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A revision of genus *Atalophlebioides* (Ephemeroptera: Leptophlebiidae)

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Atalophlebioides Phillips is redescribed as a monotypic genus endemic to New Zealand. All life stages of *A. cromwelli* (Phillips) are described, and a lectotype is designated. The relationships of the genus and the ecology of *A. cromwelli* are discussed.

INTRODUCTION

Leptophlebiidae are widespread in relatively undisturbed New Zealand streams, often dominating the invertebrate fauna (Towns 1976). However, most studies of stream invertebrate communities in New Zealand have been hampered by a lack of definitive work on the taxonomy of this family of mayflies.

This paper, in which the genus *Atalophlebioides* is redescribed, is the first of a series revising the New Zealand Leptophlebiidae.

The most recent revision of the family in New Zealand was by Phillips (1930), who described one species of *Atalophlebia*, subsequently assigned to *Zephlebia* by Penniket (1961), and seven species of *Deleatidium*, two of which were subsequently assigned to *Atalophlebioides* by Peters & Edmunds (1964). Unfortunately Phillips did not designate type specimens. We have been unable to locate his material in New Zealand or at the British Museum (Natural History), and therefore assume that most of it has been lost. However, a few specimens in the National Museum of New Zealand are almost certainly part of Phillips's original material, as indicated by collection dates, localities, and handwriting on the labels. Where appropriate, these specimens will be designated as lectotypes.

METHODS

Most material for SEM study was treated briefly (15–30 s) in an ultrasonic cleaner before mounting. Eggs prepared for the SEM were dissected from female imagos in 100% ethanol, then taken through 50 : 50 ethanol : amyl acetate to 100% amyl acetate and through a critical point drier.

Sample sizes for measurements were: body of imagos – male $n = 7$, female $n = 9$; forelegs of male imago – $n = 2$; wings – male $n = 4$, female $n = 4$; male genitalia – $n = 2$; body of nymphs – $n = 9$; mouthparts – $n = 5$.

Specimen localities are listed under the arbitrary system of area codes described by Crosby *et al.* (1976). Abbreviations of collector's names are as follows: AKW, A. K. Walker; DRT, D. R. Towns; ELT, E. L. Towns; GCH, G. C. Hayward; GFE, G. F. Edmunds, Jr; JAM, J. A. McLean; JCW, J. C. Watt; JGP, J. G. Penniket; JSD, J. S. Dugdale; KAJW, K. A. J. Wise; MB, M. Black.

Morphological terms and conventions used in the descriptions are consistent with those in Peters & Edmunds (1970) and Peters (1971), except that several additional morphological characters and descriptions of subimagos are used to further delineate genera and species.

Genus *Atalophlebioides* Phillips, 1930

IMAGO. Length: ♂ – body 6.8–8.2 mm, forewings 7.4–8.3 mm; ♀ – body 6.8–7.8 mm, forewings 7.7–8.9 mm.

Eyes: ♂ – fused on meson of head, the lower portion ¾ length of upper portion; ♀ – separated on meson of head by 2–3× maximum width of eye.

Wings (Fig. 1–3). Forewings: width 1/3 length. Vein Rs forked at 1/5 (to a little less) distance from base to margin. Vein MA forked a little less than half distance from base to margin; 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 ¼ to 1/3 distance from base to margin, base of MP_2 closer to CuA than to MP_1. Vein ICu_1 attached at base to CuA and CuP with cross veins, cross veins few in Cu–A area (Fig. 1). Hind wings: costal margin concave slightly basal to midlength (Fig. 3), the

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wing apices acute and rounded. Width of hind wings half length, and length of hindwings a little less than ¼ length of forewings. Vein Sc ¾ to 9/10 length of wings, R_1 a little less than length of wings; cross veins few.

Legs. Ratios of segments in ♂ forelegs 0.62–0.78 : 1.00(2.2–2.5 mm) : 0.03–0.06 : 0.38–0.50 : 0.41–0.50 : 0.30–0.34 : 0.11–0.13. Claws of a pair dissimilar, one apically hooked, the other pad-like with a small apical hook (Fig. 4).

Male genitalia (Fig. 5–7). Forceps: segment 2 1½× length of segment 3 and 1/5 to ¼ length of segment 1; apex of segment 3 flat, sometimes indented; base of forceps broad, inner margin forming an angular to smooth bend near midlength (Fig. 5). Styliger plate 1/3 to ½ as long medially as the maximum width, shallowly cleft at apex as in Fig. 5. Penes fused, broad at base, approximately triangular, with 2 fused, rounded, apical lobes (Fig. 5, 6) and a small midventral appendage (Fig. 5–7).

Ninth sternum of ♀ entire, rounded to slightly concave apically (Fig. 9). Terminal filament longer than cerci.

MATURE NYMPH. Length of body 6.1–7.6 mm. Head prognathous. Antennae 1½× length of head.

Mouthparts (Fig. 13–19). Labrum: length 1/3 (to a little less) maximum width, with dorsal hair as in Fig. 13, and submedian, anterosubmedian, and anterolateral areas of hair ventrally; apical margin hooded, the anteromedian emargination deep, with 5 large, flat-topped denticles (Fig. 14); lateral margins rounded (Fig. 13). Clypeus as in Fig. 13. Left mandible (Fig. 15) with a single, small, marginal hair tuft; outer margin curved; incisors with serrated apical teeth (Fig. 16); prosthecal tuft small (Fig. 15). Hypopharynx: lingua with well developed lateral processes, submedian lobes with a double row of hairs forming a crest on anterolateral margin and paired submedian longitudinal rows of long hair on internal surface, anterior margin deeply cleft, the cleavage lined with small hairs and spines (Fig. 18); superlingua as in Fig. 18, with a hair row along anterior margin and blunt lateral margins. Maxillae: apical half of galea–lacinia expanded medially, with a subapical row of 22–25 spines (Fig. 17); segment 2 of palpi subequal in length to segment 1, segment 3 a little more than half length of segment 2 (Fig. 17). Labium as in Fig. 19; palpi slender, segment 2 about equal in length to segment 1, segment 3 a little less than half length of segment 2; glossae large, on same plane as paraglossae; submentum as in Fig. 19, without spines.

Pronotum with small spines on anterolateral margin. Legs (Fig. 20): femora with pointed spines on dorsal and ventral surface and scattered over medial surface (Fig. 20, 24); inner surface of fore tibiae with double rows of coarsely and finely bipectinate spines (Fig. 25–27); inner surface of tarsi with 4 or 5 pointed spines (Fig. 20); apex of claws hooked and narrow, denticles on claws progressively larger apically (Fig. 21).

Gills (Fig. 22) on segments 1–7, alike, progressively smaller posteriorly, dorsal and ventral portions of lamellae slender, tapered towards apex; tracheae with main trunk along median line of lamellae, and with fine lateral branches. Abdomen with posterolateral spines on segments 2–9. Terminal filament a little longer than cerci, each segment with a distal whorl of prominent denticles (Fig. 23).

EGG elongate oval; chorion densely ornamented with raised tubercles (Fig. 28, 29).

TYPE SPECIES *Atalophlebioides cromwelli* (Phillips), by subsequent designation (Peters & Edmunds 1964); originally placed in *Deleatidium (Atalophlebioides).*

REMARKS

Atalophlebioides was established as a subgenus of *Deleatidium* by Phillips (1930), who placed all species with abdominal gills of double lamellae in *Atalophlebioides,* and those with abdominal gills of a single lamella in *Deleatidium* sensu stricto. Ulmer (1938), Traver (1946), and Peters & Edmunds (1964) considered *Atalophlebioides* to be worthy of generic rank, whereas Harker (1954) agreed with Phillips (1930). Peters & Edmunds (1964) designated *A. cromwelli* as the type species of *Atalophlebioides,* although they acknowledged that *Atalophlebioides* was a complex of genera with ill defined limits.

Studies of the thorax, tentorium, and abdominal terga of Gondwanian Leptophlebiidae by Tsui & Peters (1975) supported the generic status of *Atalophlebioides,* but indicated heterogeneity within the New Zealand species. Pescador (1976) also considered the New Zealand species of *Atalophlebioides* to be only tenuously related, and in his discussion of the phylogeny of Southern Hemisphere Leptophlebiidae interpreted *A. cromwelli* and *A. sepia* as separate species complexes.

Atalophlebioides can be distinguished from all other leptophlebiid genera by the following combinations of characters. In the imago: (1) hind wings without a costal projection (Fig 3), and vein Sc ¾ to 9/10 length of wings (Fig. 3); (2) penes fused (Fig. 5, 6); (3) ninth sternum of female entire, rounded to slightly concave apically (Fig. 9); (4) claws of a pair dissimilar, one apically hooked, the other pad-like with a small apical hook (Fig. 4). In the nymph: (1) labrum hooded, rounded on lateral margins (Fig. 13); (2) labrum about 1/3 as long as wide; (3) labrum with flattened denticles on anteromedian emargination (Fig. 14); (4) mandibles with a single small, marginal hair tuft (Fig. 15); (5) incisors of mandibles serrated on apex (Fig. 16); (6) prosthecal hair tuft of mandibles small (Fig. 15); (7) glossae

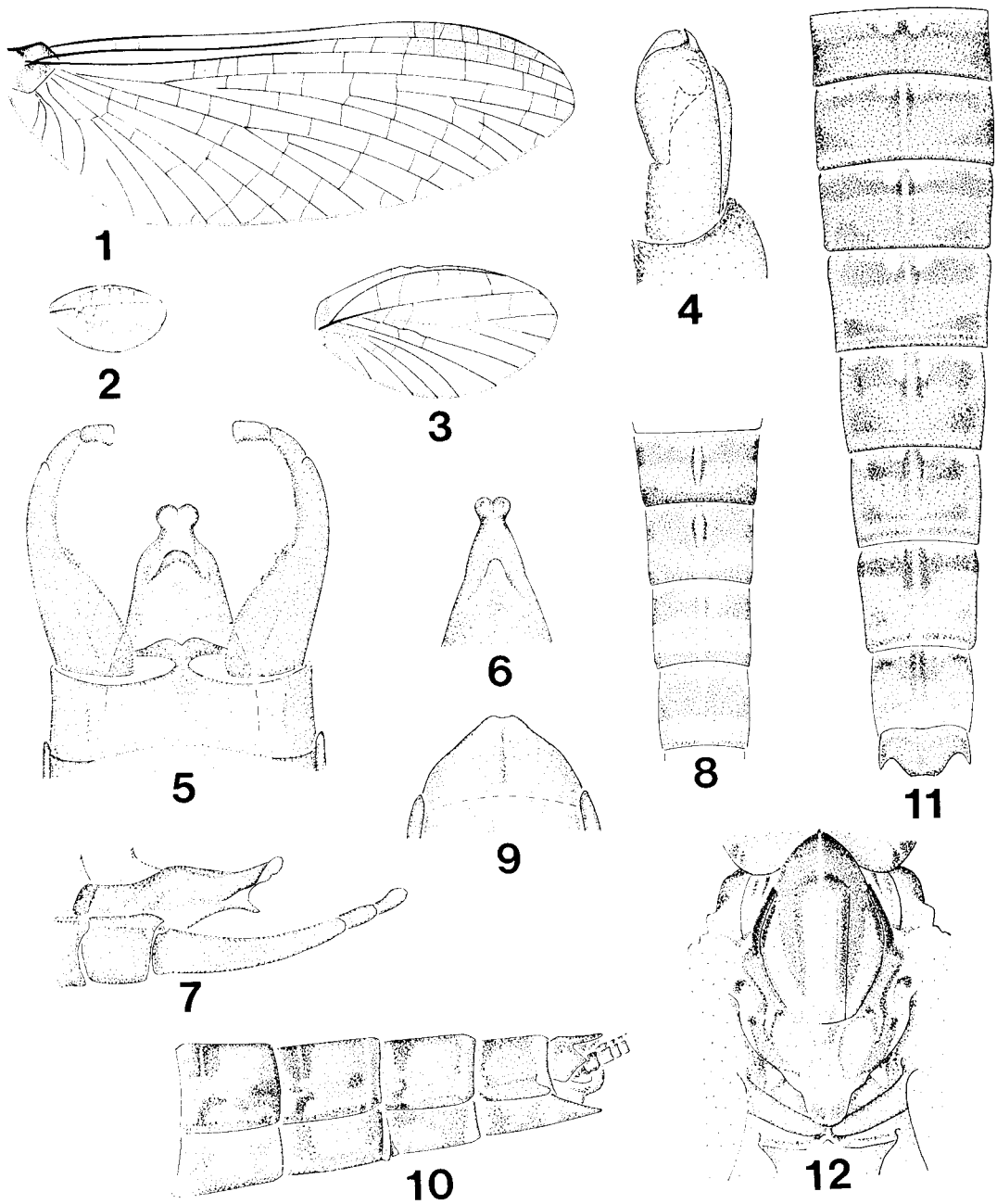

Fig. 1–12. *Atalophlebioides cromwelli.* **1–8,** ♂ imago: 1, forewing; 2, hind wing; 3, hind wing, enlarged; 4, fore claws; 5, genitalia, ventral view; 6, penes of ♂ from near Greymouth; 7, genitalia, lateral view; 8, abdominal segments 4–7, dorsal view. **9–11,** ♀ imago: 9, ninth sternum, ventral view; 10, abdominal segments 6–10, lateral view; 11, abdominal segments 2–10, dorsal view. **12,** ♂ subimago: meso- and metathorax, dorsal view.

and paraglossae of labium on same plane (Fig. 19); (8) submentum of labium without spines (Fig. 19); (9) abdominal gills with double lamellae (Fig. 22); (10) tibiae of forelegs with bipectinate spines (Fig. 25–27); (11) posterolateral spines on abdominal segments 2–9.

On the basis of published data, *Atalophlebioides* is most closely related to *Deleatidium* of New Zealand (Phillips 1930), but can be distinguished from it by the following characters. In the imago: (1) vein Sc of the hind wing less than 9/10 length of wing; (2) penes with a midventral lobe, and fused, rounded, apical lobes. In the nymph: (1) labrum rounded on lateral margins; (2) abdominal gills with double lamellae.

Two species usually placed in *Atalophlebioides*, *A. sepia* (Phillips) and *A. cromwelli* (Phillips), are known from mainland New Zealand, and a third, *A. aucklandensis* Peters, occurs on the subantarctic Auckland Islands. However, the diagnosis of *Atalo-*

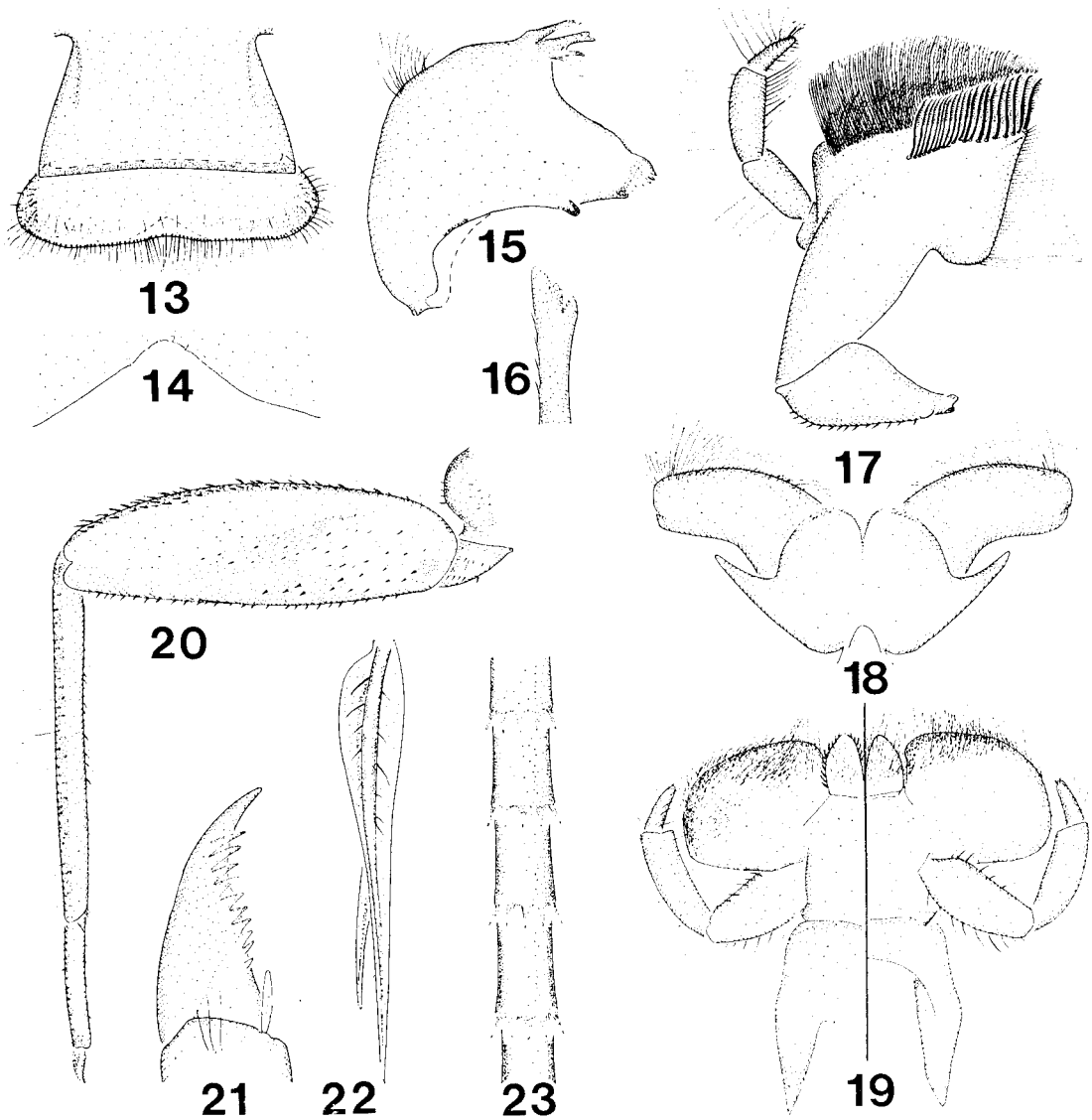

Fig. 13–23. *Atalophlebioides cromwelli*, mature nymph: 13, labrum and clypeus, dorsal view; 14, anteromedian emargination of labrum, enlarged; 15, left mandible, dorsal view; 16, right outer incisor, enlarged; 17, right maxilla, ventral view; 18, hypopharynx; 19, labium, dorsal (left) and ventral views; 20, foreleg; 21, fore claw; 22, fourth abdominal gill; 23, part of terminal filament.

phlebioides outlined above excludes *A. sepia* and *A. aucklandensis* from the genus. These species differ from *A. cromwelli* in both the nymphal and adult stages, and eventually will be placed in separate genera (Towns & Peters, in prep.). Species previously assigned to *Atalophlebioides* have also been described from Australia (Harker 1950, 1954) and Chile (Ulmer 1938), but none of them should remain in *Atalophlebioides,* which is therefore here redefined as a monotypic genus restricted to New Zealand.

Atalophlebioides cromwelli (Phillips, 1930) (Fig. 1–30)

Phillips, 1930: 385–9 (in a subgenus of *Deleatidium*). –Peters & Edmunds, 1964; 238–9. –Tsui & Peters, 1975: 555.

MALE IMAGO (in ethanol). Upper portion of eyes greyish brown, lower portion black. Head brown, carinae darker, area between antennae and ocelli dark brown. Antennae brown, flagellum paler. Basal half of ocelli black, apical half greyish white.

Thorax. Pronotum brown washed with black; mesonotum and anterior 2/3 of scutellum pale to dark brown, posterior scutellum washed with black; sutures paler; carinae dark brown to black; pleura brown, irregularly washed with dark brown or black; sterna brown washed with black. Legs pale brown, coxae irregularly washed with dark brown. Wings (Fig. 1–3): longitudinal veins of forewings and veins Sc and R of hind wings brown, remainder hyaline; all cross veins hyaline; membranes hyaline, wing bases pale brown; apical 1/3 of cells C and Sc of forewings translucent, whitish.

Abdomen washed with pale brown and black. Anterior and lateral margins of terga 2–6 and anterior margin of tergum 7 hyaline. Terga 2–7 with a pale, median, longitudinal line along entire length and a darker, broad, anterior transverse band, broken in midline (Fig. 9); area between bands and posterior margin of terga pale reddish brown to hyaline. Terga 2–5 with small, paired, posterolateral, dark maculae. Posterior margins of terga 1–6 with a narrow, transverse, dark brown to black band. Sterna 1–6 hyaline washed with pale brown, sterna 7–10 translucent pale brown. Genitalia (Fig. 5–7) pale brown, apical half of forceps paler.

FEMALE IMAGO (in ethanol). Eyes black. Head pale brown, carinae darker. Antennae pale brown, apex

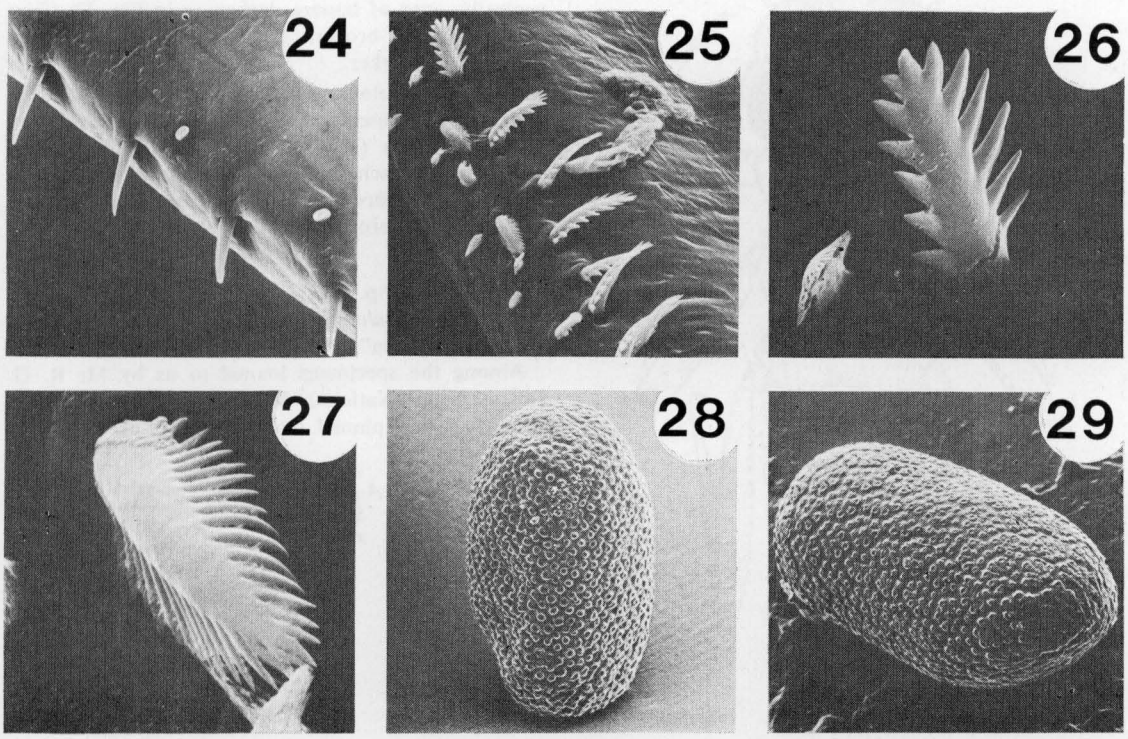

Fig. 24–29. *Atalophlebioides cromwelli,* scanning electron micrographs. **24–27,** mature nymph: 24, spines of femur (×420); 25, spines of tibia (×540); 26, coarsely bipectinate spine (×2170); 27, finely bipectinate spine (×3680). **28–29,** eggs from mature ♀♀: 28, from Kitekite Stm, Auckland (×360); 29, from Marsden, Buller (×360).

of scape and pedicel darker, flagellum paler. Colour of ocelli as in ♂ imago.

Thorax. Nota and pleura as in ♂ imago, but darker. Legs pale yellowish brown, except apex of forelegs occasionally dark brown. Wings: colour and markings as in ♂ imago.

Abdomen. Colour and markings as in ♂ imago except: general colour darker; small, pale, paired, submedian maculae occur on terga 2–9; anterior hyaline areas smaller; sterna dark brown (Fig. 10, 11).

MALE AND FEMALE SUBIMAGO (in ethanol). Head dark brown, markings as in ♂ and ♀ imago, but ocellar area darker. Antennae brown. Colour of ocelli as in ♂ imago. Eyes of ♀ black, upper portion of eyes of ♂ orange brown, lower portion black.

Thorax. Pronotum brown; anterior 1/3 of mesonotum, area between inner and outer parapsidal furrows, posterolateral mesonotum between outer parapsidal furrow and notal wing process, and anterolateral margins of scutellum brown; lateral margins of mesonotum, area between inner parapsidal furrows, and humps of scutellum whitish brown; posterior margin of scutellum washed with black (Fig. 12); pleura dark brown, edged with black, sutures pale; sterna pale, except lateral lobes of furcasternum and posterolateral margin of mesosterna brown. Wings: Longitudinal and cross veins and membranes pale grey. Legs: colour and markings as in ♂ and ♀ imago.

Abdomen. Colour and markings of terga as in ♂ and ♀ imago, except general colour darker brown, and anterior margins whitish brown; sterna pale brown, sterna 1–3 irregularly washed with dark brown. Genitalia of ♂ pale brown. Caudal filaments pale brown, darker annuations at articulations.

MATURE NYMPH (in ethanol). Head pale to dark brown, washed with darker brown or black as in Fig. 30. Ocelli coloured as in ♂ and ♀ imago. Eyes of ♀ black, upper portion of eyes of ♂ deep reddish brown, lower portion dark grey. Antennae pale yellowish brown.

Thorax. Pronotum brown, washed on posterolateral margins with dark brown; mesonotum brown, with irregular dark brown markings on anterolateral margin; metanotum brown, with a narrow, dark brown band near posterior margin (Fig. 30). Legs: pale to dark brown; basal half of femora paler ventrally, apex of femora darker, as in Fig, 30; tibiae pale to dark brown; tarsi pale brown, dorsum occasionally darker.

Abdomen. Colour and markings as in ♂ and ♀ imago, except anterior 1/3 of each tergum pale brown (Fig. 30). Gills (Fig. 22): membrane colourless to pale brown, tracheae and tracheoles black. Caudal filaments pale brown, each segment with a distal whorl of dark brown denticles.

TYPE DATA

Phillips (1930, p. 389) gives the type locality of *Deleatidium (Atalophlebioides) cromwelli* as "Streams round Wellington".

Among the specimens loaned to us by Mr R. G. Ordish from National Museum of New Zealand collections is a pinned female imago with the hand-

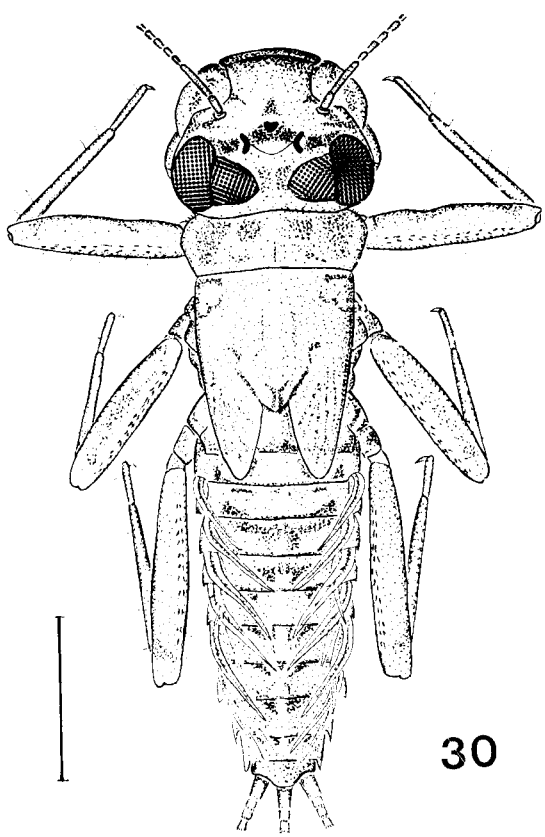

Fig. 30. *Atalophlebioides cromwelli*, mature nymph (scale line: 1 mm).

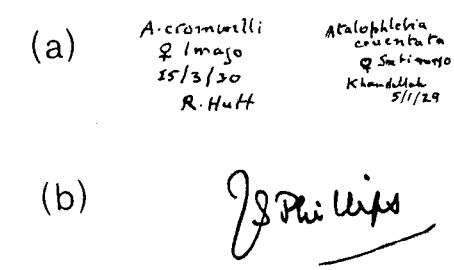

Fig. 31. (a) Unsigned handwritten labels from material in the National Museum of New Zealand; lectotype label on left. (b) Capt. J. S. Phillips's signature.

written label "*A. cromwelli*, ♀ imago, 25/3/30, R. Hutt" (Fig. 31a). On the evidence of an example of Capt. Phillips's signature (Fig. 31b) given to us by Mr P. E. S. Whalley, British Museum (Natural History), the label appears to have been written by Capt. Phillips. The specimen locality is within the generalised type locality given by Phillips, and the collection date is within the period of this study. We are satisfied, therefore, that this specimen is part of Capt. Phillips's original series. The specimen fits the description of the female given by Phillips (1930), and is the basis of our definition of *Atalophlebioides cromwelli*; all (non-type) material studied for this paper (listed below) has been compared with this specimen. We therefore designate this female imago, deposited in the collections of the National Museum of New Zealand, as the lectotype of *Atalophlebioides cromwelli*.

MATERIAL EXAMINED

North Island. ND. Waipoua State Forest: 2 ♂ and 3 ♀ imagos, light trap, 4 Feb 1975, ? coll.; 1 ♂ imago, light trap, 15 Oct 1967, JSD. **AK.** Cascade Stm: 1 ♀ imago, 8 Nov 1966, JAM; 3 ♀ subimagos, light trap, 20 Nov 1975, DRT; 1 ♀ imago, light trap, 9 Feb 1977, MB; 1 ♀ subimago, reared from nymph, 5 Apr 1975, DRT; 1 nymph, 11 Mar 1966, GFE; 2 nymphs, 18 Mar 1975, DRT; 4 nymphs, 22 Oct 1975, DRT; 3 ♂ and 4 ♀ subimagos, light trap, 9 Feb 1977, MB; 2 ♂ and 1 ♀ subimagos, light trap, 8 Nov 1966, JAM; 3 ♂ and 1 ♀ subimagos, light trap, 9 Mar 1977, MB; 1 ♀ subimago, reared from nymph, 4 Apr 1975, DRT. Waitakere R.: 1 nymph, 26 Nov 1973, DRT; 9 ♂ and 10 ♀ subimagos, light trap, 8 Feb 1977, MB; 3 nymphs, 21 Nov 1975, DRT. Small tributary of Waitakere R. near Anderson's Track; 1 ♀ subimago, light trap, 16 Feb 1977, MB. Kitekite Stm: 1 ♀ imago, reared from nymph, 25 Feb 1975, DRT; 1 nymph, riffle, 27 Dec 1976, DRT; 1 ♀ subimago, reared from nymph, 10 Feb 1974, DRT. Opanuku Stm: 1 nymph, 29 Nov 1955, KAJW. No locality or date: 1 ♂ subimago, JAM. **CL.** Kauaeranga R.: 54 nymphs, pool, 4 Jan 1977, DRT, ELT, GCH; 1 nymph, shallow riffle, 4 Jan 1977, DRT. Kapowai R.: 2 nymphs, slow riffle, 14 Jan 1977, DRT. **South Island. NN.** Aniseed Vly: 2 ♂ and 5 ♀ imagos, and 1 gynandromorph subimago, beating *Nothofagus menziesii*, 14 Jan 1976, AKW. **BR.** Mawhera State Forest, Wallaby Crk: 1 nymph, 9 Jan 1973, JCW. Kokiri: 4 ♂ and 6 ♀ imagos, reared, undated, JGP; 1 nymph, 1 ♂ and 1 ♀ imago, Dec 1961, JGP. Marsden: 2 ♀ imagos, 1 nymph, 24 Dec 1962, JGP; 1 ♂ imago, reared, 6 Jan 1962, JGP; 5 ♀ imagos, netted, 19 Jan 1962, JGP.

Association of ♂ and ♀ imagos and nymphs is based on rearing.

Repositories (all specimens are in ethanol): 1 ♂ imago, 3 ♂ and 5 ♀ subimagos, and 13 nymphs – National Museum of New Zealand, Wellington; 7 ♂ and 11 ♀ imagos, 4 ♂ and 3 ♀ subimagos, 1 gynandromorph subimago, and 12 nymphs – Entomology Division, DSIR, Auckland; 4 ♂ and 3 ♀ imagos, 1 ♂ and 2 ♀ subimagos, and 17 nymphs – Canterbury Museum, Christchurch; 3 ♂ and 2 ♀ subimagos and 11 nymphs – British Museum (Natural History), London; 2 ♂ imagos, 2 ♂ and 6 ♀ subimagos, and 13 nymphs – Florida A & M University, Tallahassee; 3 ♂ and 4 ♀ subimagos, and 1 nymph – Bernice P. Bishop Museum, Honolulu; 2 ♂ and 1 ♀ subimagos, and 7 nymphs – University of Utah, Salt Lake City.

REMARKS

The midventral appendage of the penes appeared to be distorted on slides of the male genitalia. Whole specimens had the apex entire (Fig. 5, 6), whereas in mounted specimens the appendage appeared bilobed. Penes also showed some variation in width. Male imagos collected by J. G. Penniket on the west coast of the South Island had more slender penes than specimens collected elsewhere (Fig. 6); this may be a local variation.

An unusual aberration was a gynandromorph subimago collected from Nelson. This specimen appeared to be a female, except that one eye was enlarged and divided as in males.

Thoracic and abdominal ganglia of nymphs from the Auckland area are rarely pigmented, whereas nymphs from Coromandel have pigmentation on the terminal abdominal ganglion, or the thoracic ganglia, or all ganglia.

BIOLOGY

Atalophlebioides cromwelli nymphs are most abundant on rocky substrates in slow-flowing areas of moderately large rivers (approximately 15 m wide), but also are found in pools in small streams (2 m wide).

ACKNOWLEDGMENTS

We are grateful to Dr T. K. Crosby (Entomology Division, DSIR), Mr R. G. Ordish (National Museum of New Zealand), Mr A. G. McFarlane (Canterbury Museum), and Dr G. F. Edmunds, Jr (University of Utah) for the loan of specimens. Mr Ordish, Mr P. E. S. Whalley (British Museum (Natural History)), Mr W. R. de V. Graham (Oxford University Museum), and Mr B. Cowie (University of Canterbury) kindly attempted to locate material collected by Capt. J. S. Phillips. Dr M. L. Pescador, Mrs Janice G. Peters, and Mr M. D. Hubbard of Florida A & M University offered valuable comments on the manuscript, Mrs Peters guided preparation of illustrations, Dr E. F. Riek (Canberra) discussed the identity of *Atalophlebioides* from Australia, and Ms Heather Roberts (University of Auckland) demonstrated methods of preparing mayfly eggs for SEM.

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