

Taxonomic Revision of the Genus *Metamonius* Eaton (Nesameletidae: Ephemeroptera), with Notes on its Biology and Distribution

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Abstract

The information available on the Chilean representatives of the superfamily Siphonuroidea (sensu Kluge et al., 1995) is outdated, inaccurate and incomplete. A taxonomic revision of the siphonuroid genus *Metamonius* is presented here. New material is compared with descriptions in the literature of the three species of this genus in order to determine the variability of the more relevant characters; discrepancies with the authors of the species are discussed; the synonymy of *M. anceps* and *M. fuegiensis* is proposed; removal of the species *M. hollermayeri* from the genus is also proposed; description of the previously unknown male subimago of *M. anceps* is included, as well as notes on the biology and distribution of the genus. Association of larvae and winged stages is here confirmed by rearing.

Resumen

La información disponible acerca de los representantes chilenos de la superfamilia Siphonuroidea (sensu Kluge et al., 1995) esta obsoleta, es inexacta e incompleta. Se presenta una revisión de los sifonuroideos del género *Metamonius*. El material nuevo es contrastado con las descripciones en la literatura de las tres especies de este género a fin de determinar la variabilidad de los caracteres más relevantes; se discuten discrepancias con los autores de las especies; se propone la sinonimia de *M. anceps* y *M. fuegiensis*; se propone la remoción del género de la especie *M. hollermayeri*; se incluye una descripción del subimago macho de *M. anceps*, no antes descrito, así como también notas sobre la

biología y distribución del género. Las asociaciones entre larvas y estados alados han sido confirmadas por crianzas.

Keywords: *Metamonius*, Ephemeroptera, neotropical, taxonomy, distribution.

Introduction

At the alpha taxonomy level a large portion of the aquatic insect fauna of Chile has received very little attention beyond their very first descriptions.

Amongst the Ephemeroptera several groups have hardly been dealt with in the last 50 years, so that most of the information on them is available only from the works of early authors such as Pictet (1843), Blanchard (1851), Eaton (1871, 1881, 1883–1885), Weyenbergh (1883), Ulmer (1904, 1920, 1938), Navás (1912, 1915, 1918, 1922a, 1922b, 1923, 1925, 1928, 1930a, 1930b, 1933a, 1933b, 1934, 1935), Needham and Murphy (1924), Lestage (1930, 1931, 1935a, 1935b) and Demoulin (1952, 1955a, 1955b, 1955c, 1955d, 1955e). Most of these pioneer works are no longer useful since species were often described from one developmental stage only, so that different stages were frequently described as different species. Besides, some of the old descriptions are so incomplete or inaccurate that they may fit more than one species.

Recently, the Chilean Atalophlebiinae (Leptophlebiidae) have been clarified by Peters and Edmunds (1972), Pescador and Peters (1980a, 1980b, 1982, 1985, 1987, 1991), Mis-

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erendino (1996), Pescador (1997), and Pescador and Gonser (2001), who have studied their taxonomy in detail as part of a worldwide interest in this speciose Gondwanean group. Similarly, some of the Chilean Baetidae have recently been studied by investigators such as Gillies (1990), Lugo-Ortiz and McCafferty (1996, 1999a, 1999b) and McCafferty (2000).

However, there is no recent taxonomic work available on the rest of the Chilean Ephemeroptera, so that descriptions of the species of the family Caenidae and superfamily Siphonuroidea (sensu Kluge et al., 1995) are still incomplete. Therefore, their specific diversity has not been established and, in most cases, not all the developmental stages have been described.

In addition to the purely scientific importance of this highly endemic fauna, the updating and completion of this information has become necessary so that this knowledge can be applied to environmental evaluation and monitoring of the Chilean watercourses.

This work is the first of a series of taxonomic revisions of the Chilean Siphonuroidea, which includes the Ameletopsidae, Nesameletidae and Oniscigastridae families. Each genus will be dealt with individually and information on their distribution and biology will also be included.

Bibliographical antecedents

The Ephemeroptera family Nesameletidae is part of the Gondwanean fauna of amphinotic distribution. In the Australian zone the family is represented by the Australian genus *Ameletoides* (one species) and the New Zealander *Nesameletus* (two species). In the Neotropical zone Nesameletidae is represented by the genus *Metamonius*, with three species.

The genus *Metamonius* was established by Eaton in 1885 in order to relocate in it the species *Siphylurus? anceps*, previously described by himself in 1883, which he then designated as *M. anceps*. All this was based on two winged specimens, a male imago and a female subimago from Chile, with no further locality specified. Eventually, Demoulin (1955a), with new material collected at Pichinahuel, Arauco Prov., Chile, described the female imago of the species and, in a later work (1955b) described the nymph of *Metamonius anceps* from specimens collected at Los Maitenes, Santiago, Chile; Río Gol Gol and Portezuelo de Puyehue, Osorno Prov., Chile. In that paper Demoulin (1955c) also redescribed the female subimago from one of the specimens of the Río Gol Gol. *Metamonius anceps* remains to this day the type-species of the genus.

Independently, a peculiar nymph from Tierra del Fuego, Argentina, had been described by Ulmer in 1904, who designated it only as a 'nymph des *Baëtis*-Typus.' Due to its similarity with the New Zealand species *Ameletus ornatus*, Lestage (1935a) tentatively proposed to move this larva into the genus *Ameletus*, even though, by designating it only as *fuegiensis sp. nov.*, he kept the genus as doubtful. Eventually

Lestage himself (1935b), based on characters from its mouthparts, relocated the nymph in the genus *Ameletoides*, as *A. fuegiensis*. Finally, Demoulin (1955c) placed it, with reservations, in the genus *Metamonius* as *M. fuegiensis*, thus constituting the second species of the genus.

In 1935 Navás published a very poor description of a winged male and female from Trumao, Río Bueno, Valdivia Prov., Chile, as *Metamonius hollermayeri*. This would be the third species of *Metamonius*. Unfortunately, the types have been lost.

These three species, *M. anceps*, *M. fuegiensis* and *M. hollermayeri*, constitute the diversity of the genus *Metamonius*.

The descriptions of these species are based on few specimens, from only a few localities, therefore, the variability of their characters is little known.

Not all the stages of all three species have been described, only *M. anceps* is better known although the male subimago still remains to be described. Of *M. fuegiensis* we only know the nymph. As for *M. hollermayeri*, the very scanty description of its winged stages does not even specify whether the specimens are imagoes or subimagoes.

Therefore, to this day we have no clear-cut diagnostic characters for each of the three species, in all stages of development.

Material and methods

Insect material was collected from rivers and streams in various localities from the Región Metropolitana to Magallanes and Tierra del Fuego in the XII Region, on the Chilean side of the Andes, and from Bariloche to Ushuaia on the Argentinean side. Collections were made in spring and summer 2000–2003, this material is labeled with the prefixes 'N' for nymph and 'A' for the winged stages.

Specimens from the 'Colección de Macrozoobentos del Instituto de Zoología de la Universidad Austral de Chile,' labeled with the prefix BAD, collected prior to this study were also included. Nymphs were collected using a dipnet with a mesh of 500 µm. Emerging insects were captured by means of a semi-submerged driftnet anchored to the stream bed from early afternoon until the following morning. Flying insects were captured with an aerial net. Representatives of the whole benthic community accompanying *Metamonius* were also captured and preserved in a 70% ethanol solution as complementary material for this study.

Some of the nymphs collected were reared to adults in their native streams or in our laboratory. Specimens of all stages were preserved in a 70% ethanol solution. This material is deposited in the macrozoobenthos collection at the Instituto de Zoología of the Universidad Austral de Chile in Valdivia.

Microscopic preparations were made of mouthparts, legs and rear abdomen of specimens from different localities.

Some nymphal and adult parts were clarified in KOH and mounted in Euparal.

Material examined

Chile: three male nymphs, three female nymphs, one male subimago and exuviae (reared), three female subimagoes and exuviae (reared), one male imago and exuviae (reared), one female imago and exuviae (reared), Río Quempo, altitude approx. 1500 m, El Alfalfal, Región Metropolitana, collection Numbers: N-0987, N-1773, N-1774, A-1011, A-1316, A-1317, A-1318, A-1319, A-1320; four male nymphs, 11 female nymphs; Río Claro at Parque Inglés, altitude 1082 m. (35°24'53"S; 71°03'22"W) VII Región, coll. N°: N-1872a, N°: N-1872b; four male nymphs, four female nymphs; Río Icalma, altitude 1180 m, tributary to Laguna Chica de Icalma, IX Región, coll. N°: N-1356a, N-1356b; three male nymphs, seven female nymphs; Estero Dolluco, 39°23'S; 73°05'W, Cordillera de Queule altitude 600 m, IX Región, coll. N°: N-1779a, N-1779b; 28 male nymphs, 37 female nymphs, four female subimago and exuviae (reared), three male imago and exuviae (reared), one female imago and exuviae; unnamed stream, 40°40'56"S; 72°01'13"W, Ruta Internacional Puyehue, Osorno, X Región, coll. N°: N-1770, N-1771, N-1772, N-1775, N-1776, N-1777, N-1780, N-1781, N-1782, N-1783, N-784, A-1321, A-1323, A-1324, 1325, A-1326; one female nymph, one male nymph; Río Frío, approx. 10 km south of Villa Santa Lucía, Chiloé Continental, X Región, coll. N°: N-0710; one male nymph, unnamed stream at Puente Camahueto, (42°49'33"S; 72°43'27"W) 13 km. South of Caleta Gonzalo, altitude 185 m, X Región, coll. N°: WDS-A-1512 (leg. W. Shepard); one male nymph; Río Laura, altitude approx. 500 m, Aysén, XI Región, coll. N°: BAD-9419; one nymph; Estero Acantilado, altitude approx. 150 m, tributary to Río Queulat, XI Región, coll. N°: N-0796; seven male nymphs, 15 female nymphs. Argentina: Río Tierra Mayor, approx. 11 km north of Ushuaia, Tierra del Fuego, altitude approx. 300 m, coll. N°: N-1500; microscopy preparations of a male imago identified as *Metamonius sp.* from the locality of Ushuaia, Tierra del Fuego, deposited in the collection of the Museo Miguel Lillo de Tucumán, were also reviewed, through the kindness of E. Domínguez.

Results

Genus *Metamonius* Eaton

The following diagnostic characters for the genus were gathered from the literature by Domínguez et al. (1994). Adult stages: anastomosis between the transverse veins of the stigmatic area absent; costal projections of hindwings rounded (Fig. 1b); tetrasedgmented genital forceps (Fig. 1e). Nymph: hydrodynamic body; abdominal gills oval, with a chitinized line trough the central portion and small denticles along the outer margin.

These characteristics are consistent with our observations except that our material invariably shows moderate anastomosis in the stigmatic area (Fig. 1a). This anastomosis is more intense in the subimaginal stage of both sexes and somewhat more so in males. Eaton (1885) also illustrates – in his Fig. 34b of plate 20 – just such a process in the wing of a male imago.

Further characters of diagnostic value: adult stages: last two segments of forceps combined subequal in length to the second, reduced caudal filament, claws identical for all three legs (Ulmer, 1920). This last character was also indicated by Lestage (1931) in his keys to the genera of Ephemeroptera. Nymph: Hypognathous head downwards oriented in 90° asper the longitudinal body axis (Ulmer, 1904).

Metamonius anceps (Eaton, 1883)

Siphylurus? anceps (Eaton, 1883: 209, plate 20, Fig. 34b).
Nymph des Baëtis-Typus (Ulmer, 1904: 6–7, Figs. 1, 7–11).
Ameletus? fuegiensis (Lestage, 1935a: 110).
Ameletoides fuegiensis (Lestage, 1935b: 348–349).
Metamonius fuegiensis (Lestage, 1935) new synonymy.

The descriptions of this species made by Eaton (1885) and Demoulin (1955a, 1955b, 1955c) are quite accurate and closely correspond to our new material. Therefore we will mention here only new observations and discrepancies with these authors.

Male imago

Eaton (1885), when referring to the genitalia, mentions only the forceps. We present here a complete description of the external morphology of all its components.

Genitalia (Fig. 1e). Gonobase angular with distal portion broader, margin free with a wide and shallow 'U'-shaped cleft. Forceps tetrasedgmented; segment 1 subrectangular, width approximately 3/5 of its length; segment 2 length equivalent to 1/2 of complete forceps; segment 3 length 1/3 of segment 2; segment 4 subequal to segment 3. Penis lobes fused from their base almost up to the apex, in most cases the middle part is slightly narrowed. Each lobe presents, in its distal apex, an internal and an external projection, the external being the more basal one. The apex of each lobe has a rounded apex.

Eaton (1883) gave the following tarsal proportions for the first two segments of the male imago's hind leg: segment 1 is 4/5 of the length of segment 2. Subsequently, Demoulin (1955a) questioned this proportion and D. E. Kimmins of the British Museum revised Eaton's specimen. Kimmins established that the first segment is longer than the second in a relation of 14/12. The revision of our material has shown this 14/12 relation to be accurate in most cases, though in some individuals both segments are of equal length. All the same, the variations we observed in the relative tarsal magnitudes do not alter the tarsal formulae which

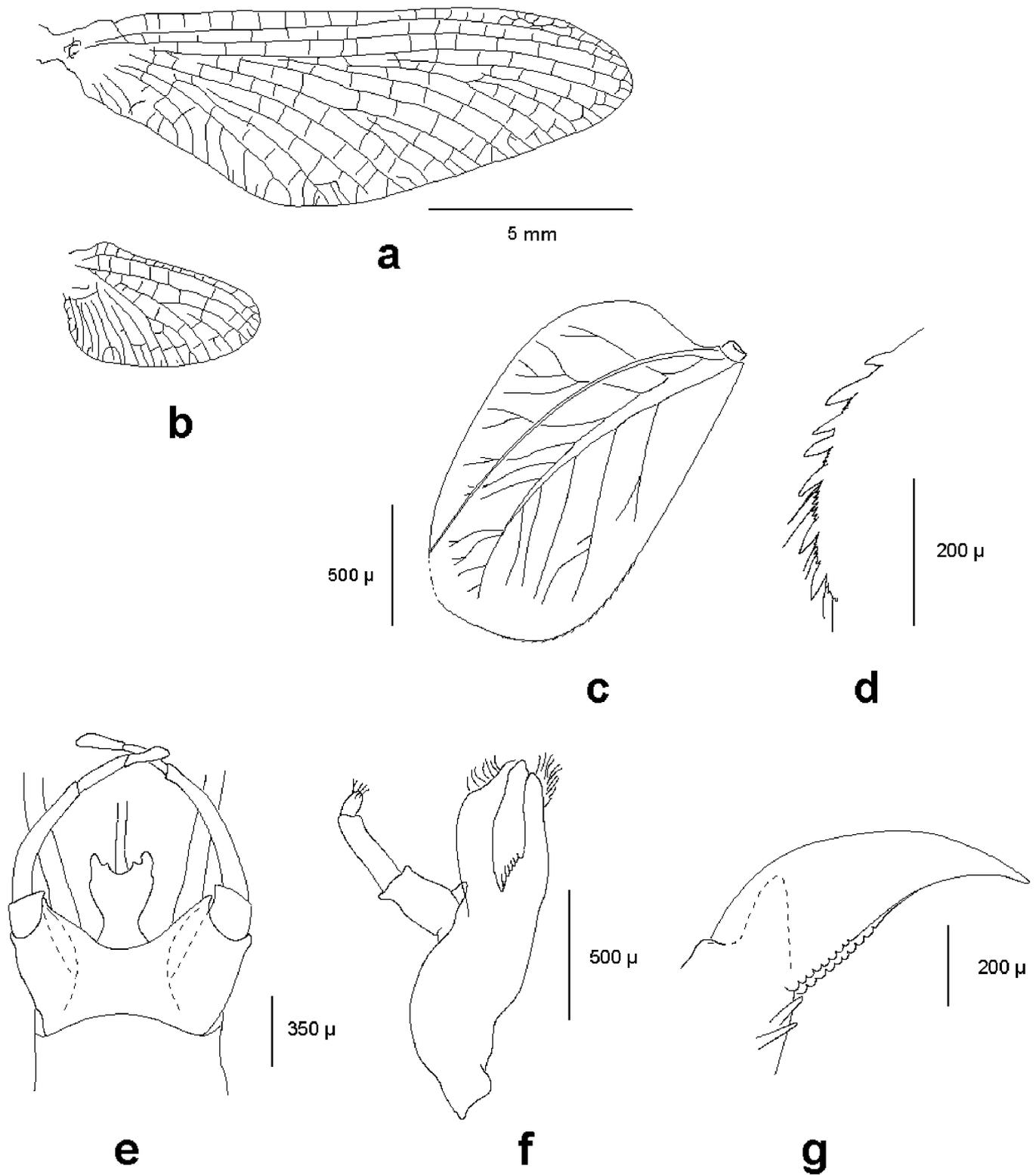


Fig. 1. *Metamonius anceps*. (a) Forewing, male imago. (b) Hindwing, male imago. (c) Gill IV, redrawn from Demoulin (1955b). (d) Gill IV, portion of margin. (e) Genitalia, male imago, ventral view. (f) Nymph, left maxilla. (g) Nymph, detail of claw in leg I.

remains: foreleg: 1 = 2, 3, 5, 4; middle and hind legs: 1, 2, 5, 3, 4.

A description of the previously unknown male subimago is now presented.

Male subimago (in alcohol)

Body length, cerci excluded: 10.5–11.5 mm.

Head. Same as imago (Eaton, 1883), only the antennae are slightly thicker than in male imago.

Thorax. Same coloring as imago. Wing venation more strongly marked than imago, with more transverse veins visible, veins shaded with dark pigmentation, membrane translucent white. Stigmatic area of forewing with notorious vein anastomosis, hind wing may or may not present anastomosis in that zone. Tarsal formulae: foreleg: 2 = 3, 4, 5, 1; middle and hind legs: 2, 1 = 5, 3, 4.

Abdomen. Dorsal markings as in imago but coloration slightly more intense. Ventrally a dark brown longitudinal band goes along all segments. Segments 1–8 with thick posterolateral projections terminated in rounded apices, segment 10 with a deep 'U'-shaped posteromedian cleft; forceps nearly straight. Paracerci similar to imago, cerci shorter than imago, all conveying a markedly pubescent aspect.

Female imago

Demoulin (1955b) indicated that in the foreleg the tibia is longer than the femur, and the tarsus subequal to the tibia. The individuals collected and reared by us presented the tibia subequal to the femur, just as in the male imago, and the tarsus subequal to the tibia in their forelegs.

Female subimago

We have found only one slight difference with Demoulin's (1955c) description of the foreleg segments: in the foreleg, the tibia is subequal to the femur but not in a 3/4 proportion as Demoulin (1955c) indicates. This seems to be an extremely variable character and in one individual we even found the tibia to be subequal to the femur in the right foreleg, but exactly the opposite in the left foreleg: the femur was subequal to the tibia.

Nymph (Fig. 2)

Demoulin (1955c) presents a complete description of the nymph including a plate with illustrations (Fig. 1a–h). His figure 'h' corresponds to the left maxilla, and shows the third palpal segment as glabrous. All the specimens reviewed by us presented the apex with setae (Fig. 1f).

Demoulin (1955c) mentions the presence of a serrated section on the basal half of the internal rim of the claws; we may add that it is composed of a double row of denticles (Fig. 1g).

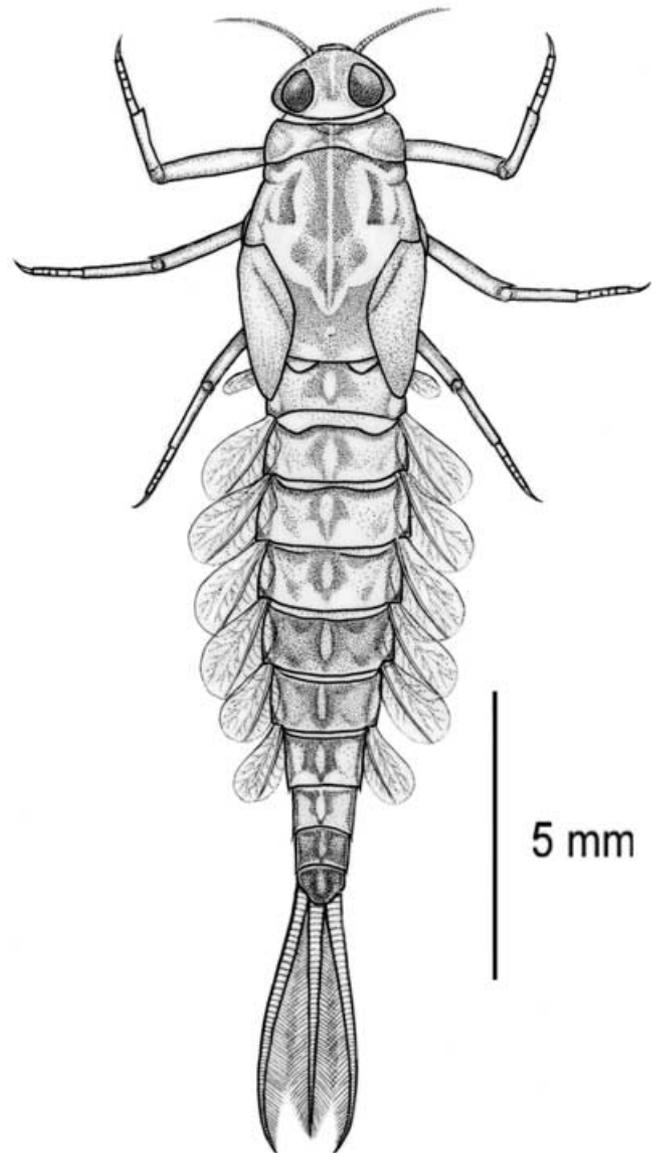


Fig. 2. Nymph of *Metamonius anceps*.

Further characters of diagnostic value for the nymphs: distal margin of the gills is nearly straight (Fig. 1c), except in the first one in which it is curved. Denticles in gills II–VII are disposed in two sections along the gill margins, as shown by Demoulin (1955c, Fig. 1c, for gill IV). The first section covers approximately 1/3 of the distal margin and continues along the straight portion, up to approximately 1/4 of its length. The other section is constituted by smaller and fewer denticles, and goes along the opposite corner of the distal portion of the gill. Serrated portions or minute denticles arranged in irregular groups occur between the larger denticles of both sections, setae also stem amongst the denticles which surpass even the larger ones (Fig. 1d). Gill I presents no denticles but only setae along its distal margin.

The maximum length amongst the nymphs collected was 19.8 mm, in a female individual from Río Quempo. In this

locality and in Dolluco the largest nymphs were found. The specimens from both localities present a darker general pigmentation, which may even obliterate their characteristic maculae.

Metamonius hollermayeri (Navás, 1935)

In spite of the very poor description Navás (1935) made of this species, whose type locality is Trumao, Valdivia province, Chile, we believe that it is possible to clarify its correct taxonomic position.

Three visits were made to the locality of Trumao in 2001 and 2003 in order to find new material of *M. hollermayeri*. Samples were taken in various rivers and streams of the area, to no avail. No *Metamonius* was found. What we did find though, is the species *Siphonella ventilans*, abundant in the rio Bueno (Trumao area), and whose characteristics happen to be completely congruent with the scant description available of *M. hollermayeri*.

The wing drawn by Navás (1935, Fig. 20) reveals the following characteristics: stigmatic area strongly anastomosed, much more so than in any *Metamonius* specimen we have reviewed; veins R and M forked, two veins originate at the base of R, the first branches at one-third of its trajectory originating R1, R2 and R3, the second one branches off around its middle course originating R4 and R; M is forked at one-third of its trajectory originating M1 and M2. This venation pattern is not to be found in the *Metamonius* material reviewed by us, nor in the literature of the genus. This pattern is characteristic of only one neotropical Siphonuroid genus: *Siphonella*. Also, the shape and proportions of the wing drawn by Navás (1935) is coincident with the wing of *Siphonella* drawn by Ulmer (1938, Fig. 11). Furthermore, the type of environment preferred by *Metamonius* is not to be found in the Trumao area. For all the above mentioned reasons we propose to relocate the species *M. hollermayeri* in the genus *Siphonella*.

Diagnosis

The combination of characters defining *Metamonius* is: nymphal body pisciform, well adapted to swimming; seven pairs of abdominal gills, each with a longitudinal reinforcement along the middle; well-developed hypognathous head angled in 90° as-per the body axis; characteristic pattern of body maculae as in Fig. 2; abdominal pattern maculae in the adults same as in nymphs; stigmatic area of the forewings with transverse veins and some anastomosis as in Fig. 1a; tetrasedgmented forceps in male genitalia, forceps and penis as in Fig. 1e.

Biology

Even though the presence of *Metamonius* is recorded in the literature in at least one medium-sized river such as the Gol Gol (Demoulin, 1955c) and, even though two larvae were

collected by the authors in the Río Frío (Palena Prov., Chile), the great majority of captures have taken place in small mountain streams with cold, clear, well-aerated waters, typically in the headwater reaches of streams well removed from and little perturbed by human activity. We should mention here that the Argentine lake localities found in the literature are area references only, all *Metamonius* nymphs having actually been found in streams entering the lakes (E. Dominguez, pers. comm.).

Metamonius nymphs are quick swimmers found mostly under large stones and boulders in rapid waters or in the slack marginal waters of swift streams, but always associated with rocks or other objects large enough to shelter under. Exceptionally, at Icalma river, nymphs were found in abundance amongst the dense *Myriophyllum* growing from the fine gravel bottom.

The adults emerge in spring, from early November to January. Reared subimagos took 48–96 h to reaching the imaginal stage. We have never observed the nuptial flight of the species.

The accompanying insect fauna collected along with our *Metamonius* material, as well as what is registered in the literature (Miserendino & Pizzolon, 2000), reflects a community structure typical of headwater reaches, dominated by representatives of the orders Plecoptera, Ephemeroptera and torrential Diptera, accompanied by species of Megaloptera and Trichoptera.

Exceptionally, *Metamonius* has been found in the sub-Antarctic forests of Western Tierra del Fuego, in the semi-arid scrubland region of Central Chile, and even in completely exposed sites above the tree line such as the Arroyo Esquel, Argentina (Miserendino & Pizzolón, 2000), but most *Metamonius* localities lie inside well-forested areas, typically within the Andean *Nothofagus* dominated assemblages known as the Nord-Patagonic rainforests. Since *Metamonius* exists outside these forests we believe that the coincidental distribution of the two is due to similar environmental requirements, found mostly along the Andean and pre-Andean slopes of South-Central Chile and Argentina.

Geographical distribution (Fig. 3)

The distributional area of *Metamonius* covers a wide latitudinal span along the Andean ranges from the province of Santiago, Chile (33°32'S) to Ushuaia in Tierra del Fuego (54°47'S), and also in the Chilean Coastal Ranges south of the Cordillera de Nahuelbuta (37°46'S), below parallel 38°S. *Metamonius* is recorded in various Argentine localities from Lago Huechulafquen (39°43'S) to Esquel 42°54'S, and then again in Ushuaia its southernmost location. This distributional area is not homogeneous as present records show a disjunct distributional area at Ushuaia, separated by some 1400 km from the Río Queulat (44°30'S). Furthermore, the Andean and Chilean coastal ranges are separate mountain systems and *Metamonius* has never been found in the valley reaches, therefore this intermediate depression should be

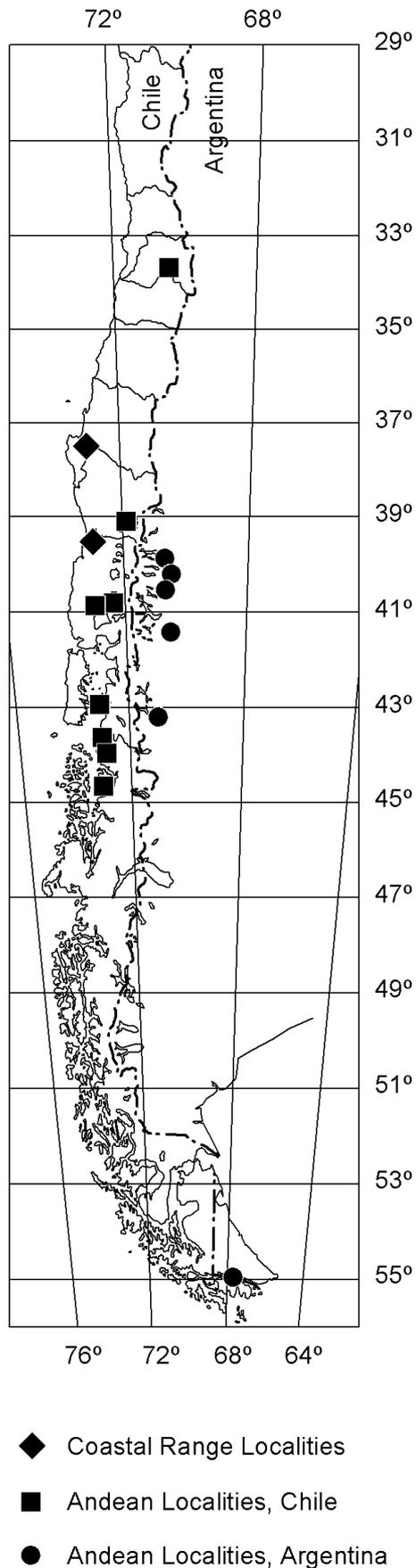


Fig. 3. Geographical distribution of *Metamonius anceps*.

considered as a dispersion barrier and the populations present in the higher reaches of the coastal ranges as distributionally disjunct also. Therefore, the distribution of *Metamonius* comprises a main distributional area along the Andean ranges, outside of which, in two distinct locations, *Metamonius* is found in a distributionally disjunct condition: Ushuaia to the South, and the coastal ranges to the West.

Discussion

Ulmer's (1904) description of his '*Nymph des Baëtis-Typus*' is completely coincident with Demoulin's (1955c) nymph of *M. anceps*, as the latter author noted. For this reason, after the various tentative denominations by Lestage (1935a, 1935b) as *Ameletus? fuegiensis* and *Ameletoides fuegiensis*, Demoulin (1955c) included this nymph in the genus *Metamonius*, with reservations.

Demoulin (1955c) also mentions three characters in the *M. anceps* nymph which he believes might be of specific value. Two of those characters are not mentioned in Ulmer's (1904) description: the serrated section on the inner margin of the claws, and a soft appendage shaped 'as gloved fingers' observable in the outer side of the cardino-stipital articulation of the maxillae. The third character is mentioned by Ulmer (1904) and, even though it is consistent with his own description of *M. anceps*, Demoulin (1955c) mentions it as a possible differentiating character: it concerns the proportions of the maxillary palp segments, in which articles I and II are subequal in length, and article III is less than half the length of article II. Besides all this, Domínguez et al. (1994) proposed that the two nymphs might be distinguished by differences in the coloration of the abdominal maculae.

We have reviewed the claw configuration of the new specimens collected in Ushuaia, type locality of *M. fuegiensis*, and all were found to have the double row of denticles aforementioned as characteristic of *M. anceps*. Also, they all possess the soft appendage on the cardino-stipital articulation, and the segments of their maxillary palps were found to conform to the proportions in *M. anceps*. The coloration of the maculae was similar to *M. anceps*, although the general pigmentation is somewhat darker.

Having carefully reviewed a male imago from this same locality in Ushuaia, we have concluded that all its characteristics are consistent with *M. anceps*. For all the above-mentioned similarities between the specimens of *M. fuegiensis* collected from the type locality, we propose here that *M. fuegiensis* is a junior synonym of *M. anceps*, the name *Metamonius anceps* remaining by priority.

Though many groups and species endemic to the Chilean coastal ranges have been identified, we were most careful in examining our material from these localities so that we can confidently ascertain that no differences whatsoever exist between Coastal and Andean *Metamonius*. Neither did we find differences among its latitudinal exponents that would substantiate different species in this genus. Therefore having

removed *M. hollermayeri* from the genus, *Metamonius* has been found to be monospecific.

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