

Overview and phylogenetic relationships of the two-winged genera of South American Leptophlebiidae (Ephemeroptera)

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Four genera of two-winged Atalophlebiinae have been described from continental South America: *Askola*, *Hagenulopsis*, *Bessierus* and *Perissophlebioides*. Of these, only *Askola* and *Hagenulopsis* are known from larvae and adults; the others only from larvae. A cladistic analysis was carried out to test the possible monophyly of these four genera, and to determine their relationships with the other South American genera known from larvae and adults. Morphological data from both larvae and adults were used for the analyses. Two different analyses were performed to check the stability of the cladogram. Results: (1) *Askola* is most closely related to *Hagenulopsis*; (2) *Perissophlebioides* is most closely related to *Bessierus*; (3) the two-winged genera do not constitute a monophyletic group; (4) *Perissophlebioides* and *Bessierus* belong to the *Farrodes* lineage, but the relationships of *Hagenulopsis* + *Askola* in this study are still unclear.

Keywords: cladistic analysis; neotropics; Atalophlebiinae

Introduction

Four genera of two-winged Atalophlebiinae have been described from continental South America: *Hagenulopsis* Ulmer (1920), *Askola* Peters (1969), *Perissophlebioides* Savage (1983), and *Bessierus* Thomas and Orth (2000). Of them, only *Askola* and *Hagenulopsis* were known from both larvae and adults. The other two genera have been described only from larvae. Just recently, the adult of *Perissophlebioides* was reared and its characters were made available to me (F. Salles, personal communication), while the adult of *Bessierus* still remains unknown.

In his biogeographic study of the Neotropical leptophlebiids, Savage (1987) made the first attempt to delimit the different 'lineages' present in South America. He stated, although without documented phylogenetic analysis, that *Hagenulopsis*, *Borinquena* and *Askola* seemed to belong to the *Hagenulopsis* lineage, while he considered *Perissophlebioides* phylogenetically enigmatic.

Thomas et al. (2000), when describing *Bessierus*, suggested its possible affinity with *Hagenulopsis* and *Perissophlebioides*, but, curiously, they did not consider *Askola* as part of the lineage.

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In the cladistic analyses of the South American Atalophlebiinae (Flowers and Domínguez 1991; Domínguez et al. 2001), no two-winged genera were included, and their relationships remained uncertain.

There are several different modifications in the shape and venation of hind wings of the Leptophlebiidae, which are apparently correlated with the phylogeny of the groups and the mating flight. For this reason, it was considered interesting to know if the hind wings disappeared only once in the South American Atalophlebiinae, as a base for other hypotheses.

In this study a cladistic analysis is carried out to investigate the phylogenetic relationships of these dipterous genera with the other South American genera.

Materials and methods

Morphological data from representatives of genera known from larvae and adults, representing all the 'lineages' delineated by Savage (1987), were studied and compiled in a data matrix. This matrix was analysed with the programs WinClada (Nixon 2002) and Pee-Wee (Goloboff 1993).

Cladistic analysis

Characters and coding

For the cladistic analysis, a matrix of 35 taxa with 59 characters was compiled, including 41 larval and 18 adult external morphological characters (Table 1). Material from the following institutions was studied: Florida A&M University, Tallahassee, Florida; Smithsonian Institution, Washington, DC; Instituto-Fundación Miguel Lillo, Tucumán, Argentina and Museu de Zoologia, Sao Paulo, Brazil. Most of the characters were the same as those used in Domínguez et al. (2001), except for a few that needed to be recoded due to new evidence. Also, more genera were included to have a broader representation of the different lineages found in South America. Binary characters were coded as 0 and 1. Multistate characters were assigned different numbers and treated in two different ways: additive or nonadditive (see list of characters). Full polymorphisms (all possible character states present in the taxon) were coded as '*', and subset polymorphisms (part of possible character states present in the taxon) coded as '\$'. Characters not comparable, or with no information available were assigned a missing code '?'.

Larval characters

Mouthparts

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); round 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). [additive].
6. *Dorsal row of setae on labrum*: absent (0); apical (1); medial (2); basal (3). [nonadditive].

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 II/segment I of maxillary palps*: subequal (0); 1.1–2 (1); > 2 (2). [additive].
15. *Ordered rows of setae on segment III of palps*: absent (0); present (1).
16. *Thick, blunt setae on segment I of maxillary palps*: absent (0); present (1).
17. *Large non-pectinate seta on inner apical margin of maxillae*: absent (0); present (1).
18. *Setae on inner margin of maxillary palps II*: 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 palps III*: present (0); absent (1).
20. *Palpifer size of maxillae*: normal (0); enlarged (1).
21. *Position of articulation of maxillary palps*: medial to apical 1/2 (0); basal (1).
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 absent (0); lateral arms present (1).
27. *Long spines on labial palps*: absent (0); on segment III only (1); on segments II and III (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 I/segment II of labial palps*: > 1.1 (0); subequal [1.1–0.9] (1); < 0.9 (2). [additive].
33. *Segment III/segment II of labial palps*: < 0.8 (0); 0.8–1.2 (1); > 1.2 (2). [nonadditive].
34. *Segment III of labial palps*: triangular (0); elongated (1); shortened (2). [nonadditive].
35. *Shape of labial palps segment II*: not elbowed (0); elbowed (1).
36. *Row of dorsal setae on labial palp segment II*: absent (0); present, < 4 (1); present, many (2). [nonadditive].

Legs

37. *Denticles on tarsal claws*: subequal (0); subapical larger (1); medial larger (2); medioapical larger (3). [nonadditive].

Abdomen

38. *Posterolateral projections on abdominal segments*: II or IV to IX (0); V or VI to IX (1); VII or VIII to IX (2); III to VI and VIII to IX (3). [nonadditive].
39. *Lateral margins of abdominal terga*: bare or with small spines (0); prominent setae or spines (1).
40. *Gill tracheae*: main tracheae present (0); tracheae divided basally (1).
41. *Rows of setae on base of terminal filaments*: absent (0); present (1).

Adult characters*Head*

42. *Dorsal portion of male eyes on stalk*: no (0); yes (1).

Wings

43. *Fork of MA of forewings*: symmetrical to slightly asymmetrical (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 in forewing*: 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 of hind wings*: in wing margin (0); in cross vein or costal projection (1).

Legs

50. *Claws of a pair*: similar (0); dissimilar (1).

♂ *Genitalia*

51. *Paired submedial projections on subgenital plate of male genitalia*: absent (0); broad (1); narrow (2). [nonadditive].
52. *Lobes of penis*: completely divided (0); apical 1/2–1/4 separated (1); fused (2). [nonadditive].
53. *Forceps sockets*: separated (0); united (1).
54. *Base of penes abruptly swollen*: absent (0); present (1).
55. *Posterolateral corners of styliger plate*: not developed (0); developed (1); strongly developed (2). [nonadditive].
56. *Styliger plate*: deeply cleft (0); fused (1).

♀ *Abdomen*

57. *9th female abdominal sternite*: strongly cleft (0); entire or shallowly cleft (1)
58. *Egg guide*: absent (0); present, short, reaching segment VIII (1); present, long, acute, reaching segment IX (2). [additive].

Hind wing pads

59. *Hind wing pads*: present (0); absent (1).

Outgroup selection

The genera *Leptophlebia* and *Habrophlebia*, representing two different lineages (Peters and Edmunds 1970) of Leptophlebiinae, the sister group of Atalophlebiinae (Peters 1980), were used to root the network.

Analysis

The computer program “PeeWee” was used for the cladistic analysis. This is a program for parsimony analysis under implied weights. It searches for trees which maximise fit across characters retaining only the trees with the highest fit. Characters are given weight in inverse relation with the amount of homoplasy (extra steps) they show in every tree examined. Trees with the highest total fit (sum of character weight) are considered the best tree. Those trees resolve character conflict in favour of the characters which have less homoplasy on the trees. In this way, it is possible to find trees with greatest explanatory power given the weights the characters deserve. The options used were ‘hold 1000; mult* 20’. The command ‘Hold’ determines the number of suboptimal trees retained in memory for the next analysis. The command ‘Mult’ randomises the order of the taxa in each replication, creating a wagner tree, and submitting it to branch-swapping, repeating the process the number of times indicated, to find all possible ‘islands’ present in the matrix. Bremer indices, indicating clade support, were calculated with the command ‘bs*’ implemented in Pee-Wee, with *n* suboptimal trees (until *n* fit worse). The program “WinClada” showed the character distribution in the resultant trees.

Two analyses were performed: the first analysis was carried out including all characters except character 59 (hind wing pads: presence / absence). Later, a second analysis was carried out adding this character to test its influence in the analysis.

Results and discussion**First analysis: (character 59 excluded)**

One tree was obtained (Figure 1), with a fit of 405.4. Although several new genera were added to the matrix used in Domínguez et al. (2001) the relationships of the main clades remained. In the present analysis, some important nodes are defined by unique synapomorphies, such as A, B, D, E, H, J, L, N, P, Q, S, and T, while there are others supported only by homoplasies (C, F, G, I, K, M and O). I will focus here only on the nodes related to the two-winged genera. Nodes A and B are separated at the base: *Terpides-Fittkaulus* (node A) is characterised by the presence of a large, nonpectinated seta on the inner apical margin of the maxilla (character 17:1); posterolateral projections on abdominal segments III–VI and VIII–IX (character 38:3); and the presence of rows of setae on base of terminal filaments (character 41:1). On the other side, the remaining genera of Atalophlebiinae included in the matrix (node B) are separated by: lateral arms present on lingua of hypopharynx (26:1); fork of MA of forewings symmetrical to slightly asymmetrical (43:0) and MP₂ attached by a cross vein to vein MP₁ in forewing (45:3). Node D separates Node C (*Massartella* (*Rhigotopus*, *Hapsiphlebia*)) from Node E, and is supported by segment III of labial palps

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

	1	5	10	15	20	25	30	35	40	45	50	55									
@ <i>Leptophlebia</i>	000000?	00	0000	0	0000	0	0000	0	0010	0	0020	0	0010	0	3000	0	0000	0	0000		
@ <i>Habrophlebia</i>	010000?	00	0000	0	0000	0	0000	0	0010	0	0020	1	0010	1	0100	1	0000	0	0010		
<i>Hermanella</i>	110013110	2	1112	1	1031	0	1230	0	1001	0	0201	1	2120	0	0012	1	0111	1	1101	0	1000
<i>Guayakia</i>	110013110	2	1112	1	1031	0	1230	0	1001	0	0201	1	2120	0	0012	1	0111	1	2101	0	1000
<i>Needhamella</i>	210013101	2	1112	1	1031	0	1220	0	1001	0	0201	1	2120	0	0012	1	0111	1	2101	0	1000
<i>Hylister</i>	110013110	2	1112	1	1031	0	1220	0	1001	0	0201	1	2120	0	0012	1	0111	1	2101	0	1000
<i>Traverella</i>	210013101	2	1112	1	1031	0	1220	1	1000	0	0111	1	1020	1	0012	1	1111	1	2101	0	1100
<i>Hydrosmylodon</i>	110013100	2	1112	1	1031	0	1220	0	1001	0	0201	1	2120	0	0012	1	0111	1	2101	0	1100
<i>T. (Zonda)</i>	210013101	2	1101	1	1031	0	1220	1	1000	0	0021	1	1020	1	0012	1	0111	1	1101	0	1100
<i>T. "bradleyi"</i>	110013100	2	1112	1	1031	0	1220	1	1000	0	0111	1	1020	1	0012	1	1111	1	0101	0	1?00
<i>Ulmeritus</i>	010103100	1	0110	0	0010	1	0111	0	1201	0	0102	0	0011	1	0001	2	1000	1	0000	0	1100
<i>Ulmeritoides</i>	010102000	1	0111	0	0010	1	0101	0	1200	0	0102	0	0011	1	0001	2	1000	1	0000	0	1100
<i>Atopophlebia</i>	010101000	0	0100	0	0010	0	0100	0	1101	0	0101	0	0000	1	0001	3	1000	1	0001	0	1100
<i>Nousia</i>	010101000	0	0100	0	0010	0	0000	0	1100	0	0011	0	0\$10	0	0000	3	0000	0	0100	0	1000
<i>Massartella</i>	010101000	0	0100	0	0010	0	0000	0	1110	0	0010	0	0000	0	0000	3	2000	0	0000	0	1000
<i>Masartellopsis</i>	110111000	1	0100	0	0010	0	0100	0	1100	0	0101	0	0000	0	0000	3	3000	0	0000	0	1100
<i>Meridialaris</i>	110111000	1	0100	0	0010	0	0100	0	1100	1	0101	0	0000	0	0000	3	3000	1	0201	0	1100
<i>Thraulodes</i>	110101000	1	0100	0	0010	0	0110	0	1000	1	0101	0	0000	0	0000	3	0100	1	0011	0	1100
<i>Terpides</i>	010101000	1	0100	0	0110	0	0030	0	0110	1	1010	0	0230	0	1110	0	1010	0	0100	1	1000
<i>Fittkaulus</i>	010101000	1	0100	0	0110	0	0030	0	0110	1	1010	0	0030	0	1110	\$	1110	0	0100	1	1000
<i>Ecuaphlebia</i>	010101000	0	0101	0	0020	0	0110	0	1100	0	0101	0	0110	0	0000	3	2100	1	0000	0	1?00
<i>Penaphlebia</i>	010101000	0	0100	0	0000	0	0000	0	1110	0	0101	0	00\$0	0	0000	3	1000	0	0000	0	1000
<i>Farrodes</i>	010101000	0	0101	0	0011	0	0010	0	1101	0	0201	0	0120	0	0010	0	0211	1	0100	2	1100
<i>Homothraulus</i>	011101000	0	0101	0	0011	0	0010	0	1101	0	0201	0	0120	0	0010	0	1211	1	0100	1	1100
<i>simothraulopsis</i>	011101000	0	0101	0	0011	0	0010	0	1101	0	0201	0	0120	0	0010	0	1211	1	0100	1	1100
<i>Rhigotopus</i>	000101000	0	0100	0	0020	0	0000	0	1110	0	0010	0	0001	1	0000	3	1000	0	0000	0	1000
<i>Demoulinellus</i>	110101000	1	0101	0	0020	0	0100	0	1100	0	1001	0	0010	0	0000	3	1000	1	0100	0	1100
<i>Hapsiphlebia</i>	000101000	0	0100	0	0010	0	0000	0	1110	0	0020	0	0001	0	0000	3	1000	0	0000	0	1010
<i>Microphlebia</i>	010101000	0	0101	0	0010	0	0010	0	1111	0	0101	0	0110	0	0110	2	1111	1	0000	0	1?00
<i>Miroculis</i>	\$10101000	0	0100	0	0011	0	0110	0	1111	0	0101	0	0100	0	*10	3	1110	1	0000	0	1000
<i>Secochela</i>	110111000	1	0100	0	0010	0	0010	0	1100	1	0101	0	0001	0	0000	3	3000	1	0100	0	1100
<i>Hagenulopsis</i>	010101000	0	0101	0	0010	0	0000	0	1101	0	0101	0	0110	0	0010	0	2???	1	0000	0	1021
<i>Askola</i>	010101000	0	0101	0	0020	0	0000	0	1101	0	0101	0	0110	0	0010	0	1???	1	0000	0	1021
<i>Perissophlebioides</i>	011121000	0	0101	0	0041	0	0100	0	1101	0	0001	0	0320	0	0???	?	????	?	????	?	???
<i>Bessierus</i>	011021100	0	0101	0	0041	0	0000	0	1101	1	0001	0	0320	0	0???	?	????	?	????	?	???

Description of characters given in text. Unknown conditions indicated by '?', subset polymorphism by '\$', and full polymorphism by '*'. Outgroups indicated by '@'.

elongated (34:1) and posterolateral projections on abdominal segments V or VI to IX (38:1). Next, Node E separates *Nousia* from the remaining genera. In this case, the characters involved are: segment I subequal to segment II of labial palps (32:1) and segment III < 0.8 of segment II of labial palps (33:0). The next node (F) is supported by two homoplasies (22:1 and 50:1), and separates two groups represented by Node G and Node J. Node G is supported by one homoplasy (57:1), and Node J, supported by apomorphy 37:1: subapical denticle of larval tarsal claw larger. Within Node J, *Ecuaphlebia* is separated from Node K, which is separated only by homoplasies. *Miroculis* is the next to separate from Node L, which is supported by character 49:1 (Sc of hind wings ending in cross vein or costal projection). Nevertheless, Node L has a low relative Bremer support (31). Next, *Microphlebia* is separated from Node M, also with low relative Bremer support (31). Two of the dipterous genera, *Askola* and *Hagenulopsis* (Node N) are separated next from Node O. Node N is characterised by one synapomorphy (egg guide present, long, acute, reaching segment IX, 58:2) and one homoplasy

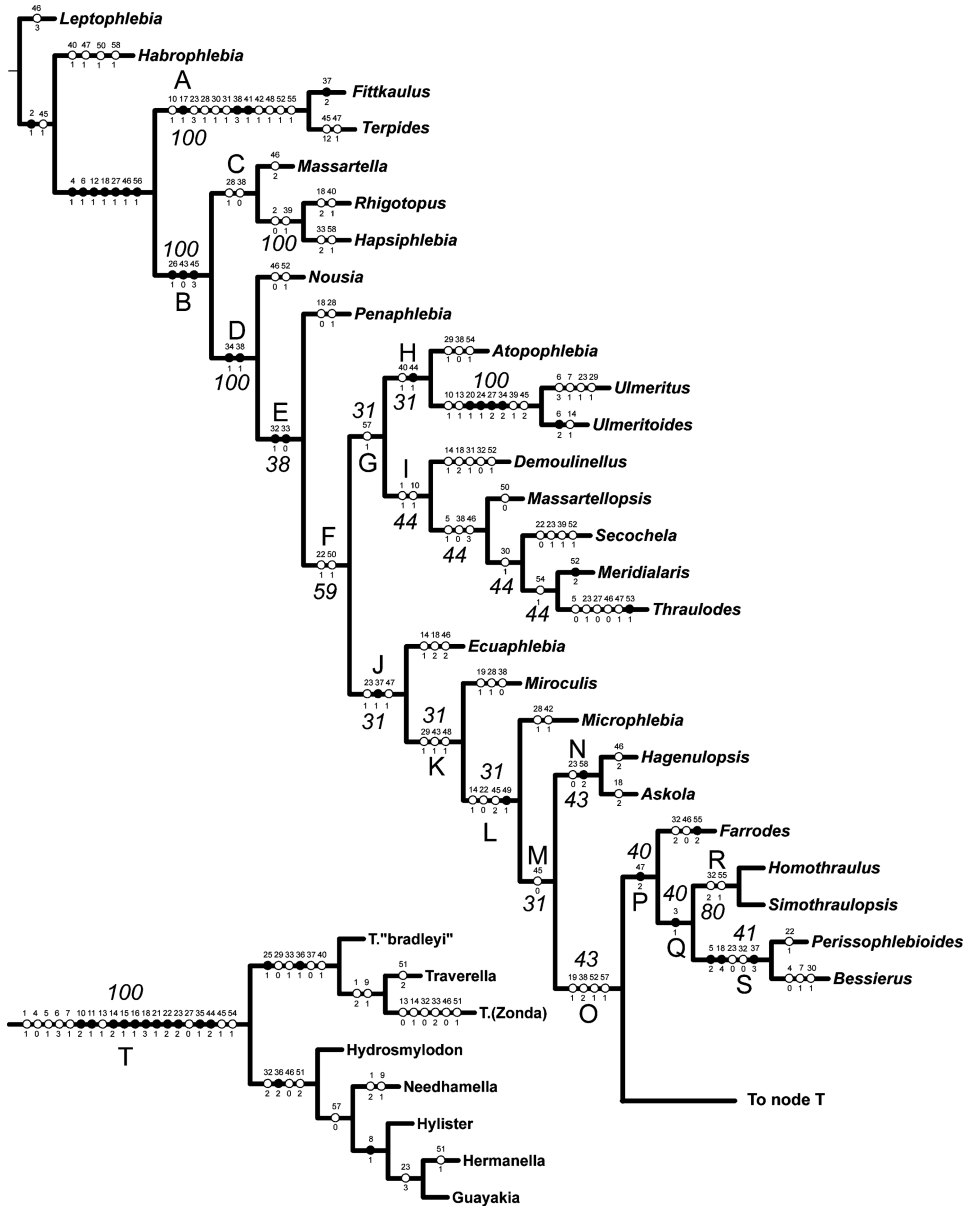


Figure 1. Cladogram showing the relationships of the genera treated. Empty circles = homoplasies, black circles = apomorphies. Numbers above circles = character number, numbers below circles = character states (see Table 1). Capital letters = nodes (see discussion). Numbers in italic = Relative Bremer Support.

(setae on 2/3 or more of outer margin of mandible, 23:0), while Node O is only supported by homoplasies, both nodes with an acceptable Bremer support (43). The two next Nodes, P and T, are both supported by synapomorphies. P that includes the *Farrodes* lineage, plus the two remaining dipterous genera, is supported by character 47:2 (costal projection of hind wings very acute). Node T that includes the

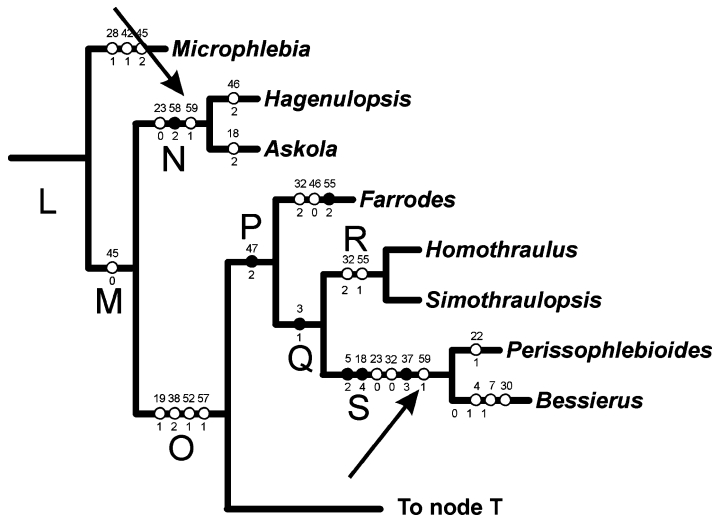


Figure 2. Portion of cladogram showing the change after addition of character 59:1 (second analysis). Arrows show where the character is added.

Hermanella-Traverella group is supported by several synapomorphies. As it has been treated elsewhere (Domínguez et al., 2001), it will not be discussed here. Within Node P, *Farrodes* is separated from Node Q, which is supported by one synapomorphy: lateral margins of labrum rounded, widest part on apical 2/3 (3:1). Finally, two nodes are separated: R composed by *Homothraululus-Simothraulopsis* on one side and S composed by *Bessierus-Perissophlebioides* on the other. Node R is supported only by homoplasies while Node S has three synapomorphies: 5:2, median cleft in labrum; 18:4, setae on inner margin of maxillary palps II absent; and 37:3, medio apical denticle on larval tarsal claws larger.

Second analysis: missing hind wing pads (character 59) included

Character 59 was not included in the first analysis, as the loss of the hind wings could have occurred independently, but would constitute a strong character uniting the four dipterous genera. Nevertheless, after the addition of this character, the analysis render a single cladogram (fit = 416.4) with the same topology of the two previous ones. The only change in the character distribution was the presence of this character appearing independently in both nodes (N and S) (Figure 2, arrows).

From these analyses, we can propose the following hypotheses:

- (1) *Askola* is more closely related to *Hagenulopsis*, as proposed by Peters (1969) and Savage (1987).
- (2) *Perissophlebioides* is closely related to *Bessierus*.
- (3) The two-winged genera of Leptophlebiidae do not constitute a monophyletic group. In this way, the loss of last wings would have occurred at least twice during the history of this group.
- (4) *Perissophlebioides* and *Bessierus* belong to the *Farrodes* lineage, while the relationship of *Hagenulopsis* + *Askola* in this study are still unclear.

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