

Michael Hubbard

Mike

# **New Zealand Journal of Zoology**

Volume 10 Number 1 1983

Department of Scientific and Industrial Research, Wellington

*Editor: C. T. Duval*

*Editorial Advisory Board*

Dr R. V. Brunson ..... Wallaceville Animal Research Centre  
Prof. W. C. Clark ..... University of Canterbury  
Dr F. M. Climo ..... National Museum  
Dr J. E. C. Flux ..... Ecology Division, DSIR  
Dr R. R. Forster ..... Otago Museum  
Prof. J. A. F. Garrick ..... Victoria University of Wellington  
Mr J. F. Longworth ..... Entomology Division, DSIR  
Prof. B. P. Springett ..... Massey University  
Prof. E. C. Young ..... University of Auckland

*New Zealand Journal of Zoology*  
*Vol. 1, No. 1 (March 1974)*

*Publication date: Vol. 9 No. 4 — 28 March 1983*

Permission to photocopy for internal or personal use or the internal or personal use of specific clients is granted by the Department of Scientific and Industrial Research for libraries and other users registered with the *Copyright Clearance Centre* (CCC), provided that the stated fee per copy is paid directly to the CCC, 21 Congress Street, Salem, MA 01970, U.S.A. Special requests should be addressed to Science Information Publishing Centre, DSIR.

The code on the first page of an article indicates the above consent and includes the fee per copy to be paid to the CCC.

ISSN 0301-4223

© *Crown Copyright*

Published by  
Science Information Publishing Centre  
Science Information Division, DSIR  
P.O. Box 9741, Wellington, New Zealand

## A revision of the genus *Zephlebia* (Ephemeroptera: Leptophlebiidae)

D. R. TOWNS\*

Department of Zoology  
University of Adelaide  
G.P.O. Box 498, Adelaide  
S.A. 5001, Australia

**Abstract** *Zephlebia* Penniket is redescribed and the status of subgenera previously recognised is assessed. The subgenus *Neozephlebia* Penniket is raised to generic rank. The only species of *Neozephlebia* recognised is *N. scita* (Walker). A new genus, *Acanthophlebia*, is established for *Zephlebia* (*Zephlebia*) *cruentata* (Hudson). Two subgenera of *Zephlebia* are recognised. A new subgenus, *Terama*, is established for *Zephlebia borealis* (Phillips), which is formally described for the first time. Five species are recognised in *Zephlebia* s.s.: *versicolor* (Eaton); *dentata* (Eaton); *inconspicua* n.sp.; *spectabilis* n.sp.; and *planulata* n.sp. All 3 genera are endemic to New Zealand. The relationships of each genus and the biology of each species are discussed. Life stages are described for all species except *Z. planulata*, of which the nymph is unknown. A key to imagos and nymphs of the species of *Zephlebia* is provided, and a possible phylogeny of the genus is discussed. A key is given to male and female imagos and nymphs of all New Zealand genera in the *Zephlebia* lineage, and to all genera with species previously placed in *Zephlebia*.

**Keywords** Ephemeroptera; Leptophlebiidae; *Zephlebia*; revision; *Neozephlebia*; new taxa; *Acanthophlebia*; subgenus *Terama*.

### CONTENTS

Introduction.....	1
Methods.....	2

Received 16 March 1982

\*Present address: Wildlife Service, Department of Internal Affairs, Private Bag, Wellington, New Zealand

Description of genus <i>Zephlebia</i> .....	3
Remarks .....	4
Key to species of <i>Zephlebia</i> .....	4
Subgenera within <i>Zephlebia</i> .....	5
Description of subgenus <i>Zephlebia</i> .....	5
<i>Zephlebia versicolor</i> .....	6
<i>Z. dentata</i> .....	9
<i>Z. inconspicua</i> n.sp. ....	12
<i>Z. spectabilis</i> n.sp. ....	14
<i>Z. planulata</i> n.sp. ....	17
Description of <i>Terama</i> n.subg. ....	18
<i>Z. (T.) borealis</i> .....	19
Phylogeny of <i>Zephlebia</i> .....	23
Description of genus <i>Neozephlebia</i> .....	23
Remarks .....	24
<i>Neozephlebia scita</i> .....	25
Description of <i>Acanthophlebia</i> n.gen. ....	28
Remarks .....	29
<i>Acanthophlebia cruentata</i> .....	29
Keys to genera of New Zealand Leptophlebiidae .....	31
Acknowledgments.....	32
References .....	33
Illustrations (Fig. 2-206).....	35

### INTRODUCTION

The genus *Zephlebia* Penniket contains some of the first mayflies described from New Zealand, and includes species which are often abundant in streams. However, most members of the genus are difficult to identify. The adults are poorly known, and nymphs of some species have never been adequately described, while other species have their identity shrouded in taxonomic confusion. The group was included in reviews by Phillips (1930) and Penniket (1961), but they provided few details of nymphal morphology. Phillips (1930) added to confusion by overlooking a valid species name and introducing a new species based on an informal description. Penniket (1961) discussed only generic and subgeneric classifications, and did not attempt to resolve specific identification problems. Unfortunately, *Zephlebia* was poorly defined by Penniket (1961) and the limits of his subgenera were not soundly based, partly because nymphal morphology was not included in his analyses. As a result, *Zephlebia* is clearly polyphyletic, encompassing some lineages with a broad austral distribution (Tsui

**Table 1** Sample sizes for measurements used in descriptions of *Zephlebia versicolor*, *Z. dentata*, *Z. inconspicua*, *Z. spectabilis*, *Z. planulata*, *Z. borealis*, *Neozephlebia scita*, and *Acanthophlebia cruentata*.

	Z.v.	Z.d.	Z.i.	Z.s.	Z.p.	Z.b.	N.s.	A.c.
IMAGO								
Length of:								
♂	5	4	4	5	3	4	5	4
♀	4	3	1	5	1	4	4	5
forelegs, ♂	2	3	2	2	—	4	3	4
wings, ♂	5	4	3	5	2	2	6	5
wings, ♀	4	3	1	5	2	4	4	4
genital extension, ♀	3	3	1	5	2	3	—	5
Genitalia measurements, ♂	3	3	2	6	1	3	6	5
NYMPHS								
Length	5	10	10	4	—	10	10	10
Measurements of mouthparts	5	5	5	4	—	6	5	5

& Peters 1975, cf. Towns & Peters 1980, Pescador & Peters 1980).

The following account attempts to remedy this confused situation by providing full redescriptions of species known in *Zephlebia*, the associations of nymph and adult, analysis of the status of elements within the genus as defined by Penniket (1961), and descriptions of new species. It is one of a series of papers revising the New Zealand Leptophlebiidae (Towns & Peters 1978, 1979a, b). A preliminary account of the phylogenetic relationships of New Zealand members of the family is given in Towns & Peters (1980).

In mayfly taxonomy there are several situations in which a subgeneric break is regarded as justified (see Edmunds 1962, Peters & Edmunds 1970). One of these was encountered during this study—a distinct character gap between nymphs of *Zephlebia* that is not reflected in the adults. It has therefore been necessary to divide *Zephlebia* into 2 subgenera, but on a different basis from the division used by Penniket (1961).

## METHODS

Methods and conventions used here follow Towns & Peters (1978, 1979a), except that the ratio of maximum labrum width to clypeus width is included to help distinguish genera. In species with the clypeus margins converging apically, clypeus width is measured slightly proximal to its articulation with the labrum. Where possible, the abdominal colour pattern descriptions of female imagos are based on specimens containing eggs, because colour changes occur following oviposition. Male genitalia were prepared for SEM study using methods previously described for eggs (Towns & Peters 1978). Association of nymphs and adults was by rearing.

Sample sizes for all measurements are given in Table 1. All illustrations were prepared by the author. Institutions providing non-type material of previously described species are listed as an abbreviation in parentheses under 'Material Examined', as follows: AMNZ, Auckland Institute and Museum; BPBM, Bernice P. Bishop Museum, Honolulu; CMNZ, Canterbury Museum, Christchurch; FAMU, Florida A & M University, Tallahassee; NMNZ, National Museum of New Zealand, Wellington; NZAC, New Zealand Arthropod Collection, Entomology Division, DSIR, Auckland; UUUS, University of Utah, Salt Lake City. Repositories for additional non-type material deposited from my collections are listed separately under 'Material Examined'.

Abbreviations of collectors' names are as follows: ACM, A. C. McLellan; AGM, A. G. McFarlane; AH, A. Hirsch; AJQ, A. J. Quinn; AKW, A. K. Walker; BAH, B. A. Holloway; BMM, B. M. May; BWH, B. W. Hayward; CEC, C. E. Clarke Collection; CP, C. Pugsley; DAC, D. A. Challis; DRT, D. R. Towns; DTL, D. T. Leaf; ELT, E. L. Towns; FMO, F. M. O'Brien; GCH, G. C. Hayward; GFE, G. F. Edmunds, Jr; GK, G. Kuschel; GW, G. Wise; IDM, I. D. McLellan; JAM, J. A. McLean; JGP, J. G. Penniket; JI, J. Illies; JIT, J. I. Townsend; JKE, J. K. Elsom; JKG, J. K. Greenfield; JM, J. Morice; JMD, J. A. Macdonald; JRH, J. R. Hutchings; JSD, J. S. Dugdale; JSP, J. S. Phillips; KAJW, K. A. J. Wise; MAC, M. A. Crozier; MGB, M. G. Black; MJW, M. J. Winterbourn; MTG, M. T. Gillies; MW, M. West; NFM, N. F. Marsh; PA, P. Aston; PMJ, P. M. Johns; PS, P. Summerhays; RGO, R. G. Ordish; RJR, R. J. Rowe; RJT, R. J. Tillyard; RWT, R. W. Taylor; SEN, S. E. Nichols; VALM, V. A. L. May; WJW, W. J. Winstanley; WTC, Wellington Teachers' College.

**Genus *Zephlebia* Penniket**

Penniket, 1961: 8.

**Imago.** Length: male – body 5.7–11.9 mm, forewings 7.4–12.2 mm; female – body 5.8–11.1 mm, forewings 7.5–13.4 mm.

Eyes: male – fused on meson of head, the lower portion a little less than two-thirds to four-fifths as long as upper portion; female – separated on meson of head by  $2\text{--}3\frac{1}{4}\times$  maximum width of eye.

Wings, Fig. 2–12. Forewing width one-third to a little more than one-third length. Vein Rs forked a little more than one-tenth to one-fifth distance from base to margin. Vein MA forked half to a little less than three-fifths distance from base to margin, the fork symmetrical. Vein MP not forked;  $MP_2$  attached at base to CuA and  $MP_1$  with a cross-vein, or attached at base to CuA but not  $MP_1$  (Fig. 8); attachment of  $MP_2$  to  $MP_1$  a little less to a little more than one-fifth distance from base to margin; base of  $MP_2$  equidistant between  $MP_1$  and CuA or closer to CuA. Vein  $ICu_1$  attached at base to CuA and CuP with cross-veins. Remainder of Cu–A area as in Fig. 2, with few cross-veins. Hind wings a little more than half to a little less than two-thirds as wide as long and a little less than one-fifth to a little less than one-quarter as long as forewings; vein Sc a little more than two-thirds to a little less than nine-tenths as long as wing;  $R_1$  a little less than nine-tenths wing length to about equal; cross-veins few; costal margin convex (Fig. 3 and 12); apex acute.

Legs. Length ratios of segments in male forelegs 0.61–0.81: 1.00 (2.3–3.7 mm): 0.03–0.07: 0.38–0.50: 0.37–0.48: 0.26–0.41: 0.08–0.15. Claws of a pair alike, apically hooked, with an opposing hook (Fig. 19).

Male genitalia (Fig. 22–33). Forceps: base broad, the inner margin with a small lobe, and forming an angular bend near midlength (Fig. 22 and 48); segment 2 two-thirds to  $1\frac{1}{3}\times$  as long as segment 3 and one-tenth to one-fifth as long as segment 1; apex of segment 3 rounded. Styliger plate a little more than one-quarter to three-fifths as long medially as maximum width; apex shallowly cleft (Fig. 22). Penes: lobes a little more than one-third to a little less than three-fifths as long as forceps segment 1, shallowly cleft to fused apically (Fig. 22 and 30); a row of hairs on ventral surface at base of each penis opening (Fig. 47 and 49).

Female with sternum 9 shallowly cleft to entire (Fig. 57–62); sternum 7 with genital extension a little more than one-tenth to two-fifths as long as sternum 8 (Fig. 64–68 and 71–76).

Terminal filament a little longer than cerci.

**Mature nymph.** Length of body 5.8–12.7 mm. Head prognathous. Antennae  $2\text{--}3\frac{1}{2}\times$  as long as head.

Mouthparts. Labrum a little less than  $1\frac{1}{4}\times$  as wide as clypeus,  $1\frac{1}{4}\text{--}1\frac{1}{2}\times$  as long as clypeus, and a little less than half to three-fifths as long as wide, with dorsal hair as in Fig. 110 and 112, and submedian, anterosubmedian, and anterolateral areas of hair ventrally; anterior margin concave, with broad-based, flat-topped denticles ventrally, the median denticle pointed (Fig. 111), or with 5 prominent pointed denticles (Fig. 113); lateral margins slightly angularly expanded (Fig. 110 and 112). Clypeus, Fig. 110 and 112. Left mandible with a large hair tuft on outer margin, with or without scattered hairs extended to base (Fig. 122); outer margin angular to smoothly curved (Fig. 122 and 123); incisors slender to stout, with unserrated apical teeth; prosthecal tuft large (Fig. 118 and 119). Hypopharynx: lingua with well developed lateral processes; apex of submedian lobes subtriangular, with sclerotised processes on each anterolateral margin (Fig. 137); superlingua, Fig. 137. Maxillae: galea–lacinia narrow in apical half, with a subapical row of 15–24 spines (Fig. 126); palp segment 2 a little more than three-quarters to  $1\frac{1}{2}\times$  as long as segment 1; segment 3 two-fifths to a little less than nine-tenths as long as segment 2 (Fig. 126 and 127). Labium, Fig. 130 and 131; palpi slender; segment 2 four-fifths to a little more than  $1\frac{1}{10}$  as long as segment 1; segment 3 two-fifths to three-quarters as long as segment 2; glossae dorsal to paraglossae, thickened subapically (Fig. 131); submentum (Fig. 130) with long spines on lateral margins, with or without spines on ventral surface.

Pronotum with prominent spines on anterolateral margin. Mesonotum and metanotum with or without dorsal submedian spines or projections (Fig. 175–177).

Legs, Fig. 155–158 and 162–168. Femora in cross-section narrowly oval to expanded on mid anterior surface (Fig. 162, 164, and 166); apical half to two-thirds indented, so tibia can draw into femur (Fig. 155); basal one-third to half with pointed and bipectinate spines over surface (Fig. 183); dorsum and apical one-third to half of anterior surface with enlarged, pointed to spatulate spines (Fig. 180, 182, 186, 189, and 190). Tibiae in cross-section suboval, the anterior surface flattened (Fig. 163, 165, and 167); fore tibiae with numerous coarsely bipectinate spines on inner surface (Fig. 181, 185, 187, and 188). Claws hooked and narrow apically; denticles well developed, progressively larger distally (Fig. 159).

Abdomen weakly oval to strongly tapered posteriorly (Fig. 106 and 107); posterolateral spines on segments 2–9 to 7–9 (Fig. 103–107). Gills (Fig. 140–150) on segments 1–6 alike, but progressively smaller posteriorly; lamellae with dorsal and ventral portions plate-like to narrowly oval, each portion terminating in a slender, submedian filament; gill 7 reduced to small, narrow lamellae, thread-like filaments, a single lanceolate lamella, or a single

filament (Fig. 141, 143, 145, 147, 149, and 150); main trunk of tracheae of gills 1–6 towards midline of lamellae and extended to filament apex; tracheae pigmented and branched. Caudal filaments  $1\frac{1}{2}$ –3 × as long as body; terminal filament a little longer than cerci, each segment with a distal whorl of small to prominent hairs.

**Egg** varying from cylindrical or elongate-oval, with rounded or stellate attachment structures over chorion (Fig. 199 and 202–204), to roughly oval or fusiform with carinae formed into folded ridges (Fig. 198, 200, and 201).

**Type species** *Zephlebia* (*Zephlebia*) *versicolor* (Eaton), by original designation (Penniket 1961); originally placed in *Atalophlebia*.

**Species included:** *Zephlebia* (*Zephlebia*) *versicolor* (Eaton); *Z.* (*Z.*) *dentata* (Eaton); *Z.* (*Z.*) *inconspicua* n.sp.; *Z.* (*Z.*) *planulata* n.sp.; *Z.* (*Z.*) *spectabilis* n.sp.; and *Z.* (*Terama*) *borealis* (Phillips) n.subg.

**Remarks.** The genus *Zephlebia* was established by Penniket (1961) to include all New Zealand species previously placed in *Atalophlebia* Eaton. Penniket divided the genus into 2 subgenera: the *scita* group of species was placed in *Zephlebia* (*Neozephlebia*), with *Z.* (*N.*) *scita* (Walker) as type species; all remaining species were placed in *Zephlebia* s.s., with *Z. versicolor* as type species. This division was based on adult characters, and included no morphological characters of nymphs beyond gill structure. From a detailed study of nymphs and adults and their relationships with genera in Australia, Chile, and New Caledonia, it is clear that *Neozephlebia* should be raised from subgenus to genus (see p. 23) and *Z.* (*Z.*) *cruentata* should be placed in a genus of its own (p. 28). Both species groups are related more closely to genera outside New Zealand than to other known members of the New Zealand fauna (see Towns & Peters 1980). This revision thus recognises 3 genera, which differ in morphology of male and female reproductive structures, wing venation, and nymphal mouthpart morphology and gill structure.

*Zephlebia* can be distinguished from all other known leptophlebiid genera by the following combinations of characters. IMAGO: (1) forewings with a distinct cloud of pigment at midlength (Fig. 2, 5, 7, 9, and 11); (2) claws of a pair similar (Fig. 19); (3) penes broad, one-third to a little less than three-fifths as long as forceps segment 1, and with apex shallowly cleft to entire (Fig. 22 and 30); (4) penes with hairs at base of each penis opening (Fig. 47 and 49); (5) sternum 9 of female with apex shallowly cleft to entire (Fig. 57–62); (6) female with genital extension a little more than one-tenth to two-fifths as long as sternum 8 (Fig. 64–68 and 71–76). NYMPH:

(1) labrum with lateral margins slightly angularly expanded and anterior margin concave (Fig. 110–112); (2) labrum with flat-topped to pointed denticles on anteromedian margin (Fig. 111 and 113); (3) mandibles with outer margin angular to smoothly curved and with prosthecal tuft well developed (Fig. 118, 119, 122, and 123); (4) galealacinia of maxillae narrow and with a subapical row of 15–24 spines (Fig. 126); (5) abdominal gills 1–6 with similar double lamellae, and gill 7 reduced to small, narrow lamellae, thread-like filaments, a single lanceolate lamella, or a single filament (Fig. 140–150); (6) claws with well developed denticles progressively larger distally (Fig. 159); (7) abdomen with posterolateral spines on segments 2–9 to 7–9.

*Zephlebia* appears to be most closely related to *Arachnocolus* of New Zealand, but can be distinguished from it by the following characters. IMAGO: (1) forewings with pigment or a distinct cloud of pigment in costal or subcostal area (Fig. 2, 5–7, 9, and 11); (2) hind wings a little less than one-fifth to a little less than one-quarter as long as forewings, and vein Sc a little more than two-thirds to a little less than nine-tenths as long as wings (Fig. 3, 4, 10, and 12). NYMPH: (1) labrum slightly angularly expanded laterally (Fig. 110 and 112) and with flat-topped to pointed denticles on anteromedian margin (Fig. 111 and 113); (2) mandibles with apical half angular to smoothly curved (Fig. 122 and 123) and with hair tuft mainly confined to mid-outer margin (Fig. 122 and 123); (3) prosthecal hair tuft large (Fig. 118 and 119); (4) legs with femora not greatly elongate (Fig. 155, 156, and 168).

*Zephlebia* appears to be closely related to a group of genera from New Caledonia and New Zealand (Towns & Peters 1980). A key to New Zealand members of this group, and to other genera from New Zealand previously referred to *Zephlebia*, is provided on p. 31.

#### KEY TO SPECIES OF *Zephlebia* s.l.

##### IMAGOS

- 1 Mid-femora of middle and hind legs unicolorous; vein  $MP_2$  attached at base to  $CuA$  and  $MP_1$  with a cross-vein (Fig. 2); genital extension of female one-fifth (or less) as long as sternum 8..... 2
- Mid-femora of all legs banded; vein  $MP_2$  usually attached at base to  $CuA$  only (Fig. 8); genital extension of female about one-quarter as long as sternum 8..... *spectabilis*
- 2 Penes more than half as long as forceps segment 1 (Fig. 24); membranes of cells C and Sc of forewings very pale yellow or hyaline..... 3
- Penes less than half as long as forceps segment 1 (Fig. 22); membranes of cells C and Sc of forewings pale yellow, with a reddish-brown cloud at midlength extended from Sc to beyond  $R_2$  (Fig. 2)..... *versicolor*

- 3 Forewings without a cloud at fork of MA (Fig. 2); penes with a shallow apical cleft (Fig. 22, 24, 26, 28, and 32); sternum 9 of female with a shallow apical cleft (Fig. 57) ..... 4  
 —Forewings usually with a cloud at fork of MA (Fig. 9); penes broad and almost flat at apex (Fig. 30); sternum 9 of female with apex entire (Fig. 60) ..... *planulata*
- 4 Body length more than 8 mm; forewings with broad clouds at cross-veins in cells C and Sc, and a diffuse reddish cloud in apical one-third (Fig. 5 and 11) ..... 5  
 —Body length less than 8 mm; forewings with a diffuse brown cloud at mid-costal area and narrow clouds at cross-veins and in apical one-third (Fig. 6) .. *inconspicua*
- 5 Forelegs with a mid-femoral band; body length more than 10 mm ..... *borealis*  
 —Forelegs without a mid-femoral band; body length less than 10 mm ..... *dentata*

#### MATURE NYMPHS

- 1 Labrum with small, flat-topped denticles, the central denticle pointed (Fig. 111); mandibles with lateral margins angular (Fig. 122) and with slender incisors (Fig. 118) ..... *Zephlebia* s.s. ... 2  
 —Labrum with large, pointed denticles (Fig. 113); mandibles with lateral margins smoothly curved (Fig. 123) and with short, stout incisors (Fig. 119) ..... *Zephlebia (Terama) borealis*
- 2 Prothorax and mesothorax with submedian projections or spines (Fig. 175–177) ..... 3  
 —Prothorax and mesothorax without projections or spines ..... *dentata*
- 3 Prothorax and mesothorax with submedian projections (Fig. 175 and 176); lateral margins of posterior abdominal terga without hairs; femora slender (Fig. 155 and 157); caudal filaments with a distal whorl of small hairs on each segment ..... 4  
 —Prothorax and mesothorax with spines (Fig. 177); lateral margins of posterior abdominal terga fringed with hairs; femora greatly expanded and with prominent spines (Fig. 158, 166, and 186); caudal filaments with distal whorls of prominent hairs on each segment ..... *spectabilis*
- 4 Prothorax and mesothorax with small submedian projections (Fig. 175); body length more than 8 mm; thread-like portions of gills shorter than lamellae (Fig. 140) ..... *versicolor*  
 —Prothorax and mesothorax with prominent submedian projections (Fig. 176); body length less than 8 mm; thread-like portions of gills about as long as lamellae (Fig. 144) ..... *inconspicua*

#### Subgenera within *Zephlebia*

The present diagnosis of *Zephlebia* includes several characters which have a wider range of variation than is normally encountered in New Zealand leptophlebiid genera. This is particularly true for nymphs, as species are included which have posterolateral abdominal spines ranging from segments 2–9 to 7–9; also, some species lack dorsal submedian spines on the thorax, others have spines (Fig. 177), and some have projections (Fig. 175 and 176). In the imago of most species sternum 9 of the

female has a shallow apical cleft (Fig. 57), but in some it is entire (Fig. 59). Vein  $MP_2$  of the forewing of one species is attached at the base only to  $CuA$  (Fig. 8), but in all other species it is attached to  $CuA$  and  $MP_1$ . Although in other groups additional generic breaks might be expected, in *Zephlebia* characters which elsewhere might partly delimit genera fluctuate within species (the cross-vein connection at the base of  $MP_2$  and the shape of sternum 9 of the female), or show change along a species gradient (dorsal submedian spines on the nymphal thorax). Even the distribution of posterolateral spines on the abdomen of nymphs, which is commonly stable within groups of genera, in *Zephlebia* differs between species.

Despite this variation, structure of the male genitalia is conservative, and mouthpart morphology of most species of *Zephlebia* remains constant. Only one species, *borealis*, has distinctive mouthparts and other nymphal characters which separate it from other species of *Zephlebia*. Because of this, *Zephlebia* is here divided into 2 subgenera, *Zephlebia (Zephlebia)* and *Zephlebia (Terama)*. Adults of the 2 subgenera cannot be separated; indeed, the similarity is so great that *Z. (T.) borealis* has commonly been confused with *Z. (Z.) dentata* (see p. 11).

In the descriptions of subgenera, the only adult characters used are body and forewing length, because all remaining variation of *Zephlebia (Terama)* falls within the range of *Zephlebia* s.s. Similarly, the only nymphal characters used are those which fall outside or partly overlap the ranges for the 2 subgenera.

#### Subgenus *Zephlebia* Penniket

**Imago.** Length: male – body 5.7–10.5 mm, forewings 7.4–11.3 mm; female – body 5.8–11.1 mm, forewings 7.5–13.3 mm.

**Mature nymph.** Length of body 5.8–10.3 mm.

Mouthparts. Labrum  $1\frac{1}{6}$  to a little less than  $1\frac{1}{4}$  as wide as clypeus; anterior margin concave, with broad-based, flat-topped denticles ventrally, the median denticle pointed (Fig. 110 and 111). Left mandible with outer margin angular (Fig. 122); incisors slender. Maxillae, Fig. 126; palp segment 2 a little more than three-quarters to a little more than total length of segment 1; segment 3 a little less than three-fifths to a little less than nine-tenths as long as segment 2 (Fig. 126). Labium, Fig. 130 and 131; palp segment 2 four-fifths to a little more than total length of segment 1, and segment 3 half to three-quarters as long as segment 2.

Mesonotum and metanotum with or without dorsal submedian spines or projections. Abdomen

weakly to strongly tapered posteriorly (Fig. 103–106); posterolateral spines on segments 2–9 to 7–9. Caudal filaments  $1\frac{1}{2}$  to  $2\frac{1}{2}$  × as long as body.

**Type species** as for the genus.

**Remarks.** It should be re-emphasised that although Penniket (1961) divided *Zephlebia* into 2 subgenera his division was based on adult characters, with little consideration of nymphs, whereas the present division is based on nymphs alone. Consequently, the above diagnosis of *Zephlebia* s.s. should be regarded as a redefinition of the subgenus.

### *Zephlebia versicolor* (Eaton)

Eaton, 1899: 286–287; –Hudson, 1904: 30–31; –Phillips, 1930: 339–344; –Mosely, 1932: 7; –Kimmins, 1960: 296; –Stout, 1969: 491; 1973: 244; 1975: 442 (in *Atalophlebia*). –Penniket, 1961: 8 (in subgenus *Zephlebia* sensu Penniket). –McLean, 1967: 100–101; –Michaelis, 1977: 366; –Townes, 1978b: 410; –Winterbourn & Towns, 1981: 18.

Not *Zephlebia versicolor*. Pendergrast & Cowley, 1966: 14–16; –Miller, 1971: 57–58.

**Male imago** (in ethanol). Length: body 8.5–10.5 (9.6) mm; forewings 10.1–10.5 (10.3) mm.

Head pale brown, occasionally dark brown on anterolateral margins and at base of antennae. Eyes with upper portion reddish-brown, lower portion greyish-black. Antennae with scape dark brown, pedicel pale to dark brown, flagellum pale brown. Ocelli with basal half black, apical half white.

Thorax. Pronotum pale brown, darker on margins and with paired, black, submedian, longitudinal lines; mesothorax and metathorax pale brown, darker along posterior half of outer parapsidal sutures and on dorsum of basal humps of scutellum, paler along midline of scutellum; lateral margins of posterior scutellum brown. Pleura dark greyish-brown to brown; carinae darker. Sterna dark brown to brown; carinae darker; membranes paler. Legs pale brownish-yellow, darker at articulation of fore femora and fore tibiae; length ratios of segments in forelegs 0.71 : 1.00 (3.2–3.6 mm) : 0.03–0.06 : 0.39–0.40 : 0.37–0.42 : 0.26–0.35 : 0.08–0.12. Wings, Fig. 2–4. Forewings 0.35–0.36 (0.35) × as wide as long; membranes of cells C and Sc pale yellow, the apical one-third translucent, the cross-veins surrounded by narrow, dark brown clouds; cells C, Sc, and R with a small, dark reddish-brown cloud at wing midlength, extended from vein Sc to beyond  $R_2$  (Fig. 2); remainder of longitudinal veins and cross-veins dark brown, and membrane hyaline. Hind wings 0.58–0.60 (0.59) × as wide as long and 0.19–0.20 (0.20) × as long as forewings; Sc 0.81–0.84 (0.82) × as long as

wing;  $R_1$  0.94–0.96 (0.96) × as long as wing. Longitudinal veins and cross-veins dark brown; membrane hyaline.

Abdomen pale brown; tergum 1 dark brown dorsally, with paired, dorsal, pale brown maculae; terga 1–9 with a narrow, transverse, brown to dark brown band on posterior margin (Fig. 39); terga 2–9 with or without dark brown lateral marks; terga 2–6 hyaline, with paired dorsal dark brown marks (Fig. 39) that are often indistinct on terga 4 and 5; terga 6–8 washed dorsally and laterally with dark brown; terga 9 and 10 pale brown dorsally, washed on dorsum and/or on lateral margins with brown. Tracheae hyaline; spiracular area black. Sterna pale to dark brown; sterna 2–5 hyaline on lateral margins; sterna 1 or 2 to 8 with paired, hyaline, submedian maculae; abdominal ganglia hyaline. Genitalia (Fig. 28, 29, 47, and 48) pale brown; styli-plate and penes darker brown on midline (Fig. 22). Caudal filaments white, with dark brown bands at articulations that become progressively wider distally.

**Female imago** (in ethanol). Length: body 9.0–10.6 (9.8) mm; forewings 11.2–12.6 (11.8) mm.

Head whitish-brown, occasionally brown on anterolateral margins, dark brown at base of antennae, and with a brown transverse band between eyes posterior to ocelli and paired, submedian, dark brown marks on posterior margins. Eyes black. Antennae and ocelli as in male imago.

Thorax and legs: colour and markings as in male imago. Forewings as in male imago, except membrane in cells C and Sc occasionally pale brown; 0.34–0.37 (0.35) × as wide as long. Hind wings 0.54–0.57 (0.56) × as wide as long and 0.19–0.21 (0.20) × as long as forewings; Sc 0.68–0.76 (0.72) × as long as wing;  $R_1$  0.90–0.96 (0.93) × as long as wing.

Abdomen: colour and markings as in male imago, except terga 2–6 not hyaline, submedian dorsal marks of terga 4 and 5 larger (Fig. 79), and tracheae of terga 6 or 7 to 9 dark brown. Sternum 7 with a small genital extension reaching one-fifth to one-quarter along sternum 8 (Fig. 64 and 71); sternum 9 with a shallow apical cleft (Fig. 57). Caudal filaments as in male imago.

**Male and female subimago** (in ethanol). Head colour and markings and ocelli as in imago, except male with a small, dark brown, mid-dorsal mark between ocelli. Antennae with scape pale to dark brown, pedicel and flagellum as in imago. Eyes black in female; in male, upper portion orange-brown, lower portion black.

Thorax. Colour and markings of pronotum as in imago; anterior one-third of mesonotum, area

between outer parapsidal sutures, and median notal suture pale brown except for a narrow, whitish band along posterior two-thirds of median notal suture and on inner margins of outer parapsidal sutures (Fig. 53); mesonotum between outer parapsidal sutures and notal wing processes pale brown, except anterior half of outer parapsidal sutures dark brown to black; basal humps of scutellum pale brown on dorsum and on lateral margins, darker towards midline, except anterior margins and midline whitish (Fig. 53); posterior scutellum and recurrent scutoscuteellar suture whitish, the lateral margins pale brown (Fig. 53). Pleura washed irregularly with dark grey or greyish-brown; carinae darker; sutures whitish. Sterna of male dark greyish-brown, except lateral lobes of furcasternum paler; sterna of female as in male, except basisternum and furcasternum occasionally whitish. Legs: colour and markings as in imago. Wings, Fig. 87 and 88; membranes of fore and hind wings translucent greyish (dried) or brownish (in ethanol), except membranes of cells C and Sc of forewings occasionally pale yellowish (dried); longitudinal veins and cross-veins dark brown, except veins in posterior half of hind wings often colourless and cross-veins in cells C and Sc of forewings darker; cross-veins of forewings with broad, lateral, dark brown clouds (Fig. 87); cross-veins of hind wings with pale greyish clouds; diffuse cloud at midlength of forewing extended from vein Sc to base of  $IM_p$  (Fig. 87) to form a rough 'Z' shape; a second cloud in apical one-third of forewing extended from  $R_2$  to  $R_3$  (Fig. 87); base of forewings pale brown; base of hind wings dark brown.

Abdomen. Colour and markings as in imago, except terga 2–6 pale brown and dorsum of terga 8–10 of male pale brown, occasionally washed with darker brown. Male genitalia: colour as in imago. Caudal filaments as in imago.

**Mature nymph** (in ethanol). Length of body 8.8–10.3(9.5) mm.

Head pale brown to dark brown with darker brown marks medial to eyes and paired, submedian, dark brown marks near posterior margin, a pale, U-shaped, brownish-white patch between antennae, and a brownish-white mark on midline posterior to ocelli (Fig. 103). Antennae 2.8–3.5(3.2) × as long as head. Ocelli with base black and apical half greyish-white. Eyes black in female; in male, upper portion reddish-brown, lower portion black.

Mouthparts. Labrum (Fig. 110) 0.48–0.53(0.51) × as long as wide, 1.32–1.53(1.41) × as long as clypeus and 1.08–1.15(1.13) × as wide. Clypeus (Fig. 110) with numerous fine hairs on lateral margin. Left mandible, Fig. 122. Maxillae: galea-lacinia with a subapical row of 18–20 spines (Fig. 126); palp segment 2 0.77–1.00(0.93) × as long as segment 1, and segment 3 0.57–0.86(0.71) × as long as segment

2. Labium, Fig. 130 and 131; submentum with spines and hairs on ventral surface (Fig. 130); palp segment 2 1.00–1.05(1.02) × as long as segment 1, and segment 3 0.55–0.61(0.59) × as long as segment 2.

Thorax pale brown to dark brown, with lateral margins of pronotum pale brown; pronotum and mesonotum paler brown on midline, with paler and darker brown spots and marks (Fig. 103) and with small, paired, dorsal, submedian blunt projections (Fig. 103 and 175); mesonotum with irregular paler brown area at base of wing pads. Legs: femora pale brown, mottled or banded with darker brown (Fig. 103 and 155); tibiae pale brown, darker brown at midlength and near apex; tarsi pale brown, the dorsum darker. Femoral and tibial spines, Fig. 180 and 181.

Abdomen. Posterolateral spines on segments 6–9. Colour and markings as in imago, except lateral margins of terga 1–9 pale brown (Fig. 103), and terga 3–8 each with a broad, pale brown band on midline for entire length (Fig. 103); terga 8–10 pale brown on dorsum to washed with dark brown (Fig. 103). Gills (Fig. 140 and 141) on segments 1–6 similar; dorsal and ventral portions of gill 7 reduced to thread-like filaments, a single lanceolate lamella, or a single filament (Fig. 141); lamellae translucent, pale yellowish brown to colourless; tracheae and tracheal branches dark grey. Caudal filaments 2.1–2.8(2.5) × as long as body, pale brown to brown with darker annulations at articulations, each segment with a distal whorl of prominent, dark brown denticles and fine hairs.

**Egg** roughly oval, carinate, the carinae formed into ridges and folded (Fig. 198).

**Type data.** Eaton (1899, p. 285) gives the type locality ("Hab.") of *Atalophlebia versicolor* as "Wellington". A male imago, designated lectotype by Kimmins (1960), is held at the British Museum (Natural History) (seen).

**Material examined.** **North Island.** ND. Waipoua State Forest: 1 ♀ imago, light trap, 4 Feb 1975, ? coll. (NZAC); 13 ♀ imagos, light trap, 11 Oct 1967, JSD (NZAC); 5 ♂ imagos, light trap, 15 Oct 1967, JSD (NZAC); 1 ♂ and 1 ♀ imago, 3 Dec 1963, PMJ (CMNZ); 1 nymph, 9 Jan 1967, RR (NZAC). Tauranga Bay, Butterfly Vly: 2 nymphs, 4–6 Apr 1969, GW (AMNZ). Under bridge S of Hikurangi: 1 ♂ imago, 17 Jan 1956, KAJW (AMNZ). **AK.** Cascade Stm: 5 ♂ imagos, 5 ♂ and 6 ♀ subimagos, light trap, 9 Mar 1977, MGB; 1 nymph, 23 Jan 1974, DRT; 7 ♂ and 4 ♀ subimagos, light trap, 9 Feb 1977, MGB; 1 ♂ and 1 ♀ subimago, light trap, 21 Nov 1966, JAM (NZAC); 2 ♂ and 1 ♀ subimagos, 30 Oct 1966, JAM (AMNZ); 1 ♀ subimago, light trap, 3 Nov 1966, JAM (NZAC); 1 imago, reared from nymph, 29 Feb 1976, DRT; 1 ♀ subimago reared from nymph, 2 nymphs, 27 Jan 1976, DRT; 1 nymph, 22 Oct 1975, DRT; 5 nymphs, 23 Jan 1974, DRT; 3 nymphs, in *Elatostema rugosum*, 22 Feb 1976, DRT; 1 ♂ imago, reared from nymph, 4 Nov 1975, DRT. Trib. of

Waitakere R. nr Anderson's Track: 1 ♂ and 1 ♀ imago, light trap, 22 Feb 1977, MGB; 1 ♀ imago, 15 Mar 1977, MGB. Kitekite Stm: 6 nymphs, pool, 27 Dec 1976, DRT, ELT, BWH, GCH. Piha Stm: 1 nymph, 18 Apr 1964, JAM (NZAC). Karamatura Stm: 3 nymphs, trailing vegetation, 9 Jan 1977, DRT, ELT. CL. Tarawaere Stm: 1 nymph, pool, 3 Jan 1977, DRT, ELT, GCH. Waterfalls Ck, trib. of Tarawaere Stm: 1 nymph, riffle, 3 Jan 1977, DRT, ELT, GCH. WO. Trib. of Waitomo R. 8 km S of Waitomo Cave: 5 nymphs, 10 Mar 1966, JGP (UUUS). Oruawai Stm nr Taumarunui: 21 nymphs, 9 Mar 1966, GFE (UUUS). In dam 5 km N of Te Anga: 1 nymph, 16 Dec 1967, JKG (NMNZ). BP. Ngamuwahine Stm, Kaimai Ra.: 9 nymphs, 30 Jun 1979, DRT, ELT, AJQ. TO. Side stream by Mahuia Rapids, 853 m, Mt Ruapehu: 1 ♂ imago, 14 Jan 1967, KAJW (AMNZ). GB. Waikaremoana, 747 m, Hopuruahine Stm: 2 nymphs, 22 Mar 1964, JM (AMNZ). Limestone Ck, Wairoa R.: 2 nymphs, 14 May 1964, JM (AMNZ). WA. Pond, Burnett's Rd: 1 nymph, WTC (NMNZ). Turanganui: 9 nymphs, 30 Aug 1965, FMO (NMNZ). WN. Khandallah: 1 ♂ imago (pinned), 7 Apr 1930, JSP? (NMNZ); 1 subimago ♀ (pinned), 4 Mar 1929, JSP? (NMNZ). Tyers Stm: 38 nymphs, 14 Jun 1979, DRT, ELT, BWH, GCH. Upper Hutt: 1 ♂ imago, 3 Apr 1964, JKE (CMNZ). Hutt R., Upper Hutt: 1 ♂ imago, Dec 1961, JKE (CMNZ). Rimutaka Forest Park, Catchpool Stm: 12 nymphs, 8 Jul 1979, DRT, BWH.

**South Island.** NN. Sml stm nr Anatori R.: 2 nymphs, 26 Oct 1969, IDM (FAMU). Kokiri: 12 ♂ imagos, Oct 1960, JGP (CMNZ); 1 ♀ imago, 27 Sep 1960, JGP (CMNZ); 2 ♂ and 2 ♀ imagos and 3 nymphs, Jan 1961, JGP (CMNZ). Outflow of L. Brunner: 1 ♂ imago, 13 Oct 1960, JGP (CMNZ). BR. Greymouth: 2 ♂ imagos, 28 Dec 1973, DTL (AMNZ). NC. Arthur's Pass, sml brook in meadow, 1000 m: 13 nymphs, 4 Mar 1966, GFE (UUUS).

Repositories of additional material (all specimens are in ethanol): 3 ♂ and 2 ♀ imagos, 1 ♂ and 1 ♀ subimago, 10 nymphs - NZAC; 1 ♂ imago, 2 ♀ subimagos, 9 nymphs - BMNH; 1 ♂ imago, 1 ♂ and 1 ♀ subimago, 12 nymphs - FAMU; 4 nymphs - BPBM; remaining material - author's collection.

**Variation.** Colour patterns of nymphs and adults are rather variable, particularly on abdominal terga 7-10. There is also some change in intensity of pigmentation as nymphs mature. In his description of colour of the nymphal abdominal terga, Phillips (1930, p. 344) stated that a "median yellow stripe runs along the surface, broadening out to the corners like a funnel on the eighth segment", and he used this as one character to separate nymphs of *Z. versicolor* and *Z. dentata*. I have found the dorsal stripe to be present in many specimens, but it occurs relatively consistently only in mature nymphs, as a pale brown line. It is usually absent in small nymphs, and is occasionally present in subimagos and imagos.

The seventh abdominal gill varies in structure, ranging from a single lanceolate or small plate-like lamella to dorsal and ventral portions of lamellae reduced to small filaments.

Most nymphs have well developed posterolateral spines only on abdominal segments 6-9. However, a few specimens also have small projections on segments 2-5.

**Remarks.** *Zephlebia versicolor* was originally described in *Atalophlebia* by Eaton (1899), but only from the imago and subimago. Hudson (1904) reproduced Eaton's description and commented on characters which could be used to distinguish imagos and subimagos of *Z. versicolor* from those of *Z. dentata*. Phillips (1930) provided an expanded description of *Z. versicolor* adults and the first description of the nymph and egg. He noted that nymphs and imagos of *Z. versicolor* may be confused with those of *Z. dentata*, and provided some distinguishing characters for nymphs. However, from the present analysis these appear not to be very reliable. More recently *Z. versicolor* nymphs have apparently been confused with those of *Z. spectabilis* (p. 15). Pendergrast & Cowley (1966) provided an excellent illustration of a nymph which they referred to *Z. versicolor*, and this figure was reproduced in Miller (1971). Although no abdominal colour patterns were illustrated, the distinctive shape of the abdomen, expanded fore femora, long hairs on the caudal filaments, and short antennae shown in their figure are more typical of *Z. spectabilis*.

*Zephlebia versicolor* appears to be most closely related to *Z. inconspicua*, but can be distinguished from it by the following characters. IMAGO: (1) body length more than 8 mm; (2) forewing membranes in cells C and Sc pale yellow (Fig. 2); (3) penes broad, about half as long as forceps segment 1 (Fig. 22). NYMPH: (1) pronotum and mesonotum with small, blunt projections (Fig. 175); (2) body length more than 8 mm; (3) gills with basal portion broad (Fig. 140); (4) submentum with spines and hairs on ventral surface (Fig. 130); (5) caudal filaments about  $2\frac{1}{2} \times$  as long as body.

**Biology.** Nymphs of *Z. versicolor* commonly occur on the bed of small, heavily forested streams in areas of low flow, or on trailing vegetation. I have occasionally observed nymphs during daylight moving slowly over the stream bed, where their brown cryptic camouflage gives them the appearance of slowly moving leaf fragments. Phillips (1930) found this species among the debris of more sluggish portions of streams, and observed that when pursued the nymphs moved with great agility into crevices or under stones.

There is no documented information on the adult emergence period. Imagos and subimagos in museum collections examined by me were taken between October and April. This almost certainly underestimates the emergence period, because little material of any life stage has yet been collected outside these months.

***Zephlebia dentata* (Eaton)**

Eaton, 1871: 80 (in *Leptophlebia*). —Eaton, 1884: 88; 1899: 287–288; —Hutton, 1898: 215; —Hudson, 1904: 31–33; —Mosely, 1932: 7–8; —Kimmins, 1960: 295 (in *Atalophlebia*). —Penniket, 1961: 9 (in subgenus *Zephlebia* sensu Penniket). —McLean, 1967: 100–101; —Michaelis, 1977: 366; —Towns, 1978b: 410; 1979: 256; —Winterbourn & Towns, 1981: 18.

Not *Zephlebia dentata*. Towns, 1978a: 367.

**Male imago** (in ethanol). Length: body 8.0–9.0(8.6) mm; forewings 8.6–11.1(9.5) mm.

Head pale brown, darker on anterolateral margins; a dark brown, narrow band between eyes posterior to antennae. Eyes with upper portion orange-brown, lower portion greyish-black. Antennae with scape pale brown to brown, pedicel dark brown, flagellum pale brown. Ocelli with basal half black, apical half white.

Thorax. Pronotum pale brown, black on margins and with paired, black, submedian longitudinal lines. Mesothorax and metathorax pale yellowish-brown; carinae darker. Scutellum with submedian, paired, dark brown marks between basal humps; dorsum of posterior scutellum whitish, the lateral margins pale brown. Metathorax with narrow, dark brown submedian and lateral marks. Pleura pale brown; carinae dark brown to black, the sutures whitish; propleuron with a broad, blackish diagonal line from dorsoposterior margin to anteroventral margin of coxae; mesopleuron dark brown from anterior margin of wing base to anterior margin of pleuron, irregularly washed with dark brown; metapleuron pale brown, irregularly washed with dark brown and black. Sterna pale brown, with carinae darker and membranes paler; area between posterior margin of prosternum and basisternum of mesothorax dark brown. Legs pale, yellowish, dark brown at apex of femora and at articulation of fore tibiae and fore tarsi, and darker at articulation of all tarsal segments; length ratios of segments in forelegs 0.75–0.81 : 1.00 (2.4–2.9 mm) : 0.04–0.07 : 0.39–0.50 : 0.39–0.48 : 0.32–0.41 : 0.13–0.15. Wings, Fig. 5. Forewings: width 0.34–0.37(0.35) × length; membranes of cells C and Sc tinted with yellow, the apical one-third translucent, the cross-veins surrounded by broad, reddish-brown clouds that are fused at wing midlength in cells C and Sc, and with diffuse clouds in pterostigmatic area (Fig. 5); remainder of longitudinal veins and cross-veins brown to dark brown, and membrane hyaline. Hind wings 0.59–0.61(0.61) × as wide as long and 0.19–0.21(0.21) × as long as forewings; Sc 0.80–0.86(0.83) × as long as wing; R<sub>1</sub> 0.94–0.97(0.95) × as long as wing. Longitudinal veins and cross-veins pale brown to brown; membrane hyaline.

Abdomen pale reddish-brown; terga 1–9 with a narrow, dark brown, posterior transverse band (Fig. 40); terga 2–8 with anterior margin hyaline and with

paired, hyaline anterior submedian maculae (Fig. 40); terga 2–7 with brown to dark brown narrow lines on either side of midline, and with dark brown lateral marks and dark brown, paired, submedian longitudinal lines (Fig. 40); terga 8 and 9 brown, darker laterally (Fig. 40); tergum 10 pale brown, darker on dorsum (Fig. 40). Tracheae hyaline to greyish-brown; spiracular area black. Sterna pale reddish-brown; sterna 2–8 with paired, anterior, submedian maculae and anterior margin hyaline. Genitalia (Fig. 24 and 25) pale brown; styliiger plate and penes darker brown on midline (Fig. 24); apex of forceps segment 1 and lateral margins of segments 2 and 3 occasionally darker brown. Caudal filaments white, with narrow, dark brown bands at articulations.

**Female imago** (in ethanol). Length: body 8.0–8.9(8.4) mm; forewings 9.5–10.5(10.1) mm.

Head colour and markings as in male imago, except dark brown posterior to lateral ocelli and on posterior margin. Eyes greyish-black. Antennae and ocelli as in male imago.

Thorax and legs: colour and markings as in male imago. Forewings 0.34–0.36(0.35) × as wide as long. Hind wings 0.60 × as wide as long and 0.20–0.22 × as long as forewings; vein Sc 0.84–0.88 × as long as wing; R<sub>1</sub> 0.96–0.98 × as long as wing.

Abdomen dark reddish-brown, with markings as in male imago except anterior margin and maculae of terga 2–8 pale reddish-brown, and dorsal and lateral marks on terga 2–7 indistinct (Fig. 72 and 80). Sternum 7 with a small genital extension reaching one-fifth to one-quarter along sternum 8 (Fig. 65 and 72); sternum 9 with a shallow apical cleft (Fig. 58). Caudal filaments yellowish-white, with markings as in male imago.

**Male and female subimago** (in ethanol). Head, antennae, and ocelli with colour and markings as in imago. Eyes black in female; in male, upper portion pale orange-brown, lower portion black.

Thorax. Colour and markings of pronotum as in imago. Anterior one-third of mesonotum, area between outer parapsidal sutures, and median notal suture pale brown except for a whitish band along posterior two-thirds of median notal suture (Fig. 53); mesonotum between outer parapsidal sutures and notal wing processes pale brown, except anterior half of outer parapsidal sutures black (Fig. 53); basal humps of scutellum whitish brown on dorsum, except for greyish-brown paired submedian marks, and with dorsolateral margins brown; posterior scutellum, recurrent scutoscuteellar suture, and lateral margins of scutellum whitish brown. Pleura: colour and markings as in imago, except irregularly washed with greyish-brown. Sterna: colour and markings as in imago, except area

between posterior margin of prosternum and basisternum of mesothorax whitish to pale brown. Legs: colour and markings as in imago. Wings, Fig. 89 and 90; membranes translucent, greyish (dried) or brownish (in ethanol), except membranes of cells C and Sc of forewings tinted with yellow; longitudinal veins and cross-veins pale brown to brown, paler in hind wings; cross-veins in cells C and Sc of forewings as in imago (Fig. 89); remainder of forewing cross-veins with pale greyish clouds, these occasionally fused at fork of vein MA; base of forewings washed with pale brown; base of hind wings greyish.

**Abdomen.** Colour and markings of terga as in imago, except abdomen of female pale brown and anterior margin and maculae of terga 2–8 of male pale brown. Sterna as in female imago. Male genitalia: colour as in imago. Caudal filaments as in imago (male only; broken off and missing in female).

**Mature nymph** (in ethanol). Length of body 5.8–9.4(7.9) mm.

Head pale brown to brown, washed with darker brown at base of antennae, paler on anterior margin of labrum and occasionally around eyes, with whitish maculae lateral to posterior ocelli and anterior to median ocellus (Fig. 105), a narrow, dark brown, transverse line from base of antennae to median ocellus, and dark brown, curved marks from posterior of lateral ocelli to base of antennae. Antennae 2.1–2.5(2.4) × as long as head. Ocelli with base black, apex greyish-white. Eyes black in female; in male, upper portion reddish-brown, lower portion black.

**Mouthparts.** Labrum (Fig. 110) 0.53–0.57(0.56) × as long as wide, 1.45–1.67(1.55) × as long as clypeus and 1.14–1.21(1.17) × as wide. Clypeus (Fig. 110) with scattered fine hairs on lateral margins. Left mandible, Fig. 110. Maxillae: galea–lacinia with a subapical row of 21–24 spines; palp segment 2 0.93–1.07(0.99) × as long as segment 1, and segment 3 0.56–0.71(0.64) × as long as segment 2 (Fig. 110). Labium, Fig. 110; submentum with spines and hairs on ventral surface (Fig. 130); palp segment 2 0.88–1.00(0.97) × as long as segment 1, and segment 3 0.50–0.64(0.57) × as long as segment 2.

Thorax pale brown, with lateral margins of pronotum and mesonotum darker; pronotum with midline whitish, and with paired submedian and mid-dorsal dark brown marks (Fig. 105); mesonotum whitish dorsally, irregularly washed with dark brown medially to base of wing pads (Fig. 105); pronotum and mesonotum without submedian spines or projections. Legs brownish-white; femora mottled or banded with greyish brown (Fig. 105 and 156); tibiae brownish-white, greyish-brown near midlength and base; tarsi brownish-white, darker

brown near base. Femoral and tibial spines, Fig. 182–184.

**Abdomen.** Posterolateral spines on segments 2–9. Terga pale brown to brown, with markings as in imago, except hyaline maculae pale brown or absent, paired submedian lines broader (Fig. 105), and no narrow lines on either side of midline. Sterna pale, whitish, often washed with dark brown marks medially and laterally on segments 2–8, the medial marks progressively larger posteriorly. Gills (Fig. 142 and 143) on segments 1–6 similar; dorsal and ventral portions of gill 7 reduced, often to thread-like filaments; lamellae grey; tracheae and tracheal branches dark brownish-grey. Caudal filaments 1.6–1.9(1.8) × as long as body, pale brown with darker annulations at articulations; each segment with a distal whorl of dark brown denticles and small hairs.

**Egg** compressed oval (Fig. 199); chorion with small nodules and regularly spaced stellate attachment structures over surface (Fig. 199).

**Type data.** Eaton (1871, p. 80) gives the type locality ("Hab.") of *Leptophlebia dentata* as "New Zealand". A male imago designated as lectotype (seen) and a female imago designated as lectoallotype by Kimmins (1960) are held at the British Museum (Natural History).

**Material examined.** **North Island. ND.** Under bridge S of Hikurangi: 3 ♂ and 2 ♀ imagos, 17 Jan 1956, 1 ♂ and 1 ♀ imago, 20 Jan 1956, KAJW (NZAC). Waipoua State Forest, Okawakawa Stm: 1 nymph, 5 Feb 1975, JCW, SEN (NZAC). **AK.** Kitekite Stm: 2 nymphs, 27 Dec 1976, DRT, ELT, BWH, GCH. Opanuku Stm, Curey's Park: 3 nymphs, 3 May 1964, JAM (NZAC). Swanson Stm: 1 nymph, 21 Jun 1964, JAM (NZAC). Cascade Stm: 1 nymph, 31 Jul 1971, KAJW (AMNZ); 1 nymph, 22 Apr 1975, DRT; 1 ♂ subimago, 9 Mar 1977, MGB; 1 ♀ subimago, 7 Nov 1966; 1 ♂ and 3 ♀ subimagos, 3 Nov 1966, 3 subimagos, 21 Nov 1966, JAM (NZAC). Sml silty trib. of Waitakere R. at Kauri Park: 3 nymphs, 22 Apr 1975, 1 ♂ and 1 ♀ subimago, reared from nymph, 5 May 1975, DRT. Sml trib. of Waitakere R. nr Anderson's Track: 3 ♂ and 1 ♀ imagos, 22 Feb 1977, MGB. **CL.** Coromandel: 1 ♂ imago, 18 Dec 1967, 1 ♂ imago, 28 Dec 1967, RJR (AMNZ). Sml silty trib. of Kauaeranga R., Coromandel Forest Park: 1 ♀ imago, 11 nymphs, 4 Jan 1977, DRT. Tarawaere Stm and trib.: 7 nymphs, 3 Jan 1977, DRT, ELT, GCH. Atuatumoe Stm: 1 nymph, 3 Jan 1977, DRT, ELT, GCH. **WO.** Rangitukia Stm, Mt Pirongia: 1 ♂ and 1 ♀ imago, reared, Jan–Feb 1980, PS; 7 nymphs, 17 Jan 1981, DRT, PS. Waitomo: 19 nymphs, 21 Nov 1966, JAM (NZAC). Trib. of Waitomo R. 8 km S of Waitomo Cave: 4 nymphs, 10 Mar 1966, JGP (UUUS). Te Kuiti, in Waipuna Cave: 1 ♂ imago, 2 Nov 1957, VALM (NZAC). Stm at Mapiu S of Te Kuiti: 2 nymphs, 28 Mar 1967, JKG (NMNZ). **BP.** Ngamuwahine Stm, Kaimai Ra.: 7 nymphs, 30 Jun 1979, DRT, ELT, AJQ. Okere, Rotorua: 1 ♂ imago (damaged), 27 Dec 1916, CEC (AMNZ; pinned). Kaingaroa Forest, Ngapuketuru, 610 m, pool on E side of lookout: 1 nymph, 30 Dec 1965, MMN (NMNZ). **WO.** Rangitukia Stm, Mt Pirongia: 1 ♂ and 1 ♀ imago, reared, Jan–Feb 1980, PS; 7 nymphs, 17 Jan 1981, DRT, PS. Waitomo: 19 nymphs, 21 Nov 1966,

JAM (NZAC). Trib. of Waitomo R. 8 km S of Waitomo Cave: 4 nymphs, 10 Mar 1966, JGP (UUUS). Te Kuiti, in Waipuna Cave: 1 ♂ imago, 2 Nov 1957, VALM (NZAC). Stm at Mapiu St of Te Kuiti: 2 nymphs, 28 Mar 1967, JKG (NMNZ). TO. Waihi Stm, L. Taupo: 1 ♂ imago, 16 Jan 1965, JGP (CMNZ). 2 km S of L. Taupo: 6 nymphs, 7 Mar 1966, GFE (US). Pungapunga Stm 12 km E of Taumarunui: 16 nymphs, 9 Mar 1966, GFE (UUUS). Trib. of Taringamotu R. 3 km E of Oruairi: 1 nymph, 9 Mar 1966, GFE (UUUS). GB. Limestone Ck, Wairoa R.: 2 nymphs, 14 Jan 1964, JM (AMNZ). Waikaremoana, 747 m, Hopuruahine Stm: 1 nymph, 22 Mar 1964, JM (AMNZ). TK. Huatoki Stm: 3 nymphs, 11 Oct 1957, AH (NMNZ). WA. Pond nr Upper Plain Rd, Masterton: 2 nymphs, 8 Jul 1968, ?coll. (NMNZ). WN. Stm in Hayward's Reserve, Lower Hutt: 75 nymphs, 13 Jul 1979, DRT. Day's Bay: 1 nymph, 23 Dec 1964, RGO (NMNZ); 6 nymphs, 9 Jul 1979, DRT, ELT, BWH, GCH. Moore's Vly Stm, Wainuiomata: 1 nymph, 30 Jan 1973, RGO (NMNZ). Rimutaka Forest Park, Catchpool Stm: 7 nymphs, 8 Jul 1979, DRT, BWH. Khandallah: 5 nymphs, 14 Apr 1963, JAM (NZAC). Tyrer's Stm: 95 nymphs, 14 Jul 1979, DRT, ELT, BWH, GCH. No data: 1 ♂ imago.

Repositories of additional material (all specimens are in ethanol): 2 ♂ and 2 ♀ imagos, 1 ♂ subimago, 7 nymphs - NZAC; 5 nymphs - CMNZ; 2 ♂ imagos, 7 nymphs - BMNH; 9 nymphs - BFBM; 54 nymphs - FAMU; remaining material - author's collection.

**Variation.** Most nymphs examined had posterolateral spines on abdominal segments 2-9, but a few had visible spines only on segments 6-9.

**Remarks.** *Zephlebia dentata* was described in *Leptophlebia* by Eaton (1871) from imagos. A description of the wings of subimagos was added by Eaton (1884), and characters distinguishing imagos and subimagos of *Z. dentata* from those of *Z. versicolor* were provided by Eaton (1899), with the type locality ("Hab") emended from New Zealand (Eaton 1871, 1884) to "Wellington". Hudson (1904) gave biological and taxonomic notes on the adults and nymphs, but his description of the nymph is insufficient to distinguish it from most other New Zealand Leptophlebiidae. Phillips (1930) did not provide a description of the nymph of *Z. dentata*, but listed characters to distinguish it from *Z. versicolor*. Unfortunately, apart from *Z. dentata* being "shorter and stouter..." than *Z. versicolor* (Phillips 1930, p. 346), the characters provided appear to be rather unreliable. Since this is the only information available on nymphs of *Z. dentata*, they have continued to be confused with other species in the genus. The leg coloration characters (pale maculae on the forelegs) used by Phillips (1930) and Pendergrast & Cowley (1966) to distinguish *Z. dentata* from *Z. versicolor* are also typical of *Z. borealis*. As a result, nymphs of *Z. dentata* have been confused with *Z. borealis* (e.g., Towns 1978a), and it is obvious from determined material that adults of the 2 species have also been confused, probably because their forewing coloration is almost identical (Fig. 5 and 11). Accordingly, distinguishing

characters are provided here for *Z. versicolor* and *Z. borealis*.

*Zephlebia dentata* appears to be most closely related to *Z. versicolor*, but can be distinguished from it by the following characters. IMAGO: (1) forewings with distinct reddish-brown clouds in cells C and Sc at midlength and in pterostigmatic area (Fig. 5); (2) penes more than half as long as forceps segment 1 (Fig. 24). NYMPH: (1) pronotum and mesonotum without submedian dorsal projections (Fig. 105); (2) legs with femora dorsoventrally expanded (Fig. 156); (3) abdomen with posterolateral projections on segments 2-9; (4) abdomen without mid-dorsum of terga 8-10 pale brown (Fig. 105). EGG: chorion without carinae, and surface with stellate attachment structures (Fig. 199). *Z. dentata* is superficially similar to *Z. borealis*, but can be distinguished from it by the following characters. IMAGO: (1) body length less than 10 mm; (2) forelegs without a broad, reddish-brown, mid-femoral band; (3) male with abdominal terga and sterna 2-7 pigmented; (4) female with a fleshy genital extension (Fig. 65-72). NYMPH: (1) mandibles with outer margin angular, and with slender incisors (Fig. 122); (2) labrum without prominent, pointed denticles in anteromedian emargination (Fig. 111).

**Biology.** The material available for this study contained no *Z. dentata* from the South Island, although the species is particularly abundant in some streams in the southern North Island. Phillips (1930) and Michaelis (1977) recorded *Z. dentata* from the Nelson region, but this remains unsubstantiated. A species similar to *Z. dentata* is widely distributed in the South Island, but only nymphs were available to me for study.

Hudson (1904, p. 32) found nymphs of *Z. dentata* to be abundant under stones in streams, but "seldom seen swimming in the open, or walking on the upper surfaces of the stones, and it is probable that, but for their secretive habits, their numerous enemies would speedily exterminate them". In contrast, I observed large numbers of *Z. dentata* moving about the substrate surface in slow to moderately flowing streams. The habits reported by Phillips (1930) for *Z. versicolor* when avoiding pursuit apply also to *Z. dentata*.

*Zephlebia dentata* is abundant around Wellington, especially in forested streams less than 2 m wide. In the Auckland and Coromandel areas it appears to be much less common, and most nymphs were collected from heavily forested streams less than 1 m wide, often with the substrate thickly coated with silt.

The flight period of adults apparently lasts from October (Hudson 1904) to April (Phillips 1930), with an emergence peak in October and November (Hudson 1904). This may underestimate the

potential flight period, because Hudson (1904) found mature nymphs throughout the year, and I have collected them in mid winter (July).

### *Zephlebia inconspicua* n.sp.

Towns, 1978a: 367 and 369 (as *Zephlebia* n.sp. B); 1978b: 410 (as *Zephlebia* sp. B).

**Male imago** (in ethanol). Length: body 7.1–7.6(7.3) mm; forewings 7.4–8.6 mm.

Head pale brown, washed with dark brown on lateral margins and posterior to antennae. Eyes with upper portion reddish-brown, lower portion greenish-black. Antennae with scape washed with dark brown, pedicel and flagellum pale brown. Ocelli with basal half black, apical half white.

Thorax. Pronotum brown, with darker submedian marks and lateral margins. Mesonotum and metanotum pale brown, darker between notal wing processes and outer parapsidal sutures and on dorsum of basal humps of scutellum. Basal humps of scutellum with dark brown, paired, submedian longitudinal lines and dark brown lateral marks; mid dorsum of scutellum and posterior scutellum pale brown; lateral margins of posterior scutellum brown. Pleura brown, irregularly washed with dark brown to black. Sterna brown; lateral lobes of furcasternum paler; carinae darker. Legs: femora pale brownish-yellow; tibiae and tarsi paler; length ratios of segments in forelegs 0.62–0.71 : 1.00 (2.3–2.6 mm) : 0.05 : 0.38–0.39 : 0.38–0.39 : 0.26–0.29 : 0.11–0.12. Wings, Fig. 6. Forewings: width 0.32–0.36 × length; membranes hyaline, except base tinted with pale brown, a diffuse, dark brown cloud at midlength between veins C and R<sub>2</sub> (Fig. 6), and apical one-third of cells C and Sc translucent. Longitudinal veins and cross-veins pale to dark brown, often paler in Cu–A area; cross-veins in cells C and Sc surrounded by narrow, dark brown clouds (Fig. 6). Hind wings 0.54–0.58 × as wide as long and 0.19–0.21 × as long as forewings; Sc 0.77–0.85 × as long as wing; R<sub>1</sub> 0.87–0.94 × as long as wing. Longitudinal veins and cross-veins colourless to pale brown; membrane hyaline, except base washed with dark brown.

Abdomen pale brown; terga 1–3, 6, and 7 with paired, submedian, dark brown marks (Fig. 41); tergum 1 dark brown on margins; terga 2–8 with paired anterolateral and posterolateral marks (Fig. 41); terga 1 to 7 or 8 with a broad, dark brown, transverse band on posterior margin (Fig. 41); terga 1–6 hyaline, and terga 7–10 pale to dark brown, with or without dark brown lateral marks (Fig. 41). Tracheae greyish-brown, darker posteriorly; spiracular area black. Sterna 2–6 pale brown; sterna 1 and 8 or 9 to 10 dark brown; sterna 1–9 with irregular dark brown marks; abdominal ganglia

hyaline. Genitalia (Fig. 26 and 27) pale whitish-brown; styliger plate dark brown on midline and penes, with dark brown submedian longitudinal marks. Caudal filaments white, with dark brown bands at articulations that become progressively wider distally.

**Female imago** (in ethanol). Length: body 6.6 mm; forewings 8.0 mm.

Head pale brown, irregularly washed with darker brown on lateral and posterior margins and posterior to ocelli; a dark brown line from pedicel of antennae to anterior margin of eyes; midline paler brown from between ocelli to posterior margin of head. Eyes dark grey. Antennae and ocelli as in male imago.

Thorax, legs, and wings: colour and markings as in male imago, except pleura paler, cloud at forewing midlength extended to IRs, and a small, faint brown cloud at fork of MA. Forewings 0.37 × as wide as long. Hind wings 0.58 × as wide as long and 0.18 × as long as forewings; vein Sc 0.71 × as long as wing; R<sub>1</sub> 0.92 × as long as wing.

Abdomen. Colour and markings as in male imago, except submedian marks broader, terga 2–6 with dark brown longitudinal lines on lateral margin (Fig. 73 and 81), terga 1–7 each with a pale brown mid-dorsal line for its entire length (Fig. 81), and terga 1–6 not hyaline. Sternum 7 with a small genital extension reaching one-fifth along sternum 8 (Fig. 66). Sternum 9 with a shallow apical cleft (Fig. 57). Caudal filaments as in male imago.

**Male and female subimago** (in ethanol). Head, antennae, and ocelli with colour and markings as in imago. Eyes black in female; in male, upper portion pale orange-brown, lower portion black.

Thorax. Colour and markings as in imago, but paler; anterior one-third of mesonotum, area between outer parapsidal sutures, and median notal suture pale brown, except for a whitish band along posterior two-thirds of median notal suture and medial to outer parapsidal sutures (Fig. 53); mesonotum between outer parapsidal sutures and notal wing processes pale brown, except anterior half of outer parapsidal sutures dark brown; basal humps of scutellum pale brown, paler towards dorsum, with the midline whitish, and bordered laterally by paired, submedian black marks; posterior scutellum whitish, with the lateral margins pale brown. Pleura pale brown, irregularly washed with dark brown to black; carinae darker; membranes whitish. Prosternum pale brown, with dark brown, paired submedian carinae; mesosternum and metasternum pale brown, washed anteriorly with darker purplish-brown. Legs: colour and markings as in imago. Wings, Fig. 91 and 92; membranes translucent, greyish (dried) or brownish

(in ethanol); forewings with a cloud at midlength as in imago, longitudinal veins and cross-veins brown to dark brown, cross-veins in cells C, Sc, and R with narrow, dark brown clouds, and all cross-veins surrounded with faint, pale brown clouds (Fig. 91); longitudinal veins and cross-veins of hind wings pale greyish-brown; base of forewings washed with brown and dark brown; base of hind wings dark brown.

Abdomen. Colour and markings as in imago, except terga 1–6 of male pale brown, and sterna 7–9 of male washed with darker brown midventrally. Male genitalia: colour as in imago. Caudal filaments as in imago.

**Mature nymph** (in ethanol). Length of body 5.8–7.8(6.7) mm.

Head brown, pale brown on midline from between ocelli to posterior margin, and often with a broad, pale brown, irregular transverse band anterior to eyes; small, dark brown marks anteromedially to base of eyes, and occasionally small, dark brown submedian marks between eyes. Antennae 2.8–3.0(2.9) × as long as head. Ocelli black at base; apical half greyish white. Eyes black in female; in male, upper portion reddish-brown, lower portion black (Fig. 104).

Mouthparts. Labrum (Fig. 110) 0.53–0.59(0.56) × as long as wide, 1.29–1.50(1.38) × as long as clypeus and 1.12–1.16(1.13) × as wide. Clypeus (Fig. 110) with scattered fine hairs on lateral margins. Left mandible, Fig. 122. Maxillae: galea–lacinia with a subapical row of 15–18 spines (Fig. 126); palp segment 2 0.88–1.00(0.93) × as long as segment 1, and segment 3 0.59–0.64(0.63) × segment 2. Labium, Fig. 130 and 131; submentum with 1 or 2 spines on ventral surface; palp segment 2 0.91–1.00(0.96) × as long as segment 1, and segment 3 0.52–0.65(0.60) × as long as segment 2.

Thorax. Pronotum and mesonotum brown, pale brown medially and dorsolaterally (Fig. 104), and with prominent, paired, mamillate, dorsal submedian projections (Fig. 104 and 176). Mesonotum with paired, submedian, dark brown marks near posterior margin (Fig. 104); metanotum pale brown. Legs: femora pale brown, with darker brown marks ventrally and near apex (Fig. 104 and 157); tibiae pale brown, darker brown at midlength; tarsi pale brown, the dorsum darker. Femoral and tibial spines, Fig. 157 and 185.

Abdomen. Posterolateral spines on segments 5 or 6 to 9. Colour and markings as in imago, except terga 4 and 5 with mid dorsum pale brown for entire length (Fig. 104), and submedian and lateral marks on terga 1–3 often joined near anterior margin (Fig. 104). Gills (Fig. 144 and 145) on segments 1–6 similar; basal portion of gills narrowly oval; dorsal and ventral portions of gill 7 reduced to a single,

thread-like filament (Fig. 145); lamellae translucent, pale yellowish-brown; tracheae and tracheal branches black. Caudal filaments 1.88–2.18(2.05) × as long as body, pale brown to brown with darker annulations at articulations; each segment with a distal whorl of small, dark brown denticles and fine hairs.

**Egg** fusiform to elongate oval, carinate, the carinae formed into ridges and folded (Fig. 200 and 201).

**Type data.** **Holotype** ♂ imago, Cascade Stream, Auckland, reared from nymph, 3 March 1976, D. R. Towns. **Allotype** ♀ imago, same data as holotype except 25 February 1976.

**Paratypes. North Island. ND.** Under bridge S of Hikurangi: 1 ♂ imago, 20 Jan 1956, KAJW. Butterfly Vly, Tauranga Bay: 2 nymphs, 28 Nov 1966, KAJW. **AK.** Cascade Stm: 1 ♂ imago, 1 ♀ subimago, reared from nymph, 25 Feb 1976, DRT; 1 ♂ imago, 9 Mar 1977, MGB; 15 nymphs, in *Elatostema*, 23 Feb 1976, DRT. Sml trib. of Waitakere R. nr Anderson's Track: 1 ♂ subimago, 28 Mar 1977, MGB. Kitekite Falls: 14 nymphs, 27 Dec 1976, DRT, ELT, BWH, GCH. **CL.** Sml trib. of Kauaeranga R.: 24 nymphs, 2 Jan 1977, DRT, ELT, BWH, GCH. **WO.** Arapuni: 1 ♂ imago, 1 Feb 1966, MJW. **TO.** Taumarunui: 1 ♂ imago, undated, PA.

Repositories (all specimens are in ethanol): holotype, allotype, 4 ♂ imaginal paratypes, 1 ♂ and 1 ♀ subimaginal paratype, 20 nymphal paratypes – NZAC; 5 nymphal paratypes – NMNZ; 1 ♂ imaginal paratype, 5 nymphal paratypes – CMNZ; 4 nymphal paratypes – BMNH; 5 nymphal paratypes – BPBM; 8 nymphal paratypes – FAMU; 8 nymphal paratypes – UUUS; 3 nymphal paratypes – author's collection.

**Variation.** Most nymphs have well developed posterolateral spines only on abdominal segments 6–9; a few also have a small projection on segment 5. Slide mounts of male genitalia show some variation in penis shape, probably due to distortion during mounting.

**Remarks.** *Zephlebia inconspicua* appears to be most closely related to *Z. versicolor*, but can be distinguished from it by the following characters. **IMAGO:** (1) body length less than 8 mm; (2) forewing membranes in cells C and Sc hyaline (Fig. 6); (3) penes narrow, more than half as long as forceps segment 1 (Fig. 26). **NYMPH:** (1) pronotum and mesonotum with prominent, mamillate projections (Fig. 176); (2) body length less than 8 mm; (3) gills with basal portion narrowly oval (Fig. 144); (4) submentum with few spines on ventral surface; (5) caudal filaments about twice as long as body.

Subimagos can be distinguished by the faint clouds surrounding the forewing cross-veins of *Z. inconspicua* and the distinctive 'Z'-shaped cloud in the forewing of *Z. versicolor* (Fig. 91).

Abdominal colour patterns of the two species are often very similar, and are not a reliable character by which to separate them.

**Etymology.** The name *inconspicua* (Latin, 'not readily visible') refers to the small size and cryptic camouflage of the nymphs.

**Biology.** *Zephlebia inconspicua* is known only from the northern North Island. The nymphs are most abundant in slow-flowing reaches of heavily forested streams, where they often dominate a distinctive mayfly fauna associated with emergent and trailing vegetation (see Towns 1978b). Their mottled pale and dark brown colour makes them difficult to distinguish from the small fragments of leaf material commonly trapped by trailing stream-bank vegetation. In some areas *Z. versicolor* occurs in this habitat with *Z. inconspicua*, but in smaller numbers. The much larger size of mature nymphs of *Z. versicolor* readily distinguishes them from those of *Z. inconspicua*.

### *Zephlebia spectabilis* n.sp.

Towns, 1979: 256; 1981: 194 (as *Zephlebia* sp.). - Pendergrast & Cowley, 1966: 14-16; -Miller, 1971: 57 and 58 (as *Zephlebia versicolor*).

**Male imago** (in ethanol). Length: 8.3-10.2(9.2) mm; forewings 9.6-11.3(10.3) mm.

Head pale brown, dark brown on lateral margins and with dark brown marks on anteromedian margin and posterior to antennae. Eyes with upper portion orange-brown to pale brown, lower portion greenish-black. Antennae with scape and pedicel pale brown washed with darker brown, flagellum pale brown. Ocelli with basal half black, apical half white.

Thorax. Pronotum pale brown, with dark brown submedian marks and lateral margins. Mesonotum and metonotum brown to dark brown, darker dorsally, laterally, and on basal humps of scutellum, and dark brown between notal wing processes and outer parapsidal sutures; basal humps of scutellum with paired, dark brown, submedian longitudinal marks; posterior scutellum with dorsum pale brown and lateral margins brown to dark brown. Pleura brown, irregularly washed with dark brown to black; propleuron with a broad, dark brown diagonal line from dorsoposterior margin to anteroventral margin of coxae; paracoxal suture and fore and hind wing base/pleura articulations whitish. Sterna brown, irregularly washed with darker brown; carinae dark

brown to black. Legs pale yellowish-brown, darker at articulation of fore tibiae and tarsi; articulation of femora and tibiae dark brown; mid-femoral area with a broad, diffuse, dark brown band; length ratios of segments in forelegs 0.61-0.65 : 1.00 (3.3-3.7 mm) : 0.04-0.05 : 0.38-0.43 : 0.38-0.39 : 0.30-0.33 : 0.09-0.14. Wings, Fig. 7 and 8. Forewings 0.34-0.36(0.35) × as wide as long; membranes of cells C and Sc tinted with pale brown, darker at cross-veins, near midlength, and in pterostigmatic area (Fig. 7); longitudinal veins and cross-veins brown to dark brown; remainder of membrane hyaline, except wing base washed with pale brown, and costal area purplish-brown (Fig. 7); vein MP<sub>2</sub> attached at base only to vein CuA (Fig. 8). Hind wings 0.58-0.63(0.60) × as wide as long and 0.20-0.24(0.22) × as long as forewings; Sc 0.74-0.86(0.79) × as long as wing; R<sub>1</sub> 0.94-0.97(0.95) × as long as wing. Longitudinal veins and cross-veins pale brown; membrane hyaline, except wing base tinted with pale brown.

Abdomen. Tergum 1 pale to dark brown; terga 2-8 pale brown, hyaline; terga 1 or 2 to 5 with paired, dark brown, submedian and lateral marks (Fig. 42); terga 1-7 with a narrow, transverse, dark brown band on posterior margin (Fig. 42); terga 6 and 7 with broad, paired, submedian dark brown marks (Fig. 42); terga 4-7 often with hyaline lateral maculae (Fig. 42); tergum 8 pale brown dorsally, and with dark brown lateral marks; terga 9 and 10 dark brown, darker on posterior and lateral margins. Tracheae hyaline; spiracular area black. Sterna pale brown, sterna 1 and 7 or 8 to 10 translucent; sterna 2 to 7 or 8 hyaline; sterna 1-8 with a narrow, dark brown, posterior transverse band and a dark brown, longitudinal median line merging with brown to dark brown area in posterior one-third to half of sternum; occasionally small, paired, submedian maculae near middle of each sternum; sternum 8 brown to dark brown; sternum 9 pale brown. Genitalia (Fig. 28 and 29) pale brown, washed with darker brown on lateral margins of forceps; styliger plate washed with darker brown on posterior and lateral margins and midline; penes with dark brown, submedian longitudinal marks. Caudal filaments pale yellowish-brown, with broad, dark brown bands at articulations that become progressively narrower distally; occasionally some segments with narrow, dark brown annulations at midlength.

**Female imago** (in ethanol). Length: body 6.5-11.1(8.1) mm; forewings 8.7-13.3(10.6) mm.

Head pale brown, with dark brown marks submedially on posterior margin, posterior to ocelli between eyes, and on midline between lateral ocelli; other markings and colour of ocelli and antennae as in male imago. Eyes black.

Thorax, legs, and wings with colour and markings as in male imago, but thorax paler, articulation of fore tibiae and tarsi pale yellowish-brown, and a faint, pale brown cloud at forewing midlength occasionally extended to vein  $R_2$ . Forewings  $0.35\text{--}0.38(0.36) \times$  as wide as long. Hind wings  $0.55\text{--}0.60(0.57) \times$  as wide as long and  $0.18\text{--}0.24(0.20) \times$  as long as forewings; Sc  $0.76\text{--}0.86(0.81) \times$  as long as wing;  $R_1$   $0.97\text{--}0.98(0.97) \times$  as long as wing.

Abdomen. Colour and markings as in male imago, except submedian marks broader (Fig. 74 and 82), and terga 1–8 not hyaline; tergum 5 occasionally without submedian marks. Sterna dark brown; sternum 7 with a genital extension reaching one-quarter to two-fifths along sternum 8 (Fig. 67 and 74); sternum 9 entire or with a very shallow apical cleft (Fig. 59). Caudal filaments as in male imago.

**Male and female subimago** (in ethanol). Head colour and markings as in imago, but paler; antennae and ocelli as in imago. Eyes black in female; in male, upper portion pale brown, lower portion black.

Thorax. Colour and markings as in male imago, but paler; anterior one-third of mesonotum, area between outer parapsidal sutures, and median notal suture pale brown except for a broad, whitish band along posterior two-thirds of median notal suture and medial to outer parapsidal sutures (Fig. 53); inner parapsidal sutures occasionally dark brown (Fig. 53); mesonotum between outer parapsidal sutures and notal wing processes pale brown, but anterior half of sutures dark brown to black; basal humps of scutellum pale brown, with whitish, paired, antero-submedian maculae and the midline whitish bordered laterally by paired, submedian, dark brown marks; posterior scutellum whitish, the lateral margins whitish to pale brown. Colour and markings of pleura as in male imago, but paler. Prosternum whitish, with dark brown, paired submedian carinae; mesosternum and metasternum pale brown to brown, washed with darker brown on basisternum and furcasternum. Legs: colour and markings as in female imago. Wings, Fig. 91 and 92; membranes translucent, brownish; longitudinal veins and cross-veins brown to dark brown, the cross-veins with diffuse, pale brown clouds that are most distinct in cells C, Sc, and R and fused at wing midlength in cells C, Sc, and R and near base of fork of MA (Fig. 91); hind wing with a diffuse, pale, brownish cloud in apical one-third (Fig. 92); wing bases and costal area of forewings as in imago.

Abdomen. Colour and markings as in female imago, but ground colour paler, and sterna washed with brown to dark brown. Male genitalia whitish, except for brown marks on midline of styliger plate and between lobes of penes. Caudal filaments whitish, with markings as in imago.

**Mature nymph** (in ethanol). Length of body 7.8–9.7(8.7) mm.

Head brown irregularly washed with darker brown towards anterior and lateral margins, with darker brown marks submedially near posterior margin and between ocelli, and dark brown to black marks near anteromedian margin of eyes (Fig. 106). Antennae  $2\frac{1}{2} \times$  as long as head. Ocelli black at base, with apical half greyish. Eyes black in female; in male, upper portion reddish-brown, lower portion black.

Mouthparts. Labrum (Fig. 110)  $0.50\text{--}0.53(0.51) \times$  as long as wide,  $1.24\text{--}1.44(1.35) \times$  as long as clypeus and  $1.11\text{--}1.18(1.16) \times$  as wide as clypeus. Clypeus (Fig. 110) with numerous short hairs on margin. Left mandible (Fig. 122) with scattered hairs extended to base of outer margin. Maxillae: galea-lacinia with a subapical row of 19–21 spines (Fig. 126); palp segment 2  $0.89\text{--}0.95(0.92) \times$  as long as segment 1, and segment 3  $0.69\text{--}0.88(0.79) \times$  as long as segment 2. Labium, Fig. 130 and 131; palp segment 2  $0.81\text{--}0.93(0.86) \times$  as long as segment 1, and segment 3  $0.64\text{--}0.75(0.70) \times$  as long as segment 2.

Thorax. Prothorax and mesothorax pale brown to brown; pronotum dark brown to black near lateral margins, and with dark brown to black mid-dorsal (and occasionally submedian) marks (Fig. 106); mesonotum irregularly washed with dark brown to black (Fig. 106); metanotum pale brown, but dark brown submedially and on lateral and posterior margins; pronotum with anterolateral margins expanded (Fig. 106) and with paired, dorsal, submedian tufts of small spines; mesonotum with dorsal submedian tufts of spines and with small spines scattered over dorsolateral surface (Fig. 106 and 177). Legs: femora broadly expanded anteriorly, with prominent, spatulate spines over surface (Fig. 158, 166, and 186), pale brown mottled and banded with darker brown (Fig. 106 and 158); tibiae pale brown banded with darker brown at base, apex, and near midlength (Fig. 106 and 158); tarsi pale brown with a broad, darker brown band. Femoral and tibial spines, Fig. 187 and 188.

Abdomen. Posterolateral spines on segments 7–9 prominent, with fine hairs on lateral margins. Colour and markings as in subimago, except submedian and lateral marks often joined near anterior margin of terga (Fig. 106). Gills (Fig. 146 and 147) on segments 1–6 similar, plate-like, becoming progressively smaller posteriorly; gill 7 with dorsal and ventral portions reduced to a single, small, thread-like filament (Fig. 147); lamellae translucent, pale grey to brownish; tracheae and their numerous branches pale to dark grey. Caudal filaments twice as long as body, pale brown; each segment with a distal whorl of dark brown denticles and prominent fine hairs.

**Egg** elongate-oval (Fig. 202); chorion with closely packed, circular attachment structures over surface (Fig. 202).

**Type data.** **Holotype** ♂ imago and **allotype** ♀ imago: Waitakere River, Auckland, light trap, 8 February 1977, M. G. Black.

**Paratypes. North Island. ND.** Waipoua Forest: 1 ♂ imago, 11 Oct 1967, JSD. Under bridge S of Hikurangi: 1 ♀ imago, 17 Jan 1956, KAJW. Kauri Park, Parauui: 1 ♂ imago, 1 ♀ subimago, 16 Mar 1968, KAJW. Whangarei Falls: 1 ♂ subimago, 16 Mar 1968, KAJW. **AK.** Kitekite Stm: 7 nymphs, 27 Dec 1976, DRT, ELT, BWH, GCH. Goldies Bush: 1 ♀ imago, 13 Mar 1966, KAJW. Stm below Fairy Falls: 1 nymph, 27 Mar 1960, KAJW. Sml trib. of Waitakere R. nr Anderson's Track: 3 ♂ and 2 ♀ imagos, 30 Mar 1977; 1 ♂ and 1 ♀ imago, 15 Mar 1977; 2 ♂ imagos, 16 Feb 1977; 1 ♂ and 1 ♀ imago, 22 Feb 1977, MGB. Waitakere R.: 3 ♂ imagos, netted, 30 Oct 1966, JAM; 2 ♂ subimagos, 12 Nov 1975, DRT; 1 ♀ imago, reared from nymph, 11 Mar 1974, DRT; 1 ♂ imago, 4 ♂ and 1 ♀ subimago, 8 Feb 1977, MGB. Cascades Track, Cascade Stm: 1 ♂ imago, 6 Apr 1957, VALM. Cascade Stm: 8 ♂ and 2 ♀ imagos, 6 May 1964, DAC; 16 ♂ and 4 ♀ imagos, 30 Oct 1966; 1 ♀ imago, 31 Oct 1966; 1 ♀ imago, 3 Nov 1966; 3 ♂ imagos, 7 Nov 1966; 2 ♂ and 2 ♀ subimagos, 21 Nov 1966; 2 ♂ imagos, 30 Nov 1966, JAM; 2 nymphs, 23 Jan 1974, DRT; 1 ♂ and 1 ♀ imago, 9 Feb 1977; 2 ♂ imagos, 5 ♂ and 1 ♀ subimagos, 9 Mar 1977, MGB; 2 ♂ imagos, 30 Oct 1975, ?coll.; 1 ♀ imago, reared from nymph, 29 Apr 1975, 1 ♀ subimago reared from nymph, 24 Oct 1975; 1 ♂ imago, reared from nymph, 5 Apr 1975; 1 ♀ subimago, 20 Nov 1975, DRT. **CL.** Kauaeranga R.: 1 nymph, 4 Jan 1977, DRT. Atuatumoe Stm: 4 nymphs, 3 Jan 1977, DRT, ELT, GCH. Sml silty trib. of Kauaeranga R.: 4 nymphs, 4 Jan 1977, DRT. Tarawaere Stm: 1 nymph, 3 Jan 1977, DRT, ELT, GCH. **BP.** Ngamuwahine Stm, Kaimai Ra.: 1 nymph, 30 Jun 1979, DRT, ELT, AJQ. **WN.** Rimutaka Forest Pk, Catchpool Stm: 14 nymphs, 8 Jul 1979, DRT, BWH.

**South Island. NN.** Little Wanganui R.: 6 nymphs, 1 Jan 1973, ACM. Hope R.: 17 nymphs, 24 Oct 1966, JI. **BR.** Baxters Stm: 2 ♂ imagos, reared, 13 Nov 1960; 5 ♀ imagos, 1 ♀ subimago, 15 Nov 1960, JGP. Kokiri Stm: 3 ♀ imagos, 4 Nov 1960, JGP; 1 ♂ imago, 4 Mar 1966, GFE. Four Mile R., betw. Westport and Greymouth: 2 nymphs, 30 Jan 1970, IDM. Greymouth: 1 ♂ imago, 28 Dec 1973, DTL. **DN.** Waipouri R.: 2 nymphs, 4 Nov 1966, JIT. **SL.** Otapiri R. (Stm): 1 nymph, Feb 1978, MTG; 1 ♂ subimago, 10 Mar 1979, NFM.

Repositories (all specimens are in ethanol): holotype, allotype, 38 ♂ and 16 ♀ imaginal

paratypes, 4 ♂ and 6 ♀ subimaginal paratypes, 17 nymphal paratypes – NZAC; 6 ♂ and 1 ♀ imaginal paratypes, 1 ♂ and 1 ♀ subimaginal paratype, 2 nymphal paratypes – AMNZ; 1 ♂ and 6 ♀ imaginal paratypes, 1 ♀ subimaginal paratype – CMNZ; 1 ♂ and 1 ♀ imaginal paratype, 3 ♂ subimaginal paratypes, 11 nymphal paratypes – NMNZ; 1 ♂ and 1 ♀ imaginal paratype, 2 ♂ and 1 ♀ subimaginal paratypes, 7 nymphal paratypes – BMNH; 2 ♂ imaginal paratypes, 2 ♂ subimaginal paratypes, 3 nymphal paratypes – BPBM; 2 ♂ and 1 ♀ imaginal paratypes, 2 ♂ and 1 ♀ subimaginal paratypes, 6 nymphal paratypes – FAMU; 2 ♂ and 1 ♀ imaginal paratypes, 2 ♂ and 1 ♀ subimaginal paratypes, 13 nymphal paratypes – UUS; 3 ♂ and 1 ♀ imaginal paratypes, 1 ♂ subimaginal paratype, 5 nymphal paratypes – author's collection.

**Variation.** The occurrence of spines on the dorsum of the thorax of nymphs appears to be related to maturity; the spines are largest in nymphs with well developed wing pads. A basal connection between forewing veins  $MP_1$  and  $MP_2$  is lacking in most specimens, but not all. In one specimen from near Greymouth, one wing lacked a connection but it was present in the other; in a second example, a complete connection was present in both wings. The occurrence and size of the apical cleft in sternum 9 of females also varies. All North Island specimens examined had sternum 9 entire (Fig. 59), whereas South Island specimens had a shallow apical cleft (Fig. 57). The degree of separation of the penes of male imagos is variable. In many specimens the penis lobes are in contact at the apex but the membranous connection is absent, leaving a small, conspicuous subapical gap.

**Remarks.** *Zephlebia spectabilis* appears to be most closely related to *Z. versicolor*, but can be distinguished from it by the following characters. **IMAGO:** (1) forewing membranes in cells C and Sc pale brown; (2) penes narrow, more than half as long as forceps segment 1 (Fig. 28); (3) forewing vein  $MP_2$  usually without a basal connection to  $MP_1$  (Fig. 8); (4) genital extension of female imago reaching one-fifth along sternum 8 (Fig. 67 and 74); (5) femora with dark brown bands. **NYMPH:** (1) pronotum and mesonotum without dorsal submedian projections, but with spines (Fig. 177); (2) abdominal segments 7–9 with posterolateral spines (Fig. 106); (4) caudal filaments with prominent fine hairs; (5) femora broadly expanded, and with prominent, spatulate spines (Fig. 158, 166, and 186).

*Zephlebia spectabilis* has a number of distinctive characters which separate it from other species of *Zephlebia*. The most obvious is the lack of a cross-vein connecting the base of  $MP_2$  with  $MP_1$ ; but this character is not completely stable. The rather

abbreviated abdominal segments of the nymph, the spines on the dorsum of the nymphal thorax, and the posterolateral spines only on abdominal segments 7–9 are also unique in the genus. However, structure and shape of the nymphal mouthparts and male genitalia, and venation and shape of the hind wings fall within the limits set by other species of *Zephlebia*. In addition, I have collected nymphs of an undescribed species of *Zephlebia* from the Kaimai Ranges, northern central North Island, which appears to have characters intermediate between *Z. spectabilis* and *Z. versicolor* or *Z. inconspicua*. This species, which I shall not describe without adult material, has posterolateral spines on abdominal segments 7–9 and plate-like gills similar to those of *Z. spectabilis*, but large projections on the thorax similar to those of *Z. inconspicua*. Nymphs of *Z. spectabilis* appear to be more closely related to this species than to other described species of *Zephlebia*.

**Etymology.** The name *spectabilis* (Latin, 'showy') refers to the colour pattern of the nymphs.

**Biology.** *Zephlebia spectabilis* appears to be most common in streams in forested areas, on stony substrates where the flow rate is less than  $0.2 \text{ m.s}^{-1}$ . This habitat is similar to that occupied by *Z. versicolor*, and both species probably occur throughout New Zealand. In the North Island, *Z. spectabilis* is considerably more common than *Z. versicolor* in northern streams (e.g., around Auckland), whereas *Z. versicolor* is more common in southern streams (e.g., around Wellington). Nymphs of *Z. versicolor* are often abundant on marginal trailing vegetation, but I have not collected *Z. spectabilis* in this habitat.

The emergence period appears to be quite long: adults have been taken from northern populations from early October to early May. In the absence of intensive collecting from any single locality, this 7-month emergence period is almost certainly an underestimate.

### *Zephlebia planulata* n.sp.

**Male imago** (in ethanol). Length: body 5.7–8.1 mm; forewings 7.8–9.0 mm.

Head pale brown to brown. Eyes with upper portion reddish-brown to orange-brown, lower portion black. Antennae entirely brown to dark brown. Ocelli with basal half black, apical half white.

Thorax. Pronotum pale brown; midline, paired dorsal marks, and anterior and posterior margins between marks dark brown. Mesonotum and metanotum pale brown to brown; sutures darker; basal humps of scutellum pale brown to brown, but

mid dorsum pale whitish, and midline dark brown. Pleura pale whitish-brown. Sterna pale brown to brown; carinae and furcasterna darker. Legs broken off and missing. Wings, Fig. 9 and 10. Forewings  $0.34 \times$  as wide as long; membranes hyaline except for a diffuse to distinct dark brown cloud at fork of vein MA and another at midlength from cell C to vein  $R_2$  (Fig. 9); distal one-third of cells C and Sc translucent; longitudinal veins and cross-veins brown; cross-veins in cells C and Sc surrounded by narrow, dark brown clouds that are darker towards wing base and apex (Fig. 9). Hind wings  $0.59 \times$  as wide as long and  $0.18\text{--}0.20 \times$  as long as forewings; Sc  $0.78 \times$  as long as wing;  $R_1$   $0.97 \times$  as long as wing. Longitudinal veins and cross-veins pale brown; membranes hyaline, but dark brown at wing base.

Abdomen pale, whitish; terga 1–7 hyaline, with brown to dark brown lateral marks (Fig. 43); terga 2–4 with paired, submedian brown marks; tergum 7 dark brown dorsally; terga 8–10 pale to dark brown. Tracheae hyaline; spiracular area black. Sterna 1–7 hyaline, whitish; occasionally sterna 6–8 with pale brownish mid-ventral marks; sterna 8–10 translucent, whitish to pale brown; abdominal ganglia hyaline, the terminal ganglion occasionally pale brown. Genitalia (Fig. 30 and 31) pale, whitish. Caudal filaments whitish.

**Female imago** (in ethanol). Length: body 5.8 mm; forewings 7.5–9.1 mm.

Head pale brown, dark brown between eyes, near posterior margin of head, and occasionally posterior to base of antennae. Eyes black. Antennae and ocelli as in male imago.

Thorax, legs, and wings with colour and markings as in male imago, except mesopleuron irregularly washed with dark brown, clouds around cross-veins in forewing cells C and Sc darker and broader, and longitudinal veins and cross-veins darker. Forelegs and middle legs broken off and missing; hind legs pale, yellowish, brown at articulation of femora and tibiae. Forewings  $0.34\text{--}0.37 \times$  as wide as long. Hind wings  $0.52\text{--}0.56 \times$  as wide as long and  $0.17\text{--}0.19 \times$  as long as forewings; Sc  $0.73\text{--}0.74 \times$  as long as wing;  $R_1$   $0.91\text{--}0.93 \times$  as long as wing.

Abdomen. Terga 1–3 dark brown, with pale brown lateral margins; terga 2–5 with midline pale brown; terga 4–6 with pale brown, submedian maculae (Fig. 83); terga 4–7 pale brown, with dark brown, curved submedian marks (Fig. 75 and 83); terga 8–10 dark brown. Tracheae hyaline; spiracular area black. Sterna pale brown, washed on lateral margins with darker brown; sternum 7 with a small genital extension reaching a little more than one-tenth along sternum 8 (Fig. 68 and 75); sternum 9 entire (Fig. 60). Caudal filaments pale, brownish, with darker brown annulations at articulations.

**Male and female subimago** (in ethanol). Head colour and markings, antennae, and ocelli as in imago, but head of female paler. Eyes black in female; in male, upper portion dark brown, lower portion black.

**Thorax.** Colour and markings of pronotum as in imago; mesonotum brown, with a broad, whitish band along posterior two-thirds of median notal suture and medially to outer parapsidal sutures (Fig. 53); mesonotum between outer parapsidal sutures and notal wing processes brown, except anterior half of outer parapsidal sutures dark brown to black; basal humps of scutellum whitish medially, the lateral half brown; posterior scutellum whitish, the lateral margins brown. Pleura whitish, except mesopleuron irregularly washed with dark brown. Sterna whitish; markings as in imago. Legs pale, yellowish, pale brown at articulations of femora and tibiae. Wings, Fig. 95 and 96; membranes of fore and hind wings whitish (in ethanol) or pale greyish (dried); markings as in imago except longitudinal veins paler and cross-veins surrounded with faint, greyish clouds (Fig. 95).

**Abdomen.** Colour and markings as in imago, except abdomen of male pale yellowish, not hyaline, and markings darker. Male genitalia and caudal filaments whitish.

**Nymph** unknown.

**Egg** elongate-oval (Fig. 204); chorion with vermiform sculpturing and with stellate attachment structures scattered over surface (Fig. 204).

**Type data.** **Holotype** ♂ imago and **allotype** ♀ imago: Glow-worm Grotto, Waitomo Caves, 27 May 1979, C. Pugsley.

**Paratypes.** Same data as holotype: 1 ♂ and 3 ♀ imagos, 7 ♂ and 13 ♀ subimagos. **TO.** Taumarunui: 1 ♂ imago, 1 ♀ subimago, 16 Dec 1963, PA.

**Repositories** (all specimens are in ethanol): holotype, allotype, 2 ♂ and 3 ♀ imaginal paratypes, 2 ♂ and 5 ♀ subimaginal paratypes – NZAC; 1 ♂ and 2 ♀ subimaginal paratypes – NMNZ; 1 ♂ imaginal paratype – CMNZ; 1 ♂ and 2 ♀ subimaginal paratypes – BMNH; 2 ♂ and 2 ♀ subimaginal paratypes – FAMU; 1 ♂ and 2 ♀ subimaginal paratypes – author's collection.

**Variation.** Abdominal colour pattern appears to be quite variable in the female subimago. Several specimens have the dorsum of terga 4 and 5 pale brown, whereas others have dark brown submedian marks. In the male imagos abdominal colour pattern has not preserved well, but it is probably closely comparable with that of female subimagos.

**Remarks.** In the absence of nymphs the relationships between *Z. planulata* and other species of *Zephlebia* are unclear. On the basis of forewing

colour pattern and body size, *Z. planulata* appears to be most closely related to *Z. inconspicua*, but can be distinguished from it by the following characters in the imago: (1) penes broad, with the apex flat (Fig. 30); (2) female genital extension reaching less than one-fifth along sternum 8 (Fig. 68); (3) sternum 9 of female entire (Fig. 60); (4) males without submedian marks on terga 6 and 7 (Fig. 43).

In the female imago and subimago of *Z. planulata* abdominal colour pattern is similar to that of *Mauilulus luma* Towns & Peters. However, the 2 species can be distinguished readily by the forewing colour pattern of *Z. planulata* and the dissimilar tarsal claws of *M. luma*.

The generic position of *Z. planulata* may have to be revised once nymphs are available for study. In *Zephlebia* it is the only species with the apex of sternum 9 in the female consistently entire, although in *Z. spectabilis* this ranges from entire to weakly cleft (Fig. 60). Moreover, the genital extension of female *Z. planulata* is the least developed in the genus, and the forewing/hindwing ratio is low (although it falls within the lower limits for *Z. inconspicua*). However, in isolation these are not sufficient grounds to place *Z. planulata* in a supraspecific category of its own.

**Etymology.** The name *planulata* (Latin, 'flat and broad') refers to the apex of the penes.

**Biology.** Most of the material examined was obtained from light traps set in a limestone cavern.

### *Terama n.subgen.*

**Imago.** Length: male – body 10.5–11.9 mm, forewings 11.9–12.2 mm; female – body 8.4–11.0 mm, forewings 13.1–13.4 mm.

**Mature nymph.** Length of body 8.5–12.7 mm.

**Mouthparts.** Labrum a little wider than clypeus; anterior margin concave, with 5 prominent pointed denticles (Fig. 112 and 113). Left mandible with outer margin curved as in Fig. 123; incisors short, stout. Maxillae, Fig. 126 and 127; palp segment 2 four-fifths to  $1\frac{1}{2}$  × as long as segment 1, and segment 3 a little more than two-fifths to two-thirds as long as segment 2, with fine hairs on outer margin (Fig. 127). Labium, Fig. 130 and 131; palp segment 2 a little more than nine-tenths to a little more than  $1\frac{1}{10}$  × as long as segment 1, and segment 3 two-fifths to a little less than three-fifths as long as segment 2.

Mesonotum and metanotum without dorsal submedian spines or projections.

Abdomen weakly oval, broadest at segments 4–6 (Fig. 107), with posterolateral spines on segments 2–9. Caudal filaments  $1\frac{1}{2}$  × to a little more than  $1\frac{3}{4}$  × as long as body.

**Etymology.** 'Te Rama', an enchanted fish-hook in Maori mythology. Refers to the large size of nymphs relative to those of *Deleatidium*, itself named from the Greek for 'a little bait' (Eaton 1899).

**Type species** *Zephlebia (Terama) borealis* (Phillips).

### *Zephlebia (Terama) borealis* (Phillips)

Phillips, 1930: 356 (in *Atalophlebia*; also as *Atalophlebia?* n.sp.). —Penniket, 1961: 9 (in subgenus *Zephlebia* sensu Penniket). —Landa et al., 1980: 171 (as *Zephlebia (Z.) cf. borealis*). —Towns, 1978a: 367 (as *Zephlebia dentata*); 1979: 256 (as gen. et sp. nov.).

**Male imago** (in ethanol). Head pale brown, blackish-brown on anterolateral margins and in a narrow band between eyes posterior to antennae. Eyes with upper portion orange-brown, lower portion black. Antennae with scape and pedicel blackish-brown, flagellum pale brown. Ocelli with basal half black, apical half white.

Thorax. Pronotum pale whitish-brown, black on margins and with paired, black, submedian longitudinal lines; mesothorax and metathorax pale yellowish-brown; carinae darker; submedian darker marks between basal humps of scutellum; posterior scutellum with dorsum whitish, lateral margins pale brown; metathorax with a broad, dark brown transverse band on posterior margin. Pleura pale brown irregularly washed with dark brown and black; carinae black; propleuron with a broad, diagonal line from dorsoposterior margin to anteroventral margin of coxae. Sterna dark brown, except prosternum pale brown, carinae darker brown to black, and lateral lobes of furcasterna paler towards lateral margins. Legs pale, yellowish-brown, dark brown at apex of femora, at apex of mid and hind tibiae, and at articulations of tarsal segments; forelegs with a broad, diffuse, reddish-brown mid-femoral band and a broad, dark brown to black band at apex of tibiae; length ratios of segments in forelegs 0.74–0.75 : 1.00 (3.6–3.8 mm) : 0.04–0.05 : 0.45–0.49 : 0.43–0.49 : 0.36–0.38 : 0.11–0.13. Wings, Fig. 11 and 12. Forewings 0.34–0.35 × as wide as long; membrane of cells C and Sc tinted with pale yellow, the cross-veins surrounded by broad, dark reddish-brown clouds that are fused at wing midlength (Fig. 11); pterostigmatic area with membrane heavily pigmented brownish-red, the pigmentation more diffuse towards wing apex; remainder of membrane hyaline, except wing base washed with pale brown, and costal area washed with purplish brown; longitudinal veins and cross-veins dark brown. Hind wings 0.60 × as wide as long and 0.19–0.20 × as long as forewings; Sc 0.79–

0.80 × as long as wing; R<sub>1</sub> 0.96–0.97 × as long as wing. Longitudinal veins and cross-veins pale brown; membrane hyaline.

Abdomen pale whitish brown, but terga 4–7 with faint, darker submedian marks (Fig. 44); terga 1–9 with a dark brown, posterior transverse band (Fig. 44); terga 1–6 hyaline; tergum 7 translucent; terga 8 and 9 dark brown, pale brown on dorsum and anterior margins; tergum 10 pale brown. Tracheae hyaline, greyish-brown posteriorly; spiracular area black. Sternum 1 dark brown, paler midventrally; sterna 2–6 hyaline, tinted with pale whitish brown; sterna 2–9 washed with darker brown on posterior margin, the darker areas becoming progressively larger on sterna 7–9; sterna 2–8 with paired, hyaline to pale brown submedian maculae near anterior margin; abdominal ganglia hyaline. Genitalia (Fig. 32 and 33) pale brown; styliger plate darker. Caudal filaments whitish to yellowish, with darker brown bands at articulations and narrow bands at midlength that become progressively wider distally.

**Female imago** (in ethanol). Head colour and markings as in male imago, but darker, and with dark brown submedian and lateral marks on posterior margin. Eyes greyish-black. Antennae and ocelli as in male imago.

Thorax, legs, and wings with colour and markings as in male imago, except pronotum dark brown on anterior and posterior margins, marks between basal humps of scutellum broader and darker, dorsum of posterior scutellum pale brown, pigmented area of wings darker, and cross-veins in forewing cell C joined by a diffuse, brownish-red cloud. Forewings 0.36–0.37 × as wide as long. Hind wings 0.56–0.61(0.59) × as wide as long and 0.19 × as long as forewings; Sc 0.73–0.84(0.79) × as long as wing; R<sub>1</sub> 0.91–0.95(0.93) as long as wing.

Abdomen pale brown, with tergum 1 darker; terga 1–9 with a broad, pale brown, mid-dorsal longitudinal line bordered with darker brown submedian marks (Fig. 76 and 84); other markings as in male imago, except terga and sterna not hyaline, and sterna darker with a pale brown midventral line. Sternum 7 with a small genital extension reaching one-fifth to one-third along sternum 8 (Fig. 69 and 76); sternum 9 apically cleft (Fig. 61). Caudal filaments as in male imago.

**Male and female subimago** (in ethanol). Head colour and markings, eyes, antennae, and ocelli as in imago, except upper portion of eyes of male pale brown to orange-brown.

Thorax. Colour and markings of pronotum as in imago; anterior one-third of mesonotum and area between outer and inner parapsidal sutures pale brown; anterior half of outer parapsidal sutures dark

brown to black; remainder of mesonotum whitish-brown (Fig. 54); basal humps of scutellum whitish-brown on dorsum, but with greyish-brown, paired submedian marks and dorsolateral area brown (Fig. 54); posterior scutellum whitish-brown, darker on lateral margins. Sterna and legs with colour and markings as in imago. Wings, Fig. 97 and 98; membranes translucent, brownish, but tinted with yellowish in forewing cells C and Sc (dried material only) (Fig. 97); longitudinal veins and cross-veins dark brown, paler in hind wings; pigmentation in forewing cells C and Sc as in imago, except clouds at cross-veins brown to dark brown, and membrane in pterostigmatic area reddish-brown; remainder of forewing cross-veins with faint, greyish clouds (Fig. 97).

**Abdomen.** Colour and markings as in imago, except terga 1–6 of male translucent, and abdomen of female paler. Sterna as in imago. Male genitalia: colour as in male imago, except base and apex of forceps segment 1 washed with dark brown. Caudal filaments as in imago.

**Mature nymph** (in ethanol). Head brown washed with darker brown at base of antennae and on dorsal surface of mandibles, with dark brown submedian marks between eyes, whitish maculae lateral to posterior ocelli and anterior to median ocellus (Fig. 107), and a dark brown transverse line from median ocellus towards anterior margins of lateral ocelli. Antennae  $2.20\text{--}3.04(2.65) \times$  as long as head. Ocelli with base black, apex whitish. Eyes black in female; in male, upper portion dark reddish-brown, lower portion black.

**Mouthparts.** Labrum (Fig. 112)  $0.49\text{--}0.60(0.55) \times$  as long as wide,  $1.33\text{--}1.60(1.48) \times$  as long as clypeus and  $1.00\text{--}1.07(1.02) \times$  as wide as clypeus. Clypeus (Fig. 112) with scattered fine hairs on lateral margins. Left mandible, Fig. 123. Maxillae: galealacinia with a subapical row of 15–18 spines; palp segment 2  $0.88\text{--}1.19(0.97) \times$  as long as segment 1, and segment 3  $0.42\text{--}0.65(0.53) \times$  as long as segment 2 (Fig. 127). Labium, Fig. 130 and 131; submentum with spines and hairs on ventral surface (Fig. 130); palp segment 2  $0.92\text{--}1.15(0.98) \times$  as long as segment 1, and segment 3  $0.40\text{--}0.56(0.51) \times$  as long as segment 2.

Thorax brown; pronotum darker towards lateral margins, with darker brown submedian marks, and lateral margins pale brown (Fig. 107); mesonotum with or without a broad, pale brown, mid-dorsal longitudinal line (Fig. 107); scutellum with paired, submedian, dark brown marks and posterior margin dark brown (Fig. 107); pronotum and mesonotum without submedian spines or projections; metanotum pale brown to brown, with a broad,

darker brown transverse band on posterior margin. Legs: femora pale brown with a small, dark brown mark at apex; fore and middle femora with paler maculae (Fig. 107 and 168); tibiae pale brown, paler towards base and apex; tarsi brown to pale brown. Femoral and tibial spines, Fig. 189 and 190.

**Abdomen.** Posterolateral spines on segments 2–9, those on segments 6–9 enlarged (Fig. 107). Colour and markings as in subimago. Gills (Fig. 148–150) on segments 1–6 similar; gill 7 reduced to a small, single lamella (Fig. 149); lamellae greyish-black; tracheae and tracheal branches darker. Caudal filaments  $1.53\text{--}1.67(1.60) \times$  as long as body, brown with darker annulations at articulations; each segment with a distal whorl of dark brown denticles and small hairs.

**Egg** cylindrical, rounded at poles (Fig. 203); chorion with single and paired stellate attachment structures over surface (Fig. 203).

**Type data.** Phillips (1930, p. 356) found *Atalophlebia borealis* in a "small woodland stream on the property of Mr F. Heaton of Tanekaha, a few miles west of Hikurangi". The only known type material comprises 2 slides of nymphal legs and gills in the collection of the British Museum (Natural History), labelled "paratype" (entry number B.M. 1933–528) (seen). I designate this nymphal material as the lectotype of *Zephlebia borealis*.

**Material examined.** **North Island.** **ND.** S. Pandora, Te Pahi Coastal Park: 1 nymph, 7 Feb 1975, AKW (NZAC). Trib. of Wekaweka R., 10 km from Waimamuku: 1 ♂ subimago, 2 Dec 1966, AGM (CMNZ). Waipoua State Forest, stm below Ige kauri tree: 9 nymphs, 9 Jan 1967, RJR (AMNZ). Butterfly Vly, Tauranga Bay: 3 nymphs, 4–6 Apr 1967, GW (AMNZ). **AK.** 'Black Leg Dam': 3 nymphs, 15 Mar 1964, JAM (NZAC). Upper Pihā Stm: 7 nymphs, off log, 18 Apr 1964 (NZAC); 2 nymphs, 13 May 1964, JAM (NZAC). Karamatura Stm: 2 nymphs, trailing vegetation, 9 Jan 1977, DRT, ELT. Cascade Stm: 1 nymph, 23 Jan 1974; 1 ♂ imago, 1 ♀ subimago, reared from nymph, 25 Feb 1976, DRT; 1 ♂ subimago, light trap, 2 Nov 1966, JAM (NZAC); 1 ♀ imago, light trap, 9 Mar 1977, MGB. Sml trib. of Waitakere R. nr Anderson's Track: 1 ♀ imago, 1 ♂ subimago, light trap, 22 Feb 1977; 1 ♀ imago, light trap, 15 Mar 1977; 2 ♂ and 3 ♀ imagos, light trap, 30 Mar 1977, MGB. Waitakere R.: 1 ♀ subimago, light trap, 3 Apr 1977; 1 ♀ imago, light trap, 4 Apr 1977, MGB. Goldies Bush, Mokoroa Stm: 1 nymph, 15 Oct 1966, JAM (NZAC). Kitekite Stm: 8 nymphs, riffle, 6 nymphs, pool below falls, 27 Dec 1976, DRT, ELT, GCH, BWH. **CL.** Little Barrier I: Awaroa Stm – 16 nymphs, 15 Feb 1977; Tirikakawa Stm – 31 nymphs, 13 Feb 1977, JMD; locality unspecified – 1 nymph, Aug 1963, JAM (NZAC). Kauaeranga R.: 1 nymph, 4 Jan 1977, DRT. Sml trib. of Kauaeranga R.: 9 nymphs, in overhanging and emergent vegetation, 2 Jan 1977, DRT, ELT, BWH, GCH. **WO.** Dam 5 km N of Te Anga, Waitomo: 1 nymph, 16 Dec 1967, JKG (NMNZ). **BP.** Ngamuwahine Stm, Kaimai Ra.: 2 nymphs, stm margin, 30 Jan 1979, DRT, ELT, AJQ. **GB.** Waiputaputa Stm, nr Tokomaru Bay: 1 nymph, 3 Apr 1980, WJW. **TK.** Huatoki

Stm: 1 nymph, 11 Oct 1957, AH (NMNZ). WN. Stm in Haywards Reserve, Lower Hutt: 52 nymphs, 13 Jul 1979, DRT. [? region]Butterfly Ck: 1 ♀ subimago, 21 Jan 1959, BAH (NMNZ). No data: 1 ♂ imago, 1 ♂ and 1 ♀ subimago (CMNZ).

Repositories of additional material (all specimens are in ethanol): 2 ♂ and 5 ♀ imagos, 1 ♂ subimago, 5 nymphs – NZAC; 2 nymphs – AMNZ; 2 nymphs – CMNZ; 31 nymphs – NMNZ; 1 ♂ and 2 ♀ imagos, 1 ♂ and 1 ♀ subimago, 10 nymphs – BMNH; 6 nymphs – BPBM; 9 nymphs – FAMU; 8 nymphs – UUUS; remaining material – author's collection.

**Variation.** In most *Zephlebia* species the attachment of the base of vein  $MP_2$  is closer to  $CuA$  than to  $MP_1$ . In *Z. borealis* it is particularly close to  $CuA$  (Fig. 11), and in some specimens the 2 veins are directly connected, so that  $CuA$  appears to be forked (Fig. 97).

Most nymphs examined by me have gill 7 reduced to a single lamella, but a few specimens, including the lectotype, have a small partial second lamella (Fig. 150).

**Remarks.** In his revision, Phillips (1930) described the nymph of a species of *Atalophlebia* as "*Atalophlebia?* n.sp." and then stated (p. 356): "This species cannot be given a name until the winged stages have been found, but for convenience, I have given it the provisional name of *A. borealis* in my notebook." Penniket (1961), citing correspondence from Kimmins, pointed out that Phillips was incorrect in assuming that naming of a nymph has no nomenclatural force, and referred *A. borealis* to *Zephlebia* (*Zephlebia*). He thus ignored the fact that, mistakenly or not, Phillips's intent was that the name should be provisional. Despite this, the incomplete nature of the type material, and the fact that the description by Phillips is apparently in parts incorrect (see below), *borealis* is clearly an available name because it was proposed before 1961 (see International Code of Zoological Nomenclature, Art. 17(8)).

The type slides are presumably from the same nymph (they have the same entry number) and they are labelled in Phillips's handwriting "*Atalophlebia borealis* gills" and "*Atalophlebia borealis* legs of nymph". My identification of *Zephlebia borealis* is based on examination of the 7 gills and 3 legs on these slides. Reference slides of nymphal legs and gills from specimens used in the present diagnosis of *Z. borealis* have been deposited in the collections of the British Museum (Natural History) and in the New Zealand Arthropod Collection.

There are several conspicuous differences between Phillips's description of many nymphal characters of *Z. borealis* and my data. Furthermore, Phillips's description of the gills is rather misleading

because there is no mention of the small, submedian filament present on gills 1–6 and clearly visible in the type material.

The following characters were noted by Phillips (p. 356) as being useful: (1) the labrum bears 5 prominent teeth; (2) the abdomen is very broad, and narrows considerably posteriorly; (3) abdominal segments 9 and 10 are telescoped; (4) abdominal segments 6–9 have posterolateral spines. However, only character (1) appears to accurately describe the species. Character (2) seems more typical of *Z. spectabilis* than of *Z. borealis*, and character (4) is apparently incorrect: the only known species of *Zephlebia* with posterolateral spines restricted to segments 6–9 is *Z. versicolor*. All specimens of *Z. borealis* examined by me had clearly visible posterolateral spines on abdominal segments 2–9, although those on segments 6–9 were particularly large (Fig. 107).

*Zephlebia borealis* appears to be most closely related to *Z. dentata*, with which it has previously been confused (p. 11), but from which it can be distinguished by the following characters. IMAGO: (1) fore femora with a broad, diffuse, reddish-brown band; (2) body length generally more than 9 mm; (3) female with a sclerotised, prominent genital extension (Fig. 76); (4) male with abdominal terga 1–6 hyaline (Fig. 44). NYMPH: (1) labrum with prominent, pointed denticles on anteromedian emargination (Fig. 113); (2) mandibles with outer margin smoothly curved, and with broad incisors (Fig. 123); (3) galea-lacinia of maxillae with a subapical row of 15–18 spines; (4) gill lamellae greyish-black (Fig. 148); (5) abdomen with posterolateral spines on segments 6–9 enlarged (Fig. 107).

A small number of nymphs and subimagos in my collections from the Waitakere River area appear to be an undescribed species of *Zephlebia* near *Z. borealis*. This species, which differs from *Z. borealis* in nymphal gill shape, abdominal colour pattern, and colour and pigmentation pattern of the forewings and fore femora of the subimago, will be described when more material is available.

**Biology.** *Zephlebia borealis* is known only from the North Island. The nymphs are often abundant in slow-flowing reaches of heavily forested streams, particularly in aggregations of wood, twigs, and leaves (see, e.g., Towns 1978b). In some streams around Wellington *Z. borealis* and *Z. dentata* occur together in large numbers, but with *Z. dentata* most common in moderate flow and *Z. borealis* most common where flow is minimal. Near Auckland, *Z. dentata* appears to be less common and *Z. borealis* is often obtained with *Z. inconspicua* and *Z. versicolor*.

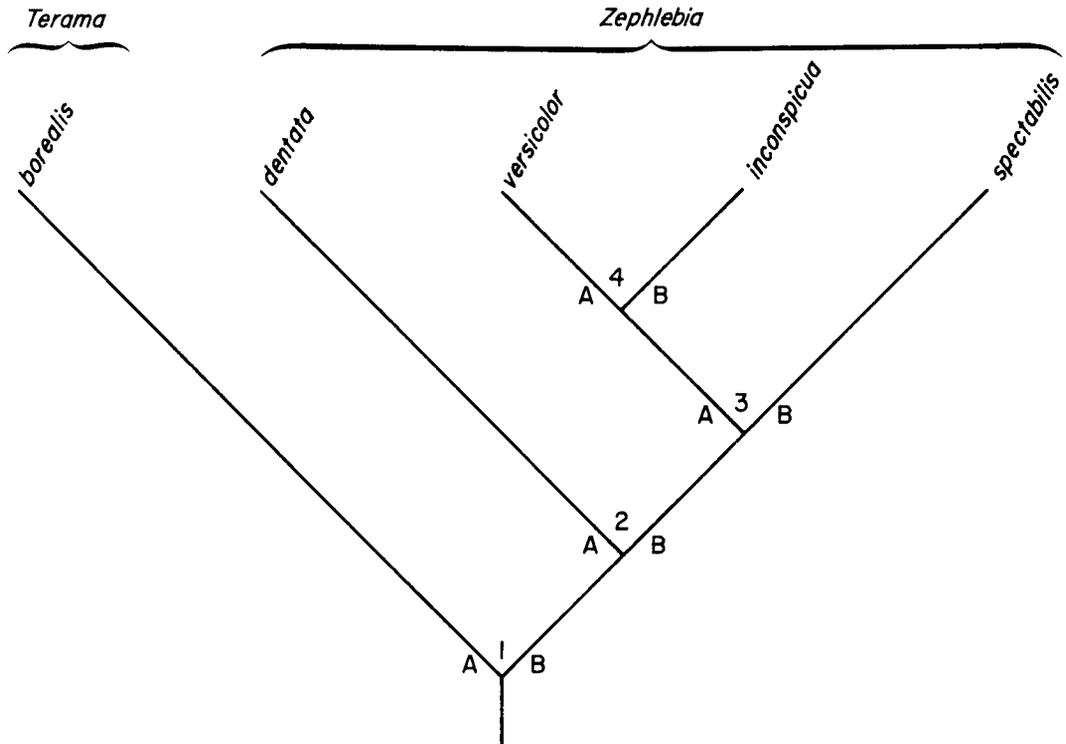


Fig. 1 Phylogenetic diagram of genus *Zephlebia*. For characters (A, B) at each furcation (1-4), see Table 2.

Table 2 Character states used in proposed phylogeny of species in *Zephlebia* s.l. (see Fig. 1); (D) derived, (P) primitive.

BRANCH A	BRANCH B
	Furcation 1
(P) abdomen narrowly oval, broadest at segments 4-6	(D) abdomen weakly to strongly tapered posteriorly
(P) incisors broad, stout (Fig. 119)	(D) incisors slender (Fig. 118)
(P) outer margin of mandibles smoothly curved (Fig. 123)	(D) outer margin of mandibles angular (Fig. 122)
	Furcation 2
(P) thoracic projections or spines absent	(D) prothorax and mesothorax with projections or spines (Fig. 175-177)
(P) abdomen with posterolateral spines on segments 2-9	(D) abdomen with posterolateral spines on segments 5 or 7 to 9
	Furcation 3
(P) abdomen weakly tapered posteriorly	(D) abdomen strongly tapered posteriorly
(P) abdomen with posterolateral spines on segments 5 or 6 to 9	(D) abdomen with posterolateral spines on segments 7-9
(D) egg carinate, the carinae formed into ridges and folded (Fig. 198 and 199)	(P) egg without carinae
	Furcation 4
(P) thoracic projections small	(D) thoracic projections large
(P) egg roughly oval (Fig. 198)	(D) egg fusiform (Fig. 201)

**PHYLOGENY OF *Zephlebia* s.l.**

A detailed phylogenetic analysis of the relationships within *Zephlebia* is premature, because I have material for at least 2 additional species, and the nymph of *Z. planulata* is unknown. The following analysis (Fig. 1) is included despite this, because it illustrates relationships within the genus as at present envisaged, and summarises possible evolutionary origins for specific character states. The derived and primitive states are given in Table 2 for each bifurcation.

This phylogeny supplements the preliminary analysis in Towns & Peters (1980). The more detailed analysis of *Zephlebia*, *Neozephlebia*, and *Acanthophlebia* carried out for the present revision showed no cause for change to the character state nomenclature used in the 1980 phylogeny. Published names for several newly established genera were not available when the 1980 paper went to press. Formally established names are now available for all genera in the 5 main lineages, plus component genera of the *Zephlebia* lineage. To avoid any possible confusion, previous and current nomenclature are listed below:

Towns & Peters (1980)	Revised names
" <i>Atalophlebioides</i> " <i>sepia</i>	<i>Austroclima</i> , <i>Mauilulus</i> (Towns & Peters 1979a)
<i>Zephlebia</i> ( <i>Neozephlebia</i> )	<i>Neozephlebia</i>
" <i>Zephlebia</i> " <i>cruentata</i>	<i>Acanthophlebia</i>
New genus I, II	<i>Arachnocolus</i> , <i>Isothraulax</i> (Towns & Peters 1979b)

The method of presenting data used here follows Towns & Peters (1980). The phylogeny is based on nymphal and egg characters alone; differences in genitalia and adult colour patterns do not form a useful basis for comparison. *Zephlebia planulata* has not been included. There is a tendency for species on the left of the cladogram (Fig. 1) to have a higher proportion of primitive characters, the proportion of derived characters increasing towards the right. This includes an evolutionary gradient in several character states; e.g., a decrease in the number of posterolateral spines on the abdomen from 2–9 to 7–9, and the appearance of thoracic spines and projections (see Table 2).

The status of mouthparts in *Z. borealis* poses a problem of interpretation (Fig. 1, Table 2). The short, stout incisors and smoothly curved mandibles can be regarded as a feeding adaptation within the genus and therefore as representing the derived condition relative to the rest of the genus (Fig. 119 and 123). Alternatively, in relation to the evolution of mouthpart structures within the family as a whole, those of *Z. borealis* represent the more primitive condition. I have taken the second approach, because the first is difficult to reconcile

with mouthpart structures in many other genera. As a result, only primitive character states separate *Terama* from *Zephlebia* s.s. The prominent denticles on the labrum of *Z. borealis* (Fig. 113) might be interpreted as the derived state, but those of *Zephlebia* s.s. are also highly distinctive (Fig. 111). I have been unable to assess the significance of these structures, and they are not included in the analysis.

**Genus *Neozephlebia* Penniket**

Penniket, 1961: 8 (as a subgenus of *Zephlebia*).

**Imago.** Length: male – body 7.3–8.9 mm, forewings 7.3–9.2 mm; female – body 6.2–8.1 mm, forewings 8.2–10.1 mm.

**Eyes:** male – fused on meson of head, the lower portion two-thirds to three-quarters as wide as upper portion; female – separated on meson of head by  $2\frac{1}{2}$  to  $3\times$  maximum width of eye.

**Wings,** Fig. 13–15. Forewings a little less than one-third to one-third as wide as long. Vein Rs forked a little less than one-fifth to one-fifth distance from base to margin. Vein MA forked a little more than two-fifths to a little more than half distance from base to margin; fork symmetrical. Vein MP not forked; ; MP<sub>2</sub> attached at base to CuA and MP<sub>1</sub> with a cross-vein; attachment of MP<sub>2</sub> to MP<sub>1</sub> a little more than one-quarter to a little more than one-third distance from base to margin; base of MP<sub>2</sub> closer to MP<sub>1</sub> than to CuA. Vein ICu<sub>1</sub> attached at base to CuA and CuP with cross-veins. Remainder of Cu–A area as in Fig. 13, with few cross-veins. Hind wings a little less than two-thirds to a little less than three-quarters as wide as long and a little more than one-tenth to a little less than one-fifth as long as forewings; Sc seven-tenths to four-fifths as long as wing; R<sub>1</sub> a little less than nine-tenths as long as wing to almost equal; cross-veins few; costal margin with blunt projection at two-fifths to half wing length (Fig. 15); apex rounded.

**Legs.** Length ratios of segments in male forelegs 0.53–0.61 : 1.00 (2.8–3.8 mm) : 0.03–0.04 : 0.37–0.43 : 0.42–0.47 : 0.34–0.39 : 0.15–0.17. Claws of a pair alike, apically hooked, with an opposing hook (Fig. 20).

**Male genitalia** (Fig. 34 and 35). Forceps: base broad, the inner margin forming an angular to smooth bend near midlength (Fig. 34); segment 2  $1\frac{1}{2}\times$  as long as segment 3 and a little less than one-fifth to a little more than one-quarter as long as segment 1; apex of segment 3 rounded. Styliger plate a little less than two-fifths to a little less than three-fifths as long medially as maximum width; apex cleft (Fig. 34). Penes: lobes divided to styliger plate, each lobe two-fifths as long as forceps

segment 1 and with a small area of spines on dorsolateral surface near penis opening (Fig. 50).

Sternum 7 of female without a genital extension; sternum 9 deeply cleft (Fig. 62).

Terminal filament a little longer than cerci.

**Mature nymph.** Length of body 6.0–8.8 mm. Head prognathous. Antennae a little less to a little more than twice as long as head.

Mouthparts. Labrum as wide as clypeus or a little wider,  $1\frac{1}{4}\times$  as long as clypeus, and a little less than two-fifths to a little less than half as long as wide, with dorsal hair as in Fig. 114, and submedian, anterosubmedian, and anterolateral areas of hair ventrally; anterior margin with a rectangular median concavity (Fig. 114) bearing 5 denticles, the median denticle largest (Fig. 115). Clypeus, Fig. 114; lateral margins subparallel. Left mandible with a few scattered hairs on outer margin in apical one-third and near base (Fig. 124); outer margin smoothly curved, slightly expanded laterally at base of incisors (Fig. 124), which are large and stout with unserrated apical teeth; prosthecal tuft large (Fig. 120). Hypopharynx: lingua with well developed lateral processes, anterior margin deeply cleft, and apex of submedian lobes acute (Fig. 138); superlingua, Fig. 138. Maxillae: galea–lacinia narrow in apical half, with a subapical row of 13–16 spines (Fig. 128); palp segment 1 with small spines on outer margin (Fig. 128); segment 2 a little shorter to a little longer than segment 1; segment 3 short, subtriangular, a little more than two-fifths to three-fifths as long as segment 2 (Fig. 128). Labium, Fig. 132–134; palpi broad; segment 2 four-fifths to a little more than nine-tenths as long as segment 1; segment 3 a little less than half to two-thirds as long as segment 2, subtriangular, the inner margin with row of short, stout spines (Fig. 132); glossae dorsal to paraglossae, the apex as in Fig. 133 and 134, the surface with prominent, blunt spines (Fig. 133); submentum, Fig. 132.

Pronotum with spines on anterolateral margin. Pronotum and mesonotum with scattered fine hairs on lateral margins (Fig. 108). Legs, Fig. 108, 169, 171, 172, and 191–193). Femora narrowly oval, the apical half deeply indented so tibia can draw into femur (Fig. 169); dorsal and lateral surface of fore femora with long, bipectinate spines (Fig. 191), ventral surface with stout, bipectinate and serrated spines (Fig. 192). Fore tibiae with large, bipectinate spines (Fig. 193). Claws hooked, narrow; denticles small, numerous, progressively larger distally (Fig. 160).

Abdomen narrowly oval, broadest at segments 4–6 (Fig. 108); posterolateral spines on segments 5 or 6 to 9; projections on segment 9 modified (Fig. 178). Gills (Fig. 151 and 152) on segments 1–7 alike, but progressively smaller posteriorly; dorsal and ventral

portions of lamellae slender, smoothly tapered to apex; main trunk of tracheae pigmented, with fine tracheal branches (Fig. 151). Caudal filaments a little longer than body; terminal filament a little longer than cerci; each segment with a distal whorl of very small denticles and fine hairs (Fig. 108).

**Egg** cylindrical with rounded poles, each pole with extremely long, irregularly coiled, thread-like attachment structures; chorion covered with small nodules (Fig. 205).

**Type species** *Neozephlebia scita* (Walker), by original designation (Penniket 1961); originally placed in *Baetis*.

**Remarks.** *Neozephlebia scita* was first described in *Baetis* by Walker (1853), then moved by Eaton (1871) to *Leptophlebia*, and again to *Atalophlebia* (Eaton 1884). Eaton (1871) described a second species, *A. nodularis*. Subsequently the identity of both species has been clouded by taxonomic confusion. Lillie (1898) described adult and nymphal material of 2 species which he determined as *Atalophlebia scita* and *A. nodularis*. However, Eaton (1899) found Lillie's "A. scita" to be an undescribed species in a new genus, and named it *Deleatidium lillii*. Lillie (1900) acknowledged the error in his 1898 paper, but Hudson (1904, p. 34) was clearly influenced by Lillie's 1898 publication when he stated that *A. scita* "appears to very closely resemble *Deleatidium lillii* in superficial appearance". Phillips (1930) took Lillie's initial misidentification one step further by assuming *A. scita* to be a synonym of *Deleatidium lillii*, and not a valid species name. The validity of both *scita* and *nodularis* was recognised by Kimmins (1960) and Penniket (1961). The 2 species were transferred by Penniket (1961) to *Neozephlebia*, a subgenus of *Zephlebia* with *N. scita* as type species. *N. scita* is the only species recognised here (see also p. 27). In separating *Neozephlebia* from *Zephlebia* s.s., Penniket (1961) recognised the many differences between the 2 groups of species, although apparently he was not aware of the extent of these differences, mainly because his analysis did not include nymphal morphology. In their phylogenetic study of Gondwanian Leptophlebiidae, Tsui & Peters (1975) found by similarity index analysis that *Zephlebia* s.s. and *Neozephlebia* differ more than would be expected within a genus. Pescador & Peters (1980) and Towns & Peters (1980) endorsed this assessment; indeed, it has been suggested that *Neozephlebia* is more closely related to the *Atalonella* lineage of Australia and South America than to other known genera in New Zealand (Pescador & Peters 1980). On the basis of these

affinities and distinctive characters of the adult and nymph, *Neozephlebia* is here raised to generic rank.

*Neozephlebia* can be distinguished from all other leptophlebiid genera by the following combinations of characters. IMAGO: (1) hind wings less than one-fifth as long as forewings, and with a blunt costal projection (Fig. 14 and 15); (2) forewing vein  $MP_2$  with base closer to  $MP_1$  than to  $CuA$  (Fig. 13); (3) penes divided to styliger plate, and with areas of spines on dorsolateral surface near penis openings (Fig. 34 and 50); (4) claws of a pair alike, apically hooked, with an opposing hook (Fig. 20); (5) sternum 9 of female deeply cleft (Fig. 62); (6) sternum 7 of female without a genital extension. NYMPH: (1) clypeus as wide as labrum or a little narrower, and with subparallel margins (Fig. 114); (2) labrum with 5 denticles on anteromedian margin, the central denticle largest (Fig. 115); (3) mandibles with outer margin smoothly curved and with a few scattered hairs in distal one-third and near base (Fig. 124); (4) galea-lacinia of maxillae narrow, and with a subapical row of 13–16 spines (Fig. 128); (5) maxillary palpi with segment 3 short and subtriangular (Fig. 132); (6) glossae of labium straight and with a large, blunt spine at apex (Fig. 133); (7) claws with numerous small denticles (Fig. 160); (8) abdominal gills 1–7 with similar, double, slender lamellae (Fig. 151 and 152); (9) abdomen with posterolateral spines on segments 5 or 6 to 9.

*Neozephlebia* appears to be most closely related to undescribed genera from New Caledonia (Peters & Peters, in prep.).

### *Neozephlebia scita* (Walker)

Walker, 1853: 570 (in *Baetis*). —Eaton, 1871: 81 (in *Leptophlebia*). —Eaton, 1884: 90; —Hutton, 1898: 216; —Eaton, 1899: 288; —Hudson 1904: 34; —Kimmins, 1960: 295 (in *Atalophlebia*). —Penniket, 1961: 9; —Winterbourn & Towns, 1981: 18 (in *Zephlebia* (*Neozephlebia*)). —Cadwallader, 1975a: 12; 1975b: 16; 1975c: 304; —Michaelis, 1977: 366 (as *Zephlebia*). —Towns, 1978b: 367 (as *Zephlebia scita/nodularis*).

Not *Atalophlebia scita*. Lillie, 1898: 167 (see Lillie, 1900: 149).

*Leptophlebia nodularis* Eaton, 1871: 81; 1884: 89; 1899: 288. —Lillie, 1898: 168; —Hutton, 1898: 216; —Hudson, 1904: 34; —Phillips, 1930: 352–355; —Mosely, 1932: 8; —Kimmins, 1960: 295; —McLean, 1967: 99 (in *Atalophlebia*). —Penniket, 1961: 9; —Winterbourn & Towns, 1981: 18 (in *Zephlebia* (*Neozephlebia*)). —Towns, 1978a: 410; 1979: 255 (as *Zephlebia*). **New synonymy.**

**Male imago** (in ethanol). Head dark brown, whitish to pale brown medially, on anterior margin, and between eyes and base of antennae. Eyes with upper portion pale brown to brown, lower portion black. Antennae with scape, pedicel, and flagellum pale brown to whitish, the scape washed with black at

apex. Ocelli with basal half black, apical half white.

Thorax. Pronotum pale brown to brown, blackish-brown submedially and on margins; mesothorax and metathorax pale yellowish-brown to dark brown, darker submedially between basal humps of scutellum; posterior scutellum darker; metathorax occasionally with a broad, darker, mid-dorsal transverse band. Pleura pale brown to dark brown, irregularly washed with darker brown; carinae black; propleuron with an irregular, dark brown band from dorsoposterior margin to antero-ventral margin of coxae. Sterna variably pale yellowish-brown washed with dark brown through to dark brown with lateral lobes of furcasternum paler. Legs pale, whitish to yellowish; fore femora sometimes darker, with dark brown marks near base and apex and a diffuse, dark brown band near midlength; fore tibiae darker at base, and with a broad, blackish-brown band at apex; fore tarsal joints darker; middle and hind femora with a diffuse band at midlength and with or without darker marks near base; middle and hind tibiae sometimes darker at articulation with femora. Wings, Fig. 13–15. Forewings: cross-veins in cells C, Sc, and  $R_1$  surrounded by brown to dark brown clouds (Fig. 13), these clouds narrower in cell  $R_1$ ; sometimes a diffuse, pale brown cloud extended from cell C to  $R_1$  at wing midlength (Fig. 13); longitudinal veins and remainder of cross-veins pale to dark brown; membrane hyaline, except base washed with pale brown to brown, and apical one-third of cells C and Sc translucent whitish. Hind wings: longitudinal veins and cross-veins hyaline to pale brown; membrane hyaline, but wing base washed with pale brown to brown.

Abdomen. Terga brown to dark brown; terga 2–8 often with darker anterolateral marks, hyaline anterior margin, and paired anterior, submedian, and lateral hyaline maculae (Fig. 45). Tracheae hyaline; spiracular area black. Sterna brown; sterna 2–7 with paired, hyaline, anterior submedian maculae; sternum 8 with paired, pale brown, anterior submedian maculae; abdominal ganglia hyaline. Genitalia (Fig. 34 and 35) pale brown to brown; styliger plate and base of penis lobes sometimes darker. Caudal filaments whitish to yellowish, with dark brown bands at articulations that become progressively wider distally.

**Female imago** (in ethanol). Head pale brown, with markings as in male imago but with dark brown areas on posterior margin, medially on anterior margin, on midline between eyes, and between antennae anterior to median ocellus. Eyes black. Antennae and ocelli as in male imago.

Thorax, legs, and wings with colour and markings as in male imago, but pronotal midline blackish.

Abdomen. Colour and markings as in male imago, but lateral maculae and anterior margin of terga 2–8 pale brown, and terga 2–9 with pale brown anterior submedian maculae. Caudal filaments as in male imago.

**Male and female subimago** (in ethanol). Head colour and markings, eyes, antennae, and ocelli as in imago.

Thorax. Colour and markings of pronotum as in imago; mesonotum pale yellowish-brown to brown, with a broad, whitish to pale brown band along inner margin of outer parapsidal sutures (Fig. 55) and pale submedian marks on dorsum (Fig. 55); anterior half of outer parapsidal sutures brown, paler posteriorly (Fig. 55); basal humps of scutellum yellowish-brown to brown submedially, dark brown on midline, pale brown on dorsum and lateral margins (Fig. 55); posterior scutellum pale, washed with greyish-brown. Sterna: colour and markings as in imago. Legs: colour and markings as in imago, but fore femora washed with brown near apex. Wings, Fig. 99 and 100. Membranes brownish; longitudinal veins and cross-veins brown, paler in hind wings; forewing cells C and Sc pigmented as in imago; remainder of forewing cross-veins with greyish clouds (Fig. 99) that are fused near fork of Rs and near base of intercalaries (Fig. 99), or mainly restricted to cross-veins.

Abdomen. Colour and markings as in imago, but terga 2–8 with translucent whitish-brown maculae and anterior margins. Sterna as in imago but pale brown to dark brown, and segments 2–7 with translucent whitish-brown maculae. Male genitalia: colour and markings as in imago, sometimes paler. Caudal filaments as in imago.

**Mature nymph** (in ethanol). Head brown washed with dark brown between ocelli, sometimes dark brown at base of antennae, and pale brown between antennae anterior to median ocellus; mandibles, labrum, and clypeus tinted with orange-brown; midline between eyes dark brown (Fig. 108). Ocelli with base black, apex greyish. Eyes black in female; in male, upper portion dark reddish-brown, lower portion black. Antennae pale, yellowish.

Thorax pale brown to brown, irregularly washed with darker brown submedially (Fig. 108), with or without dark brown marks on lateral margins; pleura and sterna as in imago. Legs pale, whitish to yellowish-brown; femora with a dark brown band near midlength (Fig. 108 and 169) that is often less distinct on middle and hind legs; sometimes a dark brown band at apex of femora and apex of fore tarsi.

Abdomen. Colour and markings as in subimago, but lateral margins of terga whitish to yellowish; terga with a narrow, yellowish, longitudinal line on mid dorsum, and at base of gills often with dark

brown to black marks (Fig. 108). Gills, Fig. 151 and 152; lamellae hyaline; tracheae dark grey to black, occasionally with very short, fine branches. Caudal filaments pale brown; each segment with a distal whorl of dark brown denticles and small hairs.

**Type data.** The only type material still in existence is a damaged male imago in the British Museum (Natural History), designated as lectotype by Kimmins and with the type data "N. Zeal." (Kimmins 1960, p. 295) (seen).

**Material examined.** **North Island.** **ND.** Mat[a]juri Bay: 8 nymphs, 23 Aug 1966, MW (NZAC). Butterfly Vly, Tauranga Bay: 4 ♀ imagos, 28 Sep 1966; 1 ♀ imago, 30 Mar 1968, KAJW (AMNZ); 6 nymphs, 4–6 Apr 1969, GW (AMNZ). Opononi, forest remnant; 1 ♂ subimago, 17 Nov 1968, KAJW (AMNZ). Whangarei Falls: 2 ♂ and 2 ♀ imagos, 11 Oct 1967; 1 ♀ imago, 14 Nov 1968, KAJW (AMNZ). **AK.** Leigh: 6 nymphs, 24 Jun 1979, DRT. Auckland: 1 ♀ imago, 9 Jan 1919, CEC (AMNZ; pinned). Cascade Stm: 7 ♂ and 18 ♀ imagos, 30 Oct 1966; 1 ♂ imago, 3 Nov 1966, JAM (NZAC); 10 ♀ imagos, 9 Feb 1977; 1 ♂ and 1 ♀ imago, 1 ♂ subimago, 9 Mar 1977, MGB. Waitakere R.: 1 ♀ imago, 7 Nov 1966, JAM (FAMU); 1 ♂ and 4 ♀ imagos, 1967; 1 ♂ and 2 ♀ imagos, 7 Nov 1967, JAM (AMNZ); 6 ♀ imagos, light trap, 12 Nov 1975; 1 ♀ imago, reared, 2 Nov 1973; 1 ♂ imago, reared, 7 Nov 1973; 1 ♂ imago, reared, 11 Nov 1973; 1 ♀ imago, reared, 18 Nov 1973, DRT; 3 ♂ and 1 ♀ imagos, light trap, 8 Feb 1977, MGB. Sml trib. of Waitakere R. nr Anderson's Track: 3 ♂ imagos, light trap, 16 Feb 1977; 1 ♀ imago, light trap, 15 Feb 1977; 1 ♂ and 1 ♀ imago, light trap, 22 Feb 1977, MGB. Kitekite Stm: 2 nymphs, 27 Dec 1976, DRT, ELT, BWH, GCH. Swanson: 1 ♀ subimago, 6 Oct 1963, JAM (NZAC). Henderson: 1 ♀ imago, 1 Dec 1958; 1 ♂ and 1 ♀ subimago, 30 Nov 1958, KAJW (NZAC). Miranda: 1 nymph, 3 Dec 1950, KAJW (NZAC). **CL.** Sml trib. of Kauaeranga R.: 3 nymphs, in overhanging and emergent vegetation, 2 Jan 1977, DRT, ELT, BWH, GCH. Sml silty trib. of Kauaeranga R.: 1 nymph, 4 Jan 1977, DRT. Wainora Stm: 1 nymph, 2 Jan 1977, DRT, ELT, BWH, GCH. **TK.** Huatoki Stm: 7 nymphs, 11 Oct 1957, AH (NMNZ). **WN.** Day's Bay: 1 nymph, 23 Dec 1964, RGO (NMNZ). Rimutaka Forest Pk, Catchpool Stm: 8 nymphs, 8 Jul 1979, DRT, BWH. Stm in Hayward's Res., Lower Hutt: 14 nymphs, 13 Jul 1979, DRT. Hutt R. nr Silverstream Hospital: 1 nymph, 12 Jul 1979, DRT, ELT, BWH, GCH. Tyer's Stm, Khandallah Res.: 17 nymphs, 14 Jul 1979, DRT, ELT, BWH, GCH.

**South Island.** **SD.** Queen Charlotte Sd: Pickersgill I. – 1 nymph, 7 Nov 1961, BAH; Blumine I. – 4 nymphs, 30 Sep 1963, MAC (NMNZ). Waikawa Bay: 1 ♀ subimago, 1 nymph, 17 Jan 1968, JRH (NMNZ). **NN.** Aniseed Vly: 3 ♂ imagos, 1 ♂ subimago, beating *Nothofagus menziesii*, 14 Jan 1976, AKW (NZAC). Spooner Ck: 3 nymphs, 23 Oct 1966, JI (UUUS). Anatori R. overflow: 20 nymphs, 26 Oct 1969, IDM (FAMU). Sml ck nr Anatori R.: 1 ♂ imago, 1 ♀ subimago, 3 nymphs, 24 Oct 1969, IDM (FAMU). Pupu Springs: 1 ♂ and 3 ♀ imagos, 1 ♀ subimago, 16 Apr 1970, GK (NZAC). Sml ck nr Matai R.: 2 ♀ subimagos, IDM (NZAC). Coal Ck, nr Owen R.: 1 nymph, 19 Jan 1973, IDM (FAMU). Gowan R. nr Gowanbridge: 2 nymphs, 6 Mar 1966, GFE (UUUS). Fuchsia Ck, Buller Gorge: 1 ♀ imago, 6 Oct 1969, JSD (NZAC); 1 nymph, 31 May 1969, IDM (FAMU). Sml ck nr Fuchsia Ck: 17 nymphs, 18 Dec 1969, IDM. Sml ck N of Hawkes Crag: 1 nymph, 14 Feb

1970, IDM. Hawkes Crag Ck: 2 nymphs, 22 Feb 1970, IDM. Dirty Mary's Ck, nr Westport: 1 ♂ and 2 ♀ subimagos, 6 nymphs, 1 Nov 1969, IDM. BR. Ikamatua, nr Reefton: 1 ♀ imago, 1 ♀ subimago, 26 Oct 1966, JIT (NZAC). Paroa Stm: 6 nymphs, 4 Mar 1966, GFE (UUUS). Kokiri: 2 ♂ and 1 ♀ imagos, 3 nymphs, 7 Oct 1960, JGP (FAMU); 1 ♀ imago, 25 Nov 1960, JGP (CMNZ); 1 ♀ imago, 4 Mar 1966, GFE (UUUS). Arnold R.: 3 nymphs, 5 Mar 1966, GFE (UUUS). WD. Otira Gorge: 1 nymph, 5 Nov 1966, JIT (NZAC). WD. Okarito R.: 1 nymph, 27 Oct 1966, JIT (NZAC). NC. Arthur's Pass, 914 m: 1 nymph, 4 Mar 1966, GFE (UUUS). SC. Orari Gorge: 2 nymphs, 5 Nov 1966, JI (UUUS). DN. Waipouri R.: 1 nymph, 4 Nov 1966, JIT (NZAC). FD. Sml stm nr Cascade Ck, 550 m: 2 nymphs, 30 Oct 1966, JI (UUUS). SL. Kuriwao Stm nr Clinton: 1 nymph, 3 Nov 1966, JIT (NZAC).

Repositories of additional material (all specimens are in ethanol): 3 ♂ and 3 ♀ imagos, 4 nymphs - NZAC; 4 ♀ imagos, 1 ♂ subimago, 6 nymphs - CMNZ; 1 ♂ and 4 ♀ imagos - NMNZ; 2 ♂ and 1 ♀ imagos, 1 ♂ subimago, 5 nymphs - BMNH; 3 ♂ and 1 ♀ imagos, 9 nymphs - BPBM; 1 ♂ and 2 ♀ subimagos, 6 nymphs - FAMU; 1 ♂ and 7 ♀ imagos - UUUS; remaining material - author's collection.

**Variation.** The colour of adults and nymphs in ethanol ranges from pale brown to dark brown, most variation occurring in the thoracic nota and abdominal terga. Examination of 54 imagos obtained in the Waitakere River catchment between October and April (light trapping, DRT, JAM, MGB) showed no clear seasonal variation in the abundance of any one colour variety. Generally both dark and pale specimens were present together, usually also with specimens of intermediate colour. The intensity and size of clouds in the forewings of adults also varies; some specimens have an indistinct cloud in one wing and a well defined cloud in the other. Intensity of colour in the femoral bands is variable, and in nymphs may be related to maturity. Nymphs with black wing pads often have much darker leg banding than less mature nymphs in the same population. Nymphs commonly appear to have a broad, dark transverse band on the posterior margin of abdominal terga, but this is the result of telescoping of the abdominal segments. Telescoping of the abdomen also commonly obscures most of the submedian maculae. The anterolateral maculae show some variation in size; in some populations they almost fuse between terga to form longitudinal lines. Occasionally similar enlargement occurs in the submedian maculae, but these fuse laterally to form a single triangular patch. The pale mid dorsal line on the nymphal abdomen is generally well developed in mature specimens, but is commonly absent in earlier instars. In small nymphs abdominal tergum 10 is often much paler than terga 1-9, in contrast to the condition in mature specimens.

**Remarks.** In his accounts of "*Atalophlebia scita*" and "*A. nodularis*", Eaton (1871, 1884) provided

illustrations of male genitalia—presumably dried material—in which the penis lobes of *A. nodularis* are fused and those of *A. scita* are divided. Kimmins (1960) gave clear illustrations of relaxed preparations of the same series which show genitalia almost identical in structure but slightly different in size. In both species the penes are divided. After examining the type material of *scita* and *nodularis*, and a large quantity of adult and nymphal material from throughout New Zealand, including SEM studies of genitalia and eggs, I can find no evidence of the presence of more than one species. Pale and dark colour varieties are common, and these may account for the 2 'species' previously described. Supposed differences between them can be accounted for by distortion of genitalia during drying and variation in both ground colour and size of the anterolateral and submedian maculae of the abdominal terga. For instance, "abdomen ... with translucent subtriangular spaces in segments 2-5" vs "segments 3-6 above marked, close to base, each with a pair of translucent yellowish spots in the midst" (see Eaton 1884, p. 89 and 90, *Atalophlebia nodularis* and *A. scita* respectively). *Leptophlebia nodularis* is accordingly considered here to be a synonym of *Neozephlebia scita*.

**Biology.** *Neozephlebia scita* occurs throughout New Zealand from near sea level to approximately 1000 m a.s.l., and has been recorded from an extremely wide range of habitats. These include springs (Michaelis 1977), clumps of algae in heavily forested streams (Towns 1978b), on soft mud (Lillie 1898), among weed (Penniket 1961), and in streams with slow to moderate flow on stones or among debris (Phillips 1930). In the Waitakere system *N. scita* occurred in the widest range of habitats of any mayfly species, from pools with no measurable flow to cascade areas with a flow rate of 2 m.s<sup>-1</sup> (Towns 1976). I have also found nymphs to be abundant in very small forested streams in riffle areas or on a silty substrate in aggregations of wood and leaf material (commonly associated with *Zephlebia borealis*) and in more open streams among aquatic and semi-aquatic macrophytes.

*Neozephlebia scita* enters drift as nymphs, and has a well synchronised diel pattern, with a peak of drift rate after sunset and a decline towards dawn (Cadwallader 1975a). Nymphal growth is poorly synchronised in the Waitakere River, producing a very long potential emergence period (Towns 1981, 1983). In the various light-trap collections from the Waitakere River area (JAM, MGB, DRT) adults were present from October to April. This is one of the few New Zealand species for which swarming behaviour has been recorded. McLean (1967) found *N. scita* swarming above *Acanthophlebia cruentata* in mid afternoon at 5-10 m, mostly over pools.

***Acanthophlebia* n.gen.**

**Imago.** Length: male - body 9.1-10.1 mm, forewings 9.3-10.5 mm; female - body 8.0-9.2 mm, forewings 9.5-10.2 mm.

Eyes: male - separated on meson of head by width of midline, the lower portion a little less than two-thirds to three-quarters as wide as upper portion; female - separated on meson of head by  $2\frac{3}{8}$  to  $3\frac{3}{8}$  × maximum width of eye.

Wings, Fig. 16-18. Forewings one-third to two-fifths as wide as long. Vein Rs forked a little more than one-tenth to one-fifth distance from base to margin. Vein MA forked a little more than two-fifths to half distance from base to margin, the fork symmetrical. Vein MP not forked;  $MP_2$  attached at base to CuA and  $MP_1$  with a cross-vein; attachment of  $MP_2$  to  $MP_1$  a little less than one-fifth to a little less than one-quarter distance from base to margin; base of  $MP_2$  equidistant between  $MP_1$  and CuA. Vein  $ICu_1$  attached at base to CuA with a cross-vein, but not attached to CuP (Fig. 16). Remainder of Cu-A area as in Fig. 16. Cross-veins in apical one-third of cell C often anastomosed (Fig. 16). Hind wings a little less than half to three-fifths as wide as long and a little more than one-fifth to one-quarter as long as forewings; vein Sc nine-tenths as long as wing or a little more or less;  $R_1$  a little shorter than wing; cross-veins numerous (Fig. 17 and 18); costal margin convex, but slightly concave on mid-costal margin (Fig. 17 and 18); apex rounded.

Legs. Length ratios of segments in male forelegs 0.66-0.71 : 1.00 (2.8 mm): 0.06 : 0.40-0.44 : 0.37-0.41 : 0.31-0.35 : 0.11. Claws of a pair alike, apically hooked, with an opposing hook (Fig. 21).

Male genitalia (Fig. 36-38). Forceps: base broad, the inner margin forming an angular bend near midlength (Fig. 38); segment 2 three-fifths to four-fifths as long as segment 3 and one-tenth to a little less than one-fifth as long as segment 1; apex of segment 3 rounded. Styli: plate one-third to a little less than two-fifths as long medially as maximum width; apex slightly cleft (Fig. 38). Penes: lobes fused except for apical one-quarter; penis openings on ventral surface, with a fringe of spines (Fig. 36 and 51).

Sternum 7 of female with genital extension reaching a little more than one-fifth to two-fifths along sternum 8 (Fig. 70 and 78); sternum 9 strongly cleft (Fig. 63).

Terminal filament a little longer than cerci.

**Mature nymph.** Length of body 7.9-10.9 mm. Head prognathous. Antennae  $2\frac{1}{2}$  × as long as head.

Mouthparts. Labrum about nine-tenths as wide as clypeus, nine-tenths to  $1\frac{1}{10}$  × as long as clypeus, and a little more than one-third to a little more than two-fifths as long as wide, with dorsal hair and spines as

in Fig. 116, and submedian, anterosubmedian, and scattered lateral areas of hair ventrally; anterior margin smoothly curved, with a rectangular median concavity (Fig. 116) containing 5 denticles, the median denticle smallest (Fig. 117). Clypeus, Fig. 116; lateral margins subparallel to slightly convergent apically. Left mandible with large hairs near mid outer margin, small hairs on dorsal surface, and spines extended to base (Fig. 125); outer margin smoothly curved (Fig. 125); incisors short, stout, the right outer incisor with prominent denticles (Fig. 121); prosthecal tuft large, its base forming a fleshy lobe (Fig. 121). Hypopharynx: lingua with well developed lateral processes; anterior margin deeply cleft; apex of submedian lobes rounded (Fig. 139); superlingua, Fig. 139. Maxillae: apical half of galealacinia narrow, with a subapical row of 9-12 spines (Fig. 129); some apical spines simple, pointed, others pectinate; palp segment 2  $1\frac{1}{2}$  to  $1\frac{3}{4}$  × as long as segment 1, broadening distally; segment 3 two-fifths to three-fifths as long as segment 2, subtriangular, with spines on outer margin and dense hairs on ventral surface (Fig. 129). Labium, Fig. 135 and 136; palpi broad; segment 2 one-third to a little less than nine-tenths as long as segment 1; segment 3 three-fifths to seven-tenths as long as segment 2, subtriangular, its inner margin with a row of short, stout spines (Fig. 135); glossae dorsal to paraglossae, rounded apically (Fig. 136), with numerous long hairs on surface and stout spines on apex and lateral margin of dorsal surface (Fig. 135 and 136); submentum, Fig. 135.

Pronotum with spines on anterolateral margin. Lateral margins and dorsum of nota with scattered fine hairs (Fig. 109). Legs, Fig. 170. Femora broad at base, narrower apically (Fig. 170); apical half indented, so tibia can draw into femur (Fig. 170); dorsal and lateral surface of fore femora with long, finely bipectinate spines (Fig. 194), ventral surface with short, bipectinate spines (Fig. 195); fore tibiae with numerous large, finely and coarsely bipectinate spines on inner surface (Fig. 196 and 197). Claws hooked and narrow apically, with well developed denticles, the distalmost 6 approximately equal in size (Fig. 161).

Abdomen narrowly oval, broadest at segment 6 (Fig. 109); posterolateral spines on segments 2 or 3 to 9; projections on segments 7-9 modified as in Fig. 179. Gills (Fig. 153 and 154) on segments 1-7 alike, but progressively smaller posteriorly; lamellae with dorsal and ventral portions broad near base, tapered towards apex; main tracheal trunk along median line of lamellae, in which tracheal branches densely ramify (Fig. 153 and 154). Caudal filaments a little longer than body; terminal filament a little longer than cerci; each segment with a distal whorl of small denticles and long, fine hairs (Fig. 109).

**Egg** elongate oval; chorion with dense, small tubercles and large, paired attachment structures (Fig. 206).

**Etymology.** The name derives from *akantha* (Greek, 'a thorn'), in reference to the large posterolateral projections of the nymphal abdomen, and *phlebos* (Greek, 'a vein'), commonly used as a suffix in this family; gender feminine.

**Type species:** *Acanthophlebia cruentata* (Hudson) n.comb.; originally placed in *Atalophlebia*.

**Remarks.** *Acanthophlebia cruentata* was originally described in *Atalophlebia* by Hudson (1904). Penniket (1961) removed all New Zealand species from *Atalophlebia* and placed them in 2 subgenera of *Zephlebia*. On the basis of the following characters in the adult, Penniket (1961, p. 8) referred *cruentata* to *Zephlebia* (*Zephlebia*): "...penes conjoined almost if not quite to tips, spines within or on rim of 'cup'; distal margin of subanal plate of female very slightly if at all emarginate". My SEM studies have shown that the spines differ in form and position from those of *Zephlebia* (see Fig. 51). The spines (and the penis openings) of *cruentata* are situated more ventrally than in *Zephlebia*. Also, *cruentata* has fleshy folds on the ventral surface of the penes similar to those in some species of *Atalophlebia* from Australia (see Suter 1980), but absent from *Zephlebia*. Further, sternum 9 ('subanal plate' of Penniket) in *cruentata* is strongly cleft, not entire or almost so as in *Zephlebia* (Fig. 63). In his characters distinguishing nymphs of *Zephlebia*, Penniket unfortunately did not consider mouthpart structure. The mouthparts of *cruentata* nymphs are highly distinctive; indeed, they are more similar to those of *Atalophlebia* than *Zephlebia*. Moreover, all species of *Zephlebia* have the derived condition of reduction of gill 7 (Towns & Peters 1980), whereas *cruentata* has the primitive condition of all gills similar (Fig. 153 and 154). Having compared adult and nymphal characters of many Gondwanian genera of Leptophlebiidae, Towns & Peters (1980) and Pescador & Peters (1980) concluded that *cruentata* is more closely related to New Caledonian, Chilean, and Australian members of the *Atalophlebia* lineage than to any known genus in New Zealand. The species has several unique characters, however, and accordingly is here placed in a genus of its own, *Acanthophlebia*.

*Acanthophlebiac* can be distinguished from all other leptophlebiid genera by the following combination of characters. IMAGO: (1) forewing without a cross-vein connection from  $ICu_1$  to  $CuP$  (Fig. 16); (2) hind wings with a slight concavity on mid costal margin, and vein Sc about nine-tenths as long as wing (Fig. 17 and 18); (3) eyes of male

separated on meson of head; (4) penes fused except for apical one-quarter, and with subapical spines (Fig. 36, 38, and 51); (5) claws of a pair alike, apically hooked, with an opposing hook (Fig. 21); (6) sternum 9 of female strongly cleft (Fig. 63); (7) sternum 7 of female with a genital extension reaching one-fifth to two-fifths along sternum 8 (Fig. 70 and 78). NYMPH: (1) clypeus broader than labrum and with subparallel margins (Fig. 116); (2) mandibles with outer margins smoothly curved, and with spines extended to base (Fig. 125); (3) outer incisor of right mandible with prominent denticles (Fig. 121); (4) galea-lacinia of maxillae narrow, and with a subapical row of 9–12 spines (Fig. 128); (5) segment 3 of maxillary palpi short, subtriangular, and with dense hair on ventral surface (Fig. 128); (6) labium with glossae straight, and segment 3 of palpi short, subtriangular, and with spines on inner margin (Fig. 135); (7) abdominal gills 1–7 with similar double lamellae, broad near base and smoothly tapered towards apex (Fig. 109, 153, and 154); (8) abdomen with posterolateral projections on segments 2 or 3 to 9, those on segments 7–9 modified (Fig. 179).

*Acanthophlebia* appears to be most closely related to *Papposa* of New Caledonia; distinguishing characters are provided by Peters & Peters (1981).

#### *Acanthophlebia cruentata* (Hudson)

Hudson, 1904: 33; -Phillips, 1930: 347; -Mosely, 1932: 8 (in *Atalophlebia*). -Penniket, 1961: 9; -Tsui & Peters, 1975: 549 (in subgenus *Zephlebia* sensu Penniket). -Landa et al. 1980: 171 (as *Zephlebia* (*Z.*) cf. *cruentata*). -Pendergrast & Cowley, 1966: 14; -McLean, 1966: 99; 1967: 100, 104; -Hopkins, 1970: 14; 1976: 633; -Towns, 1978a: 410; -Pescador & Peters, 1980: 45; -Towns & Peters, 1980: 58; -Winterbourn & Towns, 1981: 18; -Peters & Peters, 1981: 251 (as *Zephlebia*).

**Male imago** (in ethanol). Head pale yellowish-brown, the anterolateral margins with narrow, darker brown marks, the midline between ocelli and posterior margin of head black. Eyes with upper portion pale orange-brown to pale brown, lower portion greyish-black. Antennae pale yellowish-brown. Ocelli pale, whitish; basal half of median ocellus and medial half of lateral ocelli washed with brown.

Thorax. Pronotum pale yellowish-brown, with prominent submedian and lateral marks, posteromedian margin, midline, and anteromedian margin black; mesothorax and metathorax pale yellowish-brown, darker on dorsum, with carinae darker, sutures paler, and lateral margins on anterior one-third of mesonotum with broad, black longitudinal marks. Pleura pale yellowish-brown irregularly washed with darker brown towards

venter; carinae darker; sutures paler; propleuron with a broad, black diagonal line from dorsoposterior margin to anteroventral margin of coxae; mesopleuron with broad, paired, black diagonal lines from anterior margin of wing base to anterior margin of pleuron. Sterna pale yellowish-brown irregularly washed with pale reddish-brown; carinae brown to black. Legs pale yellowish-brown; fore femora darker, with a diffuse brownish band near midlength; articulations of tibiae and tarsi washed with brown; tarsal joints pale brown; brown marks broader in forelegs. Wings, Fig. 16–18. Forewings with cross-veins in cells C and Sc surrounded by narrow, dark reddish-brown clouds (Fig. 16); longitudinal veins and remainder of cross-veins dark brown to dark reddish-brown; membrane tinted with pale yellow in cell C and Sc and at wing base, brownish near costal brace, hyaline elsewhere. Hind wings, Fig. 17 and 18; longitudinal veins and cross-veins pale brown to hyaline; membrane hyaline, but proximal half in cell C tinted with pale yellow (Fig. 17 and 18).

Abdomen. Terga pale pinkish-brown to pale brown; terga 3–7 darker brown near dorsum; terga 1–7 hyaline; terga 1 to 8 or 9 with paired, dark greyish, submedian longitudinal lines (Fig. 46); terga 1–6 with posterior margin greyish; terga 2–8 with paired, greyish anterolateral marks, these often paler in terga 2 and 8 (Fig. 46); terga 8–10 translucent; terga 9 and 10 occasionally yellowish. Tracheae hyaline; spiracular area black. Sterna pinkish-brown, darker brown to greyish-brown medially; sterna 1–7 hyaline; sterna 8–10 translucent, occasionally yellowish; abdominal ganglia hyaline. Genitalia (Fig. 36–38) pale, whitish, but dark brown on midline between lobes of penes; forceps washed with pale pinkish-brown near base. Caudal filaments whitish, with dark brown annulations at articulations and a dark brown band distally on each segment, the bands becoming progressively wider apically, but broad and narrow bands often alternated.

**Female imago** (in ethanol). Head colour and markings, antennae, and ocelli as in male imago, except for broad, transverse, dark brown to black submedian marks near posterior margin of head. Eyes greyish-black.

Thorax, legs, and wings with colour and markings as in male imago, but tarsi occasionally whitish.

Abdomen with colour and markings as in male imago, but terga 1–7 translucent, the paired, greyish anterolateral marks of terga 3–7 often paler, terga 2–7 and 10 with small, paired submedian maculae near anterior margin, and sterna 1–7 translucent, with small, paler, paired submedian maculae. Caudal filaments as in male imago.

**Male and female subimago** (in ethanol). Head whitish to pale whitish-brown, with markings as in imago. Eyes black in female; in male, upper portion pale yellowish-brown to pale brown, lower portion black.

Thorax. Prothorax pale whitish-brown, with markings as in imago; mesonotum, dorsum of basal humps of scutellum, and posterior scutellum pale, whitish, with pale brown on anterior one-third of mesonotum, along inner parapsidal sutures, laterally to outer parapsidal sutures, and on lateral margins of scutellum (Fig. 56). Sterna whitish to pink-tinged; furcasternum washed with pale brown; remaining marks as in imago. Leg colour and markings as in imago, but paler. Wings, Fig. 101 and 102; membranes pale yellowish-brown; longitudinal veins yellowish-brown to hyaline; cross-veins hyaline, surrounded by narrow, pale greyish clouds (Fig. 101).

Abdomen with colour and markings as in imago, but male with markings more prominent, terga 1–7 translucent, and general colour paler. Male genitalia: colour as in imago, but paler; lobes of penes without a dark brown mark on midline. Caudal filaments as in imago.

**Mature nymph** (in ethanol). Head pale yellowish-brown to reddish-brown, darker posterior to lateral ocelli (Fig. 109); markings otherwise as in imago. Ocelli with base grey-brown to dark brown, apex greyish to whitish. Eyes of male with upper portion brown to reddish-brown, lower portion black. Antennae pale yellowish-brown to pale brown.

Thorax pale brown to brown; pronotum and mesonotum with dark brown to black marks submedially and on lateral margins (Fig. 109); sterna pale whitish-brown, but carinae on prosternum black midventrally. Legs (Fig. 109 and 170) with colour and markings as in subimago.

Abdomen pale orange-brown; terga 7–10 often reddish-brown dorsally; markings as in imago, but usually very faint. Gills, Fig. 109, 153, and 154; lamellae hyaline to translucent; tracheae and their branches dark grey to black. Caudal filaments brown; each segment with a distal whorl of small, dark brown denticles.

**Type data.** Hudson (1904) did not designate type material or provide a type locality for his "*Atalophlebia cruentata*", but the latter can be inferred from his statement that the species is "found commonly in all the streams in the vicinity of Wellington" (p. 33).

There are 4 specimens of *Acanthophlebia cruentata* from Hudson's collections in the National Museum of New Zealand, but only 2 were collected

before 1904 and probably formed part of the original series. Both are female subimagos, although one of them is listed in Hudson's register as an imago. The better preserved specimen, listed as "67e" in Hudson's register, is here designated as lectotype: ♀ subimago, Campbell's Stream, Karori, Wellington, January 1900, G. V. Hudson (NMNZ; pinned).

**Material examined.** North Island. ND. Okaihau, forest remnant: 3 nymphs, 18 Oct 1973, KAJW (AMNZ). Waipoua: 1 nymph, 30 Dec 1962, JGP (FAMU). Waiaua R. (?ND): 1 ♂ imago, reared, 29 Jan 1963, JGP (CMNZ). AK. Whangateau, forest remnant: 1 ♀ subimago, 4 Dec 1968, KAJW (AMNZ). Cascade Stm: 1 ♀ subimago, 6 Apr 1957, BMM (NZAC); 23 ♂ and 2 ♀ subimagos, 31 Oct 1966; 2 ♂ and 9 ♀ subimagos, 2 Nov 1966; 11 ♂ and 7 ♀ subimagos, 3 Nov 1966; 1 ♂ and 4 ♀ subimagos, 6 Nov 1966; 7 ♂ and 5 ♀ subimagos, 7 Nov 1966, JAM (NZAC); 1 ♂ subimago, 3 Nov 1966, JAM (AMNZ); 1 ♂ imago, reared from nymph, 28 Mar 1975; 4 ♂ and 3 ♀ subimagos, 12 Nov 1975; 5 ♂ and 3 ♀ subimagos, 20 Nov 1975, DRT; 1 ♀ subimago, 9 Feb 1977; 2 ♂ and 1 ♀ imagos, 1 ♂ subimago, 9 Mar 1977, MGB; 16 nymphs, 11 Mar 1966, GFE (UUUS). Waitakere R.: 2 ♂ subimagos, 30 Oct 1966; 4 ♀ subimagos, 1 Nov 1966, JAM (AMNZ); 2 ♀ subimagos, 31 Oct 1966; 5 ♂ and 1 ♀ subimagos, 8 Nov 1966, JAM (FAMU); 10 ♂ and 7 ♀ subimagos, 12 Nov 1975; 5 ♂ and 4 ♀ subimagos, 20 Nov 1975, DRT. Sml trib. of Waitakere R. nr Anderson's Track: 6 ♂ and 1 ♀ imagos, 4 ♂ and 2 ♀ subimagos, 16 Feb 1977; 1 ♂ subimago, 22 Feb 1977; 1 ♀ subimago, 15 Mar 1977; 1 ♂ imago, 28 Mar 1977; 2 ♂ and 9 ♀ imagos, 30 Mar 1977, MGB. Karamatura Stm: 2 nymphs, 9 Jan 1977, DRT, ELT. Kitekite Stm: 3 nymphs, 27 Dec 1976, DRT, ELT, BWH, GCH. CL. Little Barrier I.: Tirikakawa Stm - 11 nymphs, 13 Feb 1977; Awaroa Stm - 21 ♂ and 23 ♀ subimagos, 1 nymph, 5 Feb 1977, JMD. Great Barrier I.: Port Fitzroy - 1 nymph, Apr 1967; Kawa Stm, Katherine Bay - 2 nymphs, 10 Apr 1966, RGO (NMNZ). Tarawaere Stm, Coromandel Forest Pk: 2 nymphs, 3 Jan 1977, DRT, ELT, GCH. Small silty trib. of Kauaeranga R.: 1 nymph, 4 Jan 1977, DRT. WO. Giant's Cavern, Hollow Hill Cave, Te Kuiti: 1 ♀ subimago, 15 Feb 1959; 1 ♀ imago, reared from subimago, 16 Feb 1959, KAJW (NZAC). Lucky Strike Cavern, Te Kuiti: 1 ♀ subimago, 14 Feb 1959, KAJW (NZAC). BP. Motu R.: 1 nymph, Nov 1968, JAM (NZAC). TO. Pungapunga Stm: 1 ♀ imago, reared from nymph, 23 Dec 1962, PA (CMNZ). WN. Shannon: 5 nymphs, 29 Jan 1921, RJT (NZAC). Maungakotukutuku Vly: 1 nymph, 28 Jan 1973, RGO (NMNZ). Catchpool Stm, Rimutaka Forest Pk: 1 nymph, 8 Jul 1979, DRT, BWH. Stm in Hayward's Reserve, Lower Hutt: 13 nymphs, 13 July 1979, DRT. Hutt R. nr Silverstream Hospital: 4 ♂ and 3 ♀ imagos, reared from subimago, 2 ♀ subimagos, light trap, 22 Jan 1981, DRT. Khandallah: 1 ♀ subimago, 5 Jan 1929, JSP(?) (NMNZ; pinned). Tyer's Stm - 5 nymphs, 14 Jul 1979, DRT, ELT, BWH, GCH. Wilton's Bush: 2 ♂ imagos, 9 Mar 1922, GVH (NMNZ; pinned). Locality unspecified: 1 ♀ subimago, reared from nymph, Jan 1899, GVH (NMNZ; pinned).

Repositories of additional material (all specimens are in ethanol): 12 ♂ and 3 ♀ imagos, 1 ♂ and 1 ♀ subimago, 5 nymphs - NZAC; 3 ♂ and 4 ♀ subimagos, 2 nymphs - CMNZ; 1 ♂ and 1 ♀ imago, 2 ♂ and 2 ♀ subimagos - NMNZ; 1 ♂ and 1 ♀ imago, 3 ♂ and 1 ♀ subimagos, 4 nymphs - BMNH; 1 ♂ and 2 ♀ subimagos, 2 nymphs - BPBM; 1 ♂ and 1 ♀ imago, 1 ♂ and 2 ♀ subimagos, 10 nymphs - FAMU; 3 ♂ and 1 ♀ subimagos - UUUS; remaining material - author's collection.

**Variation.** The dorsal abdominal markings on mature nymphs and adults are not present in earlier instars, which are often also paler in general coloration. The labrum figured here (Fig. 116 and 117) differs slightly from the illustration in Towns & Peters (1980), which apparently was based on a specimen which tilted slightly during mounting. The shape of the glossae varies in slide-mounted material according to the extent of flattening of the mouthparts incurred during preparation.

**Remarks.** In their descriptions of *Acanthophlebia cruentata* nymphs Hudson (1904) and Phillips (1930) stated that the general coloration is bright orange-red. However, in material examined for the present study only the dorsum of abdominal segments 7-10 was reddish. No nymphs had orange legs and gill lamellae as described by Phillips (1930). Hudson (1904) also stated that nymphs have 6 pairs of gills, but Phillips (1930) correctly recognised 7 pairs.

**Biology.** All specimens of *A. cruentata* available for this study were collected in the North Island. Phillips (1930) records the species from Nelson and Canterbury, but in the absence of specimens these South Island records are open to corroboration.

*Acanthophlebia cruentata* is most abundant in slow-flowing reaches of streams (Hudson 1904, Phillips 1930), and sometimes can be collected in small forested streams by disturbing fine gravel or silty material. Although nymphs may not appear to be abundant, possibly owing to their elusiveness (Hudson 1904, Phillips 1930), subimagos are often very abundant in light-trap samples (McLean 1967). Swarming behaviour of adults occurs in mid afternoon at up to 3 m above quiet pools (McLean 1967).

## KEYS TO GENERA OF NEW ZEALAND LEPTOPHLEBIIDAE

The following keys separate New Zealand members of the *Zephlebia* lineage (see Towns & Peters 1980) and genera here removed from *Zephlebia* from other genera of New Zealand Leptophlebiidae. If these keys are used in conjunction with the key provided by Towns & Peters (1979a), it should be possible to identify adults and nymphs of all described New Zealand leptophlebiid genera.

## KEY TO NEW ZEALAND GENERA NOT IN THE *Zephlebia* LINEAGE

### IMAGOS

- 1 Forewings with membrane hyaline; claws similar or dissimilar, but if similar, hooked and without an opposing hook ..... 2

- Forewings with membrane generally pigmented in costal margin and/or with clouds at cross-veins; claws similar, hooked and with an opposing hook..... (see next key)
- 2 Claws dissimilar; hind wings less than one-third as long as forewings; male genitalia without large, fleshy ventral appendages ..... 3
- Claws similar; hind wings one-third as long as forewings; male genitalia with large, fleshy ventral appendages ..... *Penniketellus*  
(see Towns & Peters 1979b, fig. 59 and 55–57)
- 3 Sternum 9 of female with apex deeply cleft; male genitalia with penes fused, and without rounded apical lobes..... *Deleatidium*
- Sternum 9 of female with apex shallowly cleft to entire; penes fused, with rounded apical lobes, or deeply cleft and with dorsal projections .....  
... *Atalophlebioides*, *Austroclima*, *Cryophlebia*, *Mauitulus*  
(see Towns & Peters 1979a, p. 234)

#### NYMPHS

- 1 Abdominal gills with double lamellae ..... 2
- Abdominal gills with single lamellae..... *Deleatidium*
- 2 Labrum with anterior margin deeply cleft and clypeus with margins slightly divergent apically OR labrum shallowly cleft and lateral margins of clypeus strongly divergent apically; anteromedian denticles small, broad-based, appearing as slits in labral margin..... (see Towns & Peters 1979a)
- Labrum with anterior margin smoothly concave or with a rectangular anteromedian concavity (Fig. 110 and 114); margins of clypeus convergent to slightly divergent apically (Fig. 110 and 116); anteromedian denticles generally well developed to prominent, but if small, not appearing as slits ..... (see next key)

#### KEY TO NEW ZEALAND GENERA AND SUBGENERA IN THE *Zephlebia* LINEAGE, INCLUDING GENERA FORMERLY REFERRED TO *Zephlebia* IMAGOS

- 1 Forewings with membrane in costal margin pigmented pale yellow to pale brown and/or with a distinct cloud of pigment at cross-veins (Fig. 2 and 6)..... 2
- Forewings with membrane untinted and with very narrow clouds of pigment at cross-veins... *Arachnocolus*  
(see Towns & Peters 1979b, fig. 31 and 32)
- 2 Penes divided to styliger plate, and with an area of spines on dorsolateral surface (Fig. 34 and 50); sternum 7 of female without a genital extension; egg with long, irregularly coiled, thread-like attachment structures at poles (Fig. 206) ..... *Neozephlebia*
- Penes not divided to styliger plate, the penis lobes with apical or subapical spines or hairs (Fig. 22, 36, 47, 49, and 51); sternum 7 of female with a well developed genital extension (Fig. 64–70); egg without thread-like attachment structures at poles..... 3
- 3 Penes shorter than forceps segment 1; female with genital extension less than half as long as sternum 8.... 4
- Penes elongate, about as long as forceps; female with genital extension about as long as sternum 8; egg with closely packed hexagonal attachment structures over chorion..... *Isothraulius*  
(see Towns & Peters 1979b, fig. 4, 10, 25, and 26)

- 4 Eyes of male fused on meson of head; penes with hairs at apex of each opening (Fig. 22, 47, and 49); sternum 9 of female shallowly cleft to entire (Fig. 57–61); egg elongate-oval to fusiform, the chorion with circular to stellate attachment structures over surface, or carinate, the carinae formed into ridges (Fig. 198–203) *Zephlebia*
- Eyes of male slightly separated on meson of head; penes without hairs at apex (Fig. 36, 38, and 51); sternum 9 of female strongly cleft (Fig. 63); egg elongate-oval, with large, paired attachment structures (Fig. 207)..... *Acanthophlebia*

#### NYMPHS

- 1 Gills with margin entire, not fringed..... 2
- Gills with margin fringed ..... *Isothraulius*  
(see Towns & Peters 1979b, fig. 23)
- 2 Gills on abdominal segments 1–7 alike, progressively smaller posteriorly, each with double lamellae (Fig. 151–154)..... 3
- Gills on abdominal segments 1–6 alike, gill 7 reduced to a single lamella or paired small lamellae, or paired or single thread-like filaments (Fig. 141, 143, 145, 147, 149, and 150) ..... 4
- 3 Abdomen with posterolateral spines on segments 2–9, those on segments 8 and 9 greatly enlarged (Fig. 109); dorsal abdomen yellowish to reddish-brown; gills broad at base, smoothly tapered apically, and with numerous tracheal branches (Fig. 153 and 154)..... *Acanthophlebia*
- Abdomen with posterolateral spines on segments 5 or 6 to 9, that on segment 9 slightly enlarged (Fig. 108); dorsal abdomen pale to dark brown; gills slender, the tracheae sometimes with a few short branches (Fig. 151)..... *Neozephlebia*
- 4 Femora elongate; dorsal and ventral portions of gills 1–6 dissimilar; labrum with small, broad-based, rounded denticles, and the prosthecal tuft reduced *Arachnocolus* (see Towns & Peters 1979b, fig. 45, 49, 39, and 41)
- Femora not greatly elongate; dorsal and ventral portions of gills usually alike; labrum with well developed to prominent denticles, and the prosthecal tuft large..... 5
- 5 Anteromedian emargination of labrum with flat-topped lateral denticles and a pointed median denticle (Fig. 111); mandibles with outer margin angular (Fig. 122), and with slender incisors (Fig. 118 and 122); abdomen weakly to strongly tapered posteriorly (Fig. 103–106) ... *Zephlebia* (*Zephlebia*)
- Anteromedian emargination of labrum with equal-sized, prominent, pointed denticles (Fig. 113); mandibles with outer margin smoothly curved (Fig. 114), and with short, stout incisors (Fig. 119); abdomen weakly oval, broadest at segments 4–6 (Fig. 107)..... *Zephlebia* (*Terama*)

#### ACKNOWLEDGMENTS

I thank Dr W. L. and Mrs J. G. Peters, Mr M. D. Hubbard, and Dr M. L. Pescador (Florida A & M University) for their helpful comments on the manuscript. I am particularly grateful to Dr and Mrs Peters for their kindness and hospitality during my stay in Tallahassee. My thanks also to my wife Elizabeth for help in the field and for constant encouragement. The following individuals and institutions have assisted by providing material and facilities during my visits to New Zealand: Dr T. K. Crosby (Entomology Division, DSIR); Dr D. R. Cowley and

Professor E. C. Young (University of Auckland); Professor J. G. Pendergrast and Mr P. Summerhays (University of Waikato); and Dr and Mrs B. W. Hayward (who kindly acted as field assistants and hosts during visits to Wellington). Thanks also to Mr K. A. J. Wise (Auckland Institute and Museum), Mr R. G. Ordish (National Museum of New Zealand), Dr M. J. Winterbourn (University of Canterbury), Dr W. L. Peters (Florida A & M University), Dr G. F. Edmunds, Jr (University of Utah), and Dr P. C. Barnard (British Museum (Natural History)) for the loan of specimens. Professor S. Mead (Victoria University of Wellington) kindly advised on the gender of names from the Maori language. This study was supported in part by a research programme (Flax 79009) of CSRS, United States Department of Agriculture, at Florida A & M University (William L. Peters, Research Leader) and in part by an Overseas Travel Grant from the University of Adelaide Research and Publications Committee.

## REFERENCES

- Cadwallader, P. L. 1975a: Feeding habits of two fish species in relation to invertebrate drift in a New Zealand river. *New Zealand journal of marine and freshwater research* 9 : 11–26.
- 1975b: The food of the New Zealand common river galaxias, *Galaxias vulgaris* Stokell (Pisces: Salmoniformes). *Australian journal of marine and freshwater research* 26 : 15–30.
- 1975c: Feeding relationships of galaxiids, bullies, eels and trout in a New Zealand river. *Australian journal of marine and freshwater research* 26 : 299–316.
- Eaton, A. E. 1871: A monograph on the Ephemeroidea. *Transactions of the Entomological Society of London*, 1871. 164 p.
- 1884: A revisional monograph of recent Ephemeroidea or mayflies. Part II. *Transactions of the Linnean Society of London, series 2, zoology* 3 : 77–152.
- 1899: An annotated list of the Ephemeroidea of New Zealand. *Transactions of the Entomological Society of London*, 1899 : 285–293.
- Edmunds, G. F., Jr 1962: The principles applied in determining the hierarchic level of the higher categories of Ephemeroptera. *Systematic zoology* 11 : 22–31.
- Hopkins, C. L. 1970: Some aspects of the bionomics of fish in a brown trout nursery stream. *New Zealand Marine Department fisheries research bulletin* 4. 38 p.
- 1976: Estimate of biological production in some stream invertebrates. *New Zealand journal of marine and freshwater research* 10 : 629–640.
- Hudson, G. V. 1904: New Zealand Neuroptera; a popular introduction to the life histories and habits of mayflies, dragon flies and allied insects inhabiting New Zealand, including notes on their relation to angling. London, West, Newman & Co. 102 p.
- Hutton, F. W. 1898: The Neuroptera of New Zealand. *Transactions of the New Zealand Institute* 31 : 208–249.
- Kimmins, D. E. 1960: The Ephemeroptera – types of species described by A. E. Eaton, R. McLachlan, and F. Walker, with particular reference to those in the British Museum (Natural History). *Bulletin of the British Museum (Natural History), entomology* 9 : 269–318.
- Landa, V.; Soldán, T.; Peters, W. L. 1980: Comparative anatomy of larvae of the family Leptophlebiidae (Ephemeroptera) based on ventral nerve chord, alimentary canal, malpighian tubules, gonads and tracheal system. *Acta entomologica bohemoslovaca* 77 : 169–195.
- Lillie, C. O. 1898: On New Zealand Ephemeroidea: two species. *Transactions of the New Zealand Institute* 31 : 164–169.
- 1900: Notes on New Zealand Ephemeroidea. *Transactions of the New Zealand Institute* 33 : 149–150.
- McLean, J. A. 1967: Studies of Ephemeroptera in the Auckland area, Parts I & II. *Tane* 13 : 99–105.
- Michaelis, F. B. 1977: Biological features of Pupu Springs. *New Zealand journal of marine and freshwater research* 11 : 357–373.
- Miller, D. 1971: Common insects in New Zealand. Wellington, A. H. & A. W. Reed. 178 p.
- Mosely, M. E. 1932: The New Zealand mayflies. *Salmon and trout magazine* : 1–11.
- Pendergrast, J. G.; Cowley, D. R. 1966: An introduction to the freshwater insects of New Zealand. London, Collins. 100 p.
- Penniket, J. G. 1961: Notes on New Zealand Ephemeroptera. I. The affinities with Chile and Australia, and remarks on *Atalophlebia* Eaton (Leptophlebiidae). *New Zealand entomologist* 2 : 1–11.
- Pescador, M. L.; Peters, W. L. 1980: Phylogenetic relationships and zoogeography of cool-adapted Leptophlebiidae (Ephemeroptera) in southern South America. P. 45–56 in: Flannagan, J. F.; Marshall, K. E. eds, *Advances in Ephemeroptera biology*. New York, Plenum.
- Peters, W. L.; Edmunds, G. F., Jr 1970: Revision of the generic classification of the Eastern Hemisphere Leptophlebiidae (Ephemeroptera). *Pacific insects* 12 : 157–240.
- Peters, W. L.; Peters, J. G. 1981: The Leptophlebiidae: Atalophlebiinae of New Caledonia (Ephemeroptera). Part IV – Systematics. *Cahiers ORSTOM, série hydrobiologie* 14 : 245–252.
- Phillips, J. S. 1930: A revision of New Zealand Ephemeroptera, Part 2. *Transactions of the New Zealand Institute* 61 : 335–390.
- Stout, V. M. 1969: The invertebrate faunas of rivers and streams. P. 471–497 in: Knox, G. A. ed., *The natural history of Canterbury*. Wellington, A. H. & A. W. Reed.
- 1973: The freshwater environment. P. 229–250 in: Williams, G. R. ed., *The natural history of New Zealand*. Wellington, A. H. & A. W. Reed.
- 1975: The limnology. P. 405–458 in: Kuschel, G. ed., *Biogeography and ecology in New Zealand*. The Hague, Junk.
- Suter, P. J. 1980: The taxonomy and ecology of the Ephemeroptera (mayflies) of South Australia. Unpubl. PhD thesis, University of Adelaide, Australia.
- Towns, D. R. 1976: Dynamics of benthic invertebrate communities in a northern New Zealand kauri forest stream ecosystem. Unpubl. PhD thesis, University of Auckland, New Zealand.

- Towns, D. R. 1978a: First records of *Siphlaenigma janae* (Ephemeroptera: Siphlaenigmatidae) from the North Island of New Zealand. *New Zealand journal of zoology* 5 : 365–370.
- 1978b: Some little known benthic insect taxa from a northern New Zealand river and its tributaries. *New Zealand entomologist* 6 : 409–419.
- 1979: Composition and zonation of benthic invertebrate communities in a New Zealand kauri forest stream. *Freshwater biology* 9 : 251–262.
- 1981: Life histories of benthic invertebrates in a northern New Zealand kauri forest stream. *Australian journal of marine and freshwater research* 32 : 191–211.
- 1983: Life history patterns of six sympatric species of Leptophlebiidae (Ephemeroptera) in a New Zealand stream and the role of interspecific competition in their evolution. *Hydrobiologia* : in press.
- Towns, D. R.; Peters, W. L. 1978: A revision of genus *Atalophlebioides* (Ephemeroptera: Leptophlebiidae). *New Zealand journal of zoology* 5 : 607–614.
- 1979a: Three new genera of Leptophlebiidae (Ephemeroptera) from New Zealand. *New Zealand journal of zoology* 6 : 213–235.
- 1979b: New genera and species of Leptophlebiidae (Ephemeroptera) from New Zealand. *New Zealand journal of zoology* 6 : 439–452.
- 1980: Phylogenetic relationships of the Leptophlebiidae of New Zealand (Ephemeroptera). P. 57–69 in: Flannagan, J. F.; Marshall, K. E. eds, *Advances in Ephemeroptera biology*. New York, Plenum.
- Tsui, P. T. P.; Peters, W. L. 1975: The comparative morphology and phylogeny of certain Gondwanian Leptophlebiidae based on the thorax, tentorium and abdominal terga (Ephemeroptera). *Transactions of the American Entomological Society* 101 : 505–595.
- Walker, F. 1853: Ephemeroptera. P. 533–585 in: *List of the specimens of neuropterous insects in the collection of the British Museum*, 3.
- Winterbourn, M. J.; Towns, D. R. 1981: Ephemeroptera (mayflies) – key to larvae. P. 14–18 in Winterbourn, M. J.; Gregson, K. L. D., *Guide to the aquatic insects of New Zealand*. *Entomological Society of New Zealand bulletin* 5.

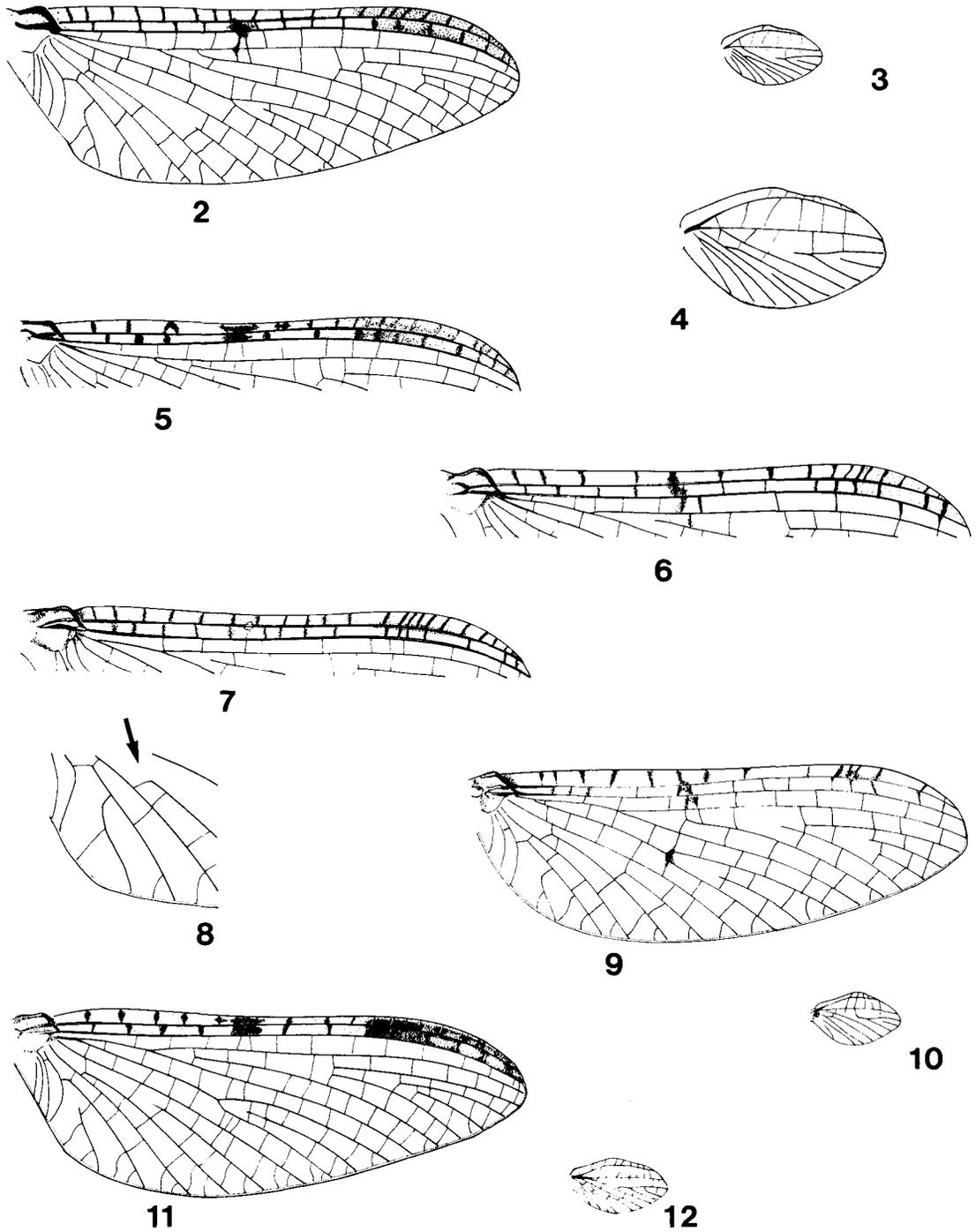


Fig. 2-12 Wings of ♂ imagos: 2-4, *Zephlebia (Z.) versicolor*, forewing, and hind wing (to scale and enlarged); 5, *Z. (Z.) dentata*, part forewing; 6, *Z. (Z.) inconspicua*, part forewing; 7, 8, *Z. (Z.) spectabilis*, part forewing, and Cu-A area (enlarged; arrow, base of vein  $MP_2$ ); 9, 10, *Z. (Z.) planulata*; 11, 12, *Zephlebia (Terama) borealis*.

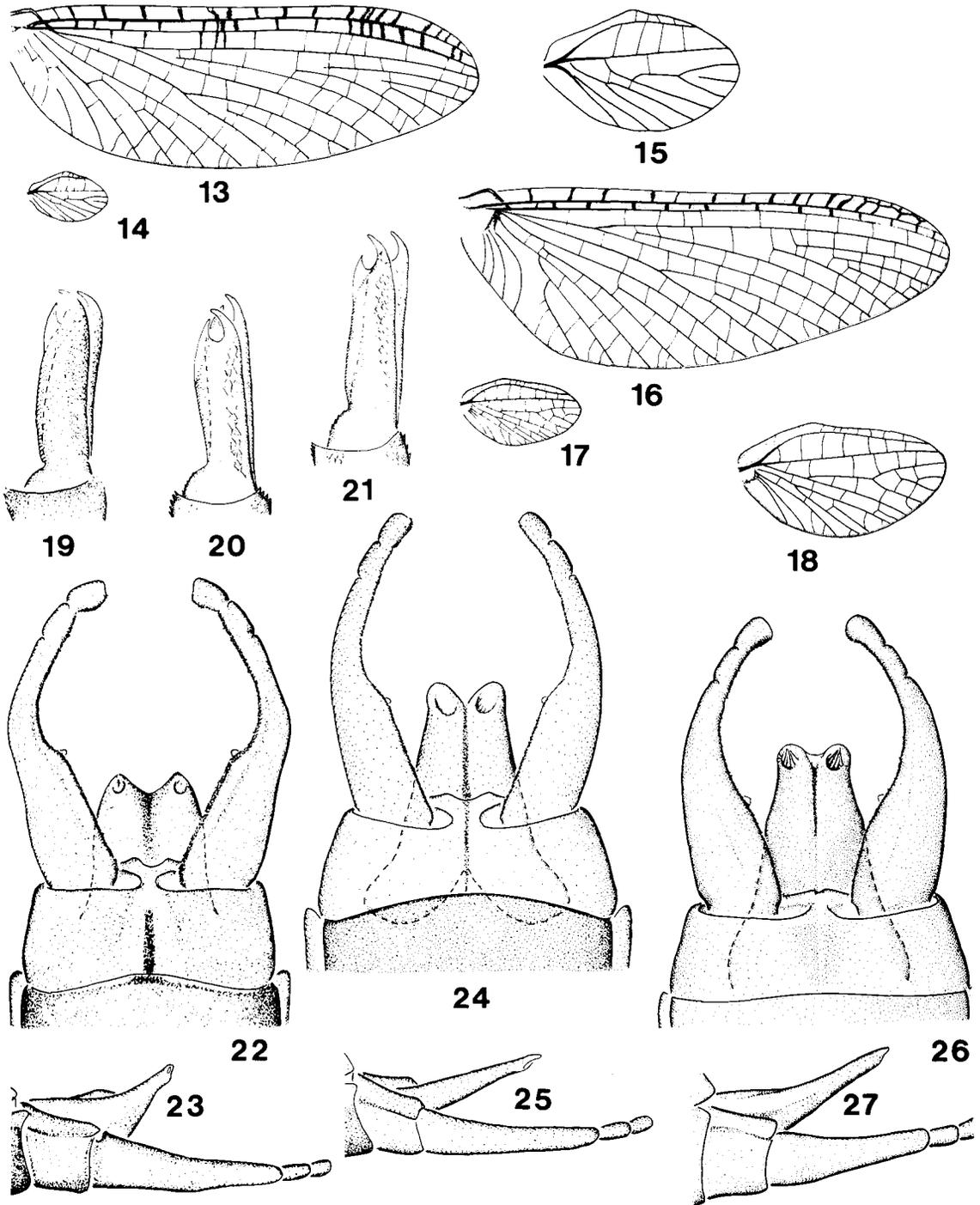


Fig. 13-18 Forewing, hind wing, and enlargement of hind wing of  $\delta$  imagos: 13-15, *Neozephlebia scita*; 16-18, *Acanthophlebia cruentata*. 19-21 Fore claw of  $\delta$  imagos: 19, *Zephlebia (Z.) versicolor*; 20, *Neozephlebia scita*; 21, *Acanthophlebia cruentata*. 22-27 Genitalia of  $\delta$  imagos, ventral and lateral views: 22, 23, *Zephlebia (Z.) versicolor*; 24, 25, *Z. (Z.) dentata*; 26, 27, *Z. (Z.) inconspicua*.

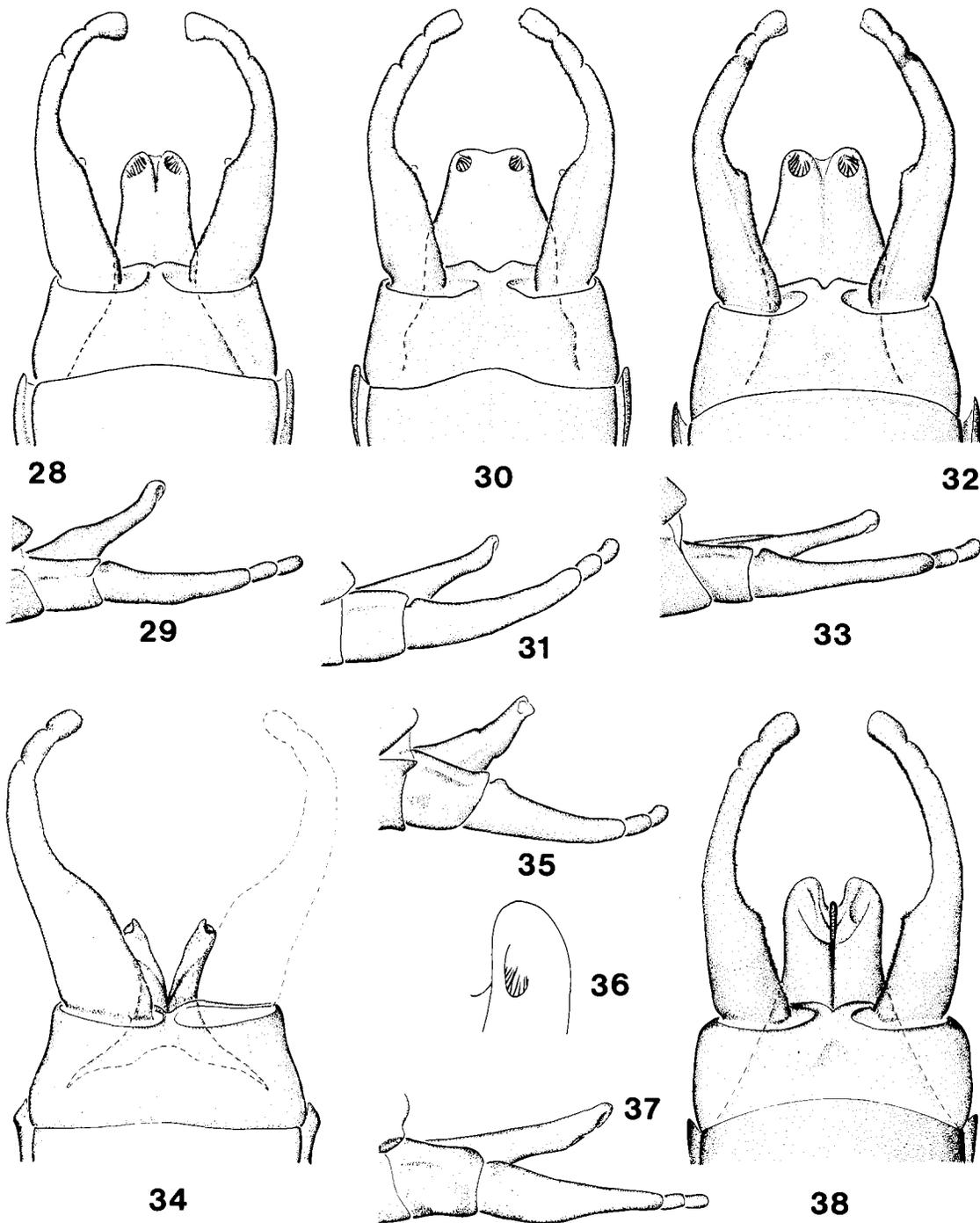


Fig. 28-38 Genitalia of  $\delta$  imagos, ventral and lateral views: 28, 29, *Zephlebia (Z.) spectabilis*; 30, 31, *Z. (Z.) planulata*; 32, 33, *Zephlebia (Terama) borealis*; 34, 35, *Neozephlebia scita*; 36-38, *Acanthophlebia cruentata* (36, penis opening, enlarged).

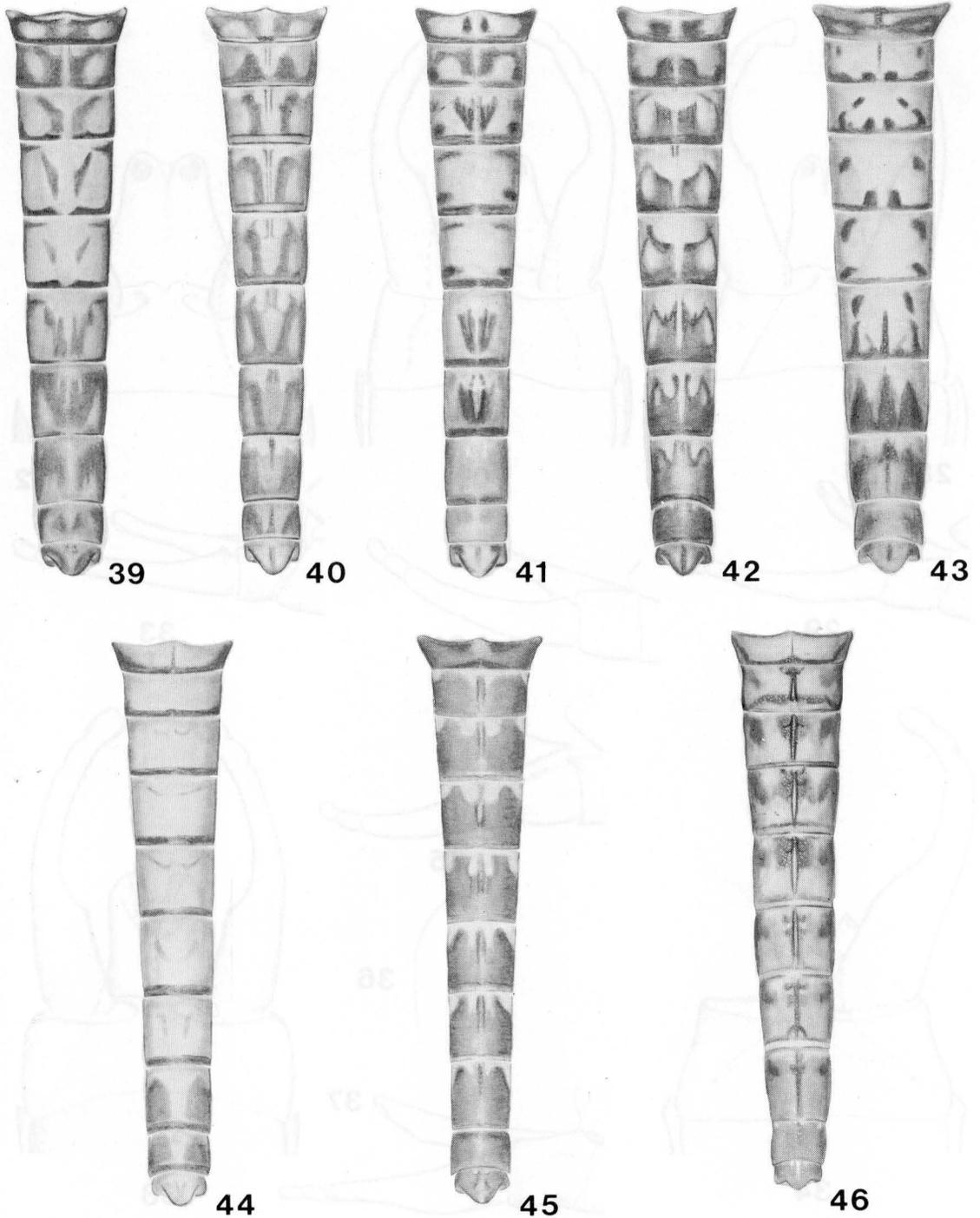


Fig. 39-46 Abdominal colour pattern of ♂ imagos: 39, *Zephlebia (Z.) versicolor*; 40, *Z. (Z.) dentata*; 41, *Z. (Z.) inconspicua*; 42, *Z. (Z.) spectabilis*; 43, *Z. (Z.) planulata*; 44, *Zephlebia (Terama) borealis*; 45, *Neozephlebia scita*; 46, *Acanthophlebia cruentata*.

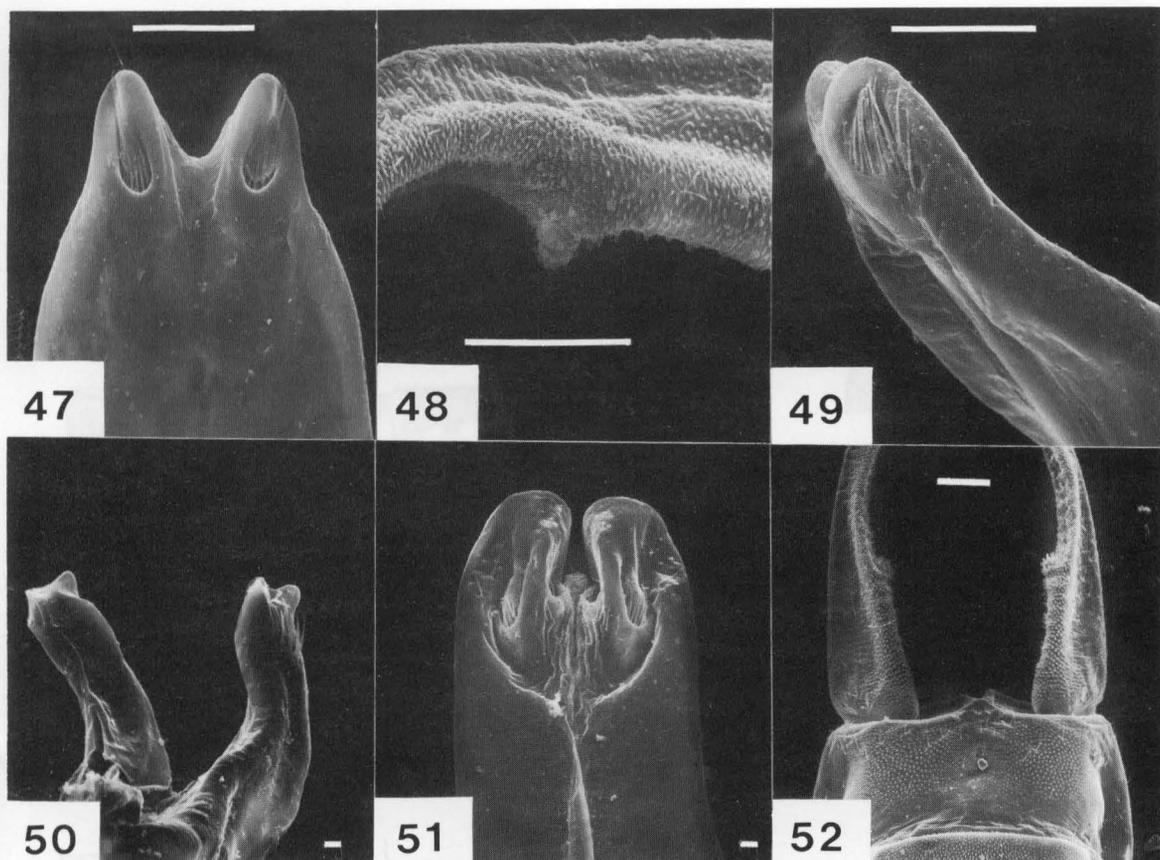


Fig. 47–52 Scanning electron micrographs of ♂ genitalia (scale lines 100  $\mu\text{m}$ , except Fig. 50 and 51, 10  $\mu\text{m}$ ). 47, 48, *Zephlebia (Z.) versicolor*, apex of penes (ventral view) and lobe on interior margin of forceps segment 1. 49, *Z. (Z.) spectabilis*, apex of penes, lateral view. 50, *Neozephlebia scita*, apex of penes, dorsal view. 51, 52, *Acanthophlebia cruentata*, apex of penes (ventral view) and forceps segment 1.

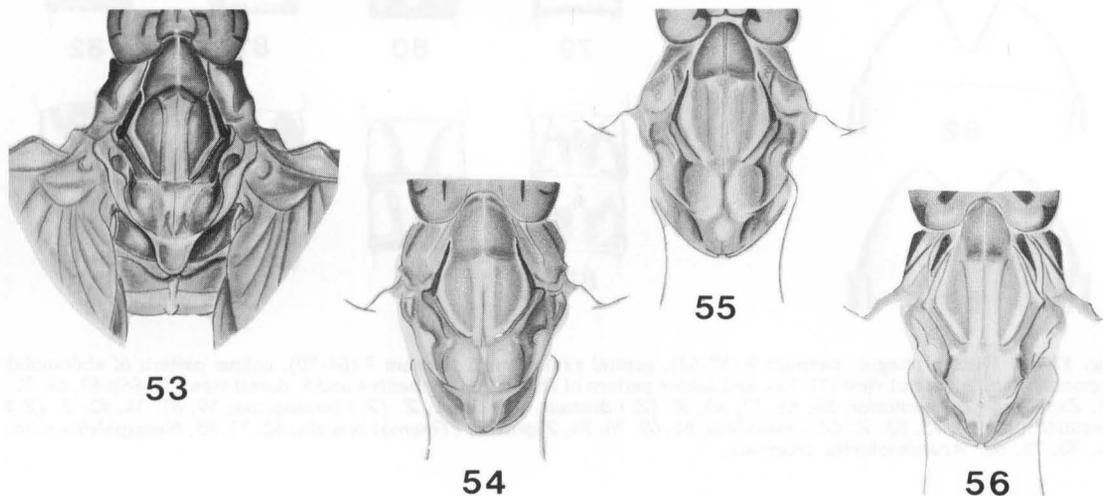
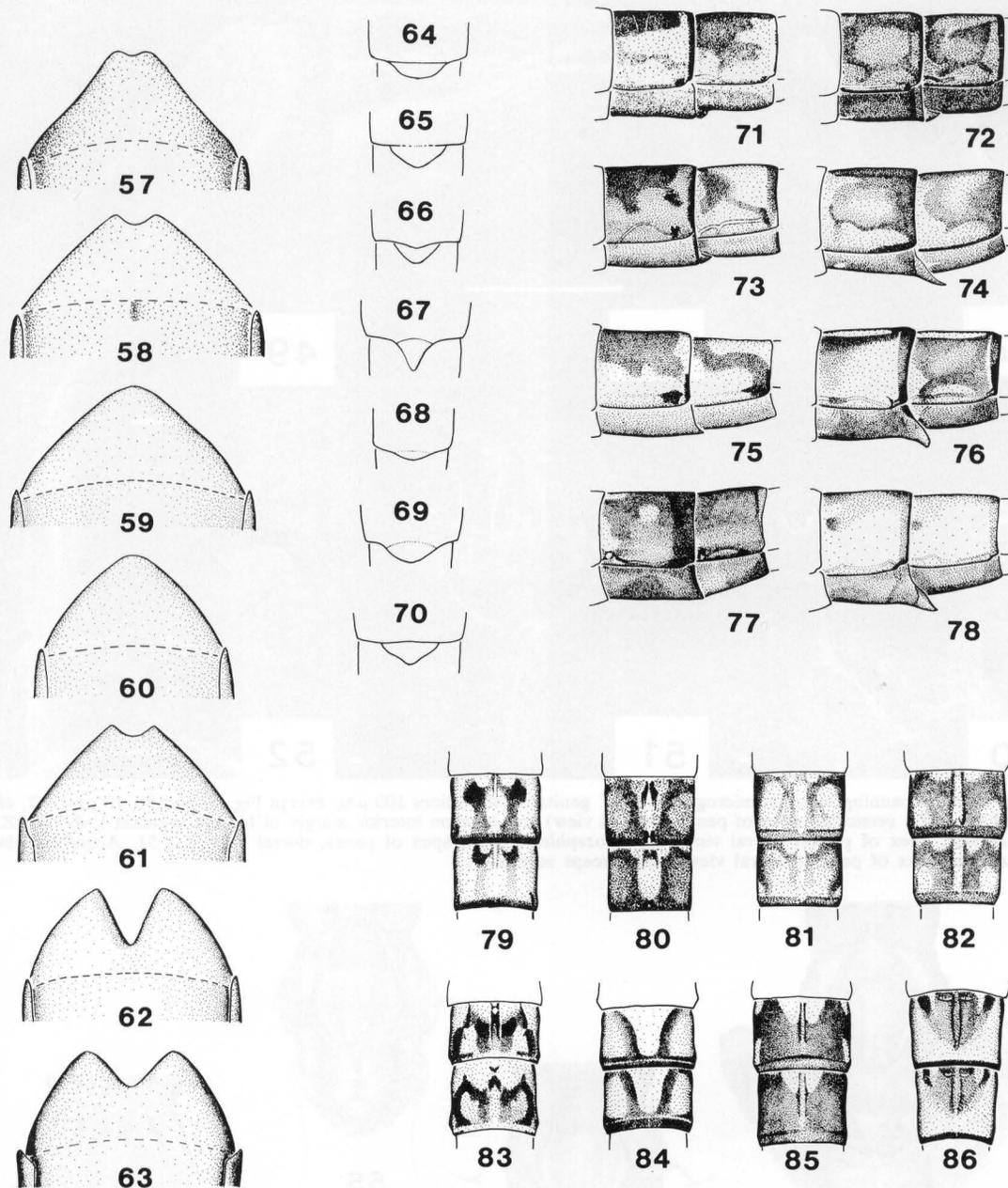
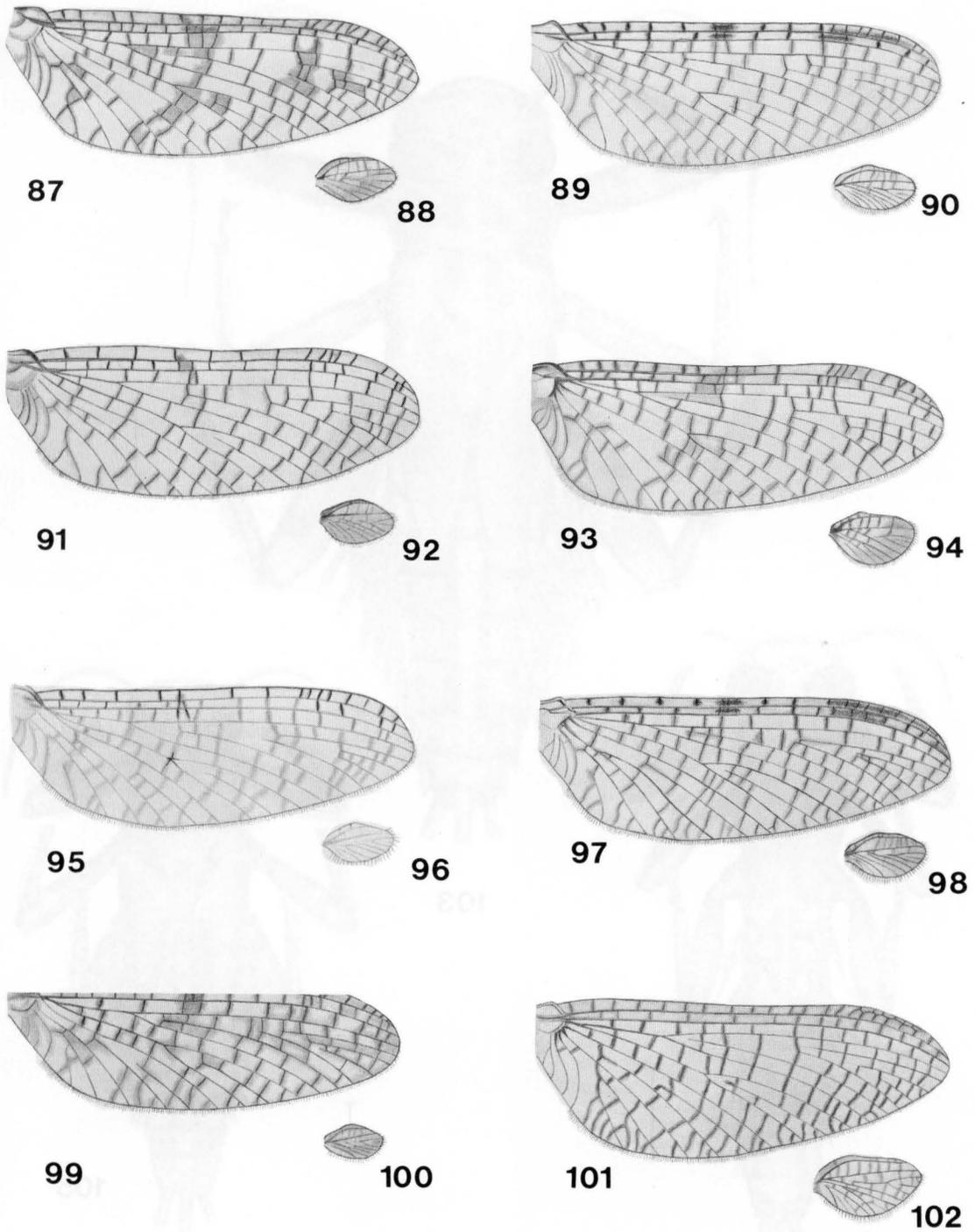


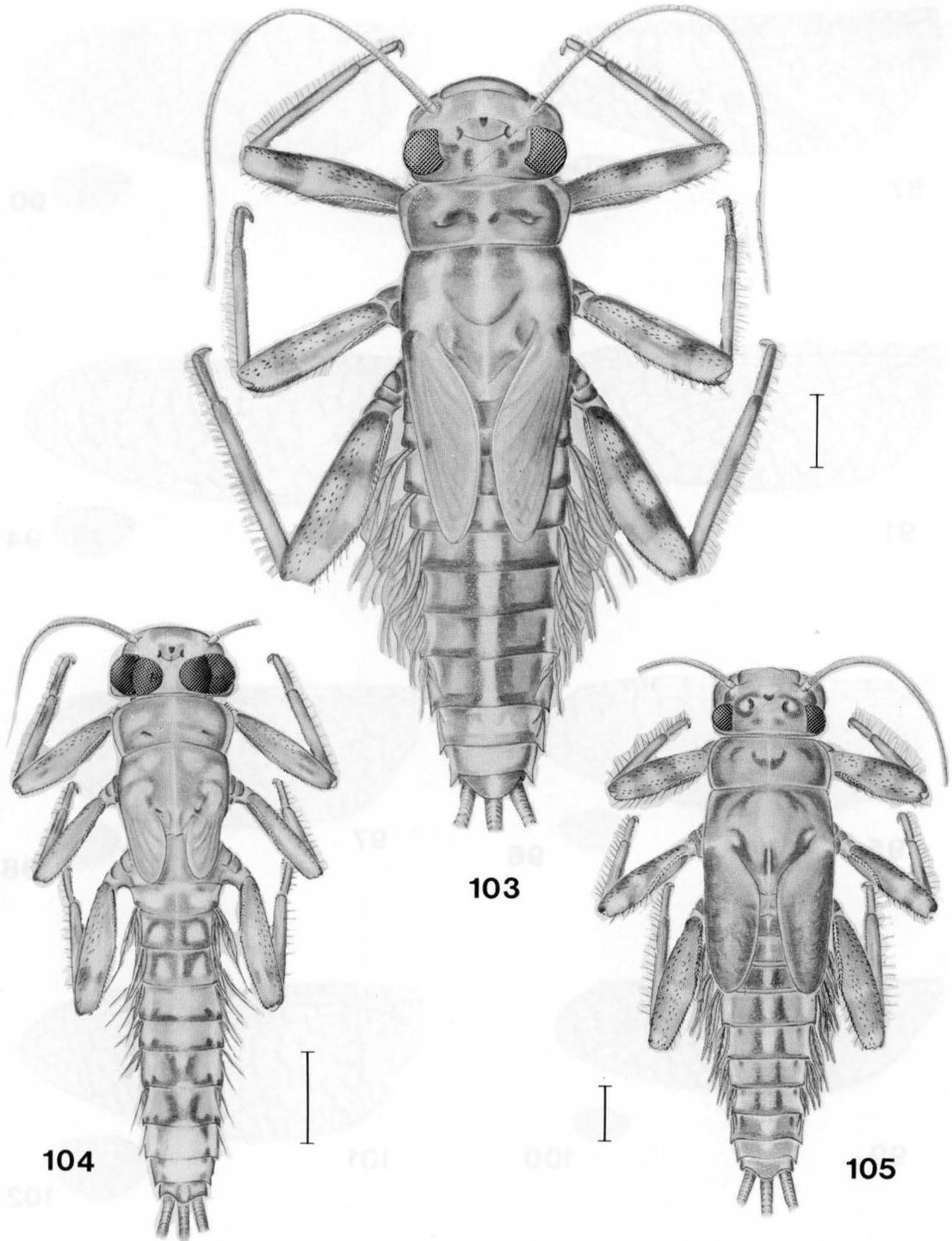
Fig. 53–56 Mesothorax of ♂ subimagos, dorsal view: 53, *Zephlebia (Z.) versicolor*; 54, *Zephlebia (Terama) borealis*; 55, *Neozephlebia scita*; 56, *Acanthophlebia cruentata*.



**Fig. 57-86** Female imagos, sternum 9 (57-63), genital extension of sternum 7 (64-70), colour pattern of abdominal segments 7 and 8, lateral view (71-78), and colour pattern of abdominal segments 4 and 5, dorsal view (79-86): 57, 64, 71, 79, *Zephlebia* (*Z.*) *versicolor*; 58, 65, 72, 80, *Z. (Z.) dentata*; 66, 73, 81, *Z. (Z.) inconspicua*; 59, 67, 74, 82, *Z. (Z.) spectabilis*; 60, 68, 75, 83, *Z. (Z.) planulata*; 61, 69, 76, 84, *Zephlebia* (*Terama*) *borealis*; 62, 77, 85, *Neozephlebia scita*; 63, 70, 78, 86, *Acanthophlebia cruentata*.



**Fig. 87-102** Forewing and hind wing of ♂ subimagos: 87, 88, *Zephlebia (Z.) versicolor*; 89, 90, *Z. (Z.) dentata*; 91, 92, *Z. (Z.) inconspicua*; 93, 94, *Z. (Z.) spectabilis*; 95, 96, *Z. (Z.) planulata*; 97, 98, *Zephlebia (Terama) borealis*; 99, 100, *Neozephlebia scita*; 101, 102, *Acanthophlebia cruentata*.



**Fig. 103–105** Mature nymphs (scale lines 1 mm): 103, *Zephlebia (Z.) versicolor*; 104, *Z. (Z.) inconspicua*; 105, *Z. (Z.) dentata*.

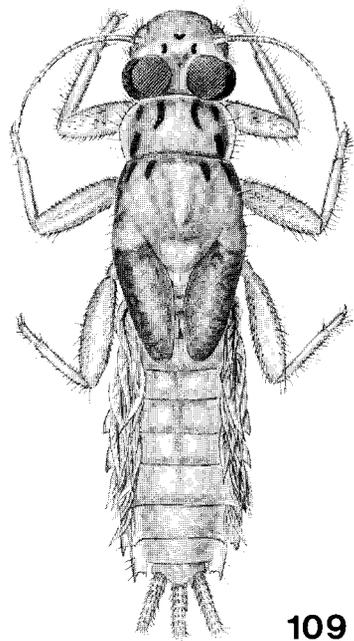
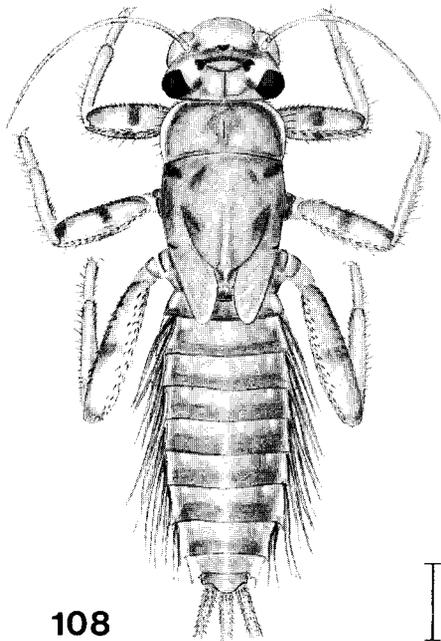
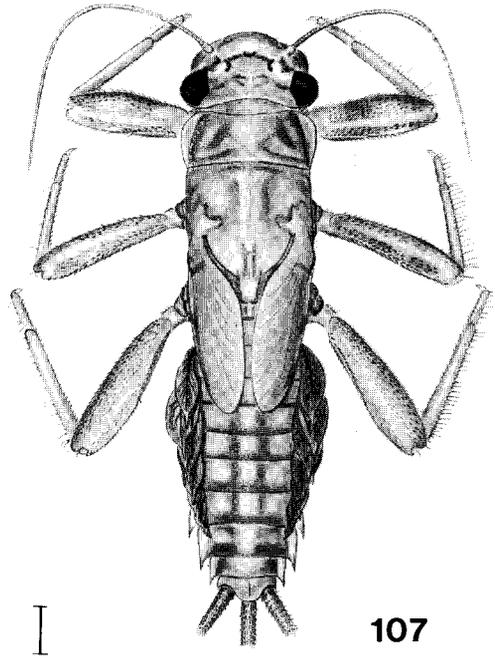
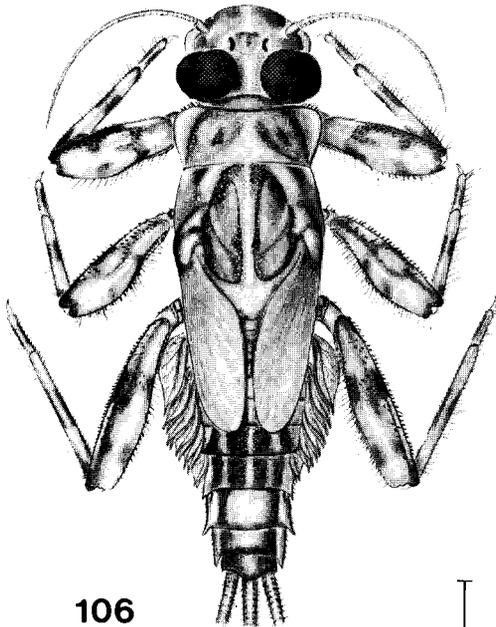
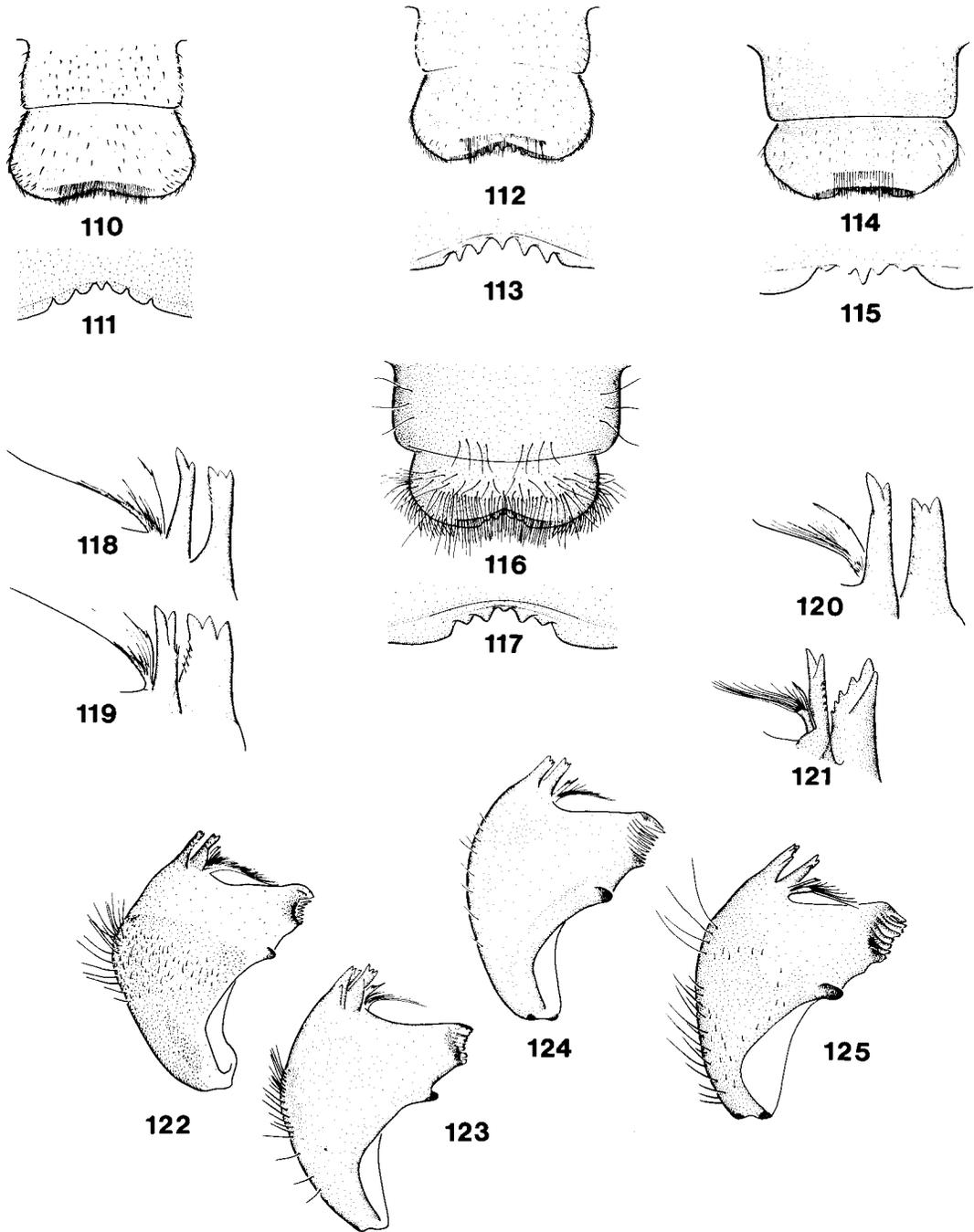


Fig. 106–109 Mature nymphs (scale lines 1 mm): 106, *Zephlebia (Z.) spectabilis*; 107, *Zephlebia (Terama) borealis*; 108, *Neozephlebia scita*; 109, *Acanthophlebia cruentata*.



**Fig. 110-117** Clypeus and labrum of nymphs, with detail of anteromedian emargination of labrum: 110, 111, *Zephlebia (Z.) versicolor*; 112, 113, *Zephlebia (Terama) borealis*; 114, 115, *Neozephlebia scita*; 116, 117, *Acanthophlebia cruentata*. **118-125** Enlargement of incisors and prosthecal tuft of right mandible (118-121), and left mandible (122-125) of nymphs: 118, 122, *Zephlebia (Z.) versicolor*; 119, 123, *Zephlebia (Terama) borealis*; 120, 124, *Neozephlebia scita*; 121, 125, *Acanthophlebia cruentata*.

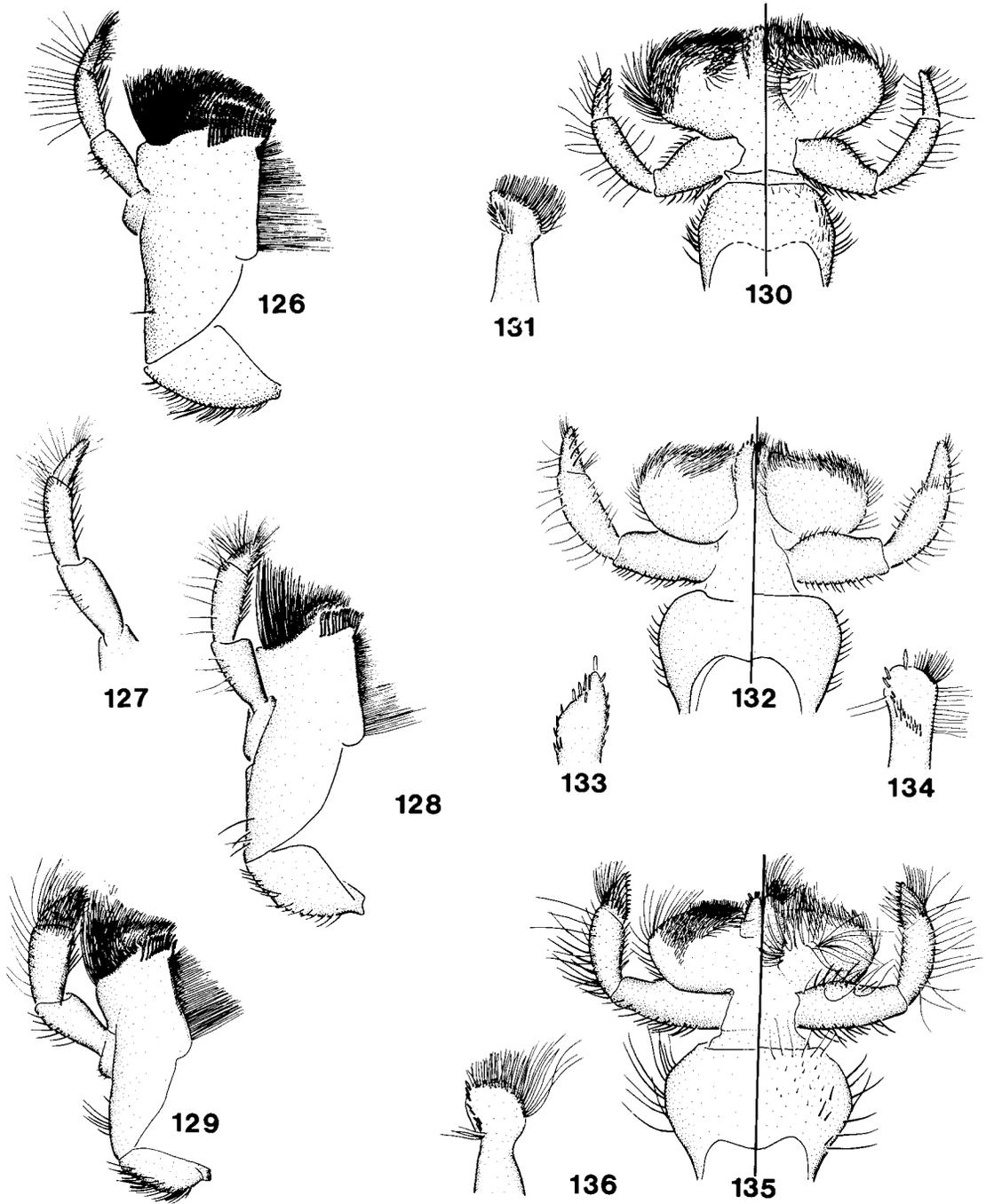
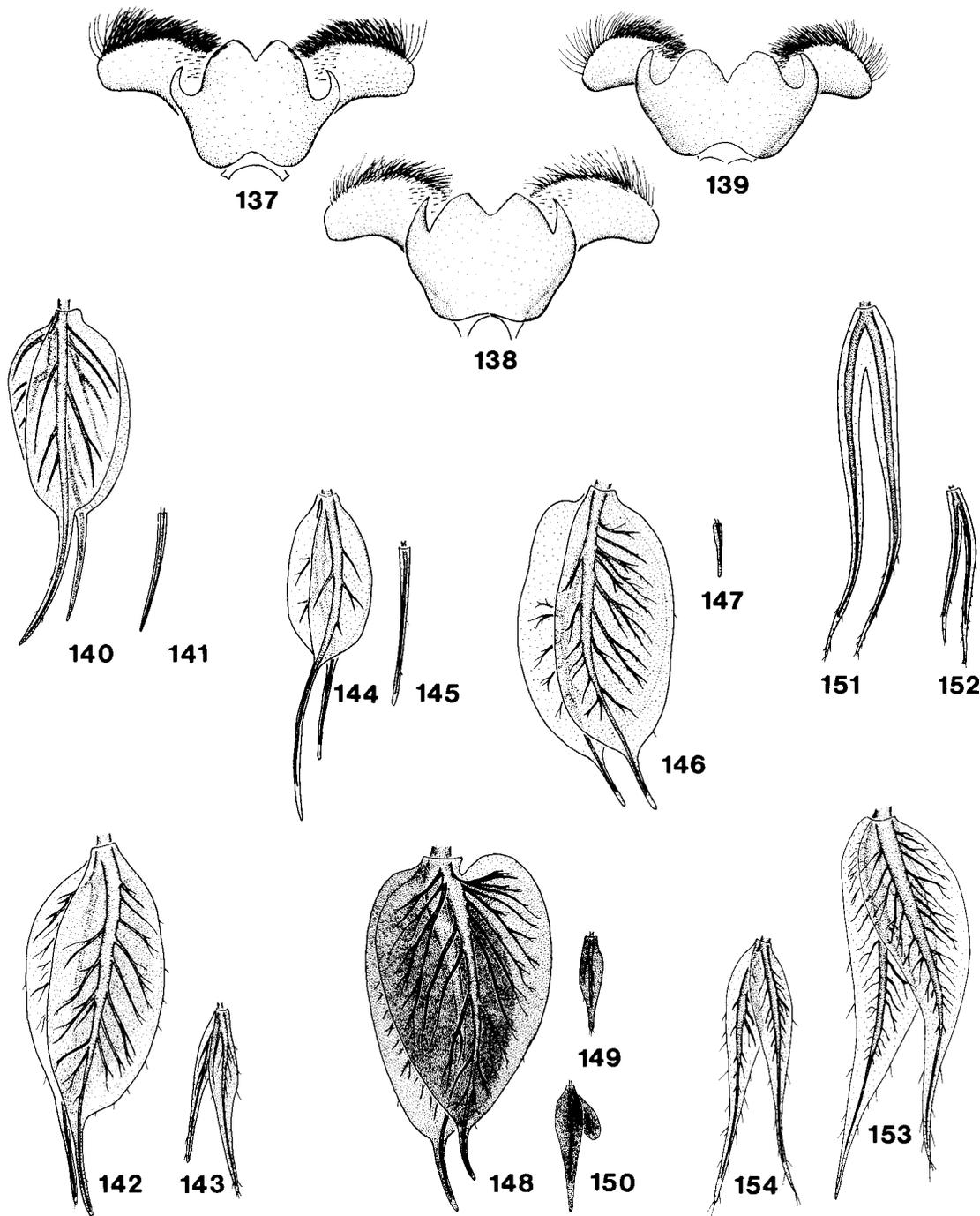


Fig. 126–129 Right maxilla of nymphs, ventral view: 126, *Zephlebia* (*Z.*) *versicolor*; 127, *Zephlebia* (*Terama*) *borealis* (palpus only); 128, *Neozephlebia* *scita*; 129, *Acanthophlebia* *cruentata*. 130–136 Labium of nymphs, dorsal (left) and ventral views, with lateral view of apex of glossa (enlarged): 130, 131, *Zephlebia* (*Z.*) *versicolor*; 132–134, *Neozephlebia* *scita* (133, apex of dorsal glossa, enlarged); 135, 136, *Acanthophlebia* *cruentata*.



**Fig. 137–139** Hypopharynx of nymphs: 137, *Zephlebia* (*Z.*) *versicolor*; 138, *Neozephlebia scita*; 139, *Acanthophlebia cruentata*. **140–153** Abdominal gills 4 and 7 of nymphs: 140, 141, *Zephlebia* (*Z.*) *versicolor*; 142, 143, *Z. (Z.) dentata*; 144, 145, *Z. (Z.) inconspicua*; 146, 147, *Z. (Z.) spectabilis*; 148–150, *Zephlebia* (*Terama*) *borealis* (150, gill 7 of lectotype); 151, 152, *Neozephlebia scita*; 153, 154, *Acanthophlebia cruentata*.

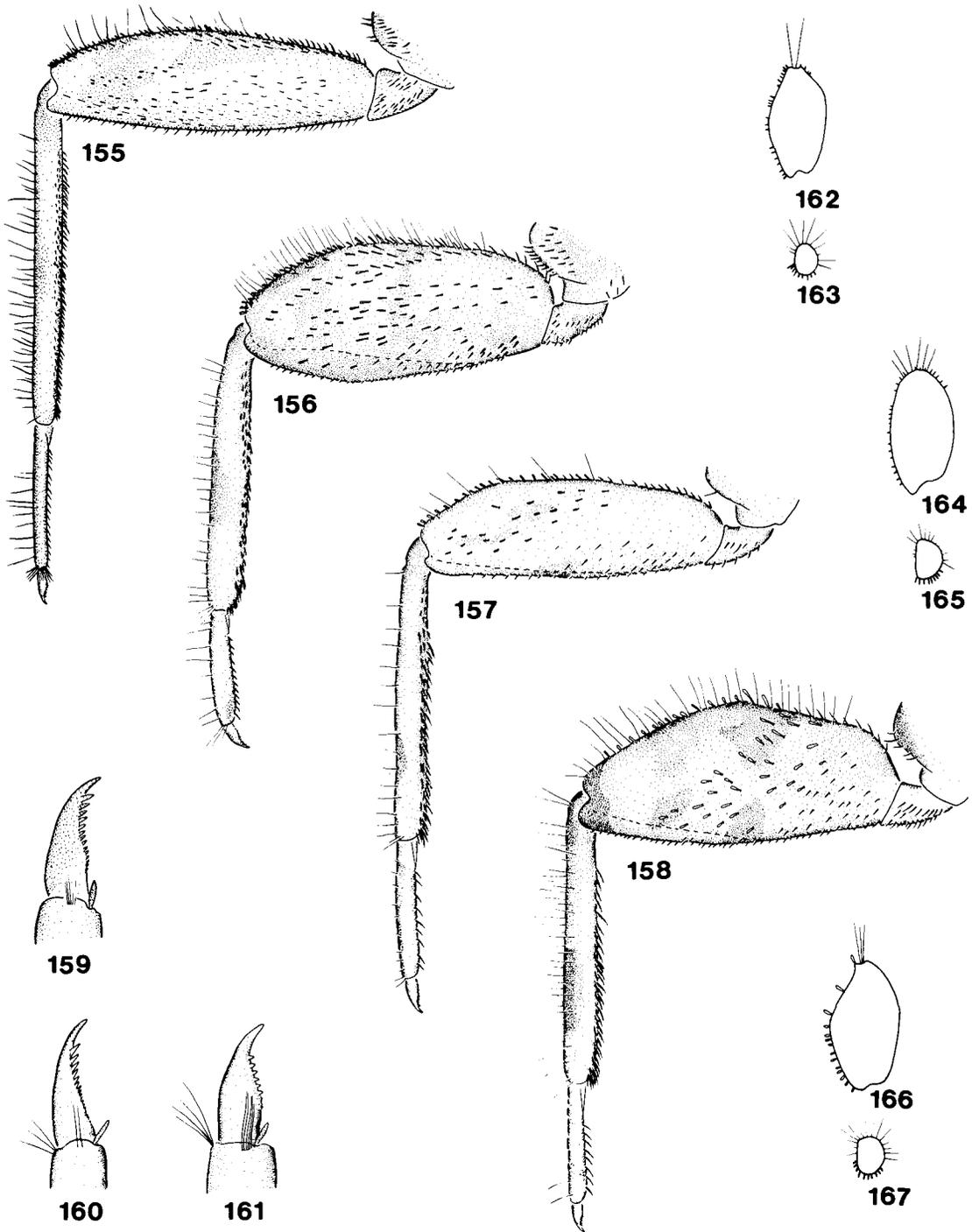


Fig. 155-167 Foreleg (155-158), fore claw (159-161), and cross-section through femur and tibia (162-167) of nymphs: 155, 159, 162, 163, *Zephlebia* (*Z.*) *versicolor*; 156, 164, 165, *Z. (Z.) dentata*; 157, *Z. (Z.) inconspicua*; 158, 166, 167, *Z. (Z.) spectabilis*; 160, *Neozephlebia scita*; 161, *Acanthophlebia cruentata*.

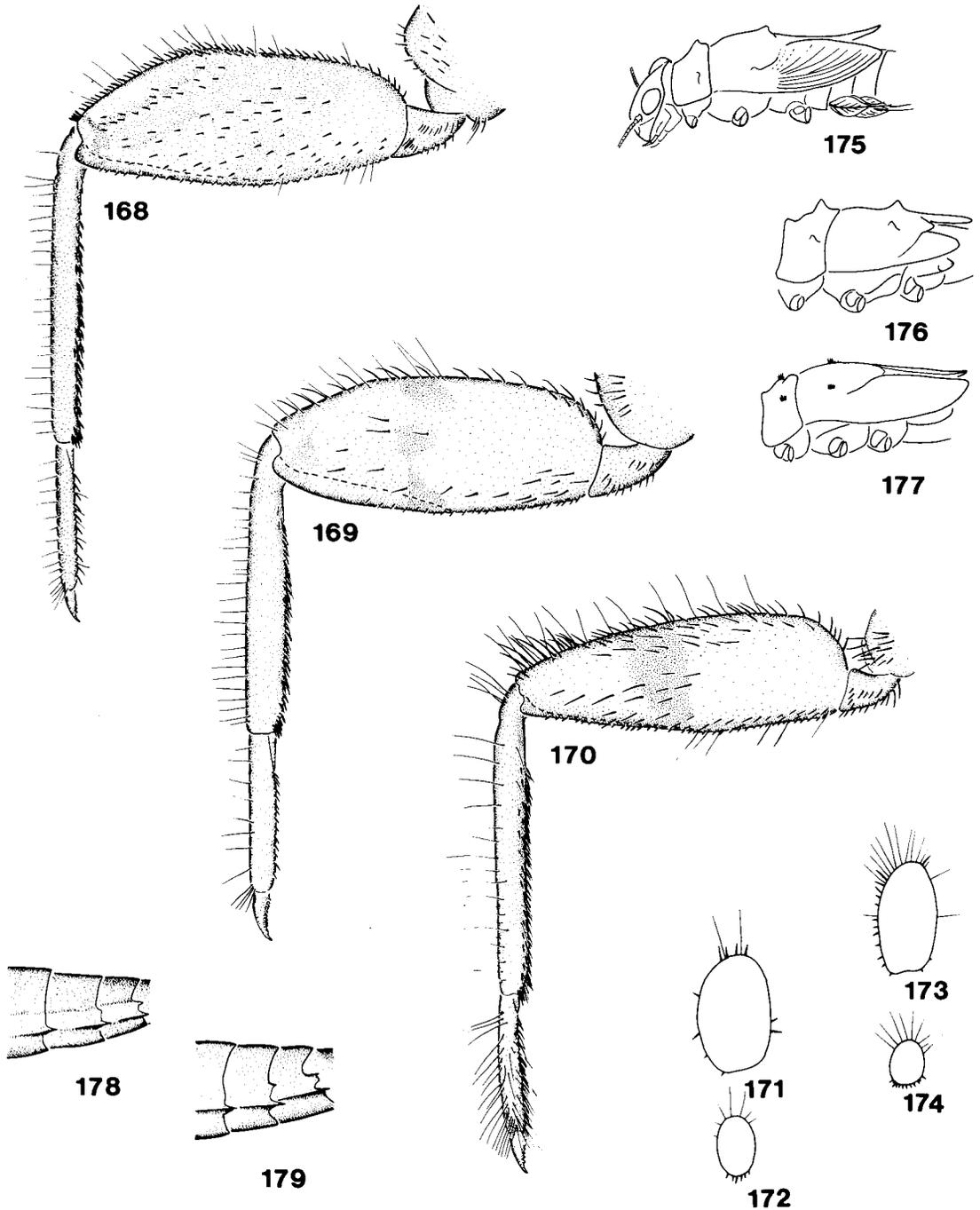
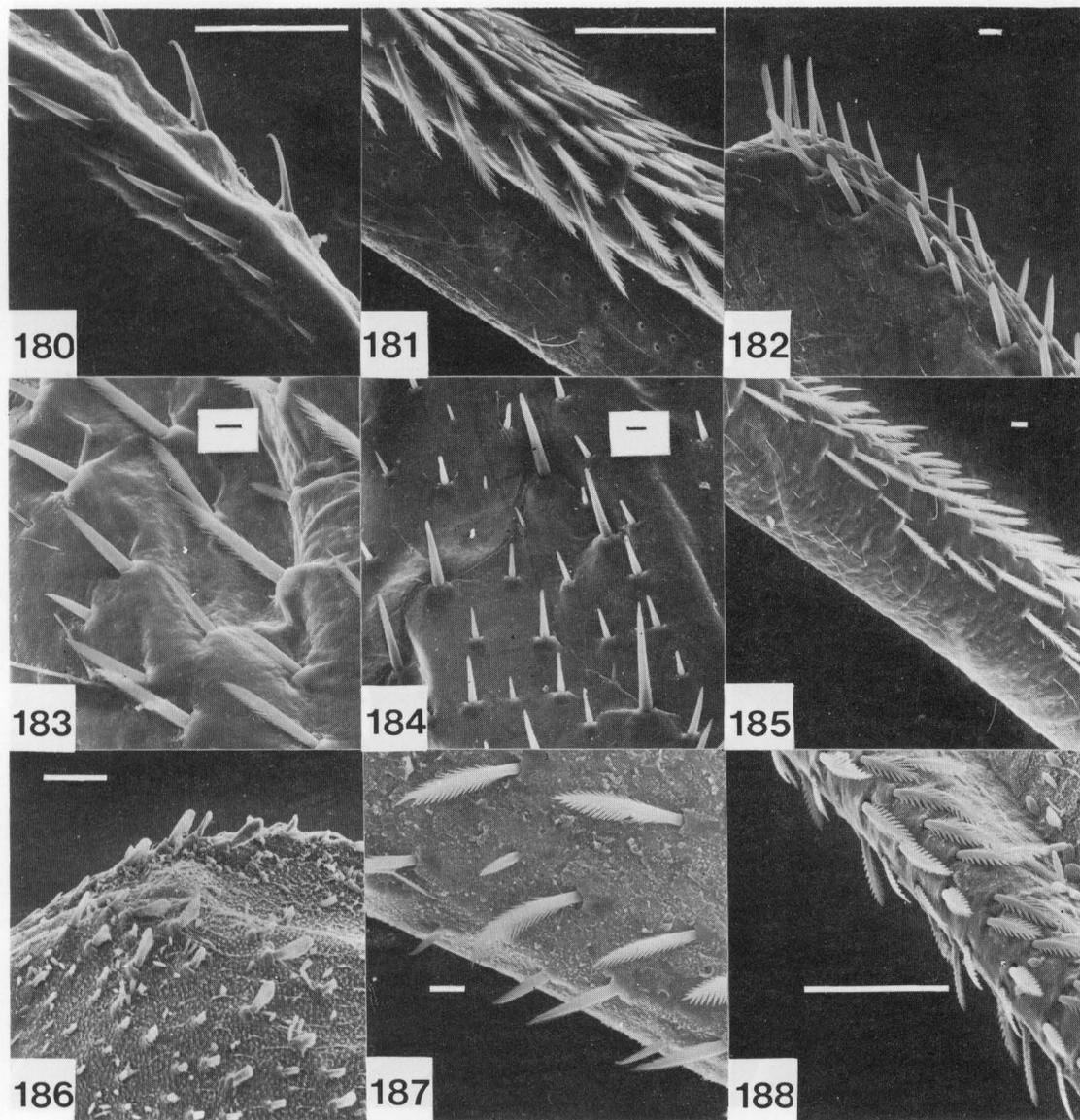


Fig. 168-174 Foreleg (168-170) and cross-section through femur and tibia (171-174) of nymphs: 168, *Zephlebia (Terama) borealis*; 169, 171, 172, *Neozephlebia scita*; 170, 173, 174, *Acanthophlebia cruentata*. 175-177 Thorax of nymphs, oblique lateral view: 175, *Zephlebia (Z.) versicolor*; 176, *Z. (Z.) inconspicua*; 177, *Z. (Z.) spectabilis*. 178, 179 Posterolateral projections of segments 7-9 of nymphal abdomen, *Neozephlebia scita* and *Acanthophlebia cruentata*.



**Fig. 180–188** Scanning electron micrographs of spines of nymphal legs (scale lines 10  $\mu\text{m}$ , except Fig. 180, 181, 186, and 188, 100  $\mu\text{m}$ ). 180, 181, *Zephlebia* (*Z.*) *versicolor*, dorsal femur near base, and tibia. 182–184, *Z.* (*Z.*) *dentata*: (182) dorsal femur near apex; (183) ventral femur near base; (184) mid femur. 185, *Z.* (*Z.*) *inconspicua*, tibia. 186–188, *Z.* (*Z.*) *spectabilis*: (186) anterior mid femur; (187) ventral femur; (188) tibia.

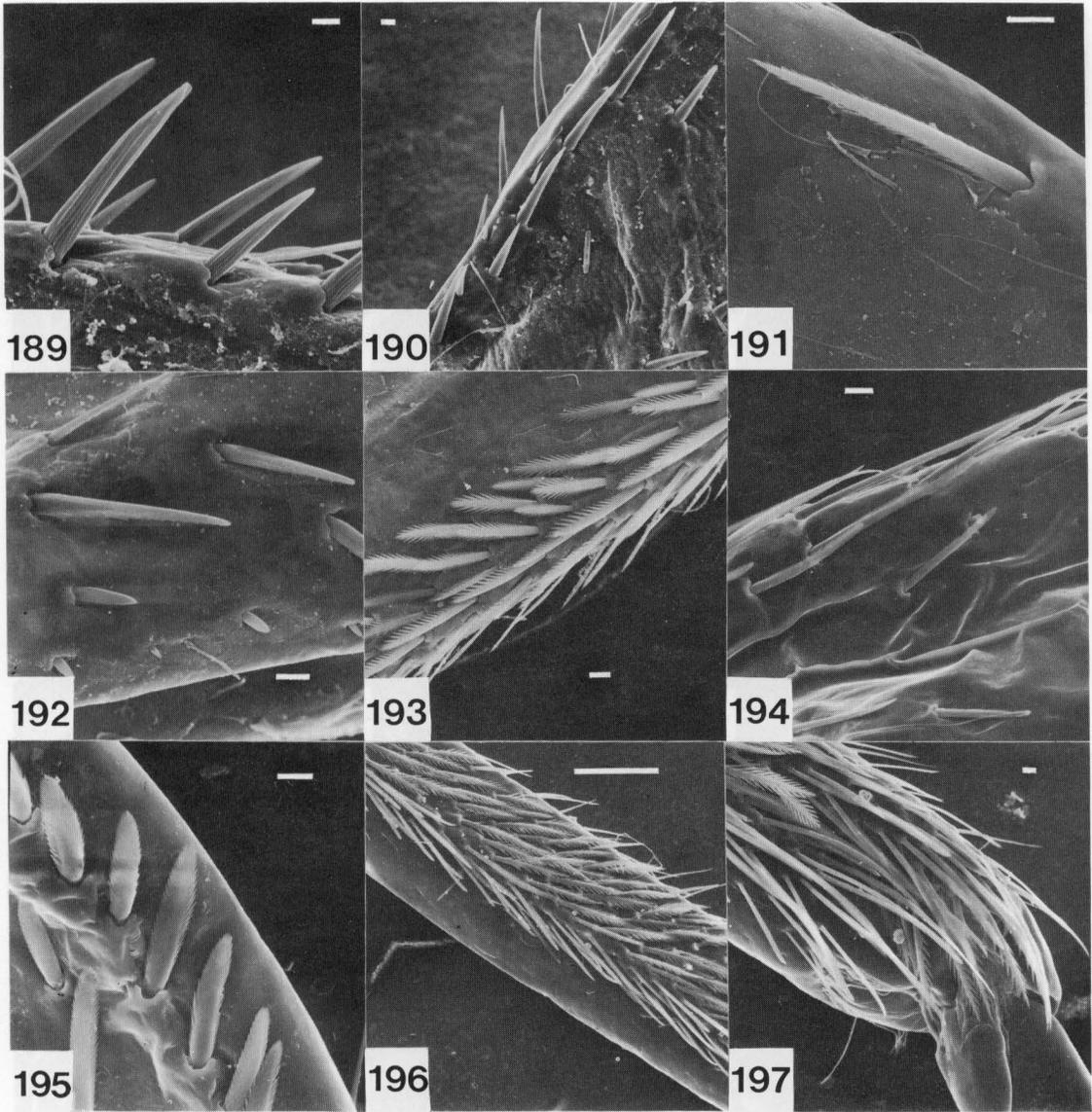


Fig. 189–197 Scanning electron micrographs of spines of nymphal legs (scale lines 10  $\mu\text{m}$  except Fig. 196, 100  $\mu\text{m}$ ). 189, 190, *Zephlebia (Terama) borealis*, dorsal femur near apex and near base. 191–193, *Neozephlebia scita*: (191) dorsal femur; (192) ventral femur; (193) tibia. 194–197, *Acanthophlebia cruentata*: (194) dorsal femur; (195) ventral femur; (196) mid tibia; (197) tibia/tarsus articulation.

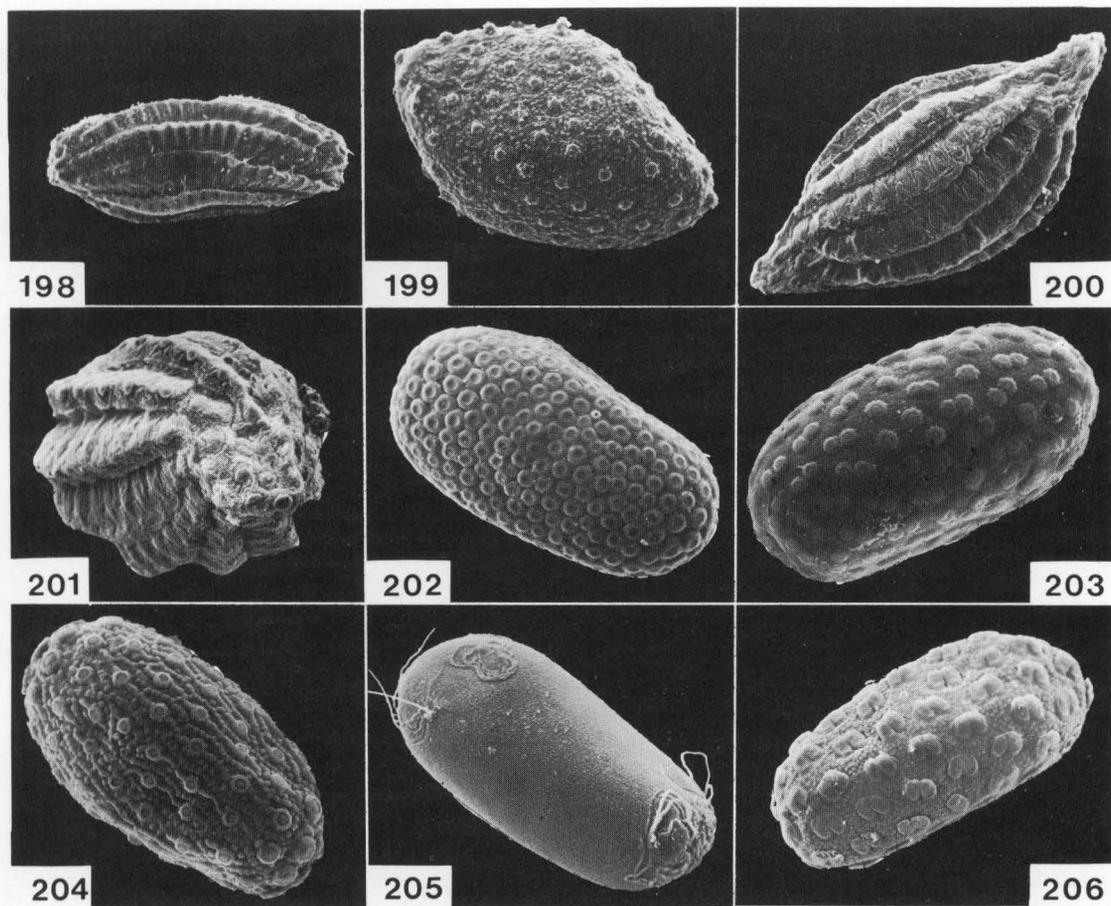


Fig. 198–206 Scanning electron micrographs of eggs. 198, *Zephlebia* (*Z.*) *versicolor*, lateral view ( $\times 160$ ). 199, *Z.* (*Z.*) *dentata* ( $\times 270$ ). 200, 201, *Z.* (*Z.*) *inconspicua*, lateral view ( $\times 210$ ) and polar view ( $\times 270$ ). 202, *Z.* (*Z.*) *spectabilis* ( $\times 250$ ). 203, *Zephlebia* (*Terama*) *borealis* ( $\times 320$ ). 204, *Z.* (*Z.*) *planulata* ( $\times 320$ ). 205, *Neozephlebia* *scita* ( $\times 250$ ); 206, *Acanthophlebia* *cruentata* ( $\times 250$ ).