REDESCRIPTION AND PHYLOGENETIC RELATIONSHIPS OF *LEENTVAARIA* DEMOULIN (EPHEMEROPTERA: LEPTOPHLEBIIDAE)

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ABSTRACT

The genus *Leentvaaria* was established by Demoulin in 1966 for a single species, *L. palpalis*, known from a few nymphs from Surinam. Since then, there was no other report on this species.

The phylogenetic relationships of the components of the *Hermanella* generic complex were studied by Flowers and Domínguez (1991). Although *Leentvaaria* almost surely belonged to this complex, it was not included because the necessary characters were not available at that time.

Recently, we have obtained new nymphal material of *Leentvaaria* from Brazil, that allowed us to obtain the nymphal characters required to establish the relationships of *Leentvaaria* with the other components of the *Hermanella* complex.
In this study *Leentvaaria* appears as the sister group of *Needhamella* and is included within the *Hermanella* complex. The nymph of *L. palpalis* Demoulin, is redescribed based on the new material.

INTRODUCTION

The genus *Leentvaaria* was established by Demoulin (1966), for a single species, *L. palpalis*, described from 3 nymphs collected in Surinam. Since then, there was no other report of this genus. The phylogenetic relationships of the *Hermanella* generic complex, a distinctive group of leptophlebiid mayflies, were studied by Flowers and Domínguez (1991). The nymphs of this group can be characterized mainly by extremely broad mouthparts, bearing even rows of long setae, and male imagoes with modified subgenital plates. Although *Leentvaaria* almost surely belonged to this complex, it was not included in that analysis because several of the

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necessary characters were not available at that time. Recently, we have obtained good nymphal material from Brazil, that allowed us to study in detail the nymphs of *Leentvaaria*. Continuing with a series of papers dedicated to the systematics of this group (Domínguez and Flowers, 1989; Flowers and Domínguez, 1992; Savage and Domínguez, 1992) we analyze and propose the phylogenetic relationships of *Leentvaaria* with the other components of the *Hermanella* complex. The nymph of the genus is also redescribed, based on the new material.

MATERIALS AND METHODS

The material used in this study is deposited in the following insitutions: INPA (Instituto Nacional de Pesquisas de Amazonia, Brazil) and IFML (Instituto Fundacion Miguel Lillo, Argentina).

The phylogenetic relationships were analyzed with the aid of the computer programs Pee-Wee (Goloboff, 1993) and CLADOS (Nixon, 1992).

Genus *Leentvaaria* Demoulin

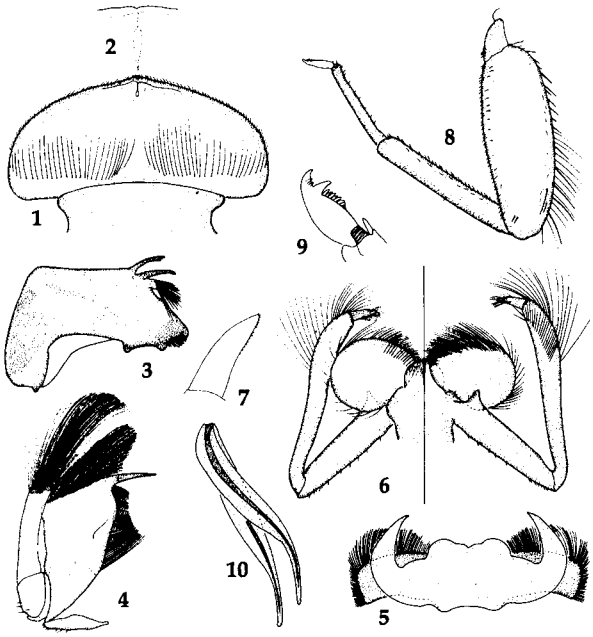
Leentvaaria Demoulin, 1966: 13.

Mature nymph: Head. Prognathous. Antennae 2.5 times length of head. Mouthparts (Figs. 1-7). *Clypeus* with lateral margins strongly concave. Maximum width of labrum 1.5-1.6 times maximum width of clypeus; length of labrum less than 0.4 maximum width, lateral margins rounded as in fig. 1, with posterolateral angulation; anteromedian emargination shallow, V-shaped dorsally, deep ventrally as in fig. 2; divided row of long dorsal setae on basal 1/5 of labrum with 25-28 setae on each side, short setae on margins. *Left mandible* (Fig. 3): outer margin angularly curved, angle sharp. *Maxillae* (Fig. 4) galea-lacinia with one long thick seta on venter, close to inner margin; subapical pectinate setae lacking; very prominent tusk on inner apical angle. Segment 1 of maxillary palpi 0.5 length of segment 2; segment 3 0.8 length of segment 2. Segment 1 with thick setae on outer margin, segment 2 with two long setae on inner apical angle, segment 3 with long setae in ordered rows. Lingua of hypopharinx with well-developed lateral processes, anterior margin with broad median V-shaped cleft; superlingua with long setae along anterior margin (Fig. 5). *Labium* (Fig. 6): Segment 1 of palpi 0.65 length of segment 2, segment 3 0.15 of segment 2. Segment 1 with a basal acute prominence; segment 2 elbowed, widened on distal 1/4 and with a dorsal row of 15-19 setae (Fig. 6); segment 3 curved, with long setae on ventral surface and external margin, short spines on inner margin (Fig. 7); glossae straight, flat, with short setae along anterior margins; paraglossae with subapical row of long setae on ventral surface. Anterolateral margins of pronotum with three large setae. Wing pads glabrous. *Legs* (Fig.8): trochanters with row of setae on apico-dorsal surface; femora with thick, long pointed setae along posterior margin and short spines along inner margin; fore and middle femora with long, fine setae along posterior margin, short spines on dorsum of middle and hind femora; tibiae with short spines along inner margin, fine setae on outer margin; tarsi with short spines on inner margin, setae on outer margin of tarsi 2 and 3. Claws hooked, narrow, ventral denticles as in fig. 9 . Gills (Fig. 10). Gills on segments 1-7, birramous, long and narrow, tapering evenly from base to apex, smaller posteriorly; trachea along median line, not branched. Posterolateral projections on abdominal segments 8 and 9. Terminal filament longer than cerci, small spines on posterior margin of each segment.

Material: BRAZIL, RR, BR 174, Km 914, Rio Paricarana, 28-X-87, Equipo Granfinale, 10 nymphs. 5 in INPA, 5 in IFML.

Distribution: Surinam and Northern Brazil.

Discussion: The type species, described by Demoulin is known only by three young nymphs. It is difficult to know if the species here used to redescribe the genus is conspecific with the type species "*L. palpalis*" and for this reason is not assigned to it. In 1992, Savage



Figs. 1-10. *Leentvaaria* sp. nymph. 1, Labrum and clypeus; 2, Labrum (detail of anteromedian emargination); 3, Left mandible; 4, Maxilla; 5, Hypopharynx; 6, Labium (right, ventral view; left, dorsal view); 7, Detail of third segment of labial palpus; 8, Foreleg; 9, Tarsal claw; 10, Gill.

and Domínguez when establishing the genus *Paramaka*, raised the possibility that *P. convexa*, its type species, could represent the unknown adult of *Leentvaaria*. After comparing the abdominal pattern from the new specimens of *Leentvaaria* with *P. convexa* it appears very improbable that they could be congeneric.

The genus *Leentvaaria* belongs to the *Hermanella* generic complex (Flowers and Domínguez, 1991) based on the following synapomorphies present in the single tree obtained: 10-11, 14-16, 18 and 21-23.

The nymphs of *Leentvaaria* can be separated from the other genera of Leptophlebiidae by the following combination of characters. Labrum as wide as head, with shape and dorsal setae as in fig. 1; long setae on maxillary palpi in even rows (Fig. 4); long row of dorsal setae on segment 2 of labial palpi present; prominent tusk on inner apical margin of maxillae; segment 1 of labial palpi shorter than segment 2 (Fig. 6); enlarged subapical denticle on tarsal claws (Fig. 9).

Leentvaaria is very close to *Needhamella*, from which it can be distinguished by the size of the maxillary tusk, the shape of the gills, and the presence of a basal prominence in segment 1 of labial palpi.

CLADISTIC ANALYSIS

Characters and Coding

For the phylogenetic analysis a matrix of 57 characters (Appendix I) was compiled, including 41 nymphal and 16 adult external morphological characters. In this study 22 taxa are treated, the same that were analyzed in Flowers and Domínguez (1991), except for

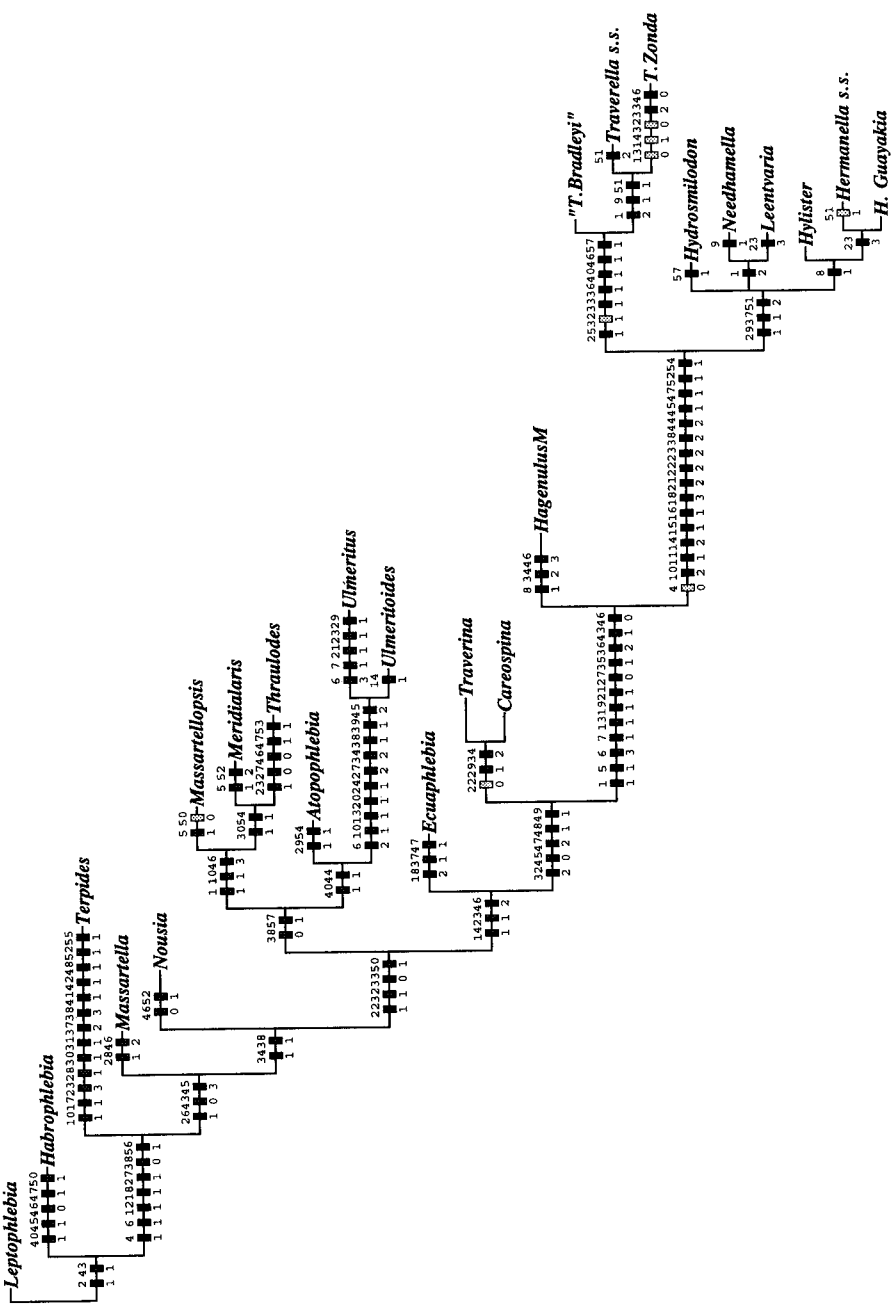
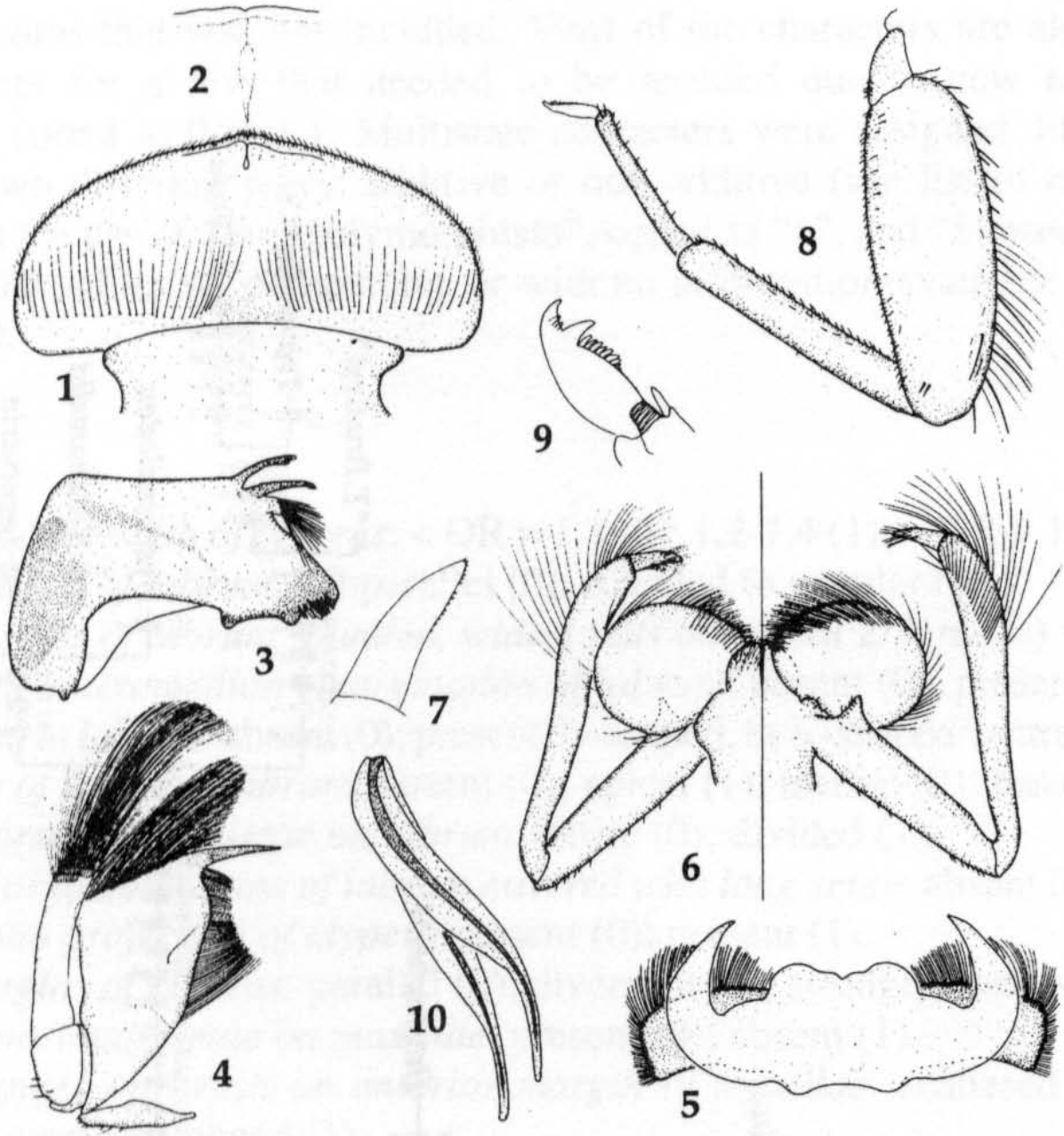


Fig. 11. Cladogram obtained from the analysis. Black boxes= apomorphies; dark grey boxes= parallelisms; light gray boxes= reversals.

Hagenulus caligatus that was not included. Most of the characters are also treated in the same way, except for a few that needed to be recoded due to new evidence. Binary characters were coded as 0 and 1. Multistate characters were assigned different numbers, and treated in two different ways: additive or non additive (see list of characters). Both programs permit the use of "Full polymorphism", coded as "*", and "Subset polymorphism" coded as "$". Characters not comparable or with no information available were assigned a missing code (?).

Character List

1. *Width of labrum/width of clypeus*: < OR = 1.1 (0); 1.2-1.4 (1); = OR > 1.5 (2)[additive].
2. *Lateral margins of labrum*: subparallel (0); rounded to angular (1).
3. *Lateral margins of labrum rounded, widest part on apical 2/3*: no (0) yes (1).
4. *Denticles on anteromedian emargination of labrum*: absent (0); present (1).
5. *Median hood in labrum*: absent (0); present, U-shaped, or V-shaped ventrally (1); cleft (2).
6. *Dorsal row of setae on labrum*: absent (0); apical (1); medial (2); basal (3)[additive].
7. *Shape of dorsal row of setae on labrum*: entire (0); divided (1).
8. *Area anterior to dorsal row of labrum covered with long setae*: absent (0); present (1).
9. *Anteromedian projection of clypeus*: absent (0); present (1).
10. *Lateral margins of clypeus*: parallel (0); divergent (1); strongly concave (2)[additive].
11. *Subapical pectinate setae on maxillae*: present (0); absent (1).
12. *Hairs or spines on brush on anterior margin of maxillae*: scattered or unevenly arranged (0); evenly arranged (1).
13. *Tusk on inner apical margin of maxillae*: absent (0); present (1).
14. *Segment 2/segment 1 of maxillary palpi*: subequal (0); 1.1 - 2 (1); >2 (2)[additive].
15. *Ordered rows of setae on segment 3 of palpi*: absent (0); present (1).
16. *Thick, blunt setae on segment 1 of maxillary palpi*: absent (0); present (1).
17. *Large non pectinated seta on inner apical margin of maxillae*: absent (0); present (1).
18. *Setae on inner margin maxillary palpi 2*: spine-like, along all margin (0); needle-like, apical 2/3 to 1/2 (1); needle-like, apical 1/5 (2); needle-like, apical corner (3); absent (4) [nonadditive].
19. *Strong setae on inner margin of palpi 3*: present (0); absent (1).
20. *Palpifer size of maxillae*: normal (0); enlarged (1).
21. *Position of articulation of palpi of maxillae*: on apical 1/2 (0); medial (1); basal (2); [additive].
22. *Shape of outer margin of mandible*: smoothly curved (0); obtuse (1); right angled (2); [additive].
23. *Setae on outer margin of mandible*: on 2/3 or more (0); on 1/2 (1); on basal 1/4 (2); absent (3); [nonadditive].
24. *Setae at base of outer incisor*: absent (0); present (1).
25. *Patch of long setae on venter of mandible*: absent (0); present (1).
26. *Shape of lingua of hypopharynx*: lateral arms lacking (0); lateral arms present (1).
27. *Long spines on labial palpi*: absent (0); on segment 3 only (1); on segment 2 and 3 (2); [nonadditive].
28. *Glossae of labium curved ventrally*: absent (0); present (1).
29. *Subapical setae row on paraglossae of labium*: absent (0); present (1).
30. *Setae or spines on submentum of labium*: present (0); absent (1).
31. *Anterolateral margins of submentum developed anteriorly*: no (0); yes (1).
32. *Segment 1/segment 2 of labial palpi*: >1.1 (0); subequal: 1.1-0.9 (1); <0.9 (2); [additive].
33. *Segment 3/segment 2 of labial palpi*: < 0.8 (0); 0.8-1.2 (1); >1.2 (2); [nonadditive].
34. *Segment 3 of labial palpi*: triangular (0); elongated (1); shortened (2); [nonadditive].
35. *Shape of labial palpi segment 2*: not elbowed (0); elbowed (1).
36. *Row of dorsal setae on palpal segment 2*: absent (0); present, <4 (1); present, many (2); [nonadditive].



Figs. 1-10. *Leentvaaria* sp. nymph. 1, Labrum and clypeus; 2, Labrum (detail of anteromedian emargination); 3, Left mandible; 4, Maxilla; 5, Hypopharynx; 6, Labium (right, ventral view; left, dorsal view); 7, Detail of third segment of labial palpus; 8, Foreleg; 9, Tarsal claw; 10, Gill.

37. *Denticles on tarsal claws*: subequal (0); subapical larger (1); medial larger (2); [nonadditive].
38. *Posterolateral projections on abdominal segments*: 2 or 4 to 9 (0); 5 or 6 to 9 (1); 7 or 8 to 9 (2); 3-6 and 8-9 (3); [nonadditive].
39. *Lateral margins of abdominal terga*: bare or with small spines (0); prominent setae or spines (1).
40. *Gills tracheae*: main tracheae present (0); tracheae divided basally (1).
41. *Rows of setae on base of terminal filaments*: absent (0); present (1).
42. *Dorsal portion of eyes of male on stalk*: no (0); yes (1).
43. *Fork of MA of forewings*: symmetrical (0); asymmetrical (1).
44. *Slanting cross vein above MA fork*: absent (0); present, ma symmetrical (1); present, ma asymmetrical (2); [nonadditive].
45. *Fork of MP of forewings*: symmetrical (0); slightly asymmetrical (1); asymmetrical (2); MP2 attached by cross vein (3); [nonadditive].
46. *Attachment of ICu1*: free basally (0); attached to CUA (1); attached to CUP (2); attached to both (3); [nonadditive].
47. *Shape of costal projection of hind wings*: obtuse (0); acute (1); very acute (2); [nonadditive].
48. *Vein MP of hind wings*: forked (0); unforked (1).
49. *Ending of Sc*: in wing margin (0); in cross vein or costal projection (1).
50. *Claws of a pair*: similar (0); dissimilar (1).
51. *Paired submedial projections on subgenital plate*: absent (0); broad (1); narrow (2); [additive].
52. *Lobes of penis*: completely divided (0); apical 1/2-1/4 separated (1); fused (2); [nonadditive].
53. *Forceps sockets*: separate (0); united (1).
54. *Base of penes abruptly swollen*: absent (0); present (1).
55. *Posterolateral corners of styliger plate*: not developed (0); developed (1).
56. *Styliger plate of males*: deeply cleft (0); fused (1).
57. *9th female abdominal sternite*: strongly cleft (0); entire or shallowly cleft (1).

Outgroup Selection

The genera *Leptophlebia* and *Habrophlebia* were used as outgroups, representing two different lineages of Leptophlebiinae, the sister group of the Atalophlebiinae. It was prefered to use two "real" taxa instead of an "hypothetical ancestor", with all "0" characters.

Analysis

The computer program "Pee-Wee" was used for the cladistic analysis, and "Clados" to show the character distribution in the resultant tree. Pee-Wee is a program for parsimony analysis under implied weights. It searches for trees which maximize fit across character retaining only the trees with highest total fit. Characters are given weight in inverse relation with the amount of homoplasy (extra steps) they show in every tree examined. Trees with the highest total fit (sum of character weight) are considered the best trees. Those trees resolve character conflict in favor of the characters which have less homoplasy on the trees. In this way it is possible to find trees with greatest explanatory power given the weights the characters deserve.

The options used with the program Pee-Wee were "Hold 1000; Mult *20". The command "Hold" determines the number of suboptimal trees retained in memory for the next analysis. The command "Mult" randomizes the order of the taxa in each replication, creating a weighted Wagner tree and submitting it to branch-swapping, repeating the process the number of times indicated, to find all possible "islands" present in the matrix.

RESULTS AND DISCUSSION

Only one tree was obtained with a fit 354.7 (Fig. 11). The topology of this tree is totally compatible with the consensus tree presented in Flowers and Domínguez (1991, Fig. 2), and is almost identical to the tree presented in fig. 3 in that paper (representing one of the 22 obtained in that analysis and used to illustrate the character distribution). The difference, besides the presence of *Leentvaaria*, is the resolution of the relationships of *Terpides*, *Massartella* and *Nousia*, that were unresolved in the previous analysis. Nevertheless, the relationships of the genera outside the *Hermanella* complex must be taken with caution as there are several genera that were not included.

As suspected, *Leentvaaria* belongs to the *Hermanella* complex, due to several synapomorphies (namely, characters 10, 11, 14-16, 18, 21-23 and 44, see Character list). The group of *"Traverella"*, composed of the two subgenera of *Traverella*, plus *"T. Bradleyi"*, that will represent a different genus, is supported by two synapomorphies: characters 25 and 36.

The *Hermanella* group does not have clear synapomorphies, but is supported by three characters that appear homoplastically: 29, 37 and 51. The relationships of *((Hydrosmilodon)*, *(Needhamella-Leentvaaria)*, *(Hylister, (Hermanella s.s.-H. Guayakia)))* are not resolved but, with the characters available *Leentvaaria* appears as the sister group of *Needhamella*. Their relationship is only supported by one homoplastic character: 1(2). It is important to remember, that at present *Leentvaaria* is only known from nymphs, so all its adult characters are missing in this analysis. When the adults of this genus became available, they will allow us to test this hypothesis. It is important to stress the fact that despite the inclusion of a new taxon and the use of different programs for the analysis of the original matrix, the monophyletic groups proposed originally (Flowers and Domínguez, 1991) remained unchanged.

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                0    5    10   15   20   25   30   35   40   45   50   55
                |    |    |    |    |    |    |    |    |    |    |    |
@Leptophlebia   -000000??0000000000000000000000010000200000001000000000000
@Habrophlebia   -010000??0000000000000000000000010000201001010100100000000
Hermanella s.s. -1100131102111211031022300100100201121200001210111111010 10
H. Guayakia     -1100131102111211031022300100100201121200001210111121010 10
Needhamella     -2100131012111211031022200100100201121200001210111121010 10
Leentvaria      -2100131002111211031022300100100201121200?????????????????
Hylister        -1100131102111211031022200100100201121200001210111121010 10
Traverella s.s. -2100131012111211031022201100000111110201001211111121010 11
Hydrosmilodon   -1100131002111211031022200100100201121200001210111121010 11
T. Zonda        -2100131012110111031022201100000021110201001210111111010 11
"T. Bradleyi"   -1100131002111211031022201100000111110201001211111110101 11
Ulmeritus       -0101031001011000010111110120100102000111000121000100000 11
Ulmeritoides    -0101020001011100010101010120000102000111000121000100000 11
Atopophlebia    -0101010000010000010001000110100101000001000131000100010 11
Traverina       -0101010000010100010000100110100202005$10000*00221110000010
Careospina      -0101010000010100010000100110100202000100000*00221110000010
Nousia          -0101010000010000010000000110000011005$1000000300000010001 0
Massartella     -0101010000010000010000000111000010000000000032000000000010
Massartellopsis -1101110001010000010001000110000101000000000033000000000011
Meridialaris    -1101110001010000001000100011001010100000000033000102010 11
Thraulodes      -1101010001010000010001100100010101000000000030100100111011
Terpides        -0101010001010000110000300011011010002300111001010001001 10
HagenulusM      -1101131100011100011011100100000202120100005*00321110000010
Ecuaphlebia     -0101010000010100020001100110000101001100000032100100000 1?
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Apendix I. Data matrix for the taxa used in this study. Description of characters given in text. Unknown conditions indicated by "?", subset polymorphism by "$" and full polymorphism by "*". Outgroups indicated by "@".

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