PHYLOGENETIC RELATIONSHIPS AND ZOOGEOGRAPHY OF COOL-ADAPTED LEPTOPHLEBIIDAE (EPHEMEROPTERA) IN SOUTHERN SOUTH AMERICA

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ABSTRACT

Twelve cool-adapted leptophlebiid genera are known to occur in southern South America. Analysis of the external morphology of both adults and nymphs indicated that cool-adapted South American leptophlebiids represent five distinct phyletic lineages, namely: the *Hapsiphlebia*, *Penaphlebia*, *Atalonella*, New Genus A and *Meridialaris* lineages. All of these, except the *Penaphlebia* lineage, presently include some genera from other areas of the Southern Hemisphere. Phylogenetic evidence indicates that cool-adapted South American Leptophlebiidae are related to confamilials occurring in the mountain waters of Southeastern Australia (including Tasmania), New Zealand, New Caledonia, Madagascar and South Africa. This study revealed that most genera from South America are more closely related to genera from Australia than to those occurring in the other continents.

INTRODUCTION

The Leptophlebiidae comprise one of the largest and most distinctive families of mayflies. The family is cosmopolitan in distribution and reaches its maximum diversity in the Southern Hemisphere.

The taxonomy of Leptophlebiidae is inadequately known in many parts of the world, particularly in southern South America. This area has been geographically defined by Hubbard and Peters (1977) as south of the Tropic of Capricorn, a section of Continental South America comprising two major biogeographic divisions; viz., a cool-adapted group and warm-adapted group, although these divisions are

not confined to southern South America. The cool-adapted group, which Illies (1969) discussed and referred to as the oligostenothermal mountain fauna, inhabits the Andes, Plains of Patagonia, Tierra del Fuego, and to a lesser extent the southern coastal mountains of Brazil. Cool mountain waters and regular periods of freezing weather prevail throughout the year. The warm-adapted group, referred to as the polystenothermal lowland fauna by Illies (1969), occupies all tropical and other areas where a stable high water temperature is maintained.

Prior to this investigation, Peters and Edmunds (1972) reported six cool-adapted leptophlebiid genera occurring in southern South America, three of which were newly established. We discovered six additional new genera making a total of twelve known to occur in this area. Pending publication of the descriptions, these six new genera are herein designated as Genera A-F.

PHYLOGENETIC RELATIONSHIPS

Detailed analysis of the external morphology of both adults and nymphs indicated that the cool-adapted South America leptophlebiids are related to several genera in the mountain streams of southeastern Australia (including Tasmania), New Caledonia, New Zealand, Madagascar and Africa. Representative genera from these areas related with the cool-adapted leptophlebiid fauna of South America, except for New Caledonia, are included in the present discussion (Table 2). One of us (WLP) is presently working on the systematics and zoogeography of the New Caledonia leptophlebiids and preliminary data show some genera that share common characters with the cool-adapted Leptophlebiidae of South America.

Figure 1 shows the proposed phylogeny of the cool-adapted leptophlebiid genera of southern South America. The sequence of branching is determined by shared possession of derived character states. The common derivation of character states used to interpret phylogeny is based on the concept that ancestral character states are generally widespread throughout the family and often throughout the order. Although the holomorphology of both nymphs and adults, when the latter were available, was analyzed, the nymphs were found to have more morphological characters applicable for phyletic and taxonomic analysis. Hence the phylogenetic reconstruction was based primarily on nymphal characters with a few complementing adult characters. Table 1 together with Figure 1 show the different phyletic lineages and corresponding character states used to interpret the phylogeny of the cool-adapted South American leptophlebiids.

The cool-adapted Leptophlebiidae of South America represent five phyletic lineages, namely: the *Hapsiphlebia*, *Penaphlebia*, *Atalonella*, New Genus A, and *Meridialaris* lineages (Fig. 1). All

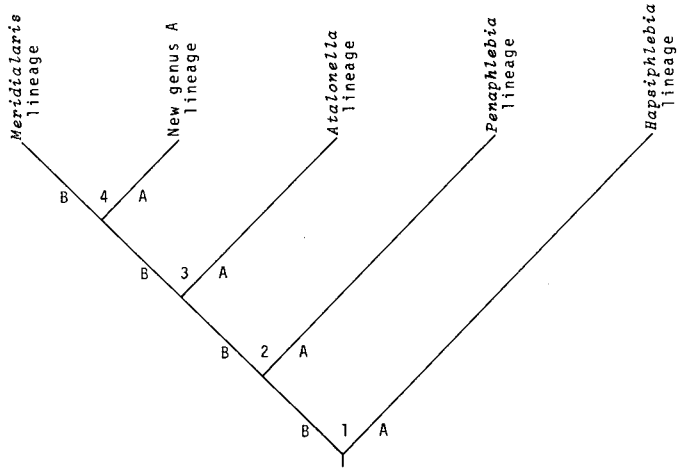


Figure 1. Phylogenetic diagram of cool-adapted Leptophlebiidae of Southern South America.

these lineages except the *Penaphlebia* lineage presently include some genera from other areas of the Southern Hemisphere (Table 2). The different lineages are arbitrarily named as such, both for convenience and since the emphasis of the present study is South American Leptophlebiidae. Therefore, it is most appropriate to simply use generic names of some of the better known leptophlebiids of southern South America.

The *Hapsiphlebia* lineage includes *Hapsiphlebia, Atalophlebia, Atalomicria, Jappa, Zephlebia cruentata* and *Aprionyx* (Table 2). Towns and Peters (personal communication) are presently revising the genus *Zephlebia* and noted that *Zephlebia cruentata* and the subgenus *Neozephlebia* not only represent two different genera but two different lineages as well. Their data and ours suggest that *Z. cruentata* and the subgenus *Neozephlebia* belong to the *Hapsiphlebia* and *Atalonella* lineages respectively. The nymphs of the *Hapsiphlevia* lineage have highly derived denticulation of incisors of the right mandible (Fig. 8) and prominent lateral hairs on the abdominal terga. Other characters differentiating this lineage from the other lineages retained the primitive states (Table 1).

The *Penaphlebia* lineage presently includes *Massartella* and *Penaphlebia* although, a few undescribed genera from Australia available to us belong to this lineage. The nymphs have derived pectinate setae on the maxillary palpi and tassel-like setae on the abdominal terga (Table 1). A phenocline ranging from almost straight outer lateral margins of the mandibles in the *Hapsiphlebia* lineage

Table 1. Character states of Figure 1. D, derived; P, primitive.

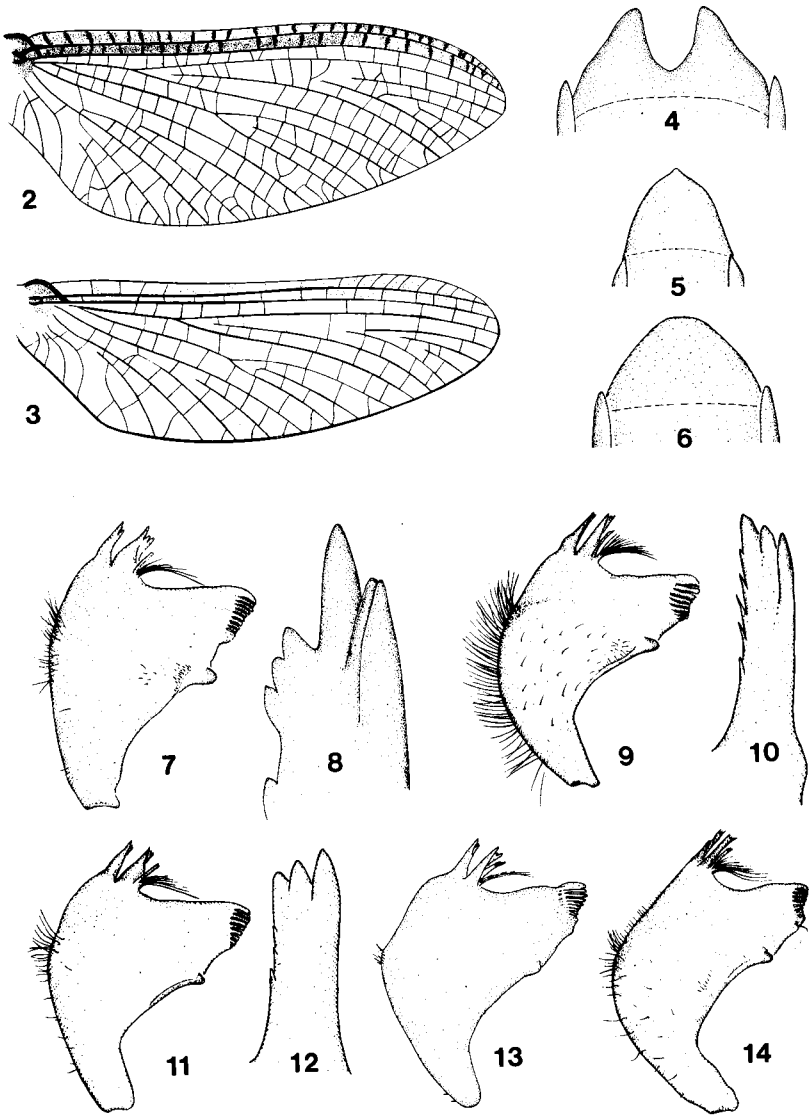
Furcation 1:	A	B
Clypeus	(P) wider than labrum (Fig. 15).	(D) narrower than labrum (Fig. 16-22).
Labrum: lateral margins	(P) subparallel (Fig. 15).	(D) rounded to angular (Fig. 16-22).
Mandible: outer margin	(P) almost straight (Fig. 7).	(D) rounded to angular (Fig. 9-14).
right outer incisor	(D) with broad subapical denticles (Fig. 8).	(P) smooth or spinose (Fig. 10, 12).
Abdominal terga: lateral margins	(D) with prominent setae.	(P) bare or with minute setae.
Furcation 2:	**A**	**B**
Clypeus	(P) subequal to slightly narrower than labrum (Fig. 16).	(D) narrower than labrum (Fig. 17-22).
Maxillary palpi: inner margin of 2	(D) with pectinate setae.	(P) with non-pectinate setae.
Abdominal terga: posterior margins	(D) with prominent spines and long tassel-like setae.	(P) with spines and scattered fine hairs.
Fore wings: vein MP_2	(P) strongly recurved (Fig. 2).	(D) moderately recurved (Fig. 3).
costal cross veins	(P) more than 25 (Fig. 2).	(D) less than 25 (Fig. 3).
Furcation 3:	**A**	**B**
Clypeus: lateral margins	(P) parallel (Fig. 17).	(D) divergent (Fig. 19,20,22).
width/labrum width	(P) less than 4/5 (Fig. 17).	(D) more than 4/5 (Fig. 19,20,22).
Labrum: lateral margins	(P) smoothly curved (Fig. 17).	(D) abruptly to angularly curved (Fig. 19,20,22).
anteromedian emargination	(D) broad, with prominent denticles (Fig. 17-18).	(P) narrow (but may be cleft or hooded), denticles reduced (Fig. 19-23).
Mandible: outer margin	(P) smoothly curved (Fig. 11).	(D) angularly curved (Fig. 13-14).
Ninth sternum of ♀	(P) deeply cleft.	(D) entire or shallowly concave.
Furcation 4:	**A**	**B**
Labrum: length/width	(P) 2/3-3/4 (Fig. 19).	(D) 1/3-1/2 (Fig. 20,22).
anteromedian emargination	(D) cleft, V-shaped dorsally and ventrally (Fig. 19).	(P) shallow U-shaped or deep V-shaped ventrally (Fig. 21-23).
Mandible: outer margin	(P) slightly angular (Fig. 13).	(D) distinctly angular (Fig. 14).
Maxilla: galea-lacinia	(P) narrow at apex (Fig. 24).	(D) broad at apex (Fig. 25).
subapical pectinate setae	(P) equal to or less than 15 (Fig. 24).	(D) more than 15 (Fig. 25).
Labium: submentum (postmentum)	(P) with thick lateral setae (Fig. 28).	(D) lateral margins bare (Fig. 29).
Body of nymph	(D) robust.	(P) flattened.

Table 2. Phyletic lineages representing the cool-adapted Leptophlebiidae of Southern South America and selected related genera from other areas of the Southern Hemisphere.

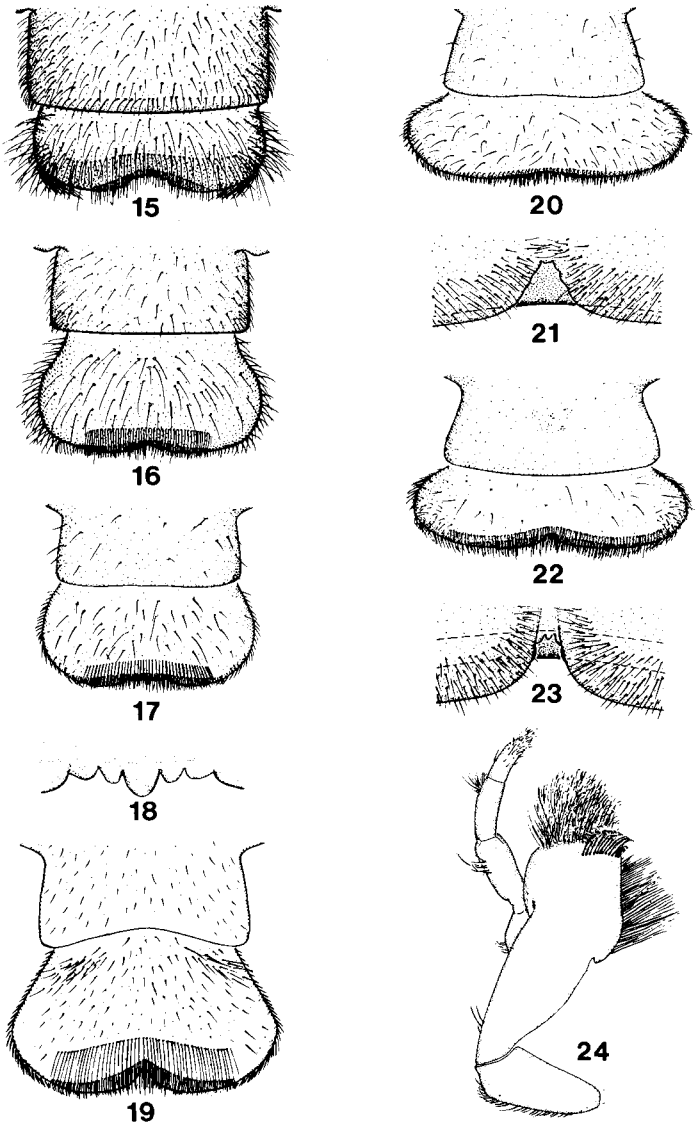
Lineage	Genera Included	Continent
1. *Hapsiphlebia*	*Hapsiphlebia*	South America
	Atalophlebia, Atalomicria	Australia
	Jappa, Ulmerophlebia	"
	"Zephlebia" cruentata	New Zealand
	Aprionyx	Africa
2. *Penaphlebia*	*Penaphlebia, Massartella*	South America
3. *Atalonella*	*Atalonella*	South America, Australia
	New genus C, New genus D	South America
	Zephlebia (Neozephlebia)	New Zealand
4. New genus A	New genus A, New genus B	South America
	"Atalophlebioides" sepia	New Zealand
5. *Meridialaris*	*Meridialaris, Massartellopsis*, New genus E	South America " "
	Atalophlebioides s.s.	New Zealand
	"Atalophlebioides"	Australia
	Petersophlebia	Madagascar

(Fig. 7), through the intermediate in the *Penaphlebia* (Fig. 9), and *Atalonella* lineages (Fig. 11), to the angularly curved lateral margins in the Genus A (Fig. 13) and *Meridialaris* lineages (Fig. 14) suggest that the straight outer margin represents the primitive character state. A similar phenoclinal pattern is observed in the clypeus as apical enlargement gradually occurs from the *Atalonella* lineage (Fig. 17) reaching its maximum in the *Meridialaris* lineage (Figs. 20 and 22) with the Genus A lineage (Fig. 19) as an intermediate stage.

The *Atalonella* lineage includes *Atalonella*, two new genera (Genus C and Genus D) and *Zephlebia* (*Neozephlebia*) (Table 2). Although nymphs of both Genus C and Genus D are still unknown, the deeply cleft ninth sternum of female imagos (Fig. 4) suggest their inclusion in this lineage. Except for the derived broad anteromedian emargination with prominent denticles (Fig. 17-18), nymphal and adult characters differentiating the *Atalonella* lineage from its



Figures 2-3, fore wing. Figures 4-6, ninth sternum of ♀ imago. Figures 7-14, left mandible and detail of outer incisor of right mandible. 2, 9, 10) *Penaphlebia*; 3, 4, 11, 12) *Atalonella*; 5, 14) *Meridialaris*; 6) *Massartellopsis*; 7, 8) *Hapsiphlebia*; 13) New genus A.



Figures 15-23, clypeus and labrum with detail of anteromedian emargination (21, 23, ventral views): 15) *Hapsiphlebia*; 16) *Penaphlebia*; 17-18) *Atalonella*; 19) New genus A; 20-21) *Meridialaris*; 22-23) *Massartellopsis*. Figure 24, maxilla of New genus A.

sister group retained the primitive states (Table 1). Progressive marginal curvature of the labrum in the five lineages forms a phenocline ranging from subparallel in the *Hapsiphlebia* lineage (Fig. 15) through rounded in the *Penaphlebia* (Fig. 16) and *Atalonella* (Fig. 17) lineages, to angular in the Genus A (Fig. 19) and *Meridialaris* (Figs. 20 and 22) lineages, suggesting that the character state in the *Meridialaris* is highly derived. A similar phenocline can be seen in the glossae: which are curved over ventrally in *Hapsiphlebia* and *Penaphlebia* (Figs. 26 and 27), knobbed in Genus A (Fig. 28) and straight in *Meridialaris* (Fig. 29).

The Genus A lineage includes two new genera (Genus A and Genus B) and the "*Atalophlebioides sepia* group" from New Zealand. Towns and Peters (in press) found two new genera that represent what Pescador (1976) referred to as "*Atalophlebioides sepia* group". Such findings complement Pescador's argument that the *Atalophlebioides* is polyphyletic. In this lineage, the nymphs have a short and chunky body, a large labrum (Fig. 19) with heavily sclerotized anterior margin and deep, V-shaped anteromedian emargination, and an apically narrow galea-lacinia of the maxillae (Fig. 24). Other characters that may have split this lineage and its sister group from a common ancestor are shown in Table 1. Genus A and Genus B are known only from nymphs.

The *Meridialaris* lineage includes *Meridialaris*, *Massartellopsis*, new Genus E, *Atalophlebioides* and the Australian "*Atalophlebioides*". Compared to the other lineages, the nymphs of the *Meridialaris* lineage possess the more derived, apically divergent clypeus (Figs. 20 and 22), short labrum (Figs. 20 and 22), distinctly angular mandibles (Fig. 14), apically broad galea-lacinia of maxillae (Fig. 25), and bare submentum (Fig. 29). Similarly, female adults have a derived ninth sternum (Figs. 5 and 6). Based on the direction of the phenocline formed by the clypeus, labrum and mandibles, the *Meridialaris* lineage appears to be the most derived among the southern South American leptophlebiid lineages.

There is one new genus (Genus F) that we consider a phyletic enigma. Pescador (1976) earlier placed it in the *Atalophlebioides* lineage which had almost the same generic composition as the *Meridialaris* lineage in this paper. However, there are also a few derived nymphal characters to include this new genus in the *Zephlebia* grouping of Towns and Peters (in press). We intend to study the morphology of the eggs of all genera representing the above phyletic lineages to determine if the egg data will offer a more concrete phyletic placement of this enigmatic genus.

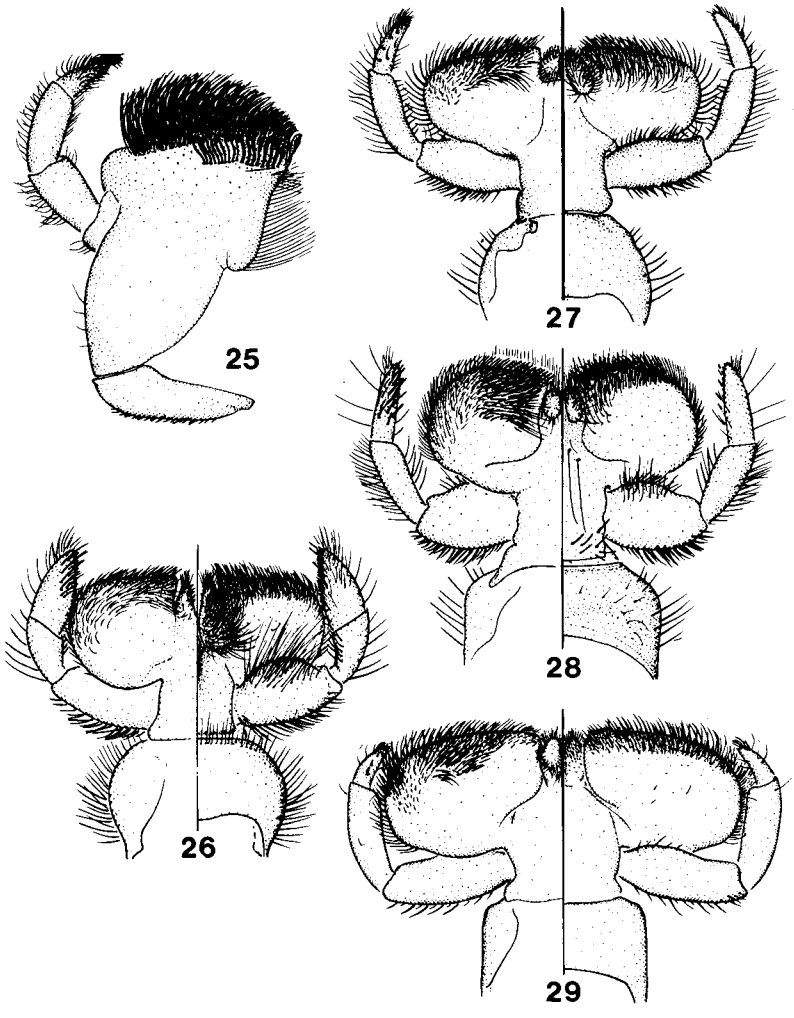


Figure 25, maxilla of *Meridialaris*. Figures 26-29, labium (dorsum on left, venter on right); 26) *Hapsiphlebia*; 27) *Penaphlebia*; 28) New genus A; 29) *Meridialaris*.

ZOOGEOGRAPHY

Phylogenetic evidence indicates that the cool-adapted South American Leptophlebiidae are closely related to confamilials occurring in the mountain waters of southeastern Australia (including Tasmania), New Zealand, New Caledonia, Madagascar and South Africa. South America and Australia still share congeneric leptophlebiid fauna, for example the genus *Atalonella*. Since mayflies have a conservative history of dispersal (Edmunds 1972), a more plausible explanation for such propinquity of a good number of extant Southern Hemisphere leptophlebiid genera leads to the argument for ancient connections or close proximity of these continents that made faunal dispersal possible. The reality of ancient Gondwanaland or a southern landmass can hardly be questioned anymore in light of overwhelming geological (Axelrod 1972, Crawford 1971, Griffiths and Varne 1972, Markl 1974, Raven and Axelrod 1972, Smith and Hallam 1970) and biological (Cracraft 1972, 1973, 1974, 1975; Edmunds 1972, 1975; Jardine and McKenzie 1972, Keast 1972, 1973; Raven and Axelrod 1972, 1974, 1975; Schlinger 1974, and Tsui and Peters 1975) data.

The five phyletic lineages represented by the cool-adapted Leptophlebiidae of southern South America includes genera from other Southern Hemisphere continents except for the *Penaphlebia* lineage (Table 2). The *Hapsiphlebia* lineage presently includes one genus from Chile, four from Australia, and one each from New Zealand and South Africa (Table 2). Genera from South America and Australia share the greatest number of shared, derived characters. For example, *Hapsiphlebia*, *Jappa* and *Ulmerophlebia* share not only morphological but to a great extent behavioral and ecological similarities. Nymphs of *Hapsiphlebia* are "semi-burrowers", partially burrowing in silt and sand. Such behavior is probably a precursor to the evolution of the burrowers as in *Jappa* and *Ulmerophlebia*. *Jappa* has derived long frontal tusks that undoubtedly improved the nymphs' burrowing efficiency.

The *Penaphlebia* lineage is presently confined to South America (Table 2), although preliminary study of some undescribed genera from Australia available to us suggests their close affinity to *Massartella* and *Penaphlebia*.

The *Atalonella* lineage presently includes genera from South America, Australia and New Zealand (Table 2). *Atalonella* occurs in South America and Australia while its sister group *Zephlebia* (*Neozephlebia*) is found in New Zealand. Two new genera (Genus C and Genus D) from South America are only known from adult specimens but available data suggest their inclusion in this lineage.

The Genus A lineage which presently includes two new genera from South America, and New Zealand, is the only cool-adapted southern South American leptophlebiid lineage not represented in Australia.

More collections and complete examination of specimens from this area available to us may give a more accurate assessment of this lineage's non-Australian representation. Genus A and Genus B from South America are only known from nymphs but they share a good number of derived characters with the "*Atalophlebioides sepia* group" from New Zealand.

The *Meridialaris* lineage presently includes three genera from South America (one new genus), and one each from Australia, New Zealand and Madagascar (Table 2). The genus *Atalophlebioides* is presently distributed in Australia and New Zealand although the Australian species were found to have more characters in common (viz. imaginal claws, ninth sternum of female imagos, nymphal clypeus and labrum) with *Meridialaris* and *Massartellopsis* than with the genus from New Zealand. Pescador (1976) indicated the Australian "*Atalophlebioides*" as a sister group of *Massartellopsis* and *Meridialaris*. Towns and Peters (1978) recently reported *Atalophlebioides*, a monotypic genus endemic to New Zealand to be the true *Atalophlebioides* and the Australian "*Atalophlebioides*" to be a different and undescribed genus. Available but limited data suggest the inclusion of *Petersophlebia* from Madagascar in the *Meridialaris* lineage, although further study is needed to ascertain its phyletic placement.

In summary, the cool-adapted leptophlebiid fauna of southern South America is related to a number of genera occurring in other areas of the Southern Hemisphere. We found most genera from South America are most closely related to genera from Australia, followed by genera from New Zealand, and Africa and Madagascar in that order. Phyletic analysis of New Caledonia Leptophlebiidae however, is yet to be completed. As mentioned earlier, such close affinities of the fauna of these areas is best explained by the presumably ancient connections or close proximity of these continents that may have facilitated faunal dispersal. Based on the degree of phylogenetic relationships of the leptophlebiid fauna of these continents, the suggested sequence of the break-up of Gondwanaland is as folows: Africa along with Madagascar, and possibly India first, followed by New Zealand with New Caledonia, and finally South America and Australia broke away from Antarctica. Inadequate fossil records make it difficult to establish the time sequence of the break-up. Geological data however, indicate the same sequential pattern of continental separation including the same approximate time of separation (see references given above).

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RESUME

Il y a douze genres de leptophlébiidés s'adaptant au froid en Amérique du Sud méridionale. L'analyse de la morphologie externe des adultes et des nymphes indique que ces leptophlébiidés représentent cinq arbres phylétiques distincts, à savoir: les familles *Hapsiphlebia*, *Penaphlebia*, *Atalonella*, le nouveau genre A et *Meridialaris*. Tous à l'exception de la famille *Penaphlebia* englobent présentement des genres provenant de régions situées en dehors de l'hémisphère sud. Les données phylogénetiques indiquent que les leptophlébiidés d'Amérique du Sud qui s'adaptent au temps froid ont des liens de parenté avec des espèces qui se rencontrent dans les eaux des montagnes d'Australie du sud-est (y compris la Tasmanie), de Nouvelle Zélande, de Nouvelle Calédonie, de Madagascar et d'Afrique du Sud. L'étude a révélé que la plupart des genres provenant d'Amérique du Sud sont plus étroitement apparentés à ceux d'Australie qu'à ceux d'autres continents.

ZUSSAMENFASSUNG

Im südlichen Sudamerika kennt man zwölf an Kälte gewöhnte Leptophlebiiden Gattungen. Eine Analyse der externen Morpholgie, sowohl von Nymphen als auch voll entwickelten Tieren ergab, daß kältegewohnte, südamerikanische Leptophlebiiden fünf verschiedene phyletische Stämme repräsentieren, nämlich: *Hapsiphlebia, Penaphlebia*, *Atalonella*, Neue Gattung A und *Meridialaris* Stämme. Alle diese, außer dem *Penaphlebia* Stamm, umfassen zur Zeit einige Gattungen von anderen Gebieten der südlichen Hemisphäre. Phylogenetisches Beweismaterial zeigt an, daß kältegewohnte, südamerikanische Leptophlebiiden verwandt sind mit Familienmitgliedern, die in den Gebirgsgewässern Sud-Ostaustraliens (Tasmanien eingeschlossen), Neuseelands, Neukaledoniens, Madagaskars und Südafrikas vorkommen. Die vorliegende Arbeit ergab, daß die meisten Gattungen Südamerikas näher verwandt sind mit Gattungen von Australien, als mit solchen, die in andern Kontinenten auftreten.

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