3/4–4/5 divided.
7. *Shape of apex of penis lobes [nonadditive]*. 0 = rounded; 1 = acutely angled; 2 = obtusely angled.
8. *Shape of base of penis lobes [nonadditive]*. 0 = not widened; 1 = widened at right angle; 2 = roundly widened.
9. *Origin of penis projections*. 0 = ventral; 1 = ventrolateral or lateral.
10. *Width of base of penis projections*. 0 = wide; 1 = narrow.
11. *Shape of penis projections [nonadditive]*. 0 = spine-like; 1 = inverted funnel; 2 = conical, curved inward; 3 = conical, curved apically upward; 4 = cylindrical, long.
12. *Structures on apex of penis projections [additive]*. 0 = absent; 1 = long apical tubule; 2 = short terminal flap.

Wings

13. *Base of vein ICu1, in forewings [nonadditive]*. 0 = Joining CuP; 1 = Joining CuA; 2 = Free.
14. *Size of costal projection of hind wings*. 0 = small (less than 0.16 of total width); 1 = large (more than 0.19 of total width).

Thorax

15. *Shape of prosternum [additive]*. 0 = deep anteriorly, median part evenly narrow; 1 = shallow anteriorly, with median constriction; 2 = shallow anteriorly, very wide posteriorly.

Abdomen

16. *Colouration of abdominal segments [nonadditive]*. 0 = all segments pigmented (non-*Farrodes* pattern); 1 = all segments pigmented (*Farrodes* pattern); 2 = at least some segments translucent.

17. *Female sternum IX [nonadditive]*. 0 = rounded, entire; 1 = conical, entire; 2 = conical, truncated apically; 3 = conical, with apical notch.

Larval characters

Mouthparts

18. *Location of widest part of labrum*. 0 = 1/2 distance base to apex; 1 = apical 2/3.
 19. *Tuft of setae on center of outer margin of mandibles*. 0 = weaker; 1 = stronger.
 20. *Two or more thick setae on margin of cardo of maxillae*. 0 = present (Figure 1); 1 = absent.
 21. *Maxillary palp segment III/II*. 0 = 0.5 or less; 1 = 0.6 or more.
 22. *Thick dorsal setae on labial palp segment III*. 0 = 5 or more; 1 = 3 (Figure 3).
 23. *Thick setae on labial palp segment III*. 0 = along outer margin (Figure 2); 1 = in basal half of outer margin only.

Legs

24. *Spines on dorsum of hind femora*. 0 = acute; 1 = blunt (Figure 4).
 25. *Pectinate spines along medial line of hind tibiae [additive]*. 0 = absent; 1 = few; 2 = numerous.
 26. *Spines on outer margin of hind tarsi [nonadditive]*. 0 = absent; 1 = short; 2 = long (Figure 5).

Gills

27. *Gill width*. 0 = wide; 1 = narrow.

Outgroup selection

The genus *Ecuaphlebia* was selected as outgroup, as in Domínguez (1999), and based on a previous phylogenetic analysis (Flowers and Domínguez 1991), where it appears as basal to members of the '*Farrodes* lineage'.

Analysis

Two analyses were performed in this study: the first including the whole matrix (analysis 1, '*all data available*') and the second with only the species with larvae and adults known (analysis 4, '*Taxa represented by both larvae and adults only, all characters*') as in Domínguez (1999). The results are compared with the equivalent ones from that paper.

The computer program 'PeeWee' was used for the cladistic analysis. This is a program for parsimony analysis under implied weights. It searches for trees which maximise fit across characters retaining only the trees with highest fit. Characters are given weight in inverse relation with the amount of homoplasy (extra steps) they show in every tree examined. Trees with the highest total fit (sum of character weight) are considered the best tree. Those trees resolve character conflict in favour of the characters which have less homoplasy on the trees. In this way, it is possible to find trees with greatest explanatory power given the weights the characters deserve. The options used were 'hold 1000; mult* 20'. The command 'Hold' determines the

number of suboptimal trees retained in memory for the next analysis. The command 'Mult' randomises the order of the taxa in each replication, creating a wagner tree, and submitting it to branch-swapping, repeating the process the number of times indicated, to find all possible 'islands' present in the matrix. The program 'WinClada' show the character distribution in the resultant trees.

The results in the two different analyses are as follows.

- (1) *All data available* (Table 1): A single tree was obtained, with a fit of 188.2. This tree (Figure 6) is totally compatible with the consensus of six trees obtained in Domínguez (1999, Figure 47), but it shows more resolution. In the *F. caribbeanus* group, the relationships of *F. savagei* and *F. roundsi* are resolved. In this way, *F. mexicanus* is the basal most species, followed by *F. savagei*, and *F. roundsi*, which appears as the sister group of *F. caribbeanus* + *F. maya*. In the *F. bimaculatus* group, the inclusion of *F. carioca* produced more resolution in the basal part of the group. In this way, *F. grenadae* remains as the basal group, then the clade *F. flavipennis* + *F. tulija* appears as the sister group of the rest. The next clades separated are *F. hyalinus*, *F. bimaculatus* and *F. maculatus* + *F. texanus*, respectively. The remaining clade (*F. iguazuanus*, *F. yungaensis* (*F. carioca* (*F. ochraceous*, *F. longispinus*, *F. pakitza*, *F. xingu*, *F. tepui*))) does not present any change. It is interesting to

Table 1. Data matrix for the taxa used in this study.

		Character states									
		1	5	10	15	20	25				
* <i>Ecuaphlebia</i>	+	0000	10000	1	0000	0	0?00	0	0000	0	00
<i>H. misionensis</i>	+	10100	1020	1	0010	2	1011	0	1001	1	00
<i>S. demerara</i>	+	10000	02020	1	0021	1	2211	1	0111	1	00
<i>F. roundsi</i>	+	4121	11020	0	1021	1	2100	0	0001	2	21
<i>F. caribbeanus</i>	+	2021	12211	0	2021	1	2300	0	0010	2	21
<i>F. maya</i>		3021	12021	0	3121	1	2???	?	????	?	??
<i>F. mexicanus</i>		3021	10020	0	3121	0	1???	?	????	?	??
<i>F. savagei</i>	+	3021	12020	0	3021	1	2100	0	0111	2	11
<i>F. bimaculatus</i>	+	3021	12021	0	4220	0	2100	0	0?0?	2	?2
<i>F. grenadae</i>	+	3021	11021	0	3020	0	1100	0	0?01	2	11
<i>F. hyalinus</i>	+	3021	12021	0	4020	0	2100	0	0?01	2	11
<i>F. iguazuanus</i>		3021	12021	0	4220	0	13??	?	????	?	??
<i>F. maculatus</i>		3021	11021	0	4220	0	1???	?	????	?	??
<i>F. texanus</i>	+	3021	11021	0	4220	0	1100	0	0001	2	11
<i>F. yungaensis</i>	+	3021	12021	0	4220	0	1300	0	1001	2	11
<i>F. flavipennis</i>		3021	12121	0	4020	0	1???	?	????	?	??
<i>F. tulija</i>		3021	12121	0	4021	0	1???	?	????	?	??
<i>F. carioca</i>	+	3021	12021	0	4221	0	1300	0	1?0?	?	11
<i>F. ochraceous</i>		3021	11021	0	4221	0	1???	?	????	?	??
<i>F. longispinus</i>		3021	11021	0	4221	0	1???	?	????	?	??
<i>F. pakitza</i>		3021	11021	0	4221	0	1???	?	????	?	??
<i>F. xingu</i>		3021	11021	0	4221	0	13??	?	????	?	??
<i>F. tepui</i>		3021	11021	0	4221	0	13??	?	????	?	??

Description of character states included in text. Unknown conditions indicated by '?'. Outgroup indicated by '*'. Taxa used in analysis 2, indicated by '+'.

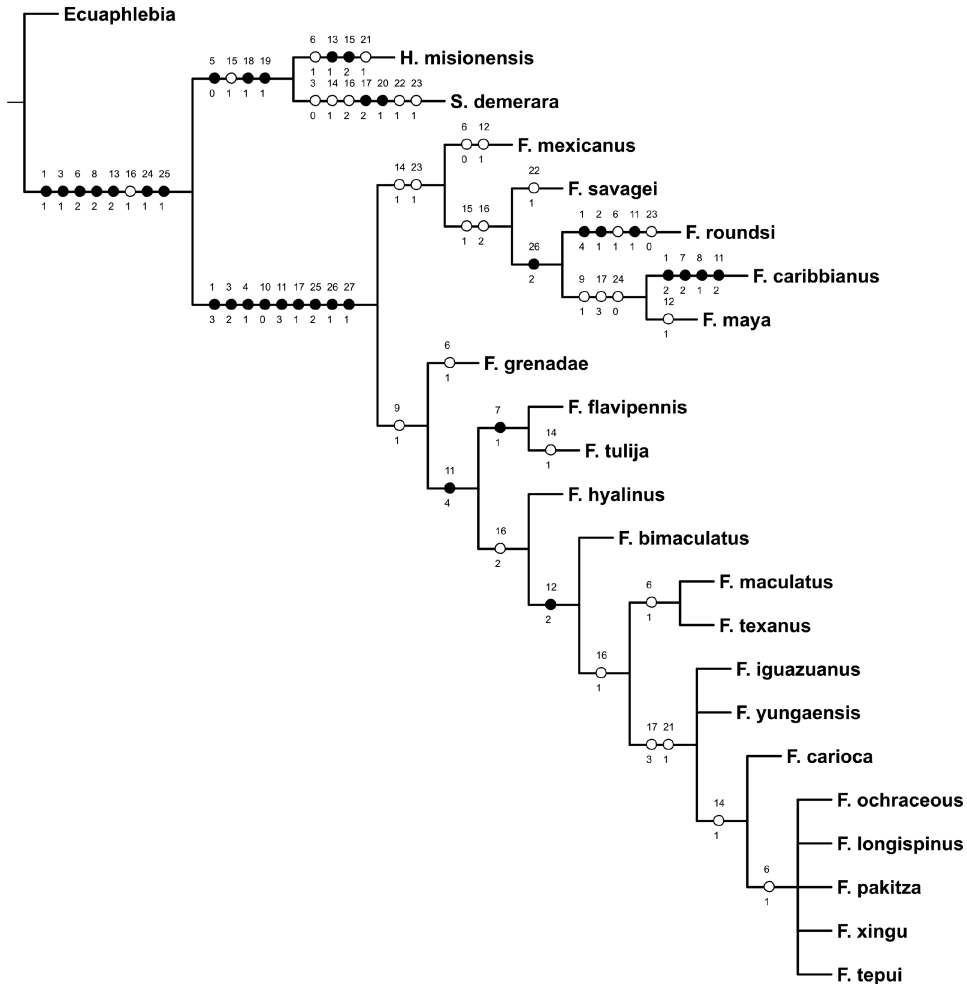


Figure 6. Cladogram obtained from data set (1). Black circles = apomorphies; empty circles = homoplasies.

note that in the last case, the inclusion of the information of the larva of *F. carioca* produced more resolution outside of the clade where this species is, instead of within its own clade.

- (2) ‘Taxa represented by both larvae and adults only, all characters’ (Table 1, taxa marked ‘+’). One tree was obtained, with a fit of 185.5. The difference between this tree (Figure 7) and the consensus of four trees obtained in Domínguez (1999) is that now all the clades are resolved. The newly added *F. roundsi* appears as the sister species of *F. caribbeanus*, and *F. carioca* appears in the same clade with *F. yungaensis*. This tree is also totally compatible with the one obtained in the first analysis.

Discussion

Domínguez (1999) proposed the existence of two species groups within the genus *Farrodes*. The larval stages of 13 out of the 23 species included were unknown at that

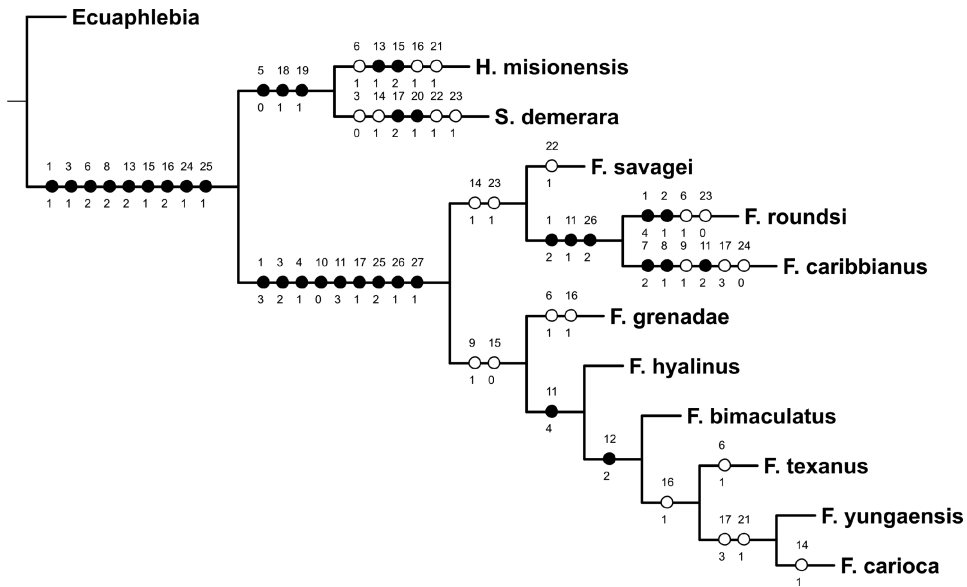


Figure 7. Cladogram obtained from data set (2) (taxa represented by adults and larvae, indicated by '+' in Table 1). Black circles = apomorphies; empty circles = homoplasies.

time, including that of the unusual species *F. roundsi*. The inclusion in this study of the data of two more larvae not only did not change the proposed relationships, but also provided more stability to the results. In both analyses, only one tree was obtained (six and four respectively in the previous one), showing the same relationships.

We can expect that even if more larval data of the treated species are included in this matrix, it will not alter the relationships already proposed, although new data will give more resolution to the cladogram.

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