

Leptophlebiidae (Ephemeroptera) of the alpine region of the Southern Alps, New Zealand

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The alpine region of the South Island of New Zealand is the habitat of a group of endemic mayfly species of the genus *Deleatidium*, which show adaptation to an alpine tundra environment. Their speciation may be best explained as the consequence of a series of Pleistocene ice advances and retreats. The larval stages of these species are well adapted to cold, fast water and high levels of ultraviolet radiation. Their distribution, restricted by geographic and climatic factors, renders the group vulnerable to climate change.

Keywords: Ephemeroptera; *Deleatidium*; alpine; distribution; global warming; ultraviolet radiation

Introduction

The Southern Alps and its lateral ranges form the backbone of the South Island, New Zealand, and lie parallel to, and close to the western coast. There is a well defined Main Divide and catchments which generally flow eastward into the Pacific Ocean or westward into the Tasman Sea. The Alps have arisen from compression between the Pacific and Australian tectonic plates (Suggate 1990) and continue to experience uplift, resulting in a steep and unstable terrain. Although distinctly lower than the European Alps, the summertime snowline descends to 1600 m in the west and 2200 m on the drier eastern side (Mark and Dickinson 1997). The western side is dominated by high rainfall (5000–12000 mm annually) and westerly winds from the Tasman Sea, which become drier Föhn winds on the eastern plains.

The alpine region extends about 700 km north–south (40°S–47°S) and 100 km east–west. Its mountains have steep gradients (0.4 or more), a dissected landscape, high geological instability, heavy rainfall and high water quality (Winterbourn 1997). The mountains are bounded by sea except for a narrow western coastal strip and a wider eastern plain created by outwash from glaciers of the Pleistocene (2–18 million years ago) (Shulmeister and McGlone 2008).

The zone considered in this paper extends from treeline to snowline (Ward 1994; Mark and Dickinson 1997). The upper limit of forest is 1200–1400 m a.s.l., and above it shrub vegetation, tussock and screes extend to permanent snow and ice. Small trickles and streams may derive from seasonal glacier and snow melt or emerge from

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scree slopes or from groundwater sources. Even in midsummer the author has found water temperatures to be only $5 \pm 3^\circ\text{C}$ in this zone. Fog and low cloud occur frequently. However, summers are reasonably sunny especially in eastern areas (Mark and Dickinson 1997). Mean global short wave radiation in the alpine zone at 43° south is about 4800 MJ/m^2 , annually (McCracken 1980), rather less than at continental alpine sites at similar latitudes (Barry, Courtin and Labine 1981).

The present New Zealand mayfly fauna includes 44 described species, all endemic, in 19 genera and eight families. The largest family, the Leptophlebiidae, is represented by more than 30 described species of which two are confined to this mountain region. In the alpine zone the genus *Deleatidium* is abundant in streams and includes several undescribed species. The absence of forest canopy above the treeline results in a paucity of terrestrially derived detritus in streams, and the abundant non-predatory invertebrates such as *Deleatidium* spp. graze mainly on epilithon (Winterbourn et al. 1981, 2008).

Studies on the taxonomy and systematics of New Zealand Leptophlebiidae have been undertaken by Phillips (1930) and by Towns and Peters whose findings have been drawn together in Towns and Peters (1996). All of these studies were carried out mainly on North Island material and it has become apparent that they do not include all taxa found in the South Island. Towns and Peters (1996) erected two subgenera, *D. (Deleatidium)* and *D. (Penniketellum)*, based mainly on differences in the tarsal claws of the adults, the former with a hooked claw and a pad, the latter with claws similar and hooked. The larval stages of the two subgenera present no such ready morphological character for identification. Species of *D. (Penniketellum)* are confined to the alpine zone of the South Island.

Materials and methods

Until recently little systematic collecting had been undertaken for alpine mayflies. Few high altitude access roads existed, but the recent development of ski-fields has made accessibility easier. Collecting sites were recorded using metric coordinates to the nearest 100 m and altitudes to the nearest 20 m from the map series NZMS 260 (1:50,000). All specimens have been stored in 80% ethanol at Canterbury Museum, Christchurch, or at Cawthron Institute, Nelson, New Zealand. Late instar larvae were associated with winged stages by rearing.

Results and discussion

Alpine Deleatidium

The genus is a very successful generalist taxon with considerable ecological flexibility (Winterbourn 1997). Many but not all *Deleatidium* species have poorly synchronised life histories (Towns 1981) and rapidly recolonise streams with highly variable flows. Larvae of alpine members of the genus are well adapted for life in mountain streams with fast, turbulent flow, highly variable discharge and unstable substrata. The larval gills are large and leaf-like, usually rounded apically and with gill 7 folded ventrally. Together, the gills form a flexible disc resembling that of some Heptageniidae (e.g. *Epeorus assimilis*) of the northern hemisphere (Milner, Taylor and Winterbourn 2001). Larvae also usually have dense abdominal hairs, particularly on sternum IX.

Subgenus *Deleatidium* (*Deleatidium*)

The first larval leptophlebiid to be described with large leaf-like gills was *D. (Deleatidium) myzobranchia* Phillips, 1930. It is distributed throughout New Zealand and is not confined to mountainous areas (Figure 1a).

Towns and Peters (1996) drew attention to morphological variations in the ornamentation of the eggs and structure of the tarsal claws of adults and subimagines, and noted that some South Island populations were darker than those in the North Island. However, they were unable to find any consistent external character to otherwise distinguish populations and concluded that they were conspecific. Earlier, Winterbourn (1978) used the term ‘*myzobranchia* group’ for larvae with rounded gills that could not be identified to species, a group that included species of the alpine subgenus *Penniketellum* that had not been recognised or described at that time. Comparisons of gene sequences in fragments of mitochondrial cytochrome oxidase I (COI) of ‘*myzobranchia* group’ larvae from various sources (D. Olsen and S. Wood, unpublished data) have indicated the likely presence of further species within the group. One new species referred to as *D. (Deleatidium)* sp. “A” in this paper is found mainly in the northern part of the Southern Alps (Figure 1b) and is being described by the author. The larva of *D. (Deleatidium)* sp. “A” has rounded gills that form an adhesion disc as in *D. myzobranchia* and appears

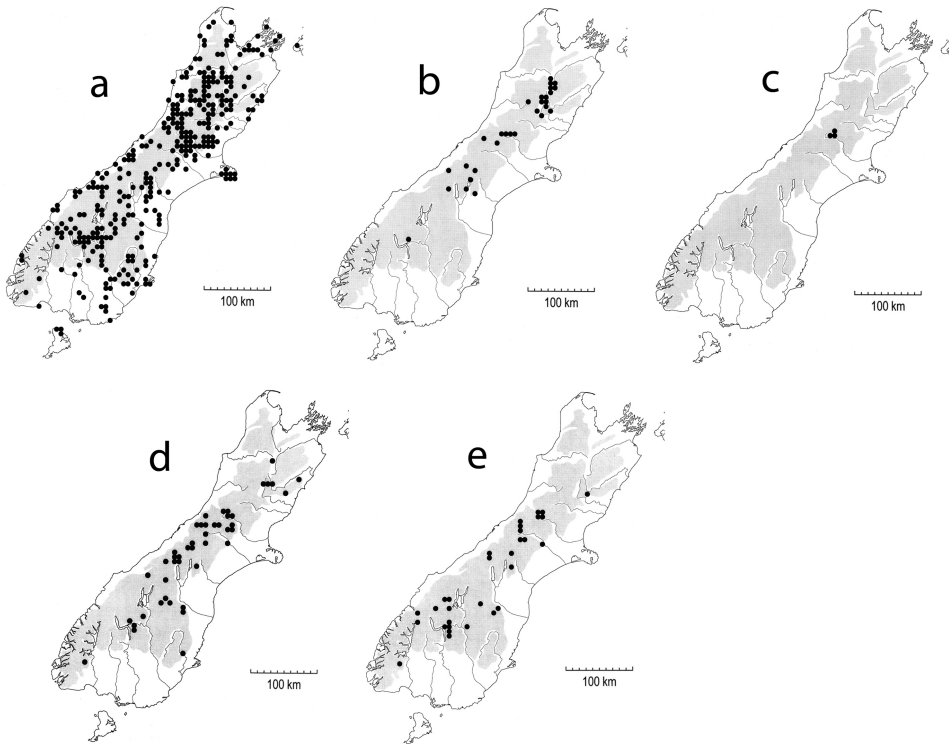


Figure 1. Collection sites for different species of *Deleatidium* in the South Island, New Zealand. Land above 700 m shaded. (a) *D. (Deleatidium) myzobranchia*; (b) *D. (Deleatidium)* sp. “A”; (c) *D. (Penniketellum) insolitum*; (d) *D. (Penniketellum) cornutum*; (e) *D. (Penniketellum) patricki*.

to be restricted to an altitudinal range of 500–1130 m in fast waters and sometimes large braided rivers. Both the larvae and adults have blackish dorsal surfaces, whereas *D. myzobranchia* is typically brownish.

Subgenus Deleatidium (Penniketellum)

The subgenus is represented by three described species: *D. (Penniketellum) insolitum* Towns and Peters, 1979; *D. (Penniketellum) cornutum* Towns and Peters, 1996 (Figure 2); and *D. (Penniketellum) patricki* (Hitchings 2008). These three species, together with *D. (Deleatidium)* sp. “A”, are all restricted to the Southern Alps and an altitudinal zone of approximately 700–1900 m (Figures 1b–e). Most larvae inhabit first and second order streams that range from trickles to glacier-fed torrents. The only large rivers with known populations are those below the terminal lakes of the Hooker and Tasman glaciers. The life history and production of a *Deleatidium (Penniketellum)* species, possibly *Deleatidium (P.) patricki*, in a South Island glacial stream, have been reported by Winterbourn et al. (2008) along with a discussion of the potential effects of climate change.

Melanistic colouration

Larvae and adults of these species in the subgenus *Penniketellum* are very darkly coloured, dorsally (Figure 2). The melanins are widespread pigments that account



Figure 2. Alpine species of *Deleatidium* with dark colouration, *Deleatidium (P.) cornutum*.

for much of the colour in the animal world. In insects the eumelanins have several important physiological functions including photoprotection (Sugumaran 2002). The tendency for alpine insects in New Zealand to have darkened sclerotised tissue is well known (Mark and Dickinson 1997). Larvae of the four leptophlebiid species that are largely restricted to the sub-alpine zone are black. Although they normally conceal themselves beneath stones, their dark colouration seems poorly adapted for predator avoidance. However, both indigenous and introduced fish are extremely rare above 1000 m (McDowell 2000) and birds that prey on the larval and winged stages of mayflies are rare at these altitudes. The main predators in this zone may be predatory stoneflies such as *Stenoperla* spp. (Eustheniidae).

Ground levels of UV radiation in New Zealand are high (McKenzie, Connor and Bodecker 1999) and increase by about 5% per kilometre of altitude in areas of unpolluted air where snow increases the radiation level a further 20–40% (R. McKenzie, personal communication). UV-B radiation penetrates water to considerable depths (Kiffney, Little and Clements 1997) and influences the behaviour of stream insects, including mayflies, which take evasive action. Increases in larval drift rates on exposure to UV can be interpreted as a strategy to avoid biological damage (Kiffney et al. 1997). Investigations on the effect of UV radiation acting on larvae of *Deleatidium* spp. at an altitude of 600 m in a clear water stream showed they were able to detect and avoid it (Johansson and Nystrom 2004). The dark colour of sub-alpine zone species is likely to help protect larvae and winged stages against potentially harmful UV radiation at high altitudes.

Hebert and Emery (1990) found that melanin prevented the transmission of >90% of incident UV radiation in two melanistic clones of the water flea *Daphnia* in Canadian arctic ponds. They also found that the melanistic clones predominated in the high arctic and in clear waters, whereas unpigmented clones were restricted to the temperate zone and ponds with high concentrations of humic materials. Furthermore, they suggested that for *Daphnia* in arctic ponds “the linkage between exposure to high near ultraviolet and melanization is so strong as to suggest that other selective agents are unimportant”.

Hebert and Emery (1990) noted that the localisation of melanin on dorsal surfaces, and the normally near horizontal movement of melanistic *Daphnia* spp. were consistent with the importance of melanin for UV interception. However, they suggest that its energetic cost may not be trivial. In waters at lower altitude and/or with significant canopy shading, melanistic individuals may compete less favourably with otherwise similar species. A comparable argument can be made for *Deleatidium*.

Biogeography

The four *Deleatidium* species considered in this paper are confined largely to the upper limits of lotic freshwaters in the Southern Alps and neighbouring ranges. They are adapted to cold, fast streams and rivers and the frequently severe conditions imposed by an unstable terrain and high winds. Although the region is often wet and with cloud cover, high levels of UV are common (McKenzie et al. 1999). Since the Alps began to form in the early Pliocene they have reached sufficient height in their central portion to establish snowfields with glaciers flowing east and west. The evidence is fragmentary, but a series of glacial advances (Carter 2008) may have driven mayfly populations adapted to this cold, hostile environment into isolated refugia at the periphery of the region where further speciation took place. In

subsequent warmer interglacial periods, retreat of the snowline may have exposed mountain streams to recolonisation by these newly evolved species. In Western Europe some elements of cold adapted fauna are considered to have speciated and developed a high degree of endemism as a consequence of similar events (Ward 1994).

Some New Zealand Leptophlebiidae have well-defined upper levels of thermal tolerance (Quinn, Steele, Hickey and Vickers 1994). Although temperature tolerances of alpine species have not been determined, a rise in temperatures associated with global warming is likely to result in a southward retreat of alpine specialists. Ryan and Ryan (2006) predicted that a 3°C warming would displace the regression of annual degree days on latitude southward by 670 km. A warming climate, reduced glaciation and the consequent loss of cold alpine streams is likely to bring about the extinction of the alpine mayfly species considered in this paper and by Winterbourn et al. (2008).

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References

- Barry, R.G., Courtin, G.M., and Labine, C. (1981), 'Tundra climates', in *Tundra Ecosystems: a Comparative Analysis*, eds. L.C. Bliss, O.W. Head and J.J. Moore, Cambridge: Cambridge University Press, pp. 81–112.
- Carter, B. (2008), 'Fleming's legacy', in *A Continent on the Move*, ed. I.J. Graham, New Zealand: Geological Society of New Zealand in association with GNS Science, pp. 264–267.
- Hebert, P.D.N., and Emery, C.J. (1990), 'The adaptive significance of cuticular pigmentation in *Daphnia*', *Functional Ecology*, 4, 703–710.
- Hitchings, T.R. (2008), 'A New Species of *Deleatidium* (*Penniketellum*) and the Adult of *D. (P.) cornutum* Towns and Peters (Ephemeroptera: Leptophlebiidae) from New Zealand', *Records of the Canterbury Museum*, 22, 29–40.
- Johansson, J., and Nystrom, P. (2004), 'Effects of Ambient UV-radiation on the Behaviour of Mayfly Larvae of the Genus *Deleatidium* from Trout Bearing and Fishless Streams of New Zealand', *Archiv für Hydrobiologie*, 161, 403–415.
- Kiffney, P.M., Little, E.E., and Clements, W.H. (1997), 'Influence of Ultraviolet-B radiation on the Drift Response of Stream Invertebrates', *Freshwater Biology*, 37, 485–492.
- Mark, A.F., and Dickinson, K.J.M. (1997), 'New Zealand Alpine Ecosystems', in *Polar and Alpine Tundra*, ed. F.E. Wielgolaski, Amsterdam: Elsevier, pp. 311–345.
- McCracken, L.J. (1980), 'Mountain Climate in the Craigieburn Range, New Zealand', in *Mountain Environments and Subalpine Tree Growth*, eds. U. Benecke and M. R. Davis, New Zealand: New Zealand Forest Service F.R.I. Technical paper. Vol. 70, pp. 41–59.
- McDowell, R.M. (2000), *The Reed Field Guide to New Zealand Freshwater Fishes*, Auckland: Raupo Publishing, p. 224.

- McKenzie, R., Connor, B., and Bodecker, G. (1999), 'Increased Summertime UV-radiation in New Zealand in Response to Ozone Loss', *Science*, 285, 1709–1711.
- Milner, A.M., Taylor, R.C., and Winterbourn, M.J. (2001), 'Longitudinal Distribution of Macroinvertebrates in two Glacier-fed New Zealand Rivers', *Freshwater Biology*, 46, 1765–1775.
- Phillips, J.S. (1930), 'A Revision of New Zealand Ephemeroptera. Part 2', *Transactions and Proceedings of the New Zealand Institute*, 61, 335–390.
- Quinn, J.M., Steele, G.L., Hickey, C.W., and Vickers, M.L. (1994), 'Upper Thermal Tolerances of Twelve New Zealand Stream Invertebrate Species', *New Zealand Journal of Marine and Freshwater Research*, 28, 391–397.
- Ryan, P.A., and Ryan, A.P. (2006), 'Impacts of Global Warming on New Zealand Freshwater Organisms; a Preview and Review', *New Zealand Natural Sciences*, 31, 43–47.
- Shulmeister, J., and McGlone, M. (2008), 'The Last Glaciation', in *A Continent on the Move*, ed. I. Graham, New Zealand: The Geological Society of New Zealand in association with GNS Science, pp. 268–269.
- Suggate, R.P. (1990), 'Late Pliocene and Quaternary Glaciations of New Zealand', *Quaternary Science Reviews*, 9, 175–197.
- Sugumaran, M. (2002), 'Comparative Biochemistry of Eumelanogenesis and the Protective Roles of Phenoloxidase and Melanin in Insects', *Pigment Cell Research*, 15, 2–9.
- Towns, D.R. (1981), 'Life Histories of Benthic Invertebrates in a Kauri Forest Stream in Northern New Zealand', *Australian Journal of Marine and Freshwater Research*, 32, 191–211.
- Towns, D.R., and Peters, W.L. (1979), 'New Genera and Species of Leptophlebiidae (Ephemeroptera) from New Zealand', *New Zealand Journal of Zoology*, 6, 431–432.
- Towns, D.R., and Peters, W.L. (1996), 'Leptophlebiidae (Insecta: Ephemeroptera)', *Fauna of New Zealand*, 36, 1–141.
- Ward, J.V. (1994), 'Ecology of Alpine Streams', *Freshwater Biology*, 32, 277–294.
- Winterbourn, M.J. (1978), 'The Macroinvertebrate Fauna of a New Zealand Forest Stream', *New Zealand Journal of Zoology*, 5, 157–169.
- Winterbourn, M.J. (1997), 'New Zealand Mountain Stream Communities: Stable yet Disturbed?', in *Evolutionary Ecology of Freshwater Animals*, eds. B. Streit, T. Stadler and C.M. Lively, Basel: Birkhauser Verlag, pp. 31–54.
- Winterbourn, M.J., Cadbury, S., Ilg, C., and Milner, A.M. (2008), 'Mayfly Production in a New Zealand Glacial Stream and the Potential Effect of Climate Change', *Hydrobiologia*, 603, 211–219.
- Winterbourn, M.J., Rounick, J.S., and Cowie, B. (1981), 'Are New Zealand Stream Ecosystems Really Different?', *New Zealand Journal of Marine and Freshwater Research*, 15, 321–328.