

PHYLOGENETIC RELATIONSHIPS OF THE LEPTOPHLEBIIDAE OF NEW ZEALAND
(EPHEMEROPTERA)

D.R. Towns* and William L. Peters

Laboratory of Aquatic Entomology
Florida A&M University
Tallahassee, Florida 32307 USA

ABSTRACT

The leptophlebiid mayfly fauna of New Zealand at present consists of three named genera, of which two are clearly polyphyletic. Analysis of these elements and addition of undescribed genera indicate the presence of at least 14 genera. The genera can be divided into five lineages which exhibit varying degrees of radiation within New Zealand and which show evolutionary progression in a number of character states. Four genera appear to be most closely related to genera in New Caledonia, two to generic groups in Chile, and the remainder to other genera in New Zealand, except for one genus for which the nearest known relatives are in New Guinea.

INTRODUCTION

The Leptophlebiidae are the largest mayfly family in New Zealand and commonly dominate the fauna of small, undisturbed stony streams and rivers. Despite this, the family is poorly known taxonomically and the phylogenetic relationships of its elements remain unclear. The discussion of the phylogeny of the Gondwanian Leptophlebiidae by Tsui and Peters (1975) included New Zealand representatives, but the poorly defined limits of these genera

* Department of Zoology, University of Adelaide, G.P.O. Box 498, Adelaide, South Australia 5001, Australia

hampered an accurate determination of their phylogenetic relationships. However, Tsui and Peters (1975) did recognize the polyphyletic nature of some New Zealand genera.

The following account presents the results of a preliminary investigation of the phylogeny of the leptophlebiids of New Zealand and discusses the relationships and possible origins of elements of the fauna. A list of some generic groups with broad austral distributions is given in Pescador and Peters (1979). Only those genera with close relationships to the New Zealand fauna are mentioned here. A series of papers revising the group are being published or are in press (Towns and Peters 1978, 1979a, b). Since none of the names of new genera we have established have appeared in print, species groups will be discussed here either in the genera to which they have been traditionally assigned, or, in the case of undescribed genera numbered as Genus I, II, etc.

THE FAUNA

To date, three New Zealand leptophlebiid genera have been recognized: *Deleatidium* Eaton, *Atalophlebioides* Phillips and *Zephlebia* Penniket. All three genera are endemic. Species previously placed in *Atalophlebioides* from Chile and Australia do not fit the present definition of the genus (Towns and Peters 1978).

Deleatidium seems to be the largest New Zealand genus and is the only one in which the species groups appear to be related. *Atalophlebioides* and *Zephlebia* are both polyphyletic and provide the largest amount of information on the relationships of the New Zealand fauna. *Atalophlebioides* consists of three species including *A. cromwelli* (Phillips), *A. sepia* (Phillips) and *A. aucklandensis* Peters. The latter two species clearly differ from *A. cromwelli* at the nymphal and adult stages and are being placed in separate genera (Towns and Peters 1979a). *Zephlebia* consists of at least three genera. When Penniket (1961) established this genus he divided it into two subgenera: *Zephlebia* s.s. and *Zephlebia* (*Neozephlebia*). *Neozephlebia* is not closely related to *Zephlebia* and should be raised to generic rank. "*Zephlebia*" *cruentata* (Hudson), referred by Penniket to *Zephlebia* s.s., has few characters in common with either subgenus of *Zephlebia*, and should have a genus of its own. A generic revision of *Zephlebia*, including the latter two species groups, is being prepared for publication (Towns and Peters in prep.). The material available to us also includes at least 6 undescribed genera. With these and analysis of the species groups of *Atalophlebioides* and *Zephlebia*, 14 genera of Leptophlebiidae can be identified from New Zealand.

A feature of the fauna is the small number of species per genus. Of the 14 genera, 11 are monotypic, and as far as we know, only two,

Deleatidium and *Zephlebia*, contain five or more species.

PHYLOGENY

The leptophlebiid fauna of New Zealand consists of five lineages shown as endpoints in Fig. 1. Derived and primitive character states are given for each furcation in Table 1. At each furcation the stated primitive condition can be assumed to occur in all other lineages unless otherwise stated. Several derived character states are given at each furcation. These include characters which will separate New Zealand genera from overseas representatives of the same lineage, as well as characters which separate the five lineages listed. However, as more overseas genera are added to the lineages shown here, modification of the terminology may, in some cases, become necessary.

The analysis is based on a combination of nymphal and adult morphological characters. Because some adult characters, which appear to be useful in a regional sense, apparently exhibit extensive parallel evolution when more widely applied, some furcations lack adult characters.

An example of parallelism of adult characters occurs in coloration of the imaginal fore wings and the structure of the imaginal claws. Imagos of *Zephlebia*, *Z. (Neozephlebia)*, and "*Zephlebia*" *cruentata* have claws of a pair similar, hooked with an opposing hook, and pigmentation in the fore wings. *Atalophlebioides* s.s. and "*Atalophlebioides*" *sepia* have the clearly derived condition of dissimilar claws and hyaline fore wings. These two sets of character states are useful in subdividing the New Zealand fauna (see Fig. 1). However, genera from outside New Zealand added to their relatives, shown as endpoints in Fig. 1, indicate that loss of pigmentation and development of dissimilar claws has developed independently on several occasions. These characters therefore become mosaics when the hypothesis is tested by adding more genera.

The suggested phylogeny presented here shows evolutionary progression of a number of characters. In "*Zephlebia*" *cruentata* the clypeus is broader than the labrum (Fig. 3) and the clypeal margins are subparallel. *Zephlebia (Neozephlebia)* retains the parallel margins of the clypeus, but the labrum is slightly broader than the clypeus (Fig. 4). The margins of the clypeus become more divergent and the labrum becomes broader with each lineage (Fig. 5-6) with the ultimate development in the *Atalophlebioides* lineage of a shallow broad labrum and a clypeus with strongly divergent margins (Fig. 7).

A similar phenocline occurs in the size and shape of the prosthecal tuft and incisors of the mandibles (Fig. 8-12). In

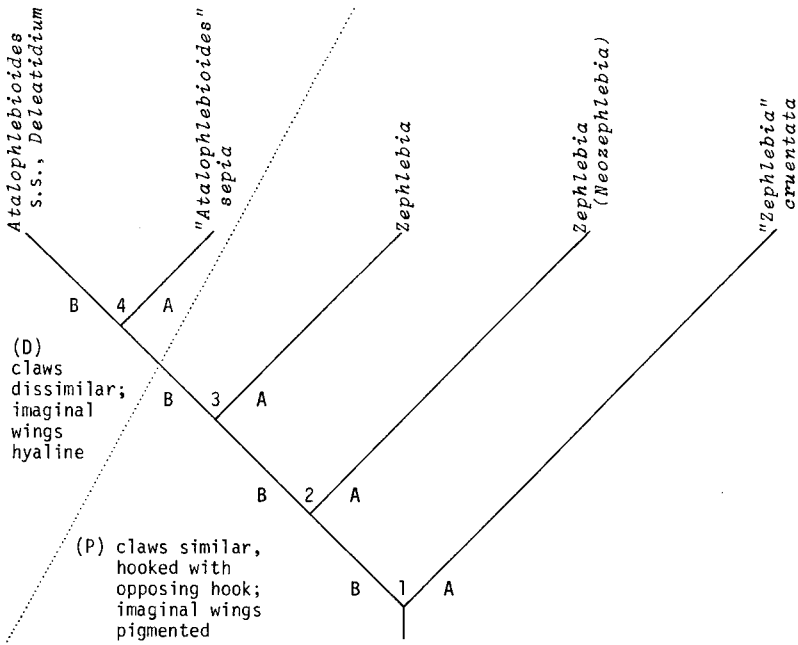


Figure 1. Phylogenetic diagram of the main generic lineages of Leptophlebiidae of New Zealand.

"*Zephlebia*" *cruentata* the prosthecal tuft has the most primitive condition, which is with the base flap-like, and hairs on the apical and lateral margins (Fig. 8); whereas, in *Z. (Neozephlebia)* it is spine-line with hairs on the anterolateral margin (Fig. 9). This spine-line shape is retained in all other lineages, but the entire prosthecal structure becomes progressively smaller (Fig. 10-11). Maximum reduction occurs in some species of *Deleatidium*, where the prosthecal tuft is reduced to a few hairs (Fig. 12). The incisors also change shape, from short and stout in "*Zephlebia*" *cruentata* to long and slender in *Atalophlebioides* (Fig. 13-17). These phenoclines generally hold when genera from outside New Zealand are included in the phylogeny (e.g. Pescador and Peters 1979). Apparent exceptions usually are clearly the result of parallel evolution. For example, a broad shallow labrum occurs outside the *Atalophlebioides* lineage in genera from New Caledonia. However, the labrum and clypeus in these genera have a number of morphological differences which separate them from the structures in the *Atalophlebioides* group.

Table 1. Character states used in proposed phylogeny of New Zealand Leptophlebiidae (Fig. 1). D, derived; P, primitives; *, occurs in furcations 1 and 2.

Furcation 1	
A	B
(D) Outer incisor of right mandible with denticles (Fig. 13).	(P) Outer incisor of right mandible smooth or spinose (Fig. 14-17).
(D) Segment 2 of maxillary palpi broad at apex.	(P) Segment 2 of maxillary palpi slender.
(P) Labrum narrower than clypeus (Fig. 3).	(D) Labrum broader than clypeus (Fig. 4-7).
(P) Base of prosthecal tuft flap-like (Fig. 8).	(D) Base of prosthecal tuft spine-like (Fig. 9-12).
(P) Segment 3 of labial palpi triangular and with stout marginal spines (Fig. 18). *	(D) Segment 3 of labial palpi slender, without stout marginal spines (Fig. 20-22).
Furcation 2	
A	B
(D) Denticles of labrum set into rectangular cavity (Fig. 4).	(P) Denticles of labrum not set into rectangular cavity (Fig. 5-7).
(P) Labrum and clypeus subequal in width (Fig. 4).	(D) Labrum broader than clypeus (Fig. 5-7).
(D) Glossae of labium with enlarged peg-like spines.	(P) Glossae of labium with pointed spines or fine hairs.
(D) Mandibles with few scattered hairs on outer margin.	(P) Mandibles with numerous hairs on outer margin.
(D) Margins of clypeus subparallel (Fig. 4).	(P) Margins of clypeus divergent (Fig. 5-7).
Furcation 3	
A	B
(D) Penes with hairs at margins of penis openings.	(P) Penes without hairs at margins of penis openings.
(P) Genital extension present to very well developed (also in furcation 1A).	(D) Genital extension absent.
(P) Labrum slightly broader than clypeus (Fig. 5).	(D) Labrum significantly broader than clypeus (Fig. 6-7).
Furcation 4	
A	B
(D) Labrum with extremely broad-based denticles on anterior margin and with deeply cleft anteromedian emargination (Fig. 6).	(P) Labrum with narrow-based denticles on anterior margin (Fig. 7).
(P) Margins of clypeus slightly divergent apically (Fig. 6).	(D) Margins of clypeus strongly divergent apically (Fig. 7).
(P) Galea-lacinia of maxillae narrow.	(D) Galea-lacinia of maxillae broad.
(P) Apex of incisors smooth (Fig. 16).	(D) Apex of incisors serrated (Fig. 17).
(P) Prosthecal tuft well developed (Fig. 11).	(D) Prosthecal tuft greatly reduced (Fig. 12).

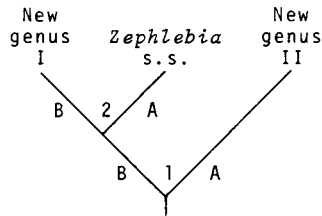


Figure 2. Phylogenetic diagram of the genera of the *Zephlebia* lineage in New Zealand.

Table 2. Character states of Fig. 2. Conventions as in Table 1.

Furcation 1	
A	B
(D) Length of penes greater than length of forceps segment 1.	(P) Length of penes less than length of forceps segment 1.
(D) Gill lamellae with fringed margins.	(P) Gill lamellae with margins entire.
(D) Female imago with long ovipositor or egg guide.	(P) Female imago with small genital extension.
(P) Abdominal gill 7 not reduced.	(D) Abdominal gill 7 reduced (single, plate-like; or paired or single thread-like filaments).
(P) Forceps of male imago without accessory lobe on segment 1.	(D) Forceps of male imago with accessory lobe on segment 1.
Furcation 2	
A	B
(D?) Projections on posterior margin of abdominal terga large.	(P) Projections on posterior margin of abdominal terga small.
(P) Femora of nymphs broad.	(D) Femora of nymphs extremely long and thin.
(P) Dorsal and ventral portions of abdominal gills similar.	(D) Dorsal and ventral portions of abdominal gills dissimilar.
(P) Labrum with well developed anteromedian denticles.	(D) Labrum with shallow, broad-based, anterosubmedian denticles.
(P) Hind wing of imago not greatly reduced (> 1/5 length of fore wing).	(D) Hind wing of imago reduced (< 1/5 length of fore wing).
(2) Mandibles with margin smoothly curved.	(D) Mandibles with apical half of outer margin straight.

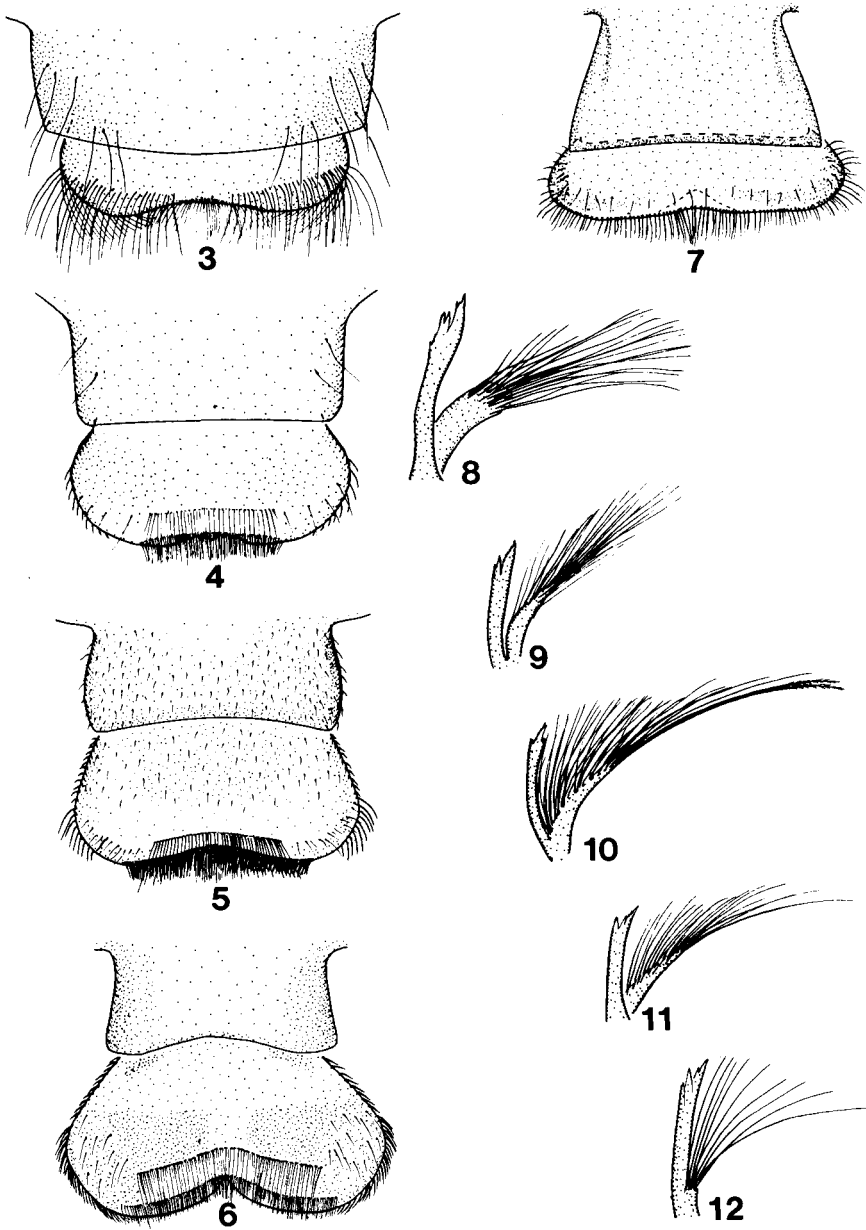


Fig. 3-7, clypeus and labrum. Fig. 8-12, prosthecal tuft of left mandible. 3,8) "*Zephlebia*" *cruentata*; 4,9) *Z. (neozephlebia)* group; 5,10) *Zephlebia* s.s.; 6,11) "*Atalophlebioides*" *septa*-group; 7,12) *Atalophlebioides* s.s. group.

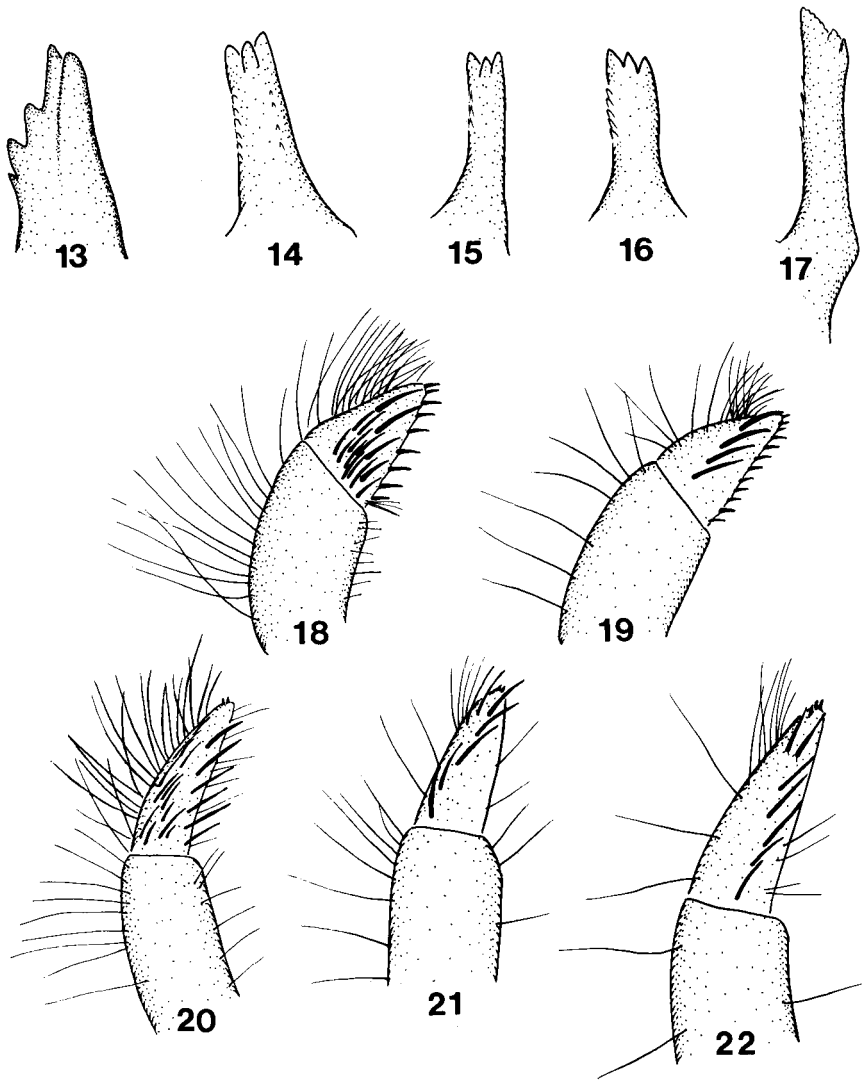


Fig. 13-17, outer incisor of right mandible. Fig. 18-22, dorsal surface of third labial palpi. 13,18) "*Zephlebia*" *cruentata*; 14,19) *Z.* (*Neozephlebia*) group; 15,20) *Zephlebia* s.s.; 16, 21) "*Atalophlebioides*" *sepia*-group; 17-22) *Atalophlebioides* s.s. group.

Two primitive character states link "*Zephlebia*" *cruentata* and *Zephlebia* (*Neozephlebia*): both genera retain the triangular shaped third labial palpal segment with heavy spines along the inner margin (Fig. 18-19) and both also have hairs or spines along the outer margin of the stipes of the maxilla. All other New Zealand genera have a labium with the third palpal segment slender without stout marginal spines (Fig. 20-22), and rarely more than a single spine near the base of the stipes of the maxilla.

Only two of the lineages listed here show any marked degree of radiation within New Zealand. The *Atalophlebioides* s.s. lineage has clear relationships outside New Zealand, but the five New Zealand genera so far identified are most closely related to each other, although at least two genera have relationships which remain unclear.

Conversely, the *Zephlebia* lineage has undergone considerable radiation in the New Zealand-New Caledonia region. This lineage, in New Zealand, is represented by three groups. The *Zephlebia* group contains *Zephlebia* s.s. and a closely related undescribed genus. The remaining two groups each contain a single new genus (Fig. 2, Table 2). The most curious of the new genera (Genus II) has many characters in common with the Palearctic, Oriental and Ethiopian genus *Thraulus*, but at the same time shares derived characters with *Zephlebia*. Nymphs are difficult to distinguish from *Thraulus* in gill shape and structure of the mouthparts. Characters in common with *Zephlebia* occur in the adults and include the presence of a genital extension in the females (greatly enlarged in the new genus), hairs around the penis openings and outline shape and venation of the wings. A second new genus from New Zealand (Genus I), has nymphs with distinctive thin femora, nymphal mouthparts similar to genera in New Caledonia and male genitalia similar to *Zephlebia* of New Zealand. Both Genus I and II are being described by Towns and Peters (1979b).

ZOOGEOGRAPHIC RELATIONSHIPS

The zoogeographic relationships of New Zealand members of a variety of the older aquatic families have been investigated recently. These include the mayfly family Siphonuridae (Edmunds 1975), Plecoptera (McLellan 1975), the chironomid subfamilies Podonominae and Diamesinae (Brudin 1966) and Trichoptera (Cowley 1978). Most of these show sister group relationships between New Zealand and temperate South America, and between temperate South America and Australia. In a few cases the picture appears to be confused by more recent wind drift between New Zealand and Australia (Plecoptera and Trichoptera) and possibly some dispersal from South-East Asia (Trichoptera). So far, in none of these groups has it been possible to investigate potential relationships between New Caledonia and New Zealand in detail. This is because stoneflies,

siphonurids and cold-adapted chironomids are unknown from New Caledonia (although the amphinotic relationships between the latter two groups of insects are well established), while Trichoptera, which have some links between New Zealand and New Caledonia (McFarlane 1976), are apparently too poorly known for their southern relationships to be fully understood (Cowley 1978). By contrast, leptophlebiid mayflies are well represented in New Caledonia and a close relationship between this and the New Zealand fauna has been suggested by Edmunds (1972).

Our data so far suggest that the relationship between the New Zealand and New Caledonia Leptophlebiidae is complex. Both old and recent groups (based on broad austral vs restricted distribution) are represented in New Zealand and New Caledonia, but some groups well represented in New Zealand, Chile and Australia are unknown in New Caledonia. Based on an extensive analysis of morphological characters, "*Zephlebia*" *cruentata* is most closely related to an undescribed genus in New Caledonia and both genera are part of a lineage which includes *Hapsiphlebia* (Chile), and *Atalophlebia* s.s., *Atalomicria* and other genera in Australia. A similar relationship occurs in *Zephlebia* (*Neozephlebia*), which has affinities with genera in New Caledonia and possibly also with genera in Chile and Australia. Relationships of the *Zephlebia* group remain unclear, although there appear to be a number of representatives in New Caledonia and possibly one in Chile (Pescador and Peters 1979). The "*Atalophlebioides*" *sepia* group has clear affinities with genera in Chile, but dubious links with genera in New Caledonia. Similarly, *Atalophlebioides* s.s. is related to *Deleatidium* of New Zealand, *Massartellopsis* and *Meridialaris* of Chile and "*Atalophlebioides*" of Australia but appears to lack representatives in New Caledonia. One of the new genera mentioned previously (Genus I) has close affinities with genera in New Caledonia, but no clear relationships outside this area, while the *Thraulus*-like genus (Genus II), although showing some affinities with New Caledonian genera, appears to be most closely related to a species group of *Thraulus* in New Guinea. The latter genus is particularly interesting because it is the first member of the group identified from the temperate Southern Hemisphere. It appears to share common ancestry with *Zephlebia* and related genera thus supporting the suggestion of Peters and Edmunds (1970, p. 235) that *Thraulus* is part of a group of genera "which represents ancient dispersal in the Southern Hemisphere."

The relationships between New Zealand and New Caledonia have not yet been completely analyzed. However, preliminary data suggest the New Zealand fauna does consistently show closest relationships with either New Caledonia or Chile, but not with Australia. Where distribution of sister groups is inconsistent with our proposed phylogeny (*Atalophlebioides* s.s., *Zephlebia* and "*Atalophlebioides*" *sepia*), the difficulties may be resolved once the leptophlebiid fauna outside New Zealand has been analysed in more detail, or the problems

may be partly the result of extinction in New Caledonia of cold-adapted forms (cf Edmunds 1972).

The small number of species per genus at present shown by New Zealand Leptophlebiidae requires some comment. This situation is not unique to leptophlebiid mayflies in New Zealand, but appears also in siphonurids and apparently in other aquatic orders as the limits of genera become more clearly defined (e.g. McFarlane 1976 - Trichoptera, McLellan 1977 - Plecoptera). Both leptophlebiid mayflies and Plecoptera in Chile have a similar low degree of speciation (M.L. Pescador pers. comm., Illies 1969). To some extent the number of species per genus is related to the level of taxonomic knowledge of the group. This applies to the mayflies of New Zealand, since the country has not been collected extensively. Even allowing for this, the level of speciation seems to be low and is about the same as the level reported by Illies (1969) for cool-adapted Plecoptera of South America. Illies (1969) compared the plecopteran fauna of South America with that of Europe and suggested that the considerable differences in levels of speciation between the two continents are the differential effects of glaciation on highland faunas. This hypothesis seems to have limited relevance to the mayflies of New Zealand. It seems more likely that the low level of speciation shown by the New Zealand mayflies can be attributed to a long isolation of an ancient specialized fauna which has since undergone a low level of radiation and/or a high level of extinction. The latter two influences could be associated with the considerable geological and climatic fluctuations to which the New Zealand landmass has been subjected (cf Fleming 1975).

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RESUME

Le groupe des éphéméroptères leptophlébiidés de Nouvelle Zélande comprend présentement trois genres répertoriés, dont deux sont de toute évidence polyphylétiques. L'analyse de ces éléments et l'addition de genres non encore étudiés indique la présence d'au moins quatorze genres. Les genres peuvent être divisés en cinq familles qui rayonnent à des degrés divers en Nouvelle Zélande et qui montrent des signes d'évolution progressive dans un certain nombre d'états caractéristiques. Quatre genres semblent être étroitement apparentés à des genres qui se trouvent en Nouvelle Calédonie, deux à des groupes génériques du Chili, et les autres à d'autres genres

qui se trouvent en Nouvelle Zélande, à l'exception d'un genre dont les spécimens les plus rapprochés que l'on connaisse sont en Nouvelle Guinée.

ZUSSAMENFASSUNG

Die leptophlebiide Eintagsfliegen Fauna Neuseelands besteht zur Zeit aus drei benannten Gattungen, von denen zwei eindeutig polyphyletisch sind. Die Analyse dieser Elemente und das Hinzufügen unbeschriebener Gattungen lassen die Existenz von mindestens vierzehn Gattungen erkennen. Diese Gattungen können wiederum unterteilt werden in fünf Stämme, die unterschiedlichen Streu-Radius innerhalb Neuseelands und evolutionäre Progression bei einer Anzahl von Merkmalen aufweisen. Vier genera scheinen ganz nah verwandt zu sein mit solchen in Neukaledonien und zwei mit generischen Gruppen in Chile. Die restlichen Gattungen sind mit anderen in Neuseeland verwandt, bis auf eine Gattung, deren nächste, bekannte Artverwandte sich in Neuguinea befinden.

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