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Notes on New Zealand Ephemeroptera. I. The affinities
with Chile and Australia, and remarks on *Atalophlebia*
Eaton (Leptophlebiidae)

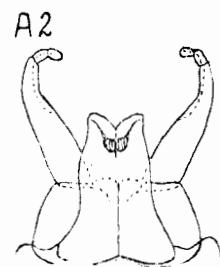
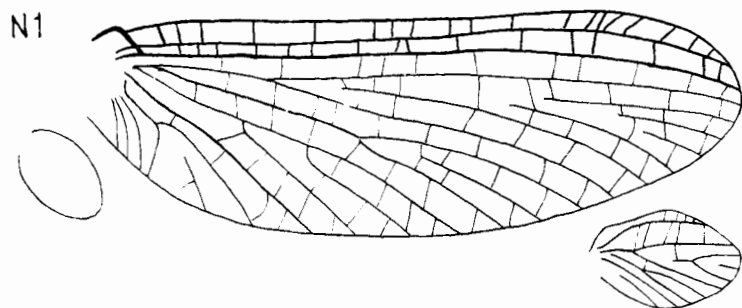
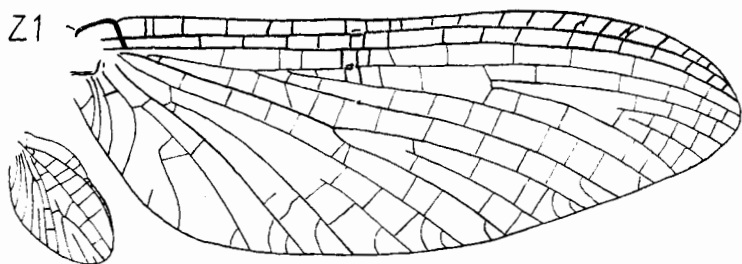
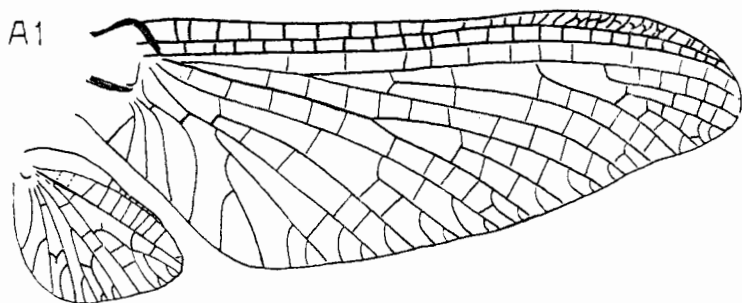
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SUMMARY

Attention is drawn to the Paleantarctic endemism of several subfamilies or tribe-equivalents, and to the sub-regional endemism of genera in these cases. All New Zealand species previously in *Atalophlebia* Eaton (Leptophlebiidae) are transferred to a new genus *Zephlebia* having two subgenera the genotypes of which are *Zephlebia* (*Zephlebia*) *versicolor* (Eaton) and *Zephlebia* (*Neozephlebia*) *scita* (Walker).

Apart from the section dealing with *Atalophlebia*, little originality is claimed for anything in this paper. The references are scattered throughout the works of Eaton, Ulmer, Tillyard, Lestage, Barnard, Traver, Needham and Murphv, Harker, Riek and Demoulin; the latter (1955) added a very great deal to what was known of the Chilean fauna, and Edmunds (1957: 245-6) first correctly analysed the relationships of the Paleantarctic Siphonuridae. Since many of the relevant papers are not readily available (indeed, in one or two cases there is no copy here at all) it is thought worth while briefly to summarise what is known in a New Zealand journal, partly as a service to local zoogeographers, and partly in the hope of stimulating others to prepare up-to-date summaries for other orders in Insecta.

Several supra-generic classifications of the order are current, usually recognising about eighteen families, only four of which are known to have representatives in New Zealand. All local genera are rather primitive, some extremely so. Considerable individual variation exists, there are known to be numerous poorly differentiated species in some of the genera, several Ephemeropteran niches appear to be more or less vacant (for example lakes and ponds), but some adaptive radiation has taken and probably still is taking place (for example *Deleatidium* has, for a Leptophlebiid,



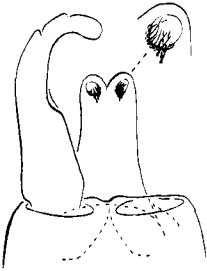
Figs. A1, A2 *Atalophlebia australis*: venation and genitalia (after Tillyard 1936: Pl. I 4; 1934: Pl. II 2 and 7.) Z1, Z2 *Zephlebia (Zephlebia) versicolor*: venation and detail of penes from Westland specimen, genitalia of type (after Kimmins 1960.) N1, N2 *Zephlebia (Neozephlebia) scita*: venation of lectotype (after Kimmins), genitalia of type (after Kimmins 1960) and detail from Westland specimen.

an atypical microhabitat (more appropriate to certain absent families such as the Heptageniidae) and some very efficient morphological adaptations to it).

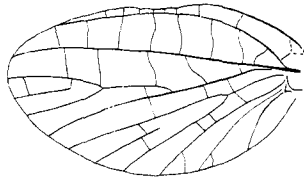
TABLE I.
Distribution of Palearctic and related genera.
(Heavy type denotes endemism.)

Group	N.Z.	Chile	Australia	Elsewhere	Remarks
Siphonuridae					
Siphonurinae A	—	—	—	8 genera	Holarctic
Siphonurinae B	Nesameletus	Metamonius	Ameletoides	—	
Oniscigastriinae	Oniscigaster	Siphonella	Tasmanophlebia	—	
Ameletopsinae	Ameletopsis	Chilopter and Chaquiha	Mirawara	—	
Isonychiidae					
Group A	Coloburiscus	Murphyella	Coloburiscoides	—	
Group B	—	—	—	Isonychia	Hol. and Oriental
Ichthybotidae	Ichthybotus	—	—	—	
Caenidae	—	(present)	Tasmanocenis	4 other	Cosmop. excl. N.Z.
Baetidae	—	3 genera	4 genera (1 endemic)	15 all told	Cosmop. excl. N.Z.
Leptophlebiidae	(See Table II.)	—	—	12 families	Various
(Other families)	—	—	—	—	—

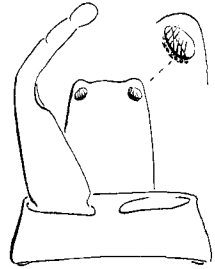
Z3



Z4



Z5



Figs. Z3, Z4 Z. (*Zephlebia*) undescribed species X: genitalia and hindwing.
Z5 Z. (*Zephlebia*) undescribed species Y: genitalia.

Table I summarises the Palearctic distribution, and should be read in conjunction with the following notes. (a) Group A of the Isonychiidae is distinguishable from Group B at about the tribal level, but this has not been fully investigated, nor have the groups received formal nomenclatural recognition. The same is true of Groups A and B of the Siphonurinae. The Isonychiidae are sometimes reduced to a subfamily of the Siphonuridae which are usually considered to be the most archaic living family in the order. (b) *Ichthybotus* is sometimes regarded as a genus of the almost cosmopolitan Ephemeridae: its eventual rank may well be that of subfamily of the latter. (c) Except possibly in the Leptophlebiidae (where the situation is somewhat obscure) and in the highly evolved and almost ubiquitous Baetidae and Caenidae, no close relationships appear to exist between the Ephemeropteran fauna of South Africa and that of any Palearctic area, nor between those of Chile and the Brazilian region, nor between those of Australia and the Sunda region. (d) Inevitably, a few genera of very doubtful occurrence or validity have had to be ignored.

It will be seen that in each of four very striking cases, a primitive tribe or subfamily, one or two genera of which occurs in each subregion, is confined to Chile, Australia and New Zealand, but no genus is common to any two of these subregions. The correspondence is so very orderly that one is almost forced to invoke either landbridges, continental subsidence, or the Wegener theory to account for it. Tillyard (1926: 64, 477-8) believed that New Zealand and Australia received all their mayflies (except the Australian Baetidae which he says are "of tropical origin") via Palearctic landbridges in Upper Jurassic or Lower Cretaceous times. The presence of Caenidae in Australia was unknown to him at that time. He did not mention the Chilean affinities.

The Chilean Baetidae and Caenidae are almost certainly later migrants from the north. Zoogeographically speaking, these are the "rats and mice" among Ephemeroptera: their mode of dispersal, the nature of which remains a mystery, must be very efficient, several Baetid genera having a very nearly world-wide distribution. In contrast to the very short adult life of most mayflies (a few days or even hours) certain Baetid females are known to have lived for several weeks; there are reports of ovoviviparity in some genera, which also suggests a longer than normal adulthood. Possibly these females conserve moisture more efficiently than do those in other families—in Ephemeroptera generally, rapid and severe desiccation is probably a major obstacle to dispersal over long distances by air.

TABLE II.

Distribution of Paleantarctic Leptophlebiidae.

Genus	N.Z.	Chile	Austr.	Elsewhere
Group A				
Zephlebia n. g.	x	—	—	—
Deleatidium	x	x ²	x ²	—
Atalophlebioides	x	x ² ¹	x ²	Madagascar ¹
Atalophlebia	—	x ²	x	Ceylon? Japan?
Atalonella	—	x	x	—
Massartellopsis	—	x	—	—
Atalomicria	—	—	x	—
Jappa	—	—	x	—
Kirrara	—	—	x	—
Ulmerophlebia	—	—	x	—
(Several other)	—	—	—	Widespread
Group B				
Thraulodes	—	x	—	New World
Thraulophlebia	—	—	x ²	—
(Many other)	—	—	—	Widespread

¹ Known from nymph only.

² Queensland.

Note: (a) The queries in the table reflect the writer's personal misgivings.

(b) No species is common to any two of the three regions.

(c) The division of the family into two groups is along the lines indicated by Traver (1946: 419); genera in Group B are probably late migrants from the north.

Examination of four pinned collections, as well as the writer's own researches, have so far failed to demonstrate the presence in New Zealand of Baetidae or Caenidae which, if they were here at all, would probably be numerous and widespread. However, a new endemic family (described in Part III of this series, but excluded from Table I) having a Baetid microhabitat, a baetoid (or siphonuroid—there is very little difference) nymph, and adult characters intermediate between those of the Siphonuridae and the Baetidae, may have descended from the former and been ancestral to the latter; in so long-isolated a region as this, such a form might well remain unchanged while its relatives elsewhere evolved into the Baetidae.

The case of the endemic Ichthybotidae is similar in some ways: this monogeneric family has some features of the Ephemeridae and some of the Polymitarcidae, both of which are almost cosmopolitan, and is slightly more generalised than either. It is interesting to note that so far nothing whatever in this phyletic line has been reported from Australia or Chile.

Oniscigaster is possibly the most archaic genus in the Ephemeroptera, even in the Pterygota (this is further considered in Part II of this series). Here again is a group which in the Paleantarctic has had to meet little or no competition: the mouthparts of the only group having a similar microhabitat (*Nesameletus* complex) suggest a different feeding pattern.

The *Coloburiscus* complex of the Isonychiidae has a torrential microhabitat from which it may have been ousted elsewhere by the Heptageniidae; the latter are sometimes considered to have descended from the Isonychiidae. *Isonychia* (Holarctic), however, seems to have avoided competition by a return to or retention of a Siphonurid microhabitat.

The situation in the Leptophlebiidae is far from clear, except that the affinities of the three faunas one with another are greater than they are with those of other regions.

Tentatively then, it seems likely that Paleantarctica evolved (or was invaded by) a characteristic archaic Ephemeropteran fauna, fortunately preserved to us almost unchanged, of which the Caenidae and the Baetidae (absent from New Zealand) were not a part, these latter having subsequently invaded Chile and Australia from the north along *two* routes.

Turning now to the Leptophlebiidae: Table II summarises the present position, with which, it is safe to say, nobody currently interested in the southern Leptophlebiidae is entirely satisfied. All the genera remain very imperfectly known, the nymphs of several are either unknown or have not been certainly associated with the adults, and species have been shuffled into and out of the second,

third and fourth listed to find a succession of uneasy resting-places; however, several overseas workers are investigating the problem, and some clarification should shortly be forthcoming. The writer is studying a large number of New Zealand species, most of them undescribed, and suspects that all New Zealand Leptophlebiidae may eventually prove to be distinct from those of Chile and Australia at subgeneric or generic levels.

As a concrete example of this the position of the New Zealand species currently in *Atalophlebia* Eaton is here briefly considered in advance of a more detailed treatment.

Atalophlebia EATON

Eaton himself (1899: 286) has said of *Atalophlebia*, "The homogeneity of this genus, alluded to with implied suspicion as long ago as 1884 in *Trans. Linn. Soc. Lond.* (2) *Zool.*, vol iii, p. 84, remains uncertain." This is almost as true today, even though many new species have been described and several homogeneous groups recognised for some of which new genera have been erected, for example *Massartella* Lestage, *Aprionyx* Barnard and *Atalonella* Needham and Murphy. Originally a large number of species, none of the nymphs of which were known, were assembled in *Atalophlebia* largely because of similarities in the hindwings in spite of gross dissimilarities in the forewings and in the genitalia.

Therefore it would be unwise to compare the New Zealand species with more than just that small homogeneous group of Tasmanian species (hereinafter referred to as *Atalophlebia* (restr.)), which comprises *A. superba* Tillyard, *A. albiterminata* Tillyard, *A. hudsoni* Tillyard and the genotype *A. australis* (Walker). (This need not imply that some mainland species do not belong in the genus; that the validity of *Atalonella* took thirty years to establish was the direct consequence of unwillingness to restrict *Atalophlebia* even temporarily to the genotype and the best-described of its nearest allies.) The characters of the group were extracted from the works of Tillyard (1934 and 1936), the excellent photographs of forewings in Plate I of the latter paper proving especially valuable. (Fig. A1 of the present paper is based on an enlargement of his photograph No. 4 of 1936, rather than on his Pl. II, Fig. 1 of 1934.)

The characters of the New Zealand groups were obtained from the study of (a) nine species, hereinafter referred to as the versicolor group, comprising *A. versicolor* Eaton (reared), *A. dentata* (Eaton), *A. cruentata* Hudson, and six undescribed species (two reared), and (b) the scita group comprising *A. scita* (Walker) (reared) and *A. nodularis* (Eaton) (no fresh material available, but the relationship of the two is certain—the venations, as well as the genitalia of the types (Kimmins 1960: Figs. 40, 41), are almost indistinguishable, and the nymph of the former proves to

agree very well with Phillips' (1930: 355 and Pl. 62 6) description of that of the latter.) All relevant literature was consulted, and attention should here be drawn to the useful photographs of forewings in Plate II of Mosely's little-known paper of 1932 (all the specific diagnoses in this plate appear to be correct except in Figs. 12 and 14 (*Nesameletus*) which will be dealt with elsewhere.)

The following key distinguishes between the groups, and erects *Zephlebia* gen. nov. with new subgenera (*Zephlebia* and *Neozephlebia*).

1. Forewing markedly triangular, broadest where posterior cubital intercalary attains margin, CuA and CuP markedly sigmoid and much closer together at two-fifths of length of CuP from origin than at one-fifth, MA fork proximally symmetrical about stem; hindwing sub-triangular, from one-quarter to one-third as long as forewing; "pockets" of penes (if present) ventral and unarmed, other accessory structures sometimes present; each gill-lamella multifid (Fig. A1, A2; Tillyard 1934: Pl. II; Tillyard 1936: Figs. 4-6, 11-13, 17-18, Pl. I, 3-9.)
Atalophlebia (restr.)

Forewing *not* markedly triangular (tornus ill-defined), broadest where CuA attains margin or distad thereof, CuA and CuP slightly sigmoid and subparallel for proximal two-fifths of CuP, MA fork proximally asymmetrical about stem (MA2 sags); hindwings oval, *less* than one-quarter as long as forewing; penes each with a conspicuous apical cup-shaped recess (gonopore) armed internally or adjacent to the rim with several small but very noticeable spines or tubercles, other accessory structures *never* present; each gill-lamella entire (References as in couplet 2) *Zephlebia* gen. nov. 2

2. Proximally, MP2 in forewing much closer to CuA than to MP1; hindwing *not less* than one-fifth length of forewing, A1 present; penes conjoined almost if not quite to tips, spines within or on rim of "cup"; distal margin of subanal plate of ♀ very slightly if at all emarginate. In the nymph, head broad and rectangular, gills broadly ovate-acuminate with tracheation much ramified, gills almost continuously rapidly vibrated (in aquarium), nymph typically clings to stones and submerged timber, transforms from surface of water (Figs. Z 1-5; Mosely 1932: Pl. II 8-11; Phillips 1930: Fig. 10, Pl. 62 2 and 3.) versicolor group=*Zephlebia* subgen. nov.
 (Genotype: *Z. (Z.) versicolor* (Eaton)).

Proximally, MP2 in forewing much closer to MP1 than to CuA; hindwing *not more* than one-sixth length of forewing, A1 absent; penes markedly divergent in distal half, tubercles slightly basad of "cup"; distal margin of subanal plate of ♀

with deep narrow cleft. In the nymph, head rounded anteriorly, gills long-lanceolate each lamella with a thick unbranched central trachea, gills very seldom vibrated and then rather slowly, nymph typically clammers amongst weed, transforms while clinging to leaf or similar situation above the surface (Figs. N 1 and 2; Mosely 1932: Pl. I 4; Phillips 1930: Pl. 62 4-6, and text 355)

..... scita group=*Neozephlebia* subgen. nov.
(Genotype: *Z. (N.) scita* (Walker)).

A number of lesser characters also separates these groups and these will be dealt with when the new species are described, but attention may here profitably be drawn to the very striking differences between *Zephlebia* and *Atalophlebia* (restr.) in the comportsment of the admittedly somewhat variable cubital intercalaries and apical veins (especially IR2 and R3b), and to the marked difference in breadth of forewing between the new subgenera.

The following new combinations are here effected: *Zephlebia (Zephlebia) dentata* (Eaton), *Zephlebia (Zephlebia) cruentata* (Hudson), *Zephlebia (Zephlebia) borealis* (Phillips) and *Zephlebia (Neozephlebia) nodularis* (Eaton). The imago of *Z. (Z.) dentata* is almost indistinguishable from *Z. (Z.) versicolor* in colour and venation, and has the characteristic *Zephlebia* penes (Kimmins 1960: Fig. 38). A dried ♂ imago of *Z. (Z.) cruentata* with a Tillyard determination label "*Atalophlebia cruentata* Huds." in the Canterbury Museum collection agrees perfectly with Hudson's (1904) and Phillips' (1930) descriptions; the species is unique among New Zealand Leptophlebiidae in that the anterior cubital intercalary is *not* attached proximally to CuP (Phillips 1930: Pl. 62 3; Mosely 1932: Pl. II 10), and in the possession of femoral bars on the forelegs but *not* the middle and hindlegs; the penes at first closely resembled Phillips' figure (1930: Fig 11) except that the apical cleft appeared much shorter, but after treatment with KOH there proved to be almost no apical cleft, and the characteristic apical "cups" and spines (not figured by Phillips) proved to be present. As for *Z. (Z.) borealis*, its author clearly found it an unremarkable New Zealand "*Atalophlebia*" and his description of the gills marks it as belonging to *Zephlebia* and not *Neozephlebia*; (Mr D. E. Kimmins points out (pers. comm.) that Phillips was incorrect in assuming that, because the adult was unknown, his (Phillips 1930: 356) description and naming of the nymph would have no nomenclatural force.) The case of *Z. (N.) nodularis* has already been discussed. No New Zealand species now remains in *Atalophlebia*.

The very characteristic penes (Figs. Z2, Z3, Z5) of the new genus at once distinguishes it from all known Leptophlebiidae from other regions. The genus with which *Zephlebia* is most

likely to be confused is *Atalonella*, from which it is distinguishable not only by the penes but also by the very strong crossveins (weaker in *Atalonella*, tending to absence in the basal half of the costal area) and the divergence of the cubital intercalaries (concentric in *Atalonella*). These characters in the latter genus are figured by Demoulin (1955) and Tillyard (1936: as *Atalophlebia brunnea*, *A. fuscula* and *A. delicatula*, all since transferred to *Atalonella*). The most zephleboïd overseas species appears to be the Tasmanian *Atalophlebia ida* Tillyard, here considered *not* to belong to *Atalophlebia* (restr.), but the male imago and the nymph remain undescribed which renders a worthwhile comparison difficult.

When the southern Leptophlebiidae are better understood, it is very possible that both *Zephlebia* and *Neozephlebia* will come to be regarded as subgenera of *Atalophlebia*, and that a new subgenus or genus may have to be erected for the Chilean species now in *Atalophlebia* by those who have access to ample material. Thanks to the great kindness of Dr. Jay R. Traver, of the University of Massachusetts, who supplied a male imago, and to the admirable figures of Dr. G. Demoulin (1955), the writer is able to draw attention to the homogeneity of the Chilean species as to absence of fusion in the penes, shortness of the stem of MP in the hindwing, and path of CuP (proximally parallel to CuA) in the forewing, characters which differ very markedly from those of the Tasmanian genotype *A. australis*. The tips of the penes defy concise verbal description, but are nevertheless recognisably peculiar to Chile, and homogeneous throughout the known species.

Alcoholic series of the nymphs and adults of the two new genotype species have been presented to the Canterbury Museum, Christchurch, and to the British Museum (Natural History), London, where Mr. D. E. Kimmins very kindly compared them with the types, confirmed the identifications and prepared a sketch of the venation of the type of one of them (Fig. N1). Additional series have been sent to the Entomology Division of the D.S.I.R. in Nelson, the California Academy of Sciences, the Institut Royal des Sciences Naturelles de Belgique, the Entomology Division of the C.S.I.R.O. at Canberra, and to a number of workers known to be investigating the Paleantarctic Leptophlebiidae.

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