

A CLADISTIC ANALYSIS OF *AUSTROPHLEBIOIDES* AND RELATED GENERA (LEPTOPHLEBIIDAE: ATALOPHLEBIINAE)

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ABSTRACT

Phylogenetic relationships among the Australian genera and species of the *Meridialaris* lineage were investigated using a cladistic analysis of 35 morphological characters, to test the monophyly of this group and determine possible placement of undescribed taxa. The monophyly of a clade containing the three Australian genera of the *Meridialaris* lineage, *Austrophlebioides* Campbell and Suter, *Kirrara* Harker and *Tillyardophlebia* Dean, was strongly supported. Several undescribed species formed a monophyletic group with *Austrophlebioides pusillus* (Harker), suggesting the placement of these species in *Austrophlebioides*. The placement of several other undescribed taxa, not easily accommodated in currently recognised genera, is discussed. The outcomes from the parsimony analysis of the Australian genera agree in part with Pescador and Peters' (1980) phylogeny.

INTRODUCTION

The Leptophlebiidae is the largest mayfly family in Australia comprising 64 described species in 15 genera. All Australian genera belong to the subfamily Atalophlebiinae and are believed to be members of a Gondwanan lineage which is distributed throughout the southern hemisphere. A phylogeny was proposed by Pescador and Peters (1980) for this southern group of genera, in which they recognised five main monophyletic lineages, the *Hapsiphlebia*, *Penaphlebia*, *Nousia*, *Dactylophlebia* and *Meridialaris* lineages. Their phylogeny was based on morphological characters of the nymphs and adults and was constructed using traditional Hennigian methods. Character polarity was inferred by reference to a hypothetical ancestor and the possession of shared derived character states was used to define each monophyletic lineage.

The *Meridialaris* lineage is argued to be the most derived (Pescador and Peters 1980), with representative genera in Australia (*Austrophlebioides* Campbell and Suter, *Kirrara* Harker and *Tillyardophlebia* Dean), South America (*Meridialaris* Peters and Edmunds, *Massartellopsis* Demoulin and *Secochela* Pescador and Peters), New Zealand

Table 1. Data matrix used in the cladistic analysis. Characters and character states are described in Appendix 1.

Taxa	Character state
<i>Leptophlebia cupida</i>	0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 1 2 2 0 2 0 0 0 1 1 0 1 0 1 0 0 0 0
<i>Atalophlebia</i>	0 0 0 2 0 0 1 0 0 1 0 1 0 0 0 0 0 1 0 2 0 3 0 0 1 1 1 0 0 0 0 0 2 0 0
<i>Jappa</i>	0 0 0 1 0 0 1 0 0 1 0 2 0 0 0 0 0 1 2 2 1 2 0 1 1 2 2 0 0 0 1 0 1 0 0
<i>Ulmerophlebia</i>	0 0 0 1 0 0 1 0 0 1 0 2 0 0 0 0 0 1 2 2 1 2 0 1 1 2 2 0 0 0 1 0 1 0 0
<i>Atalomicria</i>	0 0 0 2 0 0 1 0 1 1 0 1 0 0 0 0 0 1 2 2 0 2 0 0 1 1 0 0 0 1 0 0 2 1 0
<i>Kalbaybaria</i>	0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 2 2 0 3 0 0 1 1 1 0 1 0 0 0 2 0 0
<i>Bibulmena</i>	1 1 0 2 0 0 0 0 1 0 0 2 1 1 ? 0 0 0 1 0 0 2 0 ? 1 1 2 0 1 0 0 0 2 0 0
<i>Neboissophlebia</i>	1 1 0 1 0 0 0 0 1 0 0 2 1 0 0 0 0 1 1 0 0 1 0 0 1 1 2 1 0 0 1 0 1 ? 0
"Genus K"	1 1 0 2 0 1 0 0 1 0 0 2 1 1 0 0 0 0 2 0 0 1 0 0 1 1 2 0 0 0 0 0 2 0 0
<i>Garinjuga</i>	1 1 0 2 0 1 0 0 1 1 0 2 0 0 0 1 0 0 2 0 0 2 0 0 0 0 1 0 ? 0 0 0 0 1 0
<i>Nyungara</i>	1 1 0 2 0 0 0 0 1 0 0 1 1 1 ? 1 0 0 1 0 0 1 0 0 0 1 1 1 0 1 0 0 1 1 0
<i>Nousia</i>	1 1 0 2 0 1 0 0 1 0 0 1 1 1 1 1 0 0 1 0 0 1 0 0 0 0 1 1 0 1 0 0 1 0 0
<i>Koornonga</i>	1 1 0 2 0 1 0 0 1 0 0 1 1 1 1 1 0 0 1 0 0 1 0 0 0 0 1 1 0 1 0 0 1 0 0
<i>Kirrara procera</i>	2 2 0 2 0 2 0 1 1 0 0 2 0 1 ? 1 1 0 0 0 1 0 1 0 0 0 2 0 1 0 1 1 0 0 0
"Northern Kirrara"	2 2 0 2 0 2 0 1 1 0 0 3 0 1 1 1 1 0 0 0 1 0 1 0 0 0 2 0 1 0 1 1 0 0 0
<i>Tillyardophlebia rufosa</i>	1 1 1 2 1 1 0 ? 1 0 1 3 1 1 1 1 1 0 0 0 0 1 0 0 0 0 0 0 1 0 1 1 0 0 1
<i>Tillyardophlebia alpina</i>	1 1 1 2 1 1 0 ? 1 0 1 3 1 1 1 1 1 0 0 0 0 1 0 0 0 0 0 0 1 0 1 1 0 0 1
"WT species 1"	1 1 1 2 1 1 0 ? 1 0 1 3 1 1 1 1 1 0 0 0 0 1 0 0 0 0 2 0 0 0 1 1 1 1 0
"WT species 2"	1 1 1 2 1 1 0 1 1 0 1 3 1 1 1 1 1 0 0 0 0 1 0 0 0 0 ? 0 1 0 1 1 1 0 0
<i>Austrophlebioides pusillus</i>	2 2 1 2 1 1 0 1 1 0 1 3 1 1 1 1 1 0 0 1 0 1 0 0 0 0 2 0 1 0 1 1 1 1 0
"Paluma"	2 2 1 2 1 1 0 1 1 0 0 3 1 1 1 1 1 0 0 1 0 1 0 0 0 0 2 0 1 0 1 1 1 1 0
"Henrietta"	2 2 1 2 1 1 0 1 1 0 0 3 1 1 1 1 1 0 0 1 0 1 0 0 0 0 2 0 1 0 1 1 1 1 0
"Daintree"	2 2 1 2 1 1 0 1 1 0 0 3 1 1 1 1 1 0 0 1 0 1 0 0 0 0 2 0 1 0 1 1 1 1 0

(*Atalophlebioides* Phillips and *Deleatidium* Eaton), Sulawesi (*Sulawesi* Peters and Edmunds), southern India (*Petersula* Sivaramakrishnan) and Madagascar (*Petersophlebia* Demoulin) (Pescador and Peters 1980, 1982, 1987; Towns and Peters 1996; Campbell and Peters 1986; Campbell and Suter 1988; Peters and Edmunds 1990; Dean 1997). Members of this lineage possess the following characters: labrum broader than clypeus, clypeus with lateral margins apically divergent, lateral margins of submentum without any setae, galealacinia of maxilla apically broad and ninth sternum of the adult female entire or slightly cleft.

This investigation is part of a study in progress on the systematics of the Australian genera of the *Meridialaris* lineage, namely *Austrophlebioides*, *Kirrara* and *Tillyardophlebia*. The genus *Austrophlebioides* currently comprises five described species. *Kirrara procera* Harker is presently the only species of the monotypic genus *Kirrara*, and the recently established genus, *Tillyardophlebia*, comprises two species *T. rufosa* and *T. alpina* Dean. In addition, numerous undescribed taxa are known, some of which appear to belong to recognised genera, particularly *Austrophlebioides*, while others are not easily accommodated in any of the described genera as presently defined. Placement and rank of these taxa is uncertain. The phylogenetic relationships among the Australian genera and species of the *Meridialaris* lineage are presently unknown and the monophyly of this group has not been tested using explicit cladistic parsimony analysis.

In this study a cladistic analysis based on morphological characters of nymphs and adults was used to investigate the phylogenetic relationships of the Australian genera and species of the *Meridialaris* lineage. The aims of this analysis were to test the monophyly of this group and to determine possible placement and rank of undescribed taxa. The study also provided the opportunity to compare the tree obtained from parsimony analysis of the Australian genera with Pescador and Peters' (1980) phylogeny for the Gondwanan genera of the southern hemisphere.

METHODS

Morphological Characters

A total of 35 informative morphological characters were coded from the nymphs and adults of 23 taxa. Nymphal characters were scored from various body regions including the mouthparts, thorax, abdomen and legs. Adult characters were scored from the fore and hind wings, male genitalia and female abdomen. Characters were coded as either binary or qualitative multi-state. Characters and character states used in the analysis are listed in Appendix 1. The data matrix is given in Table 1. The terminology used in this study follows that of Edmunds *et al.* (1976). Morphological characters identified by other systematists as phylogenetically informative (Pescador and Peters 1980; Towns and Peters 1980, 1996) were included in the matrix.

Taxa

The following taxa were included in the analysis:

(1) *Austrophlebioides pusillus* (Harker) and three undescribed species which appear to belong to this genus, collected from northern Queensland and informally named after their collection localities ("Paluma", "Henrietta" and "Daintree").

(2) *Kirrara procera* and an undescribed species, "Northern Kirrara", collected by Edgar Riek from northern Queensland, that may belong in *Kirrara*.

(3) Two species of *Tillyardophlebia*, *T. rufosa* and *T. alpina*, and two undescribed taxa designated "WT species 1" and "WT species 2".

The association of adults and nymphs of all undescribed species, except "Northern *Kirrara*", was by rearing. Morphological characters were coded from nymph and adult material and from published descriptions (Campbell and Peters 1986; Campbell and Suter 1988; Dean 1997).

Representative species of the remaining genera described from Australia were also included in the analysis to investigate the higher level relationships proposed by Pescador and Peters (1980). Taxa included were: *Atalophlebia* sp., *Kalbaybaria doantrangae* Campbell, *Ulmerophlebia* sp., *Jappa edmundsi* Skedros and Polhemus, and *Atalomicria sexfasciata* (Ulmer) (*Hapsiphlebia* lineage); *Garinjuga maryannae* Campbell and Suter (*Penaphlebia* lineage); *Nousia fuscata* (Tillyard), *Koornonga inconspicua* (Eaton) and *Nyungara bunni* Dean (*Nousia* lineage); *Bibulmena kadjina* Dean and *Neboissophlebia hamulata* Dean (affinities uncertain). A species of an undescribed genus, "Genus K", was also included. Morphological characters of these taxa were coded from examination of nymphal and adult material and from the literature (Suter 1986; Campbell and Peters 1993; Campbell and Suter 1988; Dean 1987, 1988; Campbell 1993).

Phylogenetic Analysis

Cladistic analyses were performed using PAUP 3.1.1 (Phylogenetic Analysis Using Parsimony) (Swofford 1993). The branch-and-bound search option was used with characters treated as unordered and equally weighted. A representative species from the subfamily Leptophlebiinae, *Leptophlebia cupida* (Say), was used as the outgroup. Bootstrap analysis (500 randomizations) was used to assess support for each node of the tree (Felsenstein 1985; Hillis and Bull 1993).

RESULTS

Cladistic analysis resulted in eighteen most parsimonious trees, each with a length of 91 steps, a consistency index (CI) excluding uninformative characters of 0.527 and a retention

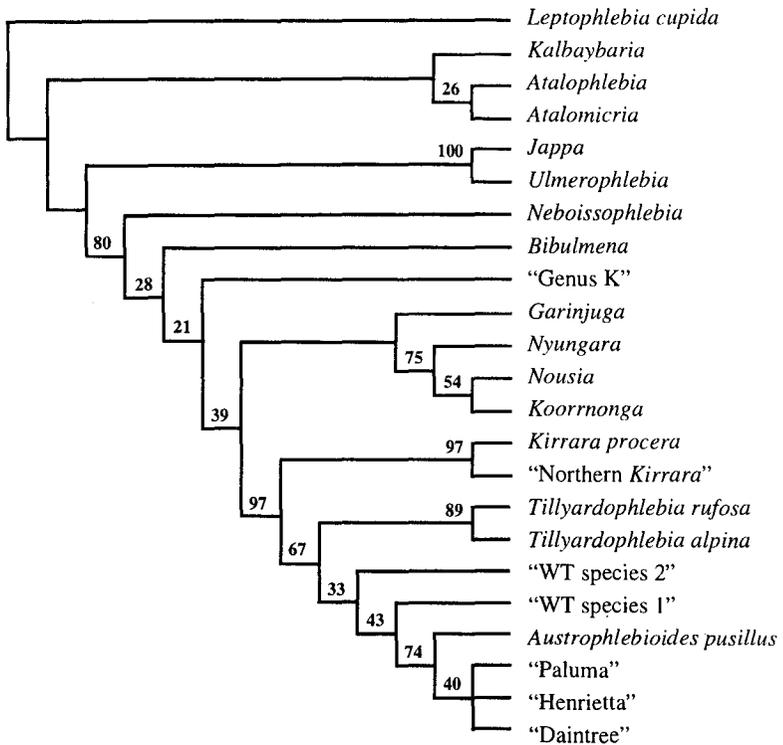


Fig. 1. One of the eighteen most parsimonious trees obtained by PAUP using a branch-and-bound search. Bootstrap values are shown above each node.

index (RI) of 0.809. One of these trees is shown in Figure 1 and a strict consensus tree is given in Figure 2.

Atalophlebia, *Kalbaybaria*, *Atalomicria*, *Ulmerophlebia* and *Jappa*, all members of the *Hapsiphlebia* lineage, occupy a basal position on the strict consensus tree (Fig. 2). Relationships among these genera were unresolved except for a sister group relationship between *Jappa* and *Ulmerophlebia* (Fig. 2).

All remaining ingroup taxa were placed in a separate clade (Fig. 2). Bootstrap support for this clade was 80%. *Nousia*, *Koornonga* and *Nyungara* formed a monophyletic group with bootstrap support of 75%. There was strong support for the monophyly of the clade containing *Kirrara*, *Tillyardophlebia* "WT species 1", "WT species 2" and *Austrophlebioides*, with a very high bootstrap value of 97% for this node. Within this clade "Northern *Kirrara*" formed a monophyletic group with *K. procera*. *A. pusillus* and the three undescribed species "Paluma", "Henrietta" and "Daintree" also formed a monophyletic group, as did the two *Tillyardophlebia* species. "WT species 1" and "WT species 2" were excluded from both the *Austrophlebioides* and the *Tillyardophlebia* groups.

Relationships among *Neboissophlebia*, *Bibulmena*, "Genus K" and *Garinjuga* were unresolved (Fig. 2). On some of the most parsimonious trees *Garinjuga* was placed as the sister group to the clade containing *Nousia*, *Koornonga* and *Nyungara* (Fig. 1), while on other most parsimonious trees (not shown) it was the sister group to the clade comprising *Kirrara*, *Tillyardophlebia* "WT species 1", "WT species 2" and *Austrophlebioides*.

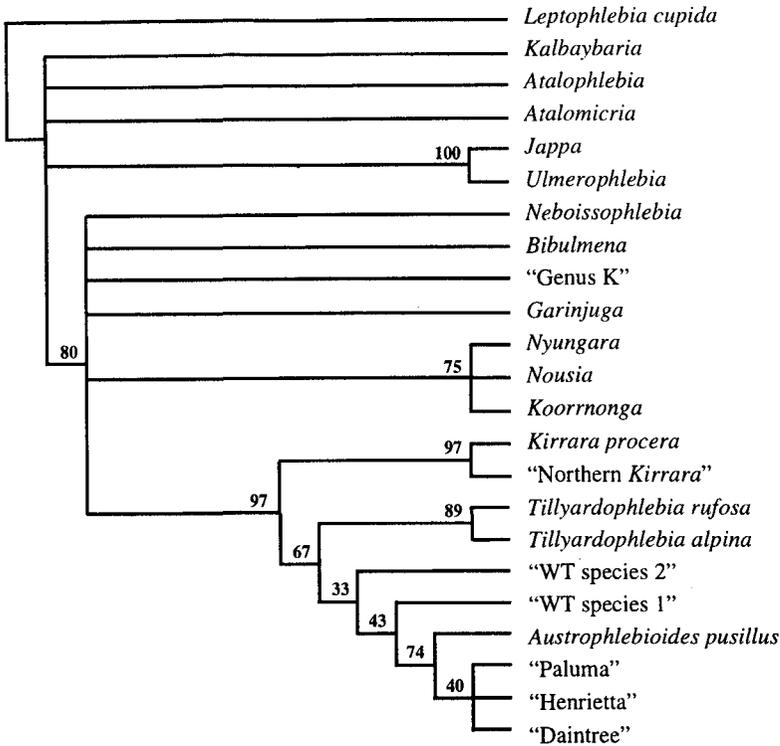


Fig. 2. Strict consensus tree of the eighteen most parsimonious trees obtained by PAUP using a branch-and-bound search. Bootstrap values are shown above each node.

DISCUSSION

Phylogenetic Relationships Among the Australian Genera of the *Meridialaris* Lineage

The findings of this study support the monophyly of a clade containing all Australian members of Pescador and Peters' *Meridialaris* lineage (*Kirrara*, *Tillyardophlebia*, *Austrophlebioides*, "WT species 1", and "WT species 2"). Character states unique to this group were the absence of hairs on the lateral margins of the submentum (character 17) and the ninth sternum of the adult female entire or only slightly cleft (character 32). These character states were identified by Pescador and Peters (1980) as synapomorphies for this group. The results indicate that "Northern *Kirrara*" and *Kirrara procera* are closely related and may be considered congeneric. The two species share many features. The nymphs of both species possess large plate-like gills with the ventral lamella of each gill greatly reduced, and mandibles with outer margin strongly right angled. Wing venation and male genitalia of the two species are also very similar. The nymphs of "Northern *Kirrara*" are easily distinguished from *K. procera* by the presence of a suction disc on the labrum and absence of median protuberances on the abdominal terga. These two species appear to be only distantly related to the other Australian members of the *Meridialaris* lineage.

Cladistic analysis supports the tentative placement of the undescribed species "Paluma", "Henrietta" and "Daintree" into *Austrophlebioides*. The three undescribed

species differ from the original diagnosis given by Campbell and Suter (1988) in the absence of a series of fine ventral spines on the penes, and lack of fine setae on the outer margin of the mandible between the setal tuft and outer incisor. Parnrong and Campbell (1997) recently modified the generic description of *Austrophlebioides* to accommodate a new species, *A. marchanti*, which also lacked ventral spines on the penes. Further revision of the generic diagnosis of *Austrophlebioides* may be necessary as additional species are described.

The exclusion of "WT species 1" and "WT species 2" from both the *Austrophlebioides* and the *Tillyardophlebia* group would suggest placement of these taxa in a new genus or genera. The nymphs of "WT species 1", and "WT species 2" are very similar to those of *Tillyardophlebia*. Shared characters states include: labrum a little broader than the clypeus, anterior margin of labrum hooded and with a U-shaped emargination, and absence of a fringe of fine setae on the lateral margins of the abdominal segments. The genitalia of the adult males, however, are unlike those of *Tillyardophlebia*. They are fused along most of their length and lack the two ventral spines present at the base of the penes of *Tillyardophlebia*. It is unclear at the present time whether these two species are congeners.

Comparison with Pescador and Peters' Phylogeny

The outcomes from the parsimony analysis of the Australian genera agreed in part with Pescador and Peters' proposed phylogeny; however, relationships among the Australian genera in the present study were far less resolved. As previously discussed, a clade comprising all of the Australian genera of Pescador and Peters' *Meridialaris* lineage is strongly supported by this study. The results also support the basal position of *Atalophlebia*, *Atalomicria*, *Kalbaybaria*, *Ulmerophlebia* and *Jappa*, relative to the other genera. However, relationships among these genera were poorly resolved, with some uncertainty as to whether these genera represent a monophyletic lineage. The exception was the sister group relationships between *Jappa* and *Ulmerophlebia*. The close relationship between these two genera has previously been discussed by Tsui and Peters (1975) and Suter (1986).

The grouping of *Nousia*, *Koornonga* and *Nyungara* into a monophyletic clade is in agreement with the current placement of these genera (Pescador and Peters 1980; Campbell and Suter 1988; Dean 1987). The relationships among *Neboissophlebia*, *Bibulmena*, *Garinjuga* and "Genus K" were unresolved and remain problematic.

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APPENDIX 1 MORPHOLOGICAL CHARACTERS USED IN THE CLADISTIC ANALYSIS

(*) Characters identified by Pescador and Peters (1980) and Towns and Peters (1980, 1996) as phylogenetically informative.

Nymph*Clypeus / labrum:*

- 1.* Labrum width / clypeus width: (0) labrum narrower than clypeus, (1) labrum subequal to slightly wider than clypeus, (2) labrum wider than clypeus.

Clypeus:

- 2.* Lateral margins: (0) parallel, (1) slightly divergent anteriorly, (2) strongly divergent anteriorly.

Labrum:

- 3.* Median hood: (0) absent, (1) present.
 4. Setae on dorsal surface of labrum: (0) scattered, (1) in 3 rows, an apical, median and basal row (2) in 1 or 2 rows, an apical plus subapical row or apical row only.
 5.* Anterior margin of labrum: (0) entire or with broad emargination, (1) with narrow U-shaped emargination.

Mandible:

- 6.* Shape of outer margin: (0) angled, (1) rounded, (2) right angled.
 7. Right outer incisor: (0) slender, parallel-sided, (1) robust, triangular.
 8.* Serrations on apex of right outer incisor: (0) absent, (1) present.
 9. Tuft of long setae midway along outer margin of mandible: (0) absent, (1) present.
 10. Long setae along outer margin: (0) absent, (1) present.
 11. Fine setae along outer margin between setal tuft and outer incisor: (0) absent, (1) present.

Maxillae:

- 12.* Galea-lacinia: (0) subapical pectinate setae absent, (1) with less than 15 subapical pectinate setae, (2) with 16 to 23 subapical pectinate setae, (3) usually with more than 24 subapical pectinate setae.
 13. Spines or long setae present on outer margin of: (0) cardo and stipes, (1) cardo only.
 14. Outer margin of cardo fringed with: (0) long setae, (1) short spine like setae.
 15. Blunt seta on outer margin of stipes: (0) absent, (1) present.

Labium:

- 16.* Glossae: (0) not on the same plane as paraglossae, (1) on about the same plane as paraglossae.
 17.* Submentum: (0) with spines or setae on lateral margins, (1) without spines or setae on lateral margins.

Thorax:

18. Setae on lateral margins of pronotum: (0) absent, (1) present.

Abdomen:

19. Postero-lateral projections on segments: (0) 2 to 9, (1) 6 to 9, (2) 7 or 8 to 9.
 20*. Lateral margin of abdominal segments: (0) bare, without fringe of fine setae, (1) fringed with fine setae only, (2) fringed with thick setae or spines.
 21. Row of setae on mid-dorsal region of segments: (0) absent, (1) present.

Gills:

22. Gill shape: (0) plate-like, (1) lanceolate, tapering gradually to a fine point, (2) lanceolate to ovate, tapering at about two-thirds the length of the gill and ending in a single apical filament, (3) divided.
 23. Gill size: (0) lower and upper gill about the same size, (1) lower gill greatly reduced.
 24. Outer margin of gill: (0) not fringed with fine setae, (1) fringed with fine setae.

Legs:

25. Tarsal claws with ventral teeth: (0) present, (1) greatly reduced to fine denticles or absent.

Caudal filaments:

26. Segments with: (0) whorls of spines, with or without short setae, (1) whorls of spines and long setae, (2) long setae only.

Adult*Fore wing:*

27. Attachment of ICu1: (0) free basally, (1) attached to CuA, (2) attached to CuA-CuP cross vein.

Hind wing:

28. Length of hind wing relative to fore wing: (0) hind wing not greatly reduced, greater than 0.2 of the length of fore wing, (1) hind wing reduced, less than 0.2 of the length of fore wing.
 29. Subcostal vein: (0) less than 0.9 of wing length, (1) greater than 0.9 of wing length.
 30. Total number of cross veins in hind wing: (0) more than 16, (1) less than 15.

Legs:

- 31.* Tarsal claws: (0) similar, (1) dissimilar.

Female abdomen:

- 32.* 9th sternite: (0) with deep to moderate cleft, (1) very shallow cleft to entire.

Male genitalia:

- 33.* Penes: (0) divided except at base, (1) separated in apical $\frac{1}{6}$ to $\frac{2}{3}$, (2) fused.
 34. Prominent spines on penes: (0) absent, (1) present.
 35. Pair of ventral spines near base of penes: (0) absent, (1) present.

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