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THE FRESHWATER INSECTS

by

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XIV. THE FRESHWATER INSECTS

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I. D. McLELLAN

Introduction

The state of entomological research in a country depends very much upon its culture and economy. Because of the former factor research on aquatic insects in New Zealand only started to gain momentum during the present century. Our reliance upon agriculture has meant that the bulk of entomological research has been turned in that direction and consequently aquatic entomology has been carried out by a small number of workers either amateur or in universities and museums. The impact of so few workers is not great and in most aquatic orders much systematic work has to be accomplished. This lack of basic knowledge has had its affect upon both zoogeographical and ecological research. The influence of the state of a taxon's systematics on its zoogeography can be illustrated by looking at the stages that the systematics of N.Z. Plecoptera have passed through. 1. Species assigned to Northern genera and families. 2. Species assigned to new genera but still in Northern families. 3. New genera now in new tribes or sub-families still in Northern families. 4. All now in Southern families. Obviously these stages have not been completely passed through in other orders and the result gives a false impression of their relationships. This is particularly so where a considerable length of time has elapsed since work was done on certain taxa and also where poor taxonomic criteria are still in use.

Most ecological work consisted of natural history notes appended to systematic works but there are a few purely ecological works and these are either theses or population studies as part of fisheries research.

In the following accounts the major aquatic orders and also the main aquatic Diptera families have been dealt with. Some taxa which are not usually found in freshwater elsewhere are given some space while others have been omitted either because they inhabit only still waters or because useful information is not available.

EPHEMEROPTERA

4 families, 9 genera, 26 species. Siphonuridae: 5 genera, 9 species. Siphlaenigmatidae: 1 genus, 1 species. Leptophlebiidae: 2 genera, 14 species. Ephemeridae: 1 genus, 2 species.

There are several undescribed genera and a number of undescribed species.

Table 1. Distribution of Austral genera of Siphonuridae.

Subfamily	New Zealand	South America	Australia
Rallidentinae	Rallidens		
Siphonurinae	Nesameletus	Metamonius	Ameletoides
Oniscigastrinae	Oniscigaster	Siphonella	Tasmanophlebia
Amelotopsinae	Ameletopsis	Chiloporter	Mirawara
		Chaquihua	
Coloburiscinae	Coloburiscus	Murphyella	Coloburiscoides

Zoogeography

All N.Z. species are endemic as are the genera in Siphonuridae and Ephemeridae. Siphonuridae also contain the endemic monotypic subfamily Rallidentinae and there is also the endemic monotypic family Siphlaenigmatidae which appears to be derived from Siphonuridae. Also endemic is the subfamily Ichthybotinae in Ephemeridae. In Leptophlebiidae the genus *Zephlebia* is endemic and probably all N.Z. Leptophlebiidae genera may eventually be found to be endemic.

Our mayfly fauna follows the usual pattern found in other aquatic orders by having a disjunctive Austral distribution of closely related groups. Part of this can be seen for Siphonuridae in Table 1. There is, however, the enigma of *Ichthybotus* which stands as the sole endemic N.Z. taxon without a sister group in S. America or Australia.

The situation in Leptophlebiidae is not as clear cut as in Siphonuridae but it is obvious that the Austral components of the family have closer affinities to each other than to those of other regions.

In N.Z. all known genera are represented at low elevations but only *Oniscigaster*, *Nesameletus* and *Deleatidium* are common at elevations much above 700 m in South Island, 1000 m in North Island. A few species occur only from 650–2000 m. It is doubtful whether any species (except perhaps *Rallidens mcfarlanei*) is restricted to a single locality or even province. There are, however, sometimes slight differences between North and South Island forms of the same species.

Ecology

Literature on ecology of N.Z. mayflies is extremely sparse, consisting mainly of notes in predominantly systematic works. The only reasonably detailed study in this field is that on the nymph of *Coloburiscus humeralis* which has brought to light some unusual facts about this siphonurid. Because of the inability of its fixed forked gills to absorb sufficient oxygen in slow streams the animal is restricted to rapid well-oxygenated waters. Its mode of obtaining sustenance also relies on water currents. Fine

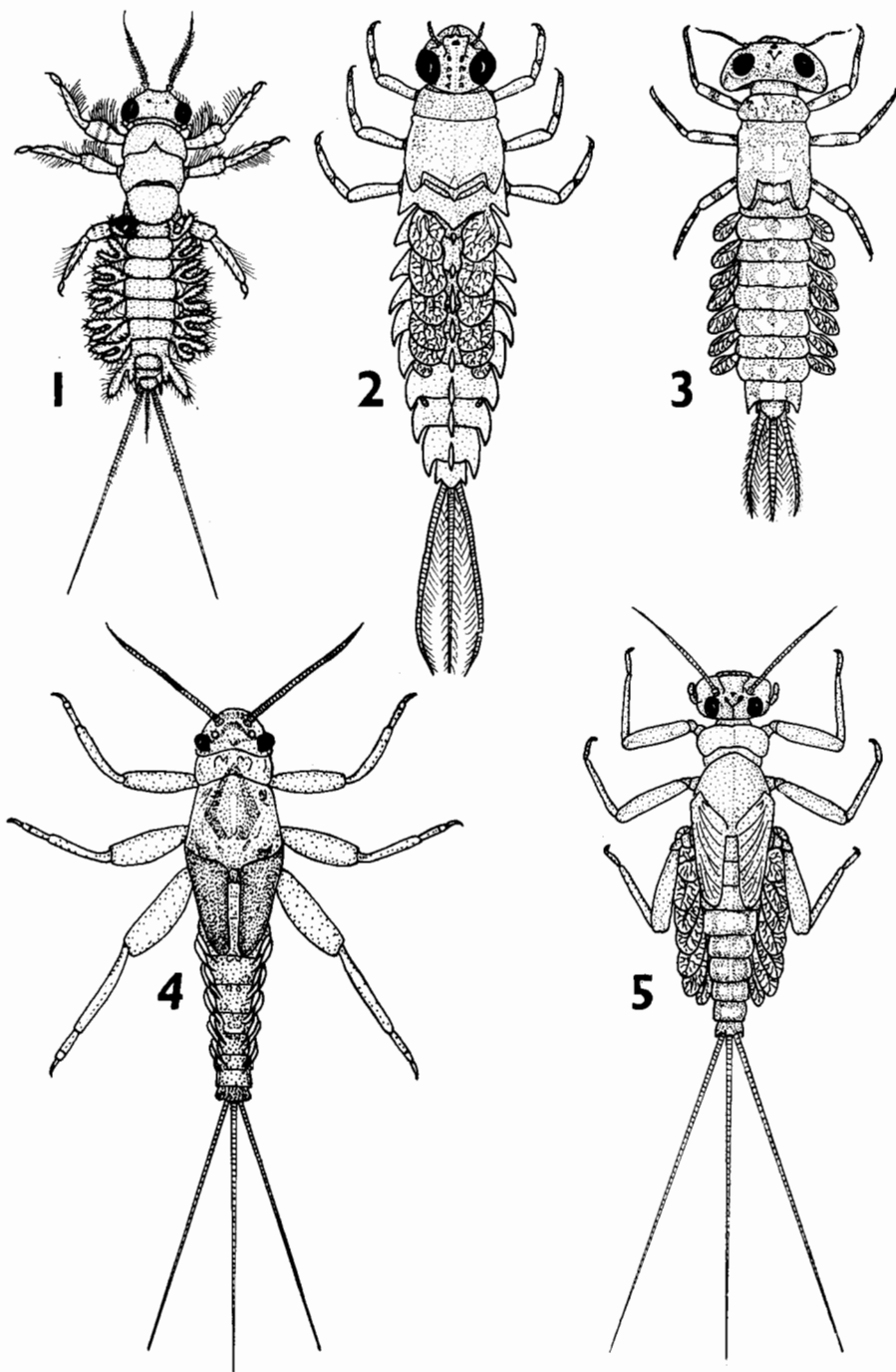


Fig. 1. Some Ephemeroptera larvae. 1: *Coloburiscus humeralis* (Siphonuridae). 2: *Oniscigaster distans* (Siphonuridae). 3: *Amelotopsis perscitus* (Siphonuridae). 4: *Zephlebia* species (Leptophlebiidae). 5: *Deleatidium myzobranchia*.

particles (diatoms and algae mainly) are swept onto the long fringes of hairs on the front and middle legs and are combed off by the brush-like mouth-parts. The eggs of this mayfly are also adapted to rapid currents being equipped with spring-like adhesive filaments to anchor the eggs to the substrate.

As far as can be ascertained the remaining nymphs of our fauna appear to be grazers on algae and other water plants apart from *Ameletopsis perscitus* (Siphonuridae) which is carnivorous and has been observed preying upon small leptophlebiid nymphs and other water insects.

The ephemerid *Ichthyobots hudsoni* occupies the same niche as that of its northern relatives. The nymphs are found in sand and mud of streams, have a similar gill structure to *Ephemera* and utilize the forelegs and mandibular tusks for digging. Several ephemeropteran niches appear to be vacant, e.g. lakes and ponds. Members of the genus *Deleatidium* (Leptophlebiidae) have atypical niches which are more or less equivalent to those of certain absent families such as Heptageniidae.

New Zealand mayfly nymphs are preyed upon by a number of invertebrate predators such as Trichoptera larvae of the family Rhyacophilidae, the larva of the Dobson Fly (*Archichauliodes diversus*) and the nymph of the stonefly *Stenoperla prasina*. Fish such as Eleotridae, *Cheimarrichthys* and *Anguilla* generally feed only on nymphs as do some Galaxiidae but the introduced Salmonidae feed both on nymphs and adults.

PLECOPTERA

4 families, 14 genera, 32 species. Eustheniidae: 1 genus, 1 species. Austroperlidae: 1 genus, 1 species. Gripopterygidae: 6 genera, 22 species including Antarctoperlinae. Notonemouridae: 6 genera, 8 species.

There are a number of undescribed species mainly in Gripopterygidae.

Zoogeography

All New Zealand genera, apart from two, are endemic to New Zealand. The two exceptions *Stenoperla* and *Spaniocerca* are shared with Australia but in *Spaniocerca* there is sufficient evidence to remove the Australian members from the genus and therefore in effect *Spaniocerca* is endemic to New Zealand. With a modern revision it is most likely that the same will happen to *Stenoperla*. ZWICK has divided the world's stoneflies into the two sub-orders Arctoperlaria and Antarctoperlaria, the latter sub-order being restricted to the southern part of the world. This southern sub-order contains the families Eustheniidae, Austroperlidae and Gripopterygidae. Although the remaining family Notonemouridae is included in the Arctoperlaria the family has a southern distribution only, which is at variance with that suggested by the sub-ordinal name.

The relationships of our sole eustheniid, *Stenoperla prasina*, presents no problems. Australia has a diverse Archiperlarian fauna and as the genus (or as it may be proved a closely related genus) is also present there, the odds are in favour of a recent Australian origin.

According to ILLIES, *Austroperla cyrene*, our only austroperlid, forms with the Chilean fauna, an evolutionary offshoot from the remainder of the Austroperlidae. This would suggest a South American origin but I hesitate to accept this for a number of reasons. SMITH & HALLAM (1970) put the dispersal of Gondwanaland about Upper Cretaceous-Tertiary times. This means that the ancestor of *A. cyrene* would have been in the New Zealand region from that time and have been subjected to division of its gene pool by geological events during the next 100 million years. Considering this and the wide range of biotopes inhabited, one would think that a number of genera, or species, would have arisen. (This speciation has occurred in the Antarctoperlinae which almost certainly came to New Zealand in this way.) Apart from a small degree of wing shortening in specimens from alpine areas this widespread species shows very little variation which is compatible with variation found in recent invaders. From this reasoning it is more likely that *A. cyrene* is one of the numerous recent travellers by wind drift from Australia.

To understand the position of the Autarctoperlinae it is necessary to refer to ZWICK (1969) who on sound evidence set this subfamily in limbo between the rest of Gripopterygidae and Austroperlidae. The Antarctoperlinae are found only in New Zealand and South America therefore dispersal must have been through the Antarctic. Our ancestral stock was most likely small in species because the same general morphological features, differing to a degree from the South American fauna, are found in all New Zealand species.

The remainder of the Gripopterygidae present a different problem. All New Zealand gripopterygids lack tibial spurs (a characteristic shared with Antarctoperlinae) and all belong to the subfamily Leptoperlinae. All Australian leptoperlinids possess tibial spurs as do those of South America except in the monotypic genus *Notoperlopsis* which bears a similarity to our *Megaleptoperla*. The Australian leptoperlinids also differ in a number of other ways from those of New Zealand. It appears that the New Zealand gripopterygids are of long established stock with a closer relationship to those of South America than to those of Australia. Like the Antarctoperlinae this presupposes dispersal through Antarctica.

The family Notonemouridae has, as intimated earlier, a possible northern origin. It is best looked at from its two elements, the *Spaniocerca* and the *Notonemoura* groups of ZWICK. The *Spaniocerca* group (named from the New Zealand genus) is found in Madagascar, South Africa, Australia, New Zealand and South America. The South Africa-Madagascar genera are less closely related to the remainder, but the Australian genera are more closely akin to the New Zealand ones than those of

South America so it is possible that they have arrived in New Zealand via Australia either by wind drift or indirectly through the Inner Melanesian Arc. (ILLIES used the idea of a route from Asia through Malaysia and Indonesia to Australia and New Zealand then to South America for the whole of Notonemouridae with the South African and Madagascan fauna as an offshoot from Asia.) It is also within reason to assume that the group was present in Gondwanaland before break up. As most exponents of Continental Drift put the breakaway of India and then Africa before that of the rest of Gondwanaland the African-Madagascan fauna would, in isolation, have had more time to develop in their peculiar line.

The *Notonemoura* group has representatives in Australia, New Zealand and South America. As there are great basic similarities between the genera of these three regions it is likely that the group had its origin in Gondwanaland. These similarities are so marked that certain genera can be easily grouped on a morphological basis e.g. *Neofulla* (South America), *Notonemoura* (New Zealand), *Varioperla* (Australia). One thing is certain, they differ greatly from the *Spaniocerca* group in that they have certain features which are decidedly apomorphic in comparison with the *Spaniocerca* group.

Excluding the Subantarctic islands which have their own endemic species the situation in New Zealand is as follows. The representatives of Austroperlidae and Eustheniidae are found throughout New Zealand and therefore this would put their arrival in New Zealand prior to the formation of Cook Strait, i.e., prior to the end of the Pleistocene and probably not long before the Pleistocene because of lack of speciation. Within the Gripopterygidae and Antartoperlinae there is an almost complete coverage of the country by some species, dependent on availability of habitat, whereas other species are restricted in range. For instance, in *Zelandoperla*, (Gripopterygidae) *Z. decorata*, *Z. fenestrata* and *Z. agnetis* are found throughout the country but *Z. denticulata* is restricted to the southwest of the South Island and in this area the four species may be collected from certain streams. *Zelandobius* (Antartoperlinae) also shows this trend. The species *Z. furcillatus* and *Z. confusus* are widespread but so far *Z. illiesi* is restricted to heavily wooded streams in the northwest of the South Island and other species are restricted to the southeast and southwest. *Aucklandobius* (Gripopterygidae) exhibits the same trend with a greater degree of endemism in the south. This applies to a lesser extent with the Notonemouridae but nevertheless the south again has its own forms. The most decisive fact to appear is that the North Island has no endemic species. In addition, the North Island lacks the apterous forms which are so common in the alpine areas of the South Island. One example of extreme brachyptery in *Aucklandobius fulvescens* has been found in the Tararua Ranges in the North Island in a species which, in the south, has never been found in that condition, even at

comparable altitudes. One of the alpine apterous forms in the South Island appears to have a discontinuous distribution in that up to the present it has been found only in Fiordland in the southwest and on the mountains in the northwest. These two areas are considered to have been refugia during the Pleistocene glaciations.

Auckland and Campbell Islands are the only Subantarctic islands having Plecoptera. Six gripopterygids are present on these islands which are endemic to the islands but the genera to which they belong (*Apteryoperla* and *Aucklandobius*) are also found on the mainland of New Zealand. These stoneflies have followed the usual trend of gripopterygids in high altitudes in that all but one species are apterous and most have terrestrial larvae. These species probably originated from New Zealand stock and they show quite marked adaptive radiation from two ancestors.

Ecology

In alpine regions and in the Subantarctic islands wingless stoneflies are common. These are found in all the species of the gripopterygid genera *Apteryoperla*, *Vesicaperla* and in some species of *Aucklandobius* (Gripopterygidae) and *Zelandobius* (Antarctoperlinae). There is a tendency for the larvae, in the first three abovementioned genera, to seek out terrestrial habitats. Some *Apteryoperla* plus *Vesicaperla* and the apterous *Aucklandobius* live in the humid atmosphere of thick alpine vegetation and *Vesicaperla* larvae have the odd habit of congregating in skeletons. Other *Apteryoperla* live under stones and in seepages. The larvae of winged *Aucklandobius* species living at low altitudes on the main New Zealand islands spend their first instars in water before moving out under stones on the flood plains of streams. This is made possible by the univoltine life cycle of these species which is as follows. The adults emerge in spring and early summer and from then until autumn no larvae are found so it is thought that the eggs remain dormant until the temperature falls to the required level. During autumn early instar larvae are found in the water but later when moist conditions and lower temperatures occur they move out into their terrestrial habitat for the remainder of their larval existence.

The larvae of the remaining gripopterygids and of *Zelandobius* inhabit a variety of biotopes in running water and we have obvious sets of associated species in certain biotopes. For example, *Zelandoperla agnetis* and *Zelandobius confusus* are associates in stony streams which carry little suspended material in flood but they are replaced by *Zelandoperla decorata* and *Zelandobius furcillatus* where the amount of suspended material is greater. The only gripopterygid which inhabits vegetation in running water is *Megaleptoperla diminuta* – a strange contrast to its generic partner *M. grandis* which lives among the boulders and stones of swift flowing streams. In the *Zelandobius* most species live in stony streams but *Z. illiesi* lives in small forest streams where dead terrestrial vegetation covers the

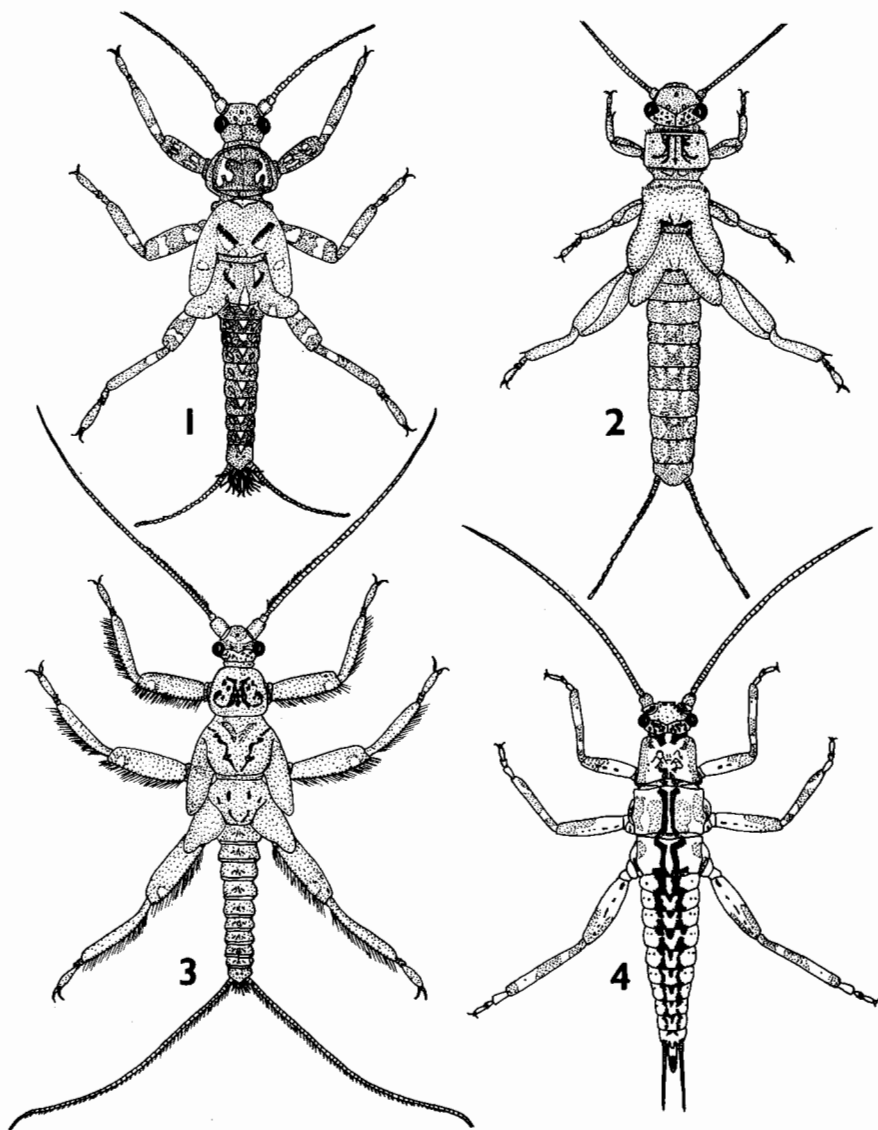


Fig. 2. Some Plecoptera. 1: Larva of *Aucklandobius trivacuatus* (Gripopterygidae). 2: Larva of *Notonemoura alisteri* (Notonemouridae). 3: Larva of *Zelandoperla decorata* (Gripopterygidae). 4: ♀ of *Vesicapera substirpes* (a wingless gripopterygid with an ovipositor).

substrate of sand, mud and stones. Here the larvae are found mainly on the fronds of a tree fern (*Cyathea smithii*).

The anal gill rosette is probably the most outstanding feature of gripopterygid and *Zelandobius* larvae. *Megaleptoperla* larvae retract and

extend the rosette rhythmically and increase the beat as the level of dissolved oxygen drops. *Zelandobius* larvae waggle the abdomen from side to side with the rosette extended and again a drop in oxygen content results in an increased speed of waggle. The other gripopterygids have no similar respiratory behaviour but are able to retract the rosette under unfavourable conditions.

In Notonemouridae all of the *Notonemoura* group inhabit hygropetric (madicole) biotopes – either in the splash zones of steep streams or in pure seepages from between strata. The adults of this group are much more alert than other New Zealand stoneflies and use their long hind legs to leap away from danger.

In the *Spaniocerca* group the larvae of *Spaniocerca zelandica* inhabit many types of running water, from sea level to about 1,000 metres. These habitats include lowland and mountain rivers and streams, in forest or grassland, and with stony, sandy or muddy substrate. Generally the larvae are found under stones, on logs, in leaf litter or moss. *Spaniocercoides hudsoni* is a little more selective but still with a wide habitat range. These consist of alpine seepages, alpine bogs of the type inhabited by *Europetala carovei* (Odonata), weedy streams and forest streams containing dead branches, twigs and leaves.

Austroperla cyrene (Austroperlidae) inhabits pockets of dead leaves, crevices in logs and aquatic vegetation in many different types of running water. Because of its ability to exist in such a variety of conditions it is our most widespread stonefly.

Stenoperla prasina (Eusteniidae) exists also in a wide range of biotopes ranging from alpine rivulets to large lowland rivers. It is important that these biotopes are well oxygenated and not too warm.

The only predatory stonefly in New Zealand is *Stenoperla prasina* which preys upon mayfly, stonefly, simuliid and blepharocerid larvae. Detritus feeders are common and one notable example, *Austroperla cyrene*, reduces dead leaves to a network of veins and can even exist on a diet of twigs. Most gripopterygid larvae are either grazers of algae or eaters of dead leaves. Some of the terrestrial larvae strip the outer layers of plant stems ingesting any algae and fungi growing thereon. The Notonemouridae follow a similar pattern. The *Notonemoura* group graze on algae but are not averse to preying on other stonefly larvae and possibly other invertebrates if the opportunity arises. The *Spaniocerca* group is not well known but the type of biotope inhabited suggests a diet of dead vegetable material such as leaves and possibly algae and fungi on its surfaces.

ODONATA

The small New Zealand fauna consists of eleven species. In the suborder Zygoptera there are two species in Coenagriidae and one in Sympecmatidae. The suborder Anisoptera contains one species in Petaluridae, two

in Aeshnidae, four in Corduliidae and one in Libellulidae. Six species are endemic but with strong affinities with the Australian fauna. The remaining species are common to both Australia and New Zealand.

Possibly the most interesting dragonfly is *Uropetala carovei* the sole member of the small family Petaluridae. (The petalurids have a preference for alpine bogs and are restricted to Chile, Australia, New Zealand, North America and Japan.) The nymphs of this species construct burrows in alpine and subalpine spring fed bogs where there is a permanent flow of water with an oxygen content of about 6.23–7.25 ml/litre which is sufficient to prevent the formation of highly acid peat from the 65–80% organic matter present. These bogs which are of recent origin, are about one metre deep with a shingle or rock base.

The nymphs, using masks as shovels together with mandibles and the lateral lobes of the labium to cut vegetation, construct burrows which are about 35 cm deep. Because of cannibalistic tendencies only one inhabitant is found in each burrow.

Early instar nymphs feed on ciliates, flagellates, rotifers, nematodes, small crustaceans and microtrichopteran larvae. Late instar nymphs feed entirely on terrestrial arthropods which are taken on their nocturnal wanderings. This most unusual food for dragonfly nymphs consists of beetles, grasshoppers, cockroaches, ants and spiders.

MEGALOPTERA

Only one megalopteron is aquatic in New Zealand. This is *Archichauliodes diversus* (Corydalidae) which is found in stony rivers and streams throughout the country. The genus has an Austral distribution in Australia, Chile and New Zealand.

Ecology

The larvae of this species are common and they rest on the undersides of rocks during the day then emerge to search for food at night. They are one of the most voracious invertebrate predators in our streams and subsist on a diet of most larval aquatic insects, particularly Ephemeroptera. The larval existence is probably over two years or more. When they are full grown they migrate to the stream edge during periods of high water in spring and early summer. As the water recedes and leaves them some distance from normal water level they construct pupal cells where they may remain in the active larval stage for several months. Pupation lasts from two to four weeks and the adults emerge from November to February. During flight adults occasionally dip onto the surface of water and rise again with little difficulty. This action plus a gliding flight high above the stream may be mistaken for egg laying behaviour, however, eggs are laid on objects directly above running water.

MECOPTERA

New Zealand's sole mecopteran *Choristella philpotti* is a member of the family Nannochoristidae which has an Austral disjunctive distribution in Australia, New Zealand and South America. The larva of this insect is aquatic and is found in muddy backwater pools in small streams in South Island localities. The aquatic habit is also found in *Nannochorista* the Australian genus. Professor PILGRIM (University of Canterbury, Christchurch, New Zealand) has just completed investigating the biology of this species.

TRICHOPTERA

14 families, 41 genera, 120 species. Rhynchoptychidae: 1 genus, 1 species. Sericostomatidae: 11 genera, 22 species. Helicopsychidae: 1 genus, 4 species. Philanisidae: 2 genera, 2 species. Pycnocentrellidae: 2 genera, 2 species. Helicophidae: 1 genus, 1 species. Philorheithridae: 1 genus, 2 species. Leptoceridae: 4 genera, 8 species. Hydropsychidae: 2 genera, 10 species. Polycentropodidae: 2 genera, 6 species. Psychomyidae: 2 genera, 2 species. Philopotamidae: 1 genus, 2 species, Rhyacophilidae: 9 genera, 54 species. Hydroptilidae: 2 genera, 4 species.

Zoogeography

Three elements constitute the New Zealand fauna. 1. Those with South-east Asian progenitors (these may be recent arrivals). 2. An element known only from both Australia and New Zealand plus certain subfamilies whose affinities and origins are difficult to determine. 3. Subfamilies or genera represented in Australia or New Zealand or both and in South America. This can be seen as each family in New Zealand is dealt with in detail.

Rhynchoptychidae: Found only in New Zealand and Chile it consists of two genera, *Kokiria* which is endemic to New Zealand and *Rynchoptysche* which is endemic to Chile.

Sericostomatidae: All eleven genera are endemic to New Zealand. The family is cosmopolitan but none of the genera occurring in the Australian-New Zealand area occur elsewhere. There is a possibility that eleven of the 26 species belong to Goeridae.

Helicopsychidae: The New Zealand species are assigned to the cosmopolitan genus *Helicopsyche*.

Philanisidae: A family of marine caddis is present only in Australia and New Zealand. *Philanisus plebeius* is common to Australia and New Zealand. *Chathamia brevipennis* (which should be transferred to the *Philanisus*) is found at the Chatham Islands.

Pycnocentrellidae: An endemic family containing the genera *Alloe-*

centrella and *Pycnocentrella* which were formerly included in Beraeidae.

Helicophidae: This family is restricted to Australia and New Zealand. The sole New Zealand genus *Zelolessica* is endemic.

Philorheithridae: A family restricted to Australia and New Zealand. The sole New Zealand *Philorheithrus* is endemic to New Zealand. Four genera are endemic to Australia.

Leptoceridae: The species of this cosmopolitan family are assigned to the following genera – *Triplectides* which is of worldwide distribution excluding Africa, the Palaearctic and Nearctic regions. Two species are assigned to this genus, *T. cephalotes* which is also found in Australia and *T. obsoleta* an endemic species which is apparently a sister species of *T. jaffueli* in Patagonia. *T. magna* is not found in New Zealand despite earlier reports. *Triplectidina* is an Australasian genus. It is possible that the New Zealand species should be in *Triplectides*. *Hudsonema* of Austral distribution contains two endemic species.

Hydropsychidae: Two genera of this cosmopolitan family are recorded from New Zealand; *Dipletrona* with two endemic species and *Hydropsyche* with nine endemic species. There is justification for removing the New Zealand species from the latter genus; they are clearly related to *Abacaria* and *Herbertorossia* from Fiji and New Guinea.

Polycentropodidae: The two genera of this cosmopolitan family have an almost world-wide distribution but the New Zealand species assigned to them are endemic.

Psychomyidae: The genus *Ecnomina* of this widespread family is shared with Australia but the sole New Zealand species in it is endemic. *Zelandoptila* which is endemic was recently transferred from Hydroptilidae.

Philopotamidae: Two genera of this world-wide family are present in New Zealand. *Dolophilodes* is endemic to Australasia but with two endemic New Zealand species. *Neobiosella* is an endemic monotypic genus.

Rhyacophilidae: All genera are endemic and belong to Hydrobiosinae which is in New Zealand, Australia and extends through South America to Mexico (this excludes the aberrant *Apsilochorema*)

Hydroptilidae: Two genera of this cosmopolitan family are represented in New Zealand. Cosmopolitan *Oxyethira* which has one endemic species and the endemic *Paroxyethira* with two species.

Three of the above families are thought to have evolved in Australia. These are Philansidae, Philorheithridae and Helicophidae. They possibly represent developments that are known to have occurred in the Australian Upper Permian and Triassic.

Distribution within New Zealand is not well known. There are some species with a restricted range of habitat such as *Pycnocentrella* which is confined to strongly flowing water usually in forest. There are, of course, large regions where the substrate of the streams is unsuitable as caddis habitat. The large papa (blue clay) area of the central North Island is such a region. Here fine clay particles prevent the growth of diatoms by either

covering or shading them from the light and therefore disrupting possible food chains. The rivers of Canterbury frequently have a substrate of shifting sand and gravel which has a destructive affect on aquatic insects.

Ecology

As with the other aquatic orders the ecological work carried out on Trichoptera has been spasmodic and mainly concerned with life histories. There are, however, current investigations on such topics as population dynamics, ventilation mechanisms and trophic relationships.

The Trichoptera form considerable part of the first order consumers of our running waters. Sericostomatidae and Helicopsychidae make up the bulk of diatom browsers. The Hydropsychidae net drifting algae as well as other organic material. The Hydroptilidae feed on filamentous algae. Some Sericostomatidae larvae live in the crevices of submerged rotting wood eating either wood or fungi on it. Many of the algal browsers carry out their activities at night. The Hydrobiosinae (Rhyacophilidae) are the principal invertebrate carnivores of our aquatic fauna and possess chelate forelimbs to facilitate capture and holding of prey. *Neurochorema* preys on the pupae of *Hydropsyche* which are available for most of the year. Associated with this feeding on an almost inert prey it shows a reduction of the chelae of the forelimb and a narrow fore part enabling it to enter the confined space of its prey's pupal shelter (fig. 3). Species inhabiting torrents have campodeiform bodies and venters of abdominal segments modified into suction pads enabling them to move in swift currents after blepharocerid and simuliid larvae and pupae. Most of *Costachorema* and some of *Hydrobiosis* have these adaptations. Except for *Neurochorema*, which seems to be specific in its food intake, most larvae of this family take whatever they can capture. Mayfly and stonefly larvae are grist to the mill but chironomid and simuliid larvae make up the bulk of the diet. There is even a degree of cannibalism. The prey is held in the chelae and slowly cut up into chunks and swallowed. One section of the Sericostomatidae differ in body form, limbs and habitat from characteristic browsers. These are the species previously mentioned as possibly belonging to Goeridae. They inhabit semifluid organic mud and it is thought that they feed on chironomid larvae and annelids. *Hudsonema* (Leptoceridae) inhabits lakes, slow waters and stable streams with vegetation and moderate currents. The larvae of *H. aliena* swims in slow water and at times leaves the water. It eats floating dead insects or sets upon injured individuals which cannot escape. The other species work along the bottom in depressions where the current tends to be swifter. They often do this in groups and possibly pick up chironomids or eat detritus.

Some adaptations of Trichoptera have obvious uses but others have not. For example, the *Philorheithrus agilis* larva, an inhabitant of swift

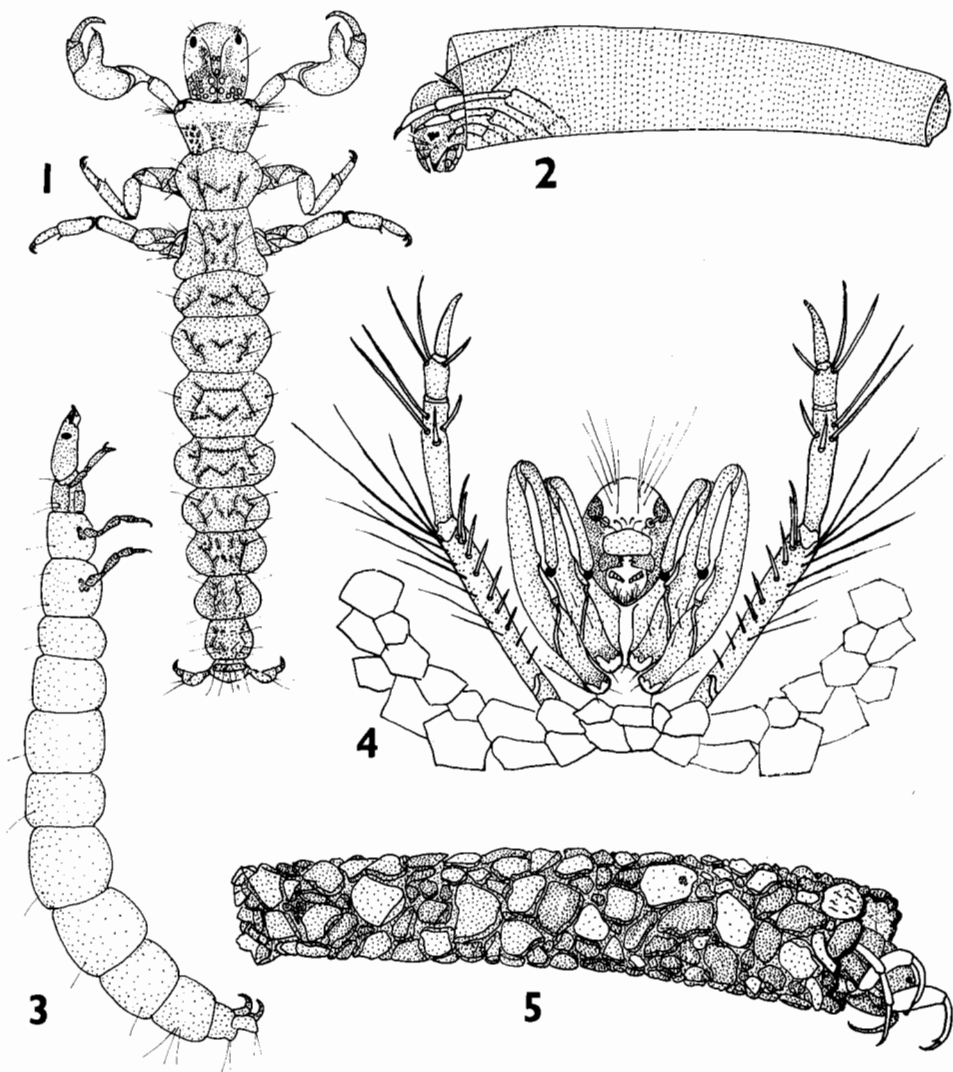


Fig. 3. Some Trichoptera larvae. 1: *Costachorema* species (Hydrobiosinae, Rhyacophilidae), a predator of swift streams. 2: *Olinga* species (Sericostomatidae), with horny case devoid of stones or vegetation. 3: *Neurochorema confusum* (Hydrobiosinae, Rhyacophilidae), a predator adapted for preying on *Hydropsyche* pupae. 4: *Kokiria miharo* (Rhynchopsychidae); note the peculiar adaptation of fore and mid limbs. 5: *Philorheithrus agilis* (Philorheithridae); an inhabitant of swift waters with a heavy case and with mid-leg tibia and tarsus fused.

streams, has a large heavy case to prevent being swept away but there is no obvious reason for fusion of tibia and tarsus of the middle limb (fig. 3). The larva of *Kokiria miharo* (fig. 3) has a puzzling adaptation. The front and middle legs have the tarsi missing and the claws reduced to thumbnail-

like remnants which rest on a raised callous-like structure on each femur. Each hind leg has a row of spines and some long hairs. All this plus the wide gaping mouth and hairs on the head suggest a funnel-like net.

Predators on Trichoptera are many. The introduced Salmonidae prey upon many species of Trichoptera at all stages. In the author's locality *Salmo trutta* of the Buller River are often found full of larval cases of *Pycnocentria evecta*. At Lake Coleridge *Oecetis* larvae, which are found 30 metres below the surface, form an important part of the diet of the trout in the lake. Elsewhere *Pycnocentrodus*, *Triplectides obseleta* and *Olinga feredayi* larvae are commonly taken by trout.

Larval Trichoptera also form an important part of the food of those native fishes mentioned previously and frequently the larval cases are encountered in the gut of *Anguilla* species. Invertebrate predators are *Uropetala carovei* (Odonata) which preys on Hydroptilidae larvae, *Archichauliodes diversus* (Megaloptera) and of course the Hydrobiosinae (Rhyacophilidae).

CHIRONOMIDAE

The New Zealand fauna consists of 63 species in 23 genera contained in the subfamilies Tanypodinae, Diamesinae, Orthoclaudiinae, Chironominae, Podonominae and Clunioninae.

Zoogeography

There is only one detailed account on the relationships of New Zealand chironomids and this deals only with the subfamilies Podonominae and Diamesinae. In these subfamilies the following conclusions have been drawn. 1. The sister group of a New Zealand group lives in South America or South America and Australia. 2. There is no direct phylogenetic connection between Australian groups and New Zealand groups. 3. South American connections to New Zealand appear to have been via West Antarctica and those to Australia via east Antarctica. 4. The New Zealand fauna shows a strong independence which is stressed by the strong relative plesiomorphy exhibited by several groups regardless of rank and by a greater degree of endemism than that of Australia.

In the previously mentioned subfamilies there are 3 endemic genera, 2 of which are the comparatively apomorphic *Maoridiamesa* and *Lobodiamesa*. The other is the peculiar *Zelandochlus* which exhibits a most interesting mosaic of plesiomorphic and apomorphic characteristics. Notable among the latter are double dististyles and a long outer spur on the hind tibia. The apomorphic podonomine genera (South American-Australian) *Rheochlus* and *Podonomopsis* and the apomorphic subfamily Aphroteniinae are absent.

Ecology

Chironomus zelandicus, a pest of sewage treatment works, is the only New Zealand chironomid which has been extensively studied but as that part of its ecology concerns its lentic biotope it will not be dealt with here.

The podonomine midges are generally cold-tolerant, rheophil and polyoxybiontic and the larvae feed on algae, diatoms and algal detritus. Two New Zealand species which show not only this cold tolerance but also tolerance to mineral particles in suspension are *Zelandochlus latipalpis* and *Parochlus glacialis* which inhabit the upper reaches of glacial torrents. The diamesine chironomids are broadly and effectively adapted to cool running waters. Although only four species are found in the mountain streams of New Zealand these are as prominent quantitatively as those in temperate South America. Generally the diamesinae are typical algal feeders, living mainly on diatoms, but one exception is *Lobodiamesa* which feeds on small arthropods plus a smaller amount of diatoms.

TONNOIR has described the most unusual chironomid in New Zealand. This is *Dactylocladius commensalis* which is a commensal on the larva of the blepharocerid *Neocurupira hudsoni*. The larvae and pupae of the chironomid inhabit the ventral surface of the blepharocerid larvae (fig. 4).

BLEPHAROCERIDAE

The New Zealand fauna consists of 8 species in the genera *Neocurupira*, *Peritheates* and *Nothohoraia* which are contained in the subfamily Apistomyiinae.

Zoogeography

TILLYARD considered Apistomyiinae was of southern origin while TONNOIR considered it was of northern origin. Both HENNIG and DUMBLETON believed the various genera of Apistomyiinae were derived independently from Paltostominae indicated a northern origin. DUMBLETON alternatively suggested *Apistomyia* may have arisen in Australia from *Neocurupira* and then migrated north. The latest author CRAIG (1969) postulated an Asian origin for *Apistomyia*, considered that the Apistomyiinae genera have a monophyletic origin and that blepharocerids entered New Zealand from the north during the Cretaceous. CRAIG also considered that when New Zealand was divided into two islands in Oligocene, *Peritheates* evolved in the northern island and the more plesiomorphic *Neocurupira* evolved in the southern island. He assumed that during the Miocene, when New Zealand was again a single land mass, *Peritheates* migrated south to at least the limits of the present South Island, and that *Neocurupira*, having evolved in the cooler south, was prevented from migrating northwards. Speciation is postulated for *Peritheates* during the Pliocene when New Zealand was again two islands.

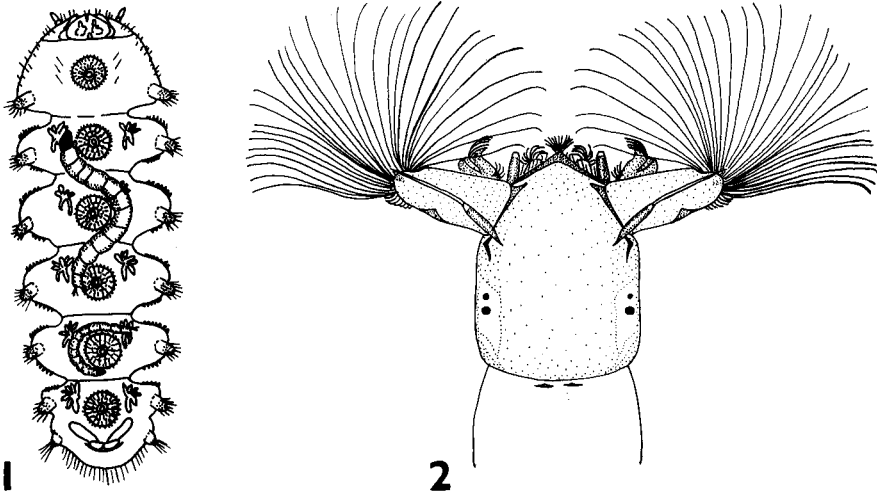


Fig. 4. 1: Larva of *Neocuripira hudsoni* (Blepharoceridae) with larval *Dactylocladius commensalis* (Chironomidae) in association. 2: Head of *Austrosimulium unguatum* (Simuliidae).

No hypothesis is given for the present distribution of *Neocuripira* species apart from *N. chiltoni* which is found on Banks Peninsula formed from the remains of two volcanoes extinct from about the Pleistocene-Holocene and connected to the East Coast plains of the South Island. Here it is considered that because the plains did not contain suitable blepharocerid habitats wind drift in the prevailing westerly was responsible for colonisation of *N. tonnoiri* type blepharocerids from the Southern Alps.

The ancestral stock of the monotypic genus *Nothohoraia* (fig. 5) which appears to be closely related to *Horaia* of the Himalayas probably constituted a separate invasion from that of the other blepharocerids.

Ecology

The chironomid previously mentioned, *D. commensalis*, has now been found on other blepharocerids and also on the rocks within the habitat and is therefore a facultative commensal. Mermithid nematodes are found in blepharocerid larvae and pupae and it is thought that they may possibly castrate males. Ryacophilid (Trichoptera) larvae are one of the most important groups of predators. These lift small larvae off the substrate and devour them whole but tear large larvae into chunks of a suitable size for consumption. Epizooic algae of the same species on the rocks cover the larvae and pupae and are eaten off by ephemeropteran nymphs. Tolerances to water velocity varies considerably in New Zealand. The range favourable for *Neocuripira chiltoni* larvae in Purau

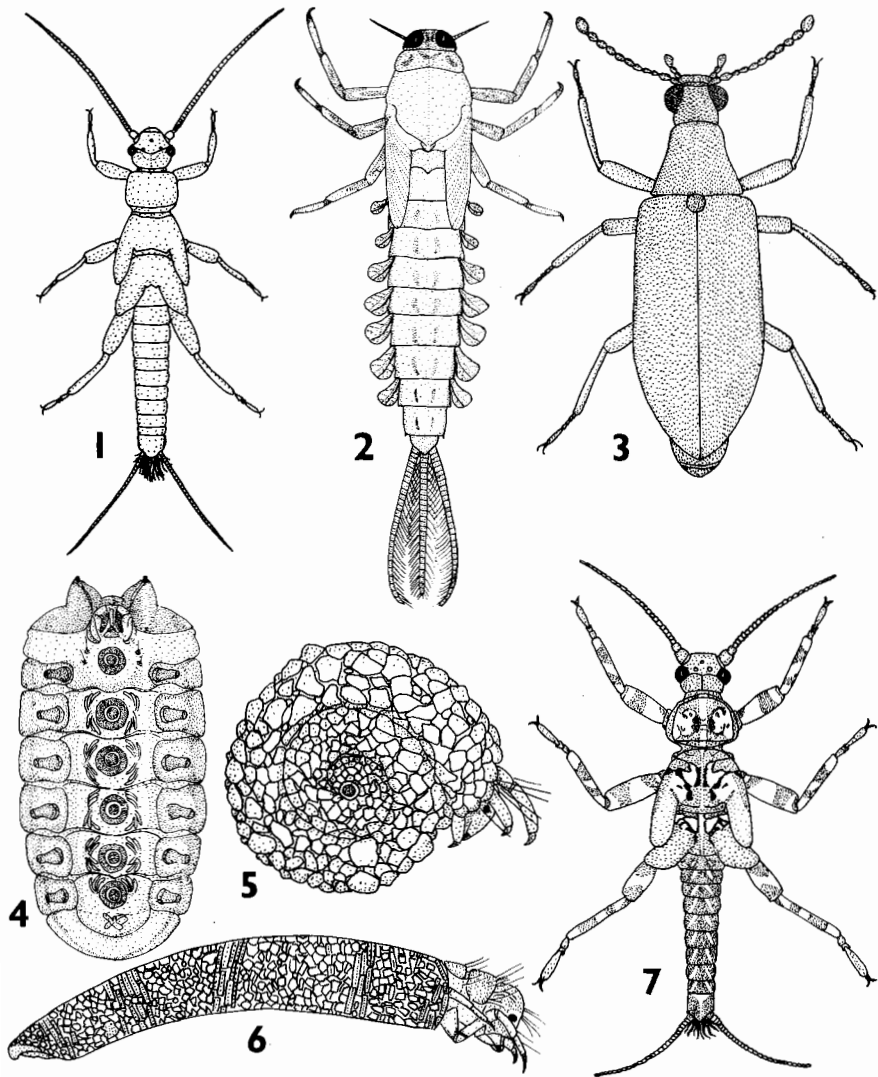


Fig. 5. Some of the fauna of a steep stony stream in lowland forest (Windy Point Creek, Buller Gorge, South Island). 1: Larva of *Zelandobius confusus* (Plecoptera, Antarcoperlinae). 2: Larva of *Nesameletus flavinictus* (Ephemeroptera, Siphonuridae). 3: Elmid species adult (Coleoptera). 4: *Nothohoraia micrognathia* larva (Blepharoceridae). 5: *Helicopsyche albescens* larva (Trichoptera, Helicopsychidae). 6: *Zelolessica chiera* larva (Trichoptera, Helicophidae). 7: *Aucklandobius fulvescens* larva (Plecoptera, Gripopterygidae).

Stream (Banks Peninsula) is 26–117 cm/sec. At Bealey Chasm (Southern Alps) larvae of other blepharocerids were not present if the water velocity was below 83 cm/sec and some larvae were found in a current of 420 cm/sec; the highest ever recorded for a blepharocerid. Water depth also has an effect in that no larvae were found in more than 30 cm of water. Apparently temperature has an effect on wing length because brachyptery in *N. campbelli* females was found to have an inverse relationship to the water temperature.

SIMULIIDAE

Zoogeography

Only one genus *Austrosimulium* occurs in New Zealand and this is one of the most specialised. The same genus occurs in Australia and there is one species in southern South America. Five species groups are recognised in Australia and New Zealand. Two are confined to Australia, one to New Zealand, and one is common to both countries. The 12 species in New Zealand do not differ markedly from one another in the adult stage but there are divergences in the larvae, pupae and cocoons.

The New Zealand fauna has its strongest affinity with that of Australia. It is not possible to identify with certainty the source and route of dispersal of the common stock from which this fauna derives. The evidence at least does not strengthen the case for a Palaeantarctic origin which was once proposed for it.

The identity or close parallelism of Australian and New Zealand taxa in this family, separated since the Cretaceous, implies a very slow or closely parallel evolution in the isolated segments. This may well be an ancient condition in this taxon. It has been suggested for instance that the simuliid genera were segregated in the Jurassic. Given such characteristics the austral distribution of this taxon could well have resulted from dispersals from the north.

A comparison of simuliid with blepharocerid fauna suggests that the New Zealand one is derived from the Australian, whatever the source and route of entry of the latter.

The New Zealand *Austrosimulium* species are distributed as follows. Kermadec and Chatham Islands have no simuliids. Stewart Island has 3 species, one endemic. Auckland Islands has one endemic species, Campbell Island has one endemic species, North Island has 4 species which are not endemic to North Island, and South Island has the 4 North Island species which are widespread plus 3 species which are endemic to South Island plus 2 species which are shared with Stewart Island.

The present southern bias in the distribution of the species of *Austrosimulium* in New Zealand, even if it is superimposed on an older original

bias, is not necessarily evidence of their southern origin. It would appear to be explicable in terms of greater and more recent speciation in the South Island, and more frequent and more widespread marine transgressions, and possibly vulcanicity also, in the North Island.

Ecology

DUMBLETON, 1972, has classified habitat preferences as follows:

A. Associated with cold snowfed streams; occasionally on boulders free of vegetation.

a. Small rivulets at high altitudes – 1550 m above bushline; stones angular *A. bicorne*

b. Larger streams, medium altitudes – 600–900 m; not predominantly glacier fed; below bushline, usually in open; stones rounded; larvae often inter-stitial *A. unicolorne*

c. Large open rivers at lower altitudes – 300 m; stones rounded *A. albovelatum*

B. Associated with cold streams often within forests.

a. Low and at high altitudes in forest or in streams with high scrub covered banks; in peaty areas or on stones *A. vexans* & *A. campbellense*

b. Small streams within forest especially in steep areas – 300–900 m; may occur in tussock sheltered streams outside forests; on angular, sub-angular or rounded stones *A. unguatum*

c. Small cold lowland streams with muddy substrate; in peaty or forested areas; on vegetation *A. stewartense*

d. Often associated with forest but sometimes in open; above or below bushline – 150–1000 m; on stones or leaves *A. multicolorne*

C. Lowland streams and larger rivers; mostly open; usually with markedly warmer summer temperature.

a. Extending into colder summer temperatures; on stones usually rounded *A. laticorne*

b. Predominantly in warmer water; stones usually rounded *A. tillyardianum*

D. Mature streams predominantly in open lowland; slower and more constant flow permitting growth of emergent vegetation or having pendant vegetation *A. australense*, *A. longicorne*

THAUMALEIDAE

The two described species belong to *Austrothaumalea* a genus peculiar to Australia, New Zealand and southern South America. TONNOIR found Thaumaleidae only in South Island but a species does exist in North Island. Up to the present the New Zealand larvae and pupae have not been described although they have been collected. They inhabit the edges of small waterfalls and seepages on steep banks.

COLEOPTERA

The Coleoptera inhabiting running waters in New Zealand consist of the following. *Huxelhydrus syntheticus* (Dytiscidae) which lives both as larva and adult at the edges of shingle rivers and the side pools of main rivers. Other Dytiscidae of the genera *Rhantus*, *Antiporus*, *Liodessus* and *Copelatus* inhabit water weed and the backwaters of small streams. Species of *Orchymontia* (Hydraenidae) are river dwelling and apparently inhabit crevices in stones or the sand under stones in the headwaters of shingle rivers. Hydrophilidae species (which appear similar to Dytiscidae in their invasion of running water) are present but are not well known. Elmidae species, which are very common in stony rivers and streams, are also in this category.

Because of the many gaps in the knowledge of New Zealand aquatic beetles, little is known of their origin. However, the presence of the Dytiscidae genera *Homoeodytes* and *Antiporus* suggest an Australian influence in that family.

There are records of a gyrenid found in New Zealand in the 1870s but none have been recorded since. It is unlikely that such conspicuous beetles could be overlooked and it is considered that the reports are either erroneous or that wind borne specimens from Australia were collected.

Population Comparisons

The surveys of populations carried out as part of research into trout streams may afford some interesting comparisons with similar work done in the Northern Hemisphere. In the best known of these surveys, (ALLAN, 1951) insect larvae and pupae make up 93% of the total invertebrate fauna of the Horokiwi Stream. Of the three main aquatic orders Trichoptera accounts for 50.77% of the total, Ephemeroptera 14.28% and Plecoptera 0.29%. These figures give a picture of the relative abundance of the three main aquatic orders in small stony rivers in New Zealand. A survey of the Tiropahi River (a similar stony stream but running through forest) gave figures of 61% for Trichoptera, 31% for Ephemeroptera and 1.64% for Plecoptera. The notable thing about these figures is the extremely small percentage of Plecoptera netted. This is consistent in the surveys I have studied. However, in the streams concerned a skilled collector working by hand can amass large numbers of nymphs of a number of species at the same times of the year as the surveys have been carried out. It is possible that the collecting methods used in the surveys do not effectively collect Plecoptera. Species numbers are interesting too. Most rivers of the above type would contain about 6 gripopterygids, 1 austroperlid, 1 eustheniid and 2 or 3 notonemourids (the species composition also is fairly uniform for a great deal of the country). This total of 10 or 11 is lower than the 17 species recorded in MIRON's survey

of Pingaratzi Stream in the Eastern Carpathians or the 31 species recorded from the survey made by SHELDON & JEWETT of Sagehen Creek in the Sierra Nevada, California. Comparison of the number of genera (Tiropahi 8, Pingaratzi 6, Sagehen 15) shows that the number of species per genus is much lower in the Tiropahi than in the Northern Hemisphere streams. The relationship of genera to species in South America and Europe is South America 1:2 and Europe 1:11. The New Zealand situation is therefore similar to that found in South American Plecoptera.

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