

PHYLOGENETIC RELATIONSHIPS OF THE AUSTRALIAN LEPTOPHLEBIIDAE

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Abstract

The phylogeny of Australian Leptophlebiidae has not been studied in detail although previous research has indicated close relationships with the Neotropical fauna. Phylogenetic relationships of Australian Leptophlebiidae were examined using a cladistic analysis of 34 morphological characters and 21 genera. Character polarity was assessed by out-group comparison and then analysed with NONA (version 2). The three most parsimonious trees produced were used to construct a strict consensus tree. Relationships among the Australian fauna specify some monophyletic groups and unresolved terminals. This study elucidates some previously unknown relationships among the Australian fauna and indicates that the currently recognised genera of Leptophlebiidae in Australia require further definition. Comparison with hypotheses previously proposed for Australian Leptophlebiidae demonstrate partial agreement, recognizing 'Meridialaris' and 'Atalonella' clades (*sensu* Pescador and Peters 1980a) and support for a sister relationship between the burrowing genera *Jappa* and *Ulmerophlebia*. Cladistic characters are tabulated and discussed with illustrations. Examined taxa, materials and comprehensive bibliographic sources are provided.

Key words: phylogeny, Australia, Leptophlebiidae, Ephemeroptera, mayflies, cladistics.

Introduction

The Leptophlebiidae, considered to be one of the most diverse mayfly families (Peters 1988), are distributed worldwide with over 100 genera, predominantly found in the Southern Hemisphere (Hubbard 1990). The monophyly of the Leptophlebiidae, within the superfamily Leptophlebioidea, is now well established (Landa and Soldán 1985, McCafferty 1991). However, phylogenetic relationships within the family have not been considered in total, due to the large number of species involved, but rather have been studied in smaller groups. These groups entail biogeographical regions such as the Southern and Eastern Hemisphere (Tsui and Peters 1975, Peters and Edmunds 1970); South America (Pescador and Peters 1980a), New Zealand (Townsend and Peters 1979, 1996), New Caledonia (Peters et al. 1978; Peters and Peters 1979, 1981a, 1981b; Peters et al. 1990, 1994), Africa (Peters and Edmunds 1964) and

Madagascar (Peters and Edmunds 1984) or genus level relations, e.g., *Meridialaris* and *Massartellopsis* (Pescador and Peters 1987), *Miroculis* (Savage and Peters 1983), *Nousia* (Pescador and Peters 1985), *Penaphlebia* (Pescador and Peters 1991), *Thraululus* (Grant 1985) and *Ulmeritus* (Domínguez 1995).

Only two studies of the evolutionary relationships of Australian genera have previously been undertaken. As part of the analysis of the cool-adapted Leptophlebiid fauna of South America, Pescador and Peters (1980a) inferred affinities between South American and Australian taxa. Later, Christidis (2001) performed an analysis of the Australian Leptophlebiidae, focussing on one evolutionary branch described by Pescador and Peters (1980a), which included several Australian representatives.

Herein we report the relationships between the Australian Leptophlebiid genera and compare and contrast the relationships of the Australian Leptophlebiid genera with hypotheses already proposed, namely the grouping of the Australian genera into five distinct evolutionary lineages based primarily on morphological similarity.

Methods

We examined representative species of the 19 known Australian genera, along with the South American subgenus *Nousia* (*Nousia*), for phylogenetic analysis. Taxa (n=21) and characters (n=34) were compiled (Appendix A). NONA version 2.0 (Goloboff 1993) was used to construct a cladogram using the tree bisection-reconnection command (mult*). A strict consensus tree (nelsen command) was constructed from the resulting most parsimonious trees. WinClada version 0.9.99i (beta) (Nixon 1999) was used to redraw the tree with the characters and character states mapped.

We borrowed type species material from the Museum of Victoria (MV), the Australian National Insect Collection (ANIC), the Australian Museum in Sydney (AM), the Queensland Department of Primary Industries (QDPI), the Natural History Museum, London (NHM), the Swedish Museum of Natural History (SMNH) and the Florida Agricultural and Mechanical University collection (FAMU). Additional specimens were borrowed from the private collections of I.C. Campbell (Campbell collection) and P.J. Suter (Suter collection). We also had specimens from our personal collections (Finlay and Bae collections).

Morphological characters and character states (Appendix B) were determined from examination of the specimens and from the species descriptions in the literature. Key sources of information for the ingroup genera included: *Atalophlebia* (Tillyard 1933; Suter 1986); *Atalomicria* (Campbell and Peters 1993), *Austrophlebioides* (Campbell and Suter 1988, Parnong and Campbell 1997), *Bibulmena* (Dean 1987), *Garinjuga* (Campbell and Suter 1988), *Jappa* (Skedros and Polhemus 1986, Bae and Finlay 2003, Bae et al. 2004), *Kalbaybaria* (Campbell 1993), *Kanina* (Dean 2000), *Kirrara* (Campbell and Peters 1986), *Koornonga* (Campbell and Suter 1988), *Loamaggalanga* (Dean et al. 1999), *Neboissophlebia* (Dean 1988), *Nousia* (Pescador

and Peters 1980a; Campbell and Suter 1988), *Nyungara* (Dean 1987), *Thraulophlebia* (Demoulin 1955a, Campbell and Suter 1988), *Thraululus* (Grant 1985, Suter 1992), *Tillyardophlebia* (Dean 1997) and *Ulmerophlebia* (Suter 1986, Bae et al. 2004). In addition, the taxa *Nousia* (*Australonousia*) and *Thraulophlebia* were recently revised (Finlay 2002) leading to the synonymisation of *Thraulophlebia* with *Koornnonga* over which it has priority (Finlay, Suter and Campbell, unpublished data) and the establishment of two new genera: 'New Genus A' and 'New Genus B' (Finlay, unpublished data).

In agreement with Edmunds and Allen (1966), Riek (1973) and Pescador, and Peters (1980a), larval characters were found to be more taxonomically informative than those of the imago, hence the disproportionately low number of adult characters. Further, wing venation, one of the major characteristics of the adult, is known to be subject to significant parallel evolution (Edmunds 1972).

Character polarities were assessed across all available outgroups (Watrous and Wheeler 1981). The nearest outgroup was the Leptophlebiinae, comprising eight genera (*Paraleptophlebia*, *Leptophlebia*, *Habroleptoides*, *Habrophlebia*, *Calliarcys*, *Habrophlebioides*, *Dipterphlebioides*, *Gillesia*) considered a primitive furcation in the evolution of the Eastern Hemisphere Leptophlebiidae (Peters and Edmunds 1970) and sufficiently different to warrant the establishment of a new subfamily (Peters 1980). Within this subfamily the plesiotypic *Paraleptophlebia* and *Leptophlebia* provided particularly valuable cladistic information.

The latest revisions of the higher classification of mayflies (McCafferty 1991, McCafferty 2002), encompassing the work of Landa and Soldán (1985), provide the next nearest outgroups within the Infraorder Lanceolata: that of the sister group Ephemeroidea (Polymitarcyidae, Euthyplociidae, Potamanthidae, Ephemeridae, Palingeniidae) followed by the superfamily Caenoidea (Ephemerellidae, Tricorythidae and Caenidae). Although the superfamily Behningoidea (containing the single family Behningiidae) is considered more closely related to Leptophlebioidea (McCafferty 1991) than the previous two superfamilies, its use as an outgroup is limited due to its highly distinctive and specialized nature in both adult and nymphal forms (Edmunds 1959).

Key literary sources of information for the outgroup taxa are as follows: Leptophlebiinae - *Paraleptophlebia*, *Leptophlebia* (Burks 1953, Peters and Edmunds 1970), *Habroleptoides*, *Habrophlebia*, *Calliarcys*, *Habrophlebioides*, *Dipterphlebioides* (Peters and Edmunds 1970), *Gillesia* (Gillies 1951, Peters and Edmunds 1970), Ephemeroidea - Ephemeridae: *Aethephemera* (McCafferty 1971a, McCafferty 1973), *Afromera* (Demoulin 1955b, McCafferty and Gillies 1979, Elouard 1986a), *Eatonica* (McCafferty 1971b, Elouard 1986b, Elouard et al. 1998), *Ephemera* (McCafferty 1973, McCafferty 1975, Hubbard 1982, Hubbard 1983; Balasubramanian et al. 1991, Kang and Yang 1994, Bae 1995, Ishiwata 1996), *Hexagenia* (Spieth 1941, McCafferty 1975, Keltner and McCafferty 1986), *Ichthybotus* (Eaton 1899), *Litobrancha* (Lestage 1939, McCafferty 1975), Euthyplociidae: *Afroplocia* (Demoulin 1952a), *Campylocia* (Demoulin 1952a,

Pereira and Da Silva 1990), *Euthyplocia* (Lestage 1918, Lestage 1939, Demoulin 1952a), *Exeuthyplocia* (Lestage 1918, Lestage 1939, Gillies 1980), *Proboscidoplocia* (Demoulin 1966), *Polyplocia* (Demoulin 1952a), *Mesoplocia* (Demoulin 1952a); Palingeniidae: *Cheirogenesia* (McCafferty and Edmunds 1976, Sartori and Elouard 1999), *Chankagenesia* (Demoulin 1952b), *Palingenia* (Sartori 1992), *Pentagenia* (Lestage 1918, McCafferty 1972, McCafferty 1975, Keltner and McCafferty 1986); Polymitarcyidae: *Campsurus* (Eaton 1868-69, McCafferty 1975), *Ephoron* (Lestage 1918, Spieth 1933, Demoulin 1952a, McCafferty 1975, Ishiwata 1996), *Tortopus* (Needham and Murphy 1924, McCafferty 1975, McCafferty and Bloodgood 1989, Lugo-Ortiz and McCafferty 1996), *Povilla* (Lestage 1918; Lestage 1939; Hubbard 1984), Potamanthidae (Bae and McCafferty 1991), *Anthopotamus* (McCafferty and Bae 1990), *Neopotamanthus* (Wu and You 1986), *Potamanthodes* (You 1984, You and Su 1987), *Potamanthus* (Uéno 1928, McCafferty 1975, Elpers and Tomka 1994, Kang and Yang 1994, Vuori 1999), *Rhoenanthus* (Soldán and Putz 2000) and *Stygifloris* (Bae et al. 1990). See Appendix C for a detailed full list of material examined.

Results

Relationships of the Australian Leptophlebiidae are shown in the strict consensus tree (length = 62; ci = 0.66; ri=0.82, Fig. 1) constructed from the three most parsimonious trees initially produced. Based on the cladogram, the Australian Leptophlebiidae are basally delineated from the outgroup by the following synapomorphies: the presence of square dorsal eye facets in the male imago, the presence of hypopharynx lateral processes and prognathous mouthparts in the nymphs.

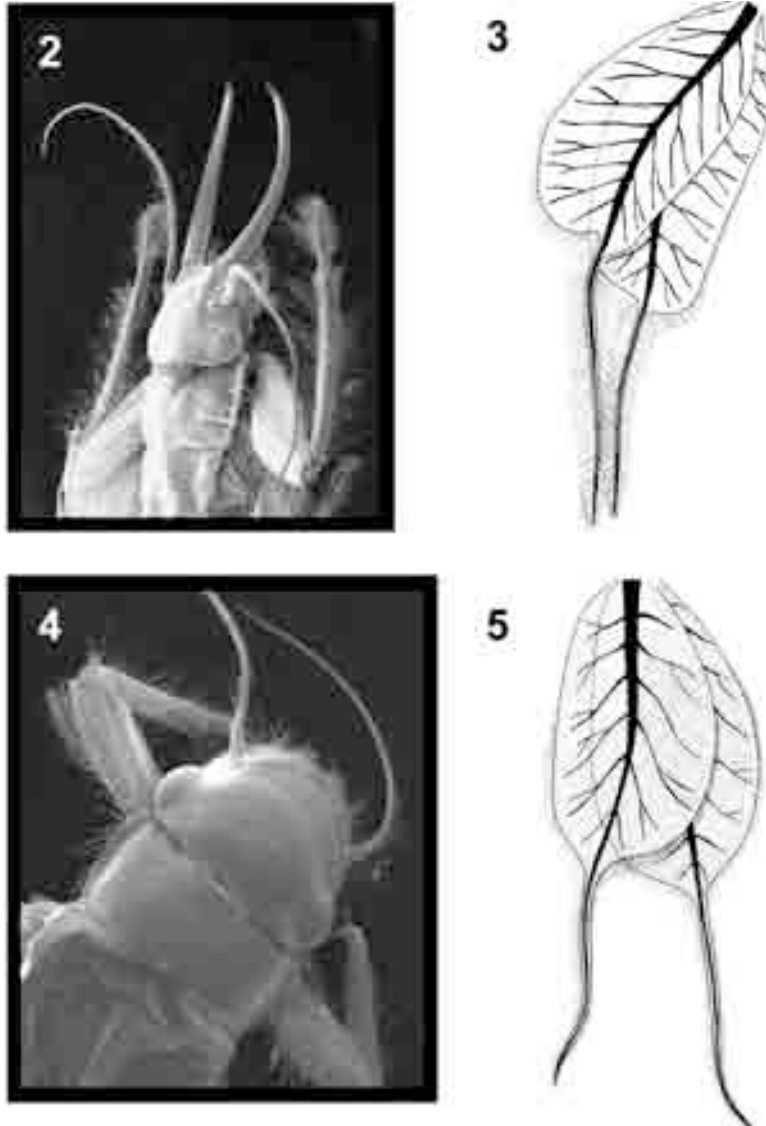
Although relationships between some groups of the ingroup taxa have not been fully resolved, certain clades are relatively well supported. *Jappa* and *Ulmerophlebia* form a monophyletic clade united by the following synapomorphies: body and gills fringed with fine setae (Figs. 2–5); abdominal terga with prominent setae on lateral margins and one prominent median denticle on the labrum (Figs. 6 and 7). *Jappa*, however, is clearly separated from *Ulmerophlebia* by the presence of autopomorphic frontal horns.

Atalomicria and *Atalophlebia* are also monophyletic, grouped together by the possession of medium, as opposed to large or contiguous, eye size (*sensu* Bae and McCafferty 1991). There is strong support for a clade, which includes three genera: *Kirrara*, *Austrophlebioides* and *Tillyardophlebia*. These are united by eight synapomorphies, including two convergences, most of which are multistate and show what are considered to be the most highly derived conditions. Thus, the labrum is much wider than the clypeus, the lateral margins of labrum are angular and the lateral margins of clypeus slightly diverge towards the anterior (Figs. 8–10), the mandibles have angular outer margins (Figs. 11–13), the maxillae galea-laciniae is broad at the apex (Figs. 14–16) and the labium submentum has no lateral setae.

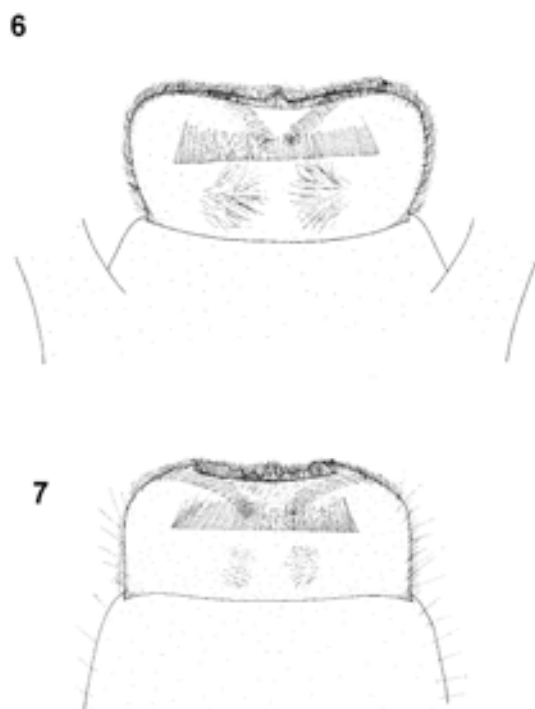


Figure 1. Strict consensus tree (length = 62; ci = 0.66; ri=0.82) of the relationships of the Australian Leptophlebiidae.

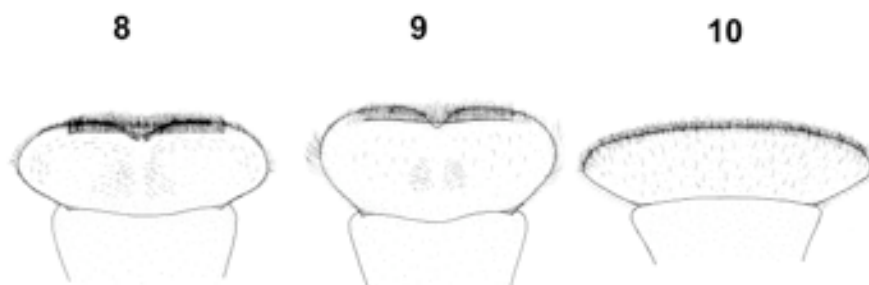
Finally, a reduction in the number of crossveins in the forewing costal space defines a clade containing the taxa *Nousia*, *Nyungara*, *Thraululus*, *Thraulophlebia* and *Neboissophlebia* (Figs. 17–22). In the present study, *Neboissophlebia* forms a tricotomy with *Thraulophlebia* and *Nousia*. These taxa, in turn, share a sister group relationship with the *Nyungara*-*Thraululus* clade. *Nousia*, *Thraulophlebia* and *Neboissophlebia* share the condition of an absence of crossveins in the male forewing costal space (Figs. 17, 18, 21 and 22). *Nyungara* and *Thraululus* are also grouped by the possession of a well-developed midlength costal projection of the hind wing (Figs. 23 and 24).



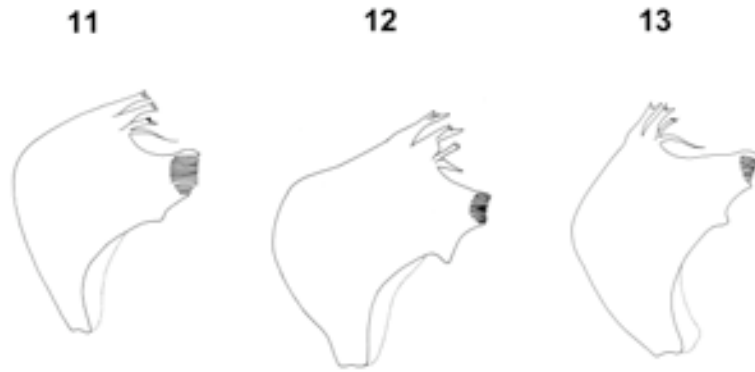
Figures 2–5. *Jappa* (Figs. 2 and 3) and *Ulmerophlebia* (Figs. 4 and 5) have bodies and gills fringed with fine setae.



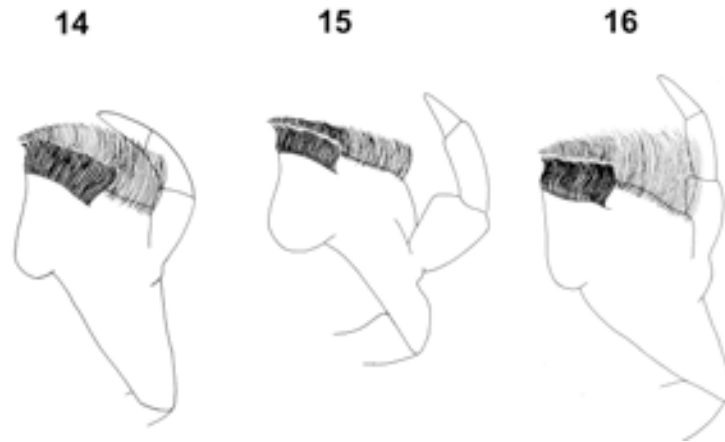
Figures 6 and 7. *Jappa* (Fig. 6) and *Ulmerophlebia* (Fig. 7) Labrum showing prominent median denticle.



Figures 8–10. Labrum and clypeus morphology of *Austrophlebioides* (Fig. 8), *Kirrara* (Fig. 10) and *Tillyardophlebia* (Fig. 12).

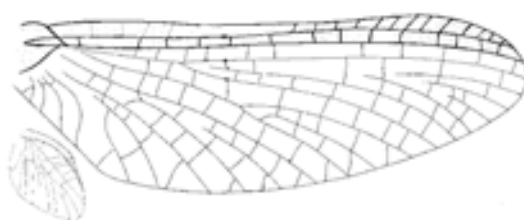


Figures 11–13. Mandible morphology of *Austrophlebioides* (Fig. 11), *Kirrara* (Fig. 12) and *Tillyardophlebia* (Fig. 13), mandible.

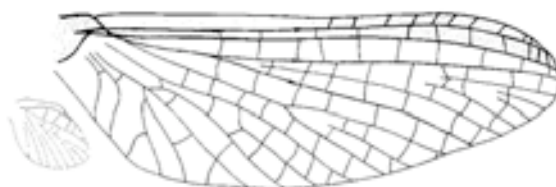


Figures 14–16. Maxilla morphology of *Austrophlebioides* (Fig. 14), *Kirrara* (Fig. 15) and *Tillyardophlebia* (Fig. 16).

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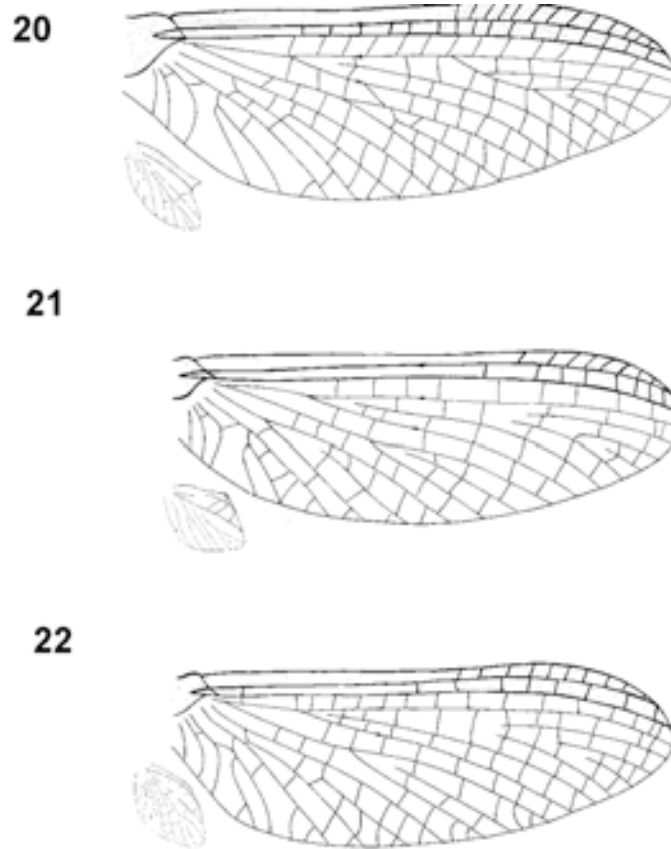
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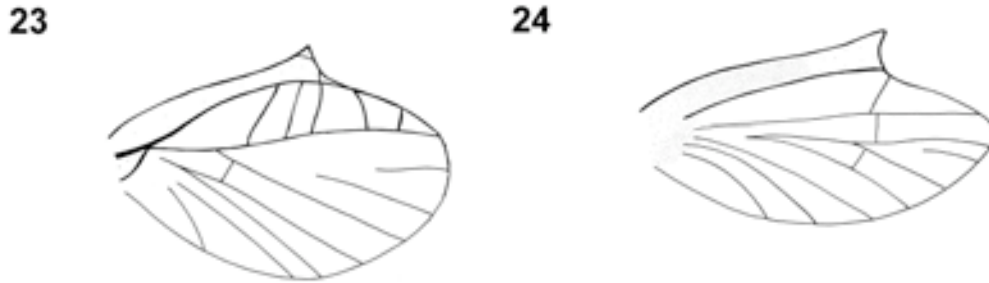
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Figures 17–19. Male imago forewings of *Nousia* (*Nousia*) (Fig 17), *Nousia* (*Australonousia*) (Fig 18), and *Nyungara* (Fig. 19). Note: reduction in the number of crossveins in the costal space, in particular the proximal half.



Figures 20–22. Male imago forewings of *Thraululus* (Fig. 20), *Thraulophlebia* (Fig. 21), and *Neboissophlebia* (Fig. 22). Note: reduction in the number of crossveins in the costal space, in particular the proximal half.



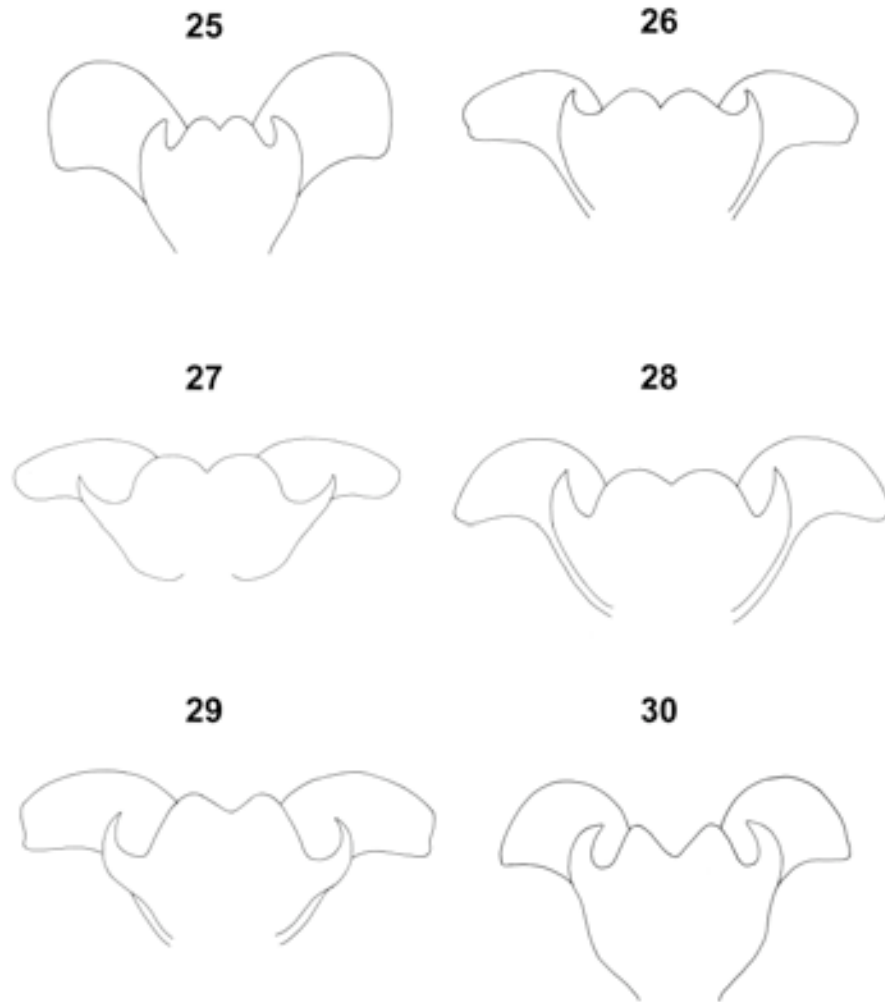
Figures 23–24. Male imago hindwings of *Nyungara* (Fig. 23) and *Thraululus* (Fig. 24) showing costal projection.

Discussion

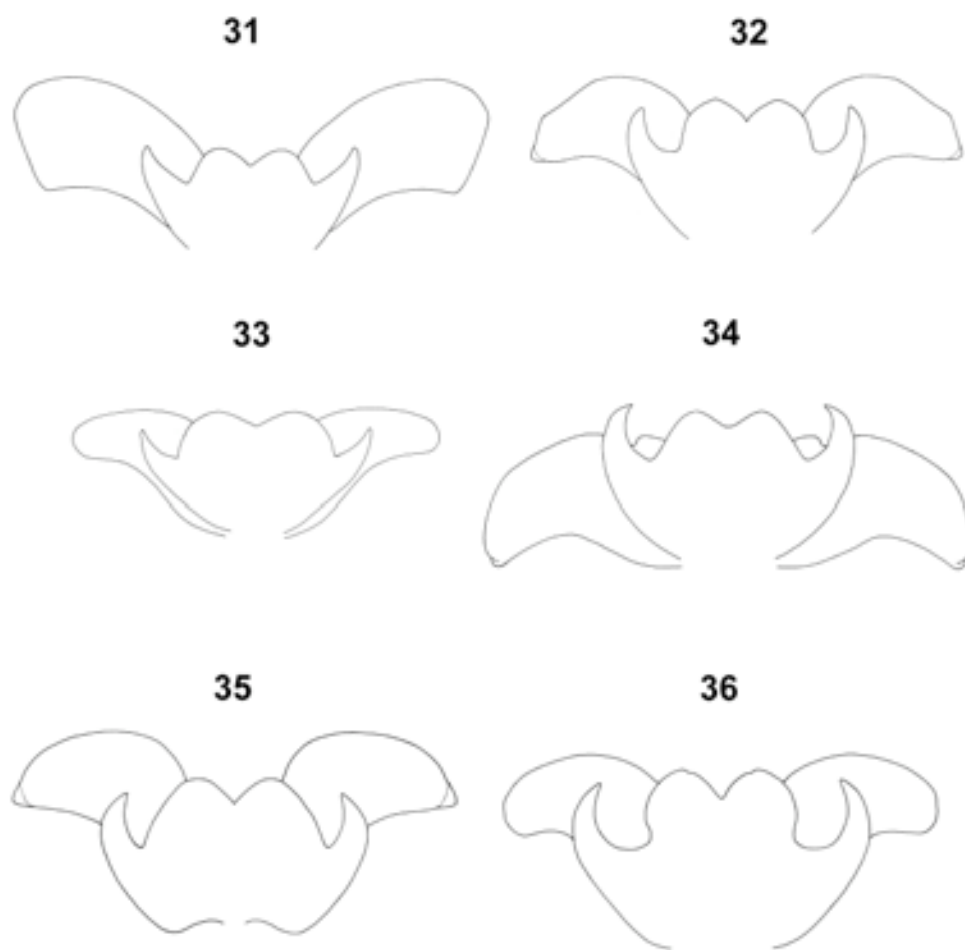
Relationships of the Australian Leptophlebiidae. The characters defining the basal clade of the ingroup (square facets, lateral processes on the hypopharynx, head position) are included in the familial definition of Leptophlebiidae as outlined by Peters and Edmunds (1964) and Towns and Peters (1996). But as these characters are present amongst the Atalophlebiinae worldwide, an analysis including all Gondwanan fauna would be required to investigate the potential monophyly of the Australian group.

Square facets are characteristic of all but one of the Atalophlebiinae taxa (Peters and Gillies 1995); a condition thought to have evolved to catch a greater proportion of the ultraviolet light available (Horridge et al. 1982). The presence of lateral processes on the hypopharynx generally applies to Atalophlebiinae worldwide and is present in all the Australian taxa (Figs. 25–43, however, it may be secondarily lost in some species (Peters and Edmunds 1970). The evolutionary function of this structure is unknown although one could presume it is related to feeding behaviour.

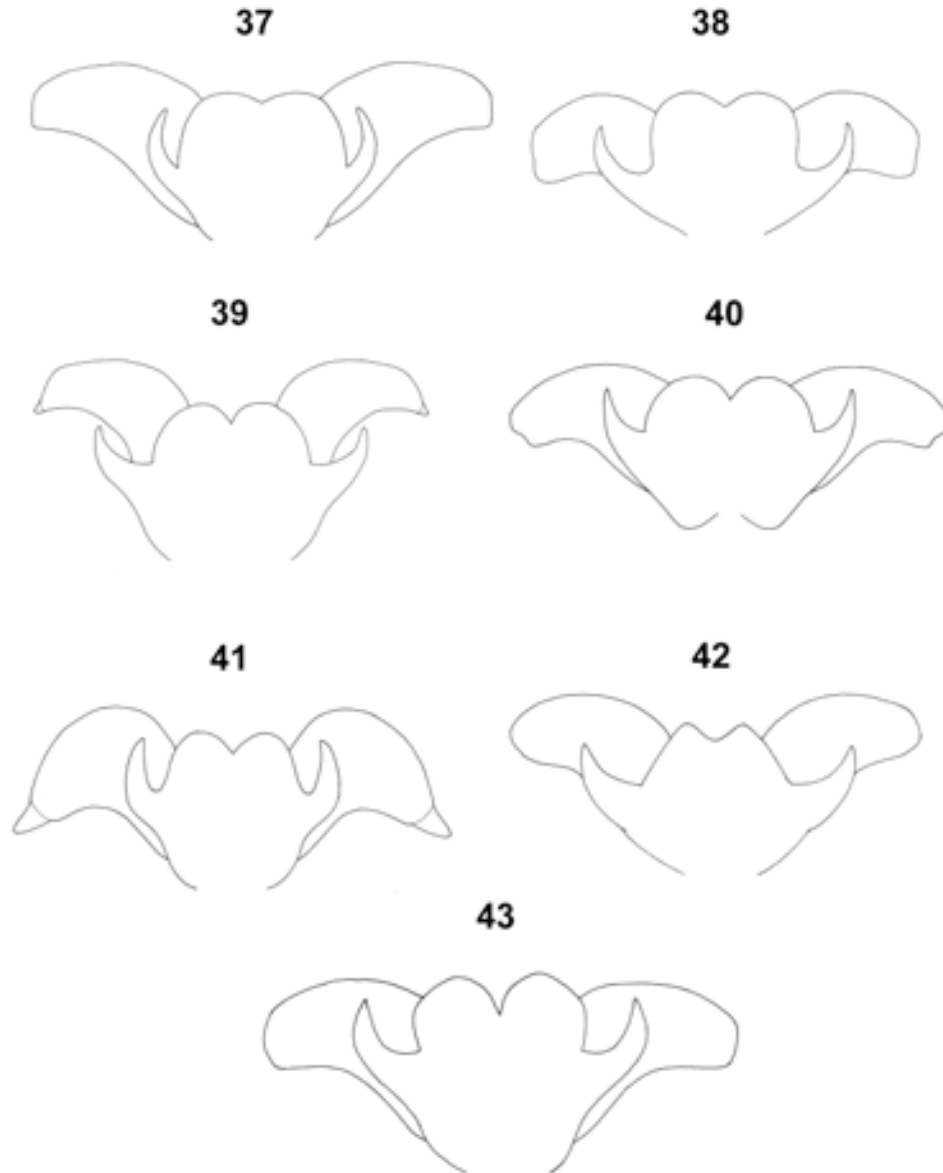
Finally, head position in the Leptophlebiidae varies widely and can be somewhat ambiguous such as the described semiprognathous of Peters and Edmunds (1964). Despite this, the mouthpart position tends to be relatively stable. For example, the position of the head of both *Jappa* and *Ulmerophlebia* can sometimes be oriented partly downwards, although the mouthparts of each are most commonly directed forward. The habit of the Atalophlebiinae as sprawlers, swimmers and clingers (Edmunds and Waltz 1996) translates into a streamlined body capable of maintaining a position of least resistance on the streambed. The Leptophlebiinae tend to be more laterally rather than dorso-ventrally flattened, often with prognathous mouthparts (Peters and Edmunds 1970). The Ephemeroidea are very robust and laterally flattened to accommodate their burrowing behavior and their mouthparts are generally hypognathous for filtering and gathering detritus.



Figures 25–43. Hypopharynx morphology of Australian genera: *Atalomicria* (Fig. 25), *Atalophlebia* (Fig. 26), *Austrophlebioides* (Fig. 27), *Bibulmena* (Fig. 28), *Garinjuga* (Fig. 29), *Jappa* (Fig. 30).



Figures 31–36. Hypopharynx morphology of Australian genera: *Kalbaybaria* (Fig. 31), *Kaninga* (Fig. 32), *Kirrara* (Fig. 33), *Loamaggalangta* (Fig. 34), *Neboissophlebia* (Fig. 35), *Nousia* (*Australonousia*) (Fig. 36).



Figures 37–43. Hypopharynx morphology of Australian genera: *Nyungara* (Fig. 37), *Thraulophlebia* (Fig. 38), *Thraululus* (Fig. 39), *Tillyardophlebia* (Fig. 40), *Ulmerophlebia* (Fig. 41), New Genus A (Fig. 42), and New Genus B (Fig. 43)

The monotypic *Kalbaybaria* is separated from the rest of the ingroup by the autapomorphy of the mandible extending anteriorly into an enlarged flattened process (Fig. 44), a feature not homologous with the horns of *Jappa*, which are derived from the head capsule. Certain Leptophlebiinae (e.g., *Paraleptophlebia*) also possess tusks derived from the outer incisor of the mandible (Needham et al. 1935, Bae and McCafferty 1995), but more work is required to establish the possible homology of *Kalbaybaria* and Ephemeroidea mandibular tusks. The distinct morphology and habitat of the tropical genus *Kalbaybaria* found only in Far North Queensland may indicate a highly evolved condition despite the obscurity of its adaptive and historical origins. There are some indications that tusk robustness and setation of the Ephemeroidea is more related to burrowing and filter feeding (Bae and McCafferty 1995) as opposed to the spatulate processes of *Kalbaybaria*, which, it is suggested, is used to navigate through leaf packs (Campbell 1993).

The sister relationship and similar characteristics of *Jappa* and *Ulmerophlebia* is presumed to be due to their similar burrowing habits. Morphological differences between the two taxa are not readily apparent apart from the highly visible frontal horns. Suggestions have been made that the two taxa are congeneric (Riek 1970, Suter 1986) due to the significant similarities other than the frontal horn, but this is currently being refuted (Bae et al. 2004).



Figure 44. Mandible morphology of *Kalbaybaria* showing enlarged flattened process.

The grouping of *Atalomicria* and *Atalophlebia* is based on their comparatively small eye size. This character has previously been noted as an apomorphy in the Potamanthidae (Bae and McCafferty 1991) but is considered liable to convergence. Interestingly, certain members of the supposed more primitive subfamily, Leptophlebiinae (*Paraleptophlebia*, *Leptophlebia*) also possess large eyes, whereas, some members of Ephemeroidea do not.

The function of the elongate maxillary palps (Fig. 45) of *Atalomicria* is unknown. Although certain ephemerid mayflies (e.g., *Ephemera*) also possess elongated maxillary palps, the morphologies of the two are quite distinct. In *Atalomicria*, segments one and two make up the majority of length, whereas, in *Ephemera* all segments are equally elongate.

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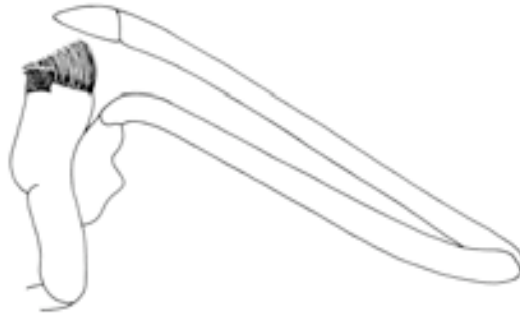


Figure 45. Maxilla morphology of *Atalomicria* showing elongate maxillary palps.

Undoubtedly, the most well supported clade is the *Kirrara*, *Austrophlebioides* and *Tillyardophlebia* trichotomy grouped by eight synapomorphies mostly relating to the nymphal mouthparts as shown above (see Figs. 8–16). Some of these characters are not independent; for example, the diverging lateral margins of the clypeus may be required to accommodate a labrum that is significantly wider than its clypeus. Pescador and Peters (1980a) have labeled a number of these characters as phenoclines, where the character states have evolved from the most primitive state through a series of intermediary stages towards the most derived condition. These character states cannot always be clearly delineated as multistate characters across all genera, but the above genera seem to possess the most highly derived character states which can be easily polarized from all the other taxa.

Austrophlebioides and *Tillyardophlebia* share an apomorphic U-shaped labrum cleft or “hood” (see Figs. 8 and 9). An unnamed Genus ‘Z’ from southeastern

Australia (Dean 1999) is not well known but also has a wide labrum and distinct V-shaped cleft with many similar characteristics to *Austrophlebioides* and may prove to be closely related.

Kirrara is distinguished from the trichotomy by the possession of a labrum, which is triangular in cross section with quite a wide anterior margin in apical view (Fig. 46). The previously named 'Genus T' (Dean and Suter 1996), which has recently been referred to *Kirrara* as an unnamed species (Christidis 2001), also possesses an apically expanded labrum where the frontal setae have been modified to form a suction disc. *Kirrara* is very similar to the highly derived *Deleatidium* of New Zealand (Townsend and Peters 1996) and *Lepegenia* of New Caledonia (Peters et al. 1978), which have laterally and apically expanded labrum and gills forming a suction disc on the venter of the abdomen. However, these structures are not present in all *Deleatidium*. These are considered adaptations to extremely rapid flow that enables the species to cling tightly to the substrate (Townsend and Peters 1996). 'Genus T', *Lepegenia* and several species of *Deleatidium*, have all been found in association with vertical rock faces of waterfalls. Other distinguishable characters of *Kirrara* include the loss of the secondary hair fringe and anteromedian denticles of the labrum, which appear to have evolved in an earlier clade in the Australian Leptophlebiidae.

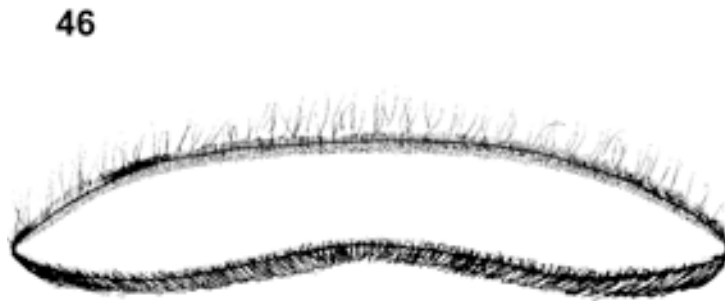


Figure 46. Apical view of *Kirrara procera* labrum; apical view.

A reduced number of crossveins in the forewing costal space defines a clade comprising the taxa *Neboissophlebia*, *Thraulophlebia*, *Nousia*, *Nyungara* and *Thraulus* (see Figs, 17–22); a state that could be related to the relatively small size of the imago where the cross support between the costal and subcostal spaces is not needed. In *Nousia*, *Thraulophlebia* and *Neboissophlebia* (see Figs. 17, 21 and 22), a maximum reduction of crossveins has occurred. They all share the condition of the absence of crossveins in the male forewing costal space. The evolutionary significance of this character state is unknown (W. L. Peters, *pers. comm.*) but as

with a reduction in the number of costal crossveins in the male forewing. This character may also be considered as the second step in the apomorphic state of the costal crossvein reduction but was analysed separately in this study because it could also be related to the relatively smaller size only in the male imago. Ecological investigation will be required to determine the significance of this character state, which is not possessed by females of the same species.

Despite the considerable morphological variation between *Thraulophlebia* and *Nousia* which warrants their separate generic status (Finlay 2002), there appear to be few phylogenetically informative characters separating the two taxa in this clade. The inclusion of the full complement of Gondwanan fauna in an analysis may elucidate more evolutionary information for these taxa in the future. Similarly, there is little phylogenetic information supporting the subgeneric separation of *Nousia*, but as the latest revision of Australian *Nousia* is preliminary, largely due to lack of material (Finlay, unpublished data) the subgenera should remain separate based on the consistent nymphal character states outlined by Campbell and Suter (1988).

Nyungara and *Thraululus* are also grouped by the possession of a well-developed midlength costal projection of the hind wing (see Figs. 23 and 24). Although this character is also possessed by the Leptophlebiinae in some cases (e.g., *Habrophlebiodes*, *Gillesia*), it is not present in the Ephemeroidea, which usually possess an apical costal projection. The Gondwanan status of *Thraululus* is unclear, being primarily distributed throughout the Oriental and Ethiopian regions and Europe (Grant 1985) and known only in Australia from the Northern Territory, north Queensland and north Western Australia. Evidence suggests there are two centers of origin for Leptophlebiidae: one with Holarctic-Oriental distribution and the other Gondwanan (Peters and Edmunds 1970, Edmunds 1972), and the distribution of this genus suggests affinities with the former. However, only a more taxonomically inclusive analysis could address the question of its geographic origins. Further, our knowledge of *Thraululus* in Australia is rudimentary. Two morphospecies were described from the Alligator River region of Northern Territory (Suter 1992) but were subsequently considered conspecific, being referred to as *Thraululus* sp. 'AV1' (Dean 1999). From the specimens examined, it is clear that specimens of *Thraululus* sp. 'AV1' are the same as *Thraululus* sp. A. from Magela Creek of the Northern Territory (Marchant 1982). Only two other unnamed species from Queensland are recognized (Dean 1999) but are based only on nymphs. Adult material is essential to further elucidate the total contingent of species in Australia.

Garinjuga possesses strongly diverging veins ICu_1 and ICu_2 in the male forewing (Fig. 47) that are considered plesiomorphic state and tend to be associated with more triangular shaped forewings, where the junction of the anal and distal margin forms an approximate 90-degree angle. This tends to expand the length of the wing hind margin and therefore separates ICu_1 and ICu_2 as the wing margin is approached. This character is generally distributed amongst the larger sized taxa such as *Jappa*, *Ulmerophlebia*, *Atalomicria*, *Atalophlebia* and *Kirrara*, which are in possession of larger and more robust forewings.

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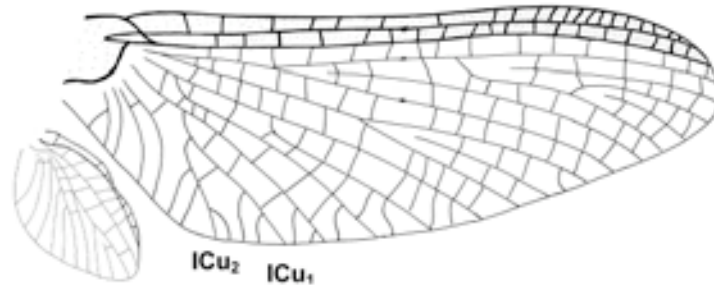
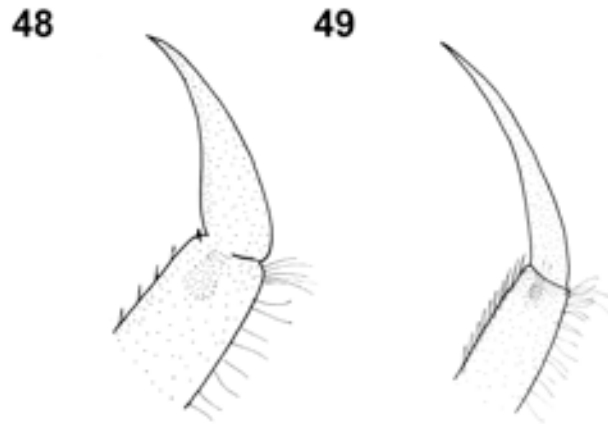
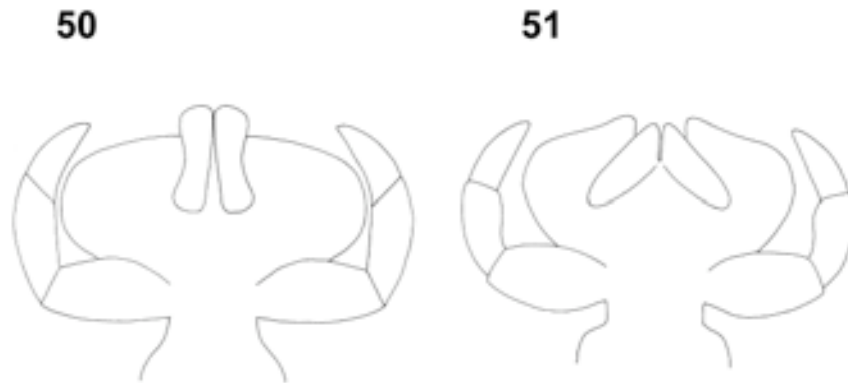


Figure 47. Male imago forewing of *Garinjuga*.

The position of the remaining taxa: *Bibulmena*, *Kaninga* and *Loamaggalangta*, 'New Genus A' and 'New Genus B' are also poorly resolved within the cladogram. *Kaninga* has only recently been established as a genus (Dean 2000) and its single species is confined to southwest Western Australia. It has been considered similar to *Bibulmena* (Dean 2000) and *Loamaggalangta* (Dean et al. 1999), but this is defined only by symplesiomorphies such as smooth tarsal claws in the nymph (Figs. 48 and 49) and the labial glossae turned over (Figs. 50 and 51). *Bibulmena* and *Kaninga* are found only in southwest Western Australia, an indication that the origins of these species may differ from their east Australian counterparts. *Loamaggalangta* has been found solely in Tasmania where it occurs only at water depths of greater than five metres clinging to submerged objects (Dean et al. 1999), which may account for some of its more unusual features such as extremely elongate leg lengths of the nymph including a long curved smooth tarsal claw (see Fig. 49), which may be used to grip tightly to the substrate. 'New Genus A' and 'New Genus B' are also unresolved in the cladogram but do not appear closely related to *Nousia* (*Australonousia*), the genus to which they were previously assigned (Dean 1999).



Figures 48 and 49. Nymph tarsal claw morphology of *Bibulmena* (Fig. 48) and *Loamaggalangta* (Fig. 49).



Figures 50 and 51. Labium morphology of *Bibulmena* (Fig. 50) and *Loamaggalangta* (Fig. 51); dorsal view.

Comparisons with previous studies of Australian Leptophlebiidae. The phylogenetic analysis of the major groups of Leptophlebiidae was first attempted by Peters and Edmunds (1970). They proposed a phylogeny for the Eastern Hemisphere genera of Leptophlebiidae including all Palaearctic, Ethiopian, and Oriental regions but excluding Australia and New Zealand as they considered these taxa to have closer affinities with the Neotropical fauna. This hypothesis had been inferred from a previous revision of the Ethiopian Leptophlebiidae (Peters and Edmunds 1964). A similar hypothesis was first intimated by Brundin (1966) while studying the

biogeography of chironomid midges and coincides with the generally accepted view of the sequential break up of Gondwana (Norton and Sclater 1979). Amongst the Leptophlebiidae, however, this has not been cladistically tested.

The proposed close affinity between Gondwanan fauna was examined in a study of the cool-adapted taxa of South America referring to cool mountain waters and regular freezing episodes (Pescador and Peters 1980a). This small but significant paper provided a basis for comparison for future phylogenetic work on the Leptophlebiidae. Five lineages, one of which was described subsequently (Pescador and Peters 1980b), were established based on an analysis of the cool-adapted Leptophlebiidae of southern South America (Fig. 52). Each lineage, although named arbitrarily after a prominent South American genus, represented a group of taxa, the names being for convenience only. The lineage at the base of the tree (*'Hapsiphlebia'*) was considered the most primitive and each successive branch more advanced until the *'Meridialaris'* lineage.

52

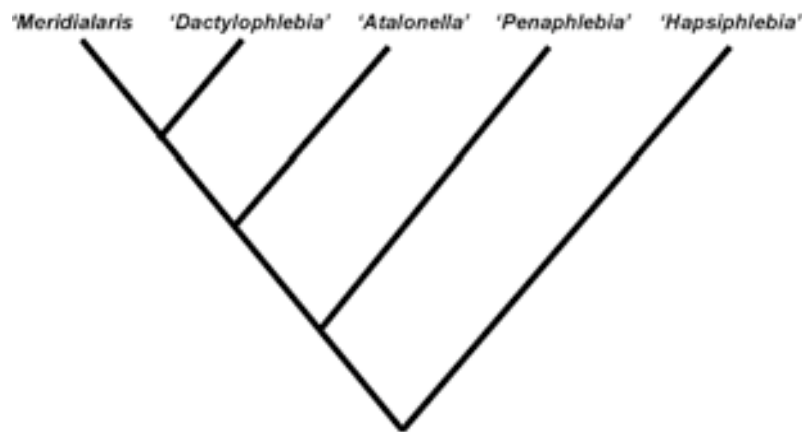


Figure 52. Proposed relationships for South American and related Southern Hemisphere fauna (reproduced from Pescador and Peters 1980a with additions from Pescador and Peters 1980b).

Although other Southern Hemisphere fauna were not included as part of the study, cursory examination of the Leptophlebiid fauna from Australia, New Zealand, New Caledonia, Madagascar and Africa inferred affinities with some of these lineages. Thus, with respect to the Australian genera, it was determined that the

genera *Jappa*, *Ulmerophlebia*, *Atalomicria* and *Atalophlebia* belonged to the 'Hapsiphlebia' lineage, *Nousia* belonged to the 'Atalonella' lineage and *Austrophlebioides* belonged to the 'Meridialaris' lineage. Based on this, it was hypothesized that the fauna of South Americas more closely related to Australia rather than New Zealand (Pescador and Peters 1980a). This is exemplified, in part, by the genus *Nousia* that Australia and New Zealand share (Hubbard 1990). Examination of the phylogenetic relationships of the entire Ephemeropteran Gondwanan fauna may lend further support to this.

Since the publication of Pescador and Peters (1980a), authors of newly erected or redescribed Australian genera have assigned placement of these taxa into the various lineages based on morphological similarities. Australian genera currently thought to belong to each of the various lineages are outlined in Table 1.

Table 1. Australian genera currently thought to belong to the five lineages outlined by Pescador and Peters (1980a). References are given for those genera added since the publication of the original paper.

Lineage	Genus	Reference
1. <i>Hapsiphlebia</i>	<i>Atalophlebia</i> <i>Atalomicria</i> <i>Jappa</i> <i>Kalbaybaria</i> <i>Ulmerophlebia</i>	Campbell 1993
2. <i>Penaphlebia</i>	<i>Garinjuga</i> <i>Bibulmena?</i>	Campbell and Suter 1988 Dean 1987
3. <i>Atalonella</i>	<i>Atalonella</i> = <i>Nousia</i> <i>Nyungara</i>	Pescador and Peters 1985 Dean 1987
4. <i>Dactylophlebia</i>	No Australian representatives	
5. <i>Meridialaris</i>	<i>Austrophlebioides</i> <i>Kirrara</i> <i>Tillyardophlebia</i>	Campbell and Peters 1986 Dean 1997

There is an inherent difficulty in comparing this cladistic analysis with the largely phyletic methods of Pescador and Peters (1980a) and where taxa in each successive lineage were compared only with taxa in the lineages above. For

comparison on an equal footing, therefore, data in the original paper was used to perform a cladistic based analysis. The lineages were used as terminal taxa (n= 6), characters (n=23) were sequentially numbered directly from Table 1 and character polarities remained unchanged. The resultant matrix (Appendix D) was used to perform an analysis using the method outlined above. Only one tree was produced (Fig. 53) (tree length of 23, ci = 1.0, ri = 1.0).

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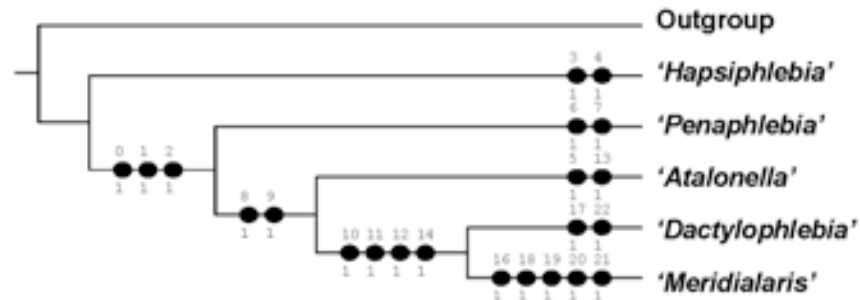


Figure 53. Cladistic based analysis of Pescador and Peters (1980a) data.

With this as a basis of comparison, there is only partial agreement between the relationships of the Australian taxa and those determined for Southern Hemisphere fauna as analyzed by Pescador and Peters (1980a). Of the four lineages considered to have representatives in Australia, only two are well supported in the current analysis; that of *'Meridialaris'* and *'Atalonella'*. The *'Hapsiphlebia'* taxa in the current analysis are basal to the rest of the ingroup as in the Pescador and Peters (1980a). There is also a question mark regarding the monophyly of the *'Penaphlebia'* lineage in Australia as *Garinjuga* is the only Australian representative.

The *'Meridialaris'* lineage is considered to include *Austrophlebioides* (Pescador and Peters 1980a), *Tillyardophlebia* (Dean 1987) and *Kirrara* (Campbell and Peters 1986) and there is strong support for such a grouping in this study. Of the six synapomorphies defining the lineage in the present study, four mirrored those of Pescador and Peters (1980a). The remaining two (lateral margins of the labrum angular and lateral margins of the clypeus divergent) identified a clade containing members of both the *'Meridialaris'* and *'Dactylophlebia'* lineages, but as there are apparently no members of the Australian *'Dactylophlebia'* fauna, these two character states became synapomorphies for Australian members of *'Meridialaris'*. Therefore

in an inclusive Gondwanan phylogeny, these characters could not be used to distinguish the 'Meridialaris' lineage as currently defined here. Pescador and Peters (1980a) also determined a greater number of subapical pectinate setae on the maxillae galea-lacinae as synapomorphic for the lineage. In the present study, however, the number of setae was somewhat subjective, varied greatly between genera and was found to be homoplastic.

The Christidis (2001) phylogeny can not be directly compared.. Her study aimed to test the monophyly only of the 'Meridialaris' taxa in Australia (*Austrophlebioides*, *Tillyardophlebia* and *Kirrara*). To this end, she studied members of the Australian 'Meridialaris' fauna at a specific level and included many undescribed species ('Northern Kirrara', 'WT species 1 & 2', 'Paluma', 'Henrietta' and 'Daintree') whose generic affinities were postulated. Note: two of these morphospecies have been recently assigned to *Austrophlebioides* (Christidis and Dean 2005). Other Australian genera were included at the generic level to investigate higher level relationships. Support was found for a monophyletic clade of the Australian representatives of the 'Meridialaris' lineage based on the absence of hairs on the lateral margins of the submentum and the ninth sternum of the female entire or only slightly cleft. An entire ninth sternum of the female imago serves as a synapomorphy for the Australian 'Meridialaris' tricotomy, although it is homoplastic in a cladistic analysis of the phylogeny of Pescador and Peters (1980a).

According to the cladistic analysis of the Pescador and Peters data, the 'Atalonella' lineage is defined by two synapomorphies: the labrum wider than the clypeus and the antero-median emargination of the labrum with broad subapical denticles. The latter character was found to be ambiguous, especially with respect to the definition of 'broad', and as it could not be objectively defined, so was not included in the phylogenetic analysis. There was some question of the affinities of the genus *Neboissophlebia*, thought to be related to the 'Hapsiphlebia' genera, *Jappa* and *Ulmerophlebia*, and the 'Atalonella' fauna (Dean 1988). We conclude that *Neboissophlebia* is more closely allied with the 'Atalonella' fauna.

Christidis (1991) also found support for the 'Atalonella' lineage where *Nyungara*, *Nousia* (*Australonousia*) and *Thraulophlebia* (as *Koornonga*) formed a monophyletic group, although there are no synapomorphies to support this. Notably, this did not include *Neboissophlebia* whose relationship was unresolved. Neither Pescador and Peters (1980a) nor Christidis (1991) included *Thraululus* in their analyses.

The cladistic analysis of the Pescador and Peters data defines the 'Penaphlebia' lineage according to the presence of pectinate setae on the inner margin of the second maxillary palp and prominent spines/tassel-like setae on the posterior margins of the abdominal terga. Both conditions are homoplastic in the present analysis. *Garinjuga* is purported to belong to the 'Penaphlebia' lineage based on the following character states (Campbell and Suter 1988): rounded labrum lateral margins, smoothly curved outer margin of mandibles, the relatively smooth right mandible inner margin of the outer incisor, inner margin of labial palp segment 3 with peg-like spines and inner

margin of maxillary palp segment 2 with pectinate spines. Again for all characters included in the present analysis, no synapomorphies were found to support these hypotheses. It has been argued that *Bibulmena* is intermediate between the 'Hapsiphlebia' and 'Atalonella' lineages sharing many characters of both and therefore belongs to 'Penaphlebia' lineage (Dean 1987), although this is not supported in the present analysis.

Loamaggalangta is considered close to *Bibulmena* (Dean et al. 1999), although it has not been formally 'allocated' a lineage *sensu* Pescador and Peters (1980a). The position of both genera remains unresolved in the present study. The evolutionary relationships of *Bibulmena*, *Loamaggalangta* (as Genus 'K') and *Garinjuga* among the Australian Leptophlebiidae are also unresolved in the Christidis (1991) phylogeny.

Conclusions

The inordinately large number of Leptophlebiid taxa worldwide (Hubbard 1990) has so far prevented an analysis of the phylogenetic relationships of the family as a whole, although assessments have been made at regional spatial scales. We followed this approach of analyzing regional fauna separately. Although there are still abundant unsolved phylogenies in the Australian Leptophlebiidae, parallel conclusions are reached between the results of this study and the findings of Pescador and Peters (1980a) and Christidis (1991) especially in relation to close relationships between *Austrophlebioides*, *Tillyardophlebia*, and *Kirrara* (the 'Meridialaris' fauna); *Nousia*, *Nyungara* and *Thraulophlebia* (the 'Atalonella' fauna), and *Jappa* and *Ulmerophlebia* (part of the 'Hapsiphlebia' lineage). The clarification of some of the phylogenetic relationships between the Australian fauna, although preliminary, is valuable as a basis for inclusion of Australian Leptophlebiidae into a future phylogenetic analysis of the Gondwanan fauna and ultimately a phylogeny of the Leptophlebiidae worldwide.

Acknowledgments

We thank Richard Marchant and Peter Lillywhite (Museum of Victoria, Melbourne), Max Moulds (Australian Museum, Sydney), Ngaire Phillips (Queensland Department of Primary Industries, Brisbane), the Collections Manager (Australian National Insect Collection Canberra), David T. Goodger (Natural History Museum, London, U.K.), Kjell Arne Johanson (Naturhistoriska Riksmuseet, Stockholm, Sweden), Bill and Jan Peters (Florida Agricultural and Mechanical University, Florida, USA), Ian Campbell, Fred Govedich and Dennis O'Dowd (Monash University), John Dean (Victoria EPA), Phil Suter (LaTrobe University) and Nigel Ainsworth (DPI Victoria) for specimen loans, assistance in the field and useful comments. Part of this research was conducted while YJB is on sabbatical at Monash University (2000–2001) supported by the Korea Research Foundation Grant (KRF-2001-013-G00007).

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Appendix A

Data matrix of phylogenetic character states for the Australian genera of Leptophlebiidae.

	11111	11111	22222	22222	3333		
	01234	56789	01234	56789	01234	56789	0123
Outgroup	00000	00000	00000	00000	00000	00000	0000
<i>Atalomicria</i>	10000	00001	10000	01001	00010	11000	1100
<i>Atalophlebia</i>	10001	00001	10000	01000	00010	11000	0100
<i>Austrophlebioides</i>	10011	22011	10220	10210	11111	01100	0001
<i>Bibulumena</i>	10000	11001	10110	10110	01010	01000	1000
<i>Garinjuga</i>	10010	11001	10110	10110	11011	01000	1000
New Genus A	10000	11001	10110	10110	11011	01100	1100
<i>Jappa</i>	11100	00001	21000	01000	00010	01000	1100
<i>Kalbaybaria</i>	10000	00000	00001	011-0	00010	01100	1000
<i>Kaninga</i>	10010	11001	10110	10110	01010	01100	1000
<i>Kirrara</i>	10001	22100	00220	-0210	11111	01000	1001
<i>Loamaggalangta</i>	10000	11001	10110	10110	01010	01100	1000
New Genus B	10000	11001	10110	10110	11011	01100	1100
<i>Neboissophlebia</i>	10000	11001	10110	10010	01010	01111	1100
<i>Nousia (Nousia)</i>	10000	11001	10110	10100	11011	01111	1100
<i>Nousia (Australonousia)</i>	10000	11001	10110	10100	11011	01111	1100
<i>Nyungara</i>	10000	11000	10110	10100	11011	01110	2110
<i>Thraulophlebia</i>	10000	11001	10110	10110	11011	01111	1100
<i>Thraulus</i>	10000	11001	10110	10110	11011	0111-	1111
<i>Tillyardophlebia</i>	10011	22011	10220	10210	11111	01100	1001
<i>Ulmerophlebia</i>	11100	00001	20000	01000	00010	01000	1100

Appendix B

Morphological characters and character states used in the cladistic analysis of Australian Leptophlebiidae.

P= plesiomorphic, A = apomorphic.

Larval Characters

Body

0. Mouthparts: 0, hypognathous (P); 1, prognathous (A).
1. Body and gills: fringed with fine setae: 0, no (P); 1, yes (A).
2. Setation or spination on lateral margins of abdominal terga: 0, bare or minute setae (P); 1 prominent spines (A).
3. Spination on posterior margins of abdominal terga: 0, none or small (P); 1, prominent (A).
4. Posterolateral spines on abdomen: 0, on segments 4, 5, 6, 7 or 8 to 9 (P); 1, on segments 8 to 9 (A).

Head and mouthparts

5. Labrum width: 0, narrower than clypeus (P); 1, subequal to slightly wider than clypeus (A); 2, significantly wider than clypeus (A).
6. Labrum lateral margins: 0, parallel (P); 1, rounded (A) ; 2 angular (A)
7. Labrum cross section: 0, oval (P); 1, parallel (A).
8. Labrum 'hood': 0, absent (P); 1, present (A).
9. Labrum secondary hair fringe: 0, absent (P); 1, present (A).
10. Labrum denticles on anteromedian emargination: 0, absent (P); 1, present (A).
11. Frontal horns: 0, absent (P); 1, present (A).
12. clypeus lateral margins: 0, converging towards anterior (P); 1, parallel (A); 2, diverging towards anterior (A).
13. Mandible outer margins: 0, relatively straight (P); 1, smoothly curved (A); 2, angular (A).
14. Mandible enlarged process: 0, absent (P); 1, present (A).
15. Mandible prosthecal tuft: 0, wide (P); 1, flap-like, setae on apical and lateral margins (A); 2, spine-like; hairs on lateral margins only (A).
16. Right mandible, outer incisor, inner margin: 0, smooth or spinose (P); 1, denticulate (A).
17. Maxillae galea-lacinae width-length ratio (W/L ratio): 0, narrow at apex, W/L <1 (P); 1, relatively broad at apex, W/L approx <1 (A); 2, very broad at apex: W/L > 1 (A).
18. Average number of pectinate setae on maxillae: 0, less than or equal to 15 (P); 1, > 17 (A).

19. Maxillary palp morphology: 0, extending just beyond galea-lacinae (P); 1, greatly elongate (A).
20. Labium glossae: 0, turned over ventrally (P); 1, straight, upright (A).
21. Spines on inner margins of labial terminal palps: 0, prominent (P); 1, minor or absent (A).
22. Labium submentum lateral setae: 0, present (P); 1, absent (A).
22. Hypopharynx lateral process: 0, absent (P); 1, present (A).
23. Tarsal claws dentition: 0, smooth or with minor processes (P); 1, denticulate (A).

Imago Characters

Head

24. Size of male imago dorsal eye lobes. $ES=B/D$ (Bae 1991): 0, eye size large, ≤ 0.2 or contiguous (P); 1, eye size medium, ≥ 0.3 (A).
25. Male dorsal eye facet shape: 0, hexagonal (P); 1, square (A).

Wings

26. Position of forewing veins ICu1 and ICu2 approaching wing margin: 0, strongly diverging (P); 1, parallel to slightly diverging (A).
27. Average number of crossveins in the costal space: 0, approx 20 or more (P); 1, approx 10-15 (A).
28. Costal crossveins present in proximal half of male forewings: 0, yes (P); 1, reduced number or absent (A).
29. Hindwing length relative to forewing: 0, hindwing large -approx 1/3th the length of forewing (P); 1, hindwing smaller - approx 1/4 to 1/5th the length of forewing (A); 2, hindwing very small -approx 1/10th the length of forewing (A).
30. Length of hindwing subcostal vein relative to hindwing: 0, more than or equal to 0.9 (P); 2, less than or equal to 0.85 (A).
31. Hindwing midlength costal projection: 0, absent (P); 1, present (A).

Abdomen

32. Sternum nine of female: 0, cleft (P); 1, entire (A).

Appendix C

Material examined:

LEPTOPHLEBIIDAE: ATALOPHLEBIINAE

***Atalomicria* Harker**

Atalomicria banjdlalama Campbell and Peters: holotype, male imago; paratypes, female imago, male and female nymphs; slide material; Booloumba Creek, Connondale Ranges, QLD, 29 xi 89, coll. I.C. Campbell (MV);

Atalomicria bifasciata Campbell and Peters: holotype, male imago; paratypes, female imago, subimagos, nymphs; slide material; Booloumba Creek, Connondale Ranges, QLD, 5 xii 89, coll. I.C. Campbell (MV);

Atalomicria dalagara Campbell and Peters: holotype, male imago; paratypes, nymphs; slide material; Booloumba Creek, Connondale Ranges, QLD, 29 xi 89, coll. I.C. Campbell (MV).

Atalomicria chessmani Campbell and Peters: holotype, male imago; paratypes, male and female imagos, nymphs; slide material; Ferntree Creek, 10km S of Goongerah, VIC, 18 i 1990, coll. I.C. Campbell (MV);

Atalomicria sexfasciata (Ulmer): holotype, male imago; paratype, female imago; Cedar Creek, QLD, Dr Mjöbergs Swedish Expedition to Australia 1910-1913 (SMNH); slide material; Yuccabine Creek, Kirrama Rd, QLD, 27 ix 87, coll. I.C. Campbell (MV);

Atalomicria uncinata (Ulmer): holotype, male imago; Cedar Creek, QLD, Dr Mjöbergs Swedish Expedition to Australia 1910-1913 (SMNH);

Atalomicria sp. 'AV1' (Dean 1999): nymphs and imagos, NSW, QLD, VIC (MV); nymphs, NSW, VIC (Finlay collection); slide material, QLD (Campbell collection).

***Atalophlebia* Eaton**

Atalophlebia albiterminata Tillyard: nymphs and imagos, reared, VIC (Finlay collection);

Atalophlebia australis (Walker): nymphs and imagos, reared, VIC, NSW, NT, TAS (MV) Finlay collection, Campbell collection); slide material, VIC (MV);

Atalophlebia sp. 'AV2', 'AV4', 'AV5', 'AV7', 'AV9', 'AV13', 'AV15', 'AV21' (Dean 1999) nymphs and imagos, reared, VIC, TAS, NSW (Finlay collection);

Atalophlebia spp.: nymphs and imagos, reared, VIC, NSW, TAS (Finlay collection).

***Austrophlebioides* Campbell and Suter**

Austrophlebioides booloumbi Parnrong and Campbell: holotype, male imago & paratypes, male and female nymphs; Booloumba Creek, Connondale Ranges, QLD, 5 xii 89, coll. I.C. Campbell (MV);

Austrophlebioides marchanti Parnrong and Campbell: holotype, male imago & paratypes, female imago, female and male nymphs; Loch River, Noojee, VIC, i

1995, coll. S. Parnrong (MV); nymphs, imagos, slide material, NSW, VIC (Finlay collection);

Austrophlebioides pusillus (Harker): nymphs, imagos, NSW, VIC (MV); nymphs, imagos, slide material, NSW, VIC (Finlay collection); slide material (Campbell collection);

Austrophlebioides sp. 'AV2' (Dean 1999): nymphs, imagos, NSW, VIC (Finlay collection);

Austrophlebioides spp: nymphs, imagos, VIC (Finlay collection).

***Bibulmena* Dean**

Bibulmena kadjina Dean: holotype, male imago, reared, North Dandalup River, North Dandalup, WA, 01 vi 1984, coll. S. Bunn (MV); paratypes, male and female imago, slide material, Foster Brook, North Dandalup, 1983, coll. S. Bunn (MV); paratype, nymph, slide material, Wungong Brook, Jarrahdale, WA, 2 xii 1981, coll. S. Bunn (MV).

***Garinjuga* Campbell and Suter**

Garinjuga maryannae Campbell and Suter: holotype, male imago & paratypes, subimagos, female and male nymphs; Thredbo River, Summit Rd at entrance to Kosciusko National Park, NSW, 19 x 1995, coll. I.C. Campbell (ANIC); nymphs, imagos, slide material, NSW, VIC (Finlay collection); nymphs, imagos, slide material, NSW (Campbell collection);

Garinjuga sp. 'AV1' (Dean 1999): nymphs, imagos, NSW, TAS, VIC (MV); nymphs, imagos, slide material, NSW, VIC (Finlay collection);

Garinjuga spp.: nymphs, imagos, slide material, NSW, VIC (Finlay collection).

***Jappa* Harker**

Jappa edmundsi Skedros and Polhemus: holotype and paratypes, nymphs, Hutchinson Creek, Cape Tribulation Rd, N of Daintree Landing, 17 viii 1983, coll. D.A. & T.J. Polhemus (ANIC); slide material, QLD (Campbell collection);

Jappa kutera Harker: nymphs, imagos, slide material, NSW, NT, QLD; nymphs, NSW, VIC (Finlay collection); slide material, VIC (Suter collection);

Jappa serrata Skedros and Polhemus: holotype, nymph, Hutchinson Creek, Cape Tribulation Rd, N of Daintree Landing, QLD, 17 viii 1983, coll. D.A. & T.J. Polhemus (ANIC); nymphs, imagos, slide material, QLD (Campbell collection);

Jappa campbelli Bae and Finlay: holotype, Licola, Wellington R., 3km upstream from Alpine National Pk entrance, VIC, 146° 37' E, 37° 34' S, 6 Jan 2002 (emerged 13 Jan 2002); paratypes, same collection data, 2 male (T-17940, 17941) and 2 female (T-17942, 17943) imagos (reared, with larval exuviae), 10 larvae, 6 male (T-17944-17949) and 4 female (T-17950-17953) larvae (MV), coll. K.J. Finlay, Y.J. Bae & N. Ainsworth (MV);

Jappa sp. 'AV3' (Dean 1999): nymphs, imagos, VIC (Finlay collection);

Jappa spp.: nymphs, imagos, VIC (Campbell collection); slide material, QLD (Campbell collection).

***Kalbaybaria* Campbell**

Kalbaybaria doantrangae Campbell: holotype, male imago; paratypes, male and female imago, nymphs; slide material, Romeo Creek, near Helenvale, QLD, 5 v 1988, coll. I.C. Campbell (ANIC); slide material, Palmer River, QLD, 20 vi 1971, coll. E.F. Riek (ANIC); slide material, Millstream Falls, W of Ravenshoe, QLD, 25 vi 1971, coll. E.F. Riek (ANIC)

Kaninga Dean

Kaninga gwabbalitcha Dean: nymphs, slide material, WA (MV);

Genus Q sp. 'AV1' (Dean 1999): 'holotype', male imago; 'paratypes', male imagos, Carey Brook, Staircase Road, WA, 15 vii 1989 coll. I. Grown (MV); nymphs, subimagos, WA (MV).

Kirrara Harker

Kirrara procera Harker: nymphs, imagos, slide material, VIC, NSW (MV); nymphs, imagos, slide material, VIC (Finlay collection);

Kirrara sp. 'AV1' (Dean 1999): nymphs, slide material, QLD (Campbell collection).

Loamaggalangta Dean, Forteath & Osborn

Loamaggalangta pedderensis Dean, Forteath & Osborn: holotype, male imago; paratypes, male imagos, subimagos; Lake Pedder, Trappes Bay, TAS, ii 1997, coll. N. Forteath (ANIC); nymphs, slide material, TAS (MV);

Genus K sp. 'AV1' & 'AV2' (Dean 1999): nymphs, NSW, VIC, QLD (MV); nymphs, TAS (Finlay collection).

Neboissophlebia Dean

Neboissophlebia hamulata Dean: holotype, male imago; paratypes, male imago, female imagos, subimagos; slide material, Tarago River, 7km W Neerim, VIC, 1 iii 1972, coll. A. Neboiss (MV); nymphs, imagos, NSW, VIC (MV); nymphs, imagos, NSW, VIC (Finlay collection);

Neboissophlebia occidentalis Dean: paratypes, male imagos, female imagos, slide material, Harvey River, 15km E Harvey, WA, 21 xi 1978, coll. A. Neboiss (MV).

Nousia Navás*, subgenus *Nousia Navás

Nousia delicata Navás: male imagos, Santiago Province, CHILE, xi 1972, coll. M.L. Pescador & G. Barria; nymphs, Río Caren, Hacienda Illapel, Coquimbo Province, CHILE, 17 xi 1972, coll. M.L. Pescador (FAMU); nymphs, Río Caren, Hacienda Illapel, Coquimbo Province, CHILE, 18 xi 1972, coll. M.L. Pescador & G. Barria (FAMU);

Nousia grandis (Demoulin): nymphs; female imago reared, male subimago reared; El Coigual, Curico Province, CHILE, i 1964, coll. L. Peña (FAMU);

Nousia minor (Demoulin): male imago, Valdivia, CHILE, 19 x 1957, coll. J. Illies; nymphs, Río Piquiquen, El Manzano, 35km W Angol, Malleco Province, CHILE, xii 1972, coll. M.L. Pescador (FAMU).

Nousia Navás*, subgenus *Australonousia Campbell and Suter

Nousia (Australonousia) fusca (Ulmer) comb. nov.; *Atalophlebia fusca* Ulmer: holotype, Cedar Creek, QLD, III 1910-1913, male imago, paralectotypes, same

collection data male and female subimago, coll. Mjöberg Expedition (SMNH); *Atalophlebia brunnea* (Tillyard): holotype, South Esk River, Clarendon, TAS, 9 III 1933, female imago; paratype, same collection data, male imago, coll by E. Scott, R.J. Tillyard collection (NHM);

Nousia (Australonousia) fuscula (Tillyard); *Atalophlebia fuscula* (Tillyard), River Shannon, TAS, male imago, 27 I 1933, coll. R.J. Tillyard (NHM).

Nousia (Australonousia) nigeli sp. nov. (Finlay, unpublished data): holotype, Taggerty River, Lady Talbot Drive, outside Marysville, VIC, 17 X 1988, 145°46'28" 37°30'20", male imago; paratypes, same collection data, 17 X 1988, male imago Donnelly Creek, Donnelly Weir Rd, VIC, 6 IV 1997, 145°32'03" 37°37'30", female imago, coll. K.J. Finlay (MV).

***Nyungara* Dean**

Nyungara bunni Dean: holotype, male imago reared; paratype, nymph; slide material, Foster Brook, North Dandalup, WA, 22 ix 1983, coll. S. Bunn (MV); paratypes, male imago, female imago, nymphs, slide material, Waterfall Gully, Jarrahdale, WA, 1981-1982, coll. S. Bunn (MV); imagos, nymphs, slide material, WA (MV)

***Thraulophlebia* Demoulin**

Thraulophlebia lucida (Ulmer) comb. nov.: *Atalophlebia lucida* Ulmer: holotype, Cedar Creek, QLD, III 1910-1913, coll. Mjöberg's expedition, male imago; paratype, same collection data, male imago, head and genitalia detached (SMNH); *Nousia pilosa* Suter: holotype, Wannon River, Grampians, VIC, 25 XI 1997, male imago; paratypes, same collection data, male imagos, female and male nymphs; Hitchcock Drain, SA, 25 XI 1997, male imago, male nymph, coll. D.N and P.J. Suter (MV);

Thraulophlebia inconspicua (Eaton) comb. nov.: Brownhill Creek, SA, 3 III 1976, 150m, 138°38' 34°59', male and female imago, coll. unknown; Bull Creek, "The Cliff", SA, 31 X 1989, nymphs, Deep Creek Tributary, Castambul, SA, 04 III 1977, 138°45' 34°52', nymphs, coll. J.E Bishop and A. Wells; Finnis River, "Riverdale" & Meadows Creek, Fingerboard corner, SA, 31 X 1989, nymphs, coll. P. Suter and S. Sheerlock; North East River, near Carnarvan, Kangaroo Island, SA, 19 XI 1977, 136°59' 35°56', male imagos, coll. J.E. Bishop; North Pava River, SA, 19 VIII 1983, nymphs, coll. P. Suter; North Pava River, Tanunda, SA, 21 X 1991, 136°59' 35°56', nymphs, coll. P. Waller; Rocky River, Flinders Chase National Park, Kangaroo Island SA, 13 XII 1976 & 18 XII 1976, , 136°44' 35°56', nymphs, coll. Bill Williams; Scott Creek, SA, 9 XI 1994, nymphs, coll. P. Goonan & C. Madden; South West River, Brigadoon, Kangaroo Island, SA, 19 XI 1977, 136°50' 35°52', male imago, coll. J.E. Bishop; Spring Creek, SA, 11 X 1995, nymphs, coll. Monitoring River Health Initiative; Stunsail Broom River, Kangaroo Island, SA, 12 XII 1976, 137°00' 35°59', nymphs, coll. Bill Williams; Sturt River, Bedford Park, SA, 27 XI 1976, 138°33' 35°02',

nymphs, coll. J.E. Bishop; Sturt River, upstream Minno Creek, SA, 26 X 1994, 138°38' 35°02', nymphs, coll. Monitoring River Health Initiative; Sturt River, Coramandel Valley SA, 29 IV 1976, 138°57' 35°03', male and female imago, coll. P. Suter; Tookayerta Creek, 22 X 1984, nymphs, coll. P. Suter; Unnamed Creek, Parawa Rd, near Yankalilla, 2 XI 1978, 138°21' 35°28', coll. J.E. Bishop and A. Wells (Suter collection);

Thraulophlebia parva (Harker) comb. nov.: *Atalophlebia parva*. Harker: holotype, Serpentine River, Point Lookout, NSW, X 1948, male imago, coll. J. Harker; paratypes, same collection data, male imago, subimago and nymph, coll. J. Harker (AM).

***Thraululus* Eaton**

Thraululus sp. 'A' sp. nov. (informal description, Grant 1985): 'holotype', male imago, Drysdale River, WA, viii 1975, coll. I.F. Common and M.D. Upton (ANIC); 'paratypes', male imagos, Nourlangie Creek, 6km W Cahill, NT, 18 xi 1972, coll. J.C. Cardale (ANIC); 'paratypes', male subimagos, Cooper Creek, 19km SE of Mt Borrdaile, NT, vi 1973, coll. J.C. Cardale (ANIC);

Thraululus sp. 'AV1' 'AV2' 'AV3' (Dean 1999): imagos, nymphs, NT, QLD (MV);

Thraululus spp.: nymphs, QLD (DPIQ).

***Tillyardophlebia* Dean**

Tillyardophlebia alpina Dean: imagos, nymphs, NSW (MV);

Tillyardophlebia rufosa Dean: holotype, male imago; paratypes, male and female imagos, nymphs; slide material, Badger Creek downstream weir, VIC, 23 ii 1984, coll. J. Dean (MV); imagos, nymphs, NSW, VIC (MV); imagos, nymphs, NSW, VIC (Finlay collection);

Tillyardophlebia spp.: imagos, nymphs, NSW, VIC (Finlay collection).

***Ulmerophlebia* Demoulin**

Ulmerophlebia pippina Suter: nymphs, subimago, VIC (Finlay collection);

Ulmerophlebia sp. 'AV2' (Dean 1999): nymphs, imagos, NSW, VIC (Finlay collection); nymphs, imagos, NSW, VIC (Finlay collection);

Ulmerophlebia sp. 'AV6' -*mjöbergi*? (Dean 1999): nymphs, imagos, QLD, (MV)

Ulmerophlebia spp.: nymphs, imagos, VIC (Finlay collection).

'New Genus A' gen. nov.

'New Genus A' *wiltkorrhingae* comb. nov.; *Nousia* (*Australonousia*) *wiltkorrhingae* Finlay: holotype, male imago, Cement Creek, Mt Donna Buang Rd, outside Warburton, VIC, 05 III 1998, 145°42'20" 37 °42'48", coll. K.J. Finlay (MV).

Paratypes; male and female imagos, subimagos and nymphs, same collection data, 1 XII 1976, EPH 1587, EPH 1588, EPH 1602; 23 XI 1978, EPH 1589, EPH 1590, EPH 1591, EPH 1592, EPH 1594, EPH 1596, EPH 1597, EPH 1598, EPH 1599; 3 III 1980, EPH 1593, coll. J. Dean (MV); 05 III 1998, 29 XI 1998, 23 I 1999, , 20 III 1999, coll. K. Finlay (MV).

'New Genus B' gen. nov.

'New Genus B' *kala* comb. nov., *Atalophlebia kala* (Harker): holotype, Lake Albina, Mount Kosciusko, NSW, 2 II 1929, male imago, coll. R.J. Tillyard (NHM);

'New Genus B' *adamus* comb. nov., holotype, Frying Pan Raceline tributary, Telmark St, Falls Creek, VIC, 5 II 1999, 1560m, 147°16'50" 36°52'00", coll. K.J. Finlay; paratypes, same collection data, male imagos, nymphs; McKay Creek tributary (waterfall), Mt McKay, Alpine National Park, VIC, 5 II 1999, 1700m, 147°15'20" 36°52'19", female imago; Tanjil River east branch headwaters, Mt Baw Baw Alpine Village, VIC, 16 II 1999, 1440m, 146°15'45" 36°50'25", male imago; coll. K.J. Finlay (MV).

LEPTOPHLEBIIDAE: LEPTOPHLEBIINAE

Gillesia hindustanica (Gillies): imagos, Assam, INDIA (FAMU);

Leptophlebia cupida (Say): nymphs, Indiana, USA (Bae collection);

Leptophlebia sp.: nymphs, Missouri, USA (Bae collection);

Paraleptophlebia bicornuta (McDonnough): nymphs, Idaho, USA (Bae collection);

Paraleptophlebia chocolata Imanishi: nymphs, imago, reared, Kyonggi-do, KOREA (Bae collection);

Paraleptophlebia packi (Needham): nymph, imago, reared, Utah, USA (Bae collection);

Paraleptophlebia sp.: nymphs, Wyoming, USA (ANIC).

EPHEMEROIDEA

Ephemera danica Müller: nymphs, near Silkeborg, DENMARK (Campbell collection);

Ephemera simulans Walker: nymphs, Wyoming, USA (ANIC);

Euthyplocia spp.: nymphs, San Martin Province, PERU (ANIC);

Ichthybotus hudsoni McLachlan: nymphs, Taupo, NEW ZEALAND (ANIC);

Povilla adusta Navás: nymphs, Lake Kivu, BELGIAN CONGO (ANIC);

Rhoenanthopsis spp.: nymphs, Chiangmai Province, THAILAND (ANIC).

Appendix D

Data matrix of Pescador and Peters (1980a)

Outgroup	00000	00000	00000	00000	000
<i>Hapsiphlebia</i>	00011	-----	-----	-----	---
<i>Penaphlebia</i>	11100	01100	-----	-----	---
<i>Atalonella</i>	11100	10011	00010	-----	---
<i>Dactyophlebia</i>	11100	00011	11101	10100	001
<i>Meridialaris</i>	11100	00011	11101	11011	110