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Systematics, cladistics and biogeography of the American genus *Farrodes* (Ephemeroptera: Leptophlebiidae: Atalophlebiinae)

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Cladistic and biogeographic analyses of the genus *Farrodes* are presented. Two species groups are delineated within *Farrodes*: *F. caribbianus* and *F. bimaculatus*. Three species formerly placed in other genera—*Thraulus caribbianus* Traver, *Thraulus roundsi* Traver and *Homothraulus maculatus* (Needham & Murphy)—are transferred to *Farrodes*. The species of the *F. caribbianus* species group are revised. Three new species are described: ***F. savagei*** from Venezuela, ***F. maya*** and ***F. mexicanus*** from Mexico. Keys to separate the two species groups of *Farrodes* and the species of the *F. caribbianus* species group are provided. Successive cladistic analyses were carried out on both adult and nymphal characters using Hennig86 and CLADOS. The matrix was composed of all available data (nymphal characters were missing for some species), from nymphal and adult stages separately and on taxa represented by both adult and nymphal characters. Species of the genera *Simothraulopsis* and *Homothraulus* (components of the *Farrodes* lineage) were included in the analyses, and *Ecuaphlebia* was used as the outgroup. Results of the four analyses are compatible. The historical biogeography of *Farrodes*, with a distribution from northern Argentina to southern Texas, is analysed using the program COMPONENT. Areas of endemism are established, and some of their relationships compared with those of other groups available in the literature.

ADDITIONAL KEY WORDS:—Neotropics – South America – phylogeny – evolution – distribution – areas of endemism – mayflies – aquatic insects.

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INTRODUCTION

The existence of the '*Farrodes* lineage' was first proposed by Savage (1987a). This complex includes the genera *Farrodes* Peters, 1971, *Simothraulopsis* Demoulin, 1966 and *Homothraulus* Demoulin, 1955 and, according to Savage was "based on initial studies without documented phylogenetic analyses". This was the first attempt to delineate some of the Leptophlebiidae lineages in northern South America. Relationships among the proposed 'warm adapted' lineages of Atalophlebiinae remained obscure. In 1991, Flowers & Domínguez studied the phylogeny of the *Hermanella* complex (Leptophlebiidae), including representatives of several other lineages, but none of the members of the '*Farrodes* lineage'. Kluge (1991) revised the Leptophlebiidae of Cuba, and based on those restricted data proposed the tribe Hagenulini, including *Farrodes* and *Homothraulus* but excluding *Simothraulopsis*. He introduced several mistakes (see Discussion) that were evident when new information about *Simothraulopsis* (Domínguez *et al.*, 1997) and *Homothraulus* (Domínguez, in prep.) became available.

In this paper I analyse the phylogenetic relationships and biogeography of the species known by adults or adults and nymphs, belonging in the genus *Farrodes*. As no previous phylogeny of the 'lineage' is available, *S. demerara* (Traver, 1947) the single component of the genus *Simothraulopsis* (Domínguez *et al.*, 1997) and *Homothraulus misionensis* (Esben-Petersen, 1912), the only species in this genus known from nymphs and adults, were also included in the analysis for the correct generic assignment of the treated species. In addition to the genera included by Savage (1987a), there are two species described in the genus *Thraulus*—*T. roundsi* Traver, 1947 and *T. caribbianus* Traver, 1943—that belong in the *Farrodes* lineage, and several new species from South and Central America that should be treated along with them. The new species belonging in the *Farrodes caribbianus* species group are described and the species transferred from *Thraulus* and *Homothraulus* are redescribed or illustrated as needed. The areas of endemism are delimited and their relationships are analysed.

MATERIAL AND METHODS

The material used in this study is deposited in the following institutions: Florida A & M University, Tallahassee, FL, U.S.A. (FAMU); National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A. (NMNH); Cornell University Insect Collection, Ithaca, NY, U.S.A. (CUIC); Fundación-Instituto Miguel Lillo, Tucumán, Argentina (IFML); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (MACN). The techniques used for mounting microscopic slides in Canada balsam were the usual for the group; however, when unique specimens were examined genitalia were first mounted in a nonpermanent medium, glycerin jelly (Guyer, 1953). This method allows examination and illustration from different perspectives, and for subsequent transfer of the specimen to Canada balsam without noticeable alteration of structures.

The phylogenetic relationships and biogeography of the taxa were analysed using the software Hennig86 (Farris, 1988), CLADOS (Nixon, 1992) and COMPONENT (Page, 1989a).

SYSTEMATICS

In this cladistic analysis, all the South American Atalophlebiinae that have variously developed postero-lateral projections on the styliger plate are included. Species of the three genera assigned by Savage (1987a) to the *Farrodes* lineage (*Farrodes*, *Homothraulus* and *Simothraulopsis*) are also included to determine the phylogenetic relationships among them and with the new taxa. Additionally, two species transferred from *Thraulus* and several new species that belong in this monophyletic group are incorporated.

The genus *Simothraulopsis* Demoulin is represented in the analysis by material recently reared (Domínguez, *et al.*, 1997), as the original description of the type species of the genus (*S. surinamensis* Demoulin) was based on only six young nymphs.

Data for the genus *Homothraulus* are from the type species, *H. misionensis* (Esben-Petersen), reared for the first time by the author and W.L. and J.G. Peters. Besides this species, only two other species were previously described: *H. larensis* (Navas), poorly described from male and female imagos, and *H. lucretiae* Traver, known only from female imagos.

All the species of *Farrodes* known from imagos are included in the analysis (only *F. taino* Lugo-Ortiz & McCaffery described solely from nymphs, is not treated), with three species transferred in this paper, two from *Thraulus* (*T. caribbianus* and *T. roundsi*) and one from *Homothraulus* (*H. maculatus*). Three new species of *Farrodes* are also included in the analysis.

Farrodes Peters

Farrodes Peters, 1971: 5; Domínguez & Savage, 1987: 43; Kluge, 1993: 247.

The genus *Farrodes* was established by Peters (1971) for three species from the Antilles. Later two more species were described from northern Argentina (Domínguez & Savage, 1987), one from Southern Texas (Davis, 1987) and one from Puerto Rico

(Lugo-Ortiz & McCafferty, 1994), the last one known only from nymphs. Recently, eight new species from Central and South America were described (Domínguez, Molineri & Peters, 1996). In this paper two species groups are delineated, namely *caribbianus* and *bimaculatus*, and three new species are described and three others are transferred and discussed or redescribed. What seemed initially to be a small genus restricted to the Antilles is proving to be widespread from Texas to South America, and it is also species rich with several new species yet to be described.

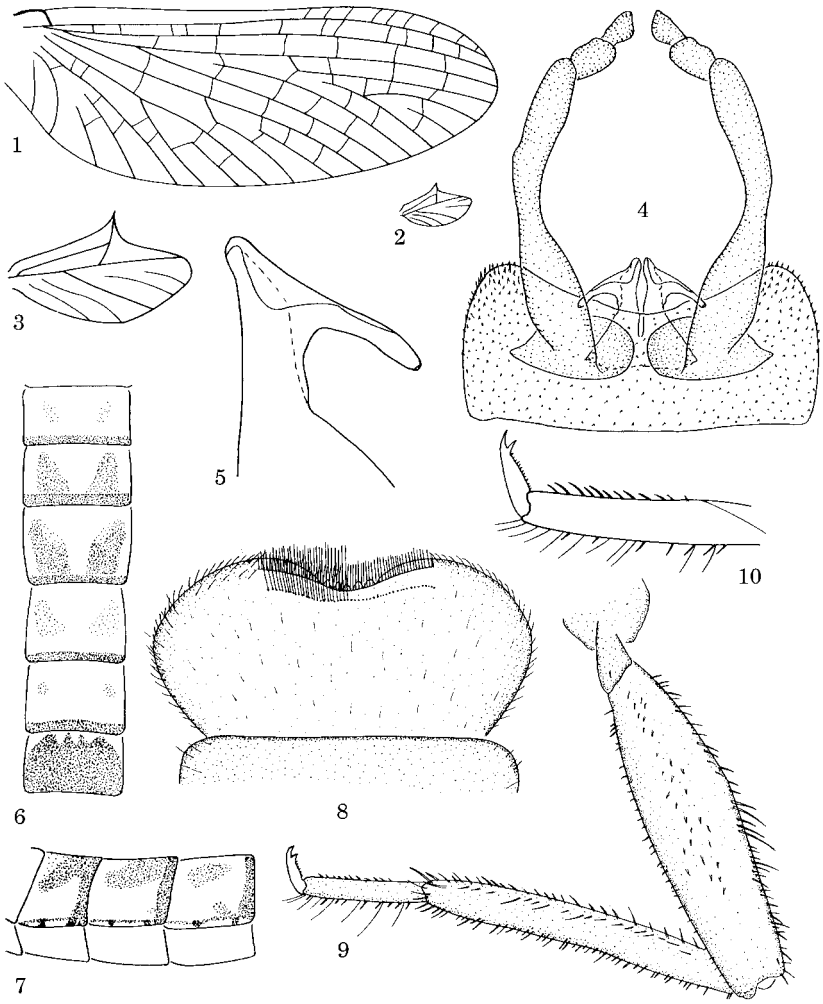
KEY FOR THE SPECIES OF THE *FARRODES CARIBBIANUS* SPECIES GROUP

♂ *Imagos*

1. Penis projections cylindrical, long (Figs 21, 60); costal projection of hind wings small (0.16 of total width) ..... *F. bimaculatus* species group
   Penis projections shaped as an inverted funnel (Figs 17, 59) or conical, curved inward (Figs 4, 57) or curved apically upward (Figs 26, 36, 61), costal projection of hind wings large (more than 0.19 of total width) ..... *F. caribbianus* species group, 2
2. Medial projection of styliger plate present (Figs 16, 59); penis projection ventral, shaped as an inverted funnel (Fig. 17); abdominal colour pattern as in Figures 14, 15 ..... *F. roundsi* **comb. nov.**
   Medial projection of styliger plate absent; penis projections lateral and conical, curved apically inward (Figs 4, 57, 58), or upward (Figs 26, 36); abdominal color pattern not as above 3
3. All abdominal segments dark coloured, as in Figures 45, 46; penis lobes completely divided (Figs 43, 44, 63, 64) ..... ***F. mexicanus* sp. nov.**
   Some abdominal segments hyaline; apical 3/4–4/5 penis lobes divided 4
4. Lateral projections of styliger plate rounded, widely based (Fig. 4); base of penis lobes widened at right angle, with small spines (Fig. 58); penis projections conical, curved inward (Figs 4, 5, 57, 58), abdominal pattern as in Figures 6, 7 ..... *F. caribbianus* **comb. nov**
   Lateral projections of styliger plate with base well defined (Figs 26, 36), apex rounded; base of penis lobes roundly widened; penis projections conical, not curved apically inward (Figs 27, 37); abdominal colour pattern not as above ... 5
5. Abdominal colour pattern as in Figures 38, 39; penis projections with a short apical tubule (Fig. 37). ..... ***F. maya* sp. nov.**
   Abdominal colour pattern as in Figures 28, 29; penis projections without apical tubule (Fig. 27) ..... ***F. savagei* sp. nov**

Nymphs

1. Long spines on outer margin of hind tarsi (Fig. 10); spines on dorsum of hind femora acute (Fig. 9); abdominal colour pattern similar to adult pattern (Figs 6, 7) ..... *F. caribbianus* comb. nov.
   Spines on outer margin of hind tarsi short (Fig. 31); spines on dorsum of hind femora blunt (Fig. 30); abdominal colour pattern similar to adult pattern (Figs 28, 29) ..... ***F. savagei* sp. nov.**



Figures 1–10. *Farrodes caribbianus*. 1, forewing; 2, hind wing; 3, hind wing, enlarged; 4, ♂ genitalia, v.v.; 5, penis lobe, detail; 6, abdominal terga II–VII; 7, abdominal segments III–V, l.v. Nymph: 8, labrum, d.v.; 9, leg III, d.v.; 10, detail tarsus III.

Farrodes caribbianus (Traver) **comb. nov.**
(*Figs 1–10, 57, 58*)

Thraulus caribbianus Traver, 1943: 79; Traver, 1960: 73; Hubbard, 1982: 267.

Thraulus caribbianus was described by Traver (1943) based on a male imago and two females, an imago and a subimago. According to the author, this species is allied to *T. maculatus* (now *Farrodes maculatus*) because of the hind wing type and the lateral appendages of the penes, although she pointed out the uniqueness of the structure of the penes.

In 1960, when commenting on the genus *Thraulus* in the New World, Traver detailed some of the similarities and differences between *Thraulus demerara*, *T. caribbianus* and *T. roundsi* and *Homothraulus*. She suggested that these species probably

were not congeneric and that there was insufficient evidence for placing them in *Homothraulus*. Therefore, she proposed to leave them provisionally in *Thraulus*.

My cladistic analysis shows *T. caribbianus* to be more closely related to the species now included in *Farrodes*. Therefore, I am here transferring *caribbianus* to *Farrodes*.

As the original descriptions of the adults are adequate, I am not redescribing them, but I am including illustrations of the genitalia (Figs 4, 5), wings (Figs 1–3) and abdomen (Figs 6, 7), as well as micrographs of the genitalia (Figs 57, 58). The nymphs are described for the first time.

Mature nymph. In alcohol. Body length: 3.8–4.6 mm. General coloration yellowish-brown, abdomen darker. *Head:* yellowish-brown, washed with black between posterior ocelli and around base of antennae. Upper portion of eyes of male light orange-brown, lower portion black. Eyes of female black. Antennae: scape and pedicel greyish-brown, flagellum yellowish, lighter toward apex. Mouthparts: yellowish-brown, molars of mandibles, crown of setae and outer margin of galea-lacinia of maxillae reddish-brown, basal 2/3 of mandibles diffusely washed with black. *Thorax:* terga light orange-brown, with pronotum, anterolateral corners of mesonotum and metanotum washed with black; pleura yellowish, with areas around coxae tinged with black; sterna yellowish-white. *Legs:* yellowish-brown, with coxae and trochanters washed with black, subapical blackish band on apex of femora, and wide brownish band on middle of tibiae. Claws light orange. Spines on dorsum of hind femora acute (Fig. 9); long spines on outer margin of hind tarsi (Fig. 10). *Abdomen:* terga light brown, males with black markings on terga III-VI resembling those of male imagos, terga VII-X almost completely washed with black, females with all terga washed with black, except anterolateral corners of terga III-VII; sterna yellowish-white, with posterolateral areas of sterna VII–VIII and sternum IX tinged with black. Gills blackish. Caudal filaments orange-brown, lighter apically.

Distribution. Venezuela, Ecuador, Costa Rica and Panama.

Material. Holotype ♂ imago: VENEZUELA, Antimano, 900 m, 13/I/1940, R. Lichy. J.R. Traver private collection (now in FAMU); also studied: VENEZUELA: 21 ♂ imagos, 3 ♀ imagos, 7 ♂ subimagos, 8 nymphs, Aragua State, P.N. Henri Pittier, Rio La Trilla, 22.5 km N of Rancho Grande on Road, 17–19/IX/1979, H.M. Savage (FAMU); COSTA RICA: 34 ♂ imagos, Guanacaste, R. Tizate, 7.2 km NE Cañas Dulces. 10.733°N; 85.449°W.275 m. 28/VI/1986, Holzenthal, Heyn, Armitage (FAMU); PANAMA: 8 ♂ imagos, 3 ♂ subimagos, 16 nymphs, Canal Zone, Pipeline Rd, Rio Frijoles, 50′, 25/XII/1977, R.W. Flowers (FAMU); 3 ♂ imagos, 18 ♂ subimagos, 2 ♀ subimagos, Bocas del Toro Prov., Rio Teribe at Zegla, 20/IV/1985, R.W. Flowers, A. Gonzalez (FAMU); 16 ♂ imagos, 3 ♀ imagos, same data, except date and collector: 23/IV/1985, R.W. Flowers (FAMU); 4 ♂ imagos, 2 ♀ imagos, Rio Changuinola at Zegla, 4–6 AM, 25–26/IV/1985, R.W. Flowers (FAMU); 17 nymphs, Chiriqui Prov., Cuenca Fortuna, Quebrada Aleman, 3900′, 18°C; 11/V/1985, R.W. Flowers; 8 nymphs, Cuenca Fortuna, str. on trail to Caldera, 6/VI/1985, 3700′, 19°C, R. W. Flowers (FAMU); 6 ♂ subimagos, San Blas, Rio Carti grande, 2 km W Nsagandi, 5/III/1985, O. S. Flint & Louton (NMNH); 1 ♂ imago and 12 ♂ subimagos, Rio Canita, 24/II/1985, O. S. Flint, Louton, (NMNH). The association of nymph and adult is by rearing, done by H. Savage in Venezuela.

Discussion. This is a very distinctive species, widely distributed in Venezuela, Costa Rica and Panama. There is rather great variation in the coloration. Some individuals have a dark pattern and others a lighter one, sometimes with the black markings on terga III–VI almost absent. Both colour morphs are sometimes present at the same locality, and no other differences are apparent. Thus, I consider these colour morphs a result of intraspecific variation.

F. caribbianus can be separated from all the other species of *Farrodes* by the following combination of characters. In the imago: (1) lateral projections of styliger plates short, blunt and widely based (Fig. 4); (2) apex of penis lobes produced in an obtuse angle (Figs 5, 57, 58); (3) base of penis lobes widened at right angle, with a few spines (Fig. 58); (4) penis projections lateral, conical, curved inward as in Figs 57, 58; (5) base of ICu_1 of forewings free basally (Fig. 1); (6) abdominal colour pattern as in Figure 6, 7.

In the nymph: (1) spines on outer margin of tarsi III long (Fig. 10); (2) spines on dorsum of hind femora acute (Fig. 9); (3) thick setae on basal half of outer margin of labial palpi II; (4) abdominal colour pattern similar to adult pattern (Figs 6, 7).

Farrodes roundsi (Traver) **comb. nov.**
(*Figs 11–17, 59*)

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

The male and female imagos of this species were described in *Thraulus* by Traver (1947), although she stated that "The genitalia are so different from most species of *Thraulus* that its affinities with other species cannot be determined. It may not belong in this genus". Later it was demonstrated that the genus *Thraulus* was not present in South America.

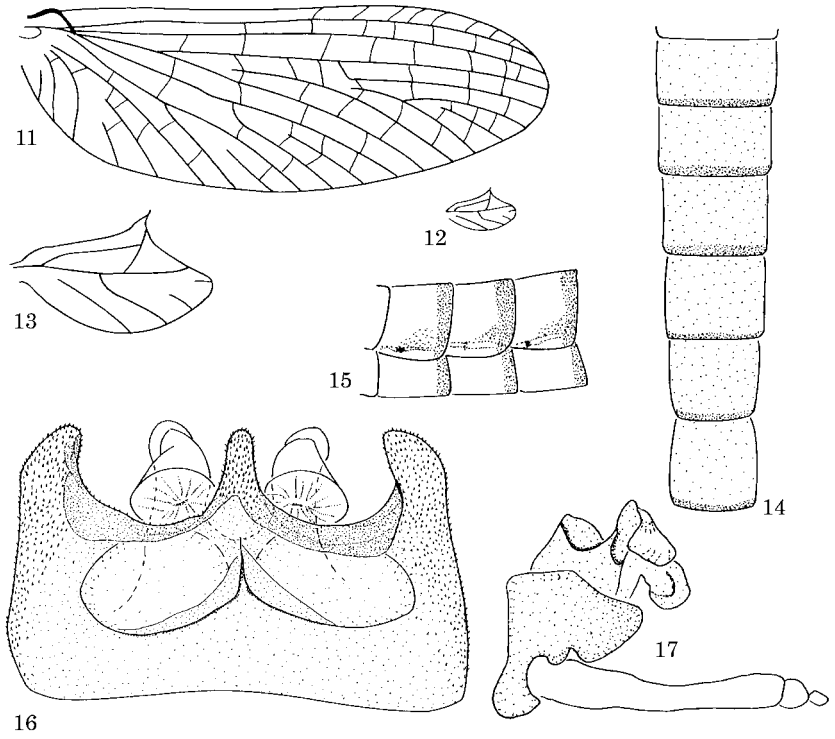
After the present revision, it is clear that this species is related to the taxa in the *Farrodes* complex. For this reason I am transferring *T. roundsi* to *Farrodes*, although it is possible that with more information, especially from the nymphal stage which is still unknown, the establishment of a new genus could be justified.

As the original descriptions are adequate, I am not redescribing this species, but I am including new drawings of the genitalia (Figs 16, 17), wings (Figs 11–13), abdomen (Figs 14, 15) and scanning micrograph of the genitalia (Fig. 59). The illustrations were made from new material which was compared with the holotype.

Discussion. The following synapomorphies place this species in the *Farrodes* complex: (1) presence of lateral projections on styliger plate (Fig. 16); (2) inner margins of forceps sockets elevated; (3) spines on venter of styliger plate larger on lateral areas, especially on lateral projections; (4) vein Icu_1 of forewings free basally (Fig. 11).

F. roundsi can be separated from all the other species of the genus by the following combination of characters: (1) lateral projections of styliger plate medium size, cylindrical and curved inwardly (Fig. 16); (2) medial projection of styliger plate present, shaped as in Figs 16, 59; (3) ventral penis projection shaped as an inverted funnel.

There is some variation in coloration among the individuals from different localities, but it is considered insufficient to separate them as discrete entities.



Figures 11–17. *Farrodes roundsi*. 11, forewing; 12, hind wing; 13, hind wing, enlarged; 14, abdominal terga II–VII; 15, abdominal segments III–V, 16, ♂ genitalia, v.v.; 17, ♂ genitalia, l.v.

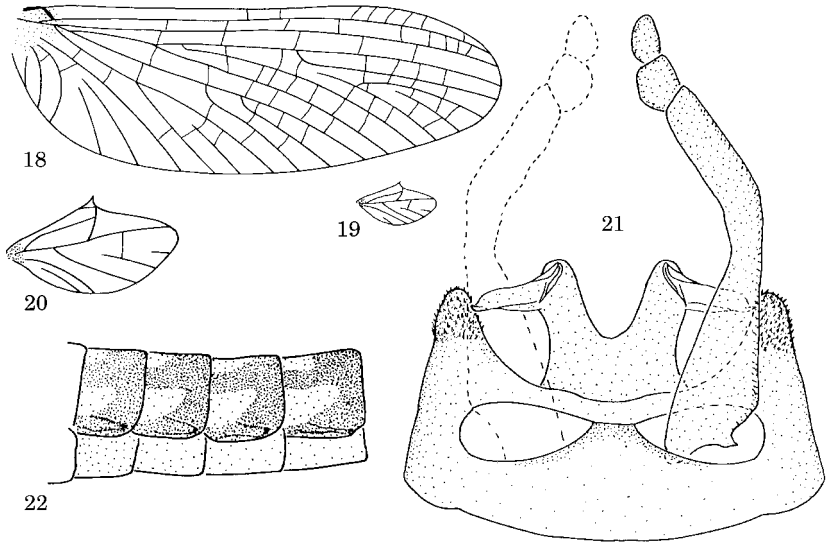
Distribution. Costa Rica and Panama.

Material. Holotype ♂ imago and Allotype ♀ imago: COSTA RICA, Rio Pedregoso, II/1939, D. L. Rounds. J.R. Traver private coll. (now in FAMU); also studied: COSTA RICA: 1 ♂ imago and 1 ♂ subimago, Guanacaste, P. N. Guanacaste, Maritza, Rio Tempisquito, 10°958′N, 85°497′W, el. 550 m, 17–18/VI/1988, Flint & Holzenthal (USNM); 2 ♂ imagos, Guanacaste, P. N. Guanacaste, Maritza, N of Liberia, 18 km E Interamerican Highway, V. Orosi, Rio Tempisquito, C. De la Rosa, 04/VII/1989 (USNM); 11 ♂ imagos, 3 ♀ imagos, Alajuela, Cerro Campana, Rio Bochinche trib., 6 km (air) NW Dos Rios, 10°945′N, 85°413′W, el. 600 m, 22–23/VII/1987, Holzenthal, Morse, Clausen (FAMU); PANAMA: 2 ♂ imagos, Prov. Chiriqui, Fortuna, 8°44′N, 82°15′W (light trap), 7/X–11/XI/1976, Henk Wolda (FAMU); 2 ♂ imagos, same data except. el. 1000 m, 12–18/X/1977.

Farrodes maculatus (Needham & Murphy) **comb. nov.**
(*Figs 18–22*)

Thraulus maculatus Needham & Murphy, 1924:45; Ulmer, 1943:28; Traver, 1947: 149.
Homothraulus maculatus; Traver, 1960: 73; Tsui & Peters, 1972: 565; Hubbard, 1982: 265.

This species was described by Needham & Murphy (1924) based solely on male imagos. These authors remarked that *T. maculatus* was "near [*Thraulus] misionensis*".



Figures 18–22. *Farrodes maculatus*. 18, forewing; 19, hind wing; 20, hind wing, enlarged; 21 ♂ genitalia, v.v.; 22, abdominal segments III–VI.

Later Traver (1960) transferred *T. maculatus* to *Homothraulus*, following Demoulin's (1955) transfer of *T. misionensis*. As the original description is inadequate, I am also including a redescription of the male imago.

Holotype ♂ imago (on slide). Length: body, 5.0–5.2 mm; forewings, 6.0 mm; hind wings, 0.9 mm. General coloration brownish, some abdominal segments translucent. *Head:* light brown, washed with black on anterior margin and behind the posterior ocelli. Upper portion of eyes orangish-brown, lower portion blackish. Ocelli white with inner margins black. *Antennae:* scape and pedicel light brown [flagellum broken-off and lost]. *Thorax:* pronotum light brown, washed with black; meso- and metanotum bright orange-brown with carinae and sutures darker; pleura and sterna orange-brown, with membranous areas lighter. *Wings* (Figs 18–20): membrane of forewings hyaline, except base washed with brown. Veins light brown, lighter posteriorly. [Hind wings folded and not observable]. *Legs:* legs I light brown with a darker spot on basal half and apex of femora; legs II and III yellowish-brown with darker spot on apex of femora II and dark brown band on subapex of femora III; claws grayish-brown. *Abdomen* (only visible from lateral view): yellowish translucent, tergum I heavily washed with black, terga II–VII with areas washed with black, as in pattern shown (Fig. 22) [remaining segments broken off and lost]. *Genitalia* (from paratype) (Fig. 21): subgenital plate light brown; forceps light brown, paler toward apex. Penis lobes same colour as apex of forceps. [Caudal filaments broken-off and lost].

Female and Nymph. Unknown.

Material. Holotype, ♂ imago, ARGENTINA, Cosquin, 8/III (CU 642.1) (Slide # 654); Paratype: Male imago, ARGENTINA, Santa Fe. (CU 642.2) (Slide # 654).

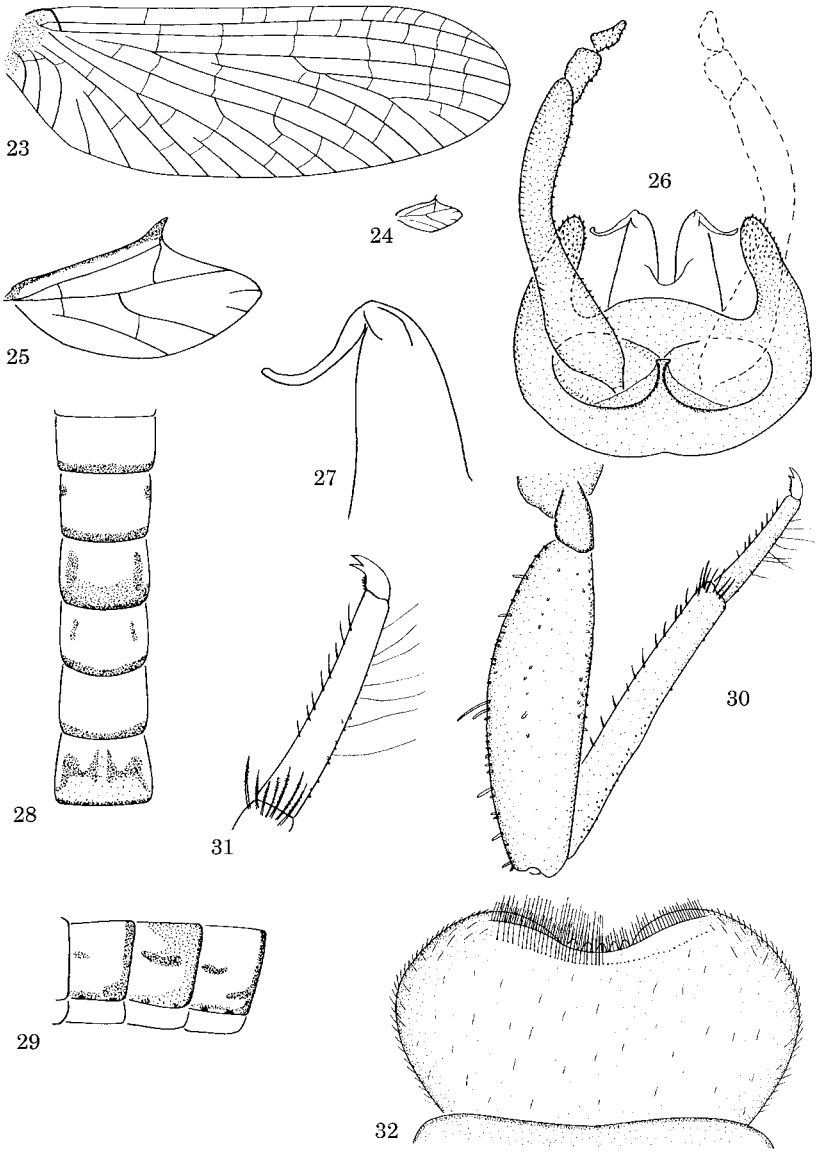
Discussion. There are only two slides, one with the holotype (body, head, legs and wing [genitalia missing]), and an extra set of fore and hind wings. The extra wings

can be distinguished because they differ in colour from the ones mounted in balsam with the body. The paratype slide contains only one set of wings, the genitalia and the body are apparently lost. The redescription was made using parts from both slides. Study of these types suggests that this species is more closely related to species in *Farrodes* than in *Homothraulus*. For this reason, I am transferring *H. maculatus* to *Farrodes*. *F. maculatus* can be separated from the other species of the genus by (1) the general shape of the penis projections (Fig. 21) and (2) the abdominal colour pattern (Fig. 20).

***Farrodes savagei* sp. nov.**
(*Figs 23–32, 61, 62*)

♂ *Imago*. In alcohol, wings and genitalia on slide. Length: body, 4.2–4.5 mm; forewings, 4.4–4.6 mm; hind wings, 0.6–0.7 mm. General coloration orange-brown, with abdominal segments translucent. *Head:* yellowish with a black band along the anterior margin and around base of antennae. Upper portion of eyes yellowish-brown, lower portion blackish. Ocelli white with a narrow basal black ring. Antennae yellowish, washed with greyish toward apex of flagellum. *Thorax:* pronotum yellowish-brown with carinae and lateral margins blackish; meso- and metanotum orange-brown, with carinae and lateral margins of mesonotum and posterior 1/2 of metanotum washed with black; pleura and sterna orange-yellow, with margins slightly darker. *Wings* (Figs 23–25): Membrane of forewings hyaline, except stigmatic area whitish translucent and wing base light brown. Veins C, Sc and R_1 light brown, lighter toward apex, remainder hyaline; 9–10 stigmatic cross veins, 1–2 costal cross veins basal to bullae. Membrane of hind wings translucent, with wing base and veins C and Sc light brown. *Legs:* Forelegs. Coxae yellowish with an anterior black spot near the base; trochanters and femora light yellow; tibiae and tarsi yellowish-white, lighter toward apex. Legs II similar to I, but tarsi light orange, darker toward apex; legs III similar to I, except with a subapical black band on femora, covering almost 1/4 of total length of femora. *Abdomen* (Figs 28, 29): Tergum I blackish; terga II–VI hyaline with posterior margins, posterolateral corners and spiracular openings tinged with black; black marks on terga IV–V as in Figure 28; terga VII–X yellowish, darker posteriorly with posterior margins, lateral corners and medial area washed with black. Sterna I–VII hyaline, remainder yellowish. *Genitalia* (Figs 26, 27, 61, 62): subgenital plate yellow-orange; forceps yellowish, lighter apically; penes yellowish. Caudal filaments light grey.

♀ *imago*. In alcohol. Length: body, 4.5–4.7 mm; forewings, 5.0–5.2 mm; hind wings, 0.7–0.8 mm. General coloration yellowish-brown. *Head:* yellowish-white, with black band along anterior margin and around base of antennae, diffusely stained with black between lateral ocelli and posterior margin of head. Eyes black. Ocelli white with a narrow basal black ring. Antennae as in ♂ imago. *Thorax:* terga, pleura, wings and legs as in ♂ imago, except black subapical band present on femora II; sterna yellowish, widely tinged with black on prosternum and basisternum II. *Abdomen:* terga orange-yellowish, with the posterior margins black and black markings occupying most of segments, delimiting a more or less rectangular area close to lateral margins, yellowish; marks on terga IV–V as in Fig. 28; sterna yellowish, with



Figures 23–32. ***Farrodes savagei* sp. nov.** 23, forewing; 24, hind wing; 25, hind wing, enlarged; 26, ♂ genitalia, v.v.; 27, penlis lobe, detail; 28, abdominal terga II–VII; 29, abdominal segments III–V, l.v. Nymph: 30, leg III, d.v.; 31, detail tarsus III; 32, labrum, d.v.

lateral margins of segments I–VII and the whole of segments VIII–X tinged with black; 9th sternum conical, entire. Caudal filaments yellowish-orange.

Mature nymph. In alcohol. Body length: 4.0–4.5 mm. General coloration yellowish-brown. *Head:* orange-brown, diffusely washed with black, heavier around base of antennae and toward anterior margins of eyes. Upper portion of eyes of male reddish-brown, lower portion black. Eyes of female blackish. Antennae: scape and

pedicel light brown, flagellum yellowish, paler toward apex. Mouthparts: yellowish-brown, molars of mandibles and crown of setae of galea-lacinia of maxillae reddish-brown, basal half of mandibles and base of cardo of maxillae heavily washed with black, remaining mouthparts slightly washed with black. Labrum as in Figure 32. *Thorax:* terga light orange-brown, heavily washed with black along lateral margins of pro- and mesonotum; pleura and sterna yellowish, with pleural sclerites washed with black. Legs (Fig. 30): yellowish-brown, with a small subapical spot on femora I and II and a wide subapical band on femora III; basal and subapical bands on tibiae. Claws orangish. Spines on dorsum of hind femora blunt (Fig. 30); spines on outer margin of hind tarsi short (Fig. 31). *Abdomen:* terga yellowish-brown, with black markings as in imagos of the corresponding sex; sterna yellowish. Gills greyish-black. Caudal filaments yellowish-brown, lighter apically.

Etymology. I name this species after my colleague, Dr Harry M. Savage, who collected and reared the material on which the description is based and kindly allowed me to study it.

Distribution. Venezuela.

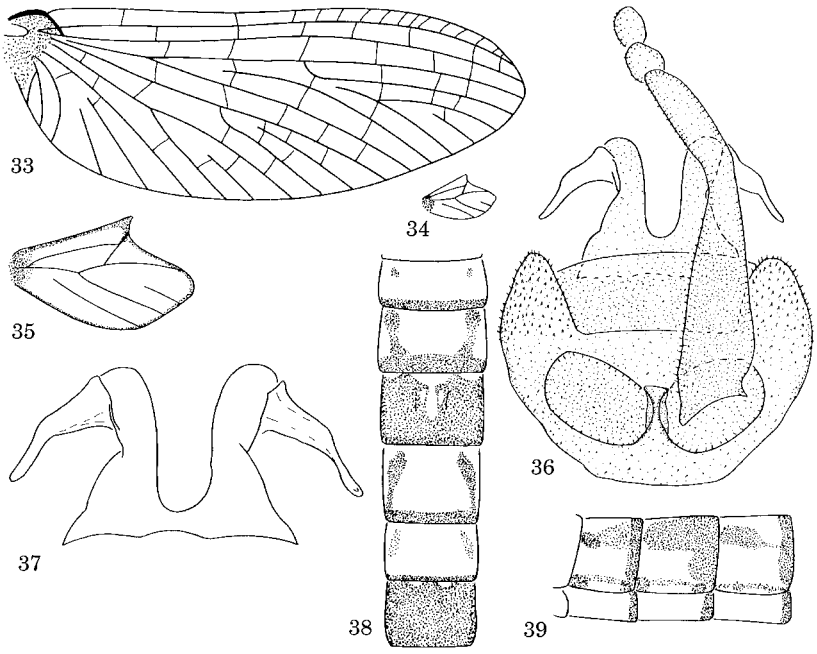
Material. Holotype ♂ imago: VENEZUELA, Zulia State, Perija, El Tucuco, Mission El Tucuco, Rio del Pelaya, 2 1/2 km from church, 28–30/XI/1979. H. M. Savage (FAMU). Allotype ♀ imago, same data as holotype. Paratypes: 6 ♂ imagos, 2 ♀ imagos, 6 nymphs, same data as holotype; 1 ♂ subimago, 6 nymphs, same data as holotype, except date: 1–5/X/1979; 2 ♀ imagos, 1 nymph, same data as holotype, except dates: 9–11/X/1979. The association of nymphs and adults is by rearing by H.M. Savage. All material deposited in FAMU, except 2 ♂ imagos and 2 nymphs in IFML.

Discussion. F. savagei can be separated from all the other species of *Farrodes* by the following combination of characters. In the imago: (1) penis lobes divided on apical 3/4–4/5; (2) ventral projections of penis conical, curved apically upward (Figs 26, 27, 61, 62); (3) lateral projections of styliger plate medium size, cylindrical, straight and rounded apically (Fig. 26); (4) abdominal terga II–VI hyaline, with black markings as in Figures 28, 29.

In the nymph: (1) spines on outer margin of tarsi short (Fig. 31); (2) thick setae on basal half of outer margin of labial palpi II; (3) abdominal pattern as in male imago (Figs 28, 29).

Farrodes maya **sp. nov.**
(*Figs 33–39*)

Holotype ♂ imago. In alcohol, one pair of wings and genitalia on slide. Length: body, 4.8–5.0 mm; forewings, 4.9–5.0 mm; hind wings, 0.4–0.5 mm. General coloration brownish, with some abdominal segments translucent. *Head:* yellowish, washed with black on anterior margin. Upper portion of eyes greyish-brown, lower portion blackish. Ocelli white with a basal black ring. Antennae whitish, washed with black on scape and pedicel. *Thorax:* pronotum light brown with margins and sublateral spots blackish; mesonotum bright yellow-brown, with lateral margins and scutellum II washed with black; metanotum yellowish, diffusely washed with black; pleura



Figures 33–39. ***Farrodes maya* sp. nov.** 33, forewing; 34, hind wing; 35, hind wing, enlarged; 36, ♂ genitalia, v.v.; 37, penis lobe, detail; 38, abdominal terga II–VII; 39, abdominal segments III–V, l.v.

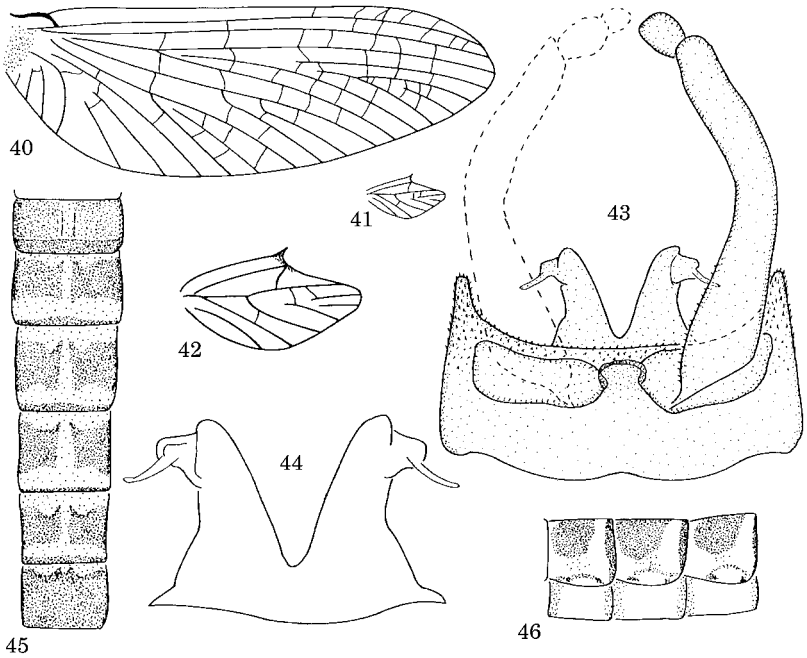
bright yellow, with sclerites around coxae tinged with black; sterna yellowish, with medial area lighter. *Wings:* (Figs 33–35): membrane of forewings hyaline, with stigmatic area translucent and wing base light brown. Longitudinal veins light brown, lighter toward posterior margin, cross veins hyaline; 13 stigmatic cross veins, 1 costal cross vein basal to bullae. Membrane of hind wings translucent with wing base and short basal portion of longitudinal veins dark brown. *Legs:* coxae light brown, washed with black; trochanter yellowish [remainder of legs broken-off and lost]. *Abdomen* (Figs 38, 39): terga I and VIII-X blackish-brown, terga II–VII hyaline with blackish sublateral longitudinal streaks on terga III and V–VI and large blackish-brown spots covering the 2/3 central of terga IV and VII; posterior margin of each segment blackish. Sternum I light yellow, sterna II–VI translucent with posterior margin blackish, sterna VII–VIII blackish-brown. *Genitalia* (Figs 36, 37): subgenital plate brown, forceps yellowish-brown, lighter toward apex; penes yellowish. [Caudal filaments broken-off and lost].

Female imago and nymph. Unknown.

Etymology. This species is named after the culture of the native people that ruled the area where the holotype was collected. Noun in apposition.

Distribution. Mexico.

Material. Holotype ♂ imago: MEXICO, Chiapas, Cascada Misolija, 20 km S Palenque, 17–18/V/1981. C.M. & O.S. Flint, Jr. (NMNH).



Figures 40–46. ***Farrodes mexicanus* sp. nov.** 40, forewing, 41, hind wing; 42, hind wing, enlarged; 43, ♂ genitalia, v.v.; 44, penis lobe, detail; 45, abdominal terga II–VII; 46, abdominal segments III–V, l.v.

Discussion. This species is known only from the holotype, but is so characteristic in its abdominal color pattern and genitalia, that it is clearly an undescribed species. The imago of *Farrodes maya* can be separated from the other species of the genus by the following combination of characters: (1) long apical tubule on penis projections (Fig. 37); (2) lateral projections of styliger plate short, with apex rounded (Fig. 36); (3) abdominal segments II–VII with markings, as in Figure 38.

***Farrodes mexicanus* sp. nov.**
(*Figs 40–46, 63, 64*)

♂ *imago.* In alcohol, one pair of wings and genitalia on slide. Length: body, 5.8–6.2 mm; forewings, 7.0–7.3 mm; hind wings, 1.3–1.5 mm. General coloration dark brown. *Head:* light brown, washed with black along anterior margin and especially between base of antennae and lower portion of eyes. Upper portion of eyes greyish-brown, lower portion blackish. Ocelli white with a narrow basal black ring. Scape and pedicel of antennae yellowish-brown [flagellum broken-off and lost]. *Thorax:* pronotum light brown, anterior margin blackish, and sublateral areas washed with black; meso- and metanotum bright brown, with sutures and scutellum II lighter; pleura bright brown, with areas around coxae washed with black; sterna yellowish-brown. *Wings:* 1(Figs 40–42): membrane of forewings hyaline, except stigmatic area whitish and base of wing tinged with brown; longitudinal vein yellowish-brown, cross veins light yellow; twelve stigmatic cross-veins. Membrane

of hind wings hyaline, with wing base tinged light brown; longitudinal veins light brown, lighter toward apex. *Legs:* coxae light brown, washed with black, trochanters yellowish [remainder of forelegs broken-off and lost]; femora, tibiae and tarsi light yellow, with subapical black spot on femora III. Claws greyish. *Abdomen* (Figs 45, 46): terga yellowish, with terga I–II and VII–X completely washed with black, in terga III–VI blackish area restricted to the medial 2/3 with a pattern as in Figure 45. Sterna translucent, with sterna I and VII–VIII light brown, sterna II–VI yellowish. *Genitalia* (Figs 43, 44, 63, 64): subgenital plate and basal 1/3 of forceps segments I light brown, remainder of forceps whitish; penes greyish. Caudal filaments yellowish.

Female imago and nymph. unknown.

Etymology. mexicanus, for the country where the specimens were collected.

Distribution. Mexico.

Material. Holotype ♂ imago: MEXICO, Veracruz, Rio Jamapa, 6 km N. Coscomatepec, 26/V/1981. C.M. & O.S. Flint, Jr. (NMNH). Paratypes: 2 ♂ imagos, 1 ♂ subimago, same data as holotype (NMNH); 11 ♂ imagos, Veracruz, Fortín de las Flores, Cervezería Moctezuma, 16–17/V/1964, Blanton, Broce & Woodruff (FAMU); 12 ♂ imagos, same data except date and collector, 18/V/64, Woodruff (7 in FAMU, 4 in IFML).

Discussion. There is some variation in the intensity of the abdominal coloration, even among specimens from the same locality, but it is always possible to identify the general pattern. The imago of *F. mexicanus* can be separated from all other species of *Farrodes* by the following combination of characters: (1) penis lobes totally separated (Figs 44, 63, 64); (2) long apical tubule at apex of penis projections; (3) lateral projections of styliger plate medium size, acute (Fig. 43); (4) abdominal terga yellowish, heavily washed with black, with pattern as in Figure 45.

CLADISTICS

Characters and coding

A matrix of 27 characters (Table 1) was compiled, including 17 adult and 10 nymphal external morphological characters. More than half of the characters are binary (14) and were coded as 0 (plesiomorphic) and 1 (apomorphic). Multistate characters were treated in two different ways: additive (characters 3, 12, 15, 25 and 26) or non-additive (characters 1, 6, 7, 8, 11, 13, 16, 17). Characters with no information available were assigned a missing code (?).

Adult characters

♂ *Genitalia*

Character 1. Lateral projection of styliger plate [nonadditive]. This character presented different degree of development in length, and varied in the form of the apex among the different species; however, in some cases it was not possible to find discrete

TABLE 1. Data matrix for the taxa used in this study. Description of character states included in text. Unknown conditions indicated by '?'. Outgroup indicated by *. Taxa used in analyses 3 and 4 indicated by '+'

Taxon		Character state 1 5 10 15 20 25 | | | | | |
**Ecuaphlebia*	+	0000100001000000?0000000000
H. misionensis	+	1010010201001021011010011 00
S. demerara	+	1000020201002112211101111 00
F. roundsi		4121110200102112 1??????????
F. caribbianus	+	2021122110202112300000102 21
F. maya		3021120210312112???????????
F. mexicanus		302110020031210 1???????????
F. savagei	+	3021120200302112100001112 11
F. bimaculatus	+	3021120210422002100 0?0?2?1
F. grenadae	+	3021110210302001100 0?01211
F. hyalinus	+	3021120210402002100 0?01211
F. iguazuanus		3021120210422001 3???????????
F. maculatus		302111021042200 1???????????
F. texanus	+	3021110210422001100000012 11
F. yungaensis	+	3021120210422001300010012 11
F. flavipennis		302112121040200 1???????????
F. tulija		3021121210402101???????????
F. carioca		3021120210422101 3???????????
F. ochraceous		3021110210422101???????????
F. longispinus		302111021042210 1???????????
F. patikza		302111021042210 1???????????
F. xingu		3021110210422101 3???????????
F. tepui		302111021042210 13??????????

states or correlations. Therefore, all straight, well developed and narrowly based projections were grouped in state 3.

0 = absent; 1 = small, slightly projected; 2 = rounded, base not well defined (Fig. 4); 3 = short to long, straight, apex blunt or acute, base well defined (Figs 21, 26, 36, 43); 4 = medium sized, cylindrical, curved medially (Fig. 16).

Character 2. Medial projection of styliger plate. Although a projection with similar position is present in *Paramaka convexa* (Spieth), because of the form and general structure of the genitalia I believe these two structures are not homologous 0 = absent; 1 = present (Fig. 16).

Character 3. Spines on ventral surface of styliger plate [additive]. Taxa with state 2 also have some large spines on medial area, which is hypothezised to be a remnant of state 1.

0 = small, equal sized; 1 = larger on medial area, between sockets; 2 = larger on lateral areas, especially on lateral projections.

Character 4. Inner margin of forcep sockets elevated. This character is easily observable in the SEM photographs (Figs 57, 59–61, 63), and in slide mounted specimens is observed as a fold (Figs 16, 21, 26, 36, 43). It is not found in any other South American leptophlebiid genera.

0 = no; 1 = yes.

Character 5. Shape of basal part of segment I of forceps. The outgroup presents the state coded 1. This coding was kept because state 0 is widely distributed within the subfamily, especially among the most plesiomorphic genera. Whether it is a true

reversal or a synapomorphy in *Homothraulus* and *Simothraulopsis* is difficult to asess at the present time, however, a reversed coding would not change the overall result.

0 = quadrangular, forming an internal angulation; 1 = not quadrangular, narrowing evenly toward apex.

Character 6. Division of penis [nonadditive]. It is not possible to hypothesize the transformation series at this point, consequently I followed the coding from Flowers & Domínguez, 1991.

0 = lobes totally separated; 1 = apical 1/2–1/3 divided; 2 = apical 3/4–4/5 divided.

Character 7. Shape of apex of penis lobes [nonadditive].

0 = rounded (Figs 16, 27); 1 = acutely angled; 2 = obtusely angled (Fig. 4).

Character 8. Shape of base of penis lobes [nonadditive].

0 = not widened; 1 = widened at right angle (Fig. 58); 2 = roundly widened (Fig. 16).

Character 9. Origin of penis projections.

0 = ventral; 1 = ventrolateral or lateral.

Character 10. Width of base of penis projections.

0 = wide; 1 = narrow.

Character 11. Shape of penis projections [nonadditive].

0 = spine-like; 1 = inverted funnel (Figs 16, 17); 2 = conical, curved inward (Figs 4, 58); 3 = conical, curved apically upward (Figs 26, 27); 4 = cylindrical, long (Figs 21, 60).

Character 12. Structures on apex of penis projections [additive]. The short terminal flap appears to be a folding of the apical tubule, and for this reason is considered as more derived in the transformation series.

0 = absent; 1 = long apical tubule (Fig. 37); 2 = short terminal flap (Fig. 21).

Wings

Character 13: Base of vein ICu_1 in forewings [nonadditive].

0 = Joining CuP; 1 = Joining CuA; 2 = free.

Character 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

Character 15. Shape of presternum [additive].

This character appears to change in the median part from narrow to wide. Its treatment as non-additive did not change the results of the analyses.

0 = deep anteriorly, median part evenly narrow; 1 = shallow anteriorly, with median constriction; 2 = shallow anteriorly, very wide posteriorly.

Abdomen

Character 16. Coloration of abdominal segments [nonadditive].

0 = all segments pigmented (non-*Farrodes* pattern); 1 = all segments pigmented (*Farrodes* pattern, Fig.22); 2 = at least some segments translucent (Figs 6, 38).

Character 17. 9th female sternum [nonadditive].

0 = rounded, entire; 1 = conical, entire; 2 = conical, truncated apically; 3 = conical, with apical notch.

Nymphal characters

Mouthparts

Character 18. Location of widest part of labrum.

0 = 1/2 distance base to apex (Figs 8, 32); 1 = apical 2/3.

Character 19. Tuft of setae on center of outer margin of mandibles. The tuft is also present in other genera within the subfamily, but is generally much stronger than the two states present in this group. For this reason, 'weaker' and 'stronger' are relative within this group.

0 = weaker; 1 = stronger.

Character 20. Two or more thick setae on margin of cardo of maxillae.

0 = present; 1 = absent.

Character 21. Palpi segment III/II of maxillae.

0 = 0.5 or less; 1 = 0.6 or more.

Character 22. Thick dorsal setae on labial palpi III.

0 = 5 or more; 1 = 3.

Character 23. Thick setae on labial palpi II.

0 = along outer margin; 1 = in basal half of outer margin only.

Legs

Character 24. Spines on dorsum of hind femora.

0 = acute; 1 = blunt.

Character 25. Pectinate spines along medial line of hind tibiae [additive]. I followed the coding from Domínguez (1995), because as in the *Ulmeritus-Ulmeritoides* group, there appears to be the same tendency to increase the number of pectinate spines.

0 = absent; 1 = few; 2 = numerous.

Character 26. Spines on outer margin of hind tarsi [additive]. State 2, autapomorphic for *F. caribbianus*, appears to be derived from 1, because the 'long' spines are relatively longer in the last nymphal instars.

0 = absent; 1 = short; 2 = long.

Gills

Character 27. Gill width.

0 = wide (3 times as long as wide); 1 = narrow (10 times as long as wide).

Outgroup selection

The genus *Ecuaphlebia* was selected as the outgroup, based on a previous phylogenetic analysis (Flowers & Domínguez, 1991) where it appears as the basal group of genera related to the '*Farrodes* lineage', not included in that study.

ANALYSIS

Initially, data were analysed using the mhenning* and bb* commands of Hennig86, combined with successive character weighting (xs w) (Farris, 1969,

TABLE 2. Behaviour of characters in the first analysis (whole matrix, Table 1). CI = Consistency Index, RI = Retention Index, Weight = weight after successive weighting

Character #	Range of steps	# of steps	CI	RI	Weight (after xs w)
1	4	4	100	100	10
2	1	1	100	100	10
3	2	3	66	66	4
4	1	1	100	100	10
5	1	1	100	100	10
6	2	7	28	50	1
7	2	2	100	100	10
8	2	2	100	100	10
9	1	2	50	80	4
10	1	1	100	100	10
11	4	4	100	100	10
12	2	4	50	89	4
13	2	2	100	100	10
14	1	4	25	66	1
15	2	3	66	80	5
16	2	5	40	50	2
17	3	4	75	80	6
18s	1	1	100	100	10
19	1	1	100	100	10
20	1	1	100	100	10
21	1	2	50	0	0
22	1	2	50	0	0
23	1	2	50	50	2
24	1	2	50	0	0
25	2	2	100	100	10
26	2	2	100	100	10
27	1	1	100	100	10

Carpenter, 1988). Successive weighting calculates the weights of the characters from the best fits, until the trees are stabilized. Later, an extra analysis was performed with the ie* option (guaranteed to find all shortest trees) instead of mh*, bb*. Although far more time consuming, ie* found more trees and was therefore preferred. When more than one cladogram was obtained, a strict consensus tree was calculated with the Nelsen option before and after the successive weighting. As the nymphal stage is unknown for several species, the data were analysed in different ways to test the informativeness of different character sets. The same analyses were performed on: (1) all taxa and available characters from adult and nymphal stages (coding characters from the missing stages as '?'); (2) only adult characters (all taxa); (3) only taxa for which nymphal characters were available (9 taxa + outgroup); (4) only taxa for which both stages were known (9 taxa + outgroup).

The results from the analyses of the different sets of taxa/characters are as follows.

(1) All data available (Table 1). The first analysis (all characters weighted equally) yielded 24 trees, each with a length (l) of 66 steps, Consistency Index (CI) of 0.68, Retention Index (RI) of 0.75. Successive weighting (xs w) was applied and resulted in six equally parsimonious trees of l = 360, CI = 0.88 and RI = 0.89 (new character weights, CI and RI shown in Table 2). After resetting the weight back to 1 with the ccode option, the length of these trees was also 66 steps, implying that they

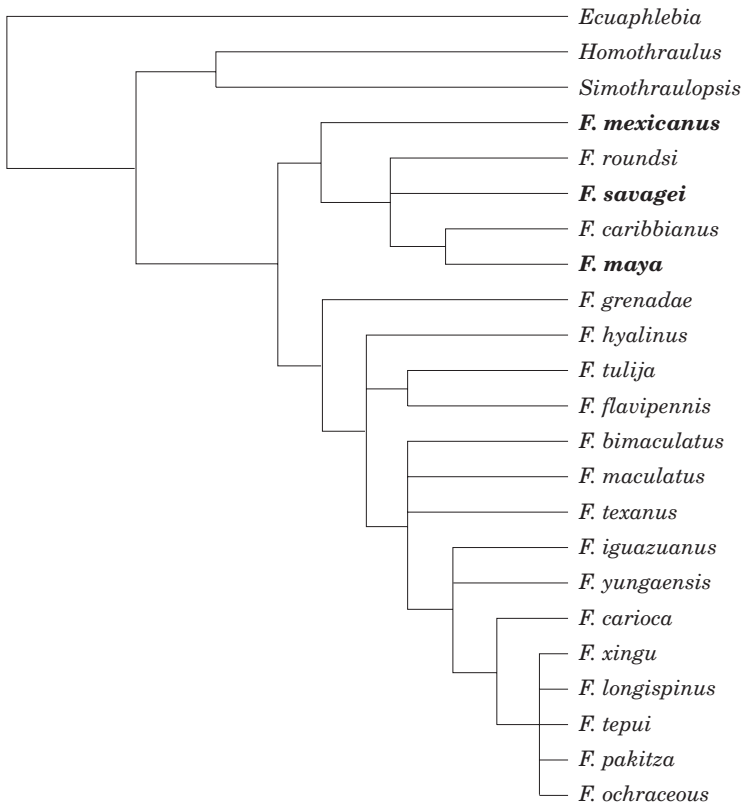


Figure 47. Consensus tree of data set (1) (all taxa and available characters).

were part of the original set of 24. The strict consensus trees for the two sets obtained before and after the successive weighting are the same (Fig. 47).

Figure 48 is one of the six equally parsimonious cladograms obtained and is used to illustrate character distributions. The differences among the topology of the resulting cladograms after successive weighting is due to the uncertain relationships of *F. bimaculatus* with *F. maculatus*, and *F. texanus* + *F. roundsi* with *F. savagei.*

(2) Adult characters only (all taxa, characters 1–17, Table 1). The first analysis (characters with equal weight) yielded six trees, each with 1 = 50, CI = 0.66 and RI = 0.77. With the successive weighting procedure the same six equally parsimonious trees remained with 1 = 276, CI = 0.85 and RI = 0.86. After recoding the weight to one, the length was again 50. These trees were identical with the topology of trees from data set (1) after successive weighting. The strict consensus tree is of course identical with the one from data set (1).

(3) Nymphal characters (taxa marked '+', characters 18–27, Table 1). The analysis resulted in two trees with 1 = 16, CI = 0.75 and RI = 0.69. The difference between these two trees results from the different values assigned to character 26 in *F. bimaculatus* (where it is actually '?'). Consequently, in one of the trees this species appears separated from the remaining *Farrodes* (assignment of state 0 to character 26). In the other tree, this branch is collapsed (character 26 with state 1) and the tree is similar to the consensus (Fig. 49). I prefer the second tree, because it is

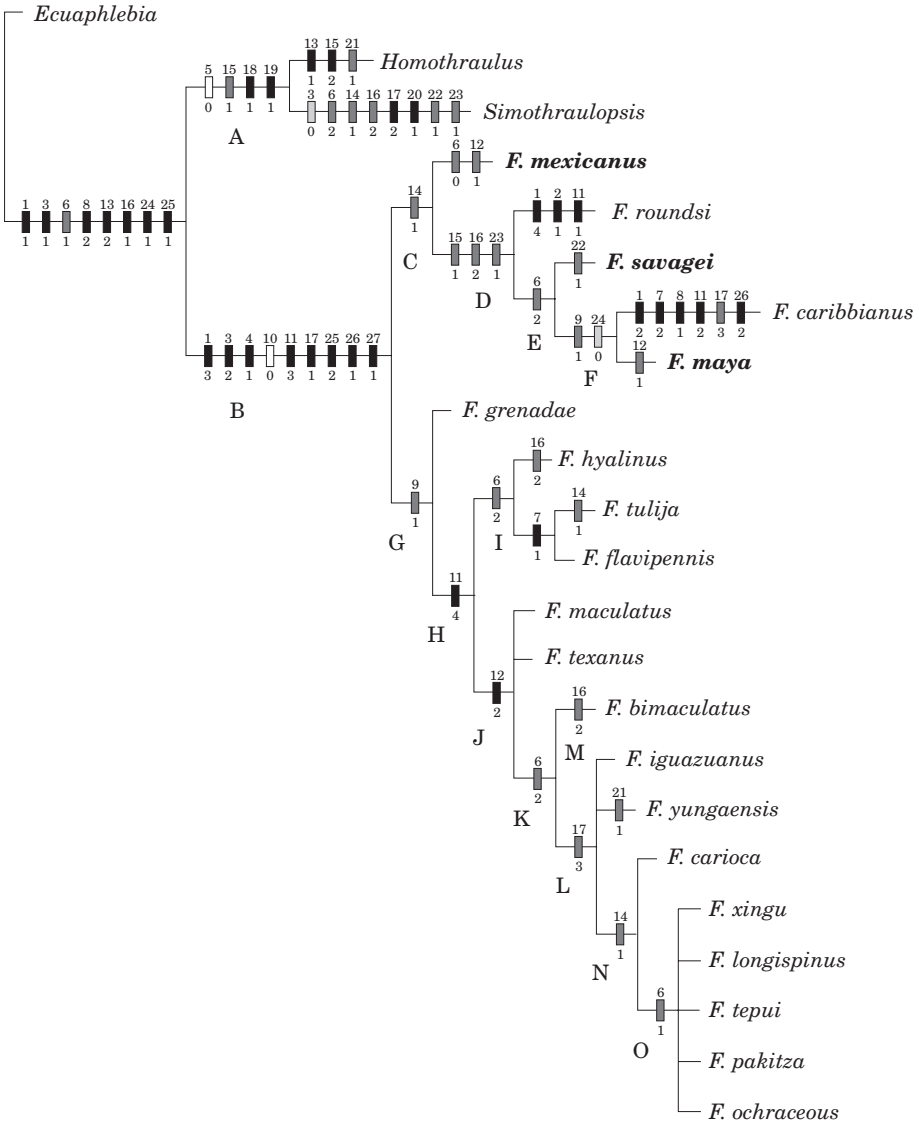


Figure 48. Preferred cladogram from data set (1), after successive weighting. ■ = apomorphies; ■ = parallelisms; ■ = reversals; □ = plesiomorphies.

deemed more likely that *F. bimaculatus* will have state 1 for character 26, as in all other species of *Farrodes*.

(4) Taxa represented by both nymphs and adults only, all characters (taxa marked '+', Table 1). The first analysis found four trees, with l = 54, CI = 0.75 and RI = 0.69. The four trees remained after the successive weighting, with l = 282, CI = 0.93 and RI = 0.93. The length of these trees was again 54 steps after resetting the weight to one. The consensus trees of both sets were identical (Fig. 50).

Although some of the terminal taxa lack scored apomorphies, they do represent isolated populations with distinct colour patterns (a trait difficult to score cladistically).

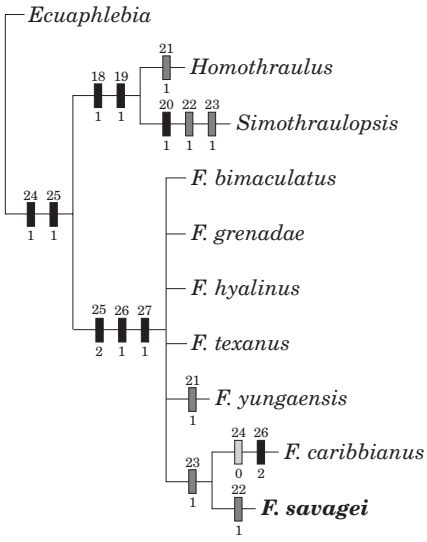


Figure 49. Consensus tree of data set (3) (nymphal characters). For key see Fig. 48.

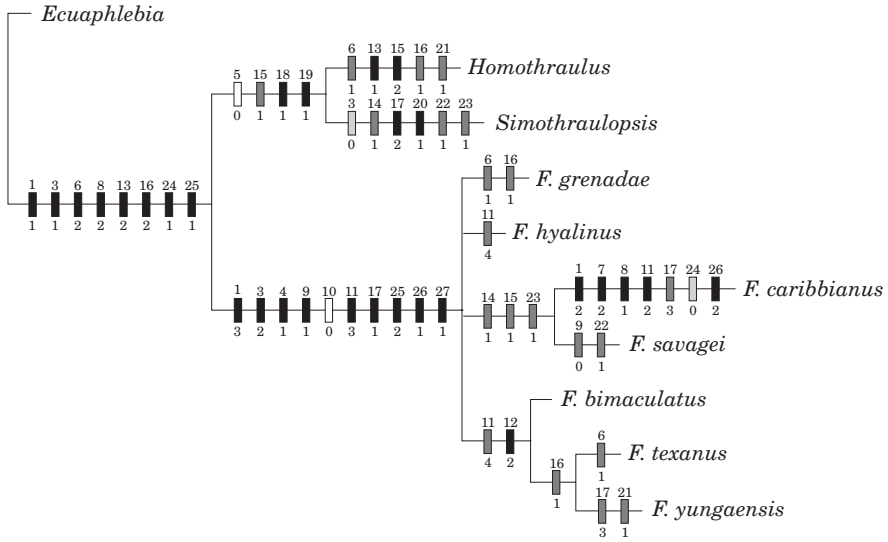


Figure 50. Consensus tree of data set (4) (taxa represented by adults *and* nymphs). For key see Fig. 48.

RESULTS

From the cladistic analysis of data set 1, as illustrated by Figure 48, the monophyly of the group is supported at the basal node by the following synapomorphies; the presence of lateral projections on the styliger plate (character 1:1); the presence of larger spines on the venter of the styliger plate (character 3:1), which reverses in *Simothraulopsis* and transforms to state 2 at node (B); the penis lobes separated in apical 1/2–1/3 (character 6:1) an attribute that changes independently several times

to alternative states, and reverses subsequently at node (O); the base of the penis roundly widened (character 8:2); the vein ICu_1 free basally, (character 13:2), transforming again in *Homothraulus*; the pattern of abdominal coloration typical of *Farrodes* (character 16:1) appears as a synapomorphy, although it changes homoplastically at several distal nodes and should be used with caution until it can be better defined; the spines on the dorsum of the hind femora are blunt (character 24:1); a few pectinate spines present along medial line of hind tibiae (character 25: 1). Two major clades are clearly separated within the in-group, one comprised of *Simothraulopsis* and *Homothraulus* (node A) and the other by all the *Farrodes* species (node B).

Node A is defined mainly by two nymphal synapomorphies: labrum widest in its apical 2/3 (character 18:1) and mandibular tuft strong (character 19:1), but also by the homoplastic character 15:1 (presternum shallow anteriorly, with a median constriction), and a reversed character 5:0 (basal part of forceps quadrangular). Each terminal taxon can be diagnosed by at least one synapomorphy, making continued generic recognition appropriate.

The second clade, considered here as the genus *Farrodes*, has several apomorphies from both adult and nymphal stages. The lateral projections of the styliger plate are straight, with base well defined (character 1:3); spines on the styliger plate are larger on lateral areas, especially on lateral projections (character 3:2); inner margin of the forceps sockets is elevated (character 4:1); penis projections are curved apically upward (character 11:3), although there are subsequent transformations; the ninth female sternum is conical, entire apically (character 17:1); the pectinate spines along medial line of hind tibiae are numerous (character 25:2); short spines on outer margin of hind tarsi present (character 26:1); and the gills are narrow (character 27:1).

Within *Farrodes* there are two species groups: the *F. caribbianus* group (node C) and the *F. bimaculatus* group (node G). Given more information, it is possible that these two groups will deserve formal categories, but because they are now characterized by homoplastic characters, I prefer to treat them as species groups. Within the *F. caribbianus* group, *F. caribbianus* is the sister species of *F. maya* (node F). It is separated from the next node (E) by the ventrolateral or lateral origin of the penis projections (character 9:1) which is a parallelism within the *F. bimaculatus* species group, and the spines on the dorsum of hind tibiae (character 24:0), a reversal. Node E is separated from its sister group (*F. roundsi*) by a parallelism: penis lobes separated on apical 3/4–4/5 (character 6:2). Node D is separated from C by the shape of the presternum, shallow anteriorly with median constriction (character 15:1); at least some abdominal segments translucent (character 16:2); and, thick setae on basal half of labial palpi II (character 23:1). These three characters appear as parallelisms. The next node (C) is characterized by a large costal projection on the hind wings (character 14:1), another parallelism.

The *F. bimaculatus* species group includes five species with insufficient information to establish their pattern of relationships (*F. xingu*, *F. longispinus*, *F. tepui*, *F. patikza* and *F. ochraceous*). They share the penes separated on apical 1/2–1/3 (character 6:1), which is a parallelism. *F. carioca* is the sister group and Node N is separated from the next by the large size of the costal projection of the hind wings (character 14: 1), a parallelism present also in clade C. The relationships between *F. iguazuanus* and *F. yungaensis* remain unresolved. They are the next to join the former taxa, their monophyly supported by the conical ninth ♀ sternum, notched apically (character

17:3), a parallelism. *F. bimaculatus* is the sister group of this clade. Node (L) is separated from the next (K) by the penes divided on apical 3/4–4/5 (character 6: 2), a parallelism. The next node is formed by *F. maculatus* and *F. texanus* (with no resolution) whereas the node K is supported by a synapomorphy, a short terminal flap on apex of penis projections (character 12:2). In a sister clade (node I), *F. tulija* and *F. flavipennis* are the most apomorphic species, their relationship being established by the apex of the penis lobes projecting in an acute angle (character 7:1). The next member of the clade is *F. hyalinus*, grouped in node I by character 6:2 (penis lobes separated on apical 3/4–4/5), a parallelism. These two clades are supported at node H by character 11:4, the penis projections cylindrical and long, and are grouped at node G with *F. grenadae*, the last member of this clade by character 9:1, a parallelism.

The differences between this tree (Fig. 48) and the consensus tree (Fig. 47) is the lack of resolution between *F. bimaculatus* and *F. maculatus* + *F. texanus*, between *F. hyalinus* and *F. tulija* + *F. flavipennis*, and the collapse of the base of the group and between *F. roundsi* and *F. savagei* in the consensus; however, these differences do not affect the topology of the three main groups.

In the single tree obtained from the analysis of data set 3 (nymphal characters, Fig. 49), the two main groups (*Simothraulopsis* + *Homothraulus*) and *Farrodes* are still separated. Within *Farrodes*, *F. caribbianus* + *F. savagei* (representing the *F. caribbianus* species group) are also separated from the remaining *Farrodes*.

Similarly, the topology of the consensus tree obtained from data set 4 (only adults *and* nymphs, Fig. 50) was similar to the one obtained from the data set (3), except that the relationship between *F. texanus* and *F. yungaensis* is resolved.

It is worth noting that the results of the 'reduced' data sets were identical (only adults, data set 2), or totally compatible (data sets 3 and 4) with the complete one. This situation provides more support for the phylogeny obtained from the complete data set (1), and suggests that the results are due to good character support in all stages, rather than to artifacts resulting from more weight from the adult set, or of interacting missing characters from the nymphal data set.

DISCUSSION

Peters (1971), in his treatment of the Leptophlebiidae of the West Indies, revised *Borinquena*, *Hagenulus* and *Neohagenulus* and established three new genera: *Careospina*, *Traverina* and *Farrodes*. He pointed out that although the six genera show similarities, basic morphological differences exist, especially among adults. Peters was aware that at that time there was not enough information available to propose a phylogeny of the group, but he considered that *Farrodes* could represent a separate evolutionary lineage from other Antillean genera, although part of the same complex. At that time, none of the treated genera (*Farrodes*, *Neohagenulus*, *Hagenulus*, *Borinquena*, *Traverina* or *Careospina*) had been recorded from continental Central or South America. Presently, *Farrodes* seems to be one of the most speciose and most widely distributed genera in South and Central America, with localities from northern Argentina to southern Texas.

In 1993, Kluge revised the Leptophlebiidae of Cuba. He proposed subgeneric status for *Borinquena*, *Careospina* and *Traverina* and proposed two non character-based subgenera (see his fig. 223, p. 284, captioned 'Phylogeny of the Cuban Hagenulini'). I would like to point out only a few of the mistakes he introduced in his paper.

He did not consider *Simothraulopsis* part of his tribe Hagenulini, because the fork of vein MP is asymmetrical and the claws of a pair are similar and hooked in all legs. He was probably misled by Demoulin's (1966) description of the wings based on the nymphal wingpads, but there is no mention of the adult tarsal claws in the description, which are actually dissimilar (one apically hooked, the other pad-like) as in the rest of the lineage. In his characterization of the tribe, he gave as character: (1) fork of vein MA of fore wing asymmetrical (yet he fails to mention that it is symmetrical in the females of *Careospina*, *Traverina* and *Hagenulus*); (2) hind wing with long acute costal projection, costal field not extended distally over the base of costal projection (. . .) this character allows Hagenulini to be distinguished from all other Leptophlebiidae except for the forms without hind wings. He did not mention that *Simothraulopsis*, which he considered not to form part of this tribe, has this character very clearly marked. In his paper, Kluge (1993) presented a 'phylogeny' of the subgenera of *Hagenulus*, with a basal polytomy of four unresolved branches. One of these four branches is 'separated' by the character 'ovipositor of female long' that Kluge himself said is "probably a plesiomorphy or parallelism with some other Atalophlebiinae". If that is true, the relationships of 5 of the 6 subgenera included in the analyses (there are still two others not treated), remain uncertain. Furthermore, the two new subgenera he established have no synapomorphies at all. For these reasons, there is no basis for a tribe Hagenulini.

PHYLOGENETIC BIOGEOGRAPHY

There have been several attempts to explain the biogeography of various neotropical aquatic insects (Brundin, 1966; Illies, 1969, Edmunds, 1975, Pescador & Peters, 1980, Savage, 1987a, McCafferty *et al.* 1984). The intercontinental relationships of some of the taxa have long been well understood (Brundin, 1966; Edmunds, 1975), but there are still very few hypotheses of the biogeography of neotropical mayflies within South America. There are several problems that restrict the possibility of proposing rigorous and testable hypotheses of historical biogeography for South American Ephemeroptera. I cite Vari & Weitzman (1990) concerning this matter, when referring to the major limiting factors influencing the historical biogeography of freshwater fishes. For them "These [factors] are the poor state of our knowledge of the species-level systematics of most taxa; the inadequate distributional information for most species; and the sparse or nonexistent data on the phylogenetic history of most supraspecific taxa". This describes very well the state of knowledge of mayflies, although it is probably also applicable to most of the aquatic insects in the neotropics.

The biogeographic studies on South American aquatic insects are generally not based on rigorous phylogenies. Frequently, they consist of narratives of possible dispersal routes and putative centers of origin (e.g. Illies, 1965), or are restricted to descriptions of geographic distributions.

Besides the theoretical-methodological problems, the neotropical mayfly fauna remains poorly sampled. As a consequence, what the old biogeographers would call 'centers of maximum diversity' in mayflies could be easily traceable to regions sampled by expeditions with mayfly workers or collectors.

All of these problems were clear when I tried to test the universality of my area

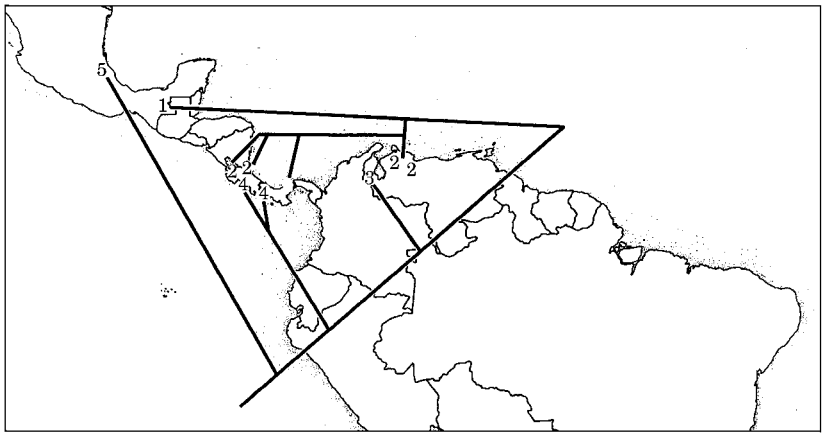


Figure 51. Distribution of *F. caribbianus* species group (cladogram superimposed). 1, ***F. maya***; 2, *F. caribbianus*; 3, ***F. savagei***; 4, *F. roundsi*; 5, ***F. mexicanus***.

cladograms, comparing them with results from other aquatic taxa with similar distributions. There were none that would apply to the whole area of distribution. For this reason, when possible, I compared the area relationships from parts of my area cladogram with results from other studies. I present my results, so that they may be subsequently contrasted with area cladograms from other groups. Although several of the cladogenetic events in the area cladograms could be explained by vicariance, dating the barriers and linking the area cladograms with the geologic history of the region lies beyond the scope of this paper.

General distribution

The genus *Farrodes* is widely distributed, ranging from central Argentina to the southern portions of the United States. A similar distribution is also found in some other leptophlebiid genera such as *Traverella* and *Thraulodes*, although both genera extend further north in North America. Unfortunately, phylogenetic hypotheses of the species of these genera are still not available for comparative purposes. The *F. caribbianus* species group of *Farrodes* is restricted to Central America and northern South America (Fig. 51, cladogram superimposed), while the *bimaculatus* species group is more widely distributed, with species in Texas, Central America, the Antilles and South America (Fig. 52, cladogram superimposed).

Delimitation of areas

Areas were delimited for the biogeographic analyses with the program COMPONENT. The areas were recognized by the species distributions and their relations with river basins. Areas with clear identity, such as the Tepuis in Venezuela or the Yungas (mountain rain forest in eastern slopes of the Andes) in NW Argentina, were treated as different, although they may be parts of the same major river basin. Although the biological elements from Cerro de la Neblina seem to form a continuum

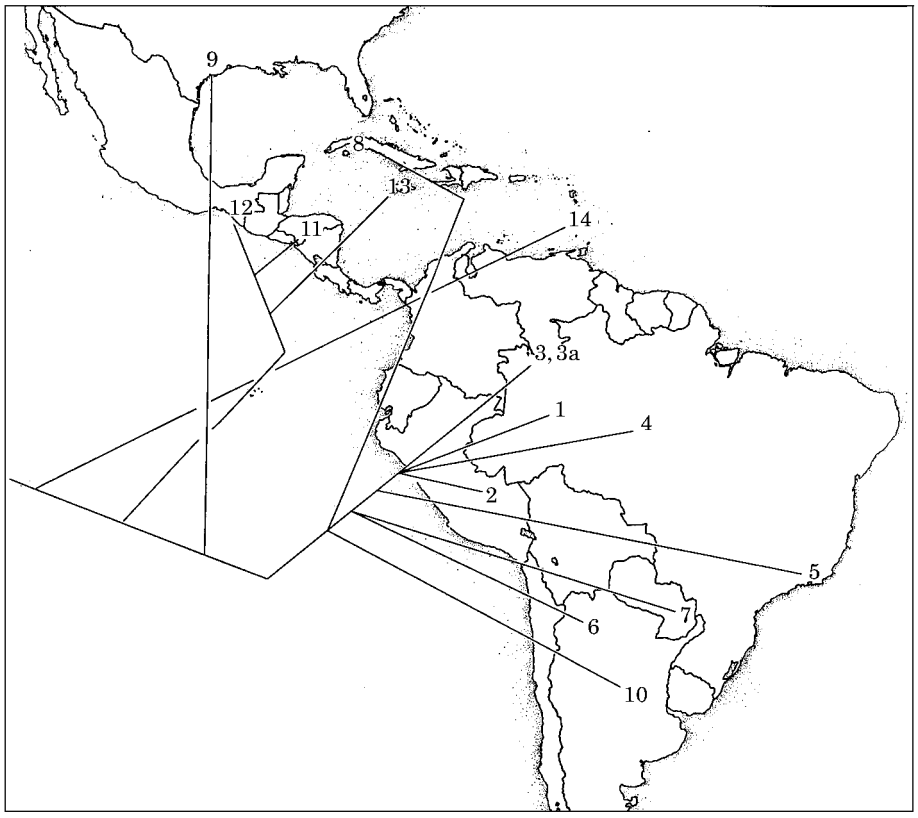


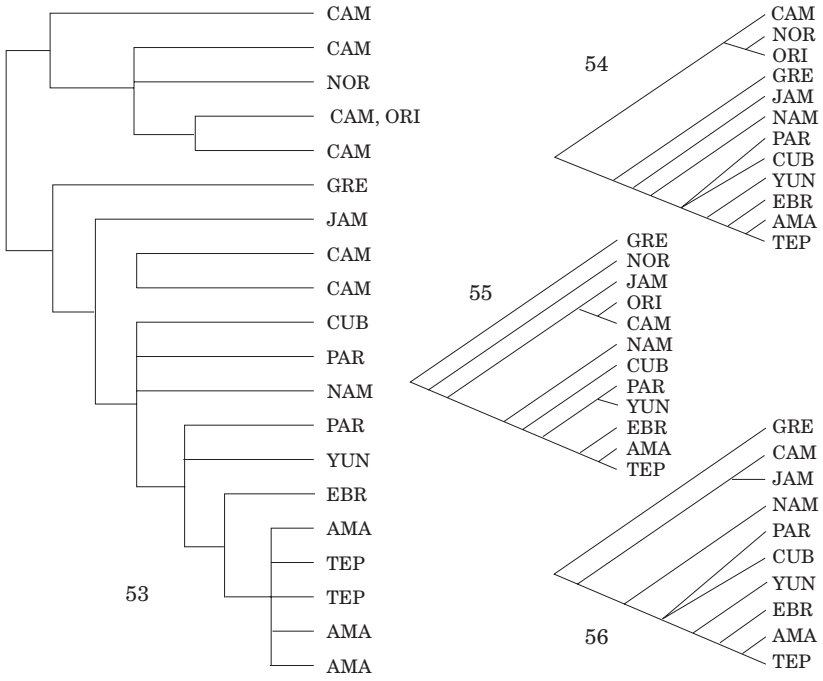
Figure 52. Distribution of *F. bimaculatus* species group (cladogram superimposed). 1, *F. ochraceous*; 2, *F. patikza*; 3, *F. longispinus*; 3a, *F. tepui*; 4, *F. xingu*; 5, *F. carioca*; 6, *F. yungaensis*; 7, *F. iguazuanus*; 8, *F. bimaculatus*; 9, *F. texanus*; 10, *F. maculatus*; 11, *F. flavipennis*; 12, *F. tulija*; 13, *F. hyalinus*; 14, *F. grenadae.*

with the surrounding areas (Huber, 1988), I have maintained them as separate due to the high number of endemic taxa (Maguire, 1955). The resultant areas coincide roughly with some of those delimited for freshwater fishes by Géry (1969) and for freshwater Decapoda (Morrone & Lopretto, 1994). Nevertheless, in some cases I had to define my areas differently from other authors. For example, Vari (1987) separated the upper Paraná from the lower Paraná, Paraguay and Uruguay rivers based on the presence of an identifiable barrier for fishes constituted by the massive Sete Quedas rapids. For mayflies, these falls do not represent an effective barrier so I could not logically divide them in a similar way. I considered it useful to restrict the areas of endemism as much as possible, because combining such areas will facilitate comparison with other taxa in the future.

Although Central America and southern Mexico (south of Veracruz) have a complex history with several areas of endemism proposed (Rosen, 1979; Liebherr, 1994) I decided to treat them as a single area (CAM). The scattered records of *Farrodes* Complex mayfly species occurring in this area do not allow further subdivisions.

The areas of endemism delimited, with the genera included, are the following:

NAM (North America: Texas): *F. texanus*



Figures 53–56. 53, Taxon-area cladogram. 54–56, Nelson consensus trees of the area cladograms obtained with COMPONENT (out-group excluded). 54, *Farrodes* (Assumption 2); 55, *Farrodes* (Assumption 1); 56, *F bimaculatus* species group (Assumption 2).

CAM (Central America: southern Mexico, Guatemala, Honduras, Costa Rica and Panama): *F. caribbianus*, *F. roundsi*, *F. maya*, *F. mexicanus*, *F. flavipennis* and *F. tulija*.

GRE (Grenada): *F. grenadae*

JAM (Jamaica): *F. hyalinus*

CUB (Cuba): *F. bimaculatus*

NOR (Northern Andes: Venezuela, Sierra de Perija): *F. savagei*

ORI (Orinoco, northern Venezuela): *F. caribbianus*

AMA (Amazon Basin, including mayor portions of Peru and Brazil): *F. ochraceous*, *F. xingu*, *F. patikza*.

TEP (Tepui: Venezuela, Cerro de la Neblina): *F. longispinus*, *F. tepui*.

EBR (Eastern Brazil: Serra do Mar in Rio de Janeiro): *F. carioca*.

PAR (Parana Basin: Uruguay, NE Argentina and SE Brazil): *F. maculatus*, *F. iguazuanus*.

YUN (Yungas: western slope of the Andes, in northwestern Argentina): *F. yungaensis*.

Biogeographic analysis

A taxon-area cladogram (Fig. 53) was constructed by replacing taxa with the areas they inhabit. As there were redundant distributions (occurrence of an area at more than one place in the cladogram) and widespread taxa (taxa occurring in more than one area) it was necessary to perform a biogeographical analysis to

convert this taxon-area cladogram into a resolved area cladogram (Nelson & Platnick, 1981). I applied component analysis (Platnick & Nelson, 1978) using the program COMPONENT ver. 1.5 (Page, 1989a).

There are three analytical methods (Assumptions) for dealing with redundant areas and widespread taxa: assumption 1 and 2 of Platnick & Nelson (1978) and assumption 0 of Zandee & Roos (1987). These assumptions differ in the way they handle widespread taxa, redundant distributions and missing areas. With only one taxon-area cladogram, it was not necessary to deal with missing areas.

Platnick & Nelson (1978) considered widespread taxa uninformative in comparison with endemics. Assumption 1 allows in this case the area relationship to be mono- or paraphyletic (Page, 1990), assuming that speciation or extinction have occurred, or that the vicariant event was not followed by speciation. Because assumption 2 allows each redundant area to be placed separately in several positions on the resolved area cladogram; it has the potential to best reflect speciation, extinction, dispersal, and failure to vicariate. The resultant areas can be mono-, para- or polyphyletic. Assumption 0 considers areas occupied by widespread taxa to be sister areas and for this reason monophyletic. In the case of redundant distributions, assumptions 0 and 1 consider every occurrence as valid, while assumption 2 treats each occurrence separately.

Assumption 2 is the one that allows for more solutions and deals more realistically with history by permitting dispersal (Page, 1990) (although sometimes redundancy and widespread taxa can interact to produce fewer trees). For this reason, I used this assumption with COMPONENT, while for comparative purposes area cladograms under assumptions 0 and 1 were also generated. Two successive analyses were performed on (a) the genus *Farrodes* as a whole and (b) the *F. bimaculatus* species group, to check variation in the results.

Version 1.5 of COMPONENT accepts only fully dichotomous trees, so the unresolved nodes were resolved by hand in all the possible combinations (six possibilities) and entered as different trees in each different analysis that involved the unresolved nodes.

Results

Each of the different taxon-area cladograms yielded six trees under assumption 2. They were combined and using the Compare/Consensus/Nelson option of COMPONENT a Nelson Consensus Tree (Page, 1989b: 177; Nelson's combinable majority tree *sensu* Nixon & Carpenter, 1996: 307) from the set of 36 was obtained and is illustrated in Figure 54. Nelson Consensus maximizes the resolution of the tree. A strict consensus tree separated only one group composed of (YUN, PAR, CUB, NAM (EBR, (AMA, TEP))), with only the relationships among the last three areas resolved. Under assumption 1, 97 trees were obtained from each taxon-area cladogram entered. The resultant Nelson Consensus Tree obtained from the 582 cladograms is totally different from the Nelson tree constructed under assumption 2, except for the relationships among (EBR, (AMA, TEP)). In this cladogram, (Fig. 55) PAR is the sister area of YUN, and JAM forms a separate group with ORI–CAM. The analysis under assumption 0 yielded only one area cladogram for each entered tree. A Nelson consensus was obtained for these six area cladograms, the difference

with the one obtained under assumption 2 being that CUB is the sister group of (PAR, YUN (EBR (AMA, TEP))), with (PAR, YUN) unresolved.

The second analysis was performed on the *F. bimaculatus* species group alone. Two area cladograms were obtained under assumption 2 for each of the six entered trees. The Nelson consensus tree is illustrated in Figure 56. With the strict consensus tree in this case, the resolution of PAR, NAM, CUB and YUN is lost. The same tree was obtained under assumption 1 and 0. Again as in the former analysis with assumption 0, the relationship between PAR–YUN is not resolved, and CUB becomes the sister group of (PAR, YUN (EBR (AMA, TEP))).

Discussion

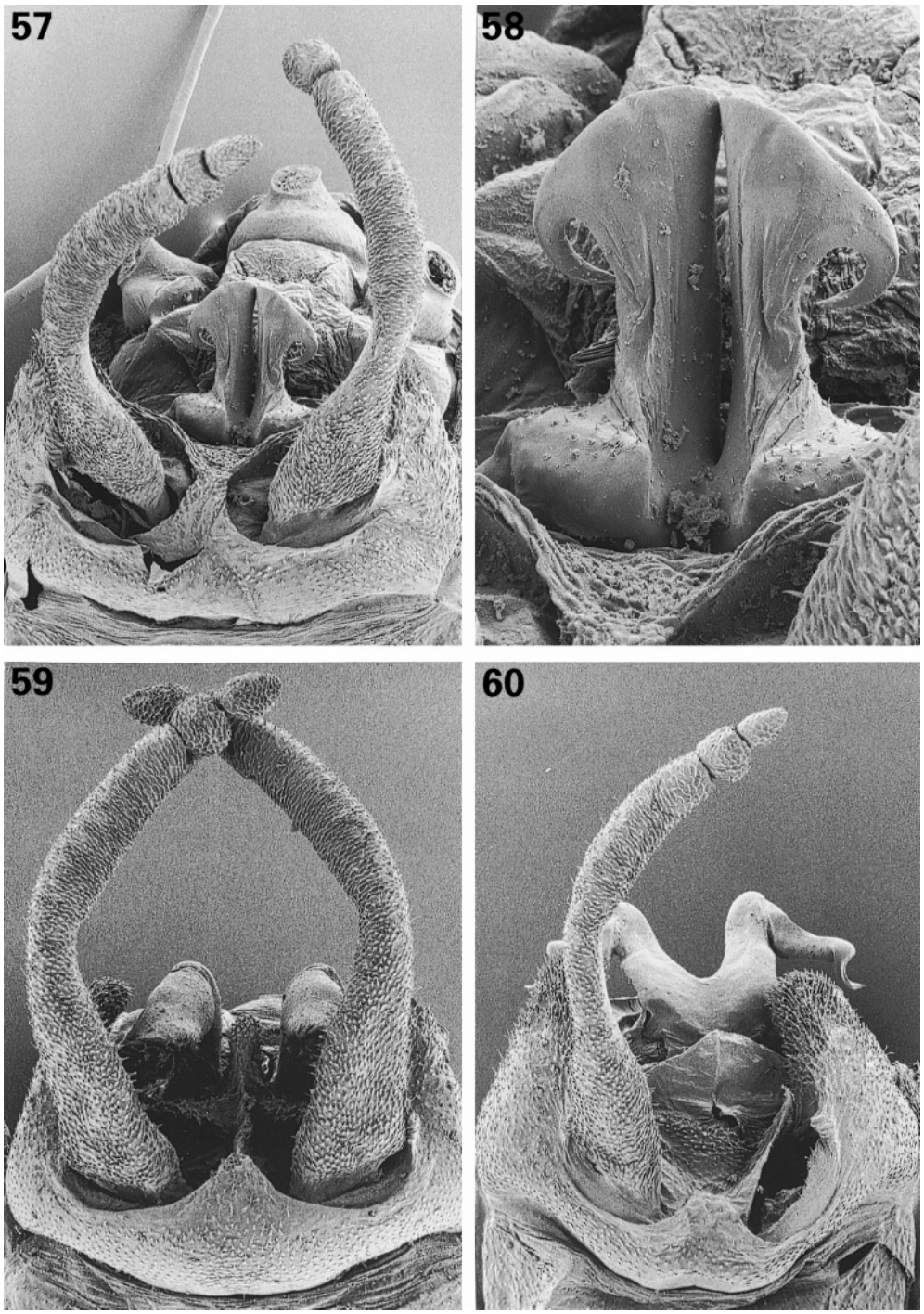
In the two Nelson consensus trees obtained under assumption 2 (Figs 54, 56), the four terminal areas are consistently related in the following way: TEP and AMA are the most closely related. The sister area of AMA–TEP is EBR, with records in the northern part of Serra do Mar, in Rio de Janeiro State, and the next related area is YUN. The relationship between TEP and AMA is not surprising if, as postulated by Huber (1988), taxa in the tepuis seem to have a continuous distribution throughout the lowlands. Savage (1987b) also found species of *Miroculis* (Leptophlebiidae) from Cerro de la Neblina belonging in subgenera widespread in the Amazon Basin. *Farrodes* is distributed in most of subtropical and tropical South America, but no species of this genus are known from the southern part of the Serra do Mar, where several other leptophlebiid genera have been found (W.L. Peters, pers. comm.) despite intensive collections. Therefore, this area is restricted to the northern portion of the Serra do Mar.

The relationships of the next three areas: CUB, NAM and PAR are not so clear. In Figures 54 and 56 (assumption 2), PAR and CUB are unresolved, and NAM is basal to them. In Figure 54 JAM and GRE are basal to the already mentioned areas and a monophyletic group is formed by NOR–ORI as the terminals, with CAM as their sister group. In Figure 56 the situation is different because NOR and ORI were removed and CAM and JAM are sister groups, and GRE is the most basal area.

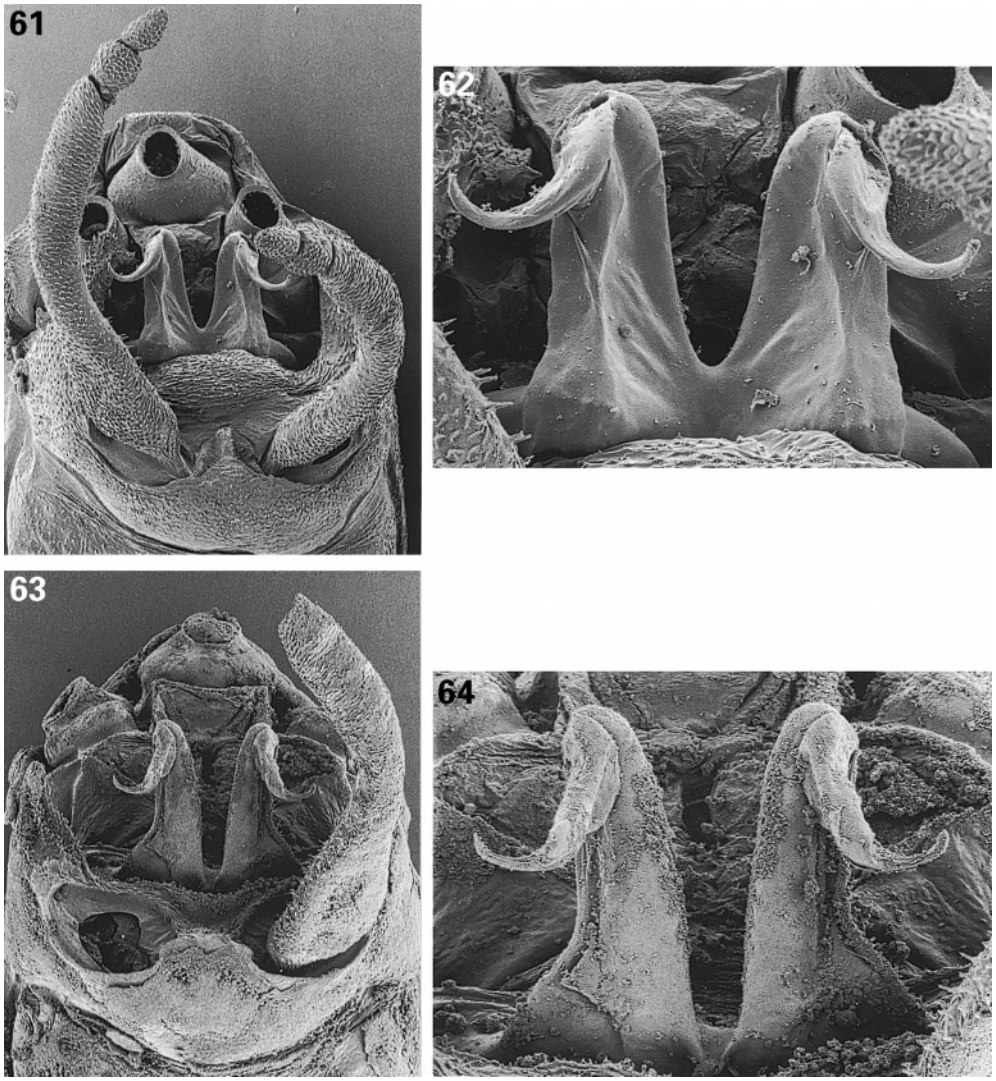
It is not possible to test the universality of these analyses or choose one of them as preferable based on my data because only one mayfly phylogeny was available. Nevertheless, some of the relationships here depicted correspond with the findings of other studies, although sometimes not based on explicit phylogenies. For example, in the areas common to the three area cladograms, the relations between the Amazon Basin (AMA) and the base of Cerro de la Neblina (TEP) have also been proposed for plants (Prance & Johnson, 1992), or can be deduced from Huber (1988) and Savage (1987b).

In the area cladogram in Figure 54 the close relationship between NOR (Lago Maracaibo basin) and the Orinoco basin (ORI) corresponds with the data for fishes presented by Vari (1995) with sister species in each area. Conversely, the relationship of CAM–JAM and NAM with South America of Figure 56 is coincident with the study of Savage & Lips (1993), based on lizards.

With regard to the Caribbean components, there remain various conflicting ideas on the details on the sequence of geologic events that may have determined the sequence of vicariant events of the biota in the region. But again, in Figure 56 the



Figures 57–60. Scanning photographs of ♂ genitalia, v.v. 57, *F. caribbianus*, 210×; 58, same, detail of penis lobes, 600×; 59, *F. roundsi*, 210×; 60, *F. xingu*, 210×.



Figures 61–64. Scanning photographs of ♂ genitalia, v.v. 61, *F. savagei*, 210×; 62, same, detail of penis lobes; 600×; 63, *F. mexicanus*, 170×; 64, same, detail of penis lobes, 375×.

sister group relationship between CAM–JAM agrees with the proposed distinctive nature of Jamaica relative to Cuba (e.g. Rosen, 1985).

CONCLUSIONS

Phylogenetic analysis has been used for some time now—credible theoretical bases have been established and the results have proved to be testable (Farris, 1983). In this study, the phylogenetic relationships emerging from the analyses of the complete and partial matrices appear stable. *Homothraulus* and *Simothraulopsis* are

always sister groups and separated from *Farrodes*. Within *Farrodes*, the two species groups are separated in the analyses of the first two data sets (Figs 47, 48), and the *F. caribbianus* group maintains its identity in the other two (Figs 49, 50).

There are some problems with the biogeographical methods presently available (Morrone & Carpenter, 1994), but still the most limiting aspects are the scarcity of accurate distributional data and phylogenetic hypotheses on different taxa. In the present situation, I utilized phylogenies or biogeographical studies available from other aquatic taxa because the distributions of terrestrial groups are in most cases not comparable with the areas of the aquatic ones.

Some of the biogeographic results obtained here are supported with other studies, as for example the relationship between AMA and TEP (all analyses); NOR–ORI (Fig. 54) or CAM–JAM (Fig. 56). Other cases like EBR–(AMA–TEP), remain as hypotheses to be tested. The generality of the areas of endemism and the area relationships proposed, will only be assessed when more comparable studies are available.

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