

PRELIMINARY CLADISTICS OF THE *HERMANELLA* COMPLEX  
(EPHEMEROPTERA: LEPTOPHLEBIIDAE, ATALOPHLEBIINAE)

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**ABSTRACT**

A preliminary phylogeny of the *Hermanella* complex was constructed using the PAUP computer program. A cladogram of the 8 taxa in this complex known from both adults and nymphs shows two separate monophyletic groups: *Traverella* s.l.; and *Hermanella* s.l., *Hylister*, *Needhamella*, and a new group containing "*Traverella*" *primana*. *Traverella* s.l. includes two closely related forms of *Traverella* and a more distantly related taxon that contains *T. bradleyi*.

The position of the *Hermanella* complex within the Atalophlebiinae remains problematical. Some alternative trees are proposed. These show the West Indian *Hagenulus* s.l. to be more closely related to the *Hermanella* complex than previously suspected and that *Ulmeritus* and related genera are not closely allied with *Hermanella*. Some advantages and drawbacks of computer-assisted systematics are mentioned.

**INTRODUCTION**

The *Hermanella* complex of the Leptophlebiidae is a group of distinctive mayflies distributed primarily in the neotropics and also extending into the Nearctic Region. Nymphs are distinguished by extremely broad mouthparts bearing ordered rows of long setae, while male imagines of most species have modified subgenital plates. In addition, nymphs of some species have a clypeal projection which can be quite striking. For many years, work on the *Hermanella* complex has been hindered by the fact that the imagines of only a few of the distinctive nymphs were known with certainty. Edmunds (1948) associated the nymph and adults of the widespread genus *Traverella* Edmunds, and Dominguez and Flowers (1989) associated nymphs and

adults of *Hermanella* Needham and Murphy and described two new genera in this complex from southern Brazil. A complete review of the taxonomy of the *Hermanella* complex can be found in Dominguez and Flowers (1989).

As with any group of insects that exhibits striking morphological features, the *Hermanella* mayflies have induced authors to speculate about their biology and evolution. The nymphal mouthparts have been assumed to function in filter-feeding but this use has yet to be demonstrated unambiguously (Dominguez and Flowers 1989). Traver (1960) noted similar mouthpart structures in *Hermanella* and the West Indian *Hagenulus* Eaton. However, Peters (1971) stated that *Hagenulus*, despite its similarity to *Hermanella* in mouthpart modifications, is unrelated to the *Hermanella* complex. Traver's efforts were hampered by the erroneous inclusion by Spieth (1943) of *Hermanellopsis incertans* Spieth in *Hermanella* (a mistake rectified by Savage and Peters 1982), and by the general lack of knowledge of many of the adult-nymph associations of the other species. Among the other Neotropical genera of the Leptophlebiidae, only *Ulmeritus* Traver shows an apparently intermediate state of development of the nymphal mouthparts; Savage (1987) felt that this genus may be related to the *Hermanella* complex.

In recent years our field work in Argentina and Panamá has led to a much better understanding of the genera within the *Hermanella* complex (cf. Dominguez & Flowers 1989). While there are many other species still to be studied, enough genera are now known in enough detail so that a preliminary phylogenetic analysis can be attempted. In this paper we present a phylogeny of the genera and subgenera of the *Hermanella* complex that are known from both the nymph and adult stages and we attempt to locate the *Hermanella* complex within a general phylogeny of Neotropical Leptophlebiidae. Some taxa of the *Hermanella* complex currently are under revision by Dominguez, Flowers, and Savage; for this reason they will not bear valid names in this paper.

## MATERIALS AND METHODS

We used 35 nymphal and 18 adult characters for cladistic analysis of the genera. Most are binary characters but some multi-state characters are included. Binary characters were coded as plesiomorphic (0) or apomorphic (1). Multi-state characters were assigned different numbers indicating different apomorphies. Quantitative characters that cannot be separated into discrete states were omitted even though some are taxonomically useful. Polarities were determined by outgroup comparison using a generalized South American Atalophlebiinae as a hypothetical ancestor. A number of character polarities have been established in previous studies of cool-adapted Southern Hemisphere Atalophlebiinae (Pescador and Peters 1978, Towns 1978) and these conclusions are followed here. The data matrix is shown in Table 1. A complete list of characters, character states and codes can be found in Appendix 1. In the 12 characters discussed below, unambiguous polarities could not be established and these are treated as unordered in the

cladistic analyses.

*Nymphal Characters:*

Setae on outer margin of maxillary stipes (15): both presence and absence of this feature are widespread among Atalophlebiinae genera.

Setae on outer margin of mandibles (18): a variable character exhibiting a wide variety of patterns. In one of the most plesiomorphic genera (*Terpides* Demoulin) these setae are lacking while in most other genera they are present in some form. They are absent in *Hermanella*, where they are presumed to have been secondarily lost. To avoid a plethora of character states, four states based on the extent of the marginal setae were scored and the character was treated as unordered.

Ratios of segments 2 and 3 of labial palpi (27): segments subequal is the plesiomorphic state. There is a tendency in various genera for segment 2 to become longer and for reduction in segment 3. On the other hand, *Traverella* "San Juan" has a greatly elongated third segment.

Gills (33) are present on segments 1-7 in most genera but may be vestigial or absent on segment 7 in some cases.

Gill shape (34) is extremely variable and can be quite different even among closely related genera. Scoring each of the many shapes exhibited by the genera in this study would result in a unwieldy, non-additive multistate character. Therefore, all specific modifications were ignored and only two states were scored: the plesiomorphic state which is a paired plate-like structure, and one apomorphic condition which includes any change from the plesiomorphic state.

Posterolateral spines on abdominal segments (35): present on segments 2-9, only 8-9, or various intermediate conditions. Evidence suggests that the spines on anterior segments have been reduced repeatedly in the Atalophlebiinae.

*Adult Characters:*

Attachment of vein ICu<sup>1</sup> of fore wing (39), with several possible conditions: free at base, attached to both CuA and CuP, or attached to either. This character is non-additive and was treated as unordered.

Penes (47, 49-52): in the plesiomorphic condition they are totally divided, lacking apical lobes and spines or basal swellings. However, these modifications are so widely distributed through the entire Leptophlebiidae that these characters were treated as unordered. An additional problem is that even for genera with these modifications, often there is no information on whether the structures are truly homologous or not.

**GENERA INCLUDED**

In the *Hermanella* complex the following genera and subgenera, known from both adults and nymphs are included: *Hermanella* (*Hermanella*), *Hermanella* (*Guayakia*), *Hylister*, *Needhamella*, and *Traverella* (Dominguez &

Flowers 1989, Edmunds 1948). Also included are *Traverella primana* (Eaton), and the undescribed taxa *Traverella* "Bradley" and an Argentinian species of *Traverella* designated *Traverella* "San Juan". *Leentvaaria* Demoulin, known only from nymphs is not included in this study.

*Traverella primana* is widespread in Central America and has been associated with its nymphs by one of us (RWF); related species have been collected as nymphs in the northern Andes. *T.* "Bradley" actually represents a group of species in Central and South America of which only one adult - *Traverella bradleyi* (Needham and Murphy) - has been described. This group is distinguished by a shelf-like projection of the subgenital plate above the penes. An undescribed species of this group has been reared from western Panamá by one of us (RWF).

The other 14 Neotropical Atalophlebiinae taxa included in this study were selected because they show some degrees of morphological intermediacy between plesiomorphic lineages (represented here by the genera *Massartella* Lestage, *Nousia* Navás, and *Terpides* Demoulin) and the *Hermanella* complex. We purposely excluded genera outside the *Hermanella* complex that have not been described from both nymph and imago, as well as several generic groups (such as the *Farrodes-Homothraulius* and *Hagenulopsis* lineages) where the few described species may not be representative of the group.

Three genera (*Hagenulus* Eaton, *Ulmeritus*, and *Ulmeritoides* Thew) show distinctive adaptations of the mouthparts that are intermediate between those of most Atalophlebiinae and those of the *Hermanella* complex. For *Hagenulus* we used two species, *caligatus* Eaton and *morrisoni* Peters. *Traverina* Peters and *Careospina* Peters are West Indian genera which show a slight degree of flattening and broadening of the head and mouthparts. *Ecuaphlebia*, recently described by Dominguez (1988), is an Andean genus with affinities to some West Indian genera. Nymphs of other genera are "generalized sprawlers", typified by nymphs of *Thraulodes* Ulmer. For *Thraulodes* (a large and variable genus) we used *Thraulodes paysandensis* Dominguez, recently reared, which is typical of the majority of described *Thraulodes* species. *Meridialaris* Peters & Edmunds and *Massartellopsis* Demoulin are cold-adapted genera that are thought to be related to *Thraulodes*. The recently described *Atopophlebia* Flowers resembles *Thraulodes* in general appearance but has a number of unique modifications (Flowers 1980, 1987). In addition to our own rearing studies and the collections of the Florida State Collection of Arthropods and Fundación Miguel Lillo, the following publications were used to establish character states for the genera: Peters (1971) - *Hagenulus*; Pescador and Peters (1987) - *Meridialaris* and *Massartellopsis*; Pescador and Peters (1985) - *Nousia*.

Cladistic analyses were performed using the computer program PAUP (Phylogenetic Analysis Using Parsimony), written by David L. Swofford, Illinois State Natural History Survey. Options used on all runs were: Hold=3; Swap=Global; MULPARS, with all characters unweighted. The taxa of the *Hermanella* complex were first run alone and a single cladogram was ob-

tained. Then the matrix was run in its entirety. Once cladograms were obtained, individual character states were mapped on them using data from the APOLIST and CHGLIST options of PAUP.

## RESULTS AND DISCUSSION

When the *Hermanella* complex alone was analyzed using PAUP, a single cladogram was found (Fig. 1). The cladogram has a length of 73 steps and a consistency index of 0.781. This cladogram shows two distinct groups within the complex: *Traverella* (including the forms "San Juan" and "Bradley", and a monophyletic group that includes *Hermanella* s.l., *Hylister*, *Needhamella* and "*Traverella primana*").

Apomorphies of the *Traverella* group are long setae on the venter of the mandibles, a dense row of long setae on the outer margins of the femora and tibiae, and the 9th female sternite entire. *Traverella* "Bradleyi" is the plesiomorphic sister group of [*Traverella* + *T.* "San Juan"] and is distinguished by the vestigial seventh gill in the nymph. The clade *Traverella* + *T.* "San Juan" has as synapomorphies in the nymph a projection on the clypeus, and labrum broad. In *Traverella* the projections of the subgenital plate in the male are long and narrow; in *T.* "San Juan" the tusk on the maxilla is lost, segment 2 of the maxillary palpi is short, segment 3 of the labial palpi is elongate, the dorsal side of tibia 1 has a row of spines, gills are absent on segment 7, and ICu<sup>1</sup> of the forewings is attached to both CuA and CuP.

The sister clade of the *Traverella* group has the following synapomorphies: a subapical row of setae on the paraglossae, segment 1 of the labial palpi shorter than segment 2, segment 3 subequal to segment 2, a long row of dorsal setae on segment 2 of the labial palpi, an enlarged subapical denticle on the tarsal claws, costal projection beyond basal half of hind wings, and development of spines on the subgenital plate. *Traverella primana* is distinguished from the other members of this clade by vestigial gills on abdominal segment 7 and denticles on the outer incisor of the mandibles. The remaining genera have the following synapomorphies: denticles absent on the outer incisors of the nymphal mandibles, dorsal spines present on the fore tibiae, and in the adult fore wing vein ICu<sup>1</sup> free basally.

*Needhamella* is separated from [*Hermanella* + *Hylister*] by its broad labrum, clypeal projection, dense rows of setae on the outer margins of the femora and tibiae, and slender subgenital plate spines in the adult male. *Hermanella* and *Hylister* are united by the numerous long setae of the labrum which cover the entire area between the dorsal row of setae and the anterior margin. *Hylister* lacks gills on the seventh abdominal segment and has secondarily lost the spines on the subgenital plate.

*Hermanella* has lost all setae on the outer margin of the mandibles, and the apex of the costal projection of the hind wing is located at half the wing length. Within *Hermanella* the two subgenera are distinguished by the subgenital plate spines: broad in *H.* (*Hermanella*) and slender in *H.* (*Guayakia*).

Based on the cladogram, "*Traverella*" *primana*" represents a distinct genus not closely related to *Traverella* but allied to *Needhamella*. *Traverella* "Bradley" and *T.* "San Juan" on the other hand, form a monophyletic group with true *Traverella*. The relationships of *Hermanella*, *Hylister*, and *Needhamella* confirmed the conclusions of our previous study (Dominguez & Flowers 1989).

When all 22 genera were included in the computer run, 22 equally parsimonious trees were found. All trees had the same basic topology. The consensus tree (Fig. 2) shows that 22 trees were output because there were three points where PAUP was unable to resolve polychotomies: [*Thraulodes* + *Massartellopsis* + *Meridialaris*], [*Massartella* + *Nousia* + *Terpides* + remaining genera], and the placement of *Atopophlebia*.

The *Hermanella* complex consistently appears as a monophyletic unit at the apex of our cladograms. Surprisingly, our data indicate that *Ulmeritus* (or [*Ulmeritus* + *Ulmeritoides* Thew]) is *not* related to the *Hermanella* complex, as Savage (1987) has hypothesized and we ourselves believed when we began this study. Indeed, our cladograms place *Ulmeritus* in a relatively distant position from *Hermanella*. Another surprise is that the sister-group of the *Hermanella* complex is the West Indian *Hagenulus*. This appears to contradict Peters' (1971) assertion that *Hagenulus* merely shows convergent evolution with *Hermanella*. A final answer to this problem must await additional studies of both West Indian and continental species of *Hagenulus* and its related genera. Nevertheless, we believe our results warrant a re-examination of the relationships between the *Hermanella* complex and some West Indian Atalophlebiinae. There is at least the possibility that *Hermanella* and *Hagenulus* had a distant common ancestor in the Andean region.

Figure 3 shows one of the 22 trees with the character state changes in all branches except in the unresolved basal area of the cladogram. *Atopophlebia* appears as a sister genus of *Ulmeritus* + *Ulmeritoides*. In the majority of the 22 trees *Atopophlebia* was placed here, in apparent contradiction to Flowers' (1988) supposition of a close relationship between *Atopophlebia* and *Thraulodes*. The resolution of [*Massartellopsis* + *Meridialaris* + *Thraulodes*] is consistent with available evidence (M.L. Pescador, pers. comm.).

There are many taxa in the Atalophlebiinae still to be analyzed. Particularly important will be the as yet undescribed taxa of the *Hermanella* complex, *Hagenulopsis* and related genera, the large and relatively unknown *Homothraululus-Farrodes* complex, and several aberrant *Thraulodes* species. When a new taxon is added to an existing PAUP matrix, the results are not simply the old cladogram with the new taxon inserted at the appropriate place. A new taxon can produce significant changes throughout a cladogram. We began this study without *Ecuaphlebia*, whose description had not yet appeared in print. Our initial results were six trees with two topologies, due to instability in the *Thraulodes*-related genera (Fig. 4). When *Ecuaphlebia* was finally added, the number of trees rose from 6 to 22, but with a single topology. Note that none of this variation affected *Ecuaphlebia* itself or its neighboring genera.

In our analysis we have not used the weighted character option of PAUP (despite the urgings of some of our colleagues) because with so many unanalyzed taxa we feel character weighting premature and because we wanted to see what a phylogenetic program free of *a priori* assumptions would do with the Atalophlebiinae. Even so, unintended weighting can creep into a PAUP analysis: selection of characters, the way characters are coded and the selection of taxa all affect the outcome. We have attempted to keep these influences as minimal as possible in our study and to identify those that we could not exclude. The version of PAUP used in this study also is limited in its abilities in handling polymorphic characters and in flexibility in dealing with character reversals and parallelisms. A new version of PAUP (which we have not seen) promises much greater power and flexibility in character handling.

Despite some limitations, we have found PAUP to be an extremely useful tool for studying mayfly phylogeny. We hope our experiences will stimulate others to try PAUP, or one of the other available programs, on their own favorite mayfly group.

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Appendix. Characters used in cladistic analysis. Unordered characters indicated by an asterisk (\*).

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1. Width of labrum/width of clypeus: 0(< or = 1.1), 1(1.2 - 1.4), 2(=or > 1.5)

LABRUM

2. Denticles on anteromedian emargination: 0(absent), 1(present).  
 3. Median hood: 0(absent), 1(present).  
 4. Dorsal row of setae: 0(apical), 1(medial), 2(basal).  
 5. Dorsal row of setae: 0(entire), 1(divided).  
 6. Area anterior to dorsal row covered with long setae: 0(absent), 1(present).

CLYPEUS

7. Anteromedian projection: 0(absent), 1(present).  
 8. Lateral margins: 0(parallel), 1(divergent), 2(strongly concave).

MAXILLAE

9. Subapical pectinate setae: 0(present), 1(absent).  
 10. Tusk on inner apical margin: 0(absent), 1(present).  
 11. Segment 2/segment 1 of palpi: 0(subequal), 1(1.1 - 2), 2(>2).  
 12. Ordered rows of setae on segment 3 of palpi: 0(absent), 1(present).  
 13. Thick, blunt setae on segment 1 of palpi: 0(absent), 1(present).  
 14. Palpifer size: 0(normal), 1(enlarged).

- \*15. Setae on outer margin of stipes: 0(present), 1(absent).

16. Position of articulation of palpi: 0(on apical 2/3), 1(medial), 2(basal).

MANDIBLE

17. Shape of outer margin: 0(smoothly curved), 1(obtuse), 2(right angled).  
 \*18. Setae on outer margin: 0(on 2/3 or more), 1(on 1/2), 2( on basal 1/4),  
 3(absent).

19. Denticles on outer incisor: 0(present), 1(absent).

20. Patch of long setae on venter: 0(absent), 1(present).

HYPOPHARYNX

21. Lingua shape: 0(lateral arms lacking), 1(lateral arms present).

LABIUM

22. Spines on palpi: 0(absent), 1(on seg. 3 only), 2(on 2 and 3).

23. Glossae curved ventrally: 0(absent), 1(present).



24. Subapical seta row on paraglossae: 0(absent), 1(present).  
 25. Setae or spines on submentum: 0(present), 1(absent).  
 26. Segment 1/segment 2 of palpi: 0(>1.1), 1(subequal, 1.1-0.9), 2(<0.9).  
 \*27. Segment 3/segment 2 of palpi: 0(<0.8), 1(0.8-1.2), 2(>1.2).  
 28. Shape of palpi segment 2: 0(not elbowed), 1(elbowed).  
 29. Row of dorsal setae on palpal segment 2: 0(absent), 1(present, <4),  
 2(present, many).

## LEGS

30. Dorsal spines or setae on fore tibia: 0(absent), 1(setae present), 2(spines present).  
 31. Dense row of setae on outer margins of femora and tibiae: 0(absent), 1(present).  
 32. Denticles on tarsal claws: 0(subequal), 1(subapical larger), 2(medial larger).

## GILLS

- \*33. Gills on abdominal segments: 0(1-7), 1(7th vestigial), 2(1-6).  
 \*34. Gill shape: 0(plate-like, no processes), 1(otherwise).

## ABDOMEN

- \*35. Posterolateral projection on segments: 0(2 or 4 to 9), 1(5 or 6 to 9), 3(7 or 8 to 9).

## ADULTS

## FORE WINGS

36. Fork of MA: 0(symmetrical), 1(asymmetrical).  
 37. Slanting cross-vein above MA fork: 0(absent), 1(present, MA symm.),  
 2(present, MA asymm.).  
 38. Fork of MP: 0(symmetrical), 1(asymmetrical).  
 \*39 Attachment of ICu<sup>1</sup>: 0(free basally), 1(attached to CuA), 2(attached to Cup),  
 3(attached to both).

## HIND WINGS

40. Shape of costal projection: 0(obtuse), 1(acute), 2(very acute).  
 41. Location of apex of costal projection: 0(in basal 1/2), 1(beyond basal 1/2).  
 42. Vein MP: 0(forked), 1(unforked).  
 43. Length of Sc: 0(> than 0.6 of wing length), 1(< than 0.6 of wing length).  
 44. Ending of Sc: 0(in wing margin), 1(in cross vein or costal projection).

## LEGS

45. Claws of a pair: 0(similar), 1(dissimilar).

## MALE GENITALIA

46. Paired projections on subgenital plate: 0(absent), 1(broad), 2(narrow).  
 \*47. Division of penes: 0(completely divided), 1(apical 1/2-1/4 separate),  
 2(fused).  
 48. Forceps sockets: 0(separate), 1(united).  
 \*49. Segment 1 of forceps: 0(broader in basal 1/3-1/4), 1(subcylindrical),  
 2(basal swelling).  
 \*50. Spines on penes: 0(absent), 1(present).

- \*51. Lobes on apex of penes: 0(absent), 1(present).
- \*52. Base of penes abruptly swollen: 0(absent), 1(present).
- ABDOMEN
- 53. 9th female sternite: 0(strongly cleft), 1(entire or shallowly cleft).

Table 1. Data matrix for taxa of Atalophlebiinae used in this study. Description of character states given in Appendix I. Unknown conditions indicated by 9.

Taxon	Character state (characters 1-53)
HYPANC	0000000000000000000000000090000000000090000000009990
HERMANELLA	1112110211211012231010010201220101211001011111011010
GUAYAKIA	11121102112110122310100102012201012110010111121011010
NEEDHAMELLA	21121012112110122210100102012211012110011111121011010
HYLISTER	11121102112110122210100102012201212110011101121011010
TRAVERELLA	2112101211211012221100001111110012110110111121011011
T. PRIMANA	1112100211211012220010010201210111211011111121011019
T. "SAN JUAN"	2112101210111012221110000021121021211001011111011011
T. "BRADLEY"	11121002112110122211100001111110112110110111101011019
ULMERITUS	00021001010001012110120101000000011020100000100020101
ULMERITOIDES	00010001010001001010120001000000011020100010100020001
ATOPOPHLEBIA	00000000000000101000110101000010110020101000100000111
TRAVERINA	000000000100000110110102000010011001211101100001000
CAREOSPINA	00000000001000100110110102000011001001211101100000000
HAGENULUS C.	20121000011000112100100002012100001001221111100001000
NOUSIA	00000900000000000000011000010000900100000000001000000
MASSARTELLA	00000900000000000000011100010001021000020000000001000
MASSARTELLOPSIS	10100901000000101000110001000110000000300000000001001
MERIDIALARIS	10100901000000101000110011000110000000300000102001001
THRAULODES	10000901000000101100100011000110000000010010100111111
TERPIDES	00000900000000100310011010100002100100101100001020000
HAGENULUS M	10121100011000011100100092012101001001321101100000000
ECUAPHLEBIA	0000000001000001100110001000001001001211000100000109

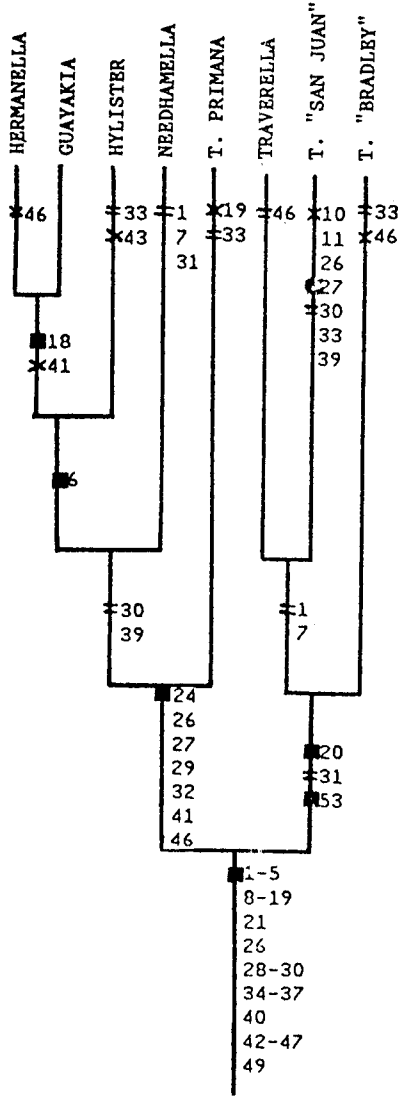


Figure 1. Cladogram of the *Hermanella* complex. Numbers refer to characters in Appendix 1. Symbols: ?, synapomorphy; =, parallelism; X, apparent reversal.

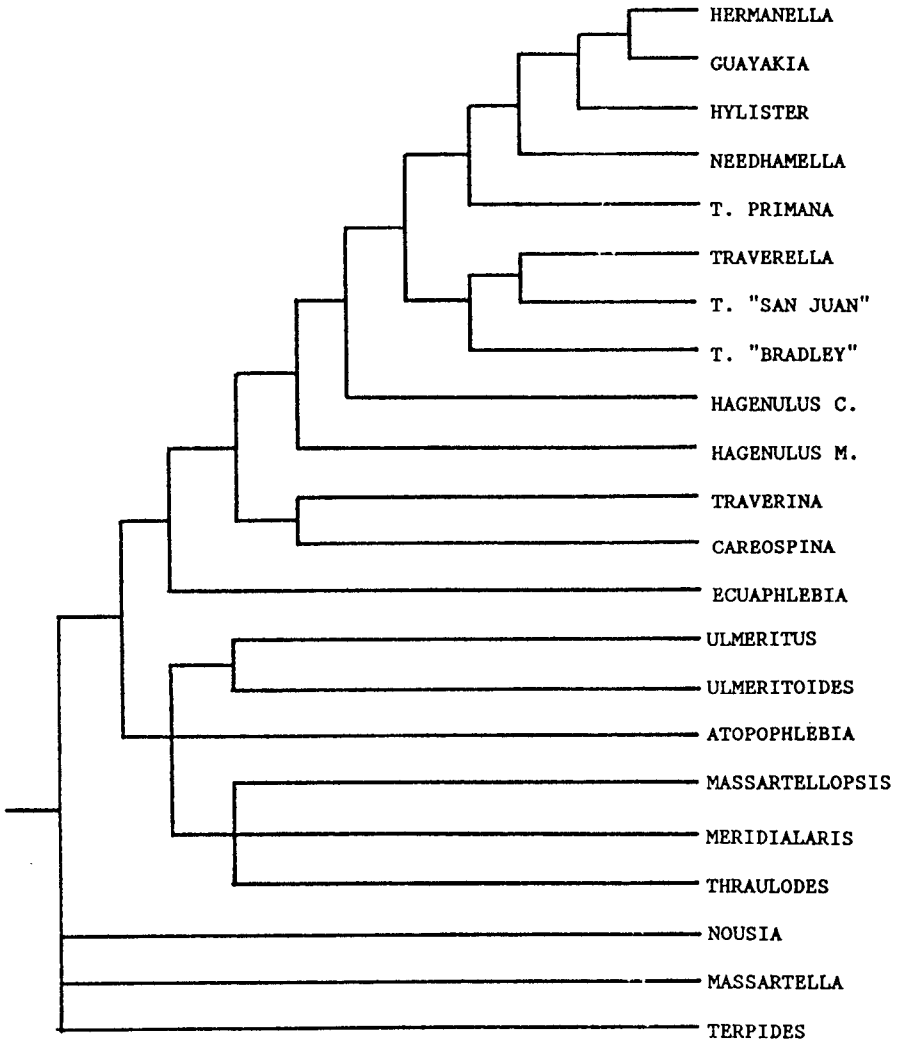


Figure 2. Consensus tree of selected Neotropical Atalophlebiinae based on data matrix in Table 1.

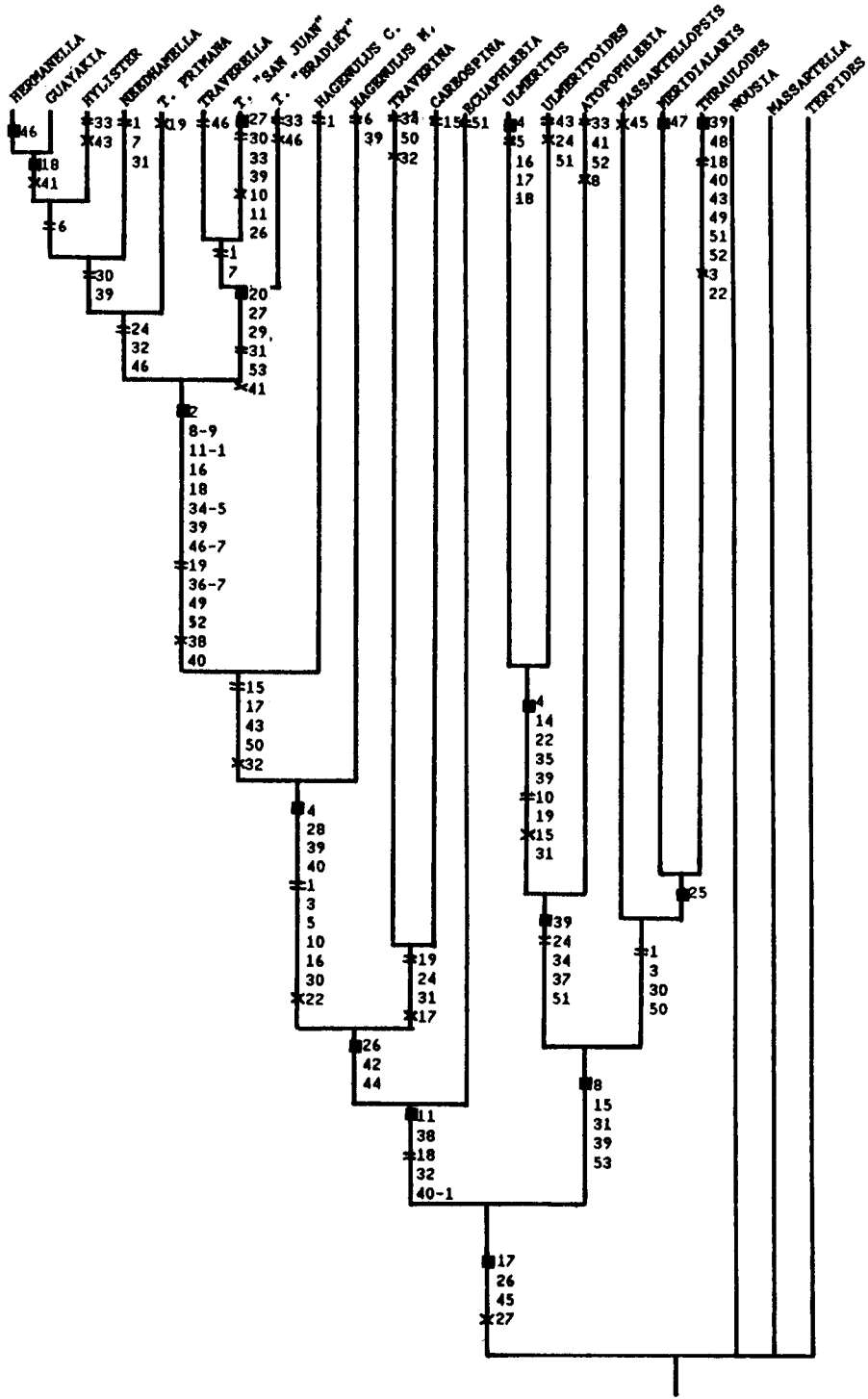


Figure 3. One of 22 equally parsimonious trees of Neotropical Atalophlebiinae showing distribution of character states. Symbols as in Fig. 1.

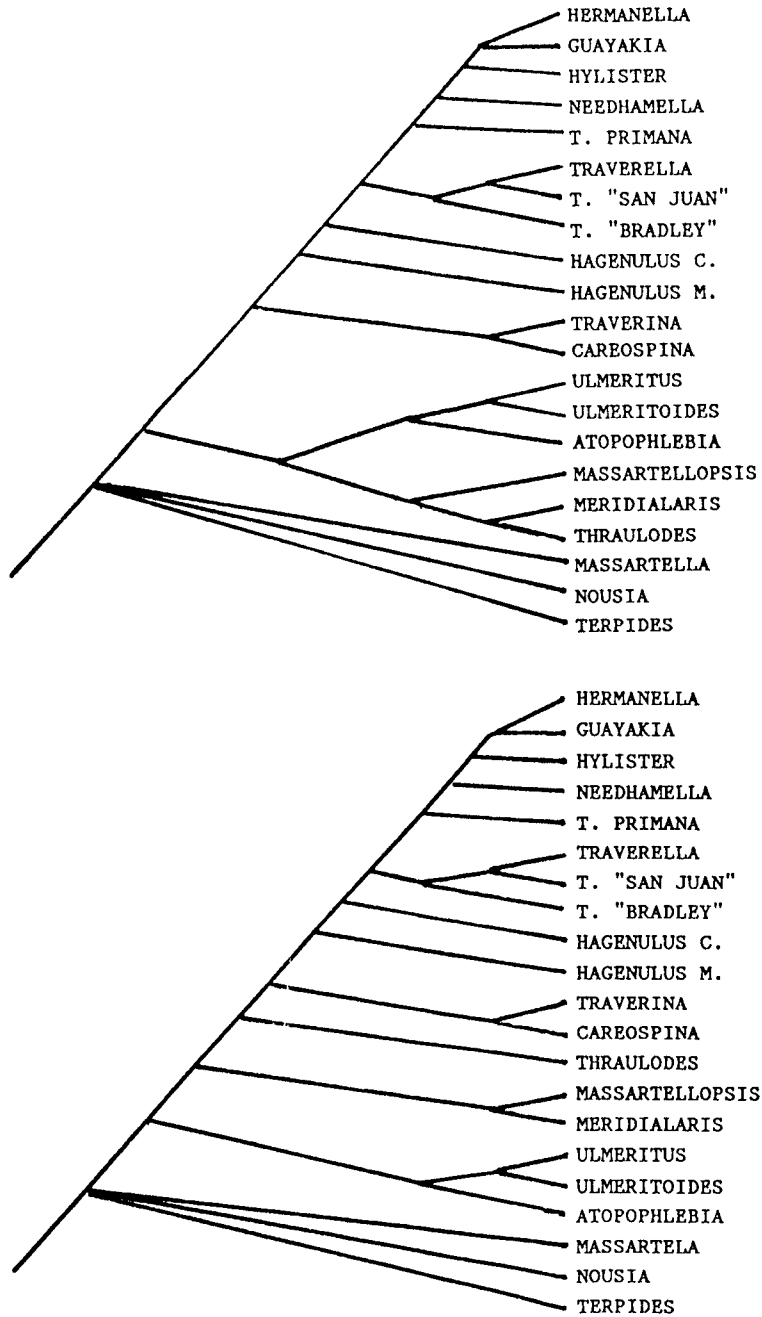


Figure 4. Examples of differing tree topologies found before *Ecuaphlebia* was added to the data matrix.