

ORIGINAL ARTICLE

A new species of the genus *Paramaka* Savage & Dominguez, 1992 with some comments on related genera (Ephemeroptera, Leptophlebiidae, Atalophlebiinae)

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Abstract

The genus *Paramaka* Savage & Dominguez, 1992 has been established to accommodate the species *P. convexa* (Spieth, 1943) described from Surinam. Here, we describe a new species, *Paramaka antonii* nov. sp. from (former British) Guyana. A cladistic analysis is performed on *Paramaka* and related genera such as *Hydrosmilodon* (four species), *Needhamella ehrhardti* (Ulmer, 1920) and *Leentvaaria palpalis* Demoulin, 1966. Our results put forward *Hydrosmilodon* as paraphyletic, with species recently described from French Guyana more closely related to *L. palpalis* than to others. The description of the winged stages of *Leentvaaria* is needed before carrying out any reassignment.

Keywords: Guyana, *Paramaka*, *Hydrosmilodon*, new species, cladistic analysis

Introduction

The *Hermanella* complex, as defined by Dominguez and Flowers (1989), Flowers and Dominguez (1991) and Dominguez et al. (2001) encompasses several apotypic species easily recognizable by their highly modified and enlarged mouthparts. *Traverella* Edmunds, 1948 is the most diversified and the most widespread with 12 species dispersed from Argentina to Canada. The genus *Hermanella* Needham & Murphy, 1924 is composed of four species distributed between Brazil, Argentina and Paraguay. The genus has also been recently reported from French Guyana (Orth et al. 2001). *Leentvaaria palpalis*, known only from nymphs, and recognizable to its elongated labial palps was described by Demoulin (1966) from Surinam. The genus *Needhamella* Dominguez & Flowers, 1989 was established to accommodate the species *N. ehrhardti* (Ulmer, 1920) found in Southern Brazil, Northern Argentina and Uruguay. The genus *Hylister* Dominguez & Flowers, 1989 was created for a single species from South-eastern Brazil. The genus *Hydrosmilodon* Flowers & Dominguez, 1992 was set up for two species found in

Northern Argentina (*H. saltensis* Flowers & Dominguez, 1992) and in Central America (*H. primanus* Eaton, 1892). Recently, Thomas et al. (2004) described two new species from French Guyana that greatly enlarged the intraspecific variability of the genus *Hydrosmilodon*. Finally the species *Thraulius convexus* Spieth, 1943 was used to establish the monotypic genus *Paramaka* Savage & Dominguez, 1992 described from Surinam. The nymph of the latter has been recently described (Blanco-Belmonte et al. 2003) with material from Venezuela, Surinam and French Guyana. The genus is also known from Brazil (Savage & Dominguez 1992).

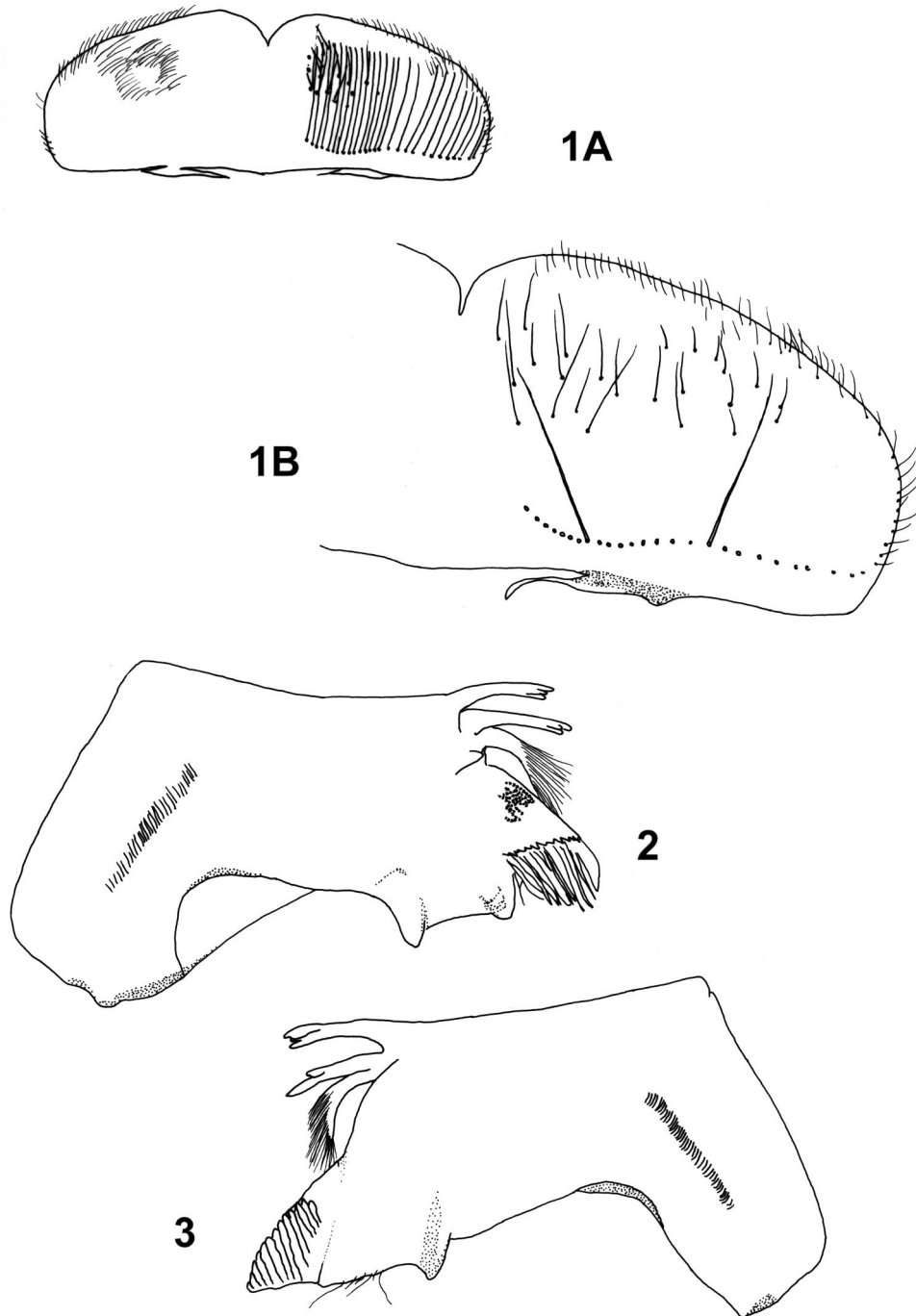
Several cladistic analyses have been proposed for the *Hermanella* complex (Flowers & Dominguez 1991; Dominguez et al. 2001; Dominguez & Cuezco 2002) that suggest *Hylister* and *Hermanella* as sister groups, and *Leentvaaria* related to *Needhamella*; the analysis remaining unclear concerning the position of *Hydrosmilodon*. No attempt has been made to reconstruct the whole clade since description of the nymph of *Paramaka*.

In the Museum of Zoology in Lausanne is deposited a small collection of mayflies from (former

British) Guyana; among them several nymphs have been previously assigned by me to the “*Needhamella-Hydrosmilodon*” complex. This material has been restudied in the light of the newly described species by Thomas et al. (2004). The Guyana population clearly presents several differences with other species of the complex and is described here below as a new species. Finally a cladistic analysis is performed on

all known species of *Hydrosmilodon* and related genera.

Holotype and most of the paratypes are housed in the Museum of Zoology in Lausanne; other paratypes are also deposited in the collections of Florida A & M University, Tallahassee (FAMU) and Instituto-Fundacion Miguel Lillo, Tucuman (IFML).



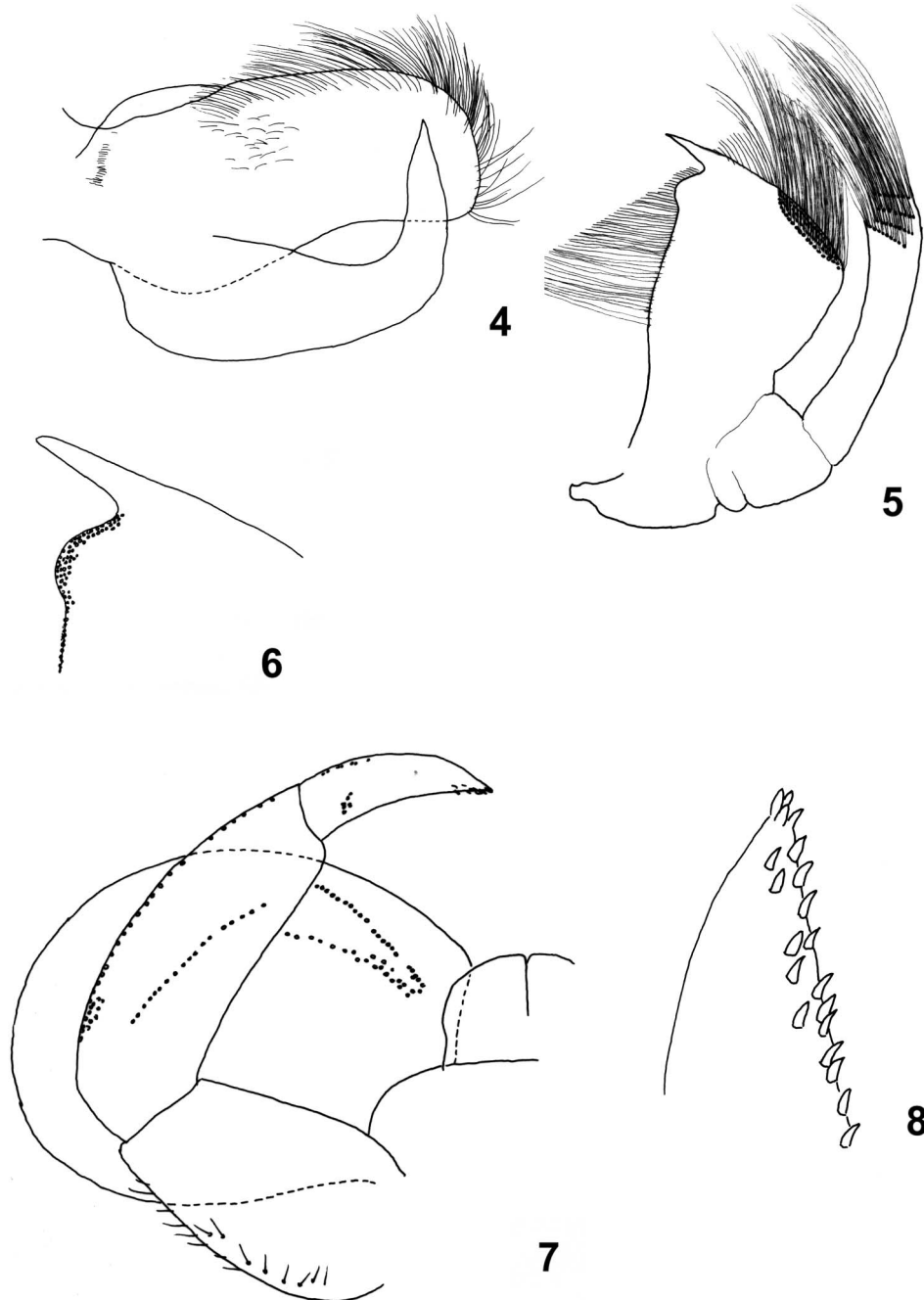
Figures 1–3. *Paramaka antonii* sp. n. nymph (d: dorsal, v: ventral view) Fig. 1a: Labrum (right, d; left, v); Fig. 1b: Half right part of the labrum (d) (most of long setae omitted); Fig. 2: Left mandible (d); Fig. 3: Right mandible (d).

***Paramaka antonii* sp. n.**

Nymph. Body length: up to 7.2 mm; cerci: up to 5.0 mm; terminal filament: up to 8.0 mm.

General coloration brown; in mature nymphs, area around the ocelli, between the compound eyes and the clypeus white, in younger this area is brown-grey. Mouthparts yellow-brown, except the setae brown. Legs yellow-brown, each with a distinct brownish spot on the distal part of the dorsal margin of the

femora; apex of the femora clouded with brown; a narrow transverse band on the proximal and subdistal parts of the tibiae, as well as the proximal third of the tarsi. Abdominal tergites brown with a dark brown median line especially well marked on tergites 6–10. Two yellowish spots near the lateral margin of tergites 6–9 (on one specimen only on tergites 6–8). Abdominal sternites uniformly yellowish. Cerci and terminal filament yellow-brown.



Figures 4–8. *Paramaka antonii* sp. n. nymph Fig. 4: Half left part of the hypopharynx (v); Fig. 5: Maxilla (v); Fig. 6: Apex of the maxilla (v) (setae omitted); Fig. 7: Half right part of the labium (v) (setae omitted); Fig. 8: Detail of the terminal segment of the labial palp (v).

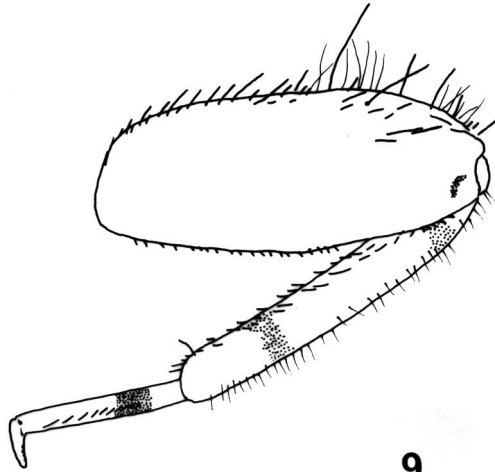
Head. Clypeus with a distinct triangular carina in the middle of the anterior margin. Ratio between clypeus vs. labrum widths, ca 1.6.

Labrum (Figure 1A, B) ca. 2.9x broader than long; antero-median incision well marked; anterior and lateral margins rounded; dorsal face with two rows of 25–26 very long and stout setae regularly arranged in the basal part; presence of scattered long and stout setae, especially near the middle of the labrum;

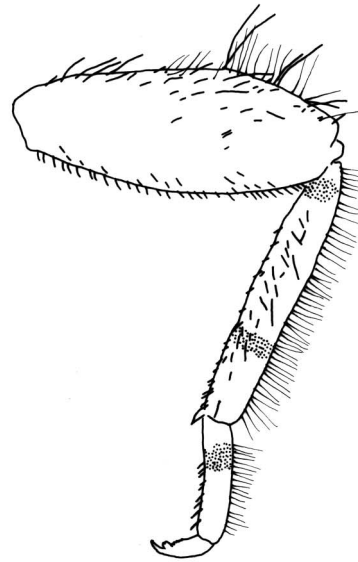
anterior and lateral margins covered with thin and short setae; ventral side covered with dense, long and thin setae.

Left mandible (Figure 2) angular, outer and inner incisors with 3 teeth each; a small distinct chagrined area under the prostheca; row of thin setae in the posterior part.

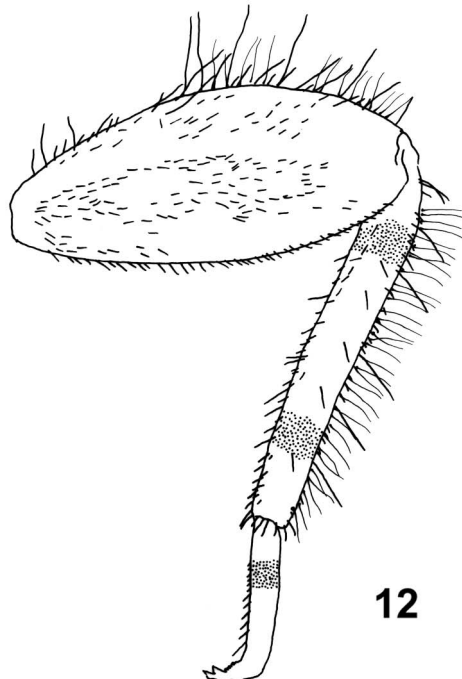
Right mandible (Figure 3) angular, outer and inner incisors with three and two teeth respectively;



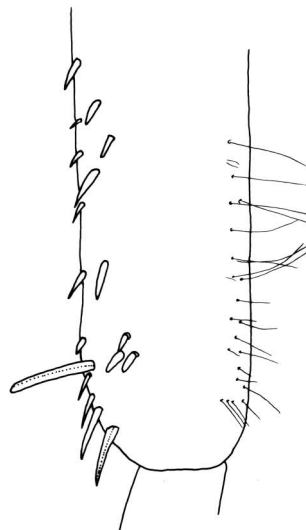
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11



12



10

Figures 9–12. *Paramaka antonii* sp. n. nymph Fig. 9: Foreleg; Fig. 10: Detail of the apex of the fore tibia; Fig. 11: Middle leg; Fig. 12: Hind leg.

scattered setae behind the mola; row of thin setae in the posterior part.

Hypopharynx as in Figure 4.

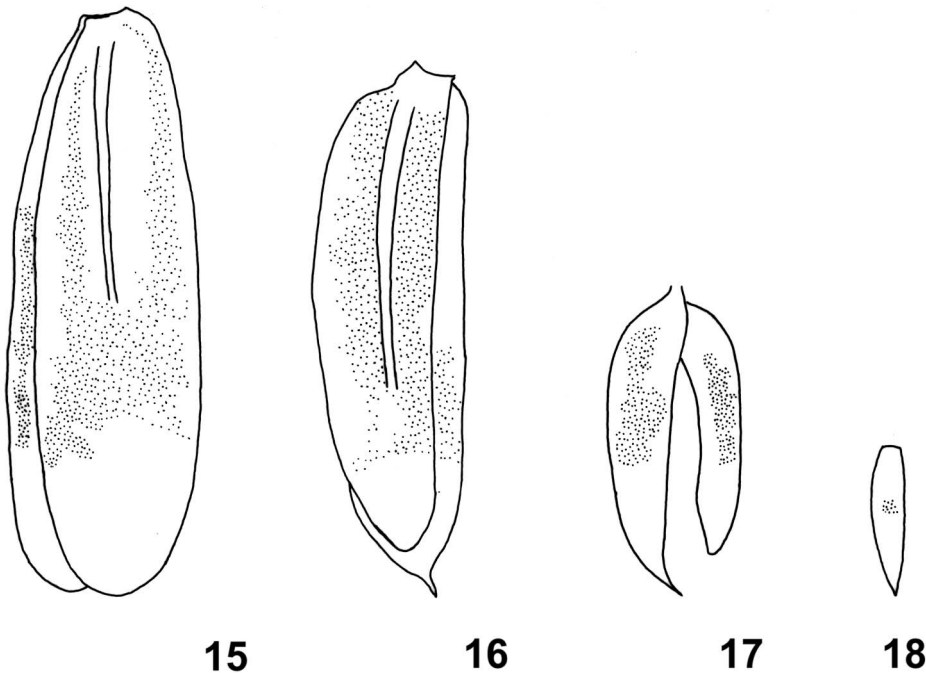
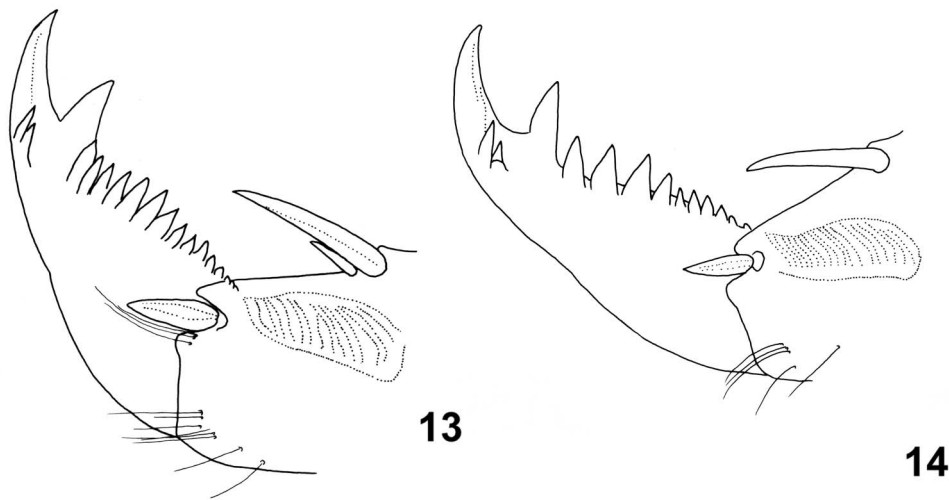
Maxillae (Figure 5) with numerous long setae on the crown of the galea-lacinia and on the apex of the palp; all these setae are arranged in regular rows; inner part of the galea-lacinia with a well-developed tooth (Figure 6).

Labium (Figure 7) also with numerous rows of long setae; glossae short, paraglossae hypertrophied, bearing two rows of setae near the anterior margin;

labial palp three-segmented, the second with a row of long setae in the middle of the dorsal face; third segment about half the length of the second one, bearing several stout setae at the apex and on the inner margin (Figure 8).

Thorax. Pronotum with 1–3 stout and pointed setae in the middle of the lateral margin.

Forelegs (Figure 9) with femora bearing long setae only on the distal part of the anterior face; dorsal margin covered with long and thin setae, some longer and thicker on the distal part; ventral



Figures 13–18. *Paramaka antonii* sp. n. nymph Fig. 13: Tarsal claw of the middle leg; Fig. 14: Tarsal claw of the hind leg; Fig. 15: Gill 1; Fig. 16: Gill 4; Fig. 17: Gill 6; Fig. 18: Gill 7.

margin with short and stout setae; dorsal margin of tibiae with a row of long and thin setae; anterior face with scattered long and stout setae; ventral margin with stout, simple setae, not pectinate (Figure 10).

Middle legs (Figure 11) as the forelegs except the dorsal margin and the anterior face of femora with more numerous long setae.

Hind legs (Figure 12) with anterior face of femora covered with stout and blunt setae; dorsal margin of tibiae with 7–8 stout and long setae, together with numerous short and stout setae, and a row of long and thin setae; tibiae ending with a crown of long and stout setae.

Tarsal claws (Figures 13 and 14) very characteristic and formed by a row of 11–15 teeth increasing in length distally: presence of a large subapical tooth, as well as two pointed teeth near the apex of the claw.

Abdomen. Posterior margin of each tergite bordered with a row of stout, acute and triangular spines, at least four times longer than broad at base.

Posterolateral projections weakly developed on segment 8, more prominent on segment 9.

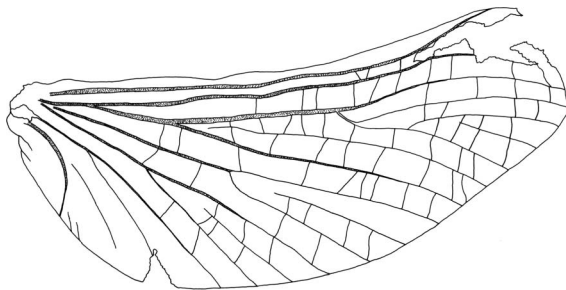


Figure 19. *Paramaka antonii* sp. n. fore wing of the subimago.

Gills present on segments 1–7, decreasing in size, all tinted with violet in the proximal $\frac{3}{4}$; gills 1–6 with two lamellae; gill 7 atrophied, with a single lamella.

Gills 1–3 similar in shape (Figure 15); apex of lamellae regularly rounded; gills 4–6 (Figures 16–17) with dorsal lamella ending with a thin and pointed process, ventral lamella obtuse; gill 7 (Figure 18) vestigial, less than half the size of gill 6.

Cerci with a row of short setae on each segment.

Winged stages: unknown except forewing (Figure 19) (extracted from a mature female nymph).

MA and MP forks asymmetrical; cubital field without intercalaries or sigmoid veins.

Material examined

Holotype: 1 male nymph, GUYANA, Ireng River, Orinduik Falls, 19.IX.2001, P. Derleth leg.

Paratypes: 7 nymphs, same data.

The new species has been collected among the dead leaves accumulated downstream the falls. Noteworthy to mention that the river in which the new species has been collected belongs to the Amazon basin drainage and forms the border between Guyana and Brazil.

Etymology

This species is dedicated to my beloved son Antoine.

Affinities

At the larval stage, genera *Traverella*, *Hylister* and *Hermanella* are easily distinguished from others, mainly based on the gill shape. Genera *Hydro-smilodon* and *Leentvaaria* are characterized by an

Table I. List of characters and character state.

Character	0	1 or 2
1	Ratio clypeus/labrum widths	≤ 1.4
2	Fronto median margin of the clypeus	Concave
3	Row of setae on the posterior half of the labrum	Absent
4	Large scattered setae on the labrum	Present
5	Anterior margin of the labrum	Rounded
6	Setae on the outer margin of the mandibles	Present
7	Shape of the mandible	Rounded
8	Apical tooth of the maxilla	ca $\frac{1}{4}$ width of apex
9	Setae on the fore tibiae	Simple
10	Apical tooth on the tarsal claws	Enlarged
11	Apex of tarsal claws	With denticles
12	Apex of gill lamellae	Multifid
13	Apex of gill lamellae 4	Regularly pointed
14	Apex of gill lamellae 1	With a digitiform process
15	Gill lamellae 7	Smaller than gill lamellae 6
16	Posterolateral projections on abdominal segments	7–9

clade is strongly supported (76%), but its placement as the sister group of ((*H. primanus* + *H. saltensis*) + *N. ehrhardti*) is weakly corroborated (24% of all reconstructions). This reconstruction also makes *Hydrosmilodon* appear paraphyletic. Bootstrap support is high for *H. saltensis* as the sister of *H. primanus* (88%), both being the sister group of *N. ehrhardti*, whereas *H. miki* is the sister group of (*L. palpalis* + *H. gilliesae*). The two species from French Guyana seem to represent another lineage, although they possess some common features, the most remarkable

being the large tooth at the apex of the maxilla. In their original description, Flowers and Dominguez (1992) mentioned as an apomorphy for the genus *Hydrosmilodon* (including at that time *H. primanus* and *H. saltensis*) the presence of denticles on the outer incisors of the mandibles. Thomas et al. (2004) said unfortunately nothing about that character, but based on their drawings (Figures 3 and 22) these denticles seem lacking in *H. gilliesae* and *H. miki*, suggesting these two taxa may belong to another clade.

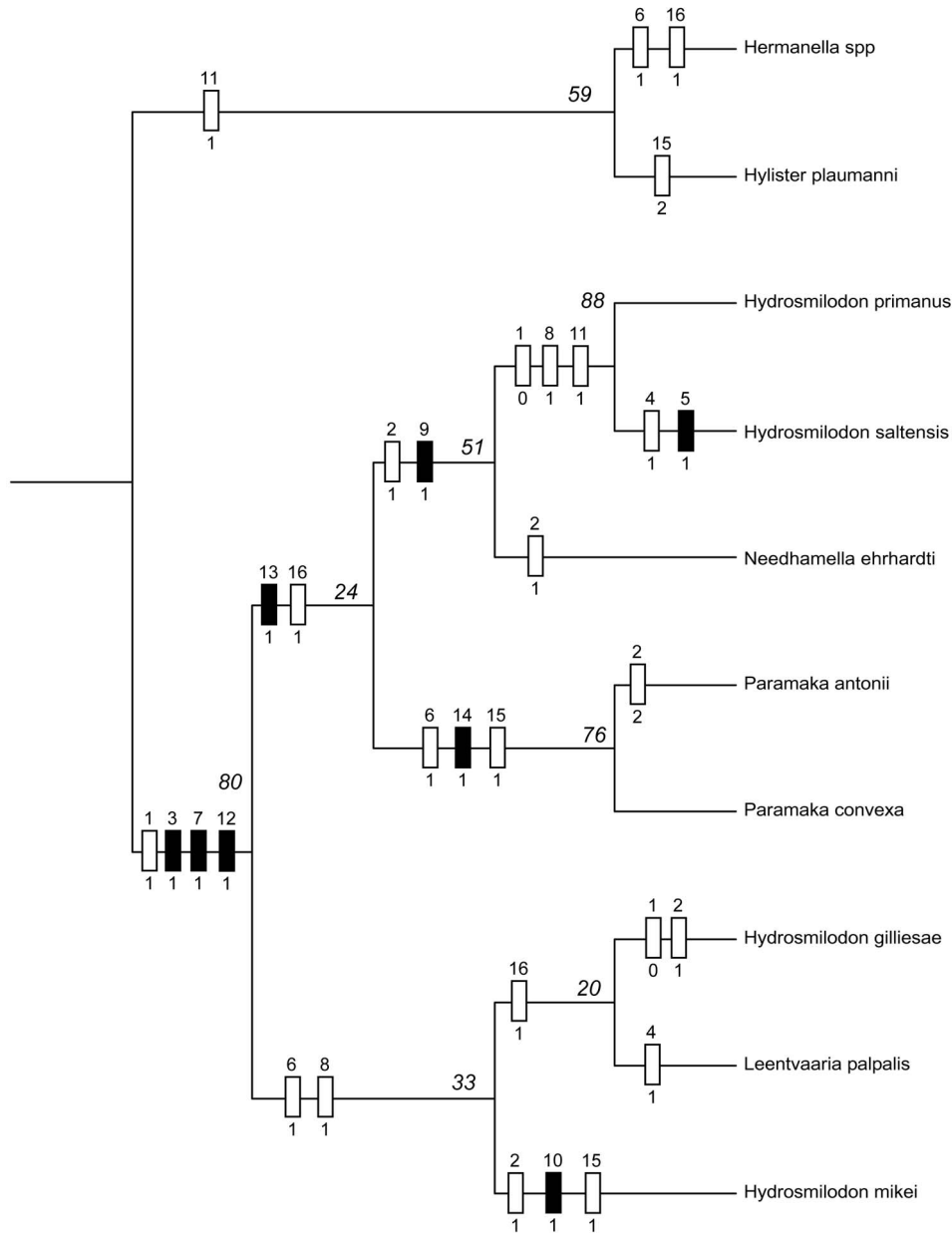


Figure 20. Cladistic reconstruction of *Paramaka* species and allied genera; black boxes: apomorphies; white boxes: homoplasies or reversions; number above boxes: character number according to Table I; number below boxes: character state; bootstrap values for each node indicated in italic.

On the basis of our results, two alternatives are possible to make them match the monophyletic concept:

- (1) Consider the eight taxa as belonging to a single genus; in this case all must bear the generic name *Leentvaaria*, *Hydrosmilodon*, *Needhamella* and *Paramaka* being considered as synonyms;
- (2) Keep the concept of *Hydrosmilodon* as proposed by Flowers and Dominguez and restrict it to the species *H. primanus* and *H. saltensis*; the genus *Needhamella* being the sister group of *Hydrosmilodon* sensu stricto; transfer the French Guyana species into the genus *Leentvaaria*. The very elongated 2nd labial palp segment may in fact be an autapomorphy to *L. palpalis* and may have no generic value.

Although the second hypothesis seems the most realistic, we will refrain using it at the moment for two main reasons:

- (1) There is no synapomorphy supporting the branch composed of these three taxa, characters 6 and 8 being subject to homoplasy, resulting in a low bootstrap value (33%)
- (2) The adult stage of *Leentvaaria* is still unknown and we suspect it to bear some autapomorphic characters that will completely reorganize our reconstruction.

Further researches are needed, especially the description of the winged stages of *Leentvaaria*, before a more complete assignment of “*H. gilliesae*” and “*H. miki*” can be proposed.

Acknowledgments

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