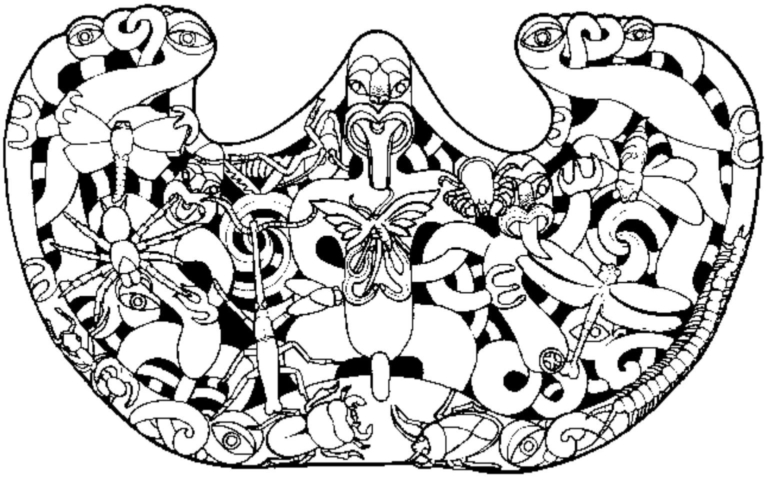

Fauna of New Zealand
Ko te Aitanga Pepeke o Aotearoa

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Number / Nama 68

Simuliidae
(Insecta: Diptera)

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Manaaki
Whenua
PRESS

Lincoln, Canterbury, New Zealand
2012

Cataloguing in publication

Craig, Douglas A.
Simuliidae (Insecta: Diptera) / Douglas A. Craig, Ruth E. G. Craig, and Trevor K. Crosby. – Lincoln, N.Z. : Manaaki Whenua Press, Landcare Research, 2012.
(Fauna of New Zealand, ISSN 0111-5383 (print), ISSN 1179-7193 (online) ; no. 68).
ISBN 978-0-478-34734-0 (print)
ISBN 978-0-478-34735-7 (online)

I. Craig, Ruth E. G. II. Crosby, Trevor K., 1946– III. Title. IV. Series.

UDC 595.771(931)

Suggested citation:

Craig, D. A.; Craig, R. E. G.; Crosby, T. K. 2012. Simuliidae (Insecta: Diptera). *Fauna of New Zealand 68*: 336 pp.

Molecular section: Craig, D. A.; Cywinska, A. 2012: Molecular analysis of New Zealand *Austrosimulium* (Diptera: Simuliidae) species. Pp. 60–65, 205–208, 298–301 *in* Craig, D. A.; Craig, R. E. G.; Crosby, T. K. 2012: Simuliidae (Insecta: Diptera). *Fauna of New Zealand 68,* 336 pp.

Dr R. J. B. Hoare of the Editorial Board oversaw the reviewing of the manuscript and accepted the revised version. Prepared for publication by the series editor and the authors using computer-based text processing, layout, and printing at Landcare Research, Private Bag 92170, Auckland, New Zealand.

To access on-line extracts from this series visit:
http://fnz.landcareresearch.co.nz/

Māori text by H. Jacob, Ōtaki.

Published by Manaaki Whenua Press, Landcare Research, P.O. Box 40, Lincoln, Canterbury, N.Z.
Website: http://www.mwpress.co.nz/

Printed by PrintLink Ltd, Wellington

Date of publication 29 June 2012

Front cover: Head of female *Austrosimulium dumbletoni* Crosby from Jackson Bay, WD (Photographer: D. A. Craig).

Publication of the *Fauna of New Zealand* series is the result of a research investment by the Ministry for Science and Innovation.

POPULAR SUMMARY

HE WHAKARĀPOPOTOTANGA

Class **Insecta**
Order **Diptera**
Suborder **Nematocera**
Family **Simuliidae**
Genus ***Austrosimulium***
Subgenus ***Austrosimulium***

Black flies, sandflies, te namu

Known in New Zealand as “sandflies” or “Te Namu” and elsewhere in the world mainly as “black flies”, Simuliidae are iconic New Zealand insects. Virtually every New Zealander has been bitten by female simuliids at some time or other, as have the many overseas tourists who have visited Fiordland.

Simuliids of New Zealand belong to the genus *Austrosimulium* known only from New Zealand, Tasmania, and mainland Australia. The nearest relative is the genus *Paraustrosimulium* in South America. This relationship has been confirmed by both morphological and molecular examination. Therefore these simuliids would appear to be of Gondwanan provenance, when South America, Australia, New Zealand, Tasmania, Africa, India, and Antarctica were co-joined in the super continent Gondwana that broke up between 120–80 million years ago. In Australia there is a small segregate of species in the subgenus *Novaustrosimulium*, with all their remaining *Austrosimulium* species in the subgenus *Austrosimulium*. Questions still remain, however, as to exactly when New Zealand simuliids arrived here, but this study indicates they are not much older than 5 million years.

Simuliid larvae require running water and in New Zealand are more or less ubiquitous, occurring in almost all running water habitats. Although there are 19 species of *Austrosimulium* in the country, the females of only 3 species are serious biters of humans. Males never bite. The females bite to obtain nutrients to produce eggs: females that do not take a blood meal can still lay a smaller number of eggs. Markedly few males have ever been collected in the field despite the equal abundance of males and females in their immature stages.

In the North Island the main biter is the New Zealand black fly, *Austrosimulium australense*, found the length

(continued overleaf)

Illustration / Whakaahua: *Austrosimulium ungulatum* Tonnoir. Brass sculpture, Milford Sound Visitor Centre, Fiordland. Artist: Elizabeth Thomson, 1991 (Photographer: Andrew Baird, Invercargill).

Te Namu

Koia tēnei ko te namu, ko tōna ingoa Pākehā i Aotearoa nei, ko te “ngaro onepū”, i tāwāhi, ko te “ngaro pango”. He ngārara ingoa araara te namu i Aotearoa — ko wai o tātou kāore anō i ngaua e te namu uwha? Tae atu anō ki te hunga haramai i tāwāhi ki Te Whakataka-kārehu-a-Tamatea — ko rātou anō e rongo kino ana i te ngau a te namu.

Nō te puninga *Austrosimulium* ngā simuliid o Aotearoa, waihoki ko Aotearoa, ko Tahimania me te tuawhenua o Ahitereiria anake ōna kāinga e mōhiotia ana. Ko ōna uri tino tata, ko te puninga *Paraustrosimulium*, i Amerika ki te Tonga. Kua whakaūngia tōna hononga ā-whakapapa ki tērā i runga i te hanga o ngā tinana me ngā mātaitanga rāpoi ngota. Nō reira, ko Te Uri Māroa pea te kāinga tuauri o ēnei puninga e rua, i te wā e whenua kotahi ana a Amerika ki te Tonga, a Ahitereiria, a Aotearoa, a Tahimania, a Āwherika, a Īnia, me Te Kōpakatanga ki te Tonga. Nō te 120–80 miriona tau ki muri i wehewehe ai a Te Uri Māroa. Tērā tētahi wehenga iti i Ahitereiria o ētahi momo nō te puninga whāiti *Novaustrosimulium*, engari ko ērā atu o ōna momo o te puninga *Austrosimulium*, nō te puninga whāiti *Austrosimulium*. Kāore anō i kitea nōnahea rawa i tau mai ai ngā namu o Aotearoa ki konei. Engari ko tā tēnei rangahautanga nei e tohu ana, nō te takiwā o te 5 miriona tau ki muri, paku neke atu rānei.

(haere tonu)

and breadth of that island, but less so in the South Island and Stewart Island. Another species in the North Island that bites to some extent is *A. tillyardianum*, but it is not found in large numbers, and then only south of Auckland. In the South Island the two main biters are *A. tillyardianum,* mainly in the north and then south through Canterbury, while in Westland and Fiordland the simuliid of notoriety is the West Coast black fly, *A. ungulatum*. The females of *A. ungulatum* will fly long distances to obtain a blood meal and their ferocity has generated many horror stories from early settlers in New Zealand, and more recently, the annual million or so overseas tourists. Few of the latter leave New Zealand unscathed if they visit Fiordland, and many tend to react badly to bites since they have not previously been exposed to the biting of this species. It has been noted that, similar to the quote regarding weather, attributed to Mark Twain (Samuel L. Clemens), that in New Zealand "Everybody talks about sandflies, but nobody does anything about them".

New Zealand *Austrosimulium* can be placed into two main species-groups, based on the presence (*ungulatum* species-group) or absence (*australense* species-group) of a basal tooth on the tarsal claws of the female. Elsewhere in the world those possessing the tooth are normally known as bird feeders, whereas those lacking the tooth are normally more mammophilic. New Zealand simuliids are opportunistic and females will generally take blood meals from whatever is available. It is well established, however, that whereas Fiordland crested penguins are heavily attacked by *A. dumbletoni,* a toothed-clawed member of the *ungulatum* species-group, its females studiously avoid biting humans. The simuliids that attack penguins are known to be a vector for a bird "malaria", *Leucocytozoon*, but are not known to be a vector for any disease to people.

Molecular analysis indicates that most New Zealand simuliid species are of relatively recent origin, probably evolving during the 5 glaciations over the last 500 000 years, and this is in agreement with some other such investigations of the New Zealand fauna. There are, however, lineages in the *ungulatum* species-group which are high altitude, cold water species; and this specialised habitat in the Southern Alps is a little more than 5 million years old. That age is in general agreement with molecular evidence from this study.

A common question is "What did New Zealand simuliids feed on before humans arrived?" Of little doubt it would be on the vast number of birds that now are greatly depleted — gone are the days of the "dawn chorus" — and probably also the large numbers of seals present then. Indeed, searching along beaches for a blood meal from either birds or seals still appears inherent behaviour of New Zealand adult female simuliids — and probably the reason for their name "sandflies".

Me wai rere e ora ai ngā punua a te namu. Me kī, kei ngā wāhi katoa o Aotearoa, me he wai e rere ana i reira. Tekau mā iwa ngā momo *Austrosimulium* kei Aotearoa, engari ko ngā uwha o ētahi momo e toru noa iho e kaha mōhiotia ana mō tā rātou ngau i te tangata. Kāore rawa ngā toa e ngau. He ngau tā te uwha, kia kaha ai tana whānau hua. Arā ētahi uwha kāore e kai toto, engari ka whakaputa hua tonu; heoi anō, he iti ake ngā hua ka whānau mai i a rātou. He ruarua noa ake ngā toa kua kohia, tēnā i ngā uwha, ahakoa e āhua rite ana te maha o ngā punua toa me ngā punua uwha.

I Te Ika-a-Māui, ko te *Austrosimulium australense* te namu kaha te ngau, kitea ai i te whāroatanga atu o tēnei motu. Kei Te Waka-a-Māui, kei Rakiura anō, engari kāore e pērā te kaha o te kitea. Ko tētahi atu namu ngau kei Te Ika-a-Māui, ko te *A. tillyardianum*, heoi anō, kāore e tini ngerongero, ka mutu kei te tonga anahe o Tāmakimakaurau. E rua ngā momo namu matua o Te Waipounamu e rongonui ana mō te ngau. Ko tētahi ko *A. tillyardianum,* kei ngā whenua mai i Te Tauihu o te Waka ahu atu ki Waitaha. Ko tērā atu, a *A. ungulatum*, e rongonui ana i Te Tai Poutini me Te Whakataka-kārehu-a-Tamatea. Ko ngā uwha o *A. ungulatum*, ka rere ki tawhiti ki te kimi toto hei kai mā rātou, ka mutu he ngārara niwha tonu. Nō konā tana uru ki ngā kōrero paki a ngā Pākehā tuatahi i whakanohonoho i Aotearoa, tae atu ki ā te hunga tāpoi o ngā tau tata ake — ko tōna kotahi miriona nei e taetae mai ana i tāwāhi i ia tau. O ngā wae tāpoi ka haere ki Te Whakataka-kārehu-a-Tamatea, he tokoiti ka hoki ki ō rātou kāinga i rāwāhi me te kore e mamae o te tinana e te ngau a namu. Ka mutu, ka āhua kino te ngau ki a rātou, he kore nō ō rātou tinana i waia ki te ngau a tērā momo namu. Kua puta te kōrero āhua pērā i tā Mark Twain (Samuel L. Clemens), tāna kōrero mō te huarere, e mea ana, i Aotearoa nei "ko te namu kei ngā ngutu o te katoa, engari kāore tētahi tangata kotahi nei i te kori ake ki te rongoā i te raruraru".

Ka noho mai ngā *Austrosimulium* o Aotearoa ki ētahi huinga momo e rua — ko ērā e whai niho ana i te pūtake o ngā matihao o te uwha (te huinga *ungulatum*) me ērā karekau he niho pērā (te huinga *australense*). I ētahi atu wāhi o te ao, ko te nuinga o ngā mea he niho pēnei ō rātou, he kai i te toto o te manu, ko ngā mea kāore he niho pēnei, he kai i te toto o te whāngote. Engari ko te nuinga o ngā simulid o Aotearoa, he whai i te ara māmā e ngata ai te hiahia, nō reira ka whāia e ngā uwha te toto o te mea e tata ana. Heoi anō, kua āta kitea i ētahi atu rangahau, ahakoa e muia ana ngā tawaki e te *A. dumbletoni,* he huānga matihao whai niho nō te rōpū *ungulatum*, kāore ngā uwha e ngau i te tangata. Ko ngā namu e urutomo ana i ngā tawaki, ko rātou ngā kaikawe i tētahi momo malaria kei te iwi manu, ko te *Leucocytozoon* te ingoa. Heoi, e ai ki ngā mātauranga

(haere tonu)

Worldwide, simuliids are notorious for their disease transmission, in particular onchocerciasis, or river blindness, in Africa and South America, but more widely for the nuisance value of their bites, especially in the northern North Hemisphere. In Canada, simuliids are celebrated in the "The Black Fly Song" written by Wade Hemworth in 1949. New Zealand has two sculptures featuring simuliids — probably unique in the world — that are remarkably accurate and most appropriate for the region. One is a set of brass adults in the visitor centre at Milford Sound, Fiordland, crafted by Elizabeth Thomson in 1991; the other is a giant 2 m long fly suspended on the outside of the Bushman's Cafe, Pukekura, Westland.

Contributors **Doug** and **Ruth** (nee **Heath**) **Craig** were born in Nelson, New Zealand, and attended their local Colleges. Doug went to the then Canterbury College, University of New Zealand, Christchurch in 1959, where, in his first year, he failed both his major subjects, Botany and Zoology, but passed well in Physics! Ruth started university a year later and they met in Botany I when Doug repeated the subject. Both were doing biology degrees with a view to becoming secondary schoolteachers, as the demographic bulge of children from the post-World War 2 'baby boom' was fast approaching and teachers were in short supply. The New Z.ealand Department of Education provided very good post-primary studentships to attend university in return for teaching an equal number of years. Ruth continued along that path and taught at Christchurch Girls' High School. Doug, however, became beguiled by the aquatic insects, the Blephariceridae, and after finishing his B.Sc. (Hons) degree in the then Zoology Department, became Vida Stout's first Ph.D. student and worked on the biology of those insects. When Vida took a sabbatical leave, and then a leave of absence in Sweden, Bob Pilgrim took over the supervisory details. As far as the secondary school teaching went, that was paid off by some 'temporary assistant lectureships' and buying the remainder out. Doug and Ruth were married in 1962. Immediately Doug finished his Ph.D. in October 1966 (with the now autonomous University of Canterbury), both left for Edmonton, in Canada; for Doug this was a sabbatical replacement position in the Department of Entomology, University of Alberta, and an opportunity for overseas experience. It was meant to last for just a single year, but with another year available, and then a position vacant, Doug was hired as departmental morphologist. So then with a family of two children (Jacqueline and Michael), two cats, and a mortgage, the stay became permanent. Good working conditions and colleagues helped too! Initially Doug worked with WHO funding on the embryology of simuliids in relation to

o nāianei, kāore e whakawhitia mai ana tētahi mate e tērā momo namu ki te tangata.

E mea ana ngā tātaritanga rāpoi ngota, ehara i te mea nō tuauriuri whāioio te nuinga o ngā namu o Aotearoa. Nō roto kē mai i ngā kapinga e 5 o te ao i te tio i te 500,000 tau kua mahue ake nei. Ā, e tautoko ana tēnei i ngā rangahautanga i ētahi atu o ngā mea oreore a Tāne. Heoi anō, arā ētahi kāwai o te huinga *ungulatum* he noho ki ngā wāhi teitei, ki te wai makariri. Ko te wāhi o Kā Puke Māeroero koirā tō rātou kāinga whāiti, kua paku neke atu i te 5 miriona tau e tū ana. E tautoko ana tēnei i ngā kitenga rāpoi ngota o tēnei mahi rangahau.

Ko tētahi pātai ka kaha te uia ake, "He aha te kai a ngā namu o Aotearoa i mua i te taenga mai o te tangata?" Kāore e kore ko te huhuatanga o te manu i te mata o te whenua i ērā wā. Kua tino kore tērā āhua iāianā, kua ngaro te pūorooro o te ngahere i ngā manu korihi o te ata. Ā, he kekeno anō pea te kai i ngā rā o nehe, inā te tini o te kekeno i ērā wā. Heoi anō, te āhua nei kei te mau tonu te whanonga a ngā uwha kātua o ngāi simuliid mā, kei te kimi tonu pea i ngā toto o te manu tai, o te kekeno i tātahi. Ā, koia anō pea i tapaina ai ki te reo Pākehā i Aotearoa nei ko te "ngaro onepū".

Puta noa i te ao, e mōhiotia ana te namu mō tana kawe i ngā tini mate. Ko tētahi ko te onchocerciasis, i Āwherika me Amerika ki te Tonga, ko te 'kāpō awa' tōna ingoa kārangaranga. E whakakinongia ana anō hoki te namu mō tana ngau, ā, ko te taha raki o te Tuakoi Raki tētahi tino wāhi i pērā ai. I titoa anō he waiata mōna i Kānata i te tau 1949, e Wade Hemworth, ko "Te Waiata Ngaro Pango" te ingoa. E rua ngā whakapakoko o te namu i Aotearoa, he mahi ahurei tonu pea huri i te ao. Me kōrero te tika o te hanga o ngā mea nei, me te hāngai ki te rohe kei reira nei rātou. Ko tētahi, he huinga kātua, he mea hanga ki te kuratea. Kei te whare manuhiri i Piopiotahi tērā, he mea waihanga e Elizabeth Thomson i te tau 1991. Ko te tuarua, he namu kaitā, e rua mita rawa te rahi, e iri mai ana i waho o te Wharekai Bushman i Pukekura, i Te Tai Poutini.

Translation by **H**. **Jacob**
Ōtaki

Doug and Ruth Craig at 7th International Congress of Dipterology, Costa Rica, 2010.

their control in Africa where the female of these insects transmits river blindness. Ruth became a technician in Plant Science until daughter Jackie was born and then, after a child-rearing stint, became a sessional instructor in the Department of Zoology for a number of years. With parents and relatives still in New Zealand, return visits were a necessity, albeit expensive with a family, so trips were restricted to various sabbatical leaves. Stopovers were, however, made in Polynesia, Rarotonga, and Fiji to collect simuliids, and that resulted in discovery of many new species, which kindled an interest in biogeography of Pacific Simuliidae. Inbetween times a childhood interest of mucking about in running water was refined, and Doug spent a decade on proximate hydrodynamics of simuliid larvae and other aquatic insects. An earlier, but important aspect to that was a detailed understanding of the shape and structure of the larvae, garnered from having one of the first Scanning Electron Microscopes (SEM) in Western Canada. Originally full of glowing vacuum tubes — now just cold transistors — that laboratory, established in 1971, is still going strong, albeit with shiny new instruments. Doug retired in 1997 after 31 years teaching, having had quite enough of the changes that are taking place in universities nowadays. As an Emeritus Professor and still active with research grants, Doug, with Ruth (now a retired Registered Nurse), in the last decade have travelled widely across the Pacific collecting simuliids for taxonomic revisions. They have been as far west as Palau in Micronesia, completely around all the Polynesian island chains, some more than once, Vanuatu twice, and Fiji a number of times. It seemed only natural to eventually do a taxonomic revision of New Zealand Simuliidae. Having daughter Jacqueline, now an anthropologist living in Auckland, and a grand-daughter there too, made the decision relatively easy.

Contributor **Trevor Crosby** was born in Cambridge, New Zealand, and grew up in the central North Island towns of Raetihi and Piriaka (attending Taumarunui High School), with a year at Whangaehu (Wanganui Boys' College). His family then moved to Karamea on the West Coast, and Trevor went to the University of Canterbury, Christchurch (in receipt of a post-primary studentship similar to his fellow contributors above) and gained his B.Sc. (Hons) in Zoology. The opportunity to do a Ph.D. on the simuliid *Austrosimulium tillyardianum* put secondary teaching on hold (subsequent employment with DSIR became approved service). He spent a year in Wellington as a DSIR science editor (bulletins and occasional publications), before moving to Auckland to join Entomology Division, DSIR as curator of NZAC, a position he held until 2009. He has been leader of the invertebrate biosystematics group (1980–1983, 1997–2007), and has been involved with the *Fauna of New Zealand* since its inception, being its editor since 1998. Collaboration with colleague Graeme Ramsay saw the publication in 1992 of the *Bibliography of New Zealand terrestrial invertebrates 1775–1985*, and later that year the database "BUGS on-disc" was published on CD as part of New Zealand's first science CD, which now forms part of the backbone of the online BUGZ literature website.

[redacted]

Trevor preparing *Fauna of New Zealand 68*, 5 June 2012 (Photograph: Birgit Rhode)

Trevor has had expert witness responsibilities in forensic entomology: his co-authored paper on using entomological evidence to prove importation of cannabis into New Zealand was awarded the 1987 Philip Allen Memorial Award by the Forensic Society of Great Britain; and the calculation of possible time of death using calliphorid maggots has assisted a number of New Zealand Police investigations. Since 1994 he has provided training in entomology and identification for phytosanitary purposes in the South Pacific (particularly Vanuatu and Samoa) and Asia (India, Cambodia, Lao PDR, Myanmar, Viet Nam, and most recently Brunei). His interest in education has continued through being a school Board of Trustee member: Gladstone Primary (1998–2004), and Western Springs College (2001–present), and with his wife Bev he has run a Dyslexia Parent Support Group since 2000. Bev and children (Cameron, Karl, and Erin) have supported his various endeavours, but sometimes remind him of the family events he has missed while away on consultancies.

Dedicated to the memory of **Lionel Jack Dumbleton** (29 December 1905 – 25 September 1976). Despite being incapacitated by a stroke shortly before he was to retire in 1970, Jack, with great determination completed his major work on New Zealand Simuliidae (1973), which provided a sound taxonomic framework for our research (see Lowe & Ramsay (1977) for his obituary).

"…no sooner had the sun risen, and we issued from our tent to wash by the river side, than those peculiarly vexatious pests, the sand-flies (*namu*), commenced their attacks on our bare hands and feet. The sand-fly is a small black insect, and swarms in such myriads, that one is never free from their vengeance, if remaining for a single instant in the same position: whilst sketching, my hands are frequently covered with blood, and their numbers being inexhaustible, one at last gets weary of killing them." (p. 21), "The horrid sand-flies attacked us to-day more unmercifully than ever, and in such clouds that I should imagine them to be a species very nearly allied to those that constituted the fourth plague of Egypt. (p. 23)"

Account about biting of *Austrosimulium australense* near the Waikato River on the AK/WO area boundary on 29 September 1844. Angas, G. F. 1847: Chapter I: pp. 21 & 23, Journey into the interior of New Zealand — The Waikato. In *Savage Life and Scenes in Australia and New Zealand Vol. II*. London, Smith, Elder & Co.

"The blood-sucking ones are all females: the male is a perfect gentleman, for it is rarely seen and never bites." Anon (1961) *New Zealand Science Review 19*: 75.

Frontispiece. Female adult of *Austrosimulium tillyardianum* feeding on the foot of DAC at Roding River, Nelson in 2007. Note the diuretic fluid extruded from the fly's anus — a mechanism for rapidly concentrating the blood meal. (Photographer: D. A. Craig).

ABSTRACT

This revision recognises 19 species of Simuliidae as being present in the New Zealand subregion, with all species assignable to *Austrosimulium* (*Austrosimulium*) Tonnoir. Added to the 13 previously described species are 2 taxa originally described by Dumbleton as subspecies which we have elevated to species rank, plus 4 new species.

The species groupings of Dumbleton (1973) are confirmed with cladistic analysis: the *australense* species-group, diagnosed in large by the lack of a basal tooth on the female tarsal claws, and the *ungulatum* species-group, characterised mainly by presence of the basal tooth on the female tarsal claws. Further subdivision of these species-groups is also confirmed. In the *australense* species-group, the *australense*-subgroup contains *Austrosimulium* (*A*). *australense* (Schiner) and *A*. (*A*.) *longicorne* Tonnoir; and that of the *tillyardianum*-subgroup contains *A*. (*A*.) *albovelatum* Dumbleton, *A*. (*A*.) *alveolatum* Dumbleton new status, *A*. (*A*.) *dugdalei* n. sp., *A. (A.) extendorum* n. sp., *A*. (*A*.) *fiordense* Dumbleton new status, *A*. (*A*.) *laticorne* Tonnoir, *A*. (*A*.) *multicorne* Tonnoir, *A*. (*A*.) *stewartense* Dumbleton, and *A*. (*A*.) *tillyardianum* Dumbleton. In the *ungulatum* species-group, the *ungulatum*-subgroup contains *A*. (*A*.) *campbellense* Dumbleton, *A*. (*A*.) *dumbletoni* Crosby, *A*. (*A*.) *ungulatum* Tonnoir, *A*. (*A*.) *vailavoense* n. sp., and *A*. (*A*.) *vexans* (Mik); and the *unicorne*-subgroup contains *A*. (*A*.) *bicorne* Dumbleton, *A*. (*A*.) *tonnoiri* n. sp., and *A*. (*A*.) *unicorne* Dumbleton. Lectotypes are designated for *A*. (*A*). *australense* and *Simulium tillyardi* Tonnoir, 1923 (= *A*. (*A*). *australense*), and a neotype is designated for *A*. (*A*). *fiordense*. Examination of specimens with the *nomen nudum,* caecutiens Walker, 1848, confirmed the synonymy with *A*. (*A*.) *australense*.

The Simuliidae of New Zealand are a segregate of species of the genus *Austrosimulium* endemic to Australia, Tasmania, and New Zealand. A small group of Australian species form the subgenus *Novaustrosimulium* Dumbleton. However, only members of subgenus *Austrosimulium* occur in the New Zealand subregion. The genus is well established as the sister taxon to the monospecific genus *Paraustrosimulium* Wygodzinsky & Coscarón in South America.

This revision is based on numerous new specimens obtained between 2006 and 2012 from over 319 localities, and 330 collections in addition to an equal number of earlier collections. Full descriptions for known stages are given for all previously described species as well as the new species. Most diagnostic characters are found in the pupal stage and involve the structure of the pupal gills, the cocoon structure, and sculpture of the thoracic cuticle. Mature final instar larvae, exhibiting dark pharate pupal gills, are also of major diagnostic value. Keys are provided to adult females and males, pupae, cocoons, final instar larvae, and larval ecological requirements. There are full illustrations of the morphological characters used.

An extensive review is provided on bionomics. For most species little is known about their biology, habitat requirements, and the factors limiting their distribution, but it appears that the requirements of the immature stages are the major determinants. *A. longicorne* larvae are found in smooth, markedly slow flowing water — quite unusual for a simuliid — and we propose the common name “slow flow black fly” for this species. Some high altitude species, such as *A. bicorne*, have quite specific habitat requirements for the immature stages. Others, such as those of *A. australense*, are habitat generalists, but normally use vegetation as a substrate. Details about recent collecting localities and their hydrological parameters are given. Typical habitats for species are illustrated, although all recent localities have an associated photograph that is accessible through <fnz.landcareresearch.co.nz>.

The biogeography of species is discussed in-depth in relation to current knowledge of the geological events that have shaped New Zealand and influenced the distribution of species.

Preliminary molecular analysis (Cytochrome oxidase subunit 1 (CO1) mitochondrial DNA barcoding, 800 base pairs) is almost in full concordance with the groupings formed through morphological cladistic analysis, but the molecular analysis could not distinguish species in the *tillyardianum*-subgroup. *Austrosimulium ungulatum*, recognised from morphological evidence to be a single entity, is shown to comprise 4 haplotypes. Similarly, some other species show multiple haplotypes. Further, *A. vexans* of the Auckland Islands is sister to an aggregate of haplotypes previously assumed to be *A. ungulatum*. *Austrosimulium dumbletoni* and *A. vailavoense,* taxonomically placed in the *ungulatum*-subgroup because of morphological characters, are shown by molecular analysis to be in the *unicorne*-subgroup; and that subgroup is sister to all remaining New Zealand *Austrosimulium*. Further, *A. australense* probably comprises 2 species, one primarily North Island, the other precinctive to the South Island and Stewart Island and that cannot be distinguished on current morphological characters.

The molecular analysis indicated that New Zealand *Austrosimulium* originally arrived by dispersal well after the so-called Oligocene Great Inundation *ca* 34–23 Mya, and the concatenation of the large *tillyardianum*subgroup even more strongly indicated that it is a segregate of recent origin. That the *unicorne*-subgroup of species require cold water, high altitude habitats in the Southern Alps, that at maximum are only some 5 million years of age, indicates that New Zealand *Austrosimulium* is unlikely to be older.

Keywords: Insecta, Diptera, Simuliidae, *Austrosimulium*, black flies, sandflies, New Zealand, morphology, molecular analysis, taxonomy, keys, fauna, relationships, biology, biogeography, New Zealand black fly, West Coast black fly, slow flow black fly.

Craig, D. A.; Craig R. E. G.; Crosby, T. K. 2012: Simuliidae (Insecta: Diptera). *Fauna of New Zealand* 68, 336 pp.

Received:2 March 2012. Accepted:1 June 2012.

CHECKLIST OF TAXA

Family **SIMULIIDAE** Newman, 1834
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  australense-subgroup Dumbleton, 1973 99
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ACKNOWLEDGMENTS

With the broad scope of this work and the length of time taken for its completion, there are many people who assisted — all much appreciated.

Doug and Ruth thank the personnel of Landcare Research, Auckland for their assistance during our 3 visits to New Zealand on this project. DAC also thanks the mycologists, who were a friendly bunch at coffee breaks.

We all thank Grace Hall for her good humour and patience in locating NZAC simuliid material, and Leonie Clunie for arranging the dispatch of specimens as required. Stephen Moore is acknowledged for assistance with the computerised imaging microscopes and sharing images of simuliids; Birgit Rhode provided advice on images also. Thomas Buckley and Rich Leschen agreed to collect simuliids on the Three Kings Islands in 2009 in an attempt to acquire mature specimens for us, but without success.

TKC acknowledges the companionship and assistance provided by his colleagues (particularly John Dugdale and other colleagues from the DSIR era) while collecting specimens, and also for the opportunities he was provided by DSIR and Landcare Research to collect in remoter parts of New Zealand and its offshore islands. For collecting and technical assistance he particularly thanks Beverley Crosby (formerly of DSIR).

Particular thanks to George Gibbs (Victoria University, Wellington) who obtained some rarely collected adults for this study, and to Shelley McMurtrie (EOS Ecology, Christchurch) for information on the Campbell Island Bicentennial Expedition and access to specimens.

Doug and Ruth thank the extended Campbell family who provided hospitality and permission to collect on property under their care, and our daughter Jacqueline Craig and her husband Matthew Campbell who provided accommodation and refuge in Auckland. The Fenwick's and Mannering's similarly did so in Christchurch. While on the road, the length and breadth of New Zealand, the main refuge for the Craigs was a VW camper van.

We all thank our librarians who have helped to track down some hard-to-find literature or publication details. We thank John Early, Ricardo Palma, and Simon Pollard, of the Auckland Museum, Te Papa, and the Canterbury Museum respectively, for allowing access to their simuliid holdings. Similarly, thanks to Uwe Kallweit (Senckenberg Naturhistorische Sammlungen, Dresden, Germany) for attempting to find the types of *A. vexans*, and Peter Sehnal (Naturhistorisches Museum, Vienna, Austria) for examining the types of *A. australense,* providing label details, and the eventual loan of that material. Heide Zwick (Schlitz, Germany) provided us with important information on early *australense* specimens obtained by Enderlein, and Joachim Ziegler (Museum für Naturkunde, Berlin, Germany) is thanked for the loan of those specimens. Elizabeth Jefferys (Macleay Museum, Sydney, Australia) provided information on the whereabouts of some Tonnoir paratypes, and Chris Manchester (CSIRO, Canberra, Australia) provided their label information. Theresa Howard (The Natural History Museum, London, England) loaned the quite startling collection of 'Simulium caecutiens', and Luis Hernandez-Triana also assisted in our requests for information on this material. We thank Alastair Dumbleton (Chief, Employment Relations Authority, Auckland) for providing us with photographs taken by his father on trips to Campbell and Auckland Islands, and allowing us to reproduce images of 2 of his collecting sites. More peripheral, but well appreciated none-the-less, was assistance to DAC by Marvin Gunderman and Robert Lee (McMaster University, Hamilton, Ontario, Canada) in locating missing Davies types of *Austrosimulium colboi*. In regard to that species, major thanks to Kevin Moulton for the loan of a rare male.

Thanks to Mark Goettel, James Becnel, and Tony Cole for help with identifying some of the parasitoids of *Austrosimulium* larvae. Trevor Worthy, Ian Jowett, and Jon Harding all graciously answered DAC's questions regarding New Zealand rivers. Similarly, thanks to Bob Carter, Andy Tulloch, Dave Craw, and others who answered questions regarding New Zealand geological history and climate. Wayne Rickets provided information on simuliids biting livestock. Geoff Tunnicliffe answered questions regarding pre-human bird populations in New Zealand. Thanks, too, to Gerald Hutchings who drew our attention to the quote by Angas and which we have used, and to Andrew Baird for allowing use of his image of the Milford Sound simuliid sculpture.

We thank Peter Adler (Clemson University, South Carolina, U.S.A.), Thomas Buckley and Robert Hoare (Landcare Research, Auckland), John Dugdale (research associate, Landcare Research, Nelson), and Michael Winterbourn (emeritus professor, University of Canterbury, Christchurch) for reviewing the manuscript before publication. Anne Austin (editor, Landcare Research, Palmerston North) is also thanked for checking the manuscript. Doug Currie and Peter Adler, fellow simuliidologists, provided a sounding board for DAC's questions, well beyond the call of duty. Similarly, DAC's long-suffering coffee and lunch groups deserve special thanks — they fielded many a query and provided much advice, some of which was taken.

The Royal Society of New Zealand expressly provided permission to use and reprint material from Dumbleton (1973), including illustrations done by John Dugdale. Thanks also to Geographx, a digital mapping company, for permission to use the digital elevation maps of New Zealand for the haplotype distribution and ecoregion maps.

For the DNA sequencing DAC and Alina Cywinska thank the Canadian Barcode of Life Network, and this work was funded, in the main, by F. F. Hunter (Brock University, Canada) and D. C. Currie (Royal Ontario Museum, Toronto, Canada), via Genome Canada through the Ontario Genomics Institute, NSERC, and other sponsors listed at <www.BOLNET.ca>.

Financial support to DAC and REGC was largely from personal funds, but also from a Discovery Grant, Natural Sciences and Engineering Research Council of Canada (NSERC) to DAC. TKC acknowledges the financial support received from the Defining New Zealand's Land Biota programme (and its predecessors) of the Ministry of Science and Innovation; likewise DAC acknowledges the partial support he received for fieldwork from this programme through Landcare Research.

INTRODUCTION

The Māori call Simuliidae "namu" (Polack 1838) and one legend, as given at Milford Sound, lays responsibility for Te Namu on Hinenuitepō, goddess of the underworld. As she gazed at the beauty crafted by Tūterakiwhanoa, the carver of Fiordland, she was fearful that humans would not want to leave such a paradise. Te Namu were to remind humans of their mortality and not linger. Miller (1952a) detailed Māori use of the word "namu" and its variants, such as "namu katipō" for mosquitoes (more commonly called waeroa — literally "long legs" or "the long-legged one"), and "naonao" for midges or small moths. In French Polynesia "no-no" or "nono" refers to bloodsucking simuliids. Māori legend has it that the mosquito advised the namu (simuliids) to wait until dark before biting — advice that was not taken.

Characterisation of the family Simuliidae

The family Simuliidae is a relatively small family of flies with only some 2 100 extant species described (Adler & Crosskey 2012). The genus *Austrosimulium* now comprises some 30 species with 19 recognised in the New Zealand subregion. Because of their economic and medical importance Simuliidae have been the focus of major investigations and reviews, and worldwide much is known (e.g., Strickland 1911; Puri 1925; Grenier 1949; Dinulescu 1966; Rivosecchi 1978; Laird 1981; Kim & Merritt 1988; Rubtsov 1989; Crosskey 1990; Takaoka 2003; Adler *et al.* 2004). The works by Crosskey and Adler *et al.* are recommended for detailed general introductions to the family.

Simuliidae are in large part characterised by shape of the adult. The body is compact with a distinct arched thorax (Fig. 1), thence the common name of "buffalo flies" in some parts of the world. The wings are broad with heavy anterior venation (Fig. 2, 3). As Adler *et al.* (2004) noted, this gestalt is ancient and known to be at least 94–90 million years old. While adults of the family are notoriously morphologically homogeneous and generally of dark colour (hence "black flies"), some are multi-coloured. The pupal stage is also generally uniform across the family and reflects the shape of the adult (Fig. 4). The prothoracic spiracular gills (respiratory organs) are amongst the most diverse structures in the family and are heavily used for diagnostic characters. The larvae (Fig. 6) have a well sclerotised head capsule, and the body is elongated and usually dumbbell-shaped. In most simuliids the head supports a pair of distinctive labral fans. There is a single anterior proleg and one posteriorly, both with hooks. Again, this body form is ancient, shown by superb fossils from the Australian Lower Cretaceous (138 million years ago) (Jell & Duncan 1986).

Systematically, Simuliidae are included in the infraorder Culicomorpha, a well-supported clade within the paraphyletic "Nematocera" or lower Diptera (Yeates & Wiegmann 2005). The Culicomorpha encompasses 2 superfamilies, with Culicoidea including Culicidae (mosquitoes), Dixidae (meniscus midges), and Corethrellidae (frog-biting midges), and its sister taxon the Chironomoidea comprising the Thaumaleidae (trickle or solitary midges), Simuliidae (black flies), Ceratopogonidae (biting midges), and Chironomidae (midges). Hennig (1973) considered Simuliidae plus Ceratopogonidae as sister to Chironomidae. Relationships of families within the 2 superfamilies are still uncertain (Yeates & Wiegmann 2005). Wood & Borkent (1989), in a widely cited phylogeny of the Nematocera based on morphological characters, placed Thaumaleidae basal to Simuliidae + (Ceratopogonidae + Chironomidae). Also in agreement with these conclusions were the studies by Borkent & McKeever (1990) and Oosterbroek & Courtney (1995). A molecular phylogeny by Beckenbach & Borkent (2003) also placed Simuliidae sister to the clade of Ceratopogonidae + Chironomidae, but the study did not include Thaumaleidae. There are, however, conflicting views. Saether (2000), using morphological characters, placed Simuliidae as sister to Chironomidae, with Thaumaleidae basal in Culicomorpha.

In a molecular study, Pawlowski *et al.* (1996) placed Thaumaleidae as sister to Simuliidae in a study based on the 28S RNA gene. Of interest also was the suggestion that evolution of the 2 families had been rapid, in particular that of Thaumaleidae. Of less significance, Miller *et al*. (1997) placed Simuliidae as sister to Dixidae, but the study suffered significantly from lack of Thaumaleidae in the taxa analysed. A Thaumaleidae + Simuliidae sister relationship was well supported by the molecular study of Moulton (2000). That relationship was again well supported by Bertone *et al*. (2008) who examined multiple nuclear genes from a wide sweep of lower Diptera. Indeed, they suggested a new superfamily for Thaumauleidae + Simuliidae, the Simulioidea.

Of relevance to this is that Mandaron (1963) in a study of eggs and larval instars of Thaumaleidae showed that the eggs are slightly triangular in shape. Adler *et al*. (2004) suggested that a distinctly triangular-shaped egg was unique to Simuliidae. Further, Mandaron (1963) showed that thaumaleids have 14–20 larval instars — very unusual for lower Diptera, where 4 is the norm. Is it surprising, then, that Simuliidae have been recorded as having between 6 and 11 larval instars, with 7 the mean number (Crosskey 1990; Colbo 1989). Not only that, but structures and chaetotaxy of the labrum of Thaumaleidae larvae appear homologous to those of the early instars of the primitive simuliid *Crozetia* Davies (Craig 1974; Craig *et al*. 2003; Craig 2005; Craig unpub. pers. obs.).

Wiegmann *et al*. (2011), in a major authoritative review of evolution of Diptera based on molecular and morphological evidence, placed Simuliidae + Thaumaleidae as sister to Chironomidae + Ceratopogonidae, in good concordance with much of the above previous work.

The family Simuliidae is overwhelmingly now arranged as 2 subfamilies (e.g., Takaoka 2003; Adler *et al*. 2004; Adler & Crosskey 2012). One, the Parasimuliinae, has but a single genus, *Parasimulium* Malloch, which consists of 4 species considered basal simuliids (Currie 1988, Moulton 2003, Adler *et al*. 2004). The other, the Simuliinae, consists of two tribes, the Prosimuliini, and Simuliini. Within the latter Crosskey (1990), Crosskey & Howard (1997), and Crosskey (1999) previously recognised only the genera *Austrosimulium* and *Simulium*, all others were placed in the Prosimuliini. Now, however, a more restricted interpretation of Prosimuliini is used with some genera from that subfamily now assigned to Simuliini (Adler *et al*. 2004; Adler & Crosskey 2012). Within Simuliini *Simulium* is the most taxon rich genus and is widespread. Although that genus and its segregates do not occur in New Zealand, they have reached New Caledonia, Fiji, Polynesia, Australia, Tasmania, and Norfolk Island (Takaoka 1996).

Composition and relationships of the endemic Simuliidae (*Austrosimulium*)

It was Tonnoir (1925) who noted that the simuliids of New Zealand and some of those in Australia formed a segregate distinct from the genus *Simulium* Latreille. In erecting the genus *Austrosimulium*, Tonnoir explicitly noted that adults of the segregate possessed 8 (rarely 7) articles on the antennal flagellum, and in his descriptions and figures drew attention to the presence of an interarm (basal) strut on the anal sclerite of larvae and the frequent occurrence of a horned condition in the pupal gill.

Austrosimulium has been well accepted by subsequent workers, the majority of whom afforded it generic status. Edwards (1931) was the first to recognise the possible relationship between a South American simuliid and *Austrosimulium,* but he considered the segregate was merely a subgenus of *Simulium*. He noted the double bend of wing vein CuA_2, the anal vein A_1 that curved but did not reach the wing margin, 8 antennal flagellomeres, and a normally developed hind tibia.

Smart (1945) on the basis of Edwards (1931) associated *Austrosimulium* with *Gigantodax* in the tribe Austrosimuliini.

The Australian *Austrosimulium* were dealt with in a series of major works by Mackerras & Mackerras (1949 *et seq*.), who extended our knowledge and definition of the genus. They recognised 3 endemic species-groups — *mirabile* Mackerras & Mackerras, *bancrofti* (Taylor), and *furiosum* (Skuse) — basing the species-groups on morphological character states from pupae and adults. They considered the New Zealand fauna to be related to the *mirabile* species-group. Dumbleton (1963b) using other pupal characters as well as those of cocoons, recognised that the *australense* and *ungulatum* species-groups were precinctive to New Zealand. Although there were 4 species undescribed, his 1964a: 36 (his Fig. 1) showed distribution in the South Island, pupal gill structure, and cocoons. He transferred 2 Australian species originally placed in the *mirabile* species-group by Mackerras & Mackerras (1949) into the *ungulatum* species-group (Dumbleton 1963b: 335, his Fig. 2). Thence, this latter group is the only one common for the two countries. Crosskey (1969) in a major reanalysis of simuliids, concentrated mainly from Africa, reaffirmed the validity of *Austrosimulium* within Simuliini, again noting the close relationship to *Simulium* Latreille s.l.

Dumbleton (1960) in an examination of previously unknown larval material of the then *Austrosimulium anthracinum* (Bigot), from Tierra del Fuego, was of the opinion that there was no strong affinity with *Austrosimulium*, but rather that *A*. *anthracinum* would eventually be assigned to *Gigantodax* Enderlein, or another genus.

Wygodzinsky & Coscarón (1962), in a detailed character analysis of *A. anthracinum* and other South American simuliids, however, disagreed with Dumbleton's conclusion. While recognising infrageneric segregates within *Austrosimulium,* they assigned it subgeneric status as *Austrosimulium* (*Paraustrosimulium*) *anthracinum*. Crosskey (1969), however, considered *Paraustrosimulium* should be considered a genus: later workers agreed (e.g., Gil-Azevedo & Maria-Herzog 2007; Coscarón *et al*. 2008; Adler & Crosskey 2012).

Dumbleton (1963b), in an assessment of relationships within Simuliidae, reexamined the question of placement of *A. anthracinum.* He was equivocal regarding its assignment to *Austrosimulium*, noting a number of apomorphic features not found elsewhere in that genus. He further noted that 2 Australian species, *A. bancrofti* and *A. furiosum,* formed a segregate with affinities to *Paraustrosimulium*. To resolve the problem of modifying the diagnosis of *Paraustrosimulium* to accommodate those 2 Australian species, in 1973 he erected the subgenus *Novaustrosimulium* for them, resulting in 3 subgenera—*Austrosimulium*, *Novaustrosimulium,* and *Paraustrosimulium*—as comprising the genus *Austrosimulium*.

Davies & Györkös (1988) described the 2 Australian species *Paracnephia pilfreyi* (as *Cnephia*) and *Austrosimulium colboi* and briefly discussed the provisional placement of these two unusual simuliids. There are unpublished notes by the authors (in possession of DAC) relating to that 1988 publication, which give a more detailed comparison of these 2 species to Australasian and South American simuliids. In the 2008 edition of the world black fly inventory Adler & Crosskey placed *Paracnephia pilfreyi* in the subgenus *Procnephia* Crosskey, but in 2009 considered it unplaced to subgenus and this has remained so (Adler & Crosskey 2012). Placement of *A. colboi* is equally uncertain and it is still unplaced to subgenus (but see Bugledich 1999), possessing a mixture of characters across current subgenera. Of note, however, is that the pupal gill of *A. colboi* is remarkably similar to that of the putative sister taxon to *Austrosimulium*, the South American *Paraustrosimulium*, having 2 annulated inflated horns and no filaments. Further, *A. colboi* males possess a well developed plate-like paramere (DAC, pers. obs.), similar to that of *P. anthracinum* and which is absent from *Austrosimulium*. We comment on this later (see Cladistic Analysis, p. 53).

Moulton (1997), in a general molecular overview of Simuliidae that included Australian members of *Austrosimulium* (*Novaustrosimulium*), *Paracnephia* Rubtsov (as "*Cnephia*"), and the South American *Paraustrosimulium anthracinum,* proposed a cautious hypothesis of phylogenetic relationships. Pertinent here was a lineage in which *P. anthracinum* plus *A. colboi* (unplaced to subgroup), was sister to *Paracnephia pilfreyi*. This was part of an unresolved clustering of "intermediate" simuliines that included other *Paracnephia*. The 2 *Novaustrosimulium* species, however, grouped 4 nodes below that lineage and were basal in the Simuliini. The lineage of *Paraustrosimulium, Paracnephia,* and *A. colboi* was supported in other scenarios he examined. After further consideration Moulton (2000) made no changes to the above scenario. There is no disagreement between the findings of Moulton and those of Davies & Györkös (1988).

However, the above placement of the 2 *Austrosimulium* (*Novaustrosimulium*) species is in some contradiction with morphological evidence (Adler *et al*. 2004). For example, *Austrosimulium* possesses a pedisulcus on the hind leg, normally associated with "higher" simuliines and which is lacking in "lower" simuliines. Moulton's placement would require evolution of the pedisulcus more than once.

Moulton (2003) again attempted the reconstruction of relationships for the Prosimuliini and Simuliini. As in his preliminary work, a tentative "best estimate" of such relationships also placed *Novaustrosimulium* sister to the rest of the Simuliini. He suggested, however, that that might be the result of "long branch attraction" which can cause misplacement of lineages. His original grouping and placement of *A. colboi*, *Paraustrosimulium anthracinum,* and *Paracnephia pilfreyi* were again fully supported.

Gil-Azevedo & Maia-Herzog (2007) in a preliminary phylogenetic analysis of simuliid genera of the Southern Hemisphere, using morphology, showed strong support for the subgenera *Austrosimulium* + *Novaustrosimulium* as sister to *P. anthracinum,* with *Cnesiamima atroparva* (Edwards) sister to those. For the present we consider *Paraustrosimulium* and *Austrosimulium* to constitute related genera.

The simuliid fauna of New Zealand all belong to the subgenus *Austrosimulium* which also occurs in Australia. Subgenus *Novaustrosimulium*, however, is precinctive to Australia.

In his revision of *Austrosimulium* Dumbleton (1973) segregated New Zealand's *Austrosimulium* species into an *australense* species-group and an *ungulatum* species-group, and these species-groups were both further subdivided. The species-groups and subgroups he erected still apply and have been further substantiated by morphological analysis and, with minor differences, molecular analyses (p. 61).

The *australense* species-group, which comprised the majority of species, was distinguished by the female lacking a basal tooth on the tarsal claw, the pupa lacking ocular setae, the cocoon lacking an anterior projection, and the larva with the accessory sclerite expanded on the semicircular sclerite. Constituents of the *ungulatum* species-group typically possessed in the female a basal tooth on the tarsal claw, a pupa with ocular setae, a cocoon with anterior projection(s), and the larva without the expanded accessory sclerite.

The 2 subdivisions of the *australense* group of species were the *australense*-subgroup (*A. australense, A. longicorne*) that have a shallow convex cephalic plate on the pupa, and the *tillyardianum*-subgroup (now comprising *A. albovelatum, A. alveolatum, A. dugdalei, A. extendorum, A. fiordense, A. laticorne, A. multicorne, A. stewartense, A. tillyardianum*) with a markedly concave cephalic plate. Within the *ungulatum* species-group, the *ungulatum*-subgroup (now comprising *A. campbellense, A. dumbletoni, A. ungulatum, A. vailavoense, A. vexans*) lack a horn on the pupal gill and the gill filaments are thick and stiff, and the semicircular sclerite of the larva has a slight expansion on its ends (larvae and pupae of *dumbletoni* and *vailavoense* unknown). The *unicorne*-subgroup (now comprising *A. bicorne, A. tonnoiri, A. unicorne*) have in females a small basal tooth on the tarsal claw, absent often in *A. unicorne*, possess a distinct horn to the pupal gill with numerous fine filaments, and the semicircular sclerite tapers finely with no expansion.

Early European references to New Zealand simuliids

The earliest European reference to New Zealand Simuliidae is that by Joseph Banks, botanist on James Cook's first voyage (1768–1771). His journal entry for 30 March 1770 stated "… sandflies maybe exactly the same as those of North America… . Of these last however, which are most Justly accounted the curse of any countrey where they abound, we never met with any great abundance; a few indeed there were in almost every place we went into but never enough to make any occupations ashore troublesome, or to give occasion for using shades for the face which we had brough[t] out to defend ourselves from them" (National Library of Australia 2004a). This appears to be the first written use of "sandflies" for New Zealand simuliids. Beaglehole (1963, vol. 2: 6) provided a footnote to this entry by biologist Averil Lysaght (Thomson 2010) which stated "The sandflies are *Austrosimulium* spp." As Beaglehole commented in another accompanying footnote, such a balanced account was no doubt due to Banks being unable to go ashore at Dusky and Doubtful Sounds, Fiordland as he wanted (see Beaglehole 1963, vol. 1: 473; and Cook's journal (National Library of Australia 2004b)). The few landings made on this voyage were mostly during the middle of the day rather than early morning or before sunset, and they did not venture far inland.

On Cook's second voyage (1772–1775) 6 1/2 weeks were spent at Dusky Sound, Fiordland, and the West Coast black fly, *Austrosimulium ungulatum* Tonnoir, came to their attention. Cook's (1777: 99) journal entry for 11 May 1773 summing up the visit noted that "The most mischievous animals here, are the small black sand flies, which are very numerous, and so troublesome, that they exceed every thing of the kind I ever met with. Wherever they bite they cause a swelling, and such an intolerable itching, that it is not possible to refrain from scratching, which at last brings on ulcers like the smallpox". Cook's quote is provided in a slightly different form in White & Doubleday (1843: 190), and editing changes were made by Beaglehole (1961: 136–137) based on Cook's manuscript journal rather than published account, which were repeated in Dumbleton (1973: 494), e.g., "sand flies" to "sandfly", "very numerous" to "exceeding numerous", and "Wherever they bite" to "wherever they light". Beaglehole again provided a footnote prepared by Averil Lysaght that expanded Cook's mention by explaining "Cook, it must be allowed, speaks with great moderation of this pest, writing as he was in pre-dimethylphthalate days. It was *Austrosimulium* sp., whose larvae breed in running water; the adults are not uncommon throughout New Zealand, but abound multitudinously in the Sounds district."

Cook's opinion was supported by the comment of (Johann) Georg Forster (1777: 135–136), a junior naturalist on that second voyage who wrote for Dusky Sound 3–5 April 1773: "Another rainy pause of three days followed this excursion, confining us to our ship, where a sort of little crane-flies (*tipula alis incumbentibus*), which had plagued us ever since our entrance into Dusky Bay, became remarkably troublesome during the bad weather. They were numerous in the skirts of the woods, not half so large as gnats or mosketoes, and our sailors called them sand-flies. Their sting was extremely painful, and often as the hand or face grew warm, caused a troublesome itching, the least irritation of which brought on a very violent swelling, attended with great pain. We were, however, not all equally affected; myself in particular, never felt any great inconvenience from them; others, on the contrary, suffered in a very violent degree, especially my father, who could not hold a pen to write down the common occurrences in a journal, and fell into a high fever at night. Various remedies were tried, but all proved ineffectual, except the simple unction with soft pomatum, and the constant use of gloves." This journal entry of Forster appears to be the first written record that not all were equally affected by the New Zealand simuliids, even among family members.

There are numerous accounts of the travails of New Zealand's early European travelers in dealing with biting *A. australense* (Schiner) in the North Island in the 1830s and 1840s. The account by Angas (1847: 21, 23; see frontispiece) is but one. Polack (1838: 319) noted that "The most disagreeable, in their acquaintance, is the *namu*, or sand-fly; these little insects are mischievously troublesome; they have no particular choice as to what part they alight on the human body—the forehead or the ankle. They contrive, with their minute invisible feelers, to make a small puncture, which soon swells, causing an itching almost intolerable. These diminutive flies are easily killed, but are seldom caught, until they are engorged with the blood of their victims. The namu are most numerous on the borders of streams or marshy places, and appear in myriads before rain. These insects are absolutely cruel to the ladies, whose apparel is of a less guarded nature to that worn by the opposite sex." Yate (1835: 72) wrote "… with a small sand-fly, not larger than a flea, but very noxious—its bite is sharp, and leaves an unpleasant itching for many hours—and they are so numerous on the beach, and by the sides of creeks and rivers, as to become, at times, almost a pest: their bite is most virulent before rain." This account was probably about *A. australense* in the Northland or Auckland area of the North Island. Others accounts are given in *Te Ara – the Encyclopedia of New Zealand* (Walrond 2009).

South Island accounts are mainly about the species *A. ungulatum* in the Fiordland area, in areas near where Cook landed in 1773 during his second voyage. Of note is an account of Carl Björk (1880–1952) who lived in Preservation Inlet, Fiordland (Dougherty 2010). He kept the simuliids at bay by periodically rubbing his face with a mixture of rancid butter and kerosene, or grease and Jeyes Cleaning Fluid! An observant and most informative account of vast numbers of simuliids biting on Pigeon Island in the Fiordland region is by pioneering conservationist Richard Henry (1896). He was caretaker of neighbouring Resolution Island, which in 1894 became a safe sanctuary for flightless native birds, for about a decade, through the efforts of the Otago Institute and the Otago Acclimatisation Society (Omerod 2010). In this newspaper article Henry related how he trapped tens of thousands of adults by applying corned beef fat to a warm iron chimney.

The depredations of female simuliids in New Zealand has not changed since those early days of exploration and settlement, but modern repellents work adequately provided all exposed skin is well covered when in areas of high numbers of flies, and remains covered using repeated applications as needed. In 1971 a television documentary "Once bitten …" was prepared by the Christchurch television section (CHTV-3) of the New Zealand Broadcasting Corporation, but it was not screened — images of the tourists being bitten in the Fiordland area, because they were not using repellent, were thought to be too graphic and would not be good for tourism; a copy of the script is in the NZAC archives. Nowadays a search of the internet's "YouTube" with the search string "sandflies New Zealand" will show that many people are still bitten and react badly to the bites.

A recent popular account regarding New Zealand sandflies is by Babirat (2011). Good general information is given, as well as some personal experiences of the biting.

Common names

Dumbleton (1973) discussed the use of the name "sandflies" by the naturalists and crew on Cook's voyages. Elsewhere in the world simuliids are usually referred to as "blackflies", "black-flies", or more so now, "black flies". Crosskey (1990) examined the use of those terms closely and Adler *et al*. (2004) listed some 28 common names for simuliids in North America. A worldwide "Blackfly Vernacular Names" can be found at http://www.blackflies.objectis.net/NamesZW/. The Oxford Dictionary defines "sandflies" as a small fly or midge, especially one belonging to the genus *Simulium*, and cites the use of the common name in this sense in Anson's (1748) "Voyage around the World". This common name probably originated because of the frequent abundance of biting Simuliidae on beaches. Crosby (1973b) noted that it is not at all clear that Anson was referring simuliids. The main problem with use of the term "sandflies" is that elsewhere in the world this is used to refer to biting Psychodidae, often of medical importance because of transmission of disease organisms. Still, the usage has persisted in New Zealand where "sandflies" is the universally employed common name for these insects. This causes no confusion, since there are no biting Psychodidae present in New Zealand, and though there is a single small biting midge (Ceratopogonidae) of localised distribution on sandy beaches, it is not sufficiently widely known to have acquired a common name.

Early collections of New Zealand simuliids

As Dumbleton commented, specimens of Simuliidae collected in New Zealand may have been present in insect collections that reached England at the end of Cook's voyages, but there is no record of this. The reference by Forster (1777) to the Dusky Sound pest of the second voyage as "a sort of little crane flies (*tipula alis incumbentibus*)" suggests that some entomologist had seen and attempted to classify them. We consider it is unlikely this entomologist was Fabricius, who examined the insect collections made during all three of Cook's voyages, as it would have been expected he would use the generic name "*Culex*" for them as he had done for other simuliids. For example, Fabricius (1775) listed 2 simuliid species on pages 800–801 under "*Culex*"; on pages 751–756 he listed 56 species under the genus "*Tipula*": species 1–23 were under the grouping "*Alis patentibus*" and the remaining species 24–56 were under the grouping of "*Alis incumbentibus*"; none of the species in this latter grouping was a simuliid.

The first simuliid specimens from New Zealand of which there are extant specimens were presented to the British Museum by Dr Andrew Sinclair, presumably as accession [18]45-61. Walker (1848) listed these specimens in such a manner ("*a*" and "*b*") that it appeared only 2 specimens were received in total (Dumbleton 1973: 495). The locality for "*a*" was recorded as New Zealand only, and no pinned specimens can be located at BMNH that can be attributed to this record (T. Howard (BMNH) pers. comm.). However, the "*b*" entry stated the locality was the Bay of Islands, and we were informed by T. Howard (pers. comm.) she had located the Walker "*b*" entry and found that in fact it referred to a pill-box and not a single specimen. With the unit tray containing the pill-box was a large note stating: "The pill box contains specimens reportedly collected at Bay of Islands (New Zealand) during the voyage of the "Erebus" and "Terror" and the basis for locality "b" cited by Walker (1848, List Dipt. Ins. Coll. Br. Mus. 1:113) attributed by Walker to White but never in fact published by the latter. See Dumbleton (1972, N.Z. Jl. Sci. 15:510) [caecutiens Walker nomen nudum]" (note [probably] by R. W. Crosskey, T. Howard, pers. comm.). Subsequent examination showed the pill-box contained about 450 specimens (Fig. 519–521). As Dumbleton (1973) correctly reported, Walker (1848) attributed authorship of the name *Simulium* caecutiens to White in the "Zoology of the Voyage of H.M.S. *Erebus* and *Terror*". The name caecutiens, however, was not used by White (1846) in the Insecta part of that work, but may have been a manuscript name given to Walker by White. Our further checking showed that only 5 Diptera species — but no simuliids — were recorded in the second part of the *Erebus* and *Terror* publication by Butler (1874; Rye 1876). Schiner (1868) referred to "*caecutiens*", attributed the authorship to Walker, and stated that to his knowledge no description of the insect existed. The name caecutiens is, therefore, a *nomen nudum* based on the Sinclair specimens. The *Erebus* and *Terror* were at the Bay of Islands 14 August–23 November 1841, and Sinclair arrived there from Australia on the *Favorite* on 24 October and collected with Hooker (Molloy 2010). It is not clear whether Sinclair gave specimens to his colleagues on the ships, but we consider this unlikely as no simuliid specimens were listed by White & Doubleday (1843). Some collections of the *Erebus* and *Terror* were sent back from the Falkland Islands on HMS *Arrow* after April 1842, but the *Erebus* and *Terror* did not get back until late 1843. We consider the caecutiens specimens were most likely collected in 1844 and presented to the British Museum in 1845 (see *australense* p. 104). On grounds of its greater abundance and biting habit, Dumbleton (1973) stated it seemed likely that of the two species known to occur in the locality the specimens were probably *A. australense,* rather than *A. longicorne,* and this has been well confirmed.

Specimens of the first New Zealand species to receive a valid name were collected at Auckland in late 1858, at the time of the visit of the Austrian ship *Novara*, and described by Schiner (1868) as *Simulia australensis*. The collector was not given, but we consider it was Sinclair (see *australense* p. 104). Specimens of a second species were collected on the Auckland Islands during a German Transit of Venus expedition in 1874 and subsequently described by Mik (1881) as *Simulium vexans*. The accounts of *australense* published by Hudson (1892) and Marshall (1896) added nothing new except Marshall's and later Hutton's (1902) observation that the antennae had 10 divisions (8 flagellomeres).

Studies on New Zealand simuliids since 1920s

The extensive studies of Tonnoir (1925) on the New Zealand and Australian Simuliidae resulted in a much more detailed knowledge of the structure and habits of all stages of the New Zealand Simuliidae and established the base for all later work. Tonnoir's work was directly aimed at obtaining information that might be used to control the bothersome "sandflies". Tonnoir (1925) found it impossible to separate the adults of some of the New Zealand species of *Austrosimulium*, although they were readily separable in their pupal stages.

The structure of the pupal respiratory organ of three of the New Zealand species was later studied by Pulikowsky (1929) in specimens supplied by Tonnoir. The work of Mackerras & Mackerras (1949 *et seq.*) while not concerned directly with the New Zealand simuliid fauna, established the existence of three species-groups in the Australian *Austrosimulium* fauna and thus provided valuable reference points for the recognition and definition of the species-groups present in New Zealand.

In the early 1950s there was interest from the Department of Agriculture in establishing myxomatosis virus to control introduced rabbits (Miller 1952b; and see p. 21). This interest in simuliids as potential disease vectors again focused attention on the need for accurate identification of the females of the various species of *Austrosimulium* which might serve as vectors for this or other virus diseases of man and animals that might gain entry to New Zealand. Dumbleton (1973) was able to separate the females of the 5 species in the *ungulatum* species-group, but had similar difficulties to Tonnoir in separating the adults of 5 of the then described 7 species of the *australense* species-group.

Also in the late 1950s pesticides were tested for controlling simuliids by Entomology Division, DSIR (Anon

1961), at which time it was commented "Experiments show the most satisfactory pesticide is DDT in a 5 per cent. diesel oil solution, which is applied to the stream water in spring and one month later." It was stated that care was needed in its use so as to not affect fish or fish food.

In spite of persistent search, Tonnoir was unsuccessful in discovering the breeding place and early stages of *A. ungulatum*, the principal pest species in the South Island, and the feasibility of controlling its breeding could not be assessed until this was done. Although Tonnoir collected in many localities, he devoted little or no attention to the southern half of the South Island or the higher elevations of the Southern Alps and this deficiency was one that Dumbleton sought to remedy (Dell 1951). Dumbleton (1973) later found the characteristic habitat of *A. ungulatum* to be smaller streams under heavy shade in the forest, and immature stages were never found in high density: we concur with these observations, and note obvious difficulties involved in effective control of pestiferous populations in such situations.

With this present work, the North Island can now be considered to be well collected with a good understanding of the distribution of taxa that can currently be recognised morphologically. The South Island is also mainly well collected, but large areas of Fiordland are still to be explored, as are the high altitudes of much of the Southern Alps which may harbour new taxa of relatively restricted distribution similar to *A. unicorne* Dumbleton. Even with the surveys by Chadderton (1988, 1990), the southern parts and higher altitudes of Stewart Island are still basically *terra incognita*, in contrast to Campbell and Auckland Islands which we consider well collected. However, at both the molecular and cytological (chromosome) level, our knowledge of New Zealand simuliids remains at an early exploratory stage.

BIONOMICS OF NEW ZEALAND *AUSTROSIMULIUM*

Little is known about general biology of *Austrosimulium*. Tonnoir (1925) made little comment and Dumbleton (1973), while he dealt with Simuliidae in general, gave little for *Austrosimulium*. Works that do deal specifically with biology of *Austrosimulium* are those of Towns (1976 *et seq.*) for *A. australense* and Crosby (1974a, b) for *A. tillyardianum*. Crosby (1974a) provided details for *A. tillyardianum* immature stages that included methods for separating the nine larval instars using morphological characters and measurements, aspects of larval biology, and the changes in population structure in relation to both water levels and the territorial behaviour of larvae that determined the availability of attachment sites. Pendergrast & Cowley (1966) gave a brief, informative account of the general life cycle and the four stages of *Austrosimulium*, including the eggs. They provided a page of figures probably based on *A. tillyardianum* given the pupal gill structure and comments about larval preferences for hard substrates: however, a drawing of a larva on a rock inaccurately portrayed the labral fans as directed towards the substrate. Since these earlier works, *Austrosimulium* is mentioned in numerous ecological studies, e.g., Collier & Winterbourn (2000) on New Zealand stream insects, however usually briefly and unidentified to species.

Adults

For most people, it is the biting of the female adult that captures attention, but few species actually bite humans (see species descriptions for details). In the North Island it is generally *A. australense* that is bothersome, although *A. tillyardianum* is also to some extent. Neither species tends to fly far from running water. *Austrosimulium longicorne,* sporadically distributed in North and South Island, is not known to bite. In a major review of host location by female simuliids, Sutcliffe (1986) broke the flying behaviour of the females into 3 parts: (1) post emergence, (2) non-oriented flight driven by endogenous activities and hunger, and (3) host-location proper, where long-, middle-, and close range (including post-landing activity) behaviours are involved. These behaviours involve attraction to exhaled carbon dioxide (CO_2), visual, and thermal cues. In New Zealand CO_2 released slowly from a gas cylinder does not attract *Austrosimulium* (TKC pers. obs.). For some simuliids, notably those attracted to birds, chemical cues along with CO_2 are involved (Adler *et al*. 2004).

The thermal cues involve infrared radiation and probably the shape of host contrasted against the background. Consequently the colour of clothing is important, with lighter shades providing some protection (see Crosby 1992; Orr 1996). The earliest record known for New Zealand is an informative newspaper article by Richard Henry (1896), who commented on the fact that light coloured clothing was less attractive — this is possibly the first written observation on this aspect of behaviour for simuliids.

Attraction to various colours by female simuliids was examined in detail by Davies (1951, 1961, 1972) who well showed that dark blue attracted the most flies and white and lighter colours the least.

Crosby (1988) noted that there was variation in numbers of *A. ungulatum* and *A. dumbletoni* attracted to moulting, individually-caged, Fiordland crested penguins. He also noted that ducklings, humans, and penguin odour were equally attractive to *A. ungulatum* when moulting penguins were present, but that virtually no *A. dumbletoni* females were attracted to these others in the presence of moulting penguins, indicating that *A. dumbletoni* was host specific to Fiordland crested penguins. We can report that *A. dumbletoni* females are attracted to humans in the absence of moulting penguins, but do not bite. Allison *et al.* (1978) noted that there were 2 peaks of biting by *A. ungulatum* on captive penguins: one peak just after dawn and the other peak before sunset. This is well known for other simuliids elsewhere (Crosskey 1990; Adler *et al*. 2004).

The blood ingested by a female simuliid is used to produce eggs and in general insects that blood-feed are categorised as "anautogenous". Those that do not blood-feed are "autogenous" and use nutrients carried through from the larval stage into the adult to produce eggs: therefore the importance of optimal feeding in the larval stage (see below). More eggs can be produced if a blood meal is taken. Of considerable importance is that *Austrosimulium* (certainly *A. tillyardianum*) can process the lymph of blood rapidly and extrude that as a diuretic fluid, allowing concentration of the more nutritive blood cells (see Frontispiece). This phenomenon has not been reported for *Austrosimulium* previously and otherwise not for simuliids either. It is, however, well known for other blood- or fluid-feeding insects (Chapman 1998).

For some simuliids and other biting flies the above behaviours are obligatory, but for others they are facultative and females will take blood meals opportunistically when possible. We surmise that *Austrosimulium* species that blood feed are of the latter kind. Still, there are many places in New Zealand where simuliids can be commonly found in large numbers in running water, but the adults do not bite, or do so in far fewer numbers than would be expected, giving rise to the possibility that there are sub-populations that do not blood feed. Whether an *Austrosimulium* species is a blood feeder, or not, can be partly judged by the size of the sclerotised abdominal tergites. These are large in the known non-blood-feeders (*cf* Fig. 70, 72). Smaller tergites presumably allow the abdomen to expand farther. Therefore, size of tergites can be used to suggest whether a species is autogenous or not (Rubtsov 1989; Dumbleton 1973).

An adult that has not laid eggs is known as "nulliparous". One that has laid eggs, whether or not it has blood-fed, is "parous", and eggs laid leave follicular remnants in the ovary, so the number of times the ovarian cycle (gonotrophic cycle) has occurred can be determined (Crosskey 1990; Adler *et al*. 2004). Some simuliids are known to repeat the gonotrophic cycle up to 6 times and are termed "multiparous". Little is known about the number of gonotrophic cycles for *Austrosimulium*, apart from those biting the Fiordland crested penguin (*Eudyptes pachyrhynchus* Gray), and infected with *Leucocytozoon tawaki* Fallis, Bisset & Allison (Craig & Crosby 2008). Transmission of *Leucocytozoon* requires at least a "biparous" situation — ingestion of blood with the leucocyte, production of eggs, oviposition, then another blood meal to transmit the parasite back to penguins.

The above discussion on blood feeding leads to two common questions; first, "What do simuliids bite when I am not around?", and second, "What did simuliids feed on before humans arrived in New Zealand?" Both are interlinked.

There is now substantive evidence that a claw with a basal tooth is a plesiomorphic condition (Currie & Grimaldi 2000) and that this equates with blood feeding on birds (Malmqvist *et al*. 2004). If *Austrosimulium* conforms to this pattern then it would be expected that members of the *ungulatum* species-group, which in large part possess a basal tooth on the claw, would be ornithophilic. However, apart from the reports of *A. dumbletoni* and *A. ungulatum* biting the Fiordland crested penguin, (e.g., Craig & Crosby 2008), there is little definitive scientific literature to indicate that this group of simuliids is, in New Zealand, bird feeding, even on poultry flocks. Instead, *A. ungulatum* is the scourge of humans in parts of the South Island and Stewart Island — clear evidence that ornithophily is not obligatory, and feeding on humans is opportunistic. This is in agreement with some of the findings of Malmqvist *et al.* (2004) for Scandinavian simuliids. Not well documented is that *A. vexans* on the Auckland Islands will, if possible, bite humans — thence its name (see p. 157). Henry (1896) made some useful observations regarding simuliids and the Māori around the time Europeans arrived in Fiordland, and speculated how Māori may have protected themselves from being bitten by covering their exposed parts with grease. But, an answer to the first question is probably, in part — "A bird if one can be found, or nothing if a bird or human is unavailable".

The second question, regarding food source before humans were available, is more substantive and primarily relates to the indigenous vertebrate fauna of New Zealand. Possible blood sources prior to arrival of humans were restricted to bats, seals, and birds. Tuatara (*Sphenodon*), leiopelmatid frogs, skinks, and geckos were probably not greatly involved, if at all, even when more widely spread than present day. Of note, though, is that *Sphenodon* uses bird burrows for shelter. Accounts of the vast number of birds originally in New Zealand and the "dawn chorus" are numerous. Worthy & Holdaway (2002) referred to New Zealand as "the land of birds". However, earlier, Holdaway (1989), rather pointedly noted that by the time Europeans arrived in New Zealand, the avifauna was but a battered remnant of that of pre-human times. Similarly, the southern fur seal *Arctocephalus forsteri* (Lesson), widespread around New Zealand, was used extensively by Māori and slaughtered in vast numbers by Europeans in the 1800s and its population is now estimated to be a mere 10% of the original (Phillips 2009). Henry (1896) also considered that seals would be a major food source for simuliids. Bats (*Mystacina*) were also much more common than at present (Holdaway 1989). Was this sparse list of vertebrate species the blood source for *Austrosimulium* prior to arrival of humans? It must have been so.

There is now, however, evidence (Worthy *et al*. 2006) that there were Miocene crocodilians and mouse-sized mammals in New Zealand before what is often referred to as the "Oligocene transgression" (25 Mya), when New Zealand was in large part, or even completely, submarine (Campbell & Landis 2001). There is no reason why such animals could not have been food items for simuliids and certainly, exquisite fossils of larval simuliids from Australia are known for the Lower Cretaceous (135 Mya) (Jell & Duncan 1986). But, this may not be the case for New Zealand, since our study here indicates *Austrosimulium* did not arrive until well after the Oligocene transgression (p. 60, 66, 86).

Another question not commonly asked, but of considerable interest, involves the ready access of female *Austrosimulium* to blood meals, notably that from humans. As discussed elsewhere, blood meals are used to produce eggs, so "Are there more simuliids in New Zealand now than before humans arrived?" A superficial answer to that would be yes, but it may be more complex. It is known (see Control section p. 30) that application of insecticides to farmlands can, via runoff, significantly alter aquatic invertebrate populations in streams (Hopkins *et al*. 1966; Stout 1975): thus, with apparent loss of predators, simuliids reoccurred in vast numbers. There is also the expectation that with enrichment (eutrophication) of waterways from fertiliser running off from farmland filter feeders such as simuliid larvae would increase in number. So, as a result of human interaction, there may well be more simuliids in some places in New Zealand.

The term "sandflies" is well chosen, because these insects are commonly a problem on beaches and at river mouths. Is this because they are searching for sea birds and seals? Maybe, but again, apart from the three species of *Austrosimulium* known to bite Fiordland crested penguins (Fallis *et al*. 1976; Craig & Crosby 2008), no scientific literature indicates that the large flocks of birds, or even seals for that matter, that still exist along New Zealand's coastlines are bitten by simuliids. Related to this, a major die-off of yellow-eyed penguins (*Megadyptes antipodes* (Hombron & Jacquinot)) on the Otago Peninsula (1989–1990) was deemed not be caused by simuliids (Gill & Darby 1993). So, it can only be assumed that birds and perhaps seals provided blood meals to female *Austrosimulium* in pre-human times, but this assumption can be made with a certain amount of assurance, because there was little else.

Currently, with abundant livestock from country-wide farming operations, it might be assumed that biting by simuliids would be serious, thence well investigated and reported. There are, however, few data on the effects of New Zealand *Austrosimulium* on introduced animals. In Australia, however, there is a small, but definitive literature mainly for the subgenus *Novaustrosimulium* Dumbleton. McCarthy (1961) noted that *A.* (*N.*) *pestilens* Mackerras & Mackerras caused deaths in macropods (e.g., wallabies) by biting around the eyes and blinding them so they dehydrated, or starved to death. He also noted, in passing, earlier reports of severe effects on humans, livestock, and pets. Lee *et al.* (1962) in an examination of Australian biting flies as possible disease vectors, were of the opinion that while *A. pestilens* was spectacular at times in its attacks on domestic animals, *A. bancrofti* was more likely to be a potential vector of livestock diseases.

Muller & Murray (1977) trapped *A. pestilens* females from live sheep, along with numerous other species of biting flies. Other adults of *A. pestilens* and *A. bancrofti* (Taylor), captured from resting places, were shown to have taken blood meals from marsupials, oxen, sheep, and goats. They commented that major attacks by *A. pestilens* could result in deaths of livestock and macropods.

A considerable suite of wide-ranging work on the two main Australian pest simuliids was done by Hunter & Moorhouse (1976b) and particularly Ballard (1988 *et seq*.) and coworkers (Ballard and others, 1988 *et seq*.). Apart from Ballard's cytological and molecular work mentioned elsewhere, investigations were made into host finding behaviour of *A. bancrofti* females and colonisation of substrates by larvae. Of interest here is the strong probability of at least 8 sibling species comprise the currently recognised *A. bancrofti*. Such a number of probable sibling species probably contributed to the differences found by Ballard in host finding behaviour of various populations of *A. bancrofti*.

Tang *et al*. (1996) examined the 16S rNA gene of nine species of simuliid known to transmit *Onchocerca*. One was *A. bancrofti,* the remainder *Simulium* species. Little was said about *A. bancrofti*, except that it was shown to be sister to *Simulium*.

For New Zealand, the first known listing of arthropods that affected humans and livestock was that by Helson (1956). Only *A. australense* and *A. ungulatum* were recorded as biting humans, and none were recorded as biting livestock of any type! Johnstone *et al*. (1992), however, investigated a series of incidents involving dermatitis in domestic cats in Nelson, and suggested that it was probably the result of biting by *A. australense*. However, while that may be so, it is more likely to have been bites from *A. tillyardianum,* larvae of which occur in astronomical numbers in the Maitai River (Tonnoir 1925; DAC pers. obs.) and may have been one reason for the early attempts to control simuliids in Nelson (see below p. 32). Johnstone *et al*. (1992) also noted that the cat dermatitis was quite similar to that on sheep on the West Coast after exposure to high densities of *A. ungulatum*. Orr (1996), a veterinarian, in a small publication on New Zealand *Austrosimulium*, noted that adults fed on owls, cranes, raptors, and small birds, such as starlings and thrushes — feeding on nestlings as well as older birds. She also noted that cattle, horse, sheep, and goats were all bitten, sometimes badly. There is, unfortunately, no attribution for this information. Henry (1896), on the other hand, was quite definite regarding the depredation of simuliid females on his dog, the impetus for his ingenious control method for the adults. More recently only *A. australense*, *dumbletoni,* and *ungulatum* are listed as ectoparasites of New Zealand vertebrates (Tenquist & Charleston 2001) and then, again, only for Fiordland crested penguins.

Still, biting by simuliids is of concern, in part because of the numbers biting humans, and especially their greater effects on those not previously bitten — tourists. TKC has often recorded biting rates equivalent to over 1000 per hour in many localities, especially just before sunset or before rain: on one occasion in February 1977 at Jackson Bay, South Westland he collected 360 specimens (nearly all *A. ungulatum*) in the act of biting his exposed arms and legs in 5 minutes, giving an equivalent biting rate of about 4000 per hour. Mackereth *et al*. (2007) in a review of potential vectors and vector-borne diseases in New Zealand listed *A. australense* and *A. ungulatum* as "medium threat", because the flies could harbour and transmit protozoans and filaroids. They noted, however, that *A. ungulatum* had been shown to not be the vector of Whataroa virus, found in south Westland, now known (Derraik & Maguire 2005) to be transmitted by endemic mosquitoes. An outbreak of psittacinepoxvirus in imported rosellas (*Platycerus* sp.) was blamed on simuliids, as was an outbreak of poxvirus in shore plovers (*Thinornis novaeseelandiae* (Gmelin)) at Pukaha Mount Bruce (Gartrell *et al*. 2003).

The ability of simuliids to transmit disease causing organisms was investigated when myxomatosis of rabbits was introduced unsuccessfully into New Zealand in the early 1950s (Miller 1952b) and was further considered for later attempts with other haemorrhagic rabbit diseases. Gurr (1953) speculated in his review that simuliids and mosquitoes could possibly act as mechanical vectors. This brief review was prepared by Gurr using his own personal observations and the Entomological Research Station files of Dumbleton. It might be expected that Dumbleton would have written this review, but in May 1952 Dumbleton left Nelson, where he had been based as entomologist since 1929, to take up a 3-year post with the South Pacific Commission, Noumea, as Plant and Animal Quarantine Officer. The trials to establish myxomatosis proved unsuccessful as there were no appropriate vectors, as was the case in the 1980s when it was rumoured that myxoma virus had been illegally imported (Parkes *et al.* 2002). Crosby & McLennan (1996) when considering potential vectors of rabbit haemorrhagic disease virus (RHDV) were of the opinion that simuliids would not be involved. Parkes *et al*. (2001) in an examination of the epidemiology of RHDV concurred, but felt that Crosby & McLennan underestimated the possibility of transmission.

Blood meals taken are not used directly for flight energy; that is derived from sugars. There is no information on sugar sources used by either female or male New Zealand *Austrosimulium*. However, an intriguing observation was made by Baughan Wisely in the Murchison Mountains area of Fiordland in early 1953 (pers. comm. to TKC 1969): at a campsite he observed "sandflies" appearing to feed on a young shoot of a fern, suggesting that plant sap might be used as a source of nutrients as has been recorded for some simuliid species (Crosskey 1990). Of relevance here, however, are a series of studies by Hunter and co-workers on Canadian simuliids. Burgin & Hunter (1977a, b, c) showed that simuliid females and males fed both on floral nectar and homopteran honeydew secretion. The honeydew feeding was based on the crop contents containing melezitose and stachyose sugars that are unique to honeydew. Flowers and nectar are not particularly abundant in New Zealand, but in the South Island there is plentiful honeydew on southern beech (*Nothofagus* Blume) produced by two species of *Ultracoelostoma* Cockerell*,* the sooty beech scale, which is widespread in *Nothofagus* forest (Kelly *et al*. 1992). There is, however, no record of New Zealand *Austrosimulium* making use of this sugar source. Stanfield & Hunter (2010) showed that honeydew sugars affected flight performance in Canadian female simuliids. Honeydew-fed adults flew farther, but the flight speed of about 0.18 m/sec was not affected by the type of sugar meal; this speed is much slower than speeds given by Hocking (1953) and Crosskey (1990).

The distance flown by female *Austrosimulium* in search of a blood meal is of some interest, given that female adults of some species can be found long distances away from suitable breeding sites. For *A. australense,* though, the females move little laterally from the immediate vicinity of the breeding stream. Within some tens of metres from running water the rate of biting adults decreases markedly, a behaviour also noted by Dumbleton. This is in full agreement with a series of studies by Cumber (e.g., 1962) on insects associated with crops in the Rangitikei and Manawatu districts, and elsewhere. Of the thousands of insects collected, only one was a simuliid, even though there were suitable breeding sites nearby. Dumbleton (1973) remarked upon *A. ungulatum* accumulating on sea and lake beaches, with the assumption being made that they return to higher elevations to oviposit. Tonnoir (1925) never discovered the immature stages of *A. ungulatum*. It was Dumbleton who showed that the larvae and pupae were found at low density in small, cold-water, heavily-shaded streams, and we have found this too. The huge numbers of adults that occur at times indicates an ability to aggregate. Hence, we suggest that for *A. ungulatum*, and perhaps other species, there is a 3-part life-history strategy: 1 — production of adults, at low densities possibly, but from multitudinous localities; 2 — dispersal, usually downstream; 3 — aggregation at lower altitude, preferably at river mouths and beaches where there is likely to be a blood source from birds and perhaps seals. This scenario requires the blood-fed female then to find a suitable running water habitat in which to oviposit. There have been some suggestions (e.g., Rothfels 1981) that simuliids return to the natal locality to oviposit. Experiments by Hunter & Jain (2000), suggested that at least for the Canadian simuliid species they investigated, there was no return to the natal site and that any suitable waterway was used. Nothing, however, is known about this for *Austrosimulium*.

Related to the above is that the emergence of simuliids elsewhere is known to be mainly diurnal (Crosskey 1990). But again, little is known about that for New Zealand *Austrosimulium*, however, Colbo (1977) recorded that Australian *A. bancrofti* emerged mainly at sunset. Still, the informative article by Henry (1896) hinted at such periodicity. He found that after trapping almost astronomical numbers of female simuliids, the numbers during the rest of the day were much reduced, returning to high numbers the next day — was this emergence and aggregation?

The time between blood meals is dictated by rate of digestion of the meal and that, in part, is determined by temperature. Fallis *et al*. (1976) and Allison *et al*. (1978) indicated that at *ca* 16°C, digestion took 10 days. Downes (1958) noted that for most species of simuliid it is assumed a blood meal is necessary for full ovarian development; but if a blood meal is not taken, some oocytes still develop fully.

Crosby (1974a, b) from his work at Wainui, Banks Peninsula, noted that female adults of *A. tillyardianum* attracted to humans were almost all parous as indicated by follicular remnants. No males were ever collected, even though the sex ratio of reared adults was approximately 1 : 1, as in all species reared to adult in the present study. Reared females showed no ovarian development after 3–4 days, suggesting obligatory anautogeny for *A. tillyardianum*.

Of relevance here is that while simuliids generally are considered not to enter structures, Adler *et al*. (2004) recorded that some species enter nest boxes of birds. They feed on the birds and then remain to digest the meal. *Austrosimulium ungulatum* certainly enters enclosed spaces. Craig (2007, 2009) recorded incidents where large numbers of *A. ungulatum* females entered a van, fed on the occupants during the night, and then attempted to escape in the morning. That experience was substantiated a number of times, with *A. ungulatum* congregating in the wheel wells of the vehicle and biting the occupants' legs, even while the vehicle was in motion (Craig, pers. obs.): a phenomenon well-known to many New Zealand residents who have stopped their vehicles in areas with simuliids. Once again, Henry (1896) was quite clear that simuliid females (without doubt *A. ungulatum*) entered his tent in large numbers and bit. We also note here for the first time that the large collection of *A. australense* (as caecutiens) made by Sinclair in 1844 was likely to have been from a tent or similar structure as they were only slightly damaged and not blood-fed, and such numbers of this species cannot be collected by sweepnetting.

It is rare to obtain a male adult in the field. They are occasionally collected at car headlights (NZAC label data), or while light trapping for Lepidoptera. Sometimes they have been collected by sweeping, once in a Malaise trap, and once attracted to headlamps deep in a cave in the Mt Arthur area. We only have one record of an *A. australense* male collected without lights, nets, or traps (St Johns, Auckland, in sunshine while inactive on a leaf of a shrub, S. E. Thorpe, 7 Oct 2011). Normally, they are obtained by rearing pupae, thence the importance of collecting and keeping live pupae.

Oviposition and mating

The number of eggs produced by a female simuliid is variable (150–600 eggs per gonotrophic cycle) and depends in part on the gonotrophy of the fly — blood meals allow larger numbers of eggs (Adler *et al*. 2004). Eggs of Simuliidae are markedly triangular in shape, a feature unique to the family (Tonnoir 1925; Craig & Crosby 2008). Tonnoir (1925) recorded dimension of eggs of *A. tillyardianum* as 0.126 × 0.189 mm, and Crosby (1974a, b) gave the dimensions for this species as falling in the ranges 0.12–0.15 × 0.20–0.24 mm.

Crosskey (1990) categorised simuliid oviposition behaviour into 4 types: scattering, dabbing, stringing, and layering. Colbo & Moorhouse (1974; 1979) noted that *A. pestilens* scattered eggs over the water, usually during a receding flood. *Austrosimulium bancrofti* was also thought to have similar behaviour since no egg masses had ever been found. Whether any New Zealand *Austrosimulium* species scatter eggs is unknown.

Crosby (1974a, b) recorded that *A. tillyardianum* females laid between 250 and 330 eggs in a single mass 6–8 × 3–5 mm on the downstream side of a protruding rock in a riffle area, about 15–100 mm below the water surface; these observations were in full agreement with Tonnoir (1925), and would be categorised as layering using Crosskey's definition. Scarsbrook (2000), based on Towns (1976), stated that *A. australense* eggs were laid on the surface of rocks and organic material below water in batches of 200–500 eggs; TKC has normally found layered egg masses on the trailing vegetation in the water. Crosby (1974a) had eggs hatching in 6–8 days at 16–19°C; this time was shorter than reported by Tonnoir (1925) who stated that eggs of *A. tillyardianum* took 14 days to embryonate and hatch, but the difference in length to hatching could be related to the time of year the observations were made. Tonnoir (1925) described the changes eggs undergo as they matured — white immediately upon oviposition, then turning yellowish, and eventually light brown when fully mature, as in other simuliids (Crosskey 1990).

Nothing is known about male *Austrosimulium* precopulatory behaviour. This is similar to other simuliids, where also little is known (Crosskey 1990). Nothing, again, is known about the mating habits of normal adults of New Zealand *Austrosimulium*, in agreement with Adler *et al.* (2004) who commented that a least-observed facet of simuliid behaviour is that of mating. Crosby (1973a), however, while commenting on a single gynandromorph specimen of *A. australense*, noted that normal females of this species, attempting to obtain blood meals and then to escape were all mated, based on spermatozoa in their spermathecae. Copulation is known to elicit blood feeding in simuliids and other dipterans (Downes 1958; Wenk 1988). Moorhouse & Colbo (1973) observed mating swarms of *A. pestilens* to be specifically associated with riparian bushes of *Callistemon* R. Br. (bottlebrush). They noted that the preponderance of females captured had mated and that blood-fed females captured elsewhere also contained spermatozoa. Therefore, the assumption which can be made for New Zealand *Austrosimulium* females that bite, is they have already copulated, as found in other simuliids.

Where mating takes place is currently unknown for New Zealand simuliids. No mating swarms or mating on the ground (Crosskey 1990) have ever been reported. An assumption might then be made that since adults seem to leave the natal stream immediately (Crosby 1974a), mate searching and copulation takes place in local vegetation as in *A. pestilens*. It has been suggested that riparian vegetation is a habitat requirement for some New Zealand *Austrosimulium* species (Dumbleton 1973).

A mated, blood-fed female will develop eggs then needs to find running water in which to oviposit. It is known that blood-fed simuliid females do not always return to the natal stream to oviposit, and appear to be opportunistic (Lake & Burger 1983; Hunter & Jain 2000), but again nothing about this is known for *Austrosimulium*.

Larvae

As Adler *et al.* (2004) pointed out, flowing water is the life blood of all simuliids and the larvae have exploited virtually every conceivable flowing water habitat. *Austrosimulium* is no exception and larvae can be found on stones in high-altitude, low-flow trickles, to low-altitude, large, braided rivers, with trailing vegetation rather than stones being the normal substrate for some species. There is even one instance (Dumbleton 1973; this work p. 40) where larvae of *A. stewartense* and *A. extendorum* were found at high tide level where a stream flowed into the sea (Fig. 466).

In New Zealand, *Austrosimulium* larvae are almost ubiquitous in running water. However, cascades and vertical flows are one habitat that *Austrosimulium* has not managed to colonise, unlike the major radiation into this habitat by the Polynesian *Simulium* Latreille species in the subgenus *Inseliellum* Rubtsov (Craig 2003).

Simuliid larvae attach themselves to the substrate using a pad of salivary silk into which the hooks on the posterior proleg are embedded. This was illustrated for *Austrosimulium* by Tonnoir (1923a, b). The functioning of the circlet of hooks and the anal sclerite of simuliids was examined in detail by Grenier (1949) and Barr (1984). Basically, a larva bends over and secretes a pad of salivary silk onto the substrate, grips it with the hooks of the prothoracic proleg and then loops the posterior proleg hooks over and onto the pad. This is the normal method of movement. Larvae can also move, or disperse, by secreting a filament of silk into the water and then releasing from the substrate. The influence of a trailing silk filament to resettlement of the larva was investigated by Fingerut *et al.* (2006), who showed that the filament helped to grab the substrate from a greater height than otherwise would be possible in turbulent flow, and unexpectedly helped passage through pools.

Crosby (1974a) noted that first instar larvae of *A. tillyardianum* drifted downstream from the oviposition site to other slower velocity localities, drifting to higher velocity positions as second and later instars. Colbo & Moorhouse (1979) also showed that size of instar of *A. bancrofti* determined the level of velocity tolerated. Fonseca & Hart (1996) fully substantiated that dispersal of simuliid larvae was mediated by flow. In the *A. tillyardianum* study by Crosby (1974a) the number of larvae per square metre was influenced mainly by water level; floods reduced the population though movement of substrate and lower water level concentrated larvae on stones in higher velocity. Sustained low water allowed growths of algae and diatoms as well as sediment to accumulate on stones, and thence made them unsuitable for colonisation by simuliid larvae. Towns (1981a) in his study on benthic invertebrates in the Waitakere Ranges, which included *A. australense*, the only simuliid, noted conspicuous periphyton growths, even in forested reaches during spring and summer (November–February). Dense periphyton is inimical to simuliid larvae, and Towns' observation that a low density of simuliid larvae occurred at peaks in periphyton growth is in accord with studies elsewhere. Casual observations by DAC and REGC of *A. australense* in the Glen Esk Stream, Piha, which also drains the Waitakere Ranges, follow those of Towns. Larvae are at maximum density in November, but by February are reduced, concomitant with lower flows and greater growth of periphyton. In part this relates to the predilection of *A. australense* larvae for trailing vegetation. Lower flows mean that bankside vegetation is not near the water, and that which is trailing in the water is covered with periphyton, unless velocity is high. Related too is the study by Death (1996) who showed that an unidentified simuliid was one of the dominant taxa in unstable streams that had clear substrate, but that this did not apply to stable streams.

In one of his studies, Towns (1981b) used a canopy to exclude light and inhibit periphyton growth. This provided a sufficiently clean substrate that a good population of *A. australense* persisted into summer, while populations elsewhere declined as normal. His observations are in full agreement with those of Quinn (2000), Crosby (1974a), and earlier observations from elsewhere on simuliids (e.g., Chutter 1968; Casey & Ladle 1976).

An unusual study by Death (1989) examined invertebrate communities outside and inside a short cave at Cave Stream in the foothills of Canterbury. The density of *A. tillyardianum* larvae was lower in the cave and larvae drifted more. As filter feeders, though, simuliid larvae should not be as affected as browsers which rely on periphyton that is reduced in the dark. Larvae of *Austrosimulium* have previously been reported from caves, in low numbers, but with no comment made (May 1963).

A more recent detailed study by Suren & Jowett (2006) on the Waipara River, Canterbury, was basically in agreement with the above, although again the species of *Austrosimulium* was not identified. They showed a moderate (*ca* 25%) decrease in populations after floods and major increases with larvae concentrated (145%) during low flow.

Quinn (2000) noted that simuliid larvae were sensitive to UV as originally substantiated by Donahue & Schindler (1998) and others later (e.g., Kelly *et al*., 2001; 2003). It had been suggested earlier by Craig (1997) that heavy pigmentation in larvae of *Simulium* (*Inseliellum*) was protection against insolation. We too have observed this for *Austrosimulium*. Larvae at high altitude will inhabit the undersides of perched stones (Fig. 487) when possible, and tend to be pale in colour (Fig. 317). If on the upper sides of stones (Fig. 474), they tend to be darker in pigmentation (Fig. 319). Larvae at lower altitudes tend to be paler (Fig. 305), but that is not always so (e.g., Fig. 314). Factors influencing colour of *Simulium vittatum* Zetterstedt larvae have been investigated by Zettler *et al*. (1998) and colour was shown to be under environmental control.

Tonnoir (1925) commented on the interaction between a larva and others that might drift within contact range. Resident larvae would attempt to dislodge the newcomer by biting its posterior. Such behaviour by simuliids has also been observed by DAC (pers. obs.). Crosby (1974a) also noted that larger larvae were territorial and kept smaller larvae from settling nearby, this behaviour having an effect on the demography of any one population on a stone. The result of this type of behaviour is well illustrated by Serra-Tosio (1967) who found that late instar larvae kept the substrate around them clear of periphyton and other larvae, and would attack chironomid larvae. At another level, Harding & Colbo (1981) showed that both intraspecific and interspecific competition between simuliid larvae could alter distribution of larvae on the substrate. This type of phenomenon has been examined by McAuliffe (1984) and others for benthic organisms in North American streams.

Such behaviours also involve hydrodynamics of flow around the larva. This is well understood for Simuliidae (Craig & Chance 1982; Chance & Craig 1986; Currie & Craig 1988; Craig & Galloway 1988; Ciborowski & Craig 1989; Eymann 1991; Lacoursière & Craig 1993) and has been examined in considerable detail by Hart (1986, 1988), Hart & Latta (1986), Finelli *et al*. (2002) and others. Hart *et al*. (1996) even measured velocity accurately within millimeters of the larval head. They showed that there is adaptive significance to territoriality by larvae. Apart from browsing the substrate, food acquisition by larvae is by the pair of elegant labral fans supported by the head which filter waterborne particles. Larvae pay particular attention to flow around the body and through the fans, and will position themselves in relation to others to achieve optimal flow conditions. Two particular patterns result. One pattern (e.g., Fig. 455, *A. australense*) is a diamond-shaped distribution where larvae are close to one body length away from others — the pattern shown by Serra-Tosio (1969). There is evidence (Thomson *et al*. 2004) that the downstream distance from one larva to the next allows the amplitude of turbulence from the upstream larva to dampen and velocity to recover, thence the upstream larva is less of an influence on flow through the fans of the downstream larva. Another pattern is for larvae to form a row with larvae side-by-side (Chance & Craig 1986; Ciborowski & Craig 1989; Eymann 1991). This is known to increase the velocity of water between the larvae, and thence through the fans, would increase particle flux (Ciborowski & Craig 1989), and was suggested as a strategy for use when food levels were low. Although not illustrated in this work, that is a common pattern for larvae of *Austrosimulium* species, such as *A. unicorne* and *A. bicorne,* which occur at low density under stones (DAC & TKC pers. obs.). Both these species occur at high altitude in pristine waters, where concentrations of particulate matter appear to be low.

Colbo & Moorhouse (1979) noted that at high population levels larvae of *A. bancrofti* and *A. pestilens* formed clumps on stones for the former and on vegetation for the latter, echoing earlier comments on those two species by Mackerras & Mackerras (1948). All other species formed spaced distribution. In general, microdistribution of *A. bancrofti* larvae depended on age of larva, water velocity, and nature of the substrate. Horne *et al*. (1992) showed that larvae of *A. furiosum* were normally found in velocities of 0.2–0.3 m/s, whereas *Simulium ornatipes* Skuse in the same habitat in velocities of 0.9–1.3 m/s. *Austrosimulium furiosum* (Skuse) larvae were particular about the choice of microhabitat and these velocity preferences were taken as evidence for microhabitat partitioning — this difference is important when benthic sampling to ensure accurate results are obtained. For New Zealand *Austrosimulium*, even for dense populations, such as occur at times with *A. tillyardianum*, larvae are always spaced.

Where velocities could be determined during this study, larvae were rarely taken at velocities below 0.3 m/sec or above 0.8 m/sec for stone-loving species (*A. tillyardianum*, *A. multicorne*) and there was a sharp cut-off below and above these limits (see Appendix 1). The upper limit appears to relate to shear stress of the water on the substrate since that was where even a thin layer of periphyton was scoured off the substrate. This can be seen in Fig. 483 (Kowhai River, Kaikoura) where larvae were only taken from the narrow dark band of stones along the edge — those with a thin layer of periphyton. Higher velocities were recorded for species on vegetation, but it was not possible to determine the exact velocity immediately proximate to the larvae. Nothing is known regarding velocity tolerances for species (e.g., *A. unicorne, A. bicorne*) living under perched stones.

Jowett (2000) gave the mean depth for larvae of an *Austrosimulium* sp. in a small stream as 0.08 m and the mean velocity as 0.18 m/s, the latter low by our observations. He also quantified that larvae in small streams prefer higher velocity than that of the mean velocity, and we agree fully. This phenomenon allows rapid assessment of a locality for the likely presence of simuliid larvae — substrates in higher velocity are examined first.

Quinn & Hickey (1990a, b) in a New Zealand-wide survey of 88 rivers showed that maximum density of unidentified *Austrosimulium* larvae was to be found on substrates with sizes up to large cobble (128–256 mm diameter). A rationale for that was the increased complexity and provision of a three-dimensional habitat; aeration is also improved. In an earlier study Pridmore & Roper (1985) examined macroinvertebrates in runs and riffles of three North Island streams. They showed statistically that unidentified *Austrosimulium* spp. were significantly more abundant in riffles than runs in the Rangitukia Stream. Although in farmland, the stream substrate was andersite and basalt cobble usually favoured by *A. tillyardianum*, and also within its distributional range.

Boothroyd & Dickie (1991), in an examination of colonisation of artificial substrates by aquatic invertebrates, showed that while chironomids dominated the drift and substrates, *A. australense* could at times comprise up to 49% of that fauna. Drifting by simuliid larvae is a well known phenomenon (Crosskey 1990) and the initial dominance by simuliids on fresh substrates is in keeping with other studies. Similarly, Death (1996, 2000) dealt with colonisation of aquatic invertebrates after substrate disturbance. *Austrosimulium* larvae colonised readily, but were eventually replaced by more slowly colonising species. This is in full agreement with Harding *et al*. (2000) and Suren (2000), with *Austrosimulium* dominating in streams after disturbances by forestry, and their occurrence in urban milieu. In his study on *A. tillyardianum* Crosby (1970) constructed a stream deviation having a substrate of small stones, and found that larvae colonised the new substrate in 3–4 days.

Collier (1995) examined some 29 lowland waterways in Northland. While an unidentified *Austrosimulium* occurred at 19 of those sites, it was not dominant enough to determine habitat requirements. Collier *et al*. (1998) also examined physical parameters in relation to macroinvertebrate fauna in 20 lowland Waikato streams. *Austrosimulium* larvae occurred at all sites. In keeping with most other such studies, larvae were found in faster water, and a range of physico-chemical parameters, such as water depth, dissolved oxygen, and temperature accounted for the greater part of larval densities on macrophytes. As usual for most such studies, the simuliid species was not identified, but was assuredly *A. australense*.

Simuliid larvae are well known to form large concentrations at lake outlets, an explanation for which has been the availability of planktonic food material (Crosskey 1990, Adler *et al*. 2004). As part of a series of studies on lake outlets, Harding (1992) examined the physico-chemical parameters and invertebrate fauna of three lakes in Westland. There were marked differences between the inlet and outlet faunas. Along with trichopterans, chironomids, and gastropods, simuliids (unidentified) dominated the outflows, but not inlets. Similarly, simuliids dominated farther downstream: these findings mirror those from elsewhere in the world, where it has been suggested food supply and temperature are optimal in these areas. Harding (1994) then examined the benthic fauna for 20 South Island lake outlets; simuliids occurred in 16 of them. He found that natural alpine lake outlets were dominated by mayflies, stoneflies, chironomids, and simuliids. Man-made lake outlets with epilimnetic (surface) discharge also had abundant simuliids, but those with hypolimnetic (subsurface) discharge had few. Regulated epilimnetic and unregulated mid- to low altitude lake outlets were similar with moderate abundances. The percentage of catchment that was forested appeared to be important, as was the amount of regulated flow. As usual with such studies, the simuliid was not identified, but listed as "Simuliidae ungulate": since the lakes were spread over the latitudinal range of the South Island more than one species may have been involved.

Life history

Tonnoir (1925) noted that larvae of *Austrosimulium* are found year round, normally with only larvae occurring during winter months. However, low numbers of female adults of the biting species may be encountered during winter. Crosby (1974a) identified 9 distinct (and two indistinct) cohorts of larvae — a strong indication that *A. tillyardianum* had a multivoltine life history at Wainui stream, Banks Peninsula. The numbers of larvae ranged from 7 000 per m^2 in March, peaked early in April at 15 000, dropped between June and September to 2 000–3 000 and then climbed to 25 000 in November. Crosby (1975) found that *A. tillyardianum* constituted up to 45% of the aquatic fauna in the Wainui stream. Towns (1981a) in a study of aquatic invertebrates (including *A. australense*) in the Waitakere River, west of Auckland, found that simuliid larvae overall constituted less than 5% of the aquatic fauna over a full year, but were a major portion of the fauna during spring (September and October), with sharp decreases over summer and into autumn and winter. He considered *A. australense* to possess the life cycle of rapid growth, high colonisation potential, and to be probably multivoltine.

Scarsbrook (2000) incorrectly stated (as *Austrosimulium* sp.) that Crosby (1974a, b) found 2 generations for *A. tillyardianum*. Crosby stated that the species was multivoltine and gave clear evidence of that. Scarsbrook also cited more than 2 generations a year for an *Austrosimulium* sp., in Otago, but gave no further information.

Number of larval instars

Tonnoir (1925) did not determine the number of larval instars for *Austrosimulium*, but thought there were 4 or more than. Crosby (1971; 1974a, b) in his detailed study of *A. tillyardianum*, showed definitely 9 instars, in good agreement with subsequent studies of simuliids, where numbers range from 6 to 11 (Crosskey 1990; Colbo 1989). Towns (1981a) could not distinguish individual instars of *A. australense* larvae using head length; he instead grouped larvae into 4 size classes, the largest being the final instar with mature pupal respiratory gill histoblasts. Ballard (1991) suggested 7 instars for *A. bancrofti*.

Pupae

The first accounts of New Zealand *Austrosimulium* pupae were by Tonnoir (1923a, b, 1925). He recorded that when ready to moult into a pupa a larva usually selected some sheltered spot on the stone they inhabited. He commented on possible negative phototropism, since larvae on leaves normally selected the undersides to pupate. Crosby's (1974a, b) investigations of *A. tillyardianum* agreed, with pupation normally on the downstream sides of stones with emergence of adults after some 7 days. There is a variance with Tonnoir (1925) who stated that about 12 days were spent as pupae, however, he did not clarify what species was involved, although probably *A. tillyardianum* from the Maitai River, Nelson, and there may have been seasonal temperature differences.

Tonnoir (1923a) made detailed observations and illustrated the pupation process, construction of the cocoon, and emergence of *A. australense*. To settle a disagreement regarding the number of prolegs in larval Diptera, he republished his findings (Tonnoir 1923b) with additional notations. Later he noted (Tonnoir 1925) that one species (probably *A. laticorne*) completely closed the cocoon except for subsequent openings for the pupal gills — behaviour quite distinct from that of *A. australense* — and he commented that construction of other forms of cocoons would be interesting to investigate. He also noted that the typical time of day to pupate was midday, with emergence at about the same time.

In a series of studies on cocoon spinning behaviour of Simuliidae, Stuart & Hunter (1995; 1998) demonstrated that components of such behaviour as originally described by Tonnoir (1923a, b) could be used as phylogenetic characters for the family. That work culminated with an examination of *A. australense* (Stuart 2002). A cladistic analysis using cocoon spinning characters of 7 genera of simuliids placed *Austrosimulium* as the sister taxon to *Eusimulium* Roubaud + *Simulium* s.s. There was strong support for that arrangement. It was also in agreement with Dumbleton (1963b, 1973) who suggested that those taxa shared a recent common ancestry. Stuart (2002) commented that the behaviour required to produce a well formed cocoon, common to and likely homologous within *Ectemnia* Enderlein*, Austrosimulium,* and *Simulium*, allowed the pharate pupae to spin a cocoon on any substrate. This is most noticeable for some species (e.g., *A. australense*) that produce distinctly different cocoons on a flat surface, such as a leaf, in contrast to the cocoon spun in the fold of a grass leaf.

Colbo & Moorhouse (1979) observed that for *A. bancrofti* pupae, which normally have the opening downstream, as also noted by Tonnoir (1925), have the openings pointing randomly in turbulent flow. It also appeared that larvae moved to pupation sites in concert, since pupae in groups were often the same age. We have also noticed this in species that have low larval density, such as *A. unicorne* and *A. bicorne*. One must assume there is some stimulus to pupate together.

Emergence of the adults

Tonnoir (1923a, b) illustrated eclosion of an adult *A. australense* (as *tillyardi*) from its pupal cuticle. The adult is surrounded by a bubble of air and floats to the surface. Most simuliids fly away instantly, with a few species known to spend a short time resting before flying away. This phenomenon is well described by Crosskey (1990) and Adler *et al*. (2004). The adults do not get wet because the body, including wings, has a vestiture of microtrichia and microsculpture (e.g., Hannay & Bond 1971a, b). The sex ratio of *Austrosimulium,* derived from rearing studies, is close to equal (Tonnoir 1925; Crosby 1974a, b; Colbo & Moorhouse 1979; this study). It is extremely rare to capture males in the wild, and Tonnoir (1925) noted that he never captured one. Neither did Crosby (1974a, b), nor we. Indeed, sweep-netting over water was not part of our standard collection protocol, since, without exception, it produced no adults except when females were biting!

Colbo (1977) investigated *A. bancrofti* in response to a lack of information on the emergence patterns of any simuliid in Australia. Males and females emerged simultaneously with a small peak mid-morning, one just after mid-day and a major one at sunset. Colbo was of the opinion that emergence was controlled by light with temperature of the water an important factor. A similar level of detail is not known for the New Zealand *Austrosimulium*, still Tonnoir (1925) noted that emergence tended to be at midday. Similarly, the observation by Henry (1896) that after reduction of adults through trapping, numbers stayed low the rest of the day, but recovered the next day, indicates a daily emergence. That observation, no doubt, was for *A. ungulatum*.

Ecological importance

Austrosimulium in New Zealand is listed as the tenth most common aquatic invertebrate in 90%, or more, of the country's running waters examined in the National River Water Quality Network (Boothroyd 2000). We fully agree. Running waters in the North Island that lack simuliids are not common and this is also the case on Stewart Island (Chadderton 1988, 1990). Places that truly lacked simuliids were usually those that had little trailing vegetation, or leaves held against rocks by the current. Similarly, and in addition, those with unstable cobble substrate that rolled frequently in floods tended not to be inhabited. Furthermore, streams and rivers that were stable and had deeply embedded or armoured bed material, and/or had encrusting vegetation were unlikely to harbour simuliid larvae. Habitat substrate preferences of New Zealand aquatic invertebrates have been examined in some detail (e.g., Death 1996; 2000) and *Austrosimulium,* in general, was deemed characteristic of unstable substrates.

One distinct restriction to higher altitudes is that of *A. unicorne.* Dumbleton noted that it only occurred above 760 m a s l. In the Arthurs Pass and Mount Cook regions this appears to be related to the presence or absence of perched stones in a stream. With a steep slope, streams in these mountainous areas change rapidly from an erosional pool–riffle profile to a depositional braided form. The former reaches contain large stable boulders, remnants from higher water flows from deglaciation, and provide stable conditions for Blephariceridae and other members of the high altitude aquatic fauna of New Zealand (Stout 1975). The mixture of substrate sizes results in a pool–riffle sequence (Frey & Church 2009) and provides the perched stones required by *A. unicorne*. The transition from this suitable habitat and the braided profile takes place at about 700 m a s l in the Mount Cook region and somewhat higher in the Arthurs Pass environs. The sharp cut-off in occurrence of *A. unicorne* is unlikely to be solely the result of preferences for lower temperature. But, recent collection of *A. unicorne* in the Haast Pass (NZS177) at only 471 m a s l does, however, indicate that temperature may be the major environmental factor, even though the substrate was suitable.

Control of simuliids

The impetus for Tonnoir's 1925 work on Australasian simuliids was control. He stated in his opening sentences that he was hired by the Cawthron Institute to accumulate information on simuliids that would lead to eventual control. As always, "knowing the enemy" is the first step in such a project, and therefore resulted in that early taxonomy.

Dumbleton (1973) briefly discussed control of *Austrosimulium*. For reducing effects of biting adults, he suggested repellents. Little has changed since then and basically the same repellents are still effective — formulations, however, have improved. Both Crosby (1992) and Orr (1996) reiterated the obvious and that is to dress appropriately. Colour of clothing is known to make a difference (Henry 1896). Darker colours, supposedly radiating more infrared radiation, are more attractive, lighter clothing less so, but there are exception for some simuliid species elsewhere (Davies 1951 *et seq*.). Such protective measures are covered well by Adler *et al*. (2004).

Managing the size of the population of immatures is a more permanent solution and has been successful in many places worldwide. The first use of DDT on simuliids was in South America by Fairchild & Barreda (1945). This became a method of choice, particularly by WHO (World Health Organisation) for control of *Simulium damnosum* Theobald and river blindness (onchocerciasis) in Africa (Crosskey 1990), until the discovery that such chlorinated hydrocarbons were concentrated up food chains. A review of early uses of DDT on simuliids is by Chance (1970). As far as is known, DDT was never used to control New Zealand simuliids, but experiments have been carried out (Anon 1961). Hopkins *et al*. (1966) examined the effects on aquatic invertebrates of DDT prill application on farmland adjacent to connected streams and found there were major effects. There was an "enormous increase" in the number of *Austrosimulium* larvae, no doubt the result of removal of controlling predator species — Dumbleton (1945) cautioned in his article on the potential usefulness of DDT that there were also potential problems such as the removal of predators in agricultural areas.

Biodegradable organophosphates (e.g., Abate™) were substituted as control agents and are still used in some situations. Again, such measures are discussed well by Adler *et al*. (2004). In the 1970s a natural toxin produced by *Bacillus thuringiensis israelensis* (Bti) was discovered to be fairly specific as a poison for simuliid larvae, with little or no effect on other aquatic invertebrates. The alkaline nature of the larval simuliid gut is thought to activate the Bti toxin, which is known to act by lysing the midgut epithelial cells (Soberóne *et al*. 2007). Since the early 1980s, Bti has become the control agent of choice, and even though it is more expensive than artificial chemicals, is extensively used in the USA (Arbegast 1994) and elsewhere. In New Zealand, Bti has only been used experimentally against simuliids. Chilcott *et al*. (1983) showed that both *A. laticorne* and *A. multicorne* were susceptible. They suggested that *A. australense* would be a good target species since its larvae occurred in large numbers in open running water. Less possible to control would be the more serious biter, *A. ungulatum*, the larvae of which tend to inhabit smaller bush-covered streams. Goodwin (1985) also obtained good results with Bti on larvae of *A. australense* and *A. longicorne*. In a review of the status of use of Bti in New Zealand, Glare & O'Callaghan (1998), made the point that there is little reason for not using it, were it not for strict regulations in place. No control programmes using Bti are currently in place in New Zealand.

Apart from deterring the biting of female sandflies by using suitable dress, repellents, or insecticides, control of simuliids elsewhere has also been attempted using natural enemies (Laird 1981; Kim & Merritt 1988). An overview of their potential usefulness for controlling New Zealand *Austrosimulium* was provided by Crosby (1989). Worldwide, there are no examples of successful control of Simuliidae using natural enemies.

Natural enemies and parasites

Predators

Predators of simuliid adults have been well examined in general (Crosskey 1990; Werner & Pont 2003). The latter authors noted that *Austrosimulium* adults were taken along with those of the South American *Lutzsimulium* d'Andretta & d'Andretta by the asilid *Holocephala oculata* (Fabricius) (Carrera & Vulcano 1961). Their *Austrosimulium* would actually be *Paraustrosimulium* Wygodzinsky & Coscarón. Dumbleton (1973) briefly mentioned predators, noting the record of Miller (1969) that empidid adults, *Thinempis otakouensis* (Miller), took *Austrosimulium* adults. There is no other substantiated record of predation on *Austrosimulium* adults.

It might be assumed though that the blue duck (*Hymenolaimus malacorhynchos* (Gmelin)) would take *Austrosimulium* individuals as part of its diet, but there seems to be no record of that, except perhaps for that of Kear & Burton (1971) who noted dipteran adult and larval remains in the duck's droppings. Pierce (1986) recorded the occasional *Austrosimulium* in the diet of stilts (*Himantopus* spp.), as did Bisset (1976) for the paradise shelduck, *Tadorna variegata* (Gmelin). Rock wrens (*Xenicus gilviventris* Pelzeln) are reported to feed on adult black flies, but accounts are anecdotal (e.g., Google Images©, YouTube©); however, flies and other insects are part of the bird's usual diet (Troup 2009).

Crosby (1974a, b, 1975) in his in-depth study on *A. tillyardianum* showed that larvae of the trichopterans *Hydrobiosis parumbripennis* McFarlane and *Hydropsyche colonica* McLachlan were the main predators of *A. tillyardianum* larvae. *Hydrobiosis parumbripennis* ate the larvae at the same relative frequency that they occurred in the fauna, but *H. parumbripennis,* when in its later instars, ate proportionally more simuliids. There was no indication of detrimental effects on the population of *A. tillyardianum*.

Harding (1997) in a study of coexistence of larvae of two species of *Hydropsysche* Pictet (Trichoptera) examined gut contents of the main predators in the habitat. The common bully (*Gobiomorphus cotidianus* McDowall) contained 64% simuliids and a hydrobiosid trichopteran (*Costachorema xanthopterum* McFarlane) 30%. It is well established that *Austrosimulium* larvae are used extensively as prey by various fish species. McIntosh (2000) listed proportional occurrence of simuliids in guts of Canterbury galaxias (*Galaxias vulgaris* Stokell) at ~25%, bluegilled bully (*Gobiomorphus hubbsi* (Stokell)) at ~12%, longfinned eel (*Anguilla dieffenbachii* Gray) at ~24%, and shortfinned eel (*Anguilla australis* Richardson) at ~11%. As usual, the simuliids were not identified. A collection of 38 mature and near mature larvae of *A. longicorne* extracted in August 1971 from the stomach of the Canterbury mudfish, *Neochanna burrowsius* (Phillipps) from Mt Somers by P. Cadwallader: these specimens are now in NZAC.

Chadderton (1990), in an examination of aquatic communties of Stewart Island, recorded in some detail predation on simuliid larvae by the isopod *Austridotea benhami* Nicholls. The examination of gut contents of individual *A. benhami* from 8 localities showed *Austrosimulium* sp. larvae occurred at a frequency of 17.5%.

Crosby (1989) analysed in detail attempts to control *Austrosimulium* larvae with predaceous larvae of the chironomid *Cardiocladius australiensis* Freeman and up to 4 species of the dragonfly genus *Austroaeschna* Selys (Anon. 1932). The latter hard-to-find publication in the 6th Annual Report of CSIRO stated on page 23:

> ”9. Section of Systematic Entomology. — During the year Mr. A. L. Tonnoir, senior entomologist of this Section, and his two assistant entomologists, Miss W. Kent Hughes and Miss L. Graham, carried out a considerable number of economic researches in addition to their systematic work. . .
>
> (iv) *New Zealand Problems*. — In return for assistance received from New Zealand in work on *Oncopera*, oak scale, and noxious weeds control, investigations on the New Zealand sandfly problem (*Simulium*) and on the . . . During the year, 270 live dragonfly larvae and 1,200 live larvae of *Cardiocladium*, both predatory on *Simulium*, were successfully transported to New Zealand; . . .”

These attempts to introduce predaceous insects to New Zealand were briefly mentioned by Miller (1969) and Dumbleton (1973), and reported in detail by Crosby (1989). Some 1 200 *Cardiocladius australiensis* larvae were collected from the Molonglo River in Canberra and sent in 2 consignments to Nelson where they were received in late January and early May 1932. The surviving 777 larvae and 19 pupae were released into the Maitai River, Nelson, at the Council Reserve.

Earlier 6 consignments of *Austroaeschna* dragonfly larvae, totalling about 500 larvae, were sent in November 1930 and October/November 1931. They were collected in Canberra at the Cotter River below the water supply dam, and possibly also from the Molonglo River. In November 1930 2 consignments were received in Nelson, held in aquaria for about 3 weeks, then the surviving 88 larvae were released at 2 sites in the Maitai River. A consignment was also sent to E. Percival at this time, but there is no information on their survival or release at Cass. In October/November 1931 further specimens were sent to Nelson, probably in 2 consignments, but only 31 survived for release into Poorman Valley Stream. A consignment was also sent to Percival: about half survived the journey and were released at Cass at the beginning of December (Anon. 1931).

Rowe (1987) suggested the *Austroaeschna* larvae were collected in Tasmania, based on a letter written by E. Percival to J. S. Armstrong on 10 July 1957. On that basis Rowe (1987) considered the species sent to New Zealand was *Austroaeschna parvistigma* Martin. Crosby (1989) did not regard the letter as reliable evidence, as it contradicted other evidence written at the time of the importations and on DSIR files.

Austroaeschna spp. and *Cardiocladius australiensis* were sent to New Zealand because of the enthusiasm of Tonnoir, as he thought they were effective in controlling larvae in Canberra where he was then based. David Miller was then in charge of the entomology group at Nelson (which included Dumbleton), and with resources overstretched he was not keen to begin this project (Crosby 1989). The releases at Nelson were therefore done under pressure, and may not have been made in optimal areas for survival. Percival would have needed to make special trips to Cass for the releases, but it is likely they were released in more ideal places. Apparently, these attempts received considerable attention at the time (Anon 1931), but were ultimately unsuccessful.

Parasitism

Parasitoids are rife in simuliids. Adler *et al*. (2004), listed 3 families of nematodes (Mermithidae, Onchoceridae, and Robertdollfusidae), 3 major groups of fungi (Classes Chytridiomycetes, Hyphomycetes, Zygomycetes) and 1 of the straminopiles (now Chromista: Oomycota), and also helicosporidia, ichthyosporeans, protists, bacteria, and viruses, not-to-mention rarer organisms such as Gordian worms. One of the most commonly occurring parasitoids, world-wide, is the blastoclad fungus, *Coelomycidium simulii* Debais. Nematodes are sufficiently pervasive to have been proposed as control agents for pest simuliids (Laird 1981; Kim & Merritt 1988; Poinar 1990). For New Zealand *Austrosimulium,* such parasitoids as above are relatively uncommon, and with one exception (Fallis *et al*. 1976) known only from larvae (Dumbleton 1973; Batson 1983; Poinar 1990). Their rarity may be the result of a narrow ecological regime tolerated by the organisms.

In an extensive chapter on pathogens of simuliids, Adler *et al*. (2004) noted that the classification of some groups of pathogenic microorganisms is undergoing considerable change. One that is relevant here is that Microsporidia is now considered a phylum in the Kingdom Fungi (Keeling & Fast 2002; Lee *et al*. 2008). More recently McCreadie *et al.* (2011) reviewed the ecology of symbionts of simuliid larvae.

Dumbleton (1973: 545) noted that a few *A. unicorne* larvae were parasitised by a probable microsporidian, but it was not mentioned in later discussion on pages 576–577. Examination of material from his collections indicates that he was referring to *Coelomycidium* Debais (Blastocladiomycota). In an unpublished study Chilcott (1979; and in Glare & O'Callaghan 1998) examined parasitoids of *Austrosimulium* and the histopathology of *Coelomycidium* and *Thelohania* Henneguy. It appears that the *Coelomycidium* species investigated was not *C. simulii*. Later Batson (1983) described two parasites of low frequency from immature unidentified *Austrosimulium* larvae from Deep Stream, west of Dunedin, South Island. One was a new genus and species, *Hirsutusporos austrosimulii* Batson (then phylum Microspora, family Nosematidae), and the second a member of the family Thelohaniidae for which no further details have ever been provided.

Both DAC and TKC (unpub. obs.) have observed *Austrosimulium* larvae packed with spherical organisms and assumed this was a result of microsporidial infection. However, by definition microsporidia are intracellular parasites (Sprague *et al*. 1992). Many of the organisms that we and Dumbleton observed were intercellular and therefore not Microsporida, e.g., Fig. 499, 500.

Kingdom Fungi

Phylum Blastocladiomycota, Class Blastocladiomycetes, Order Blastocladiales

The majority of the parasitised material on hand is with high probability, *Coelomycidium simulii* (or a closely related species), which is a widespread member of the order formerly known as Chytridiales (Poinar & Thomas 1984, Adler *et al*. 2004). Crosskey (1990) did not list it as known from Australasia, so the example provided here is a new record for the region and probably represents a new species. Crosskey (1990) gave, however, considerable detail about the known life cycle for *Coelomycidium simulii*. Typical is that the body of the simuliid larva is closely packed with individual spherical, monocentric thalli, giving a speckled appearance and usually altered colour, meaning that parasitised larvae are easily recognised (Fig. 500). In the head the thalli are less invasive (Fig. 499). At high magnification individual thalli used in this study showed virtually no internal structure and had a refractive body wall, both characters that are indicative of chytrid fungi.

Development of the parasitoid is at the expense of the internal organs of the larva and delays development: therefore, towards the end of a given cohort the frequency of parasitised larvae rises as they remain in the population. Furthermore, development of the pharate pupal gill is compromised and may result in abnormal shapes (Fig. 501, 502). If infected early with *C. simulii* a larva cannot complete development and dies.

In New Zealand, parasitised larvae have only been found in the South Island and generally at higher altitudes where water is colder. The northernmost record is at Flora Hut, Mount Arthur, where a single parasitised *A. ungulatum* larva was recovered. Along the Kaikoura Coast, *A. multicorne* larvae with *Coelomycidium* were found in Green Burn. The southernmost records for the South Island are those from Dunedin, Tuatapere Scenic Reserve, and Granity Hill.

It does seem unusual, however, for *A. stewartense* populations in low altitude streams near Dunedin to have *Coelomycidium* prevalent in some 14% of larvae. No details of water temperature were given with label data for those collections. However, calculations following Mosely (1982) indicate that although at low altitude, the mean temperature at these high latitude localities would be about 9.5°C. This is not outside the temperature range of higher altitude localities with parasitised simuliid larvae—and again indicates that low temperature is needed for the presence of parasites. This is in full agreement with Ezenwa's (1974) study of mermithid and microsporidian infections of simuliids in Newfoundland, Canada. He showed association of these parasites with cooler water; the majority of stream temperatures were below 10°C. Parasites were more prevalent in the spring and autumn in his study. He found little evidence of pH restriction, most water being slightly acidic, ranging from 5.7–6.8. Again, his findings are in general agreement with the situation in New Zealand.

No parasitised *Austrosimulium* larvae have been recovered from Stewart Island. *Coelomycidium* is now known for Campbell Island, but not yet the Auckland Islands.

Phylum Microsporidia, Class Microsporea, Order Microsporida, Family Thelohaniidae(?)

At the Homer Tunnel location (NZS32a) we recovered in *A. tonnoiri* larvae, at low frequency (<10%), a parasitic organism that packs the posterior abdominal fat bodies tightly and imparts a light pink coloration. When separated into individual organisms these are slightly dumbbell-shaped and up to 0.003 mm long (Fig. 504). Some appear to possess filaments (poorly shown in the figure).

The size and shape of these organisms agrees well with those illustrated for a hyphomycete *Tolypocladium cylindrosporum* W. Gams (e.g., Samson & Soares 1984), known from New Zealand and infecting mosquito larvae. A similar shaped organism, tentatively identified as *Tolypocladium,* isolated from *Simulium piperi* Dyar & Shannon in California was illustrated by Adler *et al*. (2004) although no size was given. Nadeau & Boisvert (1994) experimentally infected *Simulium vittatum* Zetterstedt with *T. cylindrosporum*, but achieved low mortality. However, *Tolypocladium* W. Gams is not intracellular and its hyphal bodies are free in the haemocoel, so it is most unlikely the organism we have is *Tolypocladium*.

Batson (1983), however, when describing the microsporidian *Hirsutusporos austrosimulii*, noted the presence of another microsporidian of the family Thelohaniidae, but he never gave further details. However, *Thelohania* in *Austrosimulium* had been noted by Chilcott (1979). Thelohaniids are known from mosquitoes (Andreadis & Vossbrinck 2002) where diplokaryotic meronts pack the larval fat bodies. The size and shape of the organisms we have is consistent with such stages. The filaments observed may be polar filaments known for other stages of Thelohaniidae. A major problem, though, might be that thelohaniids have a second host, often a cyclopoid copepod that is unlikely to be present in the stream in which we encountered the parasitised *A. tonnoiri*. More detailed examination will be needed to identify this organism.

Phylum Zygomycota, Subphylum Kickxellomycotina, Order Harpellales

Crosby (1974a, b) noted that the trichomycete, *Harpella melusinae* L. Léger & Duboscq was common in the alimentary tract of *A. tillyardianum* larvae, but appeared not to have any effect on populations. He also recovered *Smittium* sp. Williams & Lichtwardt (1990) studied the trichomycete gut fungi found in the New Zealand aquatic insects and found that 4 species were present in simuliids: *Harpella melusinae*, *Pennella asymmetrica* M. C. Williams & Lichtw.*,* *Smittium simulii* Lichtw., and *Smittium culicis* Tuzet & Manier ex Kobayasi. Trichomycetes are worldwide in distribution (Lichtwardt & Williams 1987; Beard *et al*. 2003) and *Stachylina litoralis* Lichtw., White & Colbo and *Smittium culicisoides* Lichtw. have even been recovered from *Crozetia seguyi* Beaucournu-Saguez & Vernon from the isolated Crozet Islands, South Indian Ocean (Reeves *et al*. 2004), and *H. melusinae* from *A. vexans* on the Auckland Islands (Crosby 1974d). The instar at which trichomycetes colonise larvae was investigated by Crosby (1974d) who showed that 50% of 2nd instar *A. tillyardianum* larvae were infested, with later instars almost completely. While trichomycetes can be detrimental to female simuliids, replacing the eggs with fungal cysts, in larvae the relationship appears to be more that of a commensual (Adler *et al*. 2004).

In a wide ranging examination of trichomycete gut fungi in Australian aquatic insects, Lichtwardt & Williams (1990) recorded *Harpella melusinae* from larvae of *Austrosimulium bancrofti*, *A. furiosum, A. mirabile, A. torrentium,* and *A. victoriae,* as well as from larvae of *Paracnephia* and *Simulium* species. *Smittium aciculare* Lichtw. was recovered from larvae of *Austrosimulium mirabile* as was *Smittium simulii* Lichtw. from those of *A. bancrofti* and *A. furiosum.* Other harpellids were taken from larvae of numbers of other simuliid species. An unusual find was an amoeboid *Paramoebidium* sp. L. Léger & Duboscq in larvae of *A. furiosum* and *A. bancrofti,* including those of some *Simulium* species. Overall, the Australian simuliid larvae had a much more diverse gut fauna than found in larvae of New Zealand *Austrosimulium* (Williams & Lichtwardt 1990).

The depauperate gut flora in larvae of New Zealand *Austrosimulium* spp. appears to be a good example of the 'enemy release hypothesis (ERH)', where a colonising organism leaves behind its parasite load (e.g., Torchin *et al*. 2003; Moran & Krasnov 2010). Can this be regarded as another indication that New Zealand *Austrosimulium* dispersed from Australia?

Aspects of endemism of gut symbionts and species of host simuliid are discussed by Nelder *et al*. (2005).

Kingdom Chromista

Phylum Myzozoa, Class Aconoidasida, Order Haemospororida, Family Plasmodiidae

Leucocytozoon tawaki is a well-studied blood parasite of the Fiordland crested penguin *(Eudyptes pachyrhynchus)* (Fallis *et al*. 1976; Allison *et al*. 1978; also see Craig & Crosby 2008) and is vectored by *A. australense*, *A. dumbletoni,* and *A. ungulatum*. It is known (Allison *et al.* 1978) that *L. tawaki* can be vectored to blue penguins (*Eudyptula minor* (Forster)) and domestic chickens (*Gallus gallus domesticus*). Allison *et al*. (1978) reported that *A. ungulatum* with heavy infections of *L. tawaki* had shorter life spans than those with lighter infection, so the organism does appear to have an effect on its host.

On the Anglem coast of Stewart Island and nearby Codfish Island, a leucocytozoon, unrelated to *L. tawaki*, is known (Hill *et al.* 2010) to cause considerable mortality of chicks of the endangered yellow-eyed penguin *Megadyptes antipodes* (Hombron & Jacquinet). From the moment they hatch, chicks of the penguin are badly bitten by simuliids. Identity of the flies is, however, unknown as is any definitive information about transmission of the disease.

Kingdom Animalia

Phylum Nematoda, Class Adenophorea, Family Mermithidae

There is only one literature record of a mermithid nematode parasitising New Zealand *Austrosimulium*, that by Poinar (1990). In Australia, similarly, there has also been only one report—that by Hunter & Moorhouse (1976a) on the feminisation of *A. bancrofti* males associated with mermithisation, a condition well known elsewhere in simuliids (Crosskey 1990; Stanfield & Hunter 2010). Although mermithids were reported from larvae, pupae, and adults of *A. bancrofti*, no details of the nematode were given.

Poinar's (1990) account was for 2 new genera of parasitic mermithids, *Austromermis namis* Poinar from larvae of *Austrosimulium multicorne,* and *Blepharomermis craigi* Poinar from larvae and pupae of *Neocurupira hudsoni* Lamb (Blephariceridae). Dumbleton had, however, collected larvae of *A. ungulatum* containing nematodes (Fig. 503) at the summit of Porters Pass (most likely from the Foggy Peak stream) on 4 March 1958. A tube with 7 larvae, of intermediate instars, with a label in Dumbleton's handwriting, was overlooked since he made no mention of it in his 1973 work. The larvae are currently in the ethanol collection of NZAC, Auckland. Although badly bleached, an examination of 2 of the larvae showed that the mermithid is that described three decades later by Poinar. So far, this collection by Dumbleton and that by Poinar are the only 2 records of nematodes in New Zealand simuliids. We found none during this study.

Poinar's mermithids were from Cave Stream, a shallow, fast, cold-water, stream in the Craigieburn Forest region, west of Christchurch. He tracked *Austromermis* development in the larvae of *A. multicorne* (then as *A. multicorne multicorne*). The parasitised simuliid larvae could be easily seen in the stream because of their white abdomens, an uncommon appearance. Infection rates in mid-January varied from 3–30%, depending on where the sample was taken. Because mature nematodes were found in smaller larvae in mid-January, Poinar concluded that there was a single generation of *Austromermis namis* per year. He further noted that the early infections by *A. namis* in November were in the Malpighian tubules of the simuliid larvae and that indicated a probable "per os" (by mouth) route of infection.

At the Craigieburn locality the mermithids had completed their development by the end of January when water temperature was 10–12°C. At the higher altitude (*ca* 950 m a s l) at Porters Pass mean water temperature would be closer to 9°C (Mosely 1982), hence it is not unexpected that the mermithids collected by Dumbleton in 1958 were still present in *A. ungulatum* larvae in early March.

GEOGRAPHICAL DISTRIBUTION AND ALTITUDINAL RANGE

New Zealand *Austrosimulium* species occur on the three main islands (North, South, and Stewart) and also on Great Island of Three Kings Islands, Great Barrier Island, and the subantarctic Auckland Islands and Campbell Island. They are not present on the Chatham Islands (Dumbleton 1973). West of Stewart Island they are known to occur on Big South Cape Island and Codfish Island, an indication that simuliids probably occur on other small islands too.

The size of island that can support a simuliid fauna is of some interest in biogeography of Simuliidae, because they are known from a variety of isolated islands worldwide (Adler & Crosskey 2012). Minimum size of island was discussed by Craig (2003, his Fig. 2) for Polynesian islands of hot spot origin, and involved the interaction of age, altitude, and size of an island in relation to the given climate and the ability to produce running water. If rainfall is sufficient, very small islands can support simuliids (Craig 2004).

A biting adult female *A. australense* was collected on Little Barrier Island by C. T. Duval on 6 April 1984, but he did not find any immature stages (NZAC record). Neither did Wise (1956) nor Winterbourn (1964). Similarly TKC found none in February 1976 when streams had very low to no water flow. But K. M. Crosby reported to TKC that while on Little Barrier Island in January 2009 he was bitten by simuliids, but did not, however, collect any specimens. These two records of biting relate to comments below on dispersal of aquatic insects (p. 42, Bunn & Hughes 1997).

The minimum size for New Zealand islands to support simuliids is not known, but we suggest that Great Island of the Three Kings is close to that for a species in which larvae are able to cope with very low water flow, and the much smaller Cuvier Island on which Riddell (1981) failed to find simuliids is below the limit. Little Barrier Island, would appear to be close to the limit for a species requiring constant water flow characteristic of most simuliid larvae.

Table 1. Summarised distributions for Simuliidae by New Zealand aquatic ecoregions. 2-letter aquatic ecoregion codes, explained on p. 38, follow Harding & Winterbourn (1997a, 1997b), and are listed in the sequence of their 1997a paper for the North Island (p. 12: Table 1) and South Island (p. 13: Table 2).

Species		North Island													South Island											
		ND	CL	HP	BP	WO	TO	EH	EL	VP	TK	CM	MN	WA	NN	NP	NE	MP	WD	SA	HC	EC	PE	CO	SL	SE
australense species-group																										
albovelatum																					HC					
alveolatum																					HC	EC				
australense		ND	CL		BP	WO	TO	EH	EL	VP	TK	CM	MN	WA	NN	NP	NE		WD		HC	EC			SL	SE
dugdalei							TO			VP																
extendorum																			WD		HC					SE
fiordense																				SA	HC					SE
laticorne															NN	NP	NE		WD		HC				SL	
longicorne	[Three Kings Is]	ND				WO	TO		EL	VP		CM	MN	WA		NP	NE	MP	WD		HC	EC		CO	SL	SE
multicorne															NN	NP	NE		WD	SA	HC	EC	PE	CO		SE
stewartense																			WD	SA	HC					SE
tillyardianum		ND	CL		BP	WO	TO	EH	EL	VP		CM	MN	WA	NN	NP	NE	MP	WD	SA	HC	EC	PE	CO		
ungulatum species-group																										
bicorne																				SA						
campbellense																									[Campbell I]	
dumbletoni																			WD							
tonnoiri																				SA						
ungulatum															NN	NP	NE		WD	SA	HC		PE	CO	SL	SE
unicorne																				SA	HC					
vailavoense																									SL	SE
vexans																									[Auckland Is]	

Table 2. Summarised distributions for Simuliidae by New Zealand area codes, from North to South and West to East. 2-letter codes follow Crosby *et al.* (1976, 1998).

Species		North Island													South Island																	
	TH	ND	AK	CL	WO	BP	TK	TO	GB	HB	RI	WI	WN	WA	SD	NN	BR	WD	MB	KA	NC	MC	SC	MK	OL	CO	DN	SL	FD	SI	AU	CA
australense species-group																																
albovelatum																				KA		MC	SC									
alveolatum																						MC										
australense		ND	AK	CL	WO	BP	TK	TO	GB	HB	RI	WI	WN	WA	SD	NN	BR	WD	MB	KA	NC	MC					DN	SL	FD	SI		
dugdalei								TO			RI																					
extendorum																														SI		
fiordense																		WD					SC						FD	SI		
laticorne															SD	NN	BR	WD	MB	KA	NC			MK	OL		DN	SL	FD			
longicorne	TH	ND	AK		WO		TK	TO	GB	HB		WI	WN	WA		NN	BR	WD	MB	KA	NC	MC				CO						
multicorne																NN	BR	WD	MB	KA	NC	MC	SC	MK	OL	CO	DN	SL	FD			
stewartense																						MC			OL	CO	DN	SL	FD	SI		
tillyardianum			AK	CL	WO	BP		TO	GB	HB	RI	WI	WN	WA	SD	NN	BR	WD	MB	KA	NC	MC	SC	MK		CO						
ungulatum species-group																																
bicorne																		WD			NC								FD			
campbellense																																CA
dumbletoni																		WD														
tonnoiri																									OL				FD			
ungulatum															SD	NN	BR	WD	MB	KA	NC	MC	SC	MK	OL	CO	DN	SL	FD	SI		
unicorne																		WD			NC	MC		MK	OL							
vailavoense																													FD	SI		
vexans																															AU	

Distributions of New Zealand *Austrosimulium* species (Maps 1–19, and summarised in Table 1) are plotted over a system of aquatic ecological regions for New Zealand (Map 20) as proposed by Harding & Winterbourn (1997a). Their ecoregions were based on overlapping parameters of geology, altitude, rainfall, and vegetation based on criteria of Biggs *et al*. (1990). They refined these regions for the South Island (Harding & Winterbourn 1997b) and then (Harding *et al*. 1997b) examined the relevance of their ecoregions to aquatic faunal assemblages, but only for the South Island. These ecoregions have been used in studies such as Duggan *et al*. (2002) and Winterbourn (2008). Where possible we discuss distribution of *Austrosimulium* spp. to these ecoregions. Although temperature is embodied in these ecoregions, we sometimes comment specifically on distribution in relation to mean annual temperatures in New Zealand (NIWA 2008).

The 2-letter codes for the aquatic ecological regions proposed by Harding & Winterbourn (1997a, b) and used on Maps 1–20 and Table 1 are as follows:

North Island: BP, Bay of Plenty Lowlands; CL, Coromandel Peninsula; CM, Central Mountains; EH, East Cape Highlands; EL, Eastern Arable Lowlands; HP, Hauraki Plains; MN, Manawatu Plains; ND, Northern Hill Country; TK, Mt Taranaki Forest; TO, Taupo Plateau; VP, Volcanic Plateau; WA, Wairarapa Highlands; WO, Waikato Hill Country. **South Island**: CO, Central Otago; EC, East Coast Plains; HC, High Country; MP, Marlborough Plains; NE, Northeast Nelson Forest; NP, Nelson Plains; NN Northwest Nelson Forest; PE, Banks Peninsula; SA, Southern Alps; SE, Southeast Forest; SL Southland Plains; WD, Westland Forest.

Arbitrary area codes proposed by Crosby *et al*. (1976) to facilitate categorising terrestrial specimen localities, and shown at the end of the monograph, are also provided in Appendix 2 and as a summary in Table 2. These area codes were updated by Crosby *et al*. (1998). They were not intended to be biogeographical regions although they followed broad climatic regions used in weather forecasts. Files containing these area codes as a data layer for use in GIS programs and Google Earth are available without cost from <http://lris.scinfo.org.nz/layer/165-nz-area-codes-for-recording-specimen-localities/>.

The distribution of the 19 New Zealand species of *Austrosimulium* recognised is disparate. While species in the *australense* species-group are found on both islands, only 4 are known from the North Island, 3 of those in common with the South Island, and the fourth, *A. dugdalei,* precinctive to central North Island. *Austrosimulium dugdalei* is, however, closely related to *A. multicorne* of the South Island. All species in the *ungulatum* species-group are precinctive to the South, Stewart, and the subantarctic Auckland and Campbell Islands. The distribution of species by ecoregion (Table 1), as with the ecological overlay on the reconstructed phylogeny (Fig. 507), well shows that some species segregates are associated with cold water and high altitude.

australense species-group

australense-subgroup

The most widely distributed simuliid is *A. australense*. It is found, literally, from the most northeastern part of Northland to the southernmost edge of South Island and onto Stewart Island (Map 3). It is particularly widely spread in the North Island. Absences are in the Wairarapa Highlands aquatic ecoregion, that of the Hauraki Plains, and the central part of Waikato Hill Country. The first two absences appear related to lack of suitable running water, in large part due to intense agriculture, whereas the latter is related to lack of collecting. Recent collections indicate that *A. australense* does occur in Waikato Hill Country, however sporadically and at low frequency. Similarly, in the South Island there are distributional gaps and unexamined areas.

Larvae of *A. australense* typically use trailing vegetation as a substrate. Therefore, larger braided rivers that have little trailing vegetation tend not to have this species: this applies to running water habitats of North, Mid and South Canterbury, and Otago areas. An outlier locality in Canterbury was the North Branch, Ashburton River where larvae and pupae were recovered from trailing branches of willow trees; we consider this record provides an indication that *A. australense* may occur elsewhere in that area, but with spotty distribution related to riparian vegetation. Sinton (2008) reported simuliids from irrigation (stock) water races on the Canterbury Plains, but did not identify the species. In general *A. australense* occurs sporadically along the ecoregions of Westland Plains, north in Nelson Plains, and Northeast Nelson Forest. It is, with few exceptions, absent from those of Marlborough Plains, High Country, Eastern Plains, Central Otago, and Southern Alps; however, it is arrayed along the southern edge of the South Island and positively identified from a few localities on Stewart Island.

Dumbleton noted that *A. australense* was restricted to an upper altitude of 610 m a s l on the Volcanic Plateau, North Island. This does seem to be the general upper limit, since we recovered *A. australense* adults from 680 m a s l on Mount Taranaki; however, we have collected immatures at 900 m a s l on Mount Ruapehu, Ohakune. While we have collected this species from near sea level, the majority of localities lie between 100–200 m a s l (Appendix 1).

Molecular analysis indicates that *A. australense* is probably two separate cryptic species. One clade is exclusively in the South Island. The other clade is almost completely in the North Island, but with apparent exemplars in the South Island; perhaps indicative of precinctive evolution of that clade in the North Island with subsequent dispersal to the South Island (see p. 63 and 77, Molecular Analysis and Biogeography sections).

The related species *A. longicorne* is also found on both main islands and similarly the molecular lineages differ on each island — a single one in the North Island. This species has specialised habitat requirements and, although widespread, is not common (Map 11). However, recent collections indicate that the species is more common than previously thought. *Austrosimulium longicorne* is the northernmost species found, occurring on Great Island of the Three Kings Islands (not the common *A. australense* as might be assumed). However, while *A. longicorne* seems to require specific habitats (see species description), it can survive in intermittently-flowing streams (e.g., Fig. 472, 473), and these occur on the Three Kings Islands.

tillyardianum-subgroup

The most widely distributed species in this subgroup is *A. tillyardianum* (Map 14), but it is restricted to south of Auckland in the North Island and north of Dunedin in the South Island. The northern distribution may well be determined by temperature, falling almost exactly within small areas of 12–14°C mean annual temperature (NIWA 2008). However, annual temperatures in the 14–16°C range do occur around the coast of East Cape where *A. tillyardianum* is found. There is a gap in the mid Waikato Hill Country aquatic ecoregion, which relates to both a paucity of collecting and the substrates in streams and rivers there tending to be of soft papa (blue mudstone); not suitable for *A. tillyardianum* larvae, which typically are on hard substrates. The absence of *A. tillyardianum* from Mount Taranaki Forest aquatic ecoregion, and the Manawatu Plains, is something of a puzzle, but rivers arising on the mountain are torrential and not particularly suitable. Lower reaches, even on the Manawatu Plains, are compromised by severe and intermittent flooding and unstable substrates that again are somewhat unsuitable. Why it is *A. australense* that occurs on this mountain and at high altitude is a further puzzle. In the South Island the distribution and cut-off north of Dunedin of *A. tillyardianum* may also represent a temperature limit, with most populations occurring in areas of 10–12°C mean annual temperature. That agrees in part with distribution of *A. tillyardianum* on the Volcanic Plateau, North Island, which mainly falls into a similar temperature regime although at higher altitude, but lower latitude. On the east coast of the South Island, the majority of localities occur in the East Coast Plain, Banks Peninsula, and High Country ecoregions. Localities farther north are mainly in the Northeast Nelson Forest and Nelson Plains.

Both Tonnoir (1925) and Dumbleton (1973) considered *A. multicorne* to occur on both islands. We have, however, raised the North Island segregate of *A. multicorne* to specific status, namely *A. dugdalei* Craig, Craig & Crosby. There is no question that the two species are closely related, with *A. dugdalei* recently derived from *A. multicorne*. We make the assertion that since *A. dugdalei* occurs only on the Volcanic Plateau (Map 6), and this ecoregion is no more than 1.6–2 million years old (Thornton 2003; Campbell & Hutching 2007; Graham 2008), then divergence of these taxa has occurred within this period of time. Known from only 11 localities, the majority of collections are on the Volcanic and Taupo Plateaus (VP, TP), with one farther south at the northern edge of the Manawatu Plains. *Austrosimulium dugdalei* is restricted to an altitude distribution of 500–1 150 m a s l. The localities fall well within mean annual temperatures of 6–12°C. The species might also occur farther northeast on the Taupo Plateau, such as in the Kaimanawa Mountains, but access is difficult.

Austrosimulium multicorne in the South Island is well distributed and occurs in all areas (Map 12), and there are problems with discrimination between it and *A. stewartense* in the southern part of the island (see species description). The majority of localities fall into the High Country ecoregion and the species, with few exceptions, is absent from East Coast Plains. A surprise is that *A. multicorne* occurs on Banks Peninsula, where it was not recovered by Crosby (1974a), even during his intensive long term study, probably because *A. multicorne* occurs at higher altitudes. The ecoregions of Banks Peninsula and the High Country cluster together in terms of climatic and geomorphological characteristics (Harding & Winterbourn 1997b), so ecological parameters are suitable. Dumbleton (1973) gave the upper limit of *A. multicorne* as 1 200 m a s l at Mount Balloon, NW Nelson. We have collected it at 1 400 m a s l at Temple Basin, Arthurs Pass, and there other records of it from 1 600 m a s l, on the Old Man Range, Otago. While it has been collected close to sea level, it is normally found at 200–600 m a s l (Appendix 1), where spot temperatures range from 8 to 18°C, with most from 8 to 15°C. This is in reasonably good agreement with mean annual temperature of the High Country ecoregion between 6 to 10°C.

Farther south in the South Island is the poorly known *A. fiordense*, originally considered by Dumbleton to be a subspecies of *A. multicorne*, and raised here to full species status. Beyond the type material from the Glasinock and Stillwater Rivers, Lake Te Anau, it is known also from high altitude in the Darran Mountains, Fiordland (both in the Southern Alps ecoregion) and an isolated population from near Mesopotamia, Rangitata River Valley (High Country ecoregion) where it occurred with *A. multicorne* and *A. tillyardianum* (Appendix 1, Map 9).

Austrosimulium stewartense has a southern distribution (Map 13). The localities in the areas of the Mid Canterbury foothills and farther south in Central Otago (High Country ecoregions) are moot. As known, this species is, at some locations, hard to separate from *A. multicorne*. However, all localities fall into ecoregions with mean annual temperatures of 8–10°C. Those in the south are mainly in the Southland Plains, but they are also in the Southeast Forest and Westland Plains. Dumbleton gave no altitudinal limits, but his label data indicate 20–400 m a s l, and we have collected it from literally high tide level up to some 760 m a s l (Appendix 1). On Stewart Island, Chadderton (1990) collected aquatic invertebrates extensively around the northern half of the island and sporadically farther south. *Austrosimulium* was amongst the 5 most abundant taxa and occurred in 41 of the 45 sites samples. The species were not identified, but we assume most were *A. stewartense*.

Now separated from *A. stewartense* as a distinct species, *A. extendorum* Craig, Craig & Crosby has a restricted distribution, known from only 2 localities, one on Stewart Island, another on nearby Big South Cape Island (Map 8). *Austrosimulium extendorum,* along with *A. stewartense*, is unique; larvae have been found on cobbles at high tide mark (Fig. 466).

Austrosimulium laticorne is precinctive to the South Island (Map 10) and has a distribution not uncommon to South Island species. Localities are concentrated in the ecoregions of Northeast Nelson Forest, Northwest Nelson Forest, and Nelson Plains. Older collections show it to be arrayed centrally along the Westland Forest ecoregion. A single questionable locality is in the Mackenzie High Country. There is then a distinct gap until south of Dunedin, where it is quite common in the ecoregions of Southland Plains and along the edge of the High Country. Overall, the distribution indicates a preference for a mean annual temperature of 8–12°C. Recorded spot temperatures (Appendix 1) are, however, warmer and range from 10 to 23°C. The major gap in distribution, north of Dunedin and up to the latitude of Timaru, indicates that there might be two taxonomic entities, reminiscent of the distribution of *A. australense* in the South Island. Dumbleton made no comment about altitudinal distribution, but we have collected *A. laticorne* from sea level to 826 m a s l (Appendix 1).

The closely related *A. alveolatum* is of limited distribution, occurring only in the Mid Canterbury area (Map 2) corresponding to the central portion of the High Country ecoregion. There is a narrow altitudinal range from 250–706 m a s l in our collections, but Dumbleton's label data indicated an upper range of 920 m a s l. The localities tend to fall into the mean annual temperature range of 6–10°C, but the spot temperatures recorded were of 11–15°C (Appendix 1).

Austrosimulium albovelatum has a similar distribution in many ways to *A. alveolatum,* but with two exceptions. One known population is in the Mid Canterbury area (Map 1), the other close to sea level, at Kaikoura (Appendix 1). Of importance here is that all localities fall into the High Country aquatic ecoregion and that includes Kaikoura. Along the Seaward Kaikoura Mountains, cold-water alpine streams empty directly into the ocean. The altitudinal range of *A. albovelatum* is normally narrow, 250–616 m a s l. The temperature regime for the High Country ecoregion is 6–10°C, but spot temperatures for localities were higher, 12–18°C (Appendix 1).

ungulatum **species-group**

No members of the *ungulatum* species-group are found in the North Island. The reasons for this have been the subject of considerable speculation (Tonnoir 1925; Dumbleton 1973). Dumbleton specifically noted that the group is precinctive to South and Stewart Islands, and the subantarctic islands. The absence from North Island is surprising given the ability of *A. ungulatum* to fly kilometers (Tonnoir 1925; Craig pers. obs.). There is a expectation that with sea level depression during glaciations, it would have been a minor dispersal event to cross the narrowed or even closed Cook Strait to reach Mount Taranaki, in particular. There are ample cold-water, densely-shaded streams on that mountain, suitable for *A. ungulatum*. But no. Some authors (e.g., Worthy & Holdaway 2002) were not convinced that land fully connected the North and South Islands during the last glaciation — Cook Strait was just markedly narrowed. Further, there is evidence that weather systems, and in particular, the "Roaring Forties" were shifted northwards and intensified during glaciations (Newnham *et al*. 2003; Carter & Gammon 2004), making a crossing of even a reduced Cook Strait more fraught even than at present.

***ungulatum*-subgroup**

Austrosimulium ungulatum is found in all parts of the South Island (Map 16). There is molecular evidence that *A. ungulatum* is perhaps a complex of at least two species (see p. 64, Molecular Analysis section) and Dumbleton (1973) noted marked variation in gill filament number. In terms of aquatic ecoregions it is absent from the East Coast Plains, with one exception, however, it abuts the western edge of that ecoregion and the eastern High Country. The exception was 2 female adults recovered from Kaituna Bush, Banks Peninsula. Of note is that the typical habitat for *A. ungulatum* larvae is small, densely-shaded, cold water streams. Larvae occur at low density and Tonnoir (1925) did not discover them; it was Dumbleton (1973) who first found them. In this instance, Kaituna Bush, while physically in the East Coast Plains ecoregion, has Kaituna River flowing through it from the Banks Peninsula ecoregion: the upper reaches of the stream are heavily shaded and cold; the Bush reserve lower down is surrounded by agricultural land. Why was *A. ungulatum* not collected on Banks Peninsula previously? Was this collection from a normal dispersal event, unsuccessful because of competitive exclusion by *A. tillyardianum*? It poses a similar problem to that with *A. multicorne* which also occurs on Banks Peninsula at extremely low frequency (Map 12, Appendix 1). Or are both recent immigrants? We note elsewhere that Banks Peninsula has been heavily impacted by human activity and currently has little of the original forest cover.

The presence of *A. ungulatum* at the Kaikoura coast might seem unusual, but again the High Country aquatic ecoregion extends out to the coast there, and some streams are classic habitats for that species (Fig. 493). *Austrosimulium ungulatum* is sparsely distributed in Central Otago and the southeastern High Country ecoregions. Dumbleton gave an altitudinal range of from sea level to 920 m a s l. We found a similar range, but up to 993 m a s l (Porters Pass, NZS134). The absence of *A ungulatum* from the Southern Alps ecoregion is notable because of the lack of biting by females of this species (Crosby & Craig pers. obs.); a role filled in part by other species.

The ecoregions for *A. ungulatum* are in the mean annual temperature range of 6–10°C. Spot temperatures were, however, from 9–23°C (Appendix 1). Exceptions to the requirement for cooler temperatures are those of a population in the Marlborough Sounds area (Northeast Nelson Forest ecoregion) and those in the northwest Nelson area (Nelson Plains ecoregion).

A new species, *A. vailavoense* Craig, Craig & Crosby is restricted to Stewart Island and the extreme south of the South Island (Map 17). The localities on the South Island are within the Southland Plains, and on Stewart Island in the Southeast Forest ecoregion. Altitude ranges from close to sea level to 21 m a s l. The immature stages are as yet unknown, but the localities known are ecologically similar to those required by immatures stages of *A. ungulatum*; small, cooler (13–15°C), densely-shaded streams (Appendix 1).

In the subantarctic islands, *A. vexans* is precinctive to the Auckland Islands, and *A. campbellense* is on Campbell Island (Map 5, 19). Dumbleton (1973) gave a few details for *A. vexans*, such as its occurrence at altitudes lower than 90 m a s l and in large numbers when the stream bed was cobble. For Campbell Island, Dumbleton (1973) also gave some details, such as mean air temperatures of 9.4° in January and 4.4°C in June and July. TKC has collected *A. campbellense* larvae at 220 m a s l. Joy & Death (2000) examined stream invertebrate communities on Campbell Island and of 19 streams examined, island wide, 7 had *A. campbellense,* all at altitudes below 40 m a s l. Most streams were deeply incised, with a mean velocity of 0.6 m/s, but some were recorded as having zero velocity! Temperatures of the water were all in the 8–9°C range.

Austrosimulium dumbletoni is, on morphological grounds, currently placed in the *ungulatum* species-group (Crosby 1976a). It is known only from the Westland Forest aquatic ecoregion at Jackson Bay and at Knights Point at sea level when attracted to penguins and humans; although it does not bite humans. Immature stages are unknown. With a probable relationship to species in the *unicorne*-subgroup (p. 64, Molecular Analysis), similar to those species, the immature stages of *A. dumbletoni* may occur at high altitude.

unicorne-subgroup

These are high altitude simuliids and of relatively restricted distribution. *Austrosimulium bicorne* is only found in the southern Westland area and northern Fiordland. There is also a small locus at the western extent of North Canterbury. All these localities fall within the Southern Alps, or are at the western edge of the High Country aquatic ecoregions (Map 4). They have a mean annual temperature of 4–8°C. With one exception, spot temperatures agreed closely with that, ranging from 6–9°C. The exception was 15°C, where water flowed down a sunlit cliff into the stream habitat below (Appendix 1, Fig. 491). The altitudinal range is narrow, from 882–1 600 m a s l. The disjunction between the two populations is probably due to a lack of collecting; not easy at that altitude in the Southern Alps.

Austrosimulium unicorne has a similar ecological distribution to *A. bicorne*. Found only in the North, Mid, and South Canterbury areas, it is sharply restricted to the eastern side of the Southern Alps aquatic ecoregion and the western edge of the High Country (Map 16). With few exceptions it is only found between 700–1 677 m a s l. Lower altitude records of 20–350 m a s l are suspect and no ecological data are available for these records. Temperature data during our collecting (6–9°C) indicates it is a cold water species. Dumbleton noted that in a typical habitat, even at a lower altitude, winter temperatures were 3°C and during summer 6°C.

A. tonnoiri Craig, Craig & Crosby is another member of this *unicorne*-subgroup. Dumbleton included the specimens he had from Homer Tunnel as a variant of *A. bicorne*, but with additional specimens we found this entity should be recognised as having species status. *Austrosimulium tonnoiri* has a restricted distribution in the Southern Alps aquatic ecoregion similar to that of *A. bicorne,* but does not have mid-island populations (Map 15). It has a restricted altitudinal range, from 660–1 150 m a s l, and occurs too in markedly cold water (6–9°C) (Appendix 1).

We have noticed that repeated collections at some localities do not necessarily return the same species of *Austrosimulium*, if any at all; or a site visited unsuccessfully many times suddenly produces simuliids. This is of some significance since it means that distributions are not static. The phenomenon has been well examined by others and an example is that by Bunn & Hughes (1997). In a broadly-based study they investigated the drift downstream and movement upstream of aquatic invertebrates, as well as distance flown by adult insects. They also examined the genetic diversity of both a *Baetis* Leach mayfly and a *Tasiagma* Neboiss caddisfly. Their general expectations were — if dispersal of an organism is high there should be little genetic differentiation among populations; on the other hand, with restricted dispersal, differentiation between populations would occur through natural selection or random genetic drift (Slatkin 1985). Against expectations, they found that genetic differentiation was not necessarily a function of geographic distance and that genetic variation in a population, from which multiple samples had been taken over time, was significantly different between times. They also calculated that to produce densities of the insects studied, only a few adults would be needed. Their conclusions were that it is the adults that do the dispersing, and dispersal capabilities and stochastic effects of recruitment can be determining factors in observed spatial and temporal variation in community structure in some streams.

A similar study was by Hogg *et al.* (2002) on population genetic structure of two New Zealand stream insects, namely the megalopteran *Archichauliodes diversus* (Walker) and ephemeropteran *Coloburiscus humeralis* (Walker). Expectations were that *A. diversus* having markedly large and poor flying adults would show greater genetic divergence between populations because of poor dispersal ability. Similarly this was expected for *C. humeralis*, but there because the adults were assumed to be short lived. The expectations were met for *A. diversus* which showed moderate genetic divergence between North Island populations and a major divergence between those and the single population sampled from the South Island. *Coloburiscus humeralis* on the other hand, did not meet expectations and showed extreme lack of genetic divergence. While that could be attributed to major dispersal ability, Hogg *et al*. (2002) had other suggestions. One was that recurring glaciation and concomitant sea level fluctuation, major volcanism, and habitat fragmentation resulted in reduction of genetic diversity in remaining small populations. Recolonisation from these genetically depauperate founder populations might then explain the current low genetic diversity in *C. humeralis*; and for that matter other New Zealand fauna.

The overview by Bunn & Hughes accords with our observations. For example, the Mountain Road, Ohakune site (NZN92) was visited 3 times. The first time (March) produced larvae of *A. australense* and *A. dugdalei*. The first species was well outside its usual altitudinal range. The next 2 visits were both in November, 2 and 3 years apart respectively, and produced nothing, yet the stream appeared the same. Similarly, near Waiouru (NZN46, November) the first visit produced *A. longicorne,* but a visit 2 years later (November) produced no simuliids. The stream at the summit of Takaka Hill on the first visit (NZS103, February) produced only 3 immature larvae of *A. longicorne*, whereas a second visit 3 years later (November) produced numerous larvae of *A. ungulatum*, 1 final instar of *A. multicorne,* and numbers of unidentifiable immature larvae. The presence and absence of simuliids on Little Barrier Island, as discussed above, is a similar situation. Overall, we suggest that species composition at any one locality should not necessarily be taken as definitive from our data.

GENERAL STRUCTURE AND TERMS

Terms for morphological structures of Simuliidae are not universal in application, so we use here in large part those terms proposed by Adler *et al*. (2004), and less so Crosskey (1990) and Craig (1977). Those works should, however, be consulted for more detail on morphological structures. Dumbleton (1962) described structures for immature simuliids (larvae, pupae, and the cocoons), however, many of the terms he used have been superseded. In the following section we deal mainly with those structures that are key characters used to separate the sexes and to identify New Zealand species, and which are used in the descriptions and keys of this revision. In the main, key characters are pupal, cocoon, and larval structures. Internal structures of the larvae are of phylogenetic value, and gut morphology was used by Kim & Adler (2009) to permit generic diagnoses: we did not use this latter character.

Adults of New Zealand *Austrosimulium*, with few exceptions, are almost impossible to identify to species, even under moderate magnification, without mounting some parts for detailed examination. A hand lens of 10–15× magnification will, however, allow the sex of adults to be determined and placement of a specimen to a species-group, and possibly in one instance to species. Some pupae may also be identified to a species-group at moderate magnification, as can some final instar larvae. As males are extremely rarely encountered during collecting, they need to be reared from pupae; however, an important point to consider when examining reared male specimens killed very soon after emergence is that their structures and coloration may not be fully developed. Definitive identification usually requires specialised dissection and mounting of body parts, and then examination under high magnification; the techniques involved are provided in the Methods section (p. 49).

Adult

Body. Simuliid adults are relatively easy to distinguish from other small Diptera. The thorax is markedly humped (Frontispiece; Fig. 1) and in the U.S.A. simuliids are often called buffalo gnats for this reason. New Zealand simuliids are all evenly dark brown to black; the males are an elegant dull black with a **vestiture** of golden scales. The legs tend to be slightly lighter in colour. Females tend to be larger than males.

Head. The heads of male and female adults show a major difference in the structure of the compound eye. In females (Fig. 1, 15) the eyes are composed of arrays of equal-sized **ommatidia** (individual corneal facets), with the 2 eyes separated by the **frons** or forehead. This arrangement of the eyes in the female is known as **dichoptic**. The eyes of the male (Fig. 16) have 2 sizes of ommatidia, larger ones on the upper eye and smaller below. The larger ommatidia meet across the front of the head, a condition of the head referred to as **holoptic**. In life the male eyes tend to be more reddish than those of the female. These eye differences readily separate the two sexes. We use the **frons width** : **head width ratio** as a descriptor for head shape in females, in addition to providing measurements of **head width** and **head depth**.

Protruding from the front of the head are 2 **antennae** (Fig. 15, 16). The number of divisions of the antenna is an important diagnostic feature within Simuliidae. However, the use of terms in describing the divisions is problematic. Strictly the antenna consists of a basal **scape** (1st antennal segment), a **pedicel** (2nd antennal segment), and a **flagellum** (3rd antennal segment): this 3rd antennal segment is divided into a number of **flagellomeres** or **articles** (Fig. 18). Therein lies the problem—flagellomeres are also often referred to as segments (e.g., Dumbleton 1973; Crosby 1974b) and consequently the antenna of *Austrosimulium* has been described as “10 segmented”. Here we take the pedicel and scape as given and refer only to the number of flagellomeres; for *Austrosimulium* this is normally 8. The antenna is usually of even coloration, with occasional patterning on the antenna being of taxonomic value, particularly the 1st flagellomere (base of the 3rd segment). There are subtle differences in shape of male and female antennae; those of the male are more tapered (Crosby 1974b, Craig & Crosby 2008).

In the centre of the head and below the eyes is the **clypeus**, a domed region that internally supports muscles of the cibarial pump; hence the clypeus is larger in females than in males. The clypeus is variably setose. Below the clypeus are the **mouthparts** or **proboscis**. We use the relative length of the proboscis to the head depth as a measure of mouthpart size, as that provides an indication as to whether the female might bite or not. Articulated to the clypeus is a triangular **labrum**. The labrum has a groove on its inner surface forming the upper surface of the food channel. Apically, the labrum has a series of robust teeth that are absent in the male. Lying under the labrum and forming part of the bottom surface of the food channel is the **hypopharynx**. Articulated basally to that is the **cibarium**, a major pump for fluid ingestion. The internal end of the cibarium in *Austrosimulium* is smooth (e.g., Fig. 24–32), but in other simuliid genera there may be ornamentation. There are 2 sclerotised arms or **cornuae** laterally; these are variably sculpted apically and ornamented; of minor value here in species identification.

Hidden under the labrum are 2 flat **mandibles** (Fig. 17) with an array of minute teeth only on the inner (medial) side of the apex. This character state is of some phylogenetic importance since most other simuliids have teeth on both sides. Posterolateral to the mandibles are 2 **laciniae**, articulated 1 each on the base of a **maxillary palp**. Each lacinia has a series of sharp **retrorse** (recurved) **teeth** (Fig. 17) on each side. The number of teeth may be of some significance in regard to blood feeding. Mandibles and laciniae are untoothed in males. Protruding from the proboscis base, but often folded backwards, are 2 **maxillary palps**. These consist of 5 segments with the 2 basal ones being small. The 3rd segment is expanded to accommodate a **sensory vesicle** (Lutz’s organ). This contains odour- and carbon dioxide-sensing organs that, in blood-feeding females, are used to locate the host. The length of the 5th segment may be of significance in evolutionary relationships, but is not used by us.

Behind and tending to surround the other mouthparts is the substantial **labium**. Apically the labium is expanded into 2 fleshy **labella**. These are spread out over the skin to collect the blood when the female is biting; normally they are in a retracted position.

Thorax. The thorax of Simuliidae in almost all instances is distinctly convex, more so in the male. Of its 3 segments, the **prothorax** is much reduced, but remnants are the **postpronotal lobes** on the anterolateral margins of the larger **scutum** (2nd thoracic segment). These 2 postpronotal lobes are sometimes lighter in colour than the scutum and of minor diagnostic use. The scutum is by far the largest part of the thorax and its colour, and various patterns, are of important taxonomic use elsewhere in Simuliidae; however, the scutum is of little taxonomic value for *Austrosimulium*. The scutum is densely covered with a **vestiture** of microtrichia plus hairs that are often scale-like and of different colours; these are mainly golden in *Austrosimulium*. In older specimens the vestiture and hair may become worn and the scutum appears shiny. Posteriorly the scutum has a concave region referred to as the **scutellar depression** with vestiture of sparse, stiff, black hairs. Behind this is the **scutellum**, a raised subtriangular area with similar hairs to the scutellar depression arranged in an irregular row. The scutellum is often slightly lighter in colour than the scutum. Between the scutellum and the 1st segment of the abdomen is the bulbous **postnotum** (3rd thoracic segment), bare and usually concolorous with the scutum. In dried specimens the depression, scutellum, and postnotum appear pollinose (covered in dust) when lit from the posterior. Under such illumination lighter bands or **vittae** may appear lengthways on the scutellum. Laterally the thorax consists of the **pleuron**, derived almost entirely from the mesothorax; it is of little taxonomic importance in *Austrosimulium*, but elsewhere in Simuliidae it is useful. The pleuron is usually lighter in colour than the scutum, and under some lighting it appears pollinose. One major feature of the pleuron is a membranous region termed the **anepisternal** membrane, that in some simuliids is haired and a useful taxonomic feature, but is bare in *Austrosimulium*. Ventrally between the coxae of the hind legs is the invaginated sternum, or **furcasternum** — of reputed taxonomic value, but not so here.

Wings. The wings of *Austrosimulium* are hyaline and, as in all simuliids, clothed in microtrichia. The wing venation referred to below follows that of Adler *et al.* (2004). In some *Austrosimulium* species the wings are slightly dusky, a condition of diagnostic value. The leading veins of simuliid wings are strongly expressed — the **costa** (C), **subcosta** (Sc), and **radius** (R) (Fig. 1–3). The costa has well-developed spines as well as hairs. The subcosta has ventral hairs, either fully or partly, along its length. The basal section of R is haired on the dorsal surface and lacks spines. The anterior branch of the radius, known as **R_1**, is haired, but lacks spines. The posterior branch of R_1 is the **radial sector** (**Rs**) and is unbranched. In *Austrosimulium* there are spiniform setae on the costa and the apex of the subcosta. More posterior veins are the branched **media** (**M_1** and **M_2**), 2 anterior **cubital** veins (**CuA_1** and **CuA_2**), posterior **cubitus** (**CuP**), and single **anal** vein (**A_1**). A **false vein** (sometimes labelled medial–cubital fold or M_{3+4} or submedian fork) lies between M_2 and CuA. There is a short humeral cross vein (**hm**) between the base of the costa and subcosta. A small **basal medial cell** (**bm**) is present at the base of the media and CuA_1 veins. The remnant of the hind wing in Diptera is the haltere, a knob-like structure on a stalk. Normally in New Zealand *Austrosimulium* the halteres are tan in colour, but occasionally they are white and of diagnostic value.

Legs. The legs of *Austrosimulium* probably carry more taxonomic information than we have used here, and the implications of various patches of hairs and their expression have not been examined. Legs are generally of lighter colour than the rest of the body, but are still dark (yellowish gray and black). The cuticle at articulations tends to be darker than intervening regions. The basal **coxae** are short and conical, **trochanters** small, and the **femora** spindle-shaped. The **tibiae** are more elongated and tend to be slightly expanded apically, particularly on the hind legs. Of importance is the **basitarsus**, which is furnished with a comb along its ventral edge and apically has the **calcipala**, a variously developed flattened flange extended over the articulation to the next tarsal segment, and present in both sexes (Fig. 19). The remainder of the **tarsus** consists of 4 divisions, or **tarsomeres**, the taxonomically important tarsomere being the basal one. In some simuliids there can be an incised area termed the **pedisulcus**, partly covered by the calcipala. However, it is not particularly well developed in *Austrosimulium* (Fig. 19); it is a weakening of the leg cuticle that enables the leg to fold up under the wing pad of the pupa during development. In some genera that are thought to be related to *Austrosimulium,* the pedisulcus is poorly developed and is little more than a series of wrinkles. It is absent in even more basal simuliids such as *Helodon* Enderlein.

On the hind basitarsus there may be a ventral row of stout setae (Fig. 19, 42–49). These setae are a plesiomorphic character for Simuliidae, occurring even in the basal genus *Parasimulium*, but not distinctly. In *Austrosimulium* their absence in both sexes helps define one of the species-groups. The apical **claws** on simuliid legs are of considerable importance, taxonomically and also provide biological information. At their simplest the two claws resemble elegantly curved talons (Fig. 50–54). This state is usually seen in mammophilic species and is perhaps an adaptation for dealing with hair. The shape of such simple claws is variable, and in some *Austrosimulium* species the base of the claw is substantial and has been referred to as a **heel** (Fig. 56). Ornithophilic species have a **bifid claw** with a variously developed basal lobe (Fig. 62). Terms for the lobe differ and here we use **basal tooth** as opposed to **thumb-like lobe** (Adler *et al*. 2004). In *Austrosimulium* when a claw tooth is present the tooth has a **basal notch**. There is considerable variation in claw structure and its various states do not unambiguously indicate feeding behaviour of the female. For instance, females with bifid claws are not restricted to just bird feeding. Adler *et al.* (2004: 41–42) discussed this aspect of simuliids in some detail. Simuliid males all have a series of **grappling hooks** (claw pad) dorsal to the base of the claw (Fig. 68, 69) that are used to engage the female vestiture during copulation

(Craig & Craig 1986). Not mentioned in the literature, as far as we know, is that males possess a lobe-like structure superficially similar to the basal tooth of female claws. It is, however, more medial, so is unlikely to be a homologue (Fig. 68). There are small hairs and pegs at the junction of the claw and the lobe. This lobe-like structure appears to be plesiomorphic in simuliids since it occurs in male *Parasimulium* (Adler *et al*. 2004: Fig. 4.58).

Abdomen. The abdomen has 11 segments. The 1st segment is distinctly modified and is usually referred to as the **basal scale**. It supports a row of long fine hairs, the **basal fringe**. In males these hairs may extend back to the middle of the abdomen. Their colour can be useful taxonomically. On the **dorsum** (tergum) of each segment, a sclerotised portion is referred to as a **tergite**, and the relative size of these to each other is of considerable taxonomic value as well as indicative of feeding behaviour. Blood feeders that require the abdomen to expand during engorgement have smaller tergites (Fig. 70, 82); non-blood feeders have larger ones (Fig. 76). In males the tergites occupy the full width of the tergum (Fig. 88), as befits non-blood feeders. Vestiture is variable, mainly sparse short black hairs on the tergites, more pronounced on posterior tergites. Ventrally the sternites are poorly developed and of no taxonomic value. Membranous areas, such as the lateral **pleuron**, are pleated to allow expansion.

Female terminalia. The 8th sternite (**VIII**) is modified on its posterior edge as a pair of **hypogynial valves** that function as ovipositor lobes (Fig. 20, 22). The shape and arrangement of these is taxonomically important in simuliids, but less so in *Austrosimulium* where they are all rather similar (*cf* Fig. 90–107), but are, however, of minor use to discriminate species. The 9th tergite (**IX**) is well developed and connects laterally to a markedly modified 9th sternite, the **genital fork** (Fig. 20). This inverted Y-shaped structure is reflexed internally with its long arm directed anteriorly. The length and sclerotisation of the long arm and shape of the **lateral arms** and **plates**, and an anteriorly directed **apodeme**, are of considerable taxonomic importance both for species-groups and at higher levels (Fig. 108–125). The 10th segment (**X**) has a small tergite and its sternum consists of the **anal lobes** (paraprocts), each broadly connected posteriorly to a **cercus (**Fig. 20, 23, 90). Of importance taxonomically elsewhere in simuliids, these two structures are of minor taxonomic use in *Austrosimulium.* At the junction of the genital fork arms is the opening (e.g., Fig. 94, 95, 97) to the **spermathecal duct** that leads to the **spermatheca**. This globular structure is used to store sperm from the male. Of considerable importance taxonomically at higher levels in simuliids (Evans & Adler 2000), the spermatheca in *Austrosimulium* is rather uniform in character, albeit the clear area at the junction of the duct and spermatheca is variable in size. Although lacking external patterning, sometimes fine, sparse microtrichia can be observed internally.

Male terminalia. The terminalia of the male consist of the genitalia plus the small tergite of segment 10 and small **cerci** that arise from the reduced 11th segment (Fig. 21). The genitalia are of major importance taxonomically for Simuliidae and in large part *Austrosimulium* (Fig. 126–134). Tergite 9 (**IX**) is well expressed and connected laterally to a band-like sternite 9 (**IX**). The **gonopods** (claspers) are the most obvious part of the genitalia at first glance. These are 2-segmented appendages, with a basal **gonocoxite** and an apical **gonostylus**. The gonocoxites are subconical in structure and show some characters of taxonomic value. The gonostyli are variable in shape and have distinct numbers of substantial **terminal spines** (spinules)—both states useful in delimiting species-groups. The **aedeagus** is a complex medial structure. Most obvious is its **ventral plate**, a shield-like structure with 2 anteriorly directed **basal arms**, or apodemes. The posterior shape of the plate and the development of a median ridge are taxonomically useful. Arising from the dorsal surface of the ventral plate is a strap-like **median sclerite**; poorly expressed in *Austrosimulium,* its development and shape are important at the generic level elsewhere in other Simuliidae. The **aedeagal** membrane is a thin, transparent cuticle, which in *Austrosimulium* has extremely small microtrichia and superficially may appear bare.

In many simuliids there are sclerites that support the aedeagal membrane laterally. These are the **parameres** and they extend from an apodeme on the dorsomedial base of the gonocoxite to the apex of the basal arms of the ventral plate. In some simuliids the paramere is a quadratic or subtriangular plate. A further posterior extension may possess 1 to many **parameral spines** of various configuration. In New Zealand *Austrosimulium* the paramere is poorly expressed, merely consisting of a short rod on the gonocoxite and a difficult-to-see twisted rod of cuticle basolateral to the aedeagal membrane. There are no parameral spines (Fig. 135–142), although they occur in some Australian *Austrosimulium*.

Pupa

The pupa is basically the same shape as the adult developing within; with the appendages closely applied to the body (Fig. 4). Of importance in *Austrosimulium* is the **cephalic plate** and **antennal sheaths** (Fig. 197–201, 202–233). The cephalic plate, along with the anterior of the thorax, may be concave in some species. In males the antennal sheaths only reach halfway over the underlying eye, but fully in females, so pupae and their exuviae can be sexed relatively easily. The disposition of various setae on the cephalic cuticle is important. **Facial setae** are always present; **frontal**, **epicranial**, **genal**, and **ocular** setae may be present or absent (Fig. 196, 197–201). Thoracic setae are of good taxonomic value, but in New Zealand *Austrosimulium*, since they are more often than not damaged, or missing, they are of superficial use only. Dumbleton (1973: 481, 500) referred to 3 of the more obvious ones as **dorsocentral setae**; elsewhere such setae are known as trichomes. Of considerable importance is the sculpting of the thoracic and cephalic integument. When **microtubercles** are present they may be grouped into patterns (Fig. 234–236, 241). When tubercles are absent the cuticle can be corrugated or **mammillated** (Fig. 238, 239).

Respiratory gills are of major value for species identification, both in pupae and final instar larvae. These are bilateral cuticular projections, located anterolaterally on the pupal thorax, and are generally directed forwards and occasionally downwards. The gills can usefully be considered as 3 components (Fig. 255–267); a **base** that attaches the gill to the pupa and is usually more pale coloured; an apical black **horn** (when present); and **filaments**. The gills are covered by a very thin outer layer of cuticle and this is supported by cuticular posts, or **trabeculae**, of various sizes — on the base they show as black spots. Also on the base, and lateral, is a **basal fenestra** (Fig. 268, 271, 275) — a weak spot that bursts at the **larva–pupal ecdysis** (moult), thought to equalise water pressure inside and out of the gill. The shape of surface sculpting (often of small sharp cones, termed **scobinate**) of the black horn can be of considerable diagnostic value (Fig. 268, 278). The number of gill filaments is variable in *Austrosimulium*, as is their manner of taper. Furthermore, the surface of the gill along its length can be **annulated** or **reticulated** (Fig. 286–302); these are characters states of good taxonomic use.

The **chaetotaxy** (disposition of hairs and spines) of the abdomen is of considerable taxonomic importance in Simuliidae, but of little importance within *Austrosimulium* where all species are close to the same (Fig. 194). Of note, however, is that the genus lacks spine combs that are rows of sharp projections across the posterior abdominal terga. However, some pupae possess **grapnel hooks**. These are modified, curly, sharply-pointed hairs (Fig. 195) on the last segment (**IX**) and are of value in defining species-groups.

Cocoon

The cocoon is spun by the **pharate pupa**, that is, while the pupa is still inside the final larval instar cuticle. The larva–pupa ecdysis takes place within this cocoon. The cocoon fabric is salivary-gland silk, and while the strand-like nature of the silk can usually be observed in the cocoon (Fig. 185), in some *Austrosimulium* species the fabric appears to be foamy (giving an alveolate appearance) (Fig. 184); in others it appears to have a waxy consistency where the original strands of silk are not obvious. Cocoons in Simuliidae range from a mere strand or two of silk holding the pupa to the substrate, to complex woven structures covering the complete pupa except for the gills. Some may have fenestrae, probably to allow water flow to ventilate the gills. The basic cocoon shapes in *Austrosimulium* are relatively conservative and range from slipper- to shoe-shaped. The former has little in the way of a ventral connection around the front edge of the cocoon opening, whereas the latter can have a considerable edge. Normally, the cocoon in the shoe shape is high and fits moderately closely around the pupa. However, in some species (Fig. 143, 160) the cocoon is patellate (round and flattened like a knee cap; Crosskey 1990). There is a considerable range of projections from the anterodorsal edge of the cocoon including ridges along the dorsal surface (Fig. 154–159); so distinct are these that they are species-defining characters for some *Austrosimulium*. Indeed, Dumbleton (1973: 522) only listed the cocoon as holotype for a subspecies he erected, although he also had the pupa that formed this cocoon and the pharate female (*alveolatum* p. 117). Cocoon-spinning behaviour of Simuliidae is of considerable phylogenetic importance (Stuart & Hunter 1995, 1998). *Austrosimulium australense* was investigated by Stuart (2002) who showed that it was the sister to *Simulium* in terms of cocoon-spinning, differing in one behavioural characteristic. Stuart's work is of significance since she showed that a similar end-product shape of cocoon spinning could be achieved by different spinning behaviours. Therefore, using shape for phylogenetic purposes, but lacking knowledge of the spinning behaviour, might result in use of homoplasious characters. Since spinning behaviour has been reported only for *A. australense*, we did not use cocoon shape in the phylogenetic analysis.

Larva

The general habitus of a simuliid larva is that of a well developed cuticular head capsule and a dumbbell- or amphora-shaped body (e.g., Fig. 6, 303–319). With few exceptions the head bears 2 anterodorsal **labral fans** (cephalic or head fans). These are often considered as mouthparts, and although intimately connected with food gathering, they are actually markedly modified parts of the lateral labrum and are homologous with the lateral palatal brushes of Culicidae and Dixidae larvae (Craig 1974). The fan proper is held away from the head by a substantial fan **stalk**, or stem (Fig. 9, 10, 362). Fans consist mainly of an array of variable-length, elegantly curved rays, beset with a row of microtrichia along the ventral edge (Fig. 7, 7a). There are other minor rows of rays, variously developed. Since larvae tend to turn the body so the fans intercept the water flow, the microtrichia are on the leading edge of the ray and in large part responsible for capture of particles in the water.

Immediately posteromedial of the fan stalks are the anterolaterally-directed **antennae**. In later instar larvae these consist of a **basal**, **medial**, and **apical** article and an apical **sensillum** (Fig 10, 367–383). The proportional length of the apical article provided in descriptions does not include the apical sensillum. In 1st instar larvae there is only the apical article and sensillum; the other articles are added in subsequent instars (Dumbleton 1964b; Crosby 1974a, b; Adler *et al*. 2004). The long, narrow, apical article is unusual for simuliids: although of only minor use taxonomically within *Austrosimulium*, it is an important phylogenetic link to the South American *Paraustrosimulium*.

The mouthpart structures are the medial **labrum**, paired **mandibles** and **maxillae**, and a fused **labium** and **hypopharynx**. All these structures are underlain by a **hypostoma** (Fig. 8, 9, 13). The **labrum** is the anterior continuation of the cephalic apotome and there is no delimitation between the two. Ventromedially the labrum merges with the **labropalatum**, or epipharynx. The **mandibles** (Fig. 14) are apically complex (Craig 1977), and in *Austrosimulium* show useful characters at the species-group level. Apically and protruding is the **apical tooth**, aborally are 3 variously developed **outer teeth**, adorally and more basal are 3 **preapical teeth**, then 9–11 sharp **spinous teeth**. In other simuliid larvae that have been examined there is normally a single substantial **serration** with a basal **sensillum** and finally a **blade** region (Fig. 421). In *Austrosimulium,* and probably diagnostic for the genus, the sensillum and serration are complex and which structure is which is not obvious. The **maxillae** are mitten-shaped with the palp representing the thumb. Maxillae show no useful variation and are not dealt with here, and neither is the complex **labiohypopharynx**.

The **hypostoma** is the anteroventral portion of the head capsule and underlies the labiohypopharynx. A trapezoidal toothed structure, it is delimited posteriorly from the **postgenal bridge** by the **hypostomal groove** (Fig. 13). Laterally, the hypostoma has an array of **sublateral setae** on each side, some 4 or 5 in *Austrosimulium*, often more in other genera. They are of little taxonomic interest here. However, family-wide, the 11–13 teeth on the dorsal side of the hypostoma are of considerable importance and of some importance for *Austrosimulium.* There is a single **median tooth**, 3 **sublateral teeth** on either side of it and usually of lower prominence, and then a single more prominent **lateral tooth** on each side. Next are variously developed **paralateral teeth** — 1 is normally obvious; a 2nd may or may not be so. Not part of the teeth series, and actually on the ventral wall of the hypostoma, are sporadically-developed, rounded **lateral serrations** (Fig. 404). The teeth are more often than not (*cf* Fig. 408 and 418) obscured by the ventral wall of the hypostoma, and the degree of this obscuring is of some diagnostic significance for *Austrosimulium*.

The region posterior to the hypostomal groove (Fig. 388) is termed the **genal bridge** and is generally featureless except for some colour patterning of moderate diagnostic value. Posterior to that is a region of the head capsule which is weakly sclerotised and non-pigmented — the **postgenal cleft**. It is defined laterally by the **posterior tentorial pits** — 2 heavily sclerotised and pigmented areas continuous laterally with the postocciput; and anteriorly, usually, by the ill-defined edge of the postgenal bridge. The shape and depth of the cleft are of major taxonomic importance in Simuliidae and can be used with value in *Austrosimulium*. However, the cleft is not significantly developed, if at all, in some species. Of some diagnostic use is that in the *australense* species-group the **suboesophageal ganglion**, which is pigmented, shows through the cleft (*cf* Fig. 401, 402).

Perhaps of most taxonomic use elsewhere, and for *Austrosimulium* larvae, is the **frontolabral apotome** (cephalic apotome), the central area of the head delimited laterally and posteriorly by ecdysial lines (Fig. 10, 321, 334). Muscle attachments for the mouthparts on the apotome are often pigmented (positive) (Fig. 320), or unpigmented (negative and neutral) (Fig. 322), and their patterns and arrangement are of considerable diagnostic value. The spots are usually described as an **anteromedial**-, **posteromedial**-, **anterolateral**-, and **posterolateral group**. Sometimes this latter group is fused with pigment along the posterior of the apotome and continuous with the well-sclerotised, rim-like **postocciput** laterally and ventrally around the back of the head (Fig. 320–325). There may be other pigmentation that is of use, such as an irregular gray mottling anterior to the muscle spots (Fig. 332). The course taken by the ecdysial lines and consequent shape of the apotome are often of use. Posterior to the apotome are 2 **cervical sclerites**. In some simuliids these are part of the postocciput, but in most simuliines they are separate. Their shape is of minor diagnostic use in *Austrosimulium*. There is occasional sexual dimorphism in head pigmentation, the female usually being the darker (*cf* Fig. 320 and 321).

Laterally on the head capsule are the 3 **stemmata** (ocelli or eye spots), although they appear as 2; a large and a smaller one (Fig. 321). Above them can be a curved pigmented **eyebrow stripe**. These characters are not of diagnostic value in *Austrosimulium*.

Immediately behind the head on the ventral surface of the thorax is the single **thoracic proleg** (Fig. 6, 306). Armed with a circlet of hooks apically, this structure is important to the larvae in dealing with salivary silk and locomotion. It is not of taxonomic value in *Austrosimulium*. In later instar larvae, and in particular, mature final instar larvae, the developing histoblasts of the pupal gills, adult wings, and legs begin to show through the thoracic cuticle of the larva (Fig. 6, 305). The development of the wing and haltere histoblasts and venation was examined in detail for *Austrosimulium* by Crosby (1974c). Here, for *Austrosimulium,* the state of the **pupal gill histoblast**, when fully mature just prior to pupal **ecdysis**, is of equal importance to the pupal characters for species identification (Fig. 339–350, 351–366).

The colour of the abdomen is of minor use in diagnoses, and, as for the head, there might be sexual dimorphism in colour. Posteroventrally on the abdomen and immediately anterior to the anal proleg are 2 **ventral tubercles** (posteroventral tubercles); cone-shaped protuberances of the abdominal wall (Fig. 6, 12, 303). They are of minor use diagnostically.

Posteriorly is the **anal proleg** (Fig. 11, 12). This consists of an **anal sclerite**, **semicircular sclerite (**usually attached to an **accessory sclerite**), and a **posterior circlet** of hooks (crotchets), structures all of considerable taxonomic value (Fig. 437–453). The anal sclerite is usually X-shaped with variously developed **anterior** and **posterior arms**, and a **median plate**. In *Austrosimulium*, lateral to the median plate are rod-like **interarm struts**, also referred to as "backward struts" by Dumbleton (1973). Arising from the anterior arms the struts do not join the posterior arms, but in mounts they may appear to merge with them. The struts may taper and are of variable thickness, hence are useful for species diagnosis. The apices of the anterior arms are variously flared and emarginated as befitting a major attachment of abdominal muscles. The posterior arms taper posterolaterally, are of variable length, and are a minor diagnostic character.

Most *Austrosimulium* larvae possess a **semicircular sclerite**, a band of pigmented cuticle that surrounds the posterior circlet of hooks. All New Zealand species possess this. A superficially similar sclerite occurs in *Gigantodax* Enderlein, and sporadically in other genera. In them, more often than not, the posterior arm of the anal sclerite is continuous with this semicircular sclerite, but not so in *Austrosimulium.* The dorsolateral **terminal expansions** (= accessory sclerite) of the semicircular sclerite are variously flared and emarginated, and in some instance tapered, not flared. These states are of considerable use taxonomically.

The semicircular sclerite has been used as a character in phylogenetic analyses involving *Austrosimulium* (present in New Zealand species, absent in some in Australian), *Paraustrosimulium* (absent), *Cnesiamima* Wygodzinsky & Coscarón (absent), *Lutzsimulium* d'Andretta & d'Andretta (absent), and *Gigantodax* (present) (Dumbleton 1963b; Wygodzinsky & Coscarón 1962). There are, however, distinct possibilities that these various expressions of the sclerite are not homologous, but rather are homoplasious (arisen more than once). In all simuliid larvae examined (DAC, pers. obs. and unpublished) there is an unpigmented ring of cuticle underlying and supporting the circlet of hooks. It is this ring that is pigmented when a semicircular sclerite is deemed present, and can be seen in *A. bicorne* and *A. unicorne* where the ring is only partially pigmented (Fig. 451, 453) and the pigmented "semicircular sclerite", as such, is narrowed. Additionally, many simuliid larvae have small **accessory sclerites** ventrolateral to the posterior arms of the anal sclerite. These sclerites are where abdominal muscle insert and there are associated campaniform sensory organs. Crosby (1974b) showed in *A. tillyardianum* that the 2nd larval instar, while possessing an anal sclerite, lacked both accessory and semicircular sclerites, but the 3rd instar had accessory sclerites. The semicircular sclerite occurred in subsequent instars and incorporated the original accessory sclerites, terminally. The position of the earlier accessory sclerites shows that the terminal expansions of the semicircular sclerite are merely modified accessory sclerites and dissection shows that muscles do attach at that location (Puri 1925; DAC, pers. obs.). Adler *et al.* (2004) noted for their character #148, in *Gigantodax*—"Anal sclerite with posterior arms extended ventrally around abdomen, forming a complete ring around base of posterior circlet of hooks"—that it should not be confused with the semicircular sclerite of *Austrosimulium*. Takaoka & Craig (1999) suggested that possession of such sclerites was an adaptation to higher velocity water. Since the semicircular sclerite appears to be homoplasious, as a character it should be used with caution in higher level phylogenetic analysis.

The **posterior circlet** consists of numerous rows of hooks (Fig. 11, 12, 448). Each hook has an elegant shape —en masse designed to attach to pads of salivary silk that the larva deposits on the substrate. These are intimately involved in locomotion and filter feeding (Barr 1984). There is a strong correlation between the number of hooks and the velocity of water inhabited by larvae (Palmer & Craig 2000), with higher hook numbers found in species in higher velocity. The same applies to *Austrosimulium* larvae, so hook number appears of some significance in habitat choice by larvae; particularly so for *A. longicorne* (p. 111).

Protruding from the anus, located between the anterior arms of the anal sclerite, are thin-walled, unpigmented **rectal papillae**, used for chloride ion uptake for osmotic regulation (Fig. 6, 11, 12, 308). Usually, in specimens preserved in lower percentage ethanol, these papillae are retracted. Often multibranched elsewhere, in *Austrosimulium* they are merely 3 simple lobes and of no taxonomic value. In some simuliids considered related to *Austrosimulium,* such as *Paraustrosimulium,* there are **rectal scales** on the anal sclerite and around the base of the papillae. Such scales are absent in New Zealand *Austrosimulium* species, but in some species (Fig. 439) there are a series of small sensillae on raised bases medially on the anal sclerite. They are probably campaniform sensilla.

STUDY METHODS

Preparation of material

Freshly collected specimens are usually killed and fixed in the field in ethyl alcohol (ethanol / ETOH). Normally 70% ETOH is adequate, but not for long term preservation, or eventual DNA extraction, for which 95–100% ethanol is recommended. Such a high percentage of ethanol does, however, make specimens brittle; to soften such specimens prior to manipulation for morphological examination, partially rehydrate them in 70% (or less) ethanol.

Adults

If possible, some specimens should be dried and pinned so that colours of the adult can be accurately described. Air-drying from ethanol is not satisfactory since the specimen will collapse, and this effect also applies to killed-and-dried specimens. Preferably, recently-killed, ethanol-preserved adults should be critical-point-dried (CPD), a technique that uses liquid carbon dioxide and pressure to replace the preservative. However, CPD specimens will have slightly muted colours although they will be perfectly turgid. A technique that produces similar results to CPD is to use fluids such as hexamethyldisilazane (HMDS). These fluids evaporate extremely rapidly and do not cause collapse (Bray *et al*. 1993). Although not requiring specialised equipment beyond a fume hood, results obtained with HMDS are not quite as good as those with CPD.

To make slide mounts of structures, or to examine the genitalia, adults need to be cleared in a solution of 10% KOH (w/w potassium hydroxide) or 80% lactic acid. The former is faster, but more corrosive. A coffee mug warmer provides an ideal temperature and a timer should be set for 15 minutes. If there is no sign of any clearing, the time is repeated until the internal organs appear reddish brown and translucent. Some experience is required here since older specimens take longer, but then clear rapidly at the end. If the specimen is then transferred to distilled water, it will swell up, usually bursting somewhere, but will normally evert the genitalia. Pressure on the specimen may be required to remove the macerated internal organs, but the cuticle is elastic and returns to its original shape. Transferring the cleared specimen to ethanol hardens it sufficiently to dissect off required structures. The head can be removed and taken through a series of ethanol/glycerine concentrations and eventually into 100% glycerine on a depression slide. Examination with low magnification using a compound microscope will allow examination of most necessary details. Then, under a stereomicroscope the mouthparts can be dissected away. Transfer into ethanol to remove the glycerine and then mount on a slide. For much of the material examined here the mountant used was Gurr's original polyvinyl lactophenol (PVL). Unlike Canada Balsam, the mountant of choice, PVL shrinks slightly, but if the mountant is brought up over and around the edge of the coverslip, shrinkage does not result in air drawn under the coverslip. Euparal® mountant, if available, also makes superior microscope slides, but the longevity of both Euparal and PVL can be variable.

Legs and wings can be mounted directly out of ethanol into PVL (its major advantage). A fine pair of scissors is used to snip off the abdomen immediately behind the postnotum of the thorax. The genitalia should be removed from the posterior abdomen, cutting across at the 7th segment — for the female making sure that the spermatheca is with the genitalia. The remainder of the abdomen can be cut longitudinally down one side, spread, and the remains of tracheae removed, then mounted in PVL so that the shape and size of the tergites (Fig. 70–89) can be recorded. The genitalia are transferred to glycerine for examination.

Depending on the age and conditions of storage, specimens may be badly bleached. If that is so, then the genitalia may need staining to show some structures. Chlorazol Black (Pantin 1962) stains unsclerotised cuticle bluish/black (Fig. 20, 21). Easy to use, it can be prepared as an aqueous or alcoholic solution (the latter is better), it cannot overstain as the excess washes out, and it is permanent. Long working distance lenses of 30–50× (e.g., Leitz) are ideal for examining both male and female genitalia. Various structures (e.g., ventral plate of the male, the genital fork of the female) will need to be dissected and possibly mounted on slides for examination. Normally, after examination, all the pieces of genitalia are put into a genitalia vial and included with other parts of the adult, cleared or not; the genitalia vial can be attached to the original pin.

Pupae

Most characters of the pupae can be observed with a stereomicroscope with the specimen in ethanol. If required, a small piece of the cocoon can be slide-mounted to observe details of its fabric. The silk goes permanently brittle in ethanol, so the coverslip over the specimen might need to be weighed down while the mountant dries. Pupal exuviae usually stay within the cocoon when the adult emerges, and such exuviae are particularly useful. An informative slide mount to make is that with half the exuviae of the pupal thorax plus gill (Fig. 238–254), and similarly that of the pupal cephalic plate cuticle (Fig. 197–233). The posterior of the abdomen is often mounted to look for grapnel hooks on the last segment (Fig. 195). A fully mature pharate adult can often be dissected from the pupal cuticle, so that both can be examined. The pharate adult, though, needs to be treated with care since it is not as hardened as a mature adult would be. Pharate males are often used to describe adult male structures.

Larvae

Larvae require the most treatment and dissection technique. While they can be cleared in KOH, it is just as easy to not bother. Very fine forceps can be used to directly pull the labral fans, mandibles, and maxillae off the head and they can be mounted on slides directly. A fine pair of scissors, or a sharp blade, can be used to cut the head laterally on both sides. The muscles and internal organs usually pull off the cuticle easily with a minuten pin curved at the tip. This allows mounts of the ventral side of the head capsule for observation of the hypostoma and genal cleft. Mounting the dorsal surface is of less use, but shows the antennae. On the prothorax of mature final instar larvae, fine scissors, forceps, and minuten pins can be used to extract the black pupal gill histoblasts. When mounted in PVL the gill filaments unravel, and with manipulation using a minuten pin, a full spread of gill horn and filaments can be obtained (e.g., Fig. 270).

Mounting the posterior proleg with the anal sclerite, semicircular sclerite, and the circlet of hooks is difficult. Because it is a 3-dimensional, cone-like structure it needs to be cut to achieve a clear view of the structures. So, to obtain a mount such as in Fig. 437, in contrast to that of Fig. 448, the posterior of the abdomen is cut off at an angle from just anterior to the ventral surface of the posterior circlet of hooks, to some way along the dorsal surface of the abdomen. The circlet of hooks is then snipped at the ventral midline, spread out, and the considerable volume of muscles and gut removed with forceps and bent pins. At this stage KOH can also be used, but cleaning up manually takes less time. With one exception (Fig. 448), all the illustrations of the semicircular sclerite and circlet of hooks here have been cut at the ventral midline.

Illustrations

Dumbleton's (1973) work on New Zealand Simuliidae involved considerable contributions from others, in particular some plates of fine illustrations by J. S. Dugdale. With express permission from the Royal Society of New Zealand we reproduce some of these illustrations here. Since originals were not available, published figures were scanned at high resolution, cleaned up, and relabelled using Adobe Creative Suite®.

All photographs are digital and have been manipulated in Adobe Creative Suite®, with background removed where possible. Some images were compiled using Syncroscopy's Automontage®, but the majority used Helicon Focus® which produces fewer artifacts with this material. Lower magnification images, such as larval and pupal habitus images, were taken with a Nikon CoolPix® 4500 camera on a Wild M5A stereomicroscope with an apochromatic lens. Higher magnification images, such as the larval head and pupal gill histoblasts, were taken with the same camera using low magnification (3–10×), high resolution objectives on a Wild M20 compound microscope. For images of claws of male and female adults, a high resolution 50× oil objective was used. To achieve as close to natural colours as possible with reflected light images, a photographic gray card was used as a background to establish the white balance; that is the background reproduced here, whenever possible. Transmitted light images normally had the white level balanced for the colour temperature of illumination at any given time.

Line drawings of genitalia were made from glycerine mounts, using Leitz long-working-distance objectives, in particular that of 50×, on the Wild M20 microscope. Images were sketched using a drawing tube, traced with ink onto Mylar film, then scanned and manipulated in Adobe Creative Suite®. Unless indicated otherwise, all illustrations and images are by DAC.

General collection locations for each species are plotted on the aquatic ecoregions map (Map 20) of Harding & Winterbourn (1997a). Older collections are solid dots (e.g., NZAC collections of Dumbleton, Crosby, and others, and also from the literature); those from DAC & REGC collections since 2006 are open circles. Offshore islands do not have aquatic ecoregions yet established, however, locations are plotted over topography derived from maps from Land Information New Zealand.

For ease of use the basic molecular phylogenies are reproduced in two formats (e.g., Fig. 508a, 508b and 509a, 509b). Detailed distributions of haplotypes are plotted, separately (Fig. 510–514) on digital elevation maps (Geographx™).

Field collecting

A standard protocol (e.g., Craig *et al*. 2006) was used for the 2006–2007, 2008–2009, and 2011–2012 collections by DAC and REGC. At a flowing water locality deemed a possible habitat for simuliids, the first substrate examined was always vegetation. Trailing grass, roots, or leaves were cut off with a knife and placed into a white plastic tray. Then leaves that adhered to the substrate would be taken too. If larvae were present, they would become active after a few minutes and thrash around while still attached to the substrate and then let go. In sunlight larvae are easy to see, less so in shade. Then fist-sized stones from the edges of the water were examined where the water flow was a few centimeters deep and the velocity no less than 0.3 m/s. Recent experience indicates that slower velocities such as in seepages should also be examined. Larvae on stones tended to remain attached firmly, but curled into a protective U-shape. After a few seconds they began moving, thrashing back and forth, and then shifted position. In brighter light they are easily seen. In both situations, fine forceps were used to collect larger larvae and place them in a vial of 70–80% ethanol. If larvae were plentiful, some were fixed in Carnoy's solution (1:3 of glacial acetic acid to 98% ethanol) for future cytological (chromosomal) analysis. For both fixatives, the fluid needs to be replaced after 15–20 minutes as water and other substances leach out of the specimens, and replaced as necessary until the fixative remains clear. For ethanol-fixed specimens the final wash was always with 98–100% ethanol and this was the storage medium.

Pupae on vegetation were valuable for rearing adults, in particular males, so the first few pupae found were taken along with a small portion of the underlying leaf and placed in a tube with damp filter paper. Other pupae were placed in ethanol, particularly those taken from rocks. Pupae removed from hard substrates seemed to be easily damaged, and few if any ever emerged. However, if large plastic containers were available, pupae on rocks could be successfully reared, but with little certainty as to the pupa from which they had emerged. On emergence the adult was allowed to harden and achieve full coloration for a minimum of 2 hours prior to fixation. A sweep net could be employed to catch flying adults, but these may *not* be the same species as the immature stages in the water since adults can fly long distances. Males are occasionally known to come to car headlights at night, or to light-traps for Lepidoptera.

If there was plenty of material available at a location, 2 people could collect all the material and details necessary in 1 hour. If 2 people found no simuliids within 15 minutes, the search was abandoned.

For each locality, data recorded involved latitude, longitude, and altitude (Garmin GPSmap 60CSx®). Localities were checked on topographical maps (MapToaster Topo®) and Google Earth®. Other data recorded were place name, date, time of day, air and water temperature (CheckTemp™), pH (pHTestr 2™), conductivity (µS/cm, TDSTestr 3™, with Automatic Temperature Compensation), and mean velocity (m/sec; standpipe method, Craig 1987). A representative photograph of each collection locality was taken with emphasis on detail of the stream substrate as well as the surrounding landscape. Here representative images only are presented (Fig. 456–498), but images of all sampling localities (some exceptions) are available as part of the supplementary material for this publication at <fnz.landcareresearch.co.nz>. Each locality was assigned a consecutive number based on the island involved, e.g., NZS48 for the 48th collection in the South Island. These numbers were included on specimen collection labels and photographs, and are extensively used in this work and should be used to cross reference data. Repeat collections from the same locality were indicated with a suffixed letter, e.g., NZS48a. Some 319 localities were sampled. Further details of the Craig collections are in Appendix 1, and are also available as supplementary material in both text and spreadsheet format from <fnz.landcareresearch.co.nz>.

Geographic data recording

For the geographic distribution listing given with each species, the names of collecting localities are those used on the New Zealand topographical maps on MapToaster Topo® v.5.6 Aug 2011. In a few instances, a name is provided in square brackets also, and this indicates the bracketed name may be used on a bridge sign but is not on MapToaster Topo®. When a locality is a collecting site of DAC and REGC the corresponding collection number(s) is given immediately after it. For many streams and rivers a more detailed descriptor for the location on that waterway is provided in parentheses, e.g., "Te Awhia Stm, NZN98 (SH1 bridge)", indicates that the Te Awhia Stream collecting site NZN98 of DAC and REGC was at the State Highway 1 bridge: the geocoordinates of this collecting site can be found in either Appendix 1 or 2. Abbreviations in the listings have been used, and correspond to how waterways are referred to on MapToaster Topo®: Ck = Creek, R = River, Stm = Stream, stm = an unnamed stream, trib = an unnamed tributary. For example, "Vaila Voe Bay stm, NZS165" refers to an unnamed stream at Vaila Voe Bay on Stewart Island, the collecting site of DAC and REGC for NZS165. Many collecting localities are near roads; where this is a "State Highway" the road has been abbreviated to SH and is followed by the appropriate State Highway number as shown by MapToaster Topo®.

Dumbleton tended not to provide clear locality data on labels, but almost always gave dates, and some of his localities remain uncertain. Given, however, that many of his localities followed roadways, or involved mountaineering trips, and had consecutive dates, we attempted to provide in Appendix 2 likely latitudes and longitudes for his localities. We did that in part by using his known routes on collecting trips, Land Information New Zealand's "Place Names" website (<www.linz.govt.nz/placenames>), MapToaster Topo®, Google Earth™, and a certain amount of guesswork. Where an exact location was doubtful, the precision of the latitude and longitude was downgraded.

Locations and dates of Tonnoir's collections of Diptera were listed by Crosby (1976b).

The geocoordinates provided in Appendices 1 and 2 can be entered directly into the search boxes of Google Maps (<maps.google.co.nz>) or Google Earth, and by using "Satellite" view a user can obtain an overview of the terrain of the collecting areas and the surroundings. As many collecting sites are near roads, the "Street View" feature of Google Maps or Google Earth often can be activated, thereby allowing a user to pan 360° at eye-level around the collecting site; in addition, some sites that are away from roads may have photographs posted through Panoramio that can also be viewed in Street View. The location for the Orere Stm, NZN10 (bridge) collecting site, for example, can be found in these programs by entering the geocoordinates into the search box in different decimal degree formats (i.e., "S36.98754 E175.18852", "36.98754S 175.18852E", "-36.98754 175.18852") or degrees and minutes formats (i.e., "S36 59.242 E175 11.300", "36 59.242S 175 11.300E", "-36 59.242 175 11.300"), and the downstream view in Street View is comparable to the photograph of site NZN10 available in the Supplementary Material. Note that the geocoordinates provided in Appendix 2 rounded to the nearest minutes will go close to the collecting location, and the waterway then should be located nearby: these coordinates should be entered as "S36 59, E175 11", "36 59S, 175 11E", "36°59'S 175°11'E", or "-36 59, 175 11". An electronic version of both Appendices 1 and 2 is provided on the <fnz.landcareresearch.co.nz> website to allow users to cut and paste correctly formatted geocoordinates into these programs.

Phylogenetic Analyses

Morphological

The data matrix in Table 3 (available at <fnz.landcareresearch.co.nz>) was entered into MacClade 4.0™ with character states coded as "0", "1", "2", as required (Maddison & Maddison 2001), and analysed using PAUP* 4.0b8 (Swofford 1998). Detailed methods are given later in the Phylogenetic Analysis section (p. 54).

Molecular

See methods in Craig & Cywinska (2012, p. 60).

Material examined

Where possible slide mounts of material prepared by Tonnoir (1925) and by Dumbleton (1973) were re-examined and used. Tonnoir's slides, even though he used what appears to be glycerine jelly, are still useful, even ringed as they are with dead Psocoptera! The state of Dumbleton's slide material is variable and the mounting media for many unknown and has degenerated. There are, however, useful specimens. When used for illustrations this material is so indicated (e.g., Fig. 448). Otherwise, material used was new slide mounts made from either material in the NZAC, or collected by D. A. and R. E. G. Craig during 2006–2007, 2008–2009, and 2011–2012. This new slide material is deposited in NZAC and fully labelled.

Many thousands of specimens were examined for this revision; comprising, in the main, 330 new collections, from 319 localities, plus more than 500 vials of ethanol material and 770 pinned specimens in NZAC, mostly collected by Dumbleton. A further 280 collections mainly by TKC and colleagues during 1969–1989 were also examined. A few taxonomically important specimens were examined from other New Zealand and overseas institutions. A representative collection of species is held at the University of Alberta, Canada (UASM), and specimens also have been provided to BMNH.

Abbreviations for institutions follow Watt (1979):

AMNZ	Auckland Institute and Museum, Auckland, N.Z.
ANIC	Australian National Insect Collection, CSIRO, Canberra, Australia.
BMNH	The Natural History Museum, London (formerly British Museum (Natural History).
CMNZ	Canterbury Museum, Christchurch, N.Z.
MONZ	Museum of New Zealand Te Papa Tongarewa, Wellington, N.Z. (formerly Dominion Museum; formerly National Museum)
NHMW	Naturhistorisches Museum, Wien, Austria.
NZAC	New Zealand Arthropod Collection, Landcare Research, Auckland, N.Z. (formerly Cawthron Institute; formerly Entomology Division, DSIR)
UASM	Strickland Museum, Department of Biological Sciences, University of Alberta, Edmonton, Canada.
ZMHU	Museum für Naturkunde, Berlin, Germany (formerly Zoologische Museum, Humboldt Universitat).

Citation of type specimen label data

We give full label data for primary and secondary types. Each label is enclosed by double quote marks (" "), and the end of each line of text by a backslash (\). Male and female symbols, when occurring on labels, are transposed as {M} and {F}. Where there is a NZAC barcode, this is indicated as {barcode}. When we have provided added interpretative information within the label data, this is enclosed in square brackets "[ ]" at the point it refers; when descriptive information is provided about the label, this is enclosed in parentheses "( )" immediately following the data of that label.

General

We refer heavily to Dumbleton's (1973) seminal work on New Zealand Simuliidae. Hence, below, often we dispense with the date for that specific work. His other publications when cited have the date appended as normal.

PHYLOGENETIC ANALYSES AND HISTORICAL BIOGEOGRAPHY

Cladistic analysis based on morphology

Outgroup

Morphologically *Paraustrosimulium anthracinum* (Bigot) is considered closely related to *Austrosimulium* (e.g., Wygodzinsky & Coscarón 1962) and while Dumbleton (1973) assigned it subgeneric status in *Austrosimulium*, others since have not. Moulton (1997, 2000, 2003) using molecular analysis, showed that *P. anthracinum* was sister to the then *Austrosimulium colboi* Davies & Györkös (Davies & Györkös 1988). Examination of modern material of *A. colboi* (Moulton 2000, DAC pers. obs.), in particular the male genitalia, indicates that it is not *Austrosimulium* (by possessing a well developed paramere, which is absent in *Austrosimulium*) and should perhaps be considered as the Australian representative of *Paraustrosimulium.* Indeed, Davies & Györkös (1988) noted that their placement was provisional. However, redescription and taxonomic transfer has not yet been done, so we refer to this entity as ?*Austrosimulium colboi.* Moulton (2000) noted that placement of other Australian simuliids not in *Austrosimulium* or *Simulium* was problematic. These are the "*Cnephia*" of various authors. He makes the point that even placement in *Cnephia* is inappropriate. This segregate of some 10 species was assigned to *Paracnephia* by Crosskey & Howard (1997), but not to any subgenus. Hence, *Cnephia pilfreyi* Davies & Györkös is referred to here as ?*Paracnephia pilfreyi.* Moulton (2003) showed ?*P. pilfreyi* is sister to *P. anthracinum* + ?*A. colboi*. Placement of the above taxa in relation to the subgenera *Novaustrosimulium* and *Austrosimulium* was a number of nodes removed in Moulton's (2003) phylogeny.

Wygodzinsky & Coscarón (1973) when redescribing *Cnesiamima atroparva* (Edwards) noted that it and *P. anthracinum* form a genus pair. In a preliminary morphological cladistic analysis of the phylogeny of Simuliidae of the Southern Hemisphere, Gil-Azevedo & Maia-Herzog (2007), while not including ?*A. colboi* in their analysis, show *Cnesiamima* to be sister to *Paraustrosimulium* + *Austrosimulium*. So, we also included *Cnesiamima* in our outgroup. Therefore, the outgroup that we use here for cladistic analysis of the subgenus *Austrosimulium* is comprised of *Paraustrosimulium anthracinum,* ?*Austrosimulium colboi,* ?*Paracnephia pilfreyi,* and *Cnesiamima atroparva*.

Character scoring of these outgroup taxa is uneven. A full series of stages was available for *P. anthracinum* and ?*A. colboi* courtesy of S. Coscarón and J. K. Moulton, respectively. Of note is that the type material of ?*A. colboi* and ?*P. pilfreyi* was listed as missing by Bugledich (1999), but has, in part, been recovered (Craig 2011). The other outgroup species were scored using literature (Davies & Györkös 1988, Coscarón & Coscarón-Arias 2007); information for some characters is lacking.

Ingroup

For New Zealand *Austrosimulium* we consider 18 species. We exclude *A. vailavoense* because only females are known. Relationships of *A. vailavoense* are discussed under the species section and below under Molecular Analysis. Inclusion of *A. dumbletoni* is arguable since characters for the male were taken from gynandromorphs (Craig & Crosby 2008) and earlier stages are yet unknown. For the Australian members of the subgenus *Austrosimulium* we have chosen exemplars (Yeates 1995) from the species-groups. Choice was dictated by availability of material and level of description (Mackerras & Mackerras 1949 *et seq*.). Material available originally was of poor quality and badly bleached, so scoring of characters not provided in the literature was, at times, questionable. The Australian taxa used included *A.* (*A.*) *cornutum* Tonnoir (*ungulatum* species-group) and *A.* (*A.*) *montanum* Mackerras & Mackerras (*mirabile* species-group). New material, however, collected in 2011 allowed full characterisation of *A. montanum*. Similar problems bedeviled the Australian *Novaustrosimulium* where again we used a single exemplar from each of the two species-groups designated by Dumbleton (1973), namely *A.* (*N.*) *furiosum* (Skuse) of the *furiosum* species-group and *A.* (*N.*) *pestilens* Mackerras & Mackerras from the *bancrofti* species-group.

Given the taxon gap for the Australian material — 4 species used versus 12 known (Adler & Crosskey 2012), this cladistic analysis should be considered preliminary.

Analysis

The data matrix in Table 3 was entered into MacClade 4.0™ with character states coded as "0", "1", "2", as required (Maddison & Maddison 2001), and analysed using PAUP* 4.0b8 (Swofford 1998). All characters were equally weighted and unordered. A heuristic search was executed using the default PAUP settings. That resulted in 10 680 Equally Parsimonious Trees (EPT). We comment on the resultant Strict Consensus tree (Fig. 505). The successive weighting method (Carpenter 1988) was applied to the EPTs using the Rescaled Consistency Index (RCI) at a base weight of 10. This procedure was done once, when the number of EPTs stabilised at 815. We comment on the 50% Majority Rule Consensus from that analysis (Fig. 506). That tree was fully resolved in MacClade™ using the Resolve Polytomies function and is shown in Fig. 507 with an overlay of distribution and general ecological requirements of larvae.

Another heuristic analysis was done using the Goloboff fit at k=2. This is another method for weighting characters (Goloboff 1993). The numbers of EPTs were reduced to 816 and the Strict Consensus tree produced was the same as the 50% Majority Rule Tree above. Reweighting the characters made no difference.

Characters

Craig & Currie (1999) used 37 characters for cladistic analysis of Polynesian *Inseliellum*. That was expanded to 45 by Craig *et al*. (2001). Gil-Azevedo & Maia-Herzog (2007) used 119 for their analysis of Southern Hemisphere simuliids. While we use some of their characters, we restrict ours to 38 (see below & Table 3). Characters are fairly equally distributed among adults (characters 1–13), pupae (characters 14–26), and larvae (characters 27–38). They are listed below with the same numbers as those in the data matrix (Table 3). For each character we show the Consistency Index (CI); a measure of how well the character fits on a phylogenetic tree. Simply, if not completely compatible with the tree a character's CI will be less than unity.

Austrosimulium Character States

Adult structures

1. **Number of antennal flagellomeres** (CI 1.0)
    0. Nine
    1. Eight

Strictly, the basal 2 divisions (scape and pedicel) of the antenna are segments, containing musculature. The remaining divisions lack muscles and should be referred to as articles, or flagellomeres (Fig. 18). Character 1 of Gil-Azevedo & Maia-Herzog (2007: 42), character 5 of Py-Daniel (1982: 298). Nine flagellomeres is considered plesiomorphic for Simuliidae; lower numbers are derived. Seven in *A.* (*N.*) *bancrofti* is autapomorphic for *Austrosimulium*.

2. **Vein R1** (CI 1.0)
    0. Spiniform setae and hairs
    1. Spiniform setae absent, hairs only (Fig. 3)

Character 25 of Gil-Azevedo & Maia-Herzog (2007: 47), 10 of Py-Daniel (1989: 298).

3. **Female mandible** (CI 1.0)
    0. Teeth present on both inner and outer edges at apex
    1. Teeth only on inner edge at apex (Fig. 17)

Teeth on both sides of the mandible is plesiomorphic for simuliids. Teeth only on the inner edge of the apex is considered derived. Character 7 of Gil-Azevedo & Maia-Herzog (2007: 43), 18 of Py-Daniel (1982: 298), and 38 of Pinto-Sanchéz *et al*. (2005: 21). State (1) is synapomorphic for *Austrosimulium*. Of interest here is that female gynandromorphs of *A. dumbletoni* show a reversion to state (0) (Craig & Crosby 2008).

4. **Female hind basitarsus** (CI 0.25)
    0. Row of stout setae present (Fig. 44)
    1. Row of stout setae absent (Fig. 48)

A row of stout setae parallel to the comb of the hind basitarsus of females is widespread in basal simuliids; poorly formed in *Parasimulium*, but distinct elsewhere. Stout setae are absent in the *ungulatum* species-group of *Austrosimulium* and considered a synapomorphy for that group. Absence in *A. australense* is considered autapomorphic.

5. **Male hind basitarsus** (CI 0.17)
    0. Row of stout setae present (Fig. 43)
    1. Row of stout setae absent (Fig. 49)

State (0) is plesiomorphic for simuliids; state (1) is derived and occurs in some species-groups in *Austrosimulium.*

6. **Female tarsal claw** (CI 0.25)
    0. Basal tooth, medium–large (claw distinctly bifid) (Fig. 62)
    1. Basal tooth, absent–small (less than 1/6 length of claw) (Fig. 59)

A claw tooth is considered a plesiomorphic condition in simuliids (Currie & Grimaldi 2000; Adler *et al.* 2004) and has been clearly associated with bird biting. Character 17 of Gil-Azevedo & Maia-Herzog (2007: 44), 13 of Coscarón & Miranda-Esquival (1998:163), 142 of Adler *et al.* (2004: 152), and 48 of Pinto-Sanchéz *et al*. (2005: 22). Absence and reduction within *Austrosimulium* is considered derived.

7. **Female genital fork** (CI 1.0)
    0. Anterior arm narrow
    1. Anterior arm broad (Fig. 108)

Character 34 of Gil-Azevedo & Maia-Herzog (2007: 48) who considered state (0) plesiomorphic. State (1) is synapomorphic to *Paraustrosimulium* + *Austrosimulium*.

8. **Female genital fork apodeme** (CI 1.0)
    0. Lateral plate apodeme not markedly developed
    1. Apodeme developed (Fig. 108)

This apodeme is situated at the junction of the lateral plate and lateral arm of the genital fork and is **not** homologous to character 35 of Gil-Azevedo & Maia-Herzog (2007: 48) and 145 of Adler *et al*. (2004: 152) — vis-à-vis the extensive apodeme in *Gigantodax* Enderlein + *Pedrowygomyia* Coscarón & Miranda-Esquivel that arises from the lateral arm and extends anteriorly. Character 137 of Adler *et al*. (2004: 151) who are of the opinion that an apodeme is synapomorphic for Simuliini.

9. **Female genital fork lateral lobe** (CI 1.0)
    0. Large (Fig. 110)
    1. Small (Fig. 108)

State (1) is synapomorphic for the *australense*-subgroup in New Zealand.

10. **Male gonostylus shape** (CI 0.25)
    0. Quadratic to subtriangular–broad (Fig. 126–128)
    1. Narrower and tapered (Fig. 136–142)

The outgroup and all the *australense* species-group possess state (0), with the exception of *A*. (*A*.) *albovelatum*. State (1) is synapomorphic for the *ungulatum* species-group in New Zealand and for one of the Australian exemplars.

11. **Gonostylus terminal spine number** (CI 0.25)
    0. Two (Fig. 130)
    1. Three (Fig. 126)
    2. Four

Modified character 48 of Gil-Azevedo & Maia-Herzog (2007: 50), who considered the plesiomorphic condition for Simuliini to be two spines; more spines is considered derived.

12. **Paramere development** (CI 0.5)
    0. Present and well developed (plate-like)
    1. Only basal connection to gonocoxa present (Fig. 128, 140)
    2. Poorly developed (sometimes present as thin twisted rod) (Fig. 131)

Character 52 of Gil-Azevedo & Maia-Herzog (2007: 50), 26 of Py-Daniel (1982: 299). In part character 136 of Adler *et al*. (2004:151). Present in basal simuliids, and markedly variable in development elsewhere. Here, the poor development in *Austrosimulium* is considered derived.

13. **Paramere spines** (CI 0.33)
    0. Present
    1. Absent

Character 25 of Currie & Grimaldi (2000: 479) who considered presence of spines as synapomorphic for Simuliini. Adler *et al*. (2004), however, considered lack of spines as plesiomorphic in Simuliini and their presence derived. Character 54 of Gil-Azevedo & Maia-Herzog (2007: 50), 182 of Adler *et al*. (2004: 155). Absence in *Austrosimulium* can be considered derived.

Pupal structures

14. **Cocoon fabric** (CI 0.40)
    0. Fibrous (Fig. 178)
    1. Alveolate (Fig. 187)
    2. Alveolate and gelatinous (Fig. 191)

A fibrous (0) cocoon is plesiomorphic for simuliids and occurs here in the outgroup. The alveolate (1) and gelatinous (2) states are here considered derived. State (1) is particularly developed in *A. alveolatum* and *A. laticorne*.

15. **Anterior projections on cocoon** (CI 0.5)
    0. Absent (Fig. 160)
    1. One (Fig. 177)
    2. Two (Fig. 175)

A simple anterior opening with or without a definite rim and no projections appears plesiomorphic for simuliids. Anterior projections are, here, considered derived.

16. **Cephalic plate depression** (CI 1.0)
    0. Not concave dorsally (Fig. 202)
    1. Concave dorsally (Fig. 205)

A non-depressed cephalic plate appears plesiomorphic in simuliids. The marked concavity in the *tillyardianum* species-group of New Zealand *Austrosimulium* is considered synapomorphic.

17. **Cephalic plate shape in female** (CI 0.5)
    0. Width of frons base distinctly more than 1/2 the height of plate (Fig. 212–216)
    1. Width of frons base subequal to 1/2, or less than 1/2, height of plate (Fig. 202–215)

State (0) is considered plesiomorphic. All members of the *australense* species-group possess state (1), those of the *ungulatum* species-group state (0).

18. **Cephalic plate facial setae** (CI 0.5)
    0. Present (Fig. 214)
    1. Absent (Fig. 205)

State (0) appears plesiomorphic in simuliids. State (1) is synapomorphic to the *australense* and *tillyardianum* species-group (with the exception of *A. albovelatum*).

Table 3 Character states for morphological cladistic analysis of *Austrosimulium*.

	Character number and coded state																																					
Taxa	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**
Paraustrosimulium anthracinum	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	0	1	0	0	1	0	0	0
?Austrosimulium colboi	1	1	0	1	1	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	3	0	0	0	1	1	0	1	1	0	1	1	0	0	2
Cnesiamima atroparva	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	2
?Paracnephia pilfreyi	0	1	0	1	?	1	0	0	0	1	2	?	?	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0	2
A. (N.) furiosum	1	1	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	1	0	0	0
A. (N.) pestilens	1	1	1	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	1	0	1	1	0	0	2
A. (A.) australense	1	1	1	1	1	1	1	1	1	0	1	2	1	0	0	0	1	1	0	1	2	1	1	0	1	0	0	1	1	0	1	1	0	1	1	2	1	2
A. (A.) longicorne	1	1	1	0	0	1	1	1	1	0	1	2	1	0	0	0	1	1	0	1	2	1	1	2	1	0	0	1	1	0	1	1	0	1	1	2	1	2
A. (A.) albovelatum	1	1	1	0	0	1	1	1	0	1	0	2	1	2	0	1	1	1	1	0	1	0	1	2	1	1	0	1	1	0	1	1	0	1	1	2	1	0
A. (A.) extendorum	1	1	1	0	0	1	1	1	?	?	?	2	1	0	0	1	1	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	0	1	1	2	1	0
A. (A.) stewartense	1	1	1	0	1	1	1	1	0	0	1	2	1	0	0	1	1	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	0	1	1	2	1	0
A. (A.) fiordense	1	1	1	0	0	1	1	1	0	?	?	?	?	0	0	1	1	1	0	2	2	0	1	0	1	1	0	1	1	0	1	1	0	1	1	2	1	0
A. (A.) laticorne	1	1	1	0	0	1	1	1	0	0	1	?	1	1	0	1	1	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	0	1	1	2	1	0
A. (A.) dumbletoni	1	1	1	1	1	1	1	1	0	1	0	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
A. (A.) alveolatum	1	1	1	0	0	1	1	1	0	0	1	2	1	1	0	1	1	1	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	2	1	0
A. (A.) dugdalei	1	1	1	0	0	1	1	1	0	0	1	2	1	0	0	1	1	1	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	2	1	0
A. (A.) multicorne	1	1	1	0	0	1	1	1	0	0	1	2	1	0	0	1	1	1	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	2	1	0
A. (A.) tillyardianum	1	1	1	0	1	1	1	1	0	0	1	2	1	1	0	1	1	1	0	0	1	1	0	1	1	1	0	1	1	0	1	1	0	1	1	2	1	0
A. (A.) ungulatum	1	1	1	1	1	1	1	1	0	1	0	2	1	1	2	0	0	0	2	0	0	0	1	2	1	0	0	1	1	1	1	1	0	1	1	1	1	0
A. (A.) vexans	1	1	1	1	1	1	1	1	0	1	0	2	1	0	2	0	0	0	2	0	0	0	1	2	1	0	0	1	1	1	1	1	0	1	1	1	1	0
A. (A.) campbellense	1	1	1	1	1	1	1	1	0	1	0	2	1	0	2	0	0	0	2	0	0	0	1	2	1	0	0	1	1	1	1	1	0	1	1	1	1	1
A. (A.) unicorne	1	1	1	1	1	0	1	1	0	1	0	1	1	2	1	0	0	0	2	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	1	1
A. (A.) bicorne	1	1	1	1	1	0	1	1	0	1	0	1	1	2	2	0	0	0	2	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	1	1
A. (A.) tonnoiri	1	1	1	1	1	0	1	1	0	1	0	1	1	2	2	0	0	0	2	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	1	0	1	1
A. (A.) montanum	1	1	1	1	1	0	1	1	0	1	0	2	1	0	1	0	0	0	2	1	2	0	0	0	1	0	0	1	1	0	1	0	1	1	1	1	1	0
A. (A.) cornutum	1	1	1	1	1	0	1	1	0	1	0	0	0	0	1	0	0	0	2	0	0	0	0	0	1	0	0	1	1	0	1	0	1	1	1	0	1	0

19. **Ocular setae** (CI 1.0)
0. Absent (Fig. 203)
1. Hair-like (Fig. 204)
2. Spine-like (Fig. 214–216)

These are sensilla as shown by the dendritic sheath that is sometimes apparent (Fig. 196). State (2) is synapomorphic for the *ungulatum* species-group. State (1) in *A. albovelatum* of the *tillyardianum*-subgroup (otherwise all with state (0)) is something of a conundrum, similar to other character states of that species which tend to emulate those of the *ungulatum* species-group.

20. **Thoracic cuticle** (CI 0.67)
0. Tuberculate (Fig. 240, 253)
1. Nontuberculate (Fig. 238, 239)

State (0) is widespread in the taxa under consideration, although in some it is poorly developed. Hence tuberculation is considered plesiomorphic. State (1) in the *australense*-subgroup appears to be synapomorphic. Within the *tillyardianum*-subgroup, state (1) in *A. fiordense* is autapomorphic.

21. **Tubercle pattern** (CI 0.67)
0. Tubercles randomly arranged (Fig. 252)
1. Tubercles grouped in patterns (Fig. 240)
2. Tubercles absent

State (0) appears plesiomorphic in the taxa considered. State (1) is synapomorphic for the *tillyardianum*-subgroup.

22. **Thoracic dorsal sensilla** (CI 0.50)
0. Posterior sensilla pair stiff, spine-like (Fig. 250)
1. All sensilla fine and trichoid (Fig. 240)

Often referred to as "trichomes", the subdorsal sensilla on the scutum are state (0) in the outgroup and one clade of New Zealand *Austrosimulium.* The trichoid state (1) appears to be the derived condition, and such sensilla are often broken off.

23. **Gill base** (CI 0.33)
0. Horn-like (Fig. 270–273)
1. Not horn-like (Fig. 280–282)

State (1) is synapomorphic for the *ungulatum*-subgroup and autapomorphic for *A. longicorne* in the *australense*-subgroup. Scoring of this character is probably suboptimal.

24. **Gill filament surface** (CI 0.6)
0. Annulated (Fig. 292–293)
1. Reticulated (Fig. 297)
2. Pseudoannulated (Fig. 296)
3. Nonfilamentous gill

State (0) is plesiomorphic for the taxa considered. State (1) is autapomorphic for *A. tillyardianum*. State (2) is synapomorphic for the *ungulatum*-subgroup and autapomorphic for *A. longicorne*.

25. **Spine combs on posterior abdomen** (CI 0.6)
0. Present
1. Absent (Fig. 194)

State (1) is synapomorphic for *Austrosimulium*.

26. **Grapnel hooks on posterior abdomen** (CI 1.0)
0. Present (Fig. 195)
1. Absent

State (1) is synapomorphic for the *tillyardianum*-subgroup.

Larval structures

27. **Antenna apical article** (CI 1.0)
0. Distinctly longer than median plus basal article (Fig. 367–383)
1. Equal in length to median plus basal article

Modified character 99 of Gil-Azevedo & Maia-Herzog (2007: 56). State (1) appears synapomorphic for *Novaustrosimulium*.

28. **Mandible sensillum and serrations** (CI 1.0)
0. Single serration and sensillum
1. Serration and sensillum complex (Fig. 421)

Basically character 101 of Gil-Azevedo & Maia-Herzog (2007: 56). State (1) is synapomorphic for *Paraustrosimulium* + *Austrosimulium*.

29. **Mandible spinous teeth number** (CI 1.0)
0. Three or four
1. More than four (Fig. 421)

State (1) is synapomorphic for *Austrosimulium*.

30. **Shape of pharate pupal gill** (CI 0.5)
0. Not L-shaped (Fig. 351–360)
1. L-shaped (Fig. 361–366)

State (1) is synapomorphic for the New Zealand *ungulatum* species-group within subgenus *Austrosimulium*.

31. **Rectal scales** (CI 0.0)
0. Present
1. Absent (Fig. 437–442)

State (1) is synapomorphic for *Austrosimulium.*

32. **Anal sclerite central region** (CI 0.33)
0. Not robustly developed (Fig. 441)
1. Robustly developed (Fig. 437–440)

State (0) appears plesiomorphic for simuliids. New Zealand *Austrosimulium* with one exception (*A. dugdalei*) possess state (1). In the subgenus *Inseliellum*, in Polynesia, a robust central region appears correlated with the presence of a semicircular sclerite (Craig & Currie 1999: Figure 5).

33. **Anal sclerite arm lengths** (CI 0.33)
0. Ventral arm distinctly longer than dorsal arm (Fig. 437, 442)
1. Dorsal and ventral arms subequal in length

Character 114 of Gil-Azevedo & Maia-Herzog (2007: 59). State (0) is synapomorphic to *Paraustrosimulium* + *Austrosimulium* (with exceptions in Australia).

34. **Anal sclerite anterior arms expression** (CI 0.5)
  0. Not flared or emarginated
  1. Flared and emarginated (Fig. 447)

With the exception of ?*A. colboi*, state (0) occurs in the outgroup. State (1) occurs in ?*A. colboi* + *Austrosimulium*. Flared anterior arms, which are muscle apodemes, appear correlated to presence of a semicircular sclerite.

35. **Anal sclerite interarm strut** (CI 1.0)
  0. Absent
  1. Present (Fig. 347-440)

Character 117 Gil-Azevedo & Maia-Herzog (2007: 59), 149 of Adler *et al*. (2004: 153). State (1) is synapomorphic for *Paraustrosimulium* + *Austrosimulium.*

36. **Accessory sclerite** (CI 0.5)
  0. Absent (Fig. 451–453)
  1. Poorly developed (Fig. 448–450)
  2. Well developed (Fig. 437–442)

State (0) occurs in the *unicorne*-subgroup, state (1) in the *ungulatum*-subgroup, and state (2) in the *australense* species-group.

37. **Semicircular sclerite** (CI 1.0)
  0. Absent
  1. Present (Fig. 437–442)

The semicircular sclerite considered here is not continuous with the ventral arms of the anal sclerite. Modified character 118 of Gil-Azevedo & Maia-Herzog (2007: 59). Character 148 of Adler *et al.* (2004: 53) who make the strong point that this sclerite is **not** homologous to the condition seen in *Gigantodax*. It is similarly homoplasious in *Simulium* (*Gomphostilbia*) *palauense* Stone (Takaoka & Craig 1999), *S.* (*Inseliellum*) *cataractarum* Craig (Craig 1987), *S.* (*I.*) *concludium* Craig (Craig 1997), and *Crozetia* spp. (Craig *et al*. 2003). State (1) occurs in subgenus *Austrosimulium*, and state (0) in *Novaustrosimulium.* Of note is that in subgenus *Austrosimulium* the semicircular sclerite is continuous around the circlet of hooks, but in *A. cornutum* (Australian *ungulatum* species-group) it is not continued mid-ventrally. See Terms section (p. 42) for more explanation.

38. **Number of hooks in anal proleg circlet** (CI 0.33)
  0. More than 1 000 and up to 1 800
  1. More than 2 000
  2. Less than 999

Palmer & Craig (2000) showed a strong correlation between the number of the hooks in the posterior circlet and the velocity of water experienced by larvae of particular species. This shows particularly in larvae of *A. longicorne* which inhabit flows of markedly low velocity and possess the smallest number of hooks.

Results and discussion

Because of the considerable taxon data gap for Australian *Austrosimulium* species, in particular that of subgenus *Novaustrosimulium*, results from this morphological cladistic analyses should be considered preliminary even though there is especially strong support (Fig. 506) for the backbone of the phylogeny.

Consensus Tree

Analysis of the data matrix (Table 3) produced 10 680 equally parsimonious trees (TL 99, CI 0.5). The strict consensus tree is shown in Fig. 505. The outgroup is fully resolved with *Cnesiamima atroparva* + ?*Paracnephia pilfreyi* and *Paraustrosimulium anthracinum* + ?*Austrosimulium colboi* as sister clades; not at variance to relationships suggested by Moulton (2003) and Gil-Azevedo & Maia-Herzog (2007). Within *Austrosimulium* the exemplars of *Novaustrosimulium* (Australian only)*, A.* (*N.*) *furiosum* (*furiosum* species-group) and *A.* (*N.*) *pestilens* (*bancrofti* species-group) are in polytomy with subgenus *Austrosimulium* (Australia and New Zealand). This is perhaps an indication that *Novaustrosimulium* needs taxonomic revision. Within the *australense* species-group, Dumbleton's *australense*- and *tillyardianum*-subgroups resolve, but, the terminal taxa in the latter subgroup do so poorly. For the *ungulatum* species-group a clade of the two Australian exemplars, *A.* (*A.*) *cornutum* (*ungulatum* species-group) + *A.* (*A.*) *montanum* (*mirabile* species-group) is unresolved with respect to the remainder of the *ungulatum* species-group. The *unicorne*-subgroup is a terminally unresolved clade. The relationship of the Australian exemplars is slightly at variance to that proposed by Dumbleton, where he placed the *mirabile* species-group sister to the *ungulatum* species-group (Australia + New Zealand). Within the New Zealand *ungulatum* species-group, the constituents of the *ungulatum*-subgroup are in a polytomy with the *unicorne*-subgroup. The overall strong concordance of the backbone of this tree to that of Dumbleton's species-groupings (his Fig. 252) was expected since he used synapomorphies for his relationships within *Austrosimulium*.

50% Majority Rule Tree

A single reweighting of the original 10 680 trees, using the rescaled consistency index at a base weight of 10, resulted in 815 trees, with no further reduction. The 50% Majority Rule tree of those trees is shown in Fig 506. Extremely high to full support shows for the backbone of the tree, and more of the terminal taxa were fully resolved. We show, simply, just branch support with no other statistics, since it is known (Craig & Currie 1999, Craig *et al*. 2001) that such basic analyses produce robust trees for Simuliidae.

For the outgroup taxa, *Paraustrosimulium anthracinum* + ?*Austrosimulium colboi* are sister to *Cnesiamima* *atroparva* + ?*Paracnephia pilfreyi,* with full support for both clades. There is no disagreement with the relationships suggested by Moulton (2003) and Gil-Azevedo & Maia-Herzog (2007). For *Austrosimulium*, the *Novaustrosimulium* exemplars, *A. furiosum* and *A. pestilens* are now resolved as sister taxa (Fig. 505).

There is full support, again, for Dumbleton's *australense* and *ungulatum* species-groups. In the former, the *A. australense* + *A. longicorne* clade that comprises the *australense*-subgroup is fully supported. Similarly supported is the *tillyardianum*-subgroup, but *A. albovelatum, A. extendorum, A. stewartense*, *A. laticorne* are unresolved in relation to the clades ((*A. alveolatum* + *A. tillyardianum*) and (*A. dugdalei* +*A. multicorne*)) with *A. fiordense* sister. The latter two clades are only moderately well supported. *Austrosimulium fiordense* is sister because of the unique lack of tuberculation on the pupal thoracic cuticle. That *A. dugdalei* and *A. multicorne* are sister species was expected.

In the *ungulatum* species-group the two Australian exemplars are again sister to the remainder, and both clades have full support. For the New Zealand species the two currently recognised subgroups, *ungulatum*- and *unicorne*- of Dumbleton, resolve as sister clades; the former with little support, the latter with full support. *Austrosimulium unicorne* (*unicorne*-subgroup) is sister to *A. bicorne* + *A. tonnoiri,* the latter clade with poor support. The *ungulatum*-subgroup is poorly supported and largely unresolved, with *A. dumbletoni* sister to the other three species, and that clade too has poor support.

Shortest Possible Tree

Resolving all terminal taxa using the Resolve Polytomies function in MacClade, resulted in the tree shown in Fig. 507. We have drafted the figure to be in concordance with that of Dumbleton's Figure 252 and have overlain geographic and ecological data.

There is little difference from the Majority Rule Tree (Fig. 506). The *ungulatum* species-group resolves as for Dumbleton, with *A. unicorne* sister to *A. bicorne* + *A. tonnoiri*, and that clade is strikingly similar to that derived from molecular data (Fig. 514). Within the *tillyardianum*-subgroup of the *australense* species-group, *A. fiordense* is again sister to all the remaining species. The previously fully supported, but terminally partially unresolved clade is now resolved with *A. tillyardianum* + *A. alveolatum* as sister taxa with the sister clade of *Austrosimulium dugdalei* +*A. multicorne*, the latter expected. Sister to those is *A. albovelatum*. The latter's placement was expected as *A. albovelatum* possesses a series of unusual character states reminiscent of the *ungulatum*-subgroup. *Austrosimulium extendorum* + *A. stewartense* are sister to *A. laticorne*.

The geographic overlay shows that both lineages of the outgroup have sister taxa in Australia and South America, and indicates a Gondwanan provenance for that outgroup clade. That the subgenus *Novaustrosimulium* does not resolve into a monophyletic clade is problematic and indicates that the subgenus needs taxonomic revision. *Austrosimulium* (*A.*) *cornutum* + *A.* (*A.*) *montanum* (Australia) remain resolved as sister species, but taxonomically they are in different species-groups. Placement as sister to the New Zealand clade of the *ungulatum* species-group suggests dispersal of that clade from Australia, independent of the New Zealand *australense* species-group. The majority of *Austrosimulium* species are restricted to the South Island, Stewart Island, plus the subantarctic islands. The North Island has only one endemic species, *A. dugdalei*, which is sister to *A. multicorne* (see species descriptions). Otherwise, both *A. australense* and *A. tillyardianum* are widely spread in the North Island, with the former to the northern tip at Cape Reinga.

Of importance phylogenetically is that the South American outgroup species (*Cnesiamima atroparva, Paraustrosimulium anthracinum*) have cool to very cold water requirements for the immature stages and occur at higher altitudes, similar to immatures of the *unicorne*-subgroup in New Zealand. Both the Australian representatives of the outgroup (?*Paracnephia pilfreyi*, ?*Austrosimulium colboi*), while tending to have less cold requirements, are found in cool temperate conditions and at moderate altitudes (Davies & Györkös 1988). We are of the opinion that this is indicative of a basic ecological template for this segregate of simuliids that includes *Austrosimulium*. Also, the normal substrate for the outgroup species is vegetation of various sorts, as it is for some members of the *ungulatum* group. That preference also occurs in the *australense* species-group, namely for *A. australense*. The typical habitat of the *tillyardianum*-subgroup is, in general, hard substrate in small to open sunlit streams, with a wide range of altitudes. The phylogeny indicates this is a derived preference.

The ecological requirements of the immature stages of New Zealand simuliid species are for the most part quite distinct. For this reason Dumbleton's original ecological keys for *Austrosimulium* spp., and which we have reprised here, work quite well. Therefore it behooves aquatic ecologists to identify to species any simuliid involved in their work – something that currently is generally not done.

Of the Australian representatives involved here, *A. pestilens* occurs mainly in Queensland and also farther west of other species and can be considered a warm temperature species. *Austrosimulium furiosum* is widely distributed from Queensland south into Tasmania. However, apart from the northern localities, the majority are at higher altitudes and cooler temperatures, particularly in Tasmania. Similarly, *A. montanum* and *A. cornutum* occur at higher altitudes along the eastern coast, with the latter also being found in Tasmania.

Craig, D. A.; Cywinska, A. 2012: Molecular analysis of New Zealand *Austrosimulium* (Diptera: Simuliidae) species. Pp. 60–65, 205–208, 298–301, *in* Craig, D. A.; Craig, R. E. G.; Crosby, T. K. 2012: Simuliidae (Insecta: Diptera). *Fauna of New Zealand 68*, 336 pp.

Molecular analysis of New Zealand *Austrosimulium* (Diptera: Simuliidae) species

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Introduction

Molecular investigation of Simuliidae taxonomy has been sporadic. While interfamilial relationships of the Culicomorpha are well investigated (Pawlowski *et al.* 1996; Wiegmann *et al.* 2011), Moulton (1997, 2000, 2003) is the chief source for relationships within Simuliidae. Intrafamilial investigations are reviewed by Phayuhasena *et al.* (2010). For *Austrosimulium* there are only studies by Ballard (1994) and by Moulton, both restricted to Australian exemplars of the genus. There has been no such work on the New Zealand *Austrosimulium* fauna. Ballard's study is of interest in that he used the rRNA 12S gene. That aligned with morphological differences between *Austrosimulium* (*N.*) *pestilens* Mackerras & Mackerras and *A.* (*N.*) *bancrofti* (Taylor), but could not resolve cytoforms known for *A. bancrofti* (Ballard & Bedo 1991). This result is similar in many ways to the situation reported by Conflitti *et al.* (2010) in which molecular and cytological evidence was taxonomically contradictory.

Other works on simuliids, too, have shown confusing results. Krueger & Hennings (2006) in a study of the *Simulium damnosum* Theobald complex (Africa) found striking inconsistencies in tree topologies depending on sequences used, and there was little correlation to host preference, behaviour, or other ecological parameters. On the other hand, Ilmonen *et al.* (2009) successfully used multiple characters from cytology, cytochrome c-oxidase subunit 1 (CO1) gene sequences, ecology, and morphology to clarify species status within the European *Simulium vernum* Macquart group. Similarly, multiple genes were used successfully, for the most part, at the species level for Thai simuliids (Phayuhasena *et al.* 2010).

Here we report on an extensive molecular dataset from the mitochondrial DNA CO1 gene (standard CO1-5' barcodes and CO1-3' markers) and that of mt16S rRNA gene, for New Zealand *Austrosimulium*. Concordance between backbone topology for species relationships derived from CO1 sequences and those from morphology is high (*cf* Fig. 505–507, 508–514). The results from this section are used elsewhere in this monograph for biogeographic purposes.

We note that we had no Australian *Austrosimulium* species in the dataset, and likewise 3 New Zealand species were not included, as material was not available for *A. extendorum* and *A. fiordense* (*tillyardianum*-subgroup) or *A. campbellense* (*ungulatum*-subgroup). However, it is unknown whether the absence of these species biased the results, given there was marked concatenation of available species within the *tillyardianum* subgroup (Fig 508, 508a).

Similarly there was a dearth of Australian *Austrosimulium* taxa in the morphological cladistic analysis section in this monograph (p. 53). Indeed, that segregate of the genus needs to be taxonomically revised, morphological descriptions brought up-to-date, and then exemplars included in molecular analyses.

Methods

DNA extractions for individual simuliids were obtained from tissue contained in 1–3 legs of adult specimens, or from the thoraxes of pupae and larvae, all fixed in at least 90% ethanol. Some 350 individuals were analysed from 165 samples. Voucher specimens are deposited in the New Zealand Arthropod Collection (NZAC), Landcare Research, Auckland, New Zealand.

For each individual, 30 µL of total DNA was extracted using the GeneElute™ Mammalian Genomic DNA Miniprep Kit (Sigma-Aldrich Co., St. Louis, MO, 2003). Three pairs of primers were used to amplify the DNA extracts for standard DNA barcodes from the 5' region of mtCO1 gene, non-standard DNA barcodes from the 3' region of mtCO1, to cover the whole mtCO1 gene, and mt16S rRNA. A pair of universal primers, LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer *et al.* 1994), was used to amplify the standard CO1-5' barcodes, i.e., *ca* 650 bp fragments at the 5'-terminus of the mitochondrial gene for cytochrome c oxidase subunit 1 (CO1; Folmer standardised region), which were trimmed to 618 bp. The CO1-3'primers, C1-J-2195 (5'-TTGATTTTTTGGTCATCCAGAAGT-3') (Simons *et al.* 1994) and UEA10 –tRNA Leu gene (5'-TCCAAT-

GCACTAATCTGCCATATTA-3’) (Lunt *et al.*1996) were used to amplify an 804 bp fragment in the remaining part of the CO1 gene. The universal mt16S primers, 16SA-L (5’-CGCCTGTTTATCAAAAACAT-3’) and 16SB-H (5’-CCGGTCT GAACTCAGATCACGT-3’) (Palumbi *et al.* 1991), were used to produce DNA templates in the mt 16S gene region; originally 550 bp long they were subsequently trimmed to 502 bp.

Each PCR cocktail contained 2.3 µL of 10×PCR buffer, pH 8.3 (10 mM of Tris-HCl, pH 8.3; and 50 mM of KCl; 0.01% NP-40),1.3 µL of mM $MgCl_2$, 200 µM of each NTP, 1 unit Taq polymerase, 0.3 µM of each primer, 1–5 µL of DNA template and the remaining volume of ddH_2O up to 25 µL. The PCR thermal regime consisted of one cycle of 1 min at 95ºC; 35 cycles of 1 min at 94ºC; 1 min at 55ºC; and 1.5 min at 72ºC, and a final cycle of 7 min at 72ºC. All PCR products were subjected to dye terminator cycle sequencing reactions (30 cycles, 55ºC annealing), and sequenced on ABI 3730 automated sequencers, using terminators with Big Dye v. 3.1, forward and reverse primers.

Electropherograms of obtained sequences were edited and aligned with Sequencher™ v.4.5 (Gene Codes Corporation, Ann Arbor, MI, USA). Pairwise nucleotide sequence divergences were calculated using the Kimura 2-parameter model (Kimura 1980), while neighbour-joining (NJ) analysis (Saitou & Nei 1987) in MEGA™ 5.5 was used to examine relationships among taxa and determine bootstrap support for lineages. The tree was rooted using *Simulium latipes* (Meigen).

All sequences obtained in this study and their numbers are available on the Barcode of Life Data System <http://www.boldsystems.org/> under “New Zealand Simuliidae” in the “Completed Project” section. The sequence numbers are also available from Appendix 3 (p. 205), and on the website <fnz.landcareresearch.co.nz>.

Results and Discussion

Our molecular screening of *Austrosimulium* worked reasonably well for most of the analysed species: the target DNA was easily recovered from small amounts of insect tissue and aligned for all *Austrosimulium* species. Two groups of mtCO1 markers, the standard CO1-5’ barcodes and the non-standard barcode CO1-3’ sequences, contained no indels, their alignments were straightforward, and they lacked nonsense codons and pseudogenes. The third marker, mt16S, showed eight gaps per sequence.

Guanine-cytosine (GC) content provides a swift insight into mitochondrial genome biodiversity and nucleotide usage. Mitochondrial genomes show considerable variation in the GC contents (reflecting horizontal gene transfer or mutational bias) within phyla (Clare *et al.* 2008), a characteristic that can be utilised to measure the diversity among mitochondrial genomes in taxonomic classifications (Cywinska *et al.* 2010). The whole mitochondrial GC content can be estimated from GC variability in the standardised CO1-5’ barcodes as it is well correlated with that of full mitochondrial genomes (Clare *et al.* 2008).

In this study the standard CO1-5’ barcodes demonstrated A+T bias (average 64.3% for all codons), and was especially strong at third codon positions (average 82.4%) for all *Austrosimulium* species. The nucleotide composition varied slightly among species, with A+T content ranging in standard CO1-5’ barcodes from 63.1% (*A. stewartense*) to 65.4% (*A. australense*) for all codons, and from 79.5% to 85.2% at their third codon positions. Non-standard CO1-3’ barcodes also showed a significant A+T bias, with an average A+T content of 65.2% for all codons and 79.0% at the third codon positions.

Thus, the analysis of the *Austrosimulium* standard barcode CO1-5’ and non-standard CO1-3’ regions showed that the average GC content (35–36%) for all codon positions can be placed slightly above the centre of 22–45% GC range for the phylum Insecta (Clare *et al.* 2008). The average GC content for *Austrosimulium* species was somewhat larger than that observed in standard CO1-5’ barcodes for Tabanidae (32%; Cywinska *et al.* 2010), Canadian Culicidae (33%; Cywinska *et al.* 2006), and for Chironomidae (Ekrem *et al.* 2007).

The *Austrosimulium* CO1 sequences show skewed GC content distribution, with low GC presence at the third codon positions (average 18–21% for CO1-5’ and CO1-3’, respectively), which points to a strong shift in nucleotide usage at those sites. Still, the GC content in *Austrosimulium* is less skewed than that in mtCO1-5’ of Tabanidae with an average 3% GC at the third codon position (Cywinska *et al.* 2010).

Conspecific K2P divergence for *Austrosimulium* barcode CO1-5’ sequences averaged 2.3% (range 0–6.9%). Congeneric average divergence was at 6.7% (range 0.9%–11.4%). For non-standard CO1-3’ barcodes, the mean conspecific divergence averaged 1.4% (range 0–14.2%) and congeneric divergence averaged 7.5% (range 0.8–13.6%). Thus, conspecific average values were lower for CO1-3’ sequences in comparison to CO1-5’ sequences, with wider range of intraspecific divergence.

Austrosimulium australense, represented here by 125 specimens, showed the highest interspecific similarity in the CO1-3’ region, with 1.9% average sequence divergence (range 0– 4.5%). For the same CO1-3’ region, *A. longicorne* (14 specimens) and *A. ungulatum* (38 individuals) showed less tight conspecific groupings, with relatively high average intraspecific sequence divergence of 3.6% (range 0–9.2%) and 2.6% (range 0–14.2%) respectively.

The average conspecific values were much higher for *Austrosimulium* species than, for example, for North American mosquitoes (0.5% K2P for CO1-5' Cywinska *et al.* 2006), tabanids (0.49% for CO1-5" and 0.39% for CO1-3"; Cywinska *et al.* 2010), North American birds (0.27%; Hebert *et al.* 2004), and moths (0.25%; Hebert *et al.* 2003).

Likewise, the non-standard CO1-3' sequences for the outgroup species *Simulium latipes* used in this study showed divergences 5–7 times lower than for *Austrosimulium* with an average of 0.31% (range 0 – 6.3%).

The average congeneric divergences for *Austrosimulium* (6.7% K2P for CO1-5' and 7.5% for CO1-3') were similar to those for other simuliids (4% K2P for CO1-5' and 6.5% for CO1-3'; Ilmonen *et al.* 2009), mosquitoes (10.4% K2P for CO1-5'; Cywinska *et al.* 2006), and tabanids (6% K2P for CO1-5' and 9% for CO1-3'; Cywinska *et al.* 2010).

For the 16S gene, the average values for divergence within species and genus were 0.16% (range 0–0.8%) and 0.6% (range 0.1–1.9%), respectively, very low in comparison to CO1 sequences. As a result, NJ analysis of the 16S gene concatenated species and no comment on haplotypes can be made with confidence with the use of this gene. The 16S-based tree is not illustrated here, but is available online in Supplementary Data of this monograph; <fnz.landcareresearch.co.nz>.

Because of the size of the non-standard CO1-3' NJ Tree (Fig 508, 509), we illustrate it in sections (Fig. 510–514) when showing phylogenetic relationships among haplotypes.

Given the generally assumed conservative evolutionary nature of the 16S ribosomal gene (Simon *et al.* 1994; Trewick & Wallis 2001) and its conservative nature in this study, we assume that grouping of some of the New Zealand *Austrosimulium* species together tends to indicate that species in the subgenus *Novaustrosimulium* (see Ballard 1994) indicates the latter is the older taxon —in agreement with more basal placement in the morphological cladistic analysis section of this monograph. Of relevance to that assertion, the paramere of male *Novaustrosimulium* species is moderately developed and with spines. We recognise and number some 43 haplotype lineages within both the *australense* and *ungulatum* species-groups, occasionally arbitrarily, and mainly to assist discussion of the results.

For the CO1 mitochondrial gene, rooted NJ analysis of CO1-3' barcodes produced a tree with a backbone topology and bootstrap support which concurred well with those of the cladistic analysis of morphological characters used in this monograph (*cf* Fig 505, 508a, b & 509a, b). Of the three molecular markers tested, the non-standard barcode CO1-3' locus was more effective as a diagnostic tool than the standard barcode CO1-5', and much more effective than the more slowly evolving mt16S locus. The CO1-3' locus, with its relatively wide gap between the interspecific and intraspecific sequence divergence, more frequent amino acid changes, comparatively high number of transversional and transitional substitutions, and slightly slower rates of transitional saturation, offers a little more flexibility in the interpretation of pairwise comparisons at the conspecific and congeneric levels than the standard barcode CO1-5' locus (Cywinska *et al.* 2010).

Therefore, we focused exclusively on CO1-3' barcodes in our molecular analysis of *Austrosimulium* taxonomy. In comparison to the cladistic morphological analysis section of this monograph there were two main differences:

1. The currently recognised *unicorne*-subgroup (*ungulatum* species-group) was sister to all others and included two species (*A. dumbletoni*, *A. vailavoense*) currently assignable on morphological grounds to the *ungulatum*-subgroup (Fig. 509a, 509b, 514).

2. The *australense*-subgroup with its two constituent species (*A. australense*, *A. longicorne*), usually considered as sister taxa, resolved *A. australense* as a pair of cryptic species with *A. longicorne* sister to the South Island segregate (Fig. 510).

Taxa of the *tillyardianum*-subgroup of species examined here (*A. dugdalei*, *A. laticorne, A. multicorne, A. stewartense, A. tillyardianum*) are not usefully aggregated by species or haplotype. So, apart from Fig. 508a, 508b, they are not further illustrated here in detail, but again, are available online in Supplementary Data for this monograph, <fnz.landcareresearch.co.nz>).

australense species-group

tillyardianum-subgroup (Fig. 508a, 508b)

This clade is 4.5% divergent from the *australense*-subgroup and with high support for monophyly (at 99%). Sister to the subgroup is an *A. tillyardianum* haplotype (NZS62, Pahau River Bridge, SH7, Canterbury) divergent from other haplotypes by ~6%. Perhaps this indicates a separate species, but material from that locality was of classic *A. tillyardianum* morphology. The sister clade, with high support, consisted of two poorly divergent lineages (~1%) with little better internal differentiation, or groupings. A major problem involves clustering together of morphologically markedly distinct species, for example, *A. laticorne*, *A. tillyardianum,* and *A. multicorne* (*cf* Fig. 275, 276, 279 of pupal gills). With such poor resolution at the species level, we feel any major comment on these species is not warranted even though this clade constitutes the majority of New Zealand simuliids. Hence, we do not provide further illustrations of the subgroup beyond Fig. 508, 508a. There are, however, three distinct clusters of *A. tillyardianum*, although for reasons stated above, we do not assign them much credence. One, for the South Island, comprised six samples (NZS2a, 12, 13, 63, 68, 84) and had a restricted distribution ranging from the Marlborough Sounds, south to Kaikoura and inland to Owen River Bridge (Buller River). Given the broad distribution of *A. tillyardianum* in the South Island (Map 14) this may represent the distribution of a distinct haplotype.

Two larger North Island clusters of *A. tillyardianum* (i.e., NZN7, 8, 10, 23, 36, 38, 42, 58, 59, 87, 91, and NZN3, 20, 34, 35, 37, 39, 40, 44, 62, 65, 67, 86, 88, 91) poorly divergent from one another are both equally well distributed over the full range of *A. tillyardianum* in the North Island. Indicative perhaps of recent origin, or, superior dispersal ability. Other minor clusterings of haplotypes (e.g., NZN11, 31, 41, 61) are similarly widespread across the full range of *A. tillyardianum*.

***australense*-subgroup (Fig. 510–513)**

This well supported clade (*A. australense* + *A. longicorne*) is distinguished from the *tillyardianum*-subgroup with *ca* 4.5% divergence. The sister lineage, haplotype #1 (NZS103, Takaka Hill Walkway), with 1% divergence is somewhat problematic, since it was identified as *A. longicorne*. The material was, however, penultimate instar larvae, difficult to identify and may represent a cryptic species. The habitat was unusual. Otherwise, there is clear separation of North and South Island *A. australense* haplotypes into two, morphologically cryptic segregates, with 2% divergence, and again, strong support. Of significance is that no South Island haplotype occurred in the North Island, but there were four examples of North Island haplotypes occurring in the South Island (Fig. 509a, 509b, 511–513); none were very closely related to each other (discussed in more detail later). Of further note is that *A. longicorne* is sister to the South Island *A. australense* clade, but at only 1% divergence. That lower divergence is perhaps surprising given the major morphological difference between pupal gills of the two species (*cf.* Fig. 160, 161).

The *A. longicorne* clade is moderately well supported, indicating monophyly — in good agreement with morphology. There are two poorly supported sister lineages. One (haplotype #8, NZS14, 41), has the two constituent populations widely separated geographically. Notable is that NZS41 is from high altitude in the Old Man Range, Otago, while NZS14 is from close to sea level at Christchurch. The second lineage we consider to have three haplotypes (#9, 9a, 10); the first two from the South Island, divergent at 0.8 % from the well supported North Island haplotype (#10), which has little internal divergence.

Regarding the marked morphological divergence between pupal gills of *A. australense* and *A. longicorne*, it is now well established (Heming 2003; Carroll 2008) that a minor change in a regulator gene, can result in major differences in a structure. In the present instance (*cf.* Fig. 268, 269), this would be a reduction in the size of the pupal gill horn and a reduction in the number of filaments with increase in their thickness — nothing markedly difficult developmentally, but most different in final appearance. It would be phylogenetically useful to examine the ontogeny of the pupal gills of these two species.

Lineages of *A. australense* in the South Island have little support. The sister haplotype (#7) is from Kawhaka Creek, West Coast (NZS50). Its sister lineage we consider as five haplotypes (#2–6). Haplotype #2 (NZS51, 67, 70, 72, 73, 74, 81, 99) is restricted to the northwest of the island, ranging from the Farewell Spit region, south to Greymouth, and inland to the Rahu Saddle. The next, #3 (NZS 1, 15, 16, 54, 77, 86,101), is more widespread, from northwest Nelson to Marlborough and south to the Canterbury Plains, and is likely to be the haplotype of the synonymic name *tillyardi* Tonnoir, 1923 from Nelson. The haplotype sister to these two groups is #4 from Inangahua Junction (NZS68). The remaining major grouping is of two poorly discriminated lineages of haplotypes #5 (NZS79, 102) and #6 (NZS2, 12, 78, 82, 89) which are widespread in the north of the island, but extend south only to Green Burn, Kaikoura (NZS12).

The well supported North Island clade of *A. australense* has a number of haplotypes, most poorly discriminated (Fig. 511–513). Some have, however, distinct distributions. We consider the first three lineages as one haplotype *viz.* #11, consisting of NZN41 (Ohiwa Stream, Hastings-Taihape Road) and two from NZN63 (near Tikitiki, SH35) — an eastern distribution. One clade of haplotype #12 (NZN 70, 72, 76, 77, 82, 94) and #13 (NZN9, 84a) is largely found north from Rotorua into Northland. Any of haplotypes #12, 28, or 32 could be the haplotype for the original material named *australense* by Schiner (1868) — all are found in the Waitakere Ranges (NZN93, 94; Fig. 511, 513). There is one southern outlier of #13 at NZN84a (Mount Ruapehu). This sample is problematic in that morphologically, it is definitively *A. longicorne*. The habitat is not typical for *A. australense* either (similar to Fig. 465). Because this population occurs well south of others of that haplotype, this may be an error in analysis.

Sister to the remaining haplotypes is that from Stewart Island (#14 NZS170, Kaipipi Inlet). Something of a conundrum, this datum may well be correct given that North Island haplotype #24 (NZS29) occurs in the Catlins, southern South Island (Fig 512). Another lineage #16 (NZN3, 7, 15, 32a, 53, 61, 62, 92) has a distribution that is similar to other haplotypes, i.e., a peripheral distribution around the central portion of the North Island. The distribution of this lineage is the base of Coromandel Peninsula, East Cape, Hawkes Bay, Taranaki, and Raglan. One population from Ohakune (NZN92), more centrally on the Volcanic Plateau, is anomalous, but it is not a misidentification. A small clade of five haplotypes #17 (NZN 4, 8, 65) and its sister, #17a of two haplotypes (NZN57, 78) has a more restricted northern distribution ranging from far Northland, Coromandel Peninsula, Bay of Plenty, and East Cape. Sister to those two, #18 (NZN36, 64, 85), is distributed along the east coast from East Cape to Waihi Stream, SH52, Manawatu. One population (NZ85) is more central, just north of Taihape. Haplotype #19 (NZN63, 65, 73, 79, 80, 81, 83), that has markedly low internal divergence, has a distribution similar to haplotypes #17, 17a, and 18, occurring well north in Northland, south to the Bay of Islands, but with a gap through the Coromandel and Bay of Plenty to East Cape.

The specimens of the unavailable name 'caecutiens' Walker, 1848 (Fig. 519–521) would be part of haplotype #19. If future investigations show haplotype #19 to be taxonomically distinct from *A. australense*, then the 'caecutiens' specimens should be listed under the name assigned to haplotype #19.

Not markedly divergent from those haplotypes is that of #20, but this is a northwestern South Island population (NZS99, Green Hills, Farewell Spit region). Perhaps, again, this is a conundrum, but given a probable connection between the North and South Islands during glacial sea level depressions (Fig. 514, 516), its occurrence in the Farewell Spit area is not unexpected (and see below). That is, if simuliids manage to cross Cook Strait from the North Island, this is one area where it might have occurred.

A more southeastern haplotype in the North Island is #21 (NZS37, 39, 51), which ranges only from Hawkes Bay to near Dannevirke.

Sister to the remainder of the haplotypes is #22 (NZN30, Rangitikei River), a more south-central locality (Fig. 512). Haplotypes #23–25 show little divergence. That of #23 (NZN 20, 32, 52, 56, 58, 67, 75, 86, 89), occurs in Northland, Bay of Plenty, Hawkes Bay, Taranaki Bight, and Raglan, and again has a largely coastal distribution around the North Island. That haplotype is unresolved from what we call #25 (NZN54, 61, 74), which is found in Northland and southeastern East Cape. Probably haplotypes #23 and 25 should be considered as one. With low divergence from those haplotypes is #24 (NZN33, 35, and NZS29). Of note, of course, is that the latter population is from the Catlins, South Island.

Another tightly nested haplotype is #27, that again shows a largely peripheral distribution (Fig. 513) (NZN5, 6, 10, 11, 17, 21, 22, 24, 34, 40, 52, 71, 78, 90). Its range includes Northland, Coromandel, Hawkes Bay, Taranaki and two localities in southern Waikato. Haplotype #28 (NZN 19, 25, 27, 29, 43, 56, 93), has a more central, but still peripheral distribution that ranges from Auckland to Bay of Plenty, inland Hawkes Bay, Taranaki, and Raglan. There are no deep central localities.

A slightly more divergent group is #29 (NZN13, Raglan, NZN26, north of Mount Taranaki). Of biogeographic importance are haplotypes #30–32. Haplotype #31 (sister to #30), occurs at Totaranui, Golden Bay, South Island (NZS102); derived from probable connections between the two islands? An assumption might be that its two sister populations would be concentrated in the southern part of the North Island, but that is not so, and in fact they are in Northland (NZN75). The remaining haplotype #32 (NZN 17, 66, 69, 70, 76, 86, 93), while also with a peripheral distribution, is widespread, ranging from Northland to inland Bay of Plenty, East Cape and Raglan and, following a major gap, near Wellington.

ungulatum species-group (Fig. 514)

As noted elsewhere, the cladistic analysis of morphological characters section in this monograph showed the *ungulatum* species-group comprised two sister clades, the *ungulatum*- and *unicorne*- subgroups (Fig. 506). The molecular analysis is at slight variance to this.

unicorne-subgroup

This is the very well supported sister clade to all other New Zealand *Austrosimulium,* and is well discriminated at *ca* the 6% level from the *ungulatum*-subgroup and is not sister to it. The *unicorne*-subgroup here consists of *A. vailavoense* + *A. unicorne* as a clade with marked internal divergence (7.2%), sister to *A. bicorne* + *A. dumbletoni* + *A. tonnoiri*, also with moderate internal divergence. *Austrosimulium vailavoense* (haplotype #39) shows minor divergence between the population at Papatotara, Southland (NZS157) and the type locality at Vaila Voe Bay, Stewart Island (NZS165). In the sister clade, one population (haplotype #41) of *A. bicorne* at Temple Basin, Arthurs Pass (NZS133) is sister to the remainder of the clade at the 1% level. Another haplotype (#42) of *A. bicorne* from the Homer Tunnel (NZS32) shows minor divergence from its sister haplotype #43. That latter haplotype is shared among 3 species. This is not surprising given morphological similarities between *A. tonnoiri* and *A. bicorne*. Whether *A. dumbletoni* truly shares that haplotype is moot, but discovery of its immature stages and their habitat requirements would confirm, or not, that placement. Probable requirements of larvae and pupae of *A. dumbletoni* are discussed elsewhere in this monograph (p. 149).

ungulatum-subgroup

Sister to the *australense* species-group is a clade comprised of *A. ungulatum* + *A. vexans.* This is well separated from the *australense* species-group (*tillyardianum*- + *australense*-subgroups) at 5% and is fully supported. Two clades that diverge at the 1% level, however, are only moderately well supported. One has *A. vexans* sister (#34) to five lineages (NZS30, 46, 67, 157) of *A. ungulatum*, two from one locality. These are considered haplotype #33, and are currently all identified morphologically as classic *A. ungulatum*. If this is the correct arrangement, we consider those haplotypes to be a cryptic segregate of *A. ungulatum* that ranges from Arthurs Pass to mid-Westland and down to southern Southland.

The second, moderately well supported, and sister to all remaining *A. ungulatum* haplotypes, is haplotype #35, from near Greymouth (NZS82). Its sister clade is not well supported. We consider that clade to have three internal haplotypes, *viz* #s 36, 37, 38, all moderately-to-well supported. Haplotype #36 (NZS1, 27, 28, 35, 45, 45a, 65, 72, 79, 82, 83, 86, 104), ranges from Nelson to the west, down Westland to Jackson Bay, and in western and eastern Southland. A major part of that grouping is homogeneous. Haplotype #37 has but two widely separated populations at Greymouth (NZS33) and Hollyford Valley (NZS33). The last haplotype, #38 (NZS4, 34, 37, 47, 49, 54, 55, 56, 65, 66, 68, 70, 74, 75, 89, 106, 170), is in large part a grade. It ranges mainly over the whole of the South Island, even Stewart Island, and overlaps well with haplotype #36. As discussed elsewhere in this monograph, occurrence of that haplotype at Arthurs Pass, well indicates that a gap in its distribution on the West Coast is not the result of glaciation.

Concluding statement

Although congruence is high for the backbone of our CO1 tree and the morphology-based tree reported in this monograph for *Austrosimulium* species, cladistic phylogenies based on morphological characters and those using molecular evidence do not always agree (e.g., Hillis 1987; Trewick 2008); cytology-based trees may also diverge (e.g., Krueger & Hennings 2006; Conflitti *et al.* 2010).

A fine example of agreement between tree topologies is that of Cranston *et al.* (2010) for Podonominae midges of Gondwanan provenance. They considered the congruence of molecular and morphological phylogenies to be unusual, but pointedly suggested that, in large part, it was due to their morphological data being derived from most stages of the life cycle. They gave examples where results were spurious when only autapomorphic adults were used. That this monograph also used most life stages for the cladistic analysis of morphological characters of *Austrosimulium* is possibly why topology from that analysis concurred closely with our molecular results here, both with strong support generally in the range of 90% and higher (Fig. 506, 508a, 508b). Even the lack of discrimination in terminal branching is in good agreement! The lack of resolution for the *tillyardianum*-subgroup in the morphological analysis section of this monograph also occurred in our molecular analysis.

We note again the successful study by Ilmonen *et al.* (2009) in elucidating specific status within the *Simulium vernum* group. Morphological characters from all three stages were used. The less successful study by Krueger & Hennings (2006) used only DNA sequences.

The concordance between tree topologies for New Zealand *Austrosimulium* is a strong indication that the morphological characters used are useful phylogenetically and should be continued to be used with confidence. Strong signals from these characters are expected since they have been examined repeatedly for phylogenetic significance, in particular by Adler *et al.* (2004) and by others (e.g., Craig & Currie 1999; Gil-Azevedo & Maia-Herzog 2007; this monograph). For molecular studies, the mtDNA CO1 gene is also of value, except apparently for very recently evolved taxa.

Previous studies of North American birds and insects showed that most (98%) conspecific sequences of CO1 were <2% divergent (Cywinska *et al.* 2006). Based on those studies we can expect that well defined congeneric species will regularly show sequence divergences in the CO1 region averaging ~10% and that divergence values for conspecific individuals will usually fall below 0.5%; on average, nearly 20 times higher for congeneric species than for members of a species (Cywinska *et al.* 2006). *Austrosimulium* sequences were characterised by only ~3 times higher congeneric values than conspecific values for CO1-5'' and 5.4 times higher congeneric values for CO1-3''. Thus, their conspecific groupings were less tight than reported for other groups of organisms.

The markedly skewed ratios of both the GC content and the rate of nucleotide substitutions at the silent sites of *Austrosimulium* reflect a strong response to environmental and biological pressures from the less evolutionarily constrained nucleotide sites. Therefore, as for many other dipteran families, pairwise comparisons among *Austrosimulium* species at the congeneric level must be interpreted with caution, and/or silent sites must be excluded from an analysis if necessary.

Biogeography

Avise (2004b) in a brief overview of biogeography made the distinction between cladistic biogeography based on morphological information, that can deal with deeper temporal scales at high taxonomic levels, and phylogeography which uses molecular data and provides insights at the intraspecific level. Since both our morphological and molecular data are analysed using cladistics, we simply use the term biogeography.

A major question that faces New Zealand biogeographers is the origin of New Zealand's biota. Is it of ancient Gondwana mien (vicariant origin) or of more recent origin via dispersal? Central to this question is the suggested Oligocene Inundation (e.g., Landis *et al*. 2008), when some assert that New Zealand was completely submerged *ca* 34–23 Mya. This has been hotly debated (e.g., Cooper & Cooper 1995; Waters & Craw 2006; Wallis & Trewick 2009; Giribet & Boyer 2010; Tennyson 2010) and there is fossil evidence that shows there was a considerable vertebrate fauna present in southern New Zealand in the Miocene immediately following the Oligocene, indicative of extensive land (Worthy *et al*. 2006; Worthy *et al*. 2011). High conifer diversity in the Oligo-Miocene of New Zealand also supports considerable land being present at that time (Jordan *et al*. 2011), so complete inundation does not appear to have occurred.

For organisms lacking fossil evidence, one possible means of addressing origins is to examine relationships of biota to antecedents, namely from Australia and South America. A famous example of this is Brundin's (1966) study of podonomine midges (Chironomidae). As reiterated by Gibbs (2006) and others, closer relationships of New Zealand's biota to that of South America than to that of Australia, indicate older vicariant origins that trace back to Gondwana. Closer relationship with Australia than South America suggest more recent dispersal from Australia is likely, while not disproving earlier Gondwanan origins.

A critical part of such examinations now involves determining rates of genetic divergence between the clades of organisms of interest — the so-called "molecular clock" (e.g., Brower 1994; Gaunt & Miles 2002; Trewick & Morgan-Richards 2005; Wallis & Trewick 2009). An estimated time of divergence since the Oligocene Inundation would indicate subsequent dispersal to New Zealand. Determining time of divergence between lineages can involve invocation of significant geological events, such as the break-up of Gondwana and the splitting of Zealandia from Gondwana at some 83 Mya. For finer analysis, more recent events such as formation of the Southern Alps (*ca* 5–3 Mya), to the formation of the modern Cook Strait (*ca* 0.45 Mya), or climatic events such as glaciations can be used. Or, at times, a general rate of divergence (% change in molecular genetic bases per million years) can be applied; however, such use is problematic since rates of change may differ between lineages, and there are other caveats, some rather firmly put (Avise 2004a; Rubinoff 2006; Rubinoff *et al*. 2006).

We use both general rate of divergence and time of geological events in discussing the age of *Austrosimulium* and its intrageneric clades.

Paleological aspects and effects on New Zealand

Geological

Much has been written about the geological underpinnings of New Zealand and its rather tortuous history. The brief overview below is based, in large part, on publications by Fleming (1975, 1979), Suggate *et al*. (1978), Stevens (1980), Coates (2002), Gibbs (2006), Campbell & Hutching (2007), Graham (2008), and many other specific studies (e.g., Cook *et al*. 1999; King 2000; McLoughlin 2001, Trewick & Bland 2011). The more recent publications should be consulted for entry into the extensive literature.

Evidence derived from this study indicates that New Zealand *Austrosimulium* is at maximum 8 My old, and more likely 5 My old. For the paleogelogical aspects of New Zealand relevant to *Austrosimulium* we deal briefly with the Oligocene, but mainly from the orogeny of the Southern Alps onwards. A review of earlier events involved in the geological evolution of New Zealand, from Gondwana to the Oligocene is available online in the Supplementary Material at <fnz.landcareresearch.co.nz>.

At the end of the Oligocene (25 Mya), the Pacific Plate began to collide with and subduct beneath the Australian Plate along the north of New Zealand. This was the beginning of the Kaikoura Orogeny and a transform fault — the incipient Alpine Fault. At that time the Fault ran more or less east–west. By the late Miocene (10 Mya) that subduction had begun south of the New Zealand landmass. These events meant that movements along the Alpine Fault were sideways: currently shown by the 460 km that separate similar old geological formations in Nelson and Southland. By later Miocene and early Pliocene (8–5 Mya) the Alpine Fault began to rotate anticlockwise. The Pacific Plate, overlain with greywacke rock, moved sideways along the Australian Plate (comprised largely of granite), and began to push west against the latter leading to uplift of the Southern Alps. This is the reason for the unusual geological arrangement in the Southern Alps of granite to the west and various greywackes to the east. There is good evidence that the major orogeny of the Southern Alps started in the early Pliocene at 5 Mya (Chamberlain *et al*. 1999; Chamberlain & Poage 2000; Batt *et al*. 2000). Older dates are now thought to be incorrect (Shuster *et al*. 2011).

At that time in the North Island there was a Manukau Strait separating Northland from the rest, and the Waitakere Ranges were probably islands. Trewick & Bland (2011), however, in an examination of the geological relationships between the North and South Islands over the last 4 My, noted that previous ideas regarding broad marine separation between the two islands needed to be reconsidered. Cook Strait, as presently known, was not in existence 4 Mya; instead to the west the 2 islands were separated by a deep Wanganui Basin, and to the east by a narrow so-called Kuripapango Strait across a finger of high land extending from the South Island. There was no broad Manawatu Strait as often suggested. The South Island extension from what is now the Marlborough Sounds went northeast to about present-day Palmerston North, and has been termed the "Wanganui–Marlborough Shield". By 3 Mya (Late Pliocene) the rates of vertical tectonism had increased and what was the Wanganui Basin to the west began to rise. The Kuripapango Strait to the north closed, and farther south was a narrower Manawatu Strait that passed through the South Island extension. There is evidence for a northeast band of higher land, separated from the proto-North Island by the Ruataniwha Strait. The Wanganui–Marlborough Shield was fragmenting, and by 2.4 Mya (Early Pleistocene) there was a broad, shallow Manawatu Strait, but it appears as if it was constrained to the west and east by extremely shallow water or low land. Farther east there appears to have been a range of shoals and islands, separated from the two islands by the Ruataniwha Strait. At 1 Mya the present-day North and South Islands were close to modern configuration, and the Manawatu Strait was obliterated by the orogeny of modern south-central mountain ranges. There was a narrow land connection across the present Cook Strait. Marlborough Sounds were well foundered and near to modern conformation, and what would become the Tararua Range north of Wellington was rising. With continued land movements, the modern Cook Strait was punched through at about 0.45 Mya during a mid Middle Pleistocene interglacial. During the Waimaunga glaciation (0.30 Mya) the North Island and South Island were connected by a low, gravel-based, Marlborough–Taranaki Plain. Rivers from Taranaki, namely the Rangitikei and Wanganui, flowed out onto this plain. From the South Island the Waimea River possibly flowed northeast, but did not merge with those from the north. The plain was submerged during the late Pleistocene interglacial (0.10 Mya). During the Last Glacial Maximum (0.02 Mya) and with sea level depressed as much as 135 m, the two islands are generally considered to have again joined. However, with intertidal scouring and tectonic movements, Cook Strait was deeper and the junction narrower and well to the west — the Farewell Rise. A junction is disputed by some. Regardless, if there was a channel, or channels, across the plain, they were narrow, and the connection of land, if any, transitory (see below, p. 70; Fig. 515–518).

Volcanism

Intraplate volcanics have been important in formation of New Zealand's landscape. Subduction zones between plates normally have associated volcanic activity along the interaction zone, however, distant from the junction. This derives from the subducted plate as it is heated and rises as magma, forming a volcanic arc. Such volcanic activity began in the north of New Zealand in the Early Miocene (*ca* 23 Mya) producing volcanoes along Northland. By Middle Miocene (*ca* 20–18 Mya) the volcanism had moved to along the present-day Coromandel Peninsula and continued in various forms until the end of the Miocene (*ca* 6 Mya). In Early Pliocene times (*ca* 5–2 Mya) the volcanism had moved farther east to near the present-day Kaimai Range and Tauranga, and at 1.9–1.6 Mya (Briggs *et al.* 2005) during a fundamental rearrangement of plate movement in the New Zealand region activity switched to the Taupo Volcanic Zone (TVZ; sometimes referred to as the Central Volcanic Region). There are, however, estimates that volcanism might have started there around 3 Mya.

Vast ignimbrite eruptions associated with the currently-active Taupo Volcanic Zone continued into the early Quaternary (1 800 years BP). Some of the pyroclastic flows associated with these eruptions are considered to be amongst the largest on Earth. One, at approximately 1.0 Mya, which in part produced the (Cape) Kidnappers Ignimbrite, extended as far north as Auckland. Volcanism associated with what is now Lake Taupo has coated extensive areas of the North Island with ash and pumice many times. One pyroclastic flow at 22 000 years BP, for example, covered north to Whakatane, east to Napier and Gisborne, south to Wellington, and west to Mount Taranaki.

The three volcanic mountains at the centre of the Volcanic Plateau are relatively young and represent the southernmost extent of the Taupo Volcanic Zone. Tongariro to the north is the oldest, considered to have commenced erupting around 275 000 years BP, reaching its modern form about 65 000 years BP. Ngauruhoe, in the middle, is judged by some to be merely 2 500 years old; however, it has been continuously active, resulting in its mass. Ruapehu is thought to have started erupting about 245 000 years BP. The Volcanic Plateau, as presently known and some 500 m above the surrounding landscape in places, is a product of those volcanoes and relatively recent in its present form.

Volcanism in the Taranaki region is the westernmost extent of the northern intraplate volcanism and began in the Late Pliocene (*ca* 1.8 Mya). The iconic Mount Taranaki (0.015–0.012 Ma) and its older precursors Mounts Pouakai

(0.25 Mya), Kaitake (0.52 Mya), and the Sugar Loaf Islands (1.75 Mya) to the west are derived from deeper parts of the subducting Pacific Plate.

Formation of the volcanic Banks Peninsula on the east coast of the South Island is of relevance here because of the precinctive aquatic fauna (Winterbourn 2008), but not for simuliids. Volcanism of the peninsula began in the Middle Miocene (15 Mya) and ceased about 5-6 Mya.

The geological underpinnings of Stewart Island to the south of the South Island are ancient. Simply the island consists of two main units; the southern Fiordland Terrane (Mid Cambrian, 510 Mya), and the northern Brook Street Terrane (Permian, 265 Mya), separated by a major fault line — the Median Tectonic Line of some — currently occupied by the Freshwater River. That the island has been above sea level for a long time is illustrated by the exfoliated, rounded, granite massifs of Gog and Magog (Cretaceous, 125–105 Mya) on the southern Fiordland Terrane. There is little evidence of glaciation on the island, its overall altitude being too low (McGlone & Wilson 1996). Foveaux Strait between Stewart Island and the South Island is shallow and was exposed during glaciation maxima sea level depressions (Fig. 518). Earlier, the Strait was likely to have been deeper, having been filled with outwash gravels during glaciations.

New Zealand is geologically a restless place! The rate of uplift of the southeastern flank of the North Island, and that of the main axis of the South Island is startling, ranging from 1–10 mm/year and has had major effects on the configuration of Cook Strait in recent geological time. Slip movement along the Alpine Fault Zone and the Southern Alps is estimated at 40 mm a year in some places.

To the east of South Island are the Chatham Islands. Simuliids are not known from there, even though there is suitable running water, so we do not comment further.

Of more interest are the subantarctic islands of the Campbell Plateau, in particular the Auckland Islands and Campbell Island from which simuliids are known. These island groups are considered to be intraplate hot-spot shield volcanoes where magma penetrated the granite basement and sedimentary rocks of the Campbell Plateau. The Auckland Islands were formed from two volcanoes, Carnley and Ross, during the Middle Miocene (*ca* 19–12 Mya). In the Middle to Late Miocene (*ca* 11–6.5 Mya, mainly *ca* 7.0 Mya), volcanism shifted, with plate movements, to form Campbell Island. Earlier rocks found on these islands are considered by some to have been brought up from the underlying Campbell Plateau; such contaminants are common to intraplate volcanism.

Paleoclimate

Superimposed on the rapidly changing geology of New Zealand has been a series of glaciations — some 9–10 in the last million years (Burrows 2005). These are of relevance for a variety of reasons, but in particular to Simuliidae because of their requirement for running water. Apart from their biogeographic implications (e.g., McCulloch *et al*. 2010), New Zealand cold periods also serve as a test for models of glaciation elsewhere in the world, such as Antarctica and the Northern Hemisphere (e.g., Carter & Gammon 2004; Alloway *et al*. 2007; Schaefer *et al*. 2009). Because of the impact of glaciation on the landscape, ice ages are often considered along with the paleogeology of New Zealand (e.g. Shuster *et al*. 2011 and other citations in paleogeology section above). Environmental changes from the beginning of the Quaternary until Present have been reviewed by Newnham *et al*. (1999) and a detailed examination of glaciations and extent of glaciation for the South Island has been made by Burrows (2005); the following is based largely on these works.

Development of the Antarctic Circumpolar Current and cooling of Antarctica began at the upper end of the Eocene (34 Mya) with the opening of the Drake Passage between South America and Antarctica, and the Tasman "gateway" between Antarctica and Australia (Katz *et al*. 2011).

Dating glaciations can be difficult, since successive glaciation events obliterate earlier episodes. Therefore, dating is often done by examination of off-coast marine sediment cores, determining gamma ray emissions and oxygen isotopes, amongst other methods. The oxygen isotopes are proven proxies for temperature and, indirectly, sea levels. High sedimentation rates indicate glaciation on shore. Quartz grains in offshore sediments are indicative of strong winds, dry conditions, and loess formation (e.g., Nelson *et al*. 1993; Carter & Gammon 2004). Such signals are grouped into Marine Isotope Stages (MIS) and can have a resolution of around 100 years, although older records are at resolution of 1 000–2 000 years. For New Zealand these have been determined back to *ca* 4 Mya.

The earliest direct evidence for glaciation in New Zealand is that for the Ross Glaciation perhaps 2.55–2.45 Mya (end of the Pliocene), followed later by that of the Porika 2.15–2.10 Mya (beginning of the Pleistocene). Then there was a long period up to *ca* 900 000 years BP with some 20 alternating cool and warm periods. A period of some 9 or 10 regular glaciations (40 000–50 000 year periodicity) followed, for which there is better evidence. The last five of these glaciations, progressively, are named the Kawhaka, Nemona, Waimaunga, Waimea, and Otira Glaciations. The Otira appears to have been one of the great glaciations and was *ca* 75 000–14 500 years BP.

Temperatures are known to have fluctuated during this time and glaciers were probably at their maximum extent at 70 000 years BP. At 26 500 years BP the Taupo caldera in the North Island erupted and produced a widespread Kawakawa (Oruanui) Tephra that allows definitive dating. There were even vaster eruptions earlier (*ca* 0.34 Mya), such as that of the Rangitawa (Holt *et al*. 2010), and such eruptions have been suggested as tipping points contributing to glaciations. More recent eruptions have also proven useful for dating (Froggatt & Lowe 1990; Newnham *et al*. 2003; Manville & Wilson 2004).

During the Otira Glaciation there were brief interstadial or warmer periods. There were two distinct ice advances: one at *ca* 65 000 years BP (MIS 4) and the other more recently, at *ca* 18 000 years BP (MIS 2c) — the former being slightly more extensive (McCarthy *et al*. 2008). There is evidence that at maximum advance the Rakaia Glacier (Burrows 2005; Alloway *et al.* 2007) extended as far east as present-day Methven. Similarly, the Rangitata Glacier to the south extended to near Mayfield. Burrows (2005) and others (e.g., Soons 1994) showed that at their final advance the eastern glaciers (Waimakariri, Rakaia, and Rangitata) terminated upstream of their present-day gorges. Farther south in the Mackenzie Basin ice extended beyond the present southern ends of Lakes Tekapo, Pukaki, and Ohau, and other lakes (Burrows 2005). There is evidence that during the Waimaunga Glaciation (ending 220 000 years BP) the Waimakariri, Rakaia, and Rangitata glaciers extended even farther eastwards than during the Otira Glaciation (Burrows 2005). These glacier advances are of relevance to refugial distributions of *Austrosimulium*.

Relevant as well to this study are the drops in sea level and shifts of climatic zones during glacial maxima. Sea level depression during the Last Glacial Maximum is generally cited at -130 m (Thomas *et al*. 2009), although other work (e.g., Thompson & Goldstein 2006) suggested -135 m. This means that a considerable area of the New Zealand continental shelf was exposed. Reconstructions of land for that time usually show only that for the maximum sea level depression (e.g. Burrows 2005; Alloway *et al.* 2007). They show Stewart Island as broadly connected to the South Island (e.g. Fig. 518), but not extending far south. Foveaux Strait at present is shallow, ranging from 20–50 m in depth over much of its extent. Exposed land continued up the east coast through Dunedin and as an extensive Canterbury Plain, extended some 40 km farther east than present coastlines (Alloway *et al*. 2007). Banks Volcanoes were well connected to the Plain, as they were during other sea level depressions. That connection became permanent in late Pleistocene times (*ca* 75 000 years BP) (Shulmeister *et al*. 1999), in large part with gravel from the Southern Alps, transported and deposited by the Waimakariri River. In more recent times (e.g., 6 500 years BP), that connection has, however, occasionally been narrowed (Burrows 2005). Along the West Coast where there is less continental shelf, ice extended out to sea along Fiordland, while farther north there were small pockets of land between glaciers that extended to the sea; well illustrated by Burrows (2005). Northwest Nelson and Taranaki were at times connected via the Farewell Rise, but how well is debatable; this is discussed on p. 70. Around the North Island there was extensive land up the west coast. Many of the present smaller offshore islands, particularly to the northeast, were connected to the mainland.

Stewart Island, because of its relatively low altitude and marine influence had little glaciation (McGlone & Wilson 1996; Alloway *et al*. 2007), but the main lineage of the Southern Alps and the Kaikoura Ranges were heavily glaciated and many of the current landforms observed are a result of that, as are distributions suggested for some biota (e.g., McCulloch *et al*. 2010; and this study). In the North Island there was minor glaciation on the volcanoes central to the Volcanic Plateau and, to the west, on Mount Taranaki.

There was extensive modification to the climate and hence vegetation; both have been investigated in detail (e.g., Burrows 2005; Alloway *et al*. 2007). This is of relevance to distribution of *A. ungulatum*, that appears to rely in part on forest. Other species have particular temperature requirements.

During the Last Glacial Maximum (MIS 2) there is evidence that extremely cold air derived from Antarctica reached New Zealand along with icebergs. The "equilibrium line" (snowline) has been determined for various periods and, for example, at the middle of the Otira Glaciation, some 45 000 years BP, it was 850–1 300 m below current levels, with the mean temperature depressed by approximately 4.5–7.0 C°, with concomitant downward movement of vegetation zones (e.g., Burrows 2005; Marra 2006; Alloway *et al*. 2007).

For Stewart Island, pollen analyses by McGlone & Wilson (1996) showed a hardwood forest and many tree ferns were present prior to 9 000 years BP and up to 5 500–4 500 years BP; then there were major changes. Absence of some tree species, including the iconic southern beech, *Nothofagus*, is attributed to failure to disperse plus limited time for which suitable habitats have been available.

Much of interior Southland and the Catlins region in the South Island appear to have had extensive regions of shrub, tussock, herb, and fell fields, and to have been above the treeline. These extended north, narrowed opposite Banks Peninsula, to expand again around the Kaikoura Ranges and northwest into the Nelson area. Major glaciers, in particular the Rakaia and Rangitata, at their maxima, punched through this zone (Burrows 2005; Alloway *et al*. 2007). At lower altitudes there were extensive tracts of dry, open grassland with some shrubs, ranging from

Stewart Island, north throughout the extended Canterbury Plains, and up to Kaikoura. The distribution of plants in the Nelson–Marlborough area indicates presence of refugia (e.g., Marra *et al*. 2009)

Of particular interest to this study of *Austrosimulium* is why some South Island species do not occur on the North Island. This question too was of particular interest to Dumbleton (1973). Cook Strait is an obvious barrier to dispersal, but its present configuration is relatively modern. Using bathymetric data of the Greater Cook Strait (Lewis *et al*. 1994; Gillespie & Nelson 1996; and that from the Ministry for Primary Industries, National Aquatic Biodiversity Information Systems 2010) and high resolution sea level data for the last 250 000 years (Thompson & Goldstein 2006), the extent of the putative land bridge, the Farewell Rise, between Cape Farewell and Cape Egmont can be detailed over that period (Fig. 517). Similarly, this can be done for the Three Kings Islands (Fig. 516), and Stewart Island plus Foveaux Strait, and Auckland and Campbell Islands (Fig. 518). We assume the bathymetry in the Greater Cook Strait has not changed greatly over the period considered here; debatable given the rate at which sediments are laid down and scoured, and uplift is occurring (Lewis *et al*. 1994; Mountjoy *et al*. 2009).

For Cook Strait, a deep (-200 to -300 m) D'Urville Canyon currently extends northwest from the Cook Strait Narrows canyon to the middle of the Taranaki Bight. It shallows rapidly to the west, in narrow configuration, up to some -100 m, to approximately the same longitude as Mount Taranaki to the north. The deepest portion of the present Farewell Rise is *ca* -70 to -90 m. Depression of the sea to that level would have exposed extensive low relief land adjacent on the North and South Islands. But the westernmost extent of the D'Urville Canyon has a depth of -94 m, and depression of sea level greater than that would be needed, at present, to close the gap between the two islands.

Sea level reconstruction shows that between 250 000 and 185 000 years BP (MIS 7) levels varied between modern levels, down to -30 m. Stewart Island would probably have been partially connected to the South Island, perhaps a connection as wide as 50 km. There was then a rapid drop in level down to perhaps -70 m (detailed data are not available) with a rapid rebound to *ca* -45 m at 175 000 years BP until *ca* 165 000 years BP (early MIS 6, Waimea Glaciation). Foveaux Strait would have been well exposed off and on (50–70 km wide); Farewell Rise would not have been, although Cook Strait would have been reduced to some 70–80 km wide. Data are again sketchy between then and 135 000 years BP, and Thompson & Goldstein (2006) made no reconstruction of sea levels for that period. However, associated d^{18}O isotope data suggested sea level depression was probably the equal of following major low sea stands (see interpolated levels from Huybrecht 2002). Therefore, portions of Farewell Rise could, off and on, have been exposed during that period, but not markedly, and probably never for more than *ca* 10 000 years. At 135 000 to130 000 years BP, sea level rose and by 125 000 years BP, was at modern high stands and even higher by some +10 m (end of MIS 6 and Waimea Glaciation). Any exposed land on the Farewell Rise was well covered, as was Foveaux Strait. Levels dropped again at *ca* 115 000 years BP, to -20 m (parts of Foveaux Strait may have been variously exposed) until *ca* 100 000 years BP, with a marked depression to *ca* -60 m, at 95 000 years BP (Foveaux Strait would have been exposed and 80–90 km wide), with levels then rising again to -20 m. Sea levels were variable over the Kaihinu interglacial between the Waimea and Otira Glaciations. Beginning at 75 000 years BP (start of MIS 4, 3, 2, and the Otira Glaciation) there was a major depression of sea level, down to some -75 m, with fluctuations, at which time the Farewell Rise might have been irregularly exposed, or with a markedly narrowed Cook Strait of *ca* 60 km, for short periods around 40 000 years BP. Levels continued dropping to -90 m at about 60 000 years BP at which time there could have been a full connection between the North and South Islands, but the connection would have been narrow, a mere 20–30 km wide. From then and 30 000 years BP, levels fluctuated between -55 m and -95 m, so the Rise would have been variously exposed and connected over a period of some 30 000 years. Then, commencing at that latter time, there was a precipitous drop in sea levels down to some -135 m at *ca* 20 500 years BP. This was immediately followed by a short-lived rise to -110 m, associated with the MIS 2b interstadial, then back down to the low stand. That deep low stand is associated with MIS 2 of the Last Glacial Maximum when there was an expansion of glaciers in New Zealand (e.g., McCarthy *et al*. 2008). From then until *ca* 17 500 years BP sea levels rose rapidly, reaching -90 m and less at *ca* 18 000 years BP, at which time the Farewell Rise was inundated again and has remained completely so since.

At maximum exposure Farewell Rise might have approached 150 km wide, but for perhaps only 5 000 years. This maximum exposure is that usually illustrated (e.g., Alloway *et al*. 2007; Trewick & Bland 2011) and tends to give the wrong impression of how much and how long land was exposed during the last glaciation. But for much of its exposed existence the Rise was not much wider than 20–50 km, and this, correctly, is illustrated by Lewis *et al*. (1994) and Marra *et al*. (2009). Further, given that much of the Rise was terrigenous gravel, plus fine sediment derived from the glaciers to the southwest, brought north by the Westland Current and passed to the D'Urville Current through Cook Strait, as well that weather systems were farther north during glacial periods and strength of westerly winds exacerbated (Fitzharris *et al*. 1992; Vandergoes & Fitzsimons 2003; Carter & Gammon 2004; Toggweiler 2009; and others), we suggest that the exposed Farewell Rise, particularly when narrow, was generally wind-driven drifts of fine material not conducive as a habitat to most organisms. This is in general agreement with Alloway *et al*. (2007) and others who suggested that the Rise was a shrubland–grassland mosaic at its greatest extent. At considerable variance with this is Marra *et al*. (2009), who were of the opinion that the junction was forested. Worthy & Holdaway (2002) were of the opinion that for now extinct birds, the moa, the junction was not of great dispersal significance during the Last Glacial Maximum. Indeed, they illustrated a narrow marine passage across Farewell Rise during that period (their Fig. 1.2). We do not greatly disagree. Newnham *et al*. (2003) considered that at about 18 000–16 000 years BP there was a marked reduction and southwards contraction of the strong westerly winds that characterised the Last Glacial Maximum climate, about the time the Farewell Rise was being flooded (Fig. 515).

The present bathymetry of western Cook Strait indicates that even if well exposed and connected — but not broad — Farewell Rise most likely consisted of narrow tidal scour channels separated by low rises, certainly at the -80 to -90 m sea level (superficially indicated in Fig. 517), which was the majority of the situation during the Otira Glaciation (Fig. 515). There is no question that modern tidal scour in Cook Strait is severe, in large part because of the offset times of tidal maxima between the east and west coast of the islands. We assume it was so during glaciations, perhaps exacerbated by the northerly shifts in climate.

Detailed bathymetry of Foveaux Strait (e.g., Cullen 1967) showed that at its present depths, regions around the easterly Ruapuke Island between the South Island and Stewart Island would have been close to connected at a depression of sea level of a mere -25 m, except perhaps for a narrowed channel a kilometre wide. At sea level depression of -40 m, connection to the South Island would have been well established to the east through Ruapuke Island and well to the west. At -50 m depression the connection could have been as wide as 50–60 km, but of low altitude and relief. At -100 m depression, the connection was in excess of 150 km wide.

Also of relevance to historical biogeography of New Zealand simuliids is the possibility, during sea level depression, that rivers from the main islands merged, or were in close proximity. For the sea level depression during the Mid Pleistocene glaciation at *ca* 1.25 Mya, Lewis *et al*. (1994: their Fig. 13e) illustrated rivers from the North Island (e.g., Wanganui and Rangitikei) as flowing onto the connecting plain to the South Island. These rivers did not join, but flowed independently into the developing D'Urville Canyon. During the Last Glacial Maximum, Fleming (1975) illustrated these rivers as combined on the emergent plain; similarly rivers from the South Island. The distance between running freshwaters would have been small, and not a great impediment to most adult simuliids. Further, given the flattened terrain, these rivers were probably large, braided, and with substrate of cobble and gravels, habitats quite suitable for at least current-day *A. tillyardianum* larvae, a species that occurs on both main islands.

At maximum sea level depression, Stewart Island would have extended southwest some 140 km, but does not appear to have incorporated Snares Island (Fig. 518). Both Auckland and Campbell Islands were many times their present size (*ca* 6 800 versus 626 km^2, and *ca* 4 000 versus 113 km^2, respectively) and each extended towards the northeast. There was, however, a marine gap between the southernmost extent of Stewart Island land and that of Auckland Islands of some 100 km. The distance between the then Auckland Island land mass and that of Campbell Island was some 200 km. In all, much smaller distances than at present.

Great Barrier Island off the northeast coast of the North Island was well connected to the North Island during sea level depressions — the Jellicoe Channel between it and the mainland is a mere 50–60 m in depth over much of its extent (not illustrated here). Therefore the present-day occurrence of *A. australense* on Great Barrier Island is to be expected.

To the north of the North Island the Three Kings Islands were separated by *ca* 11 km at maximum sea level depression (Fig. 516), so the occurrence of simuliids on these islands is not unexpected. However, only *A. longicorne* is present, and not the more ubiquitous *A. australense.* This is perhaps related to the ability of *A. longicorne* to survive in intermittent and slow-flowing streams, such as those found on the Three Kings Islands.

Historical Biogeography of New Zealand

New Zealand biogeography has long been of interest (e.g., Cockayne 1909; Kuschel 1975) and not just to New Zealanders. The country is considered important for the resolution of major questions regarding historical biogeography of islands; in particular, should New Zealand be considered as just an island, or as a continent (e.g., Gillespie & Roderick 2002; McDowell 2008; Wallis & Trewick 2009)? In recent decades, with the advent of increasingly sophisticated molecular techniques, research on New Zealand biogeography has undergone a major resurgence. The subject is extremely contentious and the literature considerable and oncoming. Recent reviews that provide an entry to the literature are by Trewick *et al*. (2007), Goldberg *et* *al*. (2008), Wallis & Trewick (2009), and Giribet & Boyer (2010). Broad topics dealt with revolve around what has been referred to as "Moa's Ark" (Bellamy *et al*. 1990) where New Zealand as an ancient land mass possessed a similarly aged biota derived from its original formation as part of Zealandia, that is, a continental landmass which split off the eastern side of Gondwana some 120–80 Mya (Mid to Late Cretaceous). There is no question that proto-New Zealand, as part of Zealandia, possessed Gondwanan biota. Fossils point to this, an example being dinosaur fossils found on the Chatham Islands (Campbell & Hutchings 2007) and an array of dinosaur and plant fossils on the mainland (Molnar & Wiffen 1994, Worthy *et al*. 2011; Jordan *et al*. 2011).

However, geological evidence (Landis *et al*. 2008) that there was major peneplaining and marine erosion of the New Zealand landmass in the Oligocene (34–23 Mya) and a possible "Great Inundation", has lead to re-examination of the age of New Zealand's biota. That the country's biota is largely ancient has now in part been discounted, and other scenarios suggested, such as New Zealand being the "Fly-paper of the Pacific" (Didham 2005; Giribet & Boyer 2010), "Goodbye Gondwana" (McGlone 2005), and "Hello New Zealand" (Trewick *et al*. 2007). These recent considerations have New Zealand being colonised by dispersal since the country rose from the sea after the "Great Inundation". That is, the biota is much younger than previously considered, and has speciated rapidly under the influence of sequential glaciation (e.g., Plecoptera, McCulloch *et al*. 2010; and others).

As noted there are problems associated with organisms that do not appear to have any great dispersal ability, such as the iconic *Sphenodon* (tuatara), Onychophora (velvet worms), and the leiopelmatid frogs. Molecular examination of some of these and others (e.g., Allwood *et al*. 2010; Boyer & Giribet 2007, Buckley *et al.* 2011) indicates that they have a long history in New Zealand, suggesting that New Zealand was not entirely submerged during the Oligocene. This is in keeping with fossil evidence (Worthy *et al*. 2006, Worthy *et al*. 2011) from the southern South Island, which showed there was already a considerable vertebrate biota in the Early to Mid Miocene (19–16 Mya).

There are also problems associated with using single molecular markers for biogeographic purposes, undersampling which can produce spurious patterns of haplotypes, and unknown extinct lineages, which can affect inferred phylogenies. Of relevance here is that it is common to use but a single exemplar from a population to establish haplotype distribution, such as we have done in large part. Populations where more specimens were used show other haplotypes present. Consequently, our distributions of haplotypes and biogeographic comments must be taken as preliminary hypotheses.

Apart from the obvious barrier of modern Cook Strait to distribution of New Zealand biota, there are other well established broad distribution patterns that appear to indicate restriction of biota at times (e.g., Wardle 1963; Goldberg *et al*. 2008; Marra *et al*. 2009). The general term "beech gap" is sometimes applied to one such disjunction for the reason that in the South Island, the iconic *Nothofagus* (southern beech) is absent from a 300 km gap between north of Greymouth to south of Paringa (e.g., Trewick & Wallis 2001; Burrows 2005).

Trewick & Wallis (2001) used molecular data for 11 New Zealand invertebrates with gap distributions to test *a priori* hypotheses regarding these so-called "beech gaps". There have been numerous other examinations of the Westland beech gap (e.g., Leschen *et al*. 2008) and the causes for other disjunctions (e.g., Marra *et al*. 2009; McCulloch *et al*. 2010).

From early times (Cockayne 1909) the general explanation for these gaps has been considered to involve Pleistocene climate extremes, namely glaciation and its effects. At considerable odds with that is a panbiogeographic explanation, involving geological movements along the Alpine Fault that forms the Southern Alps (Heads 1989, 1998). Both scenarios make different predictions regarding historical biogeographic relationships of taxa involved. In brief, if glaciation was involved, then sister taxa should be relatively young, if it were the Alpine Fault, then genetic distance between populations would be older.

Trewick & Wallis' (2001) examination concluded that there was no evidence at all to support hypotheses involving the Alpine Fault and they proposed three broad patterns for the various distributions: **Gap**—north and south populations that have failed to unite; **Colonisation**—recently dispersed taxa that have closed the gap; **Regional**—distinct lineages that do not appear to reflect any history of a gap corresponding to Pleistocene glaciation. We add to these patterns; **Refugia** —restricted distributions that can be related to glaciation.

Similarly, Neiman & Lively (2004) and Neiman *et al*. (2005), as part of an in-depth examination of sexuality of the aquatic snail *Potamopyrgus antipodarum* (J. E. Gray), demonstrated that genetic divergence between lineages on either side of the Alpine Fault and Southern Alps were not involved in present-day distributions of the snail. Their data pointed directly to Pleistocene glaciation as the main factor for the current distributions. Their studies are rather unusual in that considerable numbers of snail individuals from each of the localities were subjected to DNA analysis (Neiman *et al*. 2005), rather than the normal single individual as is commonly done elsewhere and which we have done in large part for our study.

The biota of the New Zealand subantarctic islands has long been of interest, because of the marked endemism across and within the islands, and also the presence of apparent older flora and fauna. Of interest here, because of the presence of *Austrosimulium,* are the Auckland and Campbell Islands. Michaux & Leschen (2005) in a substantial "biogeological" analysis of the flora and fauna of the subantarctic islands, considered the biota to be a depauperate, unusual paleo-endemic biota mixed with recent precinctive forms. For biota they used as far as possible groups for which phylogenetic information was available. Their review of the paleogeology of the Campbell Plateau is, however, somewhat at variance with other previously discussed accounts (King *et al*. 1999; Cook *et al*. 1999). For example, while Michaux & Leschen acknowledged the presence of the Great South Basin, a feature which is considered by others to be the original rift of Zealandia from east Gondwana and has been open sea since that original rifting, they did not consider it to be a major barrier for biota between the Plateau and proto-New Zealand. After rifting from Gondwana the Campbell Plateau was above sea level and possessed a biota that has been well established by known coal seams (Zhu *et al*. 2006) and fossil pollen from *Nothofagus* and *Araucaria* (Michaux & Leschen 2005). As Zealandia rotated away from east Antarctica, the continental crust that constituted the Campbell Plateau was stretched and thinned, a warm mantle plume moved away towards the east, and the Plateau foundered. Timing for that seems well established, although the rate of submergence is not clear. Still, the process was rapid and by the Late Eocene (40 Mya) (Sutherland *et al*. 2010: their Fig. 2) the Plateau was under water. The problem for biota is that the volcanism which produced first the Auckland Islands and then Campbell Island, did not commence at earliest 19 Mya (Late Oligocene). There is little question that the islands were much more extensive than their current heavily eroded remnants. Further, they probably have submerged to some extent as is normal for cooling, aging, hot-spot islands (Craig 2003). Nevertheless, the question remains: where did the Plateau biota go for that considerable period of time?

In their discussion on biogeology, which involved interweaving biogeography, paleogeology, and paleoclimates, Michaux & Leschen (2005) invoked ideas from Gillespie & Roderick (2002) that dealt with the evolutionary consequences of reduction and fragmentation of landscape, so-called "relaxation", to explain the overall depauperate nature of the biota of the Campbell Plateau. Michaux & Leschen were of the opinion that the Plateau sank at the Oligocene (*ca* 25 Mya) and that some land must have been above sea level until then to account for the persistence of paleo-endemics. No mention is made of the 16 million year gap between sinking of the Plateau and formation of the islands. Still, they illustrated (their Fig. 3) the juxtaposition between the Plateau and the southern portion of the South Island as it might have been at 71 Mya (end Late Cretaceous) and raised the point that perhaps the New Zealand alpine fauna might have originated from the cold-adapted Campbell Plateau paleofauna. However, they placed orogeny of the Southern Alps as commencing at 10 Mya; a time at considerable variance with the 5 Mya estimates of others (e.g., Chamberlain *et al*. 1999; Chamberlain & Poage 2000).

Michaux & Leschen (2005) in dealing with arthropods of these subantarctic islands included Plecoptera and Trichoptera. They deduced that the Plecoptera was a mixture of older endemic species with the possibility of other taxa being wind-borne from New Zealand with subsequent loss of wings. They also discussed Diptera, but not Simuliidae, even though there was a cladistic phylogeny available for *Austrosimulium* (Dumbleton 1973). Of interest is that loss of flight (brachyptery), common in subantarctic island Diptera, has never been observed for simuliids anywhere, even under extreme conditions (Craig *et al*. 2003).

Of relevance here for *Austrosimulium* is Michaux & Leschen's suggestion that relationships of the fauna of the subantarctic islands is often with the southern South Island. We too see that relationship; however, given the molecular divergences in the *ungulatum* species-group, evidence from pollen rain (McGlone 2002), and tephra reaching subantarctic islands (Alloway *et al*. 2007), plus ages of those islands, we are firmly of the opinion that *Austrosimulium* reached Auckland and Campbell Islands by wind dispersal from New Zealand; in agreement with Dumbleton (1963b). That is, presence of the genus on these subantarctic islands is not related to a relictual Gondwanan fauna suggested for the Campbell Plateau.

Towns & Peters (1996) and Hitchings (2005) in discussing the leptophlebiid mayfly *Cryophlebia aucklandensis* (Peters), endemic to the Auckland Islands, noted that it had close affinities to New Zealand genera. Hitchings followed Michaux & Leschen (2005) in concluding that it was relictual and a remnant of a Campbell Plateau fauna.

Previous studies on *Austrosimulium* relationships

It has long been recognised (Edwards 1931) that there is a relationship between some members of Australasian and Chilean simuliids, originally *Austrosimulium* and *Paraustrosimulium,* and then *Cnesiamima*. This has been amply confirmed by morphological and molecular studies (e.g., Wygodzinsky & Coscarón 1962; Dumbleton 1973; Davies & Györkös 1988; Moulton 2003; Gil-Azevedo & Maria-Herzog 2007) and again here (Fig. 506). More recent re-examination (DAC, pers. obs.) of the enigmatic

?*Austrosimulium colboi* Davies & Györkös shows that entity is most likely to be the Australian representative of *Paraustrosimulium.* Possession of remarkable inflated pupal gills and well developed parameral plates in the adult male, both absent from *Austrosimulium*, point in that direction; a conclusion fully consistent with Moulton's molecular findings. Such relationships are generally taken as indicative of vicariance mediated by the breakup of Gondwana in the Cretaceous. Further, a fully supported sister relationship (Fig. 506) between ?*Paracnephia pilfreyi* (Australia) and *Cnesiamima atroparva* (South America), strengthens that assertion for these Austral simuliids. Gil-Azevedo & Maia-Herzog (2007) also showed *C. atroparva* to be sister to *Paraustrosimulium* +*Austrosimulium*. Gibbs (2006) was of the opinion that New Zealand *Austrosimulium* was a "Ghost of Gondwana" and nothing appears to completely discredit that; however, as discussed below, it is more probable that New Zealand simuliids are "Ghosts of Gondwana" once removed.

Tonnoir (1925) commented briefly on geographic distribution of *Austrosimulium,* pointing out that with the state of knowledge at the time he could only be general. He noted that there were no species common to Australia and New Zealand. There was, however, a curious parallelism between Tasmanian *Austrosimulium* and New Zealand species, notably in female and pupal structures. Habitat choice of the larvae differed, however. He noted that *A. australense* and *A. ungulatum* were the most prevalent species in the North and South islands, respectively.

Dumbleton (1963b), in a major consideration of distribution of Simuliidae with emphasis on *Austrosimulium*, was not sure that New Zealand was colonised by *Austrosimulium* via aerial dispersal from Australia, given that it did not reach New Caledonia. He was of the opinion that presence of *Austrosimulium*'s sister taxon *Simulium* in Fiji and New Caledonia was the result of dispersal along the Melanesian Arc, and concluded that *Austrosimulium* reached New Zealand via overland connection, not significantly later than the Cretaceous.

Failure of *Simulium* to reach New Zealand was suggested as the result of the genus not reaching Australia from the north until after separation of New Zealand from Australia. That there are no species of *Austrosimulium* in common between the two countries, but one species-group that is, suggested to Dumbleton that New Zealand's simuliid fauna arose from a derived Australian group rather than a more plesiomorphic group. Perhaps entry of *Austrosimulium* stock into Australia was from the north, their current absence from Malaysia and other parts of Asia paralleling the distribution of other taxa. He mused on why there are not more primitive simuliid taxa in New Zealand, and wondered if it was from filtering effects along dispersal routes. He also commented that Tonnoir (1925) was of a similar mind. One must remember, however, that in Dumbleton's time (1963) events involving dismemberment of Gondwana were uncertain. Dumbleton did not specifically comment about absence of Australian *Paracnephia* from New Zealand, but lack of that as well as *Simulium*, could well be interpreted as indicating New Zealand *Austrosimulium* were derived from a disperal event.

Whereas Mackerras & Mackerras (1950) were of the opinion that Pleistocene cold climate was responsible for extinction of some biota, Dumbleton (1963) felt that Australian simuliids such as the *furiosum* species-group of *Austrosimulium* would not have gone extinct in New Zealand during cold periods since they are well adapted to such conditions, as are the sister taxa *mirabile* and *ungulatum* species-groups. He considered various scenarios for the southern bias in species numbers, noting the obvious barrier of Cook Strait, suggesting that the more active speciation in the South Island perhaps had been accentuated in the Pleistocene, but not necessarily confined to that period. Subsequent dispersal had not obscured the bias since there appeared to be little ecological reason why South Island species had not occupied the North Island. He also commented that the Auckland Islands species *A. vexans* must be derived from *A. ungulatum* via post-Pleistocene aerial colonists. Dumbleton observed that *A. ungulatum* appeared to need forest, which was largely absent from the Canterbury Plains and Banks Peninsula, and further that it was probably the oldest of the *ungulatum* species-group. As discussed later (p. 83), depauperate forest on the Peninsula is recent. At the time, Dumbleton felt that since *A. australense* had a markedly disjunctive distribution (then known only in the north and south of the South Island), it was probably a relict segment of a pre-Pleistocene species that had not managed to re-colonise the east coast of the South Island from either end; he suggested a similar scenario for *A. laticorne*.

Later, Dumbleton (1970), in a broadly-based Presidential address given to the Entomological Society of New Zealand 1969 conference, considered Pleistocene climates and their effect on New Zealand insect distributions. He mentioned a problem in dealing with taxa of warm-temperature adaptations (Malayo-Pacific, Australian) and those which were of apparent southern origin and cold-temperature adapted. He noted that it would be very bold to assume that species that appeared to have remained morphologically consistent through the Tertiary were unchanged in temperature tolerance. Another problem of uncertainty that he noted was the rate of speciation and the morphological differentiation by which species were then recognised. Specifically referring to *Austrosimulium* and the Australasian–South American relationship, he noted that the rate of divergence since the Cretaceous had been remarkably slow. He did not elaborate on this point; however, it appears he was of the opinion that *Austrosimulium* was of Cretaceous origin.

The South Island was commented upon as having more species of biota than the North Island and Dumbleton suggested that being 30% larger in area, and greater range of habitats, might provide the explanation. He considered the possibility of extinctions caused by extreme fluctuations in temperature during glaciations, noting that at that time there was no evidence for this for insects, but that plants seemed to show it. Shifts in distribution centred mainly around the effect of Cook Strait, and he noted a number of examples where the Strait formed the southern boundary to distribution. Physiological adaptations were admittedly puzzling at that time, in particular those involved with the alpine biota of the South Island. The main question revolved around how did the biota survive warm periods if the organisms were ancient, and the Southern Alps not? If the biota was of more recent origin and colonised colder habitats when they became available, from where did the organisms originate? Dumbleton also raised the question of how wingless forms of insects would arrive in New Zealand.

Some suggestions were made regarding the influence of refugial area, particularly in the South Island. He then dealt with distribution of a number of insects, including *Austrosimulium*, providing a map (1970, his Fig. 7) of the then known distributions of the various species of simuliid. His distributions of *Austrosimulium* spp. are little different from those presently known. Of note, however, is that *A. tillyardianum* is now known from much farther north in the North Island (Map 14) and *A. australense* is more widespread (Map 3) in the South Island.

In his seminal work on *Austrosimulium,* Dumbleton (1973) re-examined various aspects of origin and distribution of *Austrosimulium*. He judged *Austrosimulium* and its sister genus *Simulium* to be of equal evolutionary age and derived from lower simuliids. He considered the origin of *Austrosimulium* and whether it was derived from the same ancestral stock as *Simulium*, or had had an earlier origin perhaps from *Cnephia* or *Gigantodax,* and if similarities to *Simulium* were due to convergence. The anal sclerite of the larva was singled out for considerable examination. One possible origin he considered was that *Austrosimulium* arose in Antarctica, and was derived from *Gigantodax*. However, he reiterated that New Zealand *Austrosimulium* had their main relationship with Australia. Consideration was also given to Brundin's (1966) suggested relationships for Podonominae midges. Dumbleton showed that *Austrosimulium* did not follow Brundin's rules, in particular that stating: "there are no direct phylogenetic connections between a group of Tasmania-Australia and a group of New Zealand". Dumbleton suggested one scenario where the origin was an ancient trans-Antarctic dispersal from Australia to South America, in which case *Paraustrosimulium* and *Novaustrosimulium* would be plesiomorphic segregates and *Gigantodax*-like features (i.e., the semicircular sclerite of the anal sclerite) would be independent developments.

In summarising his ideas on relationships for his Fig. 252, Dumbleton concluded that *Paraustrosimulium* (South America) and *Novaustrosimulium* (Australia) were products of ancient geographic isolation. The close morphological relationship between Australia and New Zealand *Austrosimulium* suggested that the two countries shared undifferentiated stock of that subgenus. The *ungulatum* species-group shared by both countries could be attributed to the isolation of New Zealand with parallel evolution subsequent to that. He further concluded that the three segregates of *Austrosimulium* (as he recognised them) had been isolated since the Cretaceous. He noted for Australia that aridity would have imposed a rigour on evolution, whereas in New Zealand glacial climates would have been a driving factor. The *unicorne*-subgroup probably arose though physiological adaptation to greater cold. Geographical isolation was also no doubt involved in the restricted distribution of *A.* (*A.*) *fulvicorne* (Frazer Island, Australia), *A. vexans* (Auckland Islands), and *A stewartense* (Stewart Island), and the species were probably of Pleistocene age. He made similar observations for *A. fiordense*, then considered to be a subspecies of *A. multicorne*. He noted that the relationship between species of the *tillyardianum*-subgroup would need further investigation, probably cytological – a prescient observation given our results from molecular analysis of this subgroup.

McLellan (1975) in an overview of the freshwater insect fauna of New Zealand noted that in general relationships were firstly with Australian fauna and secondarily with South American. He was, however, clear that some chironomids had connections to South America in the first instance. Fleming (1975) also emphasised the relationship of New Zealand biota to Australia firstly, and noted clear evidence for dispersal as the origin of some biota.

Cranston (2005) while dealing with historical biogeography of Diptera noted that the *Parochlus* chironomid group has, firstly, strong New Zealand + South American connections, and secondarily, connections with Australia. He mentioned that *Austrosimulium* fitted what is referred to as the "Trans-Tasman track" by which dipterous fauna shows links between eastern Australia (including Tasmania), New Zealand, and New Caledonia. The overall distribution of *Austrosimulium* fits that track well, although the genus is absent from New Caledonia, and occurs on subantarctic islands. Cranston invoked an ancient geological scenario as an explanation for the Trans-Tasman track, namely Cretaceous timing for the disconnection of New Zealand from Antarctica. He noted that this was surely associated with speciation patterns seen in several New Zealand taxa. Further, other biotic links to Australia may indicate a hybrid origin of biota via dispersal, extinction, or ecological responses as the respective land masses moved northward.

Recently, Cranston *et al*. (2010) used multiple genes and sophisticated analyses to examine relationships of podonomine chironomids in the southern hemisphere. They were quite definite that all their sampled New Zealand taxa supported a South America + New Zealand relationship, and not one with Australia. Their dates of divergence (83-53 Mya) of some lineages supported vicariance (Cretaceous break-up of Gondwana) as the basis for distribution, and indicated that some New Zealand taxa must have survived the Oligocene Inundation. Even more recently, Krosch *et al.* (2011) used similar techniques to examine Gondwanan Orthocladiinae midges. They found a complex situation with some lineages showing the expected vicariance distribution from break-up of the super continent, and, as above, evidence that lineages survived inundation (if any) during the Oligocene. Further there were at least 3 examples of trans-Tasman Sea dispersal events post-dating the Gondwanan break-up.

Our molecular examination of *Austrosimulium* was restricted to New Zealand and does not show deep divergences, even of disparate lineages (Fig. 509a, 509b) that would indicate a Cretaceous origin. However, as mentioned elsewhere, work on *Novaustrosimulium* involving the 12S RNA gene (Ballard 1994) indicated that the Australian segregate is older. Our morphological cladistic analysis (Fig. 505–507) is not at variance with that, and adds little to what has already been suggested for *Austrosimulium*, i.e., the genus is sister to Australian + South American taxa. Still, relationship between the subgenera *Novaustrosimulium* and *Austrosimulium* is moot. In Strict Consensus the former did not resolve as a single clade (paraphyletic), indicating that taxonomy of that subgenus needs revision. It should be noted that Dumbleton (1973) erected *Novaustrosimulium* as a necessity to avoid amending the diagnosis of *Paraustrosimulium* within *Austrosimulium*.

A difference we see in our morphological analysis from that done by Dumbleton (1973) is that where he considered the Australian *mirabile* species-group as sister to the Australian plus the New Zealand *ungulatum* species-group (his Fig. 252), we show the Australian *mirabile* plus *ungulatum* species-groups to be sister lineages, and together sister to the New Zealand *ungulatum* species-group.

We note basic limitations of our phylogenetic investigations. The morphological analysis lacked data for many of the Australian species and the molecular analysis had no Australian data. Similarly, various New Zealand species were not included. For the molecular analysis (Craig & Cywinska 2012, pp. 60–65), material was not available for *A. campbellense, A. extendorum*, or *A. fiordense*, and the CO1 gene did not provide useful discrimination between species of the *tillyardianum*-subgroup (see Fig 508a, 508b). *Austrosimulium vailavoense* was not included in morphological considerations because the immature stages and adult males are not known. It is clear that Australian *Austrosimulium* needs to be taxonomically revised, with descriptions brought up-to-date, and analyses repeated with the full slate of species. Of importance would be molecular analysis.

The only molecular analyses of *Austrosimulium* species are those of Ballard (1994) and Moulton (1997, 2000, 2003). Ballard used the ribosomal RNA 12S gene which was congruent with morphological differences between *Austrosimulium* (*N.*) *pestilens* and *A.* (*N.*) *bancrofti.* However, he could not resolve cytological forms known for *A. bancrofti* (Ballard & Bedo 1991).

Current molecular study on New Zealand *Austrosimulium*

Analysis of the mt16S RNA gene by Craig & Cywinska produced poor discrimination between species of New Zealand *Austrosimulium*, was of little utility, and is not shown here (however, it is available in Supplementary Material on the website <fnz.landcareresearch.co.nz>). Given the generally assumed conservative nature of ribosomal genes (Simons *et al*. 1994; Trewick & Wallis 2001), Ballard & Bedo's (1991) results indicate that *Novaustrosimulium* is older than New Zealand *Austrosimulium,* in agreement with its placement in the morphological cladistic analysis (Fig. 505, 506). There is, however, no inherent information in the cladistic analysis regarding timing of arrival of New Zealand Simuliidae. That is, is it vicariant and as old as New Zealand's geology, or is it younger and an arrival by dispersal after the Oligocene?

The molecular analysis of the CO1 gene (Fig. 508–514) for 15 of the 19 recognised species of New Zealand *Austrosimulium* by Craig & Cywinska (2012, this monograph) supports the latter, a dispersal scenario. Concatenation of the large *tillyardianum* species-group (Fig. 508a, 508b) strongly indicates that it is a segregate of recent origin, and is in strong agreement with the poorer resolution obtained for this assemblage in the morphological cladistic analysis (Fig. 505–507).

Furthermore, most species of the *tillyardianum* species-group do not occur in the North Island, suggesting that the group probably arose in the South Island.

Ages of CO1 haplotype lineages are often calculated from the rate of molecular change of the gene over time.

A rate commonly applied for animals is 2–3% per million years (McCulloch *et al.* 2010). For arthropods, 2.2–2.3% per million years has been suggested as the rate to use (Brower 1994; Gaunt & Miles 2002). Trewick & Wallis (2001) used 2.3% for their biogeographic analyses, and we do here too. There are problems with this approach. In particular, rates of change may not be the same in different lineages (Avise 2004a), and the rate of change may not be constant in any one lineage. For *Austrosimulium*, one problem relates to individual species having different numbers of generations per year, from defined univoltine to multiple generations, some unsynchronised, even to a mixture depending on location. Genetic divergence accumulates generation by generation, so voltinism of species is of some importance. Application then of a single rate of genetic divergence to lineages, some strictly univoltine and others with unsynchronised multivoltinism, will result in mis-estimations of time of divergence of lineages.

We follow a commonly used practice for New Zealand biogeography, which is to determine divergence between lineages and then apply the estimated age to the geographic/geologic history of the islands (e.g., Trewick & Wallis 2001). More recent works (e.g., Cranston 2005; Smith *et al*. 2006) are most clear that each species should be biogeographically considered separately, in part because dispersal abilities of taxa differ. When similar patterns between disparate organisms emerge, a common deterministic event may be invoked, for example, glaciations, sea gaps, volcanism (e.g., Trewick & Wallis 2001; Goldberg *et al*. 2008).

The backbone of the rooted Neighbour Joining (NJ) tree from the molecular analysis of New Zealand *Austrosimulium* (Craig & Cywinska 2012, this monograph) is largely consistent with that of the morphological character analysis (Fig. 506, 508a, 508b, 509a, 509b), probably for the very reasons that Cranston *et al*. (2010) obtained similar concordance for chironomids — namely, use of characters from all stages. As noted by Craig & Cywinska (2012, this monograph), the major difference in topology between our morphological and molecular analyses is that Dumbleton's *unicorne*-subgroup (*ungulatum* species-group) is not sister to the *ungulatum*-subgroup, rather to all of the remaining New Zealand *Austrosimulium*. Further, in the *tillyardianum*-subgroup NJ analysis does not usefully group morphologically distinct species, such *A. tillyardianum*, *A. laticorne*, and *A. multicorne* (Fig. 508a, 508b); similarly, the cladistic Strict Consensus tree (Fig. 505) that also resolves the *tillyardianum*-subgroup poorly. Dumbleton (1973) too was of the opinion that this group was in need of special attention. Lack of resolution in the molecular analysis of the *tillyardianum*-subgroup tends to discredit clustering of haplotypes such as occurs with *A. tillyardianum* (Fig. 508a, 508b). We comment on this later.

Historical Biogeography of New Zealand *Austrosimulium* species

***australense* species-group**

australense-subgroup

Austrosimulium australense

The overall distribution of *A. australense* (Map 3) shows no obvious gaps in the North Island. Indeed, the species appears relatively evenly distributed, indicative of good dispersal. However, that assertion contradicts a previous one, namely adults of this species are not found far away from breeding localities. The South Island segregate shows a distinct gap from the mid Canterbury Plains, through Otago to southern Southland. The southern distribution is markedly similar to that of other New Zealand taxa (Trewick & Wallis 2001; McCulloch *et al*. 2010) and fits the definition of a gap distribution. Absence from Fiordland may be real, but is as likely to be from lack of collecting. Dumbleton (1973) was of the opinion that overall distribution of *A. australense* was the result of recent glaciation with subsequent lack of dispersal by either of the northern or southern segregates of the species to fill that gap. This is still the common explanation for such patterns in South Island biota (e.g., Trewick & Wallis 2001). However, there is no gap for *A. australense* in Westland, so dispersal since the Last Glacial Maximum appears to have occurred there for this species. Perhaps ecological factors are also involved, since this species is typically found in open streams with trailing vegetation. Where there is a lack of vegetation *A. australense* is generally absent. Dumbleton (his p. 546) also commented about ecological factors, such as humidity and vegetation, determining distribution.

In the molecular analysis, haplotype #1 (NZS103) (Fig. 510) is sister to the *australense* species-group, but was morphologically confirmed as *A. longicorne*! Still, that collection was of scant material of immature larvae and difficult to identify, so may be a misidentification. Divergent at some 3.4% it may well represent an undescribed species. However, the sister relationship and occurrence on Takaka Hill, northwest Nelson, might be of significance. Apart from the area being geologically ancient (Cretaceous limestone) it is generally thought not to have been extensively glaciated, including the Last Glacial Maximum (e.g., Alloway *et al*. 2007). That region, in general, also had the most haplotypes (#s 2, 3, 4, 5, 6) of *A. australense*. Such diversity of haplotypes in an area is often taken as an indication of longer evolutionary time — conversely, populations with low divergence of haplotypes are considered to indicate recent dispersal. Does this diversity indicate *A. australense* and its various haplotypes perhaps arose in the northwest quadrant of the South Island?

Genetic divergence between the North and South Island segregates of *A. australense* was some 6%, giving an age for separation of 2.6 Mya (end of the Pliocene). At that time in New Zealand the Manawatu Strait was still in existence, but becoming shallowed and with remnants of the Wanganui–Marlborough Shield present. By 2.0 Mya the Strait was narrowing with mountain ranges occluding it to the east (Trewick & Bland 2011). This scenario suggests *A. australense* moved northwards along those new mountains when the Manawatu Strait eventually was closed, diverging later to become the North Island clade.

Two populations of the southern *A. australense* (NZS170, Kaipipi Inlet, Stewart Island, Fig. 511; NZS 29, Catlins, South Island, Fig. 512) for which molecular data are available, are related to separate haplotypes from the North Island, not the South Island. Is this indicative of an even older disrupted distribution or, errors in analysis? Assuming the former, those populations are divergent from North Island *A. australense* at about 1.6%, which would equate to some 700 000 years BP (Mid Pleistocene). At that time the North and South Islands were connected across the modern Cook Strait at the Marlborough and Wellington regions and the Manawatu Strait was well gone (Lewis *et al*. 1994, Trewick & Bland 2011). An assumption here is that subsequent glaciations and concomitant ecological changes produced that eastern gap to the south. The Stewart Island segregate, and that from the Catlins, of *A. australense,* have habitats for immature stages that are at considerable variance to those of more northern exemplars — namely heavily shaded streams. The southern segregate of *A. australense*, if a relictual population, deserves further investigation, perhaps with finer examination of morphological structures, as was done for cryptic species of simuliids in Britain (Day *et al*. 2008).

With few exceptions, North Island haplotypes of *A. australense* (Fig. 511, 512, 513) have a similar distribution, namely, concentrated in Northland and Coromandel, east coast and sporadically in the central regions. Again, this is a well established pattern for New Zealand biota. However, *A. australense* overall occurs in all 13 aquatic ecoregions of the North Island.

The concordance between distributions of North Island *A. australense* haplotypes (Fig. 511, 512) and those for other insects, for example, the tree weta *Hemideina thoracica* (White) (Goldberg *et al*. 2008: their fig 6) and the caddisfly *Hydropsyche fimbriata* (McLachlan) (Smith *et al*. 2006) is strong. Such similar patterns shared by such widely diverse organisms are evidence of a common strong evolutionary event.

Goldberg *et al.* (2008) suggested that the distribution for the weta is consistent with Pliocene islands being present to the north at that time, with haplotype divergence occurring on the islands, in particular with the Manukau Strait across the present Auckland region acting as a barrier. Smith *et al*. (2006) also invoked this scenario, in part, for distribution of *H. fimbriata* haplotypes, suggesting a mid Pleistocene (780 000 years BP) divergence. They also considered impact of volcanic eruptions on aquatic organisms.

Volcanic ash and pyroclastic flows can be devastating for stream-dwelling organisms as is well known for the Mount Saint Helens eruption, on the west coast North American, in 1980 (Anderson 1992). Recovery from total removal of aquatics by scouring was rapid for the St Helens streams. In New Zealand, a light volcanic ash fall had little effect on the Tongariro River after the Ruapehu eruption of 1995 (Collier 2002). McDowall (1996) examined in detail the effects of a major eruption from Lake Taupo, some 2 200 years BP, on fish fauna of the northeastern part of the North Island. He was of the opinion that rivers which were impacted would likely still reflect that disruption to their fauna, not just to fish but also to the invertebrates. He noted that there was little indication of aquatic invertebrate endemicity in the volcanic region which might indicate antiquity and survival through such eruptions. For simuliids, however, there appears to be recent endemicity of *A. dugdalei*. We also wonder if the dense and widespread populations of *A. longicorne* on the volcanic plateau, where the larvae are found in specialised habitats associated with seeps high on the slopes of the volcanoes, may be an instance of survival in refugia and then good dispersal skills. We have alluded to the good dispersal skills of *A. longicorne* elsewhere (p. 113). Further, is it possible that the abrupt change in heterozygote inversion pairs on *A. australense* chromosomes on either side of the Tarawera River (McLea & Lambert 1983, 1985) is a result of that volcanic disruption?

Later, McDowall (2005) suggested that the crayfish *Paranephros* would have been extirpated by volcanic activity, but recolonised rapidly. Be that as it may, a series of such events in the North Island must have well sterilised the central regions. These were eruptions from a now-filled caldera north of Lake Taupo. The largest was at *ca* 1 Mya and produced the (Cape) Kidnappers Ignimbrite, a term used for the distinctive remains of pyroclastic flows, and was one of the most extensive pyroclastic flows ever known for Earth. Other debris from that eruption is referred to generally as the Potaka tephra (Wilson *et al*. 1995; Wilson & Leonard 2008).

Wilson *et al*. (1995) noted that the Taupo Volcanic Zone has produced some 34 ignimbrite eruptions from some 8 calderas over the last 1.6 my. The pyroclastic flow at 1 Mya reached as far north as Auckland and well south onto the Wanganui Basin. Its extent into the northern Hawkes Bay region and that of East Cape is uncertain, but deep sea drill cores indicate that, in places, the flow went well out to sea. Higher areas, such as the Bombay Hills and Hunua Range south of Auckland, Coromandel and Kaimai Ranges to the east, Hapuakohe Range, Taupiri and Hakarimata Ranges, and farther south were spared, as were peaks just northeast of Hamilton.

The correspondence between that pyroclastic flow and distribution of *A. australense* haplotypes # 12 and # 19 is marked, and similarly, but less so for that of #17 and #18. So, we suggest that the present distribution of those haplotypes is of upper Lower Pleistocene age (*ca* 1 Mya) and resultant from volcanic activity. This does not discount the possibility of involvement of the Manukau Strait as a dispersal barrier.

However, not only were there pyroclastic flows, but volcanic ash (tephra) was common. The recent Kawakawa (Oruanui), Okareka, and Rerewhakaaitu Tephras (*ca* 26 500, 19 100, 17 600 years BP, respectively) covered large areas and are useful in dating strata (Shane 2000). The first of these eruptions laid down 20 mm of ash (up to 2 000 mm in places) from south of Auckland, all over the North Island, northeast on the South Island, out to the Chatham Islands and even some to the Auckland Islands (Manville & Wilson 2004; Lowe *et al*. 2008; Manville *et al*. 2009). The thickness of some of these deposits is hard to imagine unless actually seen.

The centre of the North Island has been constantly sterilised, disrupted, and disturbed since the commencement of volcanism in the Taupo Volcanic Zone and the Central Volcanoes (perhaps 3 Mya and 0.27 Mya, respectively). The disruption caused by pyroclastic and tephritic activities is well reviewed by Manville & Wilson (2004) and Manville *et al*. (2009) and is suggested reading. Initial perturbation to fluvial systems (running water) is extreme, but so are the long-term effects on vegetation. Of considerable importance is that these effects depend on climatic conditions. For example, effects of the Oruanui eruption, which covered most of the North Island at 26 500 years BP during, the Last Glacial maximum, were still in progress *ca* 17 000 years BP and causing major reorganisation of running water systems and geomorphology. Is it possible, then, that the basic pattern of distribution of most of the *A. australense* haplotypes, that is, the generally low diversity in the central region of the North Island, is a result of the recent tumultuous history, rather than earlier events? Are we mis-estimating times of divergences between haplotypes? *Austrosimulium australense* has more than two generations a year, and in places they are poorly synchronised (see p. 107, species bionomics).

Haplotype #20 (NZS99, Green Hills) from the Farewell Spit region, South Island is of significance. This is sister to haplotypes #17–19 that occur up the east coast and in Northland. Given that haplotype #20 is based on more than one specimen, we are assured that this is not an error, and note that another North Island haplotype also occurs nearby at Totaranui (#31, NZS102, Fig 513). However, that their North Island sister haplotypes are more northerly raises a question — were intermediate populations removed by volcanic activity? We suggest a high probability for that.

Divergence for the Green Hills population is in the order of 550 000 years BP and that for the Totaranui population 325 000 years BP, indicating that there were two separate dispersal events from separate North Island stocks. Both suggested events could have occurred at times when the two islands were connected during glaciations (e.g., Lewis *et al*. 1994). For the Green Hills population, time of divergence from its North Island sister haplotype indicates the Kawhaka Glaciation, and for the Totaranui population the end of the Nemona Glaciation. Further sampling in that region and DNA analysis might be revealing.

Of significance is that these two populations have mixed haplotypes (see also Fig. 510); Totaranui also has South Island haplotype #5 and Green Hills has #2. Does lack of mixing of the two haplotypes indicate, as we have alluded to elsewhere, that the South Island segregate of *A. australense* is actually a cryptic species? A further question, too, is why have no South Island haplotypes of *A. australense* managed to reach the North Island?

Another haplotype with broad North Island distribution, but distinctly peripheral (Fig. 512), is #23 that consists of a markedly homogeneous series of populations. Indeed, it perhaps should be considered as just part of a single haplotype comprising numbers 23, 25, and 26. With the exception of one population of haplotype #26 (NZN92, Ohakune) and that of #22 (NZN30, Mangaweka, Rangitikei River), all are peripheral. Again, was volcanism from the Taupo Volcanic Zone responsible?

Slightly divergent from the above haplotypes is #24. This is known only from two populations in the south of the North Island and has an apparent relationship with a population (NZS29) from the Catlins, southern South Island! As for the relationship of the Stewart Island *A. australense* haplotype #14 to sister haplotypes in the North Island (Fig. 511), this is something of a conundrum and needs further examination.

Along those lines, is it possible that the widespread, homogenous haplotype #27 (Fig. 513) has colonised areas since the last major extirpation by volcanic activity, for example that by the Kawakawa (Oruanui) eruption (*ca* 26 500 years BP)? Effects of that eruption were still acting 17 000 years BP, as mentioned, previously (Manville & Wilson 2004).

McLea & Lambert (1983) examined the cytogenetics of *A. australense* and suggested three zones of inversion polymorphisms (see p. 108). They noted a marked cytological change between populations north of the Tarawera River and elsewhere. There also appeared to be differences in habitats occupied by immatures of the cytotypes. We have seen no such patterns in distribution of haplotypes, or habitat differences, but our samples around the Tarawera region were not extensive. Volcanics might also be implicated here. Manville & Wilson (2004) discussed major changes in watersheds for rivers flowing out of Lake Taupo following the Oruanui eruption. Similarly, the Tarawera River had massive break-out flooding and scouring during an eruption in AD 1315, and again in 1905, following the eruption of Mount Tarawera in 1886 (Hodgson & Nain 2005).

Austrosimulium longicorne

Currently known localities (Map 11) for *A. longicorne* show a scattered distribution with apparent gaps in both main islands, absence from Stewart Island, and presence on the Three Kings Islands. It is not obvious if these are strict gap distributions as such since the ecological requirements for the larvae of this species are distinctive: namely, smoothly flowing, constant velocity water with trailing vegetation and, as discovered recently, thin films of water with markedly low velocity in seepages. Further, populations of the species can survive in intermittent streams and, as we have suggested elsewhere, the dispersal ability of the species must be considerable. That is probably the reason that it, rather than the ubiquitous generalist *A. australense*, managed to colonise the Three Kings Islands. That colonisation probably occurred during a cool period when, for example, the distance between the extended North Island and the Three Kings was as little as 11 km during the Last Glacial Maximum (Fig. 516).

Molecular evidence shows (Fig. 510) that the species arose from the South Island segregate of *A. australense*. The divergence is *ca* 2.6%, and indicates an age of origin of *ca* 1 Mya (Mid Pleistocene). Morphological divergence, particularly between the pupal gills of the two species, is marked (*cf* Fig. 268, 269) and, as referred to elsewhere, is a good example of a lack of concordance between divergence rates of morphology and molecular aspects of species (p. 63 Molecular Results and Discussion). Haplotype #8 (NZS14, NZS41) has a marked altitudinal range (Christchurch and Old Man Range), that is perhaps suspect. Neither locality can be considered old, both being only a few thousands of years, if that. Haplotypes #9 and 9a (the latter moderately divergent) are arrayed only along the east coast of the South Island, but this is probably an artifact since the analysis lacks material from known populations (Map 11). The sister haplotype, #10, is only in the North Island, and is homogeneous and widespread. Divergent from haplotype #9 at some 1.5%, this indicates the split was at *ca* 0.87 Mya (lower Mid Pleistocene), when the connection across Cook Strait was narrowing and land ranged up to the Manukau Strait in the north (Lewis *et al.*1994, Trewick & Bland 2011). That there is but that single haplotype in the North Island is indicative that this dispersal pattern is recent.

tillyardianum-subgroup

Molecular evidence for this segregate concatenates species, and therefore has weak credence. Morphological divergence in some species is strong however.

Austrosimulium tillyardianum

The distribution of *A. tillyardianum* in the South Island (Map 14) is similar to that of *A. multicorne* and shows no gaps that relate obviously to glaciation. The apparent absence of *A. tillyardianum* from mid and south Westland is more likely the result of ecological factors. This species is typically found in open, clear-water streams with cobble substrate — a habitat not generally found in Westland where large rivers tend to have turbid water, high velocity, and unstable bed substrate not suitable for *A. tillyardianum* larvae. We too are of the opinion that its absence from southern South Island is probably related to temperature. The majority of known localities are in 10–12°C mean temperature areas (NIWA 2008) and this perhaps reflects in the species' absence from Southland Plains and High Country aquatic ecoregions where the mean temperature is some 2 degrees lower. A dearth of *A. tillyardianum* localities from the central Marlborough region is likely to be an artifact of poor collecting, as the species is now known from the Awatere and Waihopai Valleys (NZS182–184).

Our expectation was that Banks Peninsula populations of *A. tillyardianum* might show, at minimum, subspecific differences to those in the remainder of the South Island. Other aquatic invertebrates have precinctive species on the Peninsula, and Winterbourn (2008) listed 5 species of caddisfly, a stonefly, a mayfly, and a blepharicerid, *Neocurupira chiltoni.* Craig (1969) was of the opinion that this blepharicerid was derived from *N. tonnoiri* Dumbleton, wind-blown from the west. Similarly, Hitchings (2008), when discussing post-glacial distributions of New Zealand Ephemeroptera considered *Nesameletus vulcanus* Hitchings & Staniczek endemic to Banks Peninsula, to be related to *N. austrinus* Hitchings & Staniczek which is found to the west in the Southern Alps. McLellan (1975) also commented on this. A precinctive biota agrees with isolation of Banks Peninsula as a volcanic island until some 75 000–20 000 years BP, when gravel outwash from glaciers filled the sea gap (Shulmeister *et al.* 1999; McCulloch *et al.* 2009). Dates given for the junction of the Banks Volcanoes to the mainland to form the peninsula are various. For *A. tillyardianum* though there are no obvious morphological characters that indicate any divergence due to isolation. This is in full agreement with the lack of molecular divergence within the *tillyardianum* species-group (Fig. 508a, 508b), again suggestive of recent origin.

In the North Island, *A. tillyardianum* is widespread from the Auckland region southwards. Our collections have extended, by a considerable extent, the range known to Dumbleton (Map 14). It is unlikely this represents recent expansion of the species' range, but rather is the result of more extensive collecting. We make that assertion since it appears the distribution of *A. tillyardianum* is constrained by temperature, its northern extent falling generally in the 12–14°C mean annual temperature range (NIWA 2008). In the North Island, one gap in distribution that is probably real, even though it also represents patchy collecting, is that encompassing the Taranaki region. Streams and rivers there are, in part, cut down through blue mudstone (papa) and hard cobble substrates — typical habitat for *A. tillyardianum* larvae are generally lacking. The same applies to the Wairarapa. Similarly, *A. tillyardianum* habitats are sparse in the Waikato, however, for different geological reasons and because of heavy agricultural usage.

Lack of divergence (Fig. 508a, 508b) in the CO1 gene means we cannot usefully comment on *A. tillyardianum* distributions from a molecular viewpoint. Such homogeneity can indicate recent origin and rapid dispersal. The presence in the central part of the North Island, a region repeatedly disrupted by volcanism, also indicates considerable dispersal ability.

Austrosimulium alveolatum

Originally considered a subspecies of *A. laticorne*, but herein raised to species status, *A. alveolatum* occurs in a restricted area around Porters Pass in Canterbury (Map 2). Most likely derived from the *A. laticorne* western population (Map 10), *A. alveolatum* could be considered a breakout population through the passes in the Southern Alps. Such areas have been ice free for a relatively short time, possibly much less than 13 000 years BP (Burrows 2005).

Both *A. albovelatum* and *A. alveolatum* show distributions that would be expected from isolation caused by glaciers, as evinced for stonefly (Plecoptera) vicariant distributions by McCulloch *et al.* (2010). There is evidence that at maximum advance the Rakaia Glacier (Burrows 2005; Alloway *et al.* 2007) extended as far east as present-day Methven. Similarly, the Rangitata Glacier to the south extended to near Mayfield. Thence both cut through ecological zones on the extended coastal plains. Burrows (2005) and others (e.g., Soons 1994) showed that even at the final advance the eastern glaciers (Waimakariri, Rakaia, and Rangitata) terminated just upstream of their present-day gorges. During the Waimaunga Glaciation (ending 220 000 years BP) the Waimakariri, Rakaia, and Rangitata glaciers extended even farther eastwards than during the Otira Glaciation (Burrows 2005). Isolation caused by glaciations has often been invoked to explain distributions of biota (e.g., Hewitt 1996; McCulloch *et al*. 2010): we are of the firm opinion that this involves *A. albovelatum* and *A. alveolatum*, and that their current distributions are refugial. Such restricted areas are analogous to the "kipuka" of Hawai'i — regions of older land surrounded by fresh lava where speciation has taken place. *Austrosimulium albovelatum* and *A. alveolatum* are not closely related phylogenetically, so the glaciers acted on separate precursors.

Austrosimulium multicorne

This species occurs sporadically along the western side of the South Island and there appear to be no gaps as such (Map 12), except perhaps southern Westland. On the eastern side of the Southern Alps, the species is common along the foothills west of the Canterbury Plains and shows no evidence of disjunct distribution. Aggregation of localities hard along the Southern Alps is a collection artifact resulting from proximity of running water to roads. With lack of molecular discrimination within the *tillyardianum*-subgroup we cannot make useful comment from that point of view, except again, that lack of internal divergence indicates recent origin of the subgroup. Superficially though, the distribution (Map 12) of *A. multicorne* appears to fit well the "colonisation" distribution of Trewick & Wallis (2001), indicative of recent events since the Last Glacial Maximum and in full agreement with the molecular data (Fig. 508a, 508b).

The low frequency occurrence of *A. multicorne* on Banks Peninsula is of interest since the species' presence there was unknown until now. Crosby (1974a), during his intensive work there on *A. tillyardianum*, did not recover *A. multicorne.* Neither did Dumbleton. It is unlikely that its presence is the result of recent colonisation, although that is possible. Its low frequency may reflect competitive exclusion by *A. tillyardianum*, which is widespread and occurs in astronomical numbers at some localities.

Austrosimulium dugdalei

Originally considered to be the North Island representative of *A. multicorne* by both Tonnoir (1925) and Dumbleton (1973), divergence of *A. dugdalei* from *A. multicorne* can perhaps be suggested as no older than 275 000 years BP, given that its precinctive distribution seems to rely on the high altitude of the Volcanic Plateau and southern Taupo Volcanic Zone (Map 6). The Volcanic Plateau consists of debris originally from the Tongariro volcano, and later from Ngauruhoe, Ruapehu, and other eruptions. Given that *A.*

dugdalei appears to prefer higher altitudes, divergence from *A. multicorne* is no doubt more recent than given above, since time was required for those volcanoes to produce the plateau. Although data are limited, *A. dugdalei* does not group with *A. multicorne* in the molecular analysis (Fig. 508a, 508b), and suggests a separate species. Again, with little credence, the small amount of genetic divergence for *A. dugdalei* indicates an origin *ca* 250 000 years BP, congruent with the age of the Volcanic Plateau.

Austrosimulium albovelatum

Austrosimulium albovelatum has a similar distribution to that of *A. alveolatum*, being restricted to the eastern side of the central Southern Alps, from Porters Pass, south to the Rangitata River (Map 1). There is, however, an unusual northern outlier (NZS11) at Kaikoura, based on a pupa and cocoon, found at sea level (p. 116). Are there populations between Kaikoura and Porters Pass? All populations fall into the High Country aquatic ecoregion, a finger of which extends out to Kaikoura from the mountain range, so we assume there will be.

Apart from this Kaikoura outlier, the body of the distribution indicates an origin in a refugium between major glaciers (Waimakariri and Rakaia), and not necessarily from the recent Otira Glaciation. The arrangement of glaciers (Burrows 2005, his Fig. 70) for the Waimaunga glaciation (300 000 years BP) was similar to that of the Otira.

Austrosimulium laticorne

Although widespread in the South Island, *A. laticorne* is precinctive and is unknown from North and Stewart Islands. It is widely distributed on the West Coast, northwest Nelson and into the Marlborough Sounds area, but is mostly absent from the rest of the island except for the most southern part (Map 10), indicating a gap distribution rather similar to the South Island *A. australense* (Map 3).

The northern population might indicate the Southern Alps acted as a barrier and that the population has not yet managed to disperse east. That central Marlborough region is poorly collected, and the current known distribution may well be an artifact as suspected for other species. Recent collections in the Marlborough region failed to discover *A. laticorne*, but they extended the distribution for *A. tillyardianum*. The outlier population east of the Southern Alps at Lake Tekapo may well represent penetration of the Southern Alps by the Westland population. Such penetrations have been suggested for the cicada *Kikihia subalpina* (Hudson) (Marshall *et al*. 2009), and elsewhere across the Southern Alps for galaxiid fish as river capture alters drainage basins (Craw *et al*. 2008).

The distribution also matches, in large part, distributions exhibited by apterous stoneflies (Plecoptera) as shown by McCulloch *et al*. (2010) that suggest late Pleistocene glaciation as a simultaneous vicariant event. We assume the same for *A. laticorne* and are of the opinion that this is a classic gap distribution with some “regional” distribution (Trewick & Wallis 2001) along mid Westland. The Southern Alps appear to have been a barrier to dispersal eastward, except for some penetration at Lake Tekapo.

Absence of *A. laticorne* from the North Island indicates the species did not reach Cook Strait until after it was formed some 450 000 years BP (mid Pleistocene) and did not manage to cross during the lowering of sea levels in subsequent glaciations. This is perhaps an indication that at such times climatic conditions across the Farewell Rise were not conducive to dispersal. We consider there are many suitable habitats for *A. laticorne* available in the North Island.

Given the occurrence of *A. australense, A. stewartense*, *A. vailavoense*, and *A. ungulatum* on both Stewart Island and in the south of the South Island, a not unreasonable expectation is that *A. laticorne* might also occur on Stewart Island; so far it is not known from there. Does this indicate that *A. laticorne* colonised the south of the South island after the Last Glacial Maximum when Foveaux Strait was re-submerged. As assumed for Cook Strait during glaciations, climatic extremes may well have made Foveaux Strait impassable to simuliids for much of the time. Suitable habitats for *A. laticorne* are not plentiful on Stewart Island; still, other species find equable localities.

Austrosimulium stewartense

The distribution of *A. stewartense* (Map 13) mimics, in many ways, that of the southern segregate of *A. australense* by occurring on Stewart Island and in the southern part of the South Island. Because of variability in the morphological features used for identifying *A. stewartense* and those of the closely related *A. multicorne* (see species descriptions), we are not confident in commenting on the identities of two apparent populations from Mid Canterbury. With a broad connection (Fig. 518) across Foveaux Strait during the Last Glacial Maximum resulting from sea level depression, and no doubt such depressions previously, the *A. stewartense* distribution pattern is indicated as being of Pleistocene age, but could have come about due to earlier lowered sea levels (e.g., Fig. 515). However, a more recent origin would be in agreement with the lack of molecular divergence within the *tillyardianum* species-group (Fig. 508a, 508b).

Austrosimulium extendorum

Austrosimulium extendorum and *A. stewartense* are sister species (Fig. 507) and morphologically similar. Little can be said about *A. extendorum*, except it is only known from Stewart Island and nearby Big South Cape Island (Map 8).

With no new material, molecular data were not available, but with the lack of discrimination in the *tillyardianum* species-group, such material would likely have been of little use.

Austrosimulium fiordense

Dumbleton (1973) considered *A. fiordense* to be a subspecies of *A. multicorne*, but we raised it to specific status on the basis of distinctive features of the pupal thorax. Known originally only from material from Fiordland with the majority lost subsequently, new material was taken by TKC at high altitude on the Darran Mountains, Fiordland and by DAC at Rangitata River (Map 9). It is not clear if this is a gap distribution, or will be found to be a colonisation distribution (Trewick & Wallis 2001). We expect the latter, with other high altitude intermediate populations being discovered between Fiordland and the Rangitata locality (NZS126). If not, then glaciations can be invoked for the gap between populations. Irrespective, all known localities were heavily glaciated during the Otira Glaciation and current presence must be recent.

ungulatum species-group

ungulatum-subgroup

A. ungulatum, *A. vexans* & *A. campbellense*

Absent from the North Island, *A. ungulatum* is well distributed in the South Island and Stewart Island (Map 16). Apparent absence from parts of Marlborough is possibly a result of lack of collecting, but it could also be due to drier conditions and a lack of forest cover, which appears to be favoured by this species. Shaded cold-water streams are also lacking from much of the Canterbury Plains and Otago where it has not been collected. However, a recent collection from the Lindis Pass (NZS181, High Country ecoregion) shows that *A. ungulatum* does not require forest, but more obviously, cold water. As with *A. multicorne*, the apparent concentration of localities in the eastern foothills merely reflects accessibility from roads (Map 12). Indeed, the distribution of roads in the South Island is all too clear from the collection records for the species.

The presence of two female *A. ungulatum* on Banks Peninsula was unexpected — and DNA data was not recoverable from the specimen examined. Opportunities for wind dispersal from the west must be common, and more so in the past during glaciations when westerly winds are thought to have been exacerbated (Fitzharris *et al.* 1992) and ecological regions pushed farther east by glaciation (Burrows 2005). While present ecological conditions at the upper Kaituna River would be suitable for *A. ungulatum*, elsewhere it is generally not. Overall ecological conditions on Banks Peninsula have been substantially altered by human intervention particularly over the last century or so (Winterbourn 2008). Is it possible that the 2 specimens are relicts of more abundant populations present when the Peninsula was well forested?

The detailed distribution of *A. ungulatum* shows a small "beech gap" of less than 100 km in Westland (Map 16). The molecular data (Fig. 514) show that haplotype #38 matches closely that overall gap distribution, with haplotype #36 being more widely separated. Such distributions are normally ascribed to the glaciation that occurred in the region during the Last Glacial Maximum, with failure to close the gap since then. However, the presence of haplotype #38 at localities in the Arthurs Pass region, well glaciated during the Last Glacial Maximum, suggests that dispersal is not the problem, and that the gap is the result of other effects such as habitat availability. Further, other species of *Austrosimulium* do not show that gap.

The morphological cladistic analysis show *A. vexans* + *A. campbellense* as sister to *A. ungulatum* with *A. dumbletoni* sister to those (Fig 507). This result conforms to that of Dumbleton (1973) and is in agreement with his contention that the first two species were derived from *A. ungulatum*. Of note, though, is that molecular evidence indicates (Fig. 514) that *A. vexans* is sister to a small segregate (haplotype #33) of *A. ungulatum*, and not that species in the aggregate (Fig. 507). Divergence between the clade of *A. vexans* + *A. ungulatum* (haplotype #33) and the remainder of the *ungulatum* haplotypes (#35–38) is *ca* 7%, indicating divergence of the two clades some 3.0 Mya (early Late Pliocene). With such divergence, the *vexans* segregate of *A. ungulatum* may well be deemed a separate species if morphological characters can be determined — none can yet be found to justify this though. Is this a good example of molecular divergence without concomitant morphological change?

The main question, though, is how did the ancestor of *A. vexans* get to the Auckland Islands, and, for that matter, *A. campbellense* to Campbell Island? For the latter while morphological evidence suggests a relationship with *A. vexans* (Fig. 507), eventual molecular data might well reveal it to be sister to another segregate of *A. ungulatum,* thus representing a separate origin to that of *A. vexans*. We consider this worth investigating.

In the early Late Pliocene the world was emerging from a markedly warm period with elevated sea levels, and was entering, from then on, regular glaciations (Haq *et al.* 1987; Naish 1997). Both the Auckland Islands and Campbell Island were well emplaced and no doubt much larger having not suffered the erosion evident now. Further, hot spot islands gradually sink as the heat from their original volcanism wanes (Craig 2003), so these two islands would have then been not only larger, but higher. However, because of lack of glaciation world-wide, sea levels were higher then than now (Haq *et al.* 1987); hence land area would have been reduced. Naish (1997) showed regular occurrence of glaciations from 2.8 Mya (upper Late Pliocene) on, and these in general reduced sea levels between some 70–100 m. Similarly, apart from the Otira and Waimea Glaciations when sea levels plummeted to possibly -135 m, over the last 250 000 years the usual depression during cold periods, has been more of the order of 70 m (Fig. 515) (e.g., Chappel 1986; Burrows 2005). So, exposed land south of Stewart Island and north of Auckland Islands during these periods, although not as extensive as that in the Last Glacial Maximum (Fig. 518), would still have reduced the distance for dispersal of an *A. vexans* precursor, and similarly for the precursor to *A. campbellense* to Campbell Island.

Dispersal by wind is a distinct possibility. McGlone (2002) had substantial evidence for long-distance pollen dispersal (pollen rain) to New Zealand's Southern Oceanic Islands, with New Zealand the dominant source. However, he also noted that the Auckland Islands show abundant evidence of glacial activity. The U-shaped valley systems of Campbell Island also indicate glaciation, though more ambiguously.

McGlone (2002) also considered problems that during recent glaciations, the marine Antarctic Convergence possibility moved 5 degrees north. This would have likely resulted in Auckland and Campbell Islands possessing climates similar to that now found on Macquarie Island; that is, summer temperatures as low as 5 to 6°C and 3 to 4°C, respectively. That would have created problems for the present flora, since cooling would have resulted in no suitable land for survival because of the depression of snow level. Not mentioned, however, is that with the major glaciation during those recent glaciations, sea level depression was marked, even down to 135 m below present levels (Fig. 518). So, while the current land areas of Campbell and Auckland Islands are 113 km^2 and 626 km^2, respectively, during the Last Glacial Maximum they would have been some 4 000 km^2 and 6 800 km^2, respectively, for perhaps 5 000–10 000 years during each of the Otira and Waimea Glaciations (Fig. 515).

Opportunities for colonisation of Auckland and Campbell Islands by *Austrosimulium* were not lacking — running water would not have been in short supply. The molecular data indicate early Late Pliocene; the probability is low that colonisation of Auckland and Campbell Islands by *Austrosimulium* was older. While the islands are some 19–12 and 11–6 million years old respectively (mid Early Miocene), the Campbell Plateau, which might have served as a biological source, was well submerged by 40–35 Mya (Middle Eocene) (Sutherland *et al.* 2010: their Fig 2). That is, there was a gap of, at maximum, 16 million years between the flooding of the plateau and formation of land via volcanoes. This presents a major problem for the origin of all the biota of these islands, some of which is thought to be old in nature (e.g., Michaux & Leschen 2005).

Dumbleton (1963b) was of the opinion that *A. vexans* was derived from *A. ungulatum* via aerial colonists, post-Pleistocene, but he did not elaborate. In 1973, he commented that origin of *A. campbellense* was probably similar to that of *A. vexans* and post-Pleistocene, at oldest post Pliocene. We agree.

The remaining moderately well supported clade of the *ungulatum* group s.s. (haplotypes #35–38) has haplotype #35 (NZS82, Lyell Creek, Buller River), sister to the remainder at 1.9% divergence; indicating the age of separation at maximum 826 000 year BP (early Late Pleistocene). This location is of interest in that the general region is considered to have harboured relictual forest during the Last Glacial Maximum (Alloway *et al.* 2007) and no doubt during others previously. *Austrosimulium ungulatum* appears to be dependent on forest, although the exact reason why is not obvious. Small, cold-water, densely-shaded streams are normal for these larvae, although shade is not necessary (e.g. NZS181). Could this region be the origin of *A. ungulatum* s.s?

The remaining *A. ungulatum* haplotypes (#36–38) had a divergence of some 3.7 % from the others, which gives an origin at *ca* 1.6 Mya (upper Lower Pleistocene). In general, the haplotypes are widely dispersed and their apparent absence, in particular from Kaikoura, Canterbury, and Otago regions, are sampling artifacts (see Map 16). There is little in the northern distribution to indicate any effect of the Southern Alps as a distributional barrier, as suggested for other invertebrates (McCulloch *et al.* 2010). Although molecular data were not available for the localities at Kaikoura (Map 16), we expect them to be probably of haplotype #38, distributed to the west.

Still, an apparent "beech gap" for *A. ungulatum* is puzzling, as is its absence from the North Island. Females of *A. ungulatum* will fly considerable distances to blood feed. They develop eggs and need to find running water to oviposit. Running water is not lacking in the region of the "beech gap", so why has *A. ungulatum* not filled that gap? Other previously glaciated areas have *A. ungulatum*. A partial reason may involve the chemistry of water in the region, much of which is brown from dissolved organic compounds. *Austrosimulium* larvae appear to be tolerant of a wide range of pH, and elevated acidity due to organic compounds does not alter presence of many invertebrate taxa (Winterbourn & Collier 1987). However, acid streams, in comparison to those that are alkaline, may have only a quarter of the density of aquatic invertebrates (Collier & Winterbourn 1987) and that too was our experience with aquatic macroinvertebrates. So, although presence of the "beech gap", is assumed to be due to glacial effects, is it really a consequence of ecological conditions, or a combination of both? That haplotype #38, which occurs on either side of the apparent gap is also found at Arthurs Pass, which recently glaciated, points to ecological reasons for the gap to the west.

Relevant to the ecological reasoning for a beech gap is the rapid fall-off in abundance of *Austrosimulium* larvae south of the Kawhaka River, Old Christchurch Road, a light brown-water river (NZS50), near the northern edge of the "beech gap". Yet, a mere 27 km directly ENE, is currently New Zealand's most species-rich simuliid locality at Jacksons Bridge, Taramakau River (NZS51). There, larvae of *A. australense, A. laticorne, A. multicorne,* and *A. tillyardianum*, together with adults of *A. ungulatum* were obtained from a small area. This is unusual even though the Taramakau River has clear water, but it is a large, braided, unstable river and not obviously suited to all those species. Still, *A. australense* (Map 3) and *A. multicorne* (Map 12) occur sporadically along the gap region.

The apparent aggregation of haplotypes in the Arthurs Pass region (Fig. 514) is a sampling artifact, as material from several nearby localities (Map 16) was not available for molecular analysis.

The two main haplotypes of *A. ungulatum* (#36, #38) are widespread and overlap in distribution. Their divergence of 2.5% represents separation of lineages at about 1 Mya (upper Lower Pleistocene). At that time New Zealand was emerging from a period of some 20 cool episodes that alternated with warm periods before entering more substantial glaciations (Burrows 2005). It was also the time of the devastating eruption that covered much of the North Island and produced the Kidnappers Ignimbrite. Is it possible that there was a genetic bottleneck at that time for *A. ungulatum* with subsequent widespread dispersal of the two haplotypes over the South Island? And attesting to the apparent considerable flight ability of the females?

Dumbleton (1973), too, puzzled over the distribution of *A. ungulatum*, in particular its absence from the North Island. For the adults, some dispersal and aggregation behaviour is well known. Part of the puzzle surrounding the absence of *A. ungulatum* in North Island is that Mount Taranaki currently has conditions that appear to be suitable for this species. But that was not so during the Last Glacial Maximum. As McGlone & Neall (1994), Alloway *et al*. (2007), and others have shown, the mountain was then covered in shrubland and grasses that do not provide optimal habitat for *A. ungulatum*. Further, the mountain is relatively young (0.015–0.012 Mya) and has been volcanically active. The change from shrubland to forest was rapid, possibly over a period of only 1 000 years around 12 000 years BP (McGlone & Neall 1994). Furthermore, conditions for an adult simuliid attempting to fly across the present Cook Strait are not amicable, and strong westerly winds that are typical will reduce the probability of dispersal from the South Island to the North. Such winds were known to have been exacerbated during glaciations. Still, such winds do not blow continuously.

A not unreasonable expectation would be for *Austrosimulium* and other aquatic insects to disperse easily between the two main islands during glacial maxima because of rivers flowing out onto the South Island–Taranaki plain. The Waimea, Motueka, Takaka, and Aorere Rivers no doubt flowed out onto the plain from the South Island, as did the Whanganui and the Rangitikei Rivers from the North Island. The exact drainage patterns are not known, but some have been suggested (Fleming 1975; Lewis *et al*. 1994; Trewick & Bland 2011). Even if the rivers did not merge, distances between them would have been short.

unicorne-subgroup

Austrosimulium vailavoense + *A. unicorne* & *A. bicorne* + *A. tonnoiri* + *A. dumbletoni*

Dumbleton (1973) considered *A. unicorne* and *A. bicorne* to constitute taxonomically the *unicorne*-subgroup, sister to the New Zealand *ungulatum*-subgroup. Our cladistic analysis is in full agreement at the Majority Rule level (Fig. 506), with minor differences when fully resolved (Fig. 507). We raised *A. tonnoiri* to species status from specimens considered by Dumbleton to be *A. bicorne*, mainly on the basis of the distinct pupal cocoon. Both *A. dumbletoni* and *A. vailavoense* are only known from adults, and morphologically appear to belong to the *ungulatum*-subgroup.

Molecular analysis (Fig. 514) is slightly at variance to the above, with *A. vailavoense* and *A. dumbletoni* clustered in what is normally considered the *unicorne*-subgroup and discussion below is centred round this point. The placement of these two species in the molecular phylogeny is perhaps not anomalous given the lack of morphological divergence in the females of the *ungulatum* species-group. Species designation is in large part based on pupal horn and larval anal sclerite characters, however, immatures of the two species of concern are not yet known. If the placement of these two species based on molecular data is correct, then we suggest that gills of pupal *A. vailavoense* and *A. dumbletoni*, when discovered, will be more similar to those of the *unicorne* species-group, with a basal horn and fine filaments (Fig. 283, 285), rather than the antlered type found in *ungulatum* species s.l. (Fig. 281).

The *unicorne*-subgroup is part of New Zealand's unusual high-alpine biota which has long been of interest (e.g., Fleming 1963, 1979; Johns 1969; Raven 1973; McGlone 1985; Given & Gray 1986; Morgan-Richards & Gibbs 1996; Trewick *et al.* 2000; Hitchings 2009). In large part the interest is because of the relatively youthful age of the Southern Alps.

There is ample tectonic evidence (e.g., King 2000; Coates 2002) to suggest that the Southern Alps are at the most perhaps 8 million years old, but more likely 5 or even 3, when uplift was accelerated to produce their present form. Batt *et al.* (2000) used K–Ar dating to determine that their age was certainly in the order of 5 million years. Of note, they commented that estimates of earlier age (e.g., 8 Mya) were based on older rock in Fiordland exposed during later exhumation erosion along the mountains, a process recently examined in detail by Shuster *et al.* (2011). Chamberlain *et al.* (1999) and Chamberlain & Poage (2000) using d^{18}O isotope also showed changes that agreed with an origin of the Alps at 5 Mya and, further, that there was a rapid 2 000 m increase in altitude at that time in the early Miocene.

Is this an acceptable age for the origin of *Austrosimulium* in New Zealand, via dispersal from Australia, probably Tasmania? Certainly, sister taxa in Tasmania are adapted to cool temperate conditions, as are those of South America (Fig 507). Preadaptation to mountainous conditions in New Zealand has been suggested already by Dumbleton (1973). Molecular evidence from divergence ages of lineages would suggest so and is not at variance with that of paleogeology.

A nagging question remains, though, in regards to the other high alpine aquatic fauna such as blephariceridids and mayflies, both considered to be older groups. Did they, too, adapt to the alpine conditions at the same time as *Austrosimulium*, or were there separate events?

The newly recognised species *A. vailavoense* from the southern South Island and Stewart Island (Map 18) shows a distribution common to southern segregates of other species, namely *A. australense, A ungulatum*, and *A. stewartense*. While we did not include *A. vailavoense* in the cladistic analysis because we lack all stages other than female adults, we currently place it in the *ungulatum*-subgroup following the same reasoning as Crosby (1976a) for *A. dumbletoni*—namely the toothed claw.

A marked molecular divergence of *ca* 16% from the *ungulatum*-subgroup proper (Fig. 513), indicates that the precursor to *A. vailavoense* was an older entity, perhaps up to some 7 million years old. The two populations of this species (NZS157, 165) separated by Foveaux Strait are divergent at only 0.7%, indicative of more recent dissociation, some 330 000 years BP (mid Middle Pleistocene), perhaps following the end of the Nemona Glaciation (Burrows 2005) when sea level depression is estimated to have reached at least -110 m and then risen rapidly (Huybrechts 2002). The older divergence from the common ancestor with *A. unicorne* presents something of a problem, since that species is now strictly a cold-water, high-altitude species. These are habitat attributes that were not available until the Early Pliocene (5 Mya) with orogeny of the Southern Alps.

Based on the slightly longer divergence of the South Island population of *A. vailavoense* one scenario is that the precursor of *A. vailavoense* diverged from that of *A. unicorne* on the South Island and then dispersed to Stewart Island. *Austrosimulium unicorne* then adapted to alpine conditions when these became available later, with *A. vailavoense* inhabiting lowland forested habitats. This latter assertion will be tested when early stages of *A. vailavoense* are discovered.

For *A. unicorne,* only a single locality (NZS132, Pegleg Creek, Arthurs Pass) was available for molecular analysis. Other localities (Map 17) show this species to be restricted to the Southern Alps in the central South Island. With one exception, all localities have cold, clear water at high altitude. Molecular data from other populations should reveal how divergent they are—if at all. At present the distribution fits the "colonisation" definition of Trewick & Wallis (2001) consistent with reinvasion of suitable habitats following the Last Glacial Maximum.

Austrosimulium unicorne (Fig. 514), as sister to *A. vailavoense,* is divergent at *ca* 9%—indicating a split of some 4 Mya, and an age similar to that of the Southern Alps.

The sister clade to the above is comprised of *A. bicorne*, *A tonnoiri*, and *A. dumbletoni*. With the exception of *A. dumbletoni*, for which there is not much information, the other two have similar ecological requirements to *A. unicorne* (Fig. 507). Divergence time for this clade from the *ungulatum* species-group is similar to that for its sister clade (*A. vailavoense* + *A. unicorne*), and is relatively consistent with formation of the Southern Alps. *Austrosimulium bicorne* is known from two regions, one (haplotype #41) in the Arthurs Pass region (NXS133) and the other (haplotypes #42, 43) in Fiordland (NZS32) (Map 4). The haplotype #41 from Arthurs Pass is divergent from haplotype #42 by some 2.8%, an age of some 1.2 million years. These two populations should be re-examined morphologically for the possibility that they are cryptic species. The Fiordland population (NZS32) shows evidence for perhaps 3 haplotypes, with #42 divergent at 1.2 % (522 000 years BP) and another at *ca* 1.0 % (435 000 years BP). Is this indicative of multiple isolation events via glaciations? Their occupation of areas that were heavily glaciated during the Otira Glaciation, indicates an ability to disperse rapidly.

For the present we consider the gap between Arthurs Pass and Fiordland to be a collecting artifact and expect other intermediate populations to be discovered. Collecting this species and *A. tonnoiri,* elsewhere in the Southern

Alps will, however, require considerable physical stamina. Mountaineering skills would not be amiss.

Austrosimulium unicorne, A. bicorne, and *A. tonnoiri* are all high altitude and cold water species. In addition, they have further markedly specialised requirements for the larvae. These immatures are large and pale. UV radiation is avoided by simuliid larvae (Donahue & Schindler 1998; Kelly *et al.* 2003), so it is likely that their usual habitat (perched stones) allows larvae to attach on the undersides, thereby avoiding UV radiation while still in full flow of water. Further, in the alpine streams inhabited by these larvae the water levels vary considerably, often on a diurnal basis as snow packs melt. Dumbleton (1973: 545) suggested that the thick pupal cocoons of these species (Fig. 175–177) would protect against temperature fluctuations; an unusual suggestion for a poikilotherm such as a simuliid. We consider that it is far more likely to be protection against desiccation from the rapidly varying water levels. Such distinctly specialised habitats cannot be older than the age of the Southern Alps and specifically require mountainous terrain to form (Frey & Church 2009). This represents physical evidence that origin of these species is no more than 5 Mya.

Known only from Westland at Jackson Bay and Knights Point some 60 km further north (Map 7), *A. dumbletoni* appears to have a refugial distribution. Burrows (2005, his Fig. 7.1) showed both areas as being non-glaciated during the Otira Glaciation, but ice extended out to sea between them. Collection efforts in similar ice-free areas farther north would test this assertion.

Age of New Zealand *Austrosimulium*

The maximum divergence (Fig. 509) between New Zealand *Austrosimulium* and *Simulium* (generally agreed to be the sister genus to *Austrosimulium* overall), is some 19%, equating to a separation *ca* 8 Mya (early Late Miocene). However, the inclusion of taxa absent from the molecular analysis, such as *Paraustrosimulium anthracinum*, *?Austrosimulium colboi*, *Cnesiamima atroparva*, and ?*Paracnephia pilfreyi* (the outgroups), and Australian exemplars of *Austrosimulium*, might well suggest a different scenario.

Given, however, that the basal groups of New Zealand *Austrosimulium*, the Australian sister taxa, and related forms in South America, have immatures that require high-altitude cold-water habitats, the New Zealand *Austrosimulium* probably arrived in New Zealand pre-adapted to those conditions, and did not adapt to the early Southern Alps as they arose starting in the Early Pliocene. So, with present understanding, we consider it is unlikely that New Zealand *Austrosimulium* are "Ghosts of Gondwana" (Gibbs 2006) — but they are first or second cousins.

FUTURE STUDIES ON *AUSTROSIMULIUM*

There are still many opportunities for research on *Austrosimulium*. At a higher level, the Australian segregate needs to be fully revised to the same level as done here for New Zealand, together with molecular analyses. Part of that revision might well include the so-called *Paracnephia* Rubtsov of Australia. There are also indications that the New Zealand *Austrosimulium* might be paraphyletic, with a separate origin for the *ungulatum*-subgroup given its unusual pupal gill structure.

Within New Zealand a more detailed examination of the human-biting species *A. australense* is in order, to see if morphological evidence can be found to assign the South Island population to a separate morphospecies from that of the North Island. This would resolve the current taxonomic conundrum from molecular analysis of the *australense* species-group (Fig. 509a, 509b, 510) with *A. longicorne*, a markedly distinct morphospecies, sister to the South Island clade of *A. australense*, but not to the whole of *A. australense*. Part of this examination should involve further collections of *A. australense* from around the north of the South Island, to clarify the occurrence of North Island haplotypes there (Fig. 511), and also collections in the south of the South Island and on Stewart Island (Fig. 511, 512). Such study should help to clarify aspects of historical biogeography.

Similarly, the important human-biting species *A. ungulatum* needs further examination, particularly the variation in its pupal gill structure. Molecular evidence indicates that *A. ungulatum* is a species complex and the gills might provide sufficient morphological evidence to assign some haplotypes to separate species. Such an examination should also include a re-examination of the relationship of *A. vexans* to its sister segregate of *A. ungulatum*. More material of *A. campbellense* is needed to answer the following question; is it directly sister to *A. vexans*, or is it related to a segregate of *A. ungulatum* haplotypes, as is *A. vexans*?

It is of phylogenetic significance to find the immature stages of *A. dumbletoni* and *A. vailavoense*, currently assigned to the *ungulatum* species-group on the basis of their morphology. In contrast, molecular evidence indicates both belong to the *unicorne*-subgroup. Early stages, in particular the pupae, could resolve to which subgroup they should really be assigned. Searches for *A. dumbletoni* immatures might well be concentrated in high-altitude localities, in keeping with known habitats of the *unicorne*-subgroup species; none have thus far been found at low altitude where adults have been collected.

High-altitude localities need to be further searched. They have been relatively poorly collected to date because of access difficulties. Such collections would no doubt reveal that some of the current disparate distributions, such as those for *A. albovelatum* and *A. fiordense*, are probably the result of lack of collecting. Areas that need much more collecting are southern Southland and Stewart Island, as simuliids from both regions indicate that these regions were refugia during glaciations. The central Marlborough region, with poor access, is also an area of concern — virtually no collections are known from there.

Ecologically, almost all species, with the exception of *A. tillyardianum* and perhaps *A. australense,* need detailed study; even the most basic investigation would add to current knowledge. One species, *A. longicorne*, would be most intriguing to investigate further. Originally thought to be widespread and disparate in distribution, it is now known to be widespread and common on the central volcanoes of the North Island. Of particular interest is the extreme habitat of the larvae: thin-film, slow-velocity flows in seepages dominated by iron bacteria. The larvae are the dominant aquatic macroinvertebrate in these habitats. One aspect of biology that is startlingly undocumented for all species is mating behaviour; what do the males do and where does copulation take place?

Ilmonen *et al*. (2009) successfully used multiple characters from cytology, CO1 gene sequences, ecology, and morphology to clarify species status within the European *Simulium vernum* group. A similar approach could perhaps be used to better elucidate species limits within the *tillyardianum* species-group of *Austrosimulium,* in particular those of the *'multicorne* assemblage', which appears to be undergoing an evolutionary radiation. Rubinoff *et al.* (2006) pointed out that nuclear genes might provide insights into relationships when mtDNA does not.

Molecular evidence showed that a haplotype from the top of the Takaka Hill, was sister to the *australense*-subgroup, but morphologically it appeared to be *A. longicorne*. Further collecting from that locality might throw some light on this conundrum.

In the central North Island, further investigations are needed on *A. australense* to explain the abrupt change in heterozygote inversion pairs between Zones 1 and 2 reported by McLea & Lambert (1983, 1985); they suggested this might represent 2 cryptic species with support provided by differing water flow conditions in the habitats the larvae occupied. However, we found no morphological evidence to substantiate the presence of 2 cryptic species, and molecular analysis of the CO1 gene also did not support it. In South Westland it would be worth investigating why this species showed a high ratio (about 1 in 170) of gynandromorphic individuals attracted to moulting Fiordland crested penguins in one study (Craig & Crosby 2008); this incidence of gynandromorphic individuals is far higher than reported for any other simuliid species (Crosskey 1990).

SYSTEMATICS

The generic and subgeneric descriptions below are based on those of Dumbleton (1973).

Simuliidae Newman, 1834: 379

Austrosimulium Tonnoir, 1925

Austrosimulium Tonnoir, 1925: 230. Edwards 1931: 143 (as subgenus of *Simulium*). Séguy 1940: 228. Smart 1945: 499 (as genus). Mackerras & Mackerras 1949: 391. Wygodzinsky & Coscarón 1962: 240. Stone 1963: 2. Dumbleton 1963b: 326. Dumbleton 1973: 481. Crosskey 1969: 25; 1991: 12. Adler & Crosskey 2012: 19.

TYPE-SPECIES: *Simulia australensis* Schiner, 1868: 15 (New Zealand), by original designation.

Small to medium-sized species of dark or grayish coloration. **Female**. **Head**: Dichoptic, facets uniform in size. Antennae with 8 flagellomeres, usually uniformly dark, exceptionally with some paler creamy articles. Mandibles toothed only on medial side of apex. Cibarium unarmed. **Thorax**: Mesonotum with fine pale decumbent hairs; antepronotal lobe haired; proepisternum (propleuron) bare; anepisternal (pleural) membrane bare; precoxal bridge (anterior basisternum) incomplete; furcasternum (between hind legs) markedly flared apically; katepisternal sulcus, complete, well defined. Wings (Fig. 1–3) with spiniform setae present on Costa (C); Subcosta (Sc) haired below for part or full length; Radius (R) not forked, basal sector with dorsal setae; M without stem or very short stem; basal end of Rs apposed to or joining R; Cubitus (Cu) doubly curved; A1 curved and not reaching wing margin; basal cell small and indistinct. Hind legs with calcipala present at apex, pedisulcus present on 2nd tarsal segment; tarsal claw with or without basal tooth; row of stout setae on hind basistarsus present or absent. **Abdomen**: Abdominal tergites (Fig. 70–87) variable in width, usually wholly dark, but in some species with pubescent or ashy patches. Sternites absent on abdominal segments 2–6. Anterior arm of genital fork broad with lateral membranous areas, tapered anteriorly; lateral arms with or without knee-bend; apotome generally sharply developed; lateral plate, with exceptions, broadly developed (Fig. 108–125). Hypogynial valves (ovipositor lobes, gonapophyses) broadly to sharply rounded apically, medial edges usually with bare area. Anal lobes, not markedly developed (with exceptions); cerci normally rounded, exceptionally truncated (Fig. 126–142).

Male. **Head**: Holoptic with larger upper and smaller lower facets. **Thorax**: Legs with hind basitarsus of normal width (except Australian *crassipes*). **Abdomen**: Abdominal tergites wide. Sternites present. Genitalia usually without well-defined parameres, or parameral spines (if present, usually delicate and pale); median sclerite usually indistinct or absent; dorsal plate absent; ventral plate broadly rounded posteriorly, keeled (markedly developed in some), and setulose in mid-ventral line, lacking posteriorly directed apodeme off basal arm; gonostyli about as long as gonocoxites, tapered or subquadratic to apex with 2–4 apical teeth.

Pupa. Setae simple. Cephalic setae (Fig. 197–201): facial 1/1 always present; frontal 1/1, epicranial 2/2, genal 1/1, and ocular setae 1/1, present or absent; clypeal setae absent. Thoracic setae: posterolateral (baso-alar) 1/1; dorsocentral 3/3 sometimes on prominent bases or apically hooked, posterior seta sometimes shorter and spine-like; post-spiracular or anterolateral 2/2; propleural 2/2; post-tracheal 1/1; pre-alar 2/2. Integument of thoracic notum without sculpture or with microtubercles, single, grouped, or sometimes mammillated. Pupal gill with filaments, usually arising from a brown or black horn, but sometimes from an undifferentiated stalk, sometimes antlered, filaments wide and tapering or narrow and parallel-sided, seldom branched except when horn absent, surface imbricated or pseudosegmented. Abdominal segments V–VIII with thin elastic integument; tergites lacking basal row of spines, apical hooks present on tergites III and IV; apical hooks or curly hairs present or absent on tergites V–VIII. Apical hooks present or absent on some sternites, when present non-bifid. Segment IX with small dorsal horns; grapnel hooks on venter present or absent.

Cocoon. Of definite shape (Fig. 143–159) and usually consisting of close-textured, thin, brown fabric; sometimes thick, fleshy, and white, or alveolate or honeycombed; never fenestrated or latticed; with or without anterodorsal process which may be short or long and single or paired; usually with larger or smaller anteroventral bridge ("collar" or "neck" of authors) aperture usually circular with definite rim, rarely flexible, constructed around gills, sometimes covered or occluded by anterodorsal process(es) with or without a ventral floor posteriorly.

First instar larva. Head and cephalic apotome of normal form. Labral fans present.

Larva. Posterior abdomen (Fig. 303–319) of fusiform shape (except Australian *magnum*); integument without scales, spines, or tubercles. Head of subrectangular shape; cephalic apotome widest posteriorly, posterolateral angles rounded; cervical sclerites small and isolated. Labral fans normally developed. Mandibles (Fig. 420–436) usually with complex array of serrations and sensillum on inner margins, mandibular hair brushes present. Hypostoma usually with 13 teeth (11 in Australian *bancrofti*) which are largely concealed from below by the anterior margin of the hypostoma which sometimes has a small median lobe; hypostomal setae unbranched distally, usually 4–6 on each side. Antennae with basal and medial articles darker;

articles subequal in length, or medial short and basal longer than apical plus medial; apical sensillum short and conical. Rectal papillae with 3 simple lobes. Rectal scales absent. Anal sclerite (Fig. 11, 437–453) X-shaped, anterior arms horizontal, posterior arms descending from median piece, interarm struts arising on each side from anterior arm and closely approaching but not fused with the posterior arm. Semicircular sclerite (Fig. 12) immediately anterior to and contouring the posterior circlet of hooks present or absent; dorsal ends simple and tapered or expanded or forked, closely approaching the ventral ends of the posterior arms of anal sclerite but separated. 1 pair of ventral tubercles anterior to the posterior circlet present or absent. Posterior circlet of hooks usually of constant width with a variable number of rows, slightly interrupted in the median dorsal line.

Distribution. Australia (but absent from islands to north, east and south of New Guinea; absent from Solomon Islands, Vanuatu, New Caledonia, and Fiji); Tasmania; New Zealand and its subantarctic islands.

Constituents. 2 subgenera. *A*. (*Austrosimulium*) and *A*. (*Novaustrosimulium*).

***Austrosimulium* (*Austrosimulium*) Tonnoir, 1925**

Austrosimulium Tonnoir, 1925: 230 (as genus); Dumbleton 1973: 483 (as subgenus *A. Austrosimulium*).

Type-species: *Simulia australensis* Schiner, 1868: 15

Adult. antennal pedicel longer than 1st antennal flagellomere; tarsal claw of female with or without a basal tooth; wings lacking spiniform setae on apical part of vein R. Male with median sclerite of aedeagus not well developed and gonostylus with 2 or 3 apical teeth. **Pupa**. Gill stalked, antlered, or horned. Abdominal sternites V–VII with hooks, but terga lacking basal row of spines. **Cocoon**. With or without a floor, with or without anterior dorsal process(es). **Larva**. Semicircular sclerite present, ventral tubercles present,; apical antennal article always longer than combined medial and basal articles.

Distribution. New Zealand, Australia.

***A*. (*Novaustrosimulium*) Dumbleton, 1973**

A. Novaustrosimulium Dumbleton, 1973: 484

Type-species: *Simulium bancrofti* Taylor, 1918: 168.

Adult. antennal pedicel shorter than 1st antennal flagellomere; tarsal claw of female lacking basal tooth, or with a small tooth only; wings lacking spiniform setae on R. Male with aedeagus as in subgenus *Austrosimulium*, gonostylus with 2–4 apical teeth (4 in *bancrofti*). **Pupa**. Gill horned; abdominal sternites V–VII lacking hooks, terga lacking basal spine rows. **Cocoon**. Without a floor, and usually without anterior processes (present in *victoriae*). **Larva**. Semicircular sclerite absent, ventral tubercles present or absent, antennal articles subequal in length.

Distribution. Australia.

The Australian *Austrosimulium* species are listed below for completeness. They do not occur in New Zealand, and are not revised in this work.

***Austrosimulium* (*Austrosimulium*) Tonnoir, 1925**

ungulatum species-group Dumbleton, 1973
cornutum Tonnoir, 1925
crassipes Tonnoir, 1925
sp. 'C' of Mackerras & Mackerras, 1949

mirabile species-group Mackerras & Mackerras, 1949
mirabile Mackerras & Mackerras, 1948
fulvicorne Mackerras & Mackerras, 1950
montanum Mackerras & Mackerras, 1952

***Austrosimulium* (*Novaustrosimulium*) Dumbleton, 1973**

furiosum species-group Mackerras & Mackerras, 1949
furiosum (Skuse, 1889)
victoriae (Roubaud, 1906)
torrentium torrentium Tonnoir, 1925
torrentium hilli Mackerras & Mackerras, 1949

bancrofti species-group Mackerras & Mackerras, 1949
bancrofti (Taylor, 1918) (complex)
pestilens Mackerras & Mackerras, 1948
magnum Mackerras & Mackerras, 1955

Unplaced to subgenus (doubtful if *Austrosimulium;* Craig 2011, unpublished observations)
colboi Davies & Györkös, 1988

NEW ZEALAND *AUSTROSIMULIUM* (*AUSTROSIMULIUM*)

Keys to New Zealand simuliids can be found in Dumbleton (1973) and Crosby (2006) and should be consulted as well. Crosby (2006) used a combination of cocoon and pupal characters in his key to pupae. However, pupae in collections are often separated from their cocoons, and empty cocoons are sometimes all that is collected from the field. We therefore provide separate keys to pupae and cocoons.

KEY TO *AUSTROSIMULIUM* SUBGENERA AND SPECIES-GROUPS

01 Adult: 1st antennal flagellomere shorter than pedicel (except *dumbletoni*); female tarsal claw with or without basal tooth. **Pupa**: gill horned, antlered, or stalked; abdominal sternites V–VII with hooks. **Larva**: antennal article 3 longer than combined basal 2 articles; semicircular sclerite present; ventral tubercles present. **Cocoon**: floor present or absent, anterior processes present or absent (Australia, N.Z.) .... … (subgenus *Austrosimulium*) … 2

—**Adult**: 1st antennal flagellomere longer than pedicel; female tarsal claw without basal tooth, or with only small tooth. **Pupa**: gill horned; abdominal sternites V–VII without hooks. **Larva**: without semicircular sclerites; with or without ventral tubercles; antennal articles 1–3 subequal in length. **Cocoon**: without floor; anterior processes usually absent (Australia) .... … (subgenus *Novaustrosimulium*) … 4

02(01) Adult: female tarsal claw lacking basal tooth. **Pupa**: lacking ocular setae and frontal setae. **Larva**: dorsal ends (accessory sclerite) of semicircular sclerite expanded or forked. **Cocoon**: no anterior processes (N.Z.) .... *australense* species-group

—**Adult**: female tarsal claw with a strong basal tooth (reduced or absent in *unicorne*). **Pupa**: ocular and frontal setae present. **Larva**: semicircular sclerites dorsally expanded or forked, or neither. **Cocoon**: with anterior dorsal process(es), sometimes short (Australia, N.Z.) 3

03(02) Adult: no antennal flagellomeres orange-coloured; abdominal tergites V–VIII without ashy tomentose patches. **Pupa**: gill horned or not horned. **Larva**: semicircular sclerite lacking dorsal accessory sclerites (Australia, N.Z.) .... *ungulatum* species-group

—**Adult**: At least 3 antennal flagellomeres (4–6) orange-coloured, or abdominal tergites V–VIII with ashy tomentose patches. **Pupa**: gill horned. **Larva**: semicircular sclerite with dorsal accessory sclerites (Australia) .... *mirabile* species-group

04 (01) Adult: 1st antennal flagellomere much wider than pedicel (except in *magnum*), abdomen with pale ashy patches of hairs. **Pupa**: abdominal tergites V–VIII with curly setae or grapnel hooks. **Cocoon**: anterior dorsal processes absent. **Larva**: ventral tubercles absent (Australia) .... *bancrofti* species-group

—**Adult**: 1st antennal flagellomere only little wider than pedicel, abdomen dark. **Pupa**: abdominal tergites V–VIII lacking grapnel hooks or curly setae. **Cocoon**: dorsal anterior processes present or absent. **Larva**: ventral tubercles present (Australia) .... *furiosum* species-group

KEYS TO NEW ZEALAND SPECIES-GROUPS AND SUBGROUPS OF *AUSTROSIMULIUM* (*AUSTROSIMULIUM*)

01 Adult: **female** tarsal claw lacking basal tooth, but possessing heel (Fig. 50–59); hind basitarsus with row of stout setae (Fig. 42, 44) (exception *A. australense*); genital fork variable from markedly broad and insubstantial, to narrowed and distinct, lateral arms of genital fork usually with knee-bend, posteromedial edges of genital fork plate rounded (Fig. 108–117); **male** with gonostyli substantial, subquadratic, not markedly tapered, possessing 2 or 3 terminal spines, rarely 4; ventral plate normally without well developed medial keel (Fig. 126–135). **Pupa**: ocular and frontal setae absent (Fig. 197–198); cephalic plate of female with or without posterior concavity (Fig. 198, 201); grapnel hook (Fig. 195) on abdominal sternite IX present (*australense*-subgroup), or absent (*tillyardianum*-subgroup). **Cocoon**: rarely white, never fleshy; anterior dorsal process(es) absent. **Larva**: suboesophageal ganglion pigmented (Fig. 401); accessory sclerites on dorsal ends of semicircular sclerite forked or expanded (Fig. 437–447); pharate pupal gill not L-shaped (Fig. 351–360) .... … (***australense*** species-group) ... 02

—**Adult**: **female** tarsal claw with basal tooth, more-or-less well developed (Fig. 60–67); hind basitarsus always lacking row of stout setae; genital fork usually broad and always insubstantial, lateral arms lacking knee-bend, posteromedial edges of fork plate angulate (Fig. 118–125); **male** with gonostyli tapered, possessing only 2 terminal spines; ventral plate normally with well developed medial keel, occasionally extreme (Fig. 136–142). **Pupa**: ocular and frontal setae present (Fig. 196, 199); cephalic plate of female flat posteriorly; grapnel hooks absent from abdominal sternite IX. **Cocoon**: fabric sometimes white and fleshy; anterior dorsal process(es) present. **Larva**: suboesophageal ganglion not pigmented, or faintly so (Fig. 402); accessory sclerites absent and dorsal ends of semicircular sclerite tapered (Fig. 448–453); pharate pupal gill L-shaped (Fig. 361–366) .... (***ungulatum*** species-group) ... 03

02(01) **Adult** female and male hind basitarsus with or without row of stout setae (Fig. 42, 43, 46, 47); female genitalia with median space of hypogynial valves broad (mid width divided by length = 0.6 or greater), anterior edge semicircular, inner edges curved posteriorly gradually with little change in width (Fig. 90, 91); anterior arm of genital fork broad, width to length proportion at midpoint 1 : 2.8 (Fig. 108, 109); male ventral plate broader than long, medial keel poorly developed; male gonostyli robust, subquadratic, not markedly tapered (Fig. 126, 127). Female **pupa** lacking dished cephalic plate posteriorly (Fig. 198, 202, 203); thoracic cuticle mammillate, not tuberculate (Fig. 238, 239) .... ***australense***-subgroup

—**Adult** female, always possessing row of stout setae on hind basitarsus (Fig. 44); male adult hind basitarsus with row of stout setae present or often absent (Fig. 45); female genitalia with median space of hypogynial valves variable, normally narrow and with decreased width posteriorly (mid width divided by length = 0.5 or less), if broad then with straight edges (Fig. 92–99), anterior edge not semicircular; genital fork narrower, width to length proportion at midpoint 1 : 3.3; male ventral plate as long as broad, median keel normally well developed (Fig. 128–135); male gonostyli more tapered, occasionally robust, but not markedly subquadratic. Female **pupa** with dished apex to cephalic plate (Fig. 201, 204–211); thorax with microtubercles (Fig. 240–249) (except *A. fiordense* Fig. 244) .... ***tillyardianum***-subgroup

03(02) Female tarsal claw with basal tooth usually 0.3× length of inner claw surface; pupal gill with small base, filaments few, substantial, non-tapered, rigid, grouped; cocoon fabric not thickened, coarse, fibrous weave. Not markedly high altitude species, sea level to maximum at 920 m a s l .... ***ungulatum***-subgroup

—Female tarsal claw with small basal tooth 0.25× length of inner claw surface (Fig. 65), usually absent in *A. unicorne* (Fig. 67); pupal gill with small basal horn, filaments numerous, fine, ungrouped, cocoon of thick, white, fine fibrous weave. High altitude species, generally found between 700–1 600 m a s l .... ***unicorne***-subgroup

Diagnosis for *australense* species-group

Adult: wings not dusky. **Female**: tarsal claw lacks basal tooth and heel, hind basitarsus with row of stout setae (absent in one species); genital fork with tendency to be narrowed, with or without knee-bend on lateral arm, posteromedial edge of lobe rounded. **Male**: hind basitarsus with or without row of stout setae; genitalia, gonocoxites without, or with poorly developed, anteromedial flutings; gonostyli quadratic or bluntly tapered; normally 3 terminal spines, occasionally 2; ventral plate with poorly developed or no medial keel; parameres virtually non existent, paramere spines absent. **Pupa**: ocular and frontal setae absent; cephalic plate of female with or without posterior concavity; thorax with or without microtubercles; sternite IX with or without grapnel hooks. **Cocoon**: rarely white and fleshy, anterior dorsal projections absent, fabric filamentous, sometimes alveolate. **Larva**: suboesophageal ganglion pigmented; accessory sclerite of semicircular sclerite expanded, more-or-less emarginated; pharate pupal gill not L-shaped.

Constituent species: *A. albovelatum, A. alveolatum, A. australense, A. dugdalei, A. extendorum, A. fiordense, A. laticorne, A. longicorne, A. multicorne, A. stewartense, A. tillyardianum*.

Cladistic analysis of morphology fully supports this species-group (Fig. 506), but with poor resolution terminally. CO1 mDNA analysis also fully supports the species-group, but the analysis concatenates species of one segregate (Fig. 508a, b) and provides no useable groupings within that.

Diagnosis for *australense*-subgroup

Pupa: female pupal cephalic plate not dished; thoracic cuticle mammillated, microtubercles absent, grapnel hooks present on sternite IX terminus. **Cocoon**: fabric filamentous, never thickened. **Female adult**: hind basitarsus with row of stout setae; genital fork broad, lateral plates not markedly developed. **Male adult**: hind basitarsus with or without row of stout setae.

Constituent species: *A. australense, A. longicorne.*

This subgroup is based on a small number of morphological characters, mainly the non dished pupal cephalic plate. Of concern is the disparate structure of the pupal gills (Fig. 268–269) of these two species. Morphological cladistic analysis (Fig. 506), however, fully supports the grouping, as does the CO1 mDNA analysis (Fig. 509a, b). The latter indicates, with strong support, that *A. australense* consists of two cryptic species. One, precinctive to the South Island, is sister to *A. longicorne*. As yet no feature has been identified that will morphologically separate the two cryptic species of *A. australense*. Therefore, we make no change to the current taxonomic status of this species.

Diagnosis for *tillyardianum*-subgroup

Pupa: female pupal cephalic plate markedly concave; thoracic cuticle with microtubercles present, with one exception; grapnel hooks absent from sternite IX terminus. **Cocoon**: fabric filamentous, occasionally thickened, white and alveolate. **Female adult**: hind basitarsus always with row of stout setae; genital fork with exceptions narrow, lateral plates extended laterally. **Male adult**: hind basitarsus with or without row of stout setae.

Constituent species: *A. albovelatum, A. alveolatum, A. dugdalei, A. extendorum, A. fiordense, A. laticorne, A. multicorne, A. stewartense, A. tillyardianum.*

This subgroup constitutes the largest lineage of New Zealand simuliids. Only moderately resolved in morphological cladistic analysis; similar results are obtained with the CO1 mDNA analysis where the constituent species do not aggregate well. Apart from *A. albovelatum*, the other species are overall morphologically similar and could be referred to as the “*multicorne* assemblage”.

Diagnosis for *ungulatum* species-group

Female: tarsal claw with tooth, occasionally lacking; haltere tan, occasionally white; hind basitarsus lacking row of stout setae; genital fork short and broad, knee-bend absent, lobe markedly developed, medial edge angulate. **Pupa**: with ocular and frontal setae on cephalic capsule; thoracic notum with fine evenly distributed microtubercles, occasionally very sparse; dorsocentral thoracic setae elongate, sometimes spine-like; cephalic plate not concave; gills with or without obvious horn; filament surface either reticulated or annulated; grapnel hooks present on abdominal sternite IX. **Cocoon**: fabric sometimes white and fleshy, anterior process(es) present. **Larva**: semicircular sclerite lacking distinct accessory sclerite, tapered; pupal gill histoblast L-shaped, directed caudally.

Constituent species: *A. bicorne, A. campbellense, A. dumbletoni, A. tonnoiri, A. ungulatum, A. vailavoense, A. vexans, A. unicorne.*

Cladistic analysis of morphology gives full support for this species-group. Strict consensus (Fig. 505) is at variance with Dumbleton’s arrangement, with the *unicorne*-subgroup, while a clade, the remaining species are in polytomy. However, the Majority Rule tree (Fig. 506) resolves the *unicorne*-subgroup as sister to the *ungulatum*-subgroup.

Molecular analysis (Fig. 509, 514) is more at variance with Dumbleton’s arrangement and that used here. *Austrosimulium vexans* and *A. ungulatum* form a highly supported clade. Apart from the segregate of *A. ungulatum* that is sister to *A. vexans*, the possibility of cryptic species within the remaining *A. ungulatum* populations is high. Basal to that is a well supported clade with *A. bicorne* + (*A. bicorne* + *A. tonnoiri* + *A. dumbletoni*) sister to *A. unicorne* + *A. vailavoense*; again, with possible cryptic species in *A. bicorne*. We make no change to Dumbleton’s arrangement on the basis that a number of the species involved have unknown immature stages which are significant in the morphological diagnosis. We note, though, that the molecular analysis suggests a quite reasonable taxonomic arrangement.

Diagnosis for *ungulatum*-subgroup

Female: all with basal tooth on tarsal claw; haltere occasionally white. **Pupa**: gills not arising from obvious horn, sparse thick filaments arranged in groups, antler-like, surface reticulated; dorsocentral pupal setae spine-like. **Cocoon**: fabric filamentous, not white. **Larva**: semicircular sclerite with slight expansion basal of tapered tip.

Constituent species: *A. campbellense, A. dumbletoni, A. ungulatum, A. vailavoense, A. vexans.*

Morphological analysis fully supports this assignment of species (Fig 506). Molecular evidence is incomplete, with none available for *A. campbellense*. Of note though is that *A. vailavoense* is placed outside of this subgroup in a sister relationship with *A. unicorne*. We make no change to the placement of *A. vailavoense* because we have no immature stages.

Diagnosis for *unicorne*-subgroup

Female: with or without basal tooth on tarsal claw; abdominal tergites broader, exceptionally broad. **Pupa**: dorsocentral thoracic setae not markedly spine-like; pupal gill with small basal horn, numerous fine non-tapered filaments, ungrouped. **Cocoon**: fabric of thick white non-fibrous weave.

Constituent species: *A. bicorne, A. unicorne, A. tonnoiri.*

Strict consensus morphological analysis shows *A. unicorne* + *A. bicorne* + *A. tonnoiri* as a clade, and in polytomy with the New Zealand members of the *ungulatum* species-group (Fig. 505). However, the Majority Rule tree (Fig. 506) places the three species in a single clade with full support and *A. bicorne* and *A. tonnoiri* as sister taxa, although with poor support. Molecular analysis overall agrees (Fig. 509a, b), but the subgroup is not sister to the *ungulatum*-subgroup, rather is sister to all other New Zealand *Austrosimulium*. Further, molecular data well support *A. vailavoense* as sister to *A. unicorne*. Until immatures of *A. vailavoense* are known, we leave that species assigned to the *ungulatum*-subgroup.

KEYS TO ADULTS, PUPAE, COCOONS, AND LARVAE OF *A. (AUSTROSIMULIUM) AUSTRALENSE* SPECIES-GROUP

ADULTS

Females (note: species are extremely difficult to separate)

01 Abdominal tergites III–V markedly wide and short (width 3× length) (Fig. 71); hind basitarsus with row of stout setae present (Fig. 42) .... …(p. 109)... ***longicorne***

—Abdominal tergites III–V not markedly wide or short (width less than 3× length); hind basitarsus row of stout setae present with one exception 02

02(01) Abdominal tergites III–V small, *ca* 0.3× width of tergite II, subequal, subquadratic (Fig. 70); hind basitarsus with row of stout setae absent (Fig. 46) .... …(p. 99)... ***australense***

—Abdominal tergites III–IV large, *ca* 0.5× width of tergite II, unequal; hind basitarsus with row of stout setae present 03

03(02) Hypogynial gap broadening posteriorly (mid-width divided by length = 0.6 or more) (Fig. 92); genital fork stem narrowed, lateral arm with moderate to obvious knee-bend (Fig. 92) 04

—Hypogynial gap generally narrowed posteriorly (mid-width divided by length = 0.5 or less); genital fork broad, lateral arm with knee-bend poorly developed or absent 05

04(03) Hypogynial gap broadening posteriorly, lateral arm of genital fork with moderate knee-bend, cercus rounded apically (Fig. 92) …(p. 113)... ***albovelatum***

—Hypogynial gap markedly broadening posteriorly, lateral arm of genital fork with distinct knee-bend; cercus truncated apically (Fig. 99) ...(p. 139)... ***tillyardianum***

05(03) Genital fork stem more narrowed, spermatheca spherical, slightly raised edge to clear area around duct (Fig. 98) .... …(p. 136)... ***stewartense***

—Genital fork stem broader, spermatheca ovoid, clear area around duct lacking raised edge 06

06(05) Genital fork not constricted at mid-length .... (Fig. 94) ....(p. 120)...***dugdalei***; ... (Fig. 95) ...(p. 125)... ***fiordense***; .. (Fig. 97) ...(p. 132)... ***multicorne***

—Genital fork stem slightly constricted at mid-length … (p. 117)... ***alveolatum***; ....(Fig. 96) ...(p. 128)... ***laticorne***

Males (rarely encountered unless bred, and in which case pupal characters provide identification)

01 Genital ventral plate with lateral protrusions, not markedly shield-shaped (Fig. 127) …(p. 109)... ***longicorne***

—Genital ventral plate lacking lateral protrusions, shield-shaped (Fig. 126, 128–135) 02

02(01) Ventral plate with median keel poorly developed, apex not pointed (Fig. 126) 03

—Ventral plate with median keel moderately developed, apex pointed (Fig. 134) 04

03(02) Ventral plate markedly wider than long; gonostylus quadratic (Fig. 126) .... …(p. 100)... ***australense***

—Ventral plate width and length subequal; gonostylus broadly tapered to apex .. .. … (Fig. 129) ...(p. 118)... ***alveolatum***; ... (Fig. 131) ...(p. 123)... ***extendorum***; . ...(Fig. 132) ...(p. 128)... ***laticorne***

04(03) Gonostylus robust, not markedly tapered to apex, 3 terminal spines, ventral plate with well developed keel (Fig. 134) 05

—Gonostylus tapered to apex, 2 terminal spines, ventral plate with moderate development of keel (Fig. 128) 06

05(04) Gonocoxite elongated (length *ca* 2.4× mid-width), ventral plate basal arms not well developed, keel not markedly developed (Fig. 134) .... …(p. 136)... ***stewartense***

—Gonocoxite broad (length *ca* 1.6× mid-width), ventral plate basal arms well developed, keel sharply defined (Fig. 135) .... …(p. 139)... ***tillyardianum***

06(05) Ventral plate broad (width to length = 1.4), V-shaped apically, keel broadly developed (Fig. 128) .... …(p. 114)... ***albovelatum***

—Ventral plate more deeply developed (width to length = 1.7), U-shaped apically, keel more distinctly developed ....(Fig. 130)... (p. 121) ... ***dugdalei***; ....(Fig. 133)...(p. 132)... ***multicorne***

PUPAE

01 Female pupa without posterior 1/2 of cephalic plate dished or concave (Fig. 198, 202, 203); thoracic integument without subcircular microtubercles or asperities, but crenulated (wrinkled) or mammillated (Fig. 238, 239); grapnel hooks present on sternite IX (e.g., Fig. 195) .... …(***australense***-subgroup)... 02

—Female pupa with posterior 1/2 of cephalic plate dished or concave (Fig. 201, 204–211); thoracic integument with microtubercles grouped, or patterned (Fig. 240–248) (one exception, *A. fiordense*); grapnel hooks absent on sternite IX .... …(***tillyardianum***-subgroup)… 03

02(01) Thoracic integument finely mammillated to crenulated (Fig. 238); gill horn broad and parallel sided (Fig. 255, 268); 35–45 fine short filaments, with annulated surface .... …(p. 100)... ***A. australense***

—Thoracic integument mammillated (Fig. 239); gill horn markedly small; 11–13 long, slender filaments, occasionally bifurcate, with surface pseudoannulated (Fig. 256, 269, 287) .... …(p. 109)... ***A. longicorne***

03(01) Thoracic integument mammillated (often difficult to determine in mature specimens); gill horn rod-like, *ca* 4× longer than wide, slightly expanded at mid length, surface scobinate; *ca* 40 fine filaments with annulated surface (Fig. 274, 292) ..... …(p. 126)... ***A. fiordense***

—Thoracic integument with microtubercles grouped, or patterned; gill horn various shapes ....… 04

04(03) Dorsal thoracic integument lacking distinct trident pattern of tubercles (Fig. 235) 05

—Dorsal thoracic integument with distinct trident pattern of tubercles (Fig. 234, 236) 07

05(04) Gill horn club-shaped and greatly expanded laterally (variable), scobinate; 36–40 fine non-tapered filaments, often in pairs (Fig. 259, 275), surface annulated (Fig. 293) .... …(p. 129)... ***A. laticorne***

—Gill not markedly expanded, surface variable 06

06(05) Gill horn rod-like, *ca* 4× as long as wide, sides parallel; 17–20 filaments (Fig. 240, 257, 270), surface pseudoannulated (Fig. 288) .... …(p. 114)... ***A. albovelatum***

—Gill horn broad, mitten-like, variable (Fig. 258, 271); 36–40 non-tapered filaments, surface annulated (Fig. 289) .... …(p. 118)... ***A. alveolatum***

07(04) Gill horn small, as wide as long (Fig. 262, 279); 12–20 filaments, thick and moderately stiff, surface reticulated (Fig. 296) ….(p. 140)... ***A. tillyardianum***

—Gill horn either rounded or rod-like and fusiform (spindle-shaped), filament surface annulated ...… 08

08(07) Gill horn small and rounded; 43–55 long fine filaments (Fig. 272, 290); thorax with distinct band of tubercles posterior to gill base (Fig. 242) .... …(p. 121)... ***A. dugdalei***

—Gill horn rod-like or fusiform (variable); fewer shorter filaments; thorax lacking distinct band of tubercles posterior to gill base (Fig. 246) ....… 09

09(08) Gill horn markedly rod-like and elongated, 8–11× longer than wide; 25–27 filaments longer than horn (Fig. 273, 291) ....(p. 124)... ***A. extendorum***

—Gill horns not rod-like and elongated, more fusiform; filament length variable 10

10(09) Gill horn with parallel sides, but often curved (Fig. 276) to moderately fusiform (Fig. 277), variable, scobinate; 30–40 filaments (not as long as in *A. dugdalei*), variable (Fig. 276, 277) . …(p. 133)... ***A. multicorne***

—Gill horn expanded at mid length, scobinate; 20–23 short fine filaments (Fig 261, 278)...................................... .... …(p. 136)... ***A. stewartense***

COCOONS

01 Cocoon white, orifice not circular, margins gathered round base of gills (high collar, 2 longitudinal dorsal ribs) (Fig. 145, 162). South Island .... …(p. 115)... ***albovelatum***

—Cocoon not white, orifice near circular. North and South Island ....… 02

02(01) Cocoon fabric distinctly alveolate or deeply honeycombed (Fig. 146, 150, 163, 168). South Island ....… 03

—Cocoon fabric not distinctly alveolate or deeply honeycombed. North and South Island ....… 04

03(02) Cocoon fabric alveolate (Fig. 150, 167, 168)........ ....(p. 128)... ***laticorne***

—Cocoon fabric deeply honeycombed (Fig. 146,163)..... .... …(p. 118)... ***alveolatum***

04(02) Cocoon usually close-fitting to pupa; oval, convex (Fig. 144, 153, 169–171) ....… 05

—Cocoon usually not close-fitting to pupa, subcircular, patellate (Fig. 143, 149, 160, 164, 166) .... …06

05(04) Cocoon with high collar and 2 poorly developed dorsal ribs; usually on stones (Fig. 153, 171). North and South Islands .... …(p. 140)... ***tillyardianum***

—Cocoon with low collar, with no dorsal ribs, usually on leaves (Fig. 144, 161). Three Kings, North, and South Islands .... …(p. 110)... ***longicorne***

06(04) On leaves or stones; when on stones often oval, convex 07

—Usually on leaves and vegetation, mainly circular 08

07(06) On stones and leaves, ovoid, not closely fitting, fabric of fine weave (Fig. 169). South Island .... …(p. 133)... ***multicorne***

—On leaves and substrate, when on substrate often with material incorporated along edge of cocoon (Fig. 164). North Island .... …(p. 121)... ***dugdalei***

08(06) When on a flat surface, markedly circular and patellate with distinct edge (Fig. 143, 160). North, South, Stewart Island 09

—More ovoid and less circular (Fig. 165, 170), edge less pronounced. South, Stewart Islands 10

09(08) Widespread distribution, North, South, Stewart Island (Fig. 143, 160) .... …(p. 101)... ***australense***

—Restricted distribution in Fiordland and South Canterbury, South Island (Fig. 149, 166). Not well known .. ..(p. 126)... ***fiordense***

10(08) Ovoid, moderately close fitting to pupa (Fig. 170) .... …(p. 137)... ***stewartense***

—Ovoid, not markedly close fitting to pupa (Fig. 165) ... . …(p. 124)... ***extendorum***

LARVAE (Mature final instar)

01 Pharate pupal gill spot with horn small, not obviously black (Fig. 340, 345) 02

—Pharate pupal gill spot with horn well developed, black (Fig. 339, 343) 03

02(01) Gill horn small, wider than long; common stem of gill filaments short or absent; with 5 or 6 long thin filaments; hypostomal teeth prominent (Fig. 404); 2nd antennal article markedly elongated (Fig. 368) (also applies to earlier instars); head usually pale at low altitude (Fig. 322), browner at high altitude (Fig. 323). Three Kings, North and South Islands .... …(p. 110)... ***longicorne***

—Gill horn longer than wide, brown; usually 6 thick filaments showing (Fig. 360), common stem longer; hypostomal teeth not prominent (Fig. 413); 2nd antennal article markedly small (Fig. 377), head usually with grey infuscation anteriorly (Fig. 332); North and South Islands .... …(p. 140)... ***tillyardianum***

03(01) Horn of large area, flattened; filaments fine and coiled on horn surface 04

—Horn of smaller area, narrowed; filaments stout, not coiled on horn surface 05

04(03) Horn parallel-sided; head pale with marked cross-shaped pigmentation (applies as well to earlier instars) (Fig. 320); 2nd antennal article *ca* 0.17× length of 1st antennal article (Fig. 367); North, South, and Stewart Islands ....(p. 101)... ***australense***

—Horn broad, club-shaped; head pale, distinct markings absent (Fig. 374); 2nd antennal article *ca* 0.24× length of 1st antennal article (Fig. 374); South Island .... …(p. 129)... ***laticorne***

05(03) Head pale and mostly devoid of pigmentation (Fig. 324); 2nd antennal article almost 0.5× length of 1st antennal article (Fig. 368). South Island .... …(p. 115)... ***albovelatum***

—Head more pigmented; 2nd antennal article 0.20–0.30× length of 1st antennal article. North, South, and Stewart Islands 06

06(05) 2nd antennal article 0.25–0.30× length of 1st antennal article (Fig. 371, 375); North and South Islands 07

—2nd antennal article 0.20× length of 1st antennal article (Fig. 372, 376); South and Stewart Islands ......… 08

07(06) Head pale, pigmented posteriorly (Fig. 325); South Island ....(p. 117)... ***alveolatum***

—Head not pale. North and South Islands 10

08(06) Head light brown anteriorly, lacking gray markings (Fig. 328) (poorly known); South Island .... …(p. 126)... ***fiordense***

—Head medium brown anteriorly, with irregular gray markings; South and Stewart Islands ....… 09

09(08) Ecdysial line broadly sinuous (Fig. 327); Stewart Island .... …(p. 124)... ***extendorum***

—Ecdysial line not broadly sinuous (Fig. 331); South and Stewart Islands .... …(p.137)... ***stewartense***

10(07) Head evenly dark brown, ecdysial line not sinuous (Fig. 326); North Island .... …(p. 122)... ***dugdalei***

—Head evenly light brown, ecdysial line sinuous (Fig. 330); South Island .... …(p. 133)... ***multicorne***

KEY TO ADULTS, PUPAE, COCOONS, AND LARVAE OF *A. (AUSTROSIMULIUM) UNGULATUM* SPECIES-GROUP

ADULTS

Females

01 Abdominal tergites III–IV subquadratic (Fig. 82–84), 1/2 width of tergite II….(***ungulatum***-subgroup)... 03

—Abdominal tergites III–IV less than 1/2 width of tergite II (Fig. 85, 86) (*unicorne* with all tergites wide and subequal, Fig. 87) .... …(***unicorne***-subgroup)... 02

02(01) Tarsal claw usually with rounded heel, occasionally a small tooth (Fig. 67). South Island .... …(p. 165). ... ***unicorne***

—Tarsal claw with distinct basal tooth (Fig. 65, 66). South and Stewart Islands .... …(p. 158, 162)... ***bicorne, tonnoiri***

03(01) Base of 1st antennal flagellomere pale, haltere white. South and Stewart Islands................................ .... …(p. 149)... ***ungulatum***

—Base of 1st antennal flagellomere not pale, haltere white or tan (*dumbletoni*). South, Stewart, and subantarctic Islands ....… 04

04(02) Large species (max. body length 4.8 mm), wing dusky, haltere tan ....…(p. 147)... ***dumbletoni***

—Medium sized species (max. body length 3.7 mm), wing not markedly dusky, haltere white ....… 05

05(04) South and Stewart Islands …(p. 153)... ***vailavoense***

—Subantarctic Islands ....… 06

06(05) Campbell Island .... …(p. 143)... ***campbellense***

—Auckland Islands .... …(p. 155)... ***vexans***

Males

Males of *A. vailavoense* unknown.

01 Large species (max. body length 4.8 mm), dusky wings, median keel of ventral plate not well developed, gonocoxite lacking anteromedial crenulations (Fig. 137) (based on gynandromorph) …(p. 147)... ***dumbletoni***

—Medium sized species (max. body length 3.0 mm), wings not markedly dusky, median keel of ventral plate well developed, gonocoxite with anteromedial crenulations (Fig. 136, 138–142) ....… 02

02(01) Keel bluntly cone-shaped, or parallel-sided (e.g., Fig. 136, 142) ....… 04

—Keel sharply cone-shaped (Fig. 138) ....… 03

03(02) Ventral plate heart-shaped (Fig. 139). Auckland Islands .... …(p. 155)... ***vexans***

—Ventral plate shield-shaped, wider than long (Fig. 138). South and Stewart Islands .. …(p. 150)... ***ungulatum***

04(02) Keel cone-shaped ....… 05

—Keel markedly developed, parallel-sided (Fig 142) .... …(p. 165)... ***unicorne***

05(04) Ventral plate as long as wide (length : mid-width ratio = 1 : 1); gonocoxite markedly broad (Fig. 136) . ... …(p. 143)... ***campbellense***

—Ventral plate wider than long (length : mid-width ratio greater than 1 : 1.6); gonocoxite more elongate … 06

06(04) Gonocoxite triangular, ventral plate domed anteriorly (Fig. 140) ....(p. 159)... ***bicorne***

—Gonocoxite elongate, ventral plate markedly wider than long (Fig. 141) ....(p. 162)... ***tonnoiri***

PUPAE

Pupae of *A. dumbletoni* and *A. vailavoense* are unknown.

01 Gill lacking horn (Fig. 263–265); 6–13 filaments, strong, not markedly tapered, rigid, surface pseudoannulated (Fig. 297–299). South, Stewart and subantarctic Islands .... …(***ungulatum***-subgroup)... 02

—Gill with black horn (Fig. 266, 267); 30–40 filaments, finely tapered, slender, flexible, surface finely annulated (Fig. 300–302). South Island ....(***unicorne***-subgroup)... 04

02(01) Thoracic integument without microtubercles (Fig. 250); modal gill filament number 10 (Fig. 281), range 9–13, basal filament directed dorsally. South and Stewart Islands .... …(p. 150)... ***ungulatum***

—Thoracic integument with microtubercles; gill filament number 6–14, basal filament directed laterally. Subantarctic Islands ....… 03

03(02) Modal gill filament number 11 (Fig. 282), range 10–12, with 6 apicoventral primary branches arising from common stem. Auckland Is .... …(p. 156)... ***vexans***

—Modal gill filament number 7 (Fig. 237, 280), range 6–9, with 4 apicoventral primary branches. Campbell Island .... …(p. 144)... ***campbellense***

04(01) Gill horn *ca* 5× longer than wide (Fig. 266, 283, 285); filaments 2–3× as long as horn ....… 05

—Gill horn *ca* 3× longer than wide (Fig. 267, 285); filaments *ca* 10× as long as horn . ...(p. 166)... ***unicorne***

05(04) Gill horn club-shaped apically (Fig. 284) ....(p. 163)... ***tonnoiri***

—Gill horn not club-shaped apically (Fig. 283) .... …(p. 159)... ***bicorne***

COCOONS

Cocoons of *A. dumbletoni* and *A. vailavoense* are unknown.

01 Fabric thin and brown; 2 thin, parallel-sided, dorsal anterior processes present. South, Stewart and subantarctic Islands .... …(***ungulatum***-subgroup)... 02

—Fabric thick and white; 1 or 2 stout, thick anterior processes. South Island .... …(***unicorne***-subgroup)... 04

02(01) Dorsal anterior processes markedly extended, curled apically and longer than diameter of anterior orifice (Fig. 155, 173). South and Stewart Islands .... …(p. 150)... ***ungulatum***

—Dorsal anterior processes straight, not extended longer than anterior orifice diameter. Subantarctic Islands ... .… 03

03(02) Auckland Islands .... …(p. 156)... ***vexans***

—Campbell Island .... …(p. 144)... ***campbellense***

04(01) Cocoon with 2 thickened longitudinal ridges on dorsum; dorsal anterior processes paired, horizontal. ....… 05

—Cocoon with a median longitudinal ridge on dorsum; dorsal anterior process single, deflexed, swollen, spatulate, occluding anterior orifice (Fig. 159, 177) .. ..(p. 166)... ***unicorne***

05(03) Dorsal anterior processes slightly divergent along midline, not occluding anterior orifice (Fig. 157, 175) .... …(p. 159)... ***bicorne***

—Dorsal anterior processes swollen and adpressed along midline, occluding anterior orifice (Fig. 158, 176) .... …(p. 163)... ***tonnoiri***

LARVAE (mature final instar)

Larvae of *A. dumbletoni* and *A. vailavoense* unknown.

01 Pharate pupal gill spot without a horn (Fig. 346–348, 361–363); accessory sclerite absent, but semicircular sclerite weakly expanded and angulated, tapered, stout (Fig. 448–450); posterior proleg often retracted; 2nd antennal article less than 2× as long as broad (Fig. 378–380). South, Stewart and subantarctic Islands ... . …(***ungulatum***-subgroup)... 02

—Pharate pupal gill spot horned (Fig. 364–366); semicircular sclerite finely tapered, not angulate subapically, slender (Fig. 451–453); 2nd antennal article usually more than 2× as long as broad (Fig. 381–383). South Island .... …(***unicorne***-subgroup)... 04

02(01) Hypostomal median tooth as long as prominent lateral teeth (Fig. 415) ....… 03

—Hypostomal median tooth shorter than prominent lateral teeth (Fig. 414); Campbell Island .... …(p. 144)... ***campbellense***

03(02) Abdomen markedly thicker at mid-length than in other species, posterior often retracted in ethanol-preserved material (Fig. 315); South and Stewart Islands .... …(p. 151)... ***ungulatum***

—Abdomen narrower at mid-length (Fig. 316), abdomen not retracted in preserved specimens; Auckland Islands .... …(p. 156)... ***vexans***

04(01) Pharate pupal gill horn 5× as long as wide (Fig. 364, 365); 2nd antennal article much shorter than 1st article (Fig. 381, 382); head margins tapered anteriorly (Fig. 336, 337). ....… 05

—Pharate pupal gill horn less than 3× longer than wide (Fig. 366); 2nd antennal article nearly as long as 1st article (Fig. 383); head margins subparallel (Fig. 338). .... …(p. 166)... ***unicorne***

05(04) Head evenly mottled brown, no marked pigmentation pattern, ecdysial line not sinuous .... …(p. 160)... ***bicorne***

—Head evenly light brown, distinct mottled median pattern, ecdysial line slightly sinuous .... …(p. 162)... ***tonnoiri***

ECOLOGICAL KEY TO SPECIES

Based on keys by Dumbleton (1973) and Crosby (2006).

1 Associated with cold streams that are snow fed, at least in spring; occurring often under (interstitial) perched cobbles and boulders, substrate free of periphyton.

—**1**.**1** Small rivulets at high altitude (1 550 m a s l) above tree line, stones angular .... ***bicorne*** (Fig. 486, 487), ***tonnoiri*** (Fig. 491)

—**1**.**2** Larger streams at medium altitude (600–900 m a s l), not predominantly glacier fed, below tree line, but usually open, with rounded cobbles.

  —**1**.**2**.**1** Larvae mainly interstitial .... ***unicorne*** (Fig. 496, 497)

  —**1**.**2**.**2** Larvae not interstitial ***alveolatum*** (Fig. 459)

—**1**.**3** Large open rivers, lower altitude (300–500 m a s l), larvae and pupae in full flow on boulders and large cobbles .... ***albovelatum*** (Fig. 456, 457)

2 Associated with cold streams, often within forest, sometimes in the open.

—**2**.**1** Lowland, at high latitude, in forest or high-banked streams, in scrub cover with peaty areas. Larvae on stones (subantarctic islands) .... ***campbellense*** (Fig. 488), ***vexans*** (Fig. 498)

—**2**.**2** Smaller streams within forest, especially in steep topography (300–900 m a s l). May occur in non-forested streams, sheltered by tussock. Larvae and pupae on cobbles and trailing vegetation .... ***ungulatum*** (Fig. 492–495)

—**2**.**3** Small cold lowland streams with mud or sand substrate.

—**2**.**3**.**1** On vegetation ... ***stewartense*** (Fig. 480, 481)

—**2**.**3**.**2** On cobbles .... ***extendorum*** (Fig. 466)

—**2**.**4** Often in the open, but sometimes associated with forest.

—**2**.**4**.**1** Above or below tree line (160–1 289 m a s l) on cobbles and vegetation .... ***dugdalei*** (Fig. 465), ... ***multicorne*** (Fig. 475–478), ***fiordense*** (high altitude)

—**2**.**4**.**2** From low altitude to above tree line, in small streams, on trailing vegetation................................... .... ***longicorne***, in part (Fig. 474)

3 Lowland streams and larger rivers, mostly open, usually with markedly warm summer temperatures.

—**3**.**1** Also in colder summer temperatures. On cobbles (usually rounded) .... ***laticorne*** (Fig. 468–469)

—**3**.**2** Predominately in warmer water. On rounded cobbles .... ***tillyardianum*** (Fig. 454, 482–485)

4 Mature streams and rivers, often lowland.

—**4**.**1** Open and with slower constant flows. With trailing vegetation and leaves plastered on rocks (Fig. 455). North Island (0–160 m a s l), South Island (sometimes to 610 m a s l) .... ***australense*** (Fig. 462–464)

—**4**.**2** Also in open streams and with slower constant flows, but sometimes in small streams and ditches with markedly constant flow, and thin films of water with low velocity in seepages, iron bacteria common (10–1 600 m a s l, in both islands) .... ***longicorne*** (Fig. 470–473)

DIAGNOSES AND DESCRIPTIONS

australense species-group

australense-subgroup

Austrosimulium (*Austrosimulium*) *australense* (Schiner, 1868) New Zealand black fly

Figures: female, 1, 3, 15, 24, 46, 47, 50, 70, 90, 108; male, 126; pupa and cocoon, 4, 5, 143, 160, 178, 197, 198, 202, 217, 238, 255, 268, 286; larva, 6–14, 303, 304, 320, 321, 339, 351, 367, 384, 403, 420, 437, 455; habitat, 461–464; specimens and labels, 519–536; Map 3.

caecutiens Walker, 1848: 113 (*Simulium*), *nomen nudum*. Hutton 1874: 165 (as White name not published, *Simulia*); 1881: 3 (as White name not published, *Simulium*). Kirby 1884: 273 (as White MS, listed under "*Simulium Australense*, Schin.", *S[imulium]*). Smart 1945: 499 (world catalogue; as White in Walker according to Kirby (1884), synonym of *australiensis* in genus *Austrosimulium*). Dumbleton 1973: 510 (*nomen nudum*, no generic name).

australensis Schiner, 1868: 15 (description female; *Simulia*). Hutton 1874: 165 (*Simulia*); 1881: 19 (mis-spelt as *australiensis*, *Simulia*). Kirby 1884: 273 (as "*Simulium Australense*"). Nowicki 1875: 5 ("*Simulium australense*", stated to be from Auckland Islands; corrected to Auckland in Mik 1881: 195 and compared with *vexans* Mik, 1881: 202). Hudson 1892: 53–54 ("*Simulium australiensis*"). Marshall 1896: 310 ("*Simulium australiensis*"). Tonnoir, 1925: 251 (*australense,* type-species for *Austrosimulium*; female, male, pupa, cocoon, larva; caption for fig. 12G (p. 228) in error states this is a new species, implying of Tonnoir). Pulikowsky 1929: 659 (pupal respiratory system). Enderlein 1930: 93 (as "*Wilhelmia australiensis*"). Smart 1945: 499 (world catalogue; listed as *australiensis* in *Austrosimulium*). Mackerras & Mackerras 1949: 403 (*australense, Austrosimulium*). Miller 1950: 145 (Auckland Is a doubtful record, with listing based on Nowicki 1875), Gurr 1953: 81; Harrison 1955: 214 (cites Miller (1950) to doubt Auckland Is record). Dumbleton 1963b: 333 (as subgenus *Austrosimulium* (*Austrosimulium*), in *australense* group). Dumbleton 1964a: 35 (relationships, distribution). Dumbleton 1964b: 32 (1st instar larva). Wise 1965: 208. Dumbleton 1973: 505. Crosby 1974b. McLea & Lambert 1983: 275 (salivary gland chromosomes). Winterbourn 2004: 7. Crosby 2006: 72 (key). Adler & Crosskey 2012: 20 (world inventory).

tillyardi Tonnoir, 1923a: 165 (as *Tillyardi*, *Simulium*, cocoon spinning, illustrations of pupal respiratory horn and cocoon shape, biological character of larvae found on vegetation, valid description, publication date before 3 April 1923 from date stamp on University of Michigan fascicle). Tonnoir 1923b: 85 (as *Tillyardi*, *Simulium*, cocoon spinning). Puri 1925: 301. Wu 1931: 552. Bequaert 1934: 189. Smart 1934: 236. Usova 1955: 846. Burton 1966: 48.

Not *australense*. Hilgendorf 1918: 141 ("*Simulium australense*", misidentification as larvae stated to be found on stones).

Diagnosis. A small to medium-sized species. **Female**: abdominal tergites III–V subquadratic, hind basitarsus lacking row of stout setae. **Male**: hind basitarsus lacking row of stout setae. **Pupa**: dorsal thoracic cuticle lacking microtubercles, but distinctly mammillated; gill with black, elongate horn directed ventrally with 35–45 non-tapered filaments; sternite IX with grapnel hooks. **Cocoon**: slipper-shaped, patellate, of low profile, fabric finely woven. **Larva**: body overall pale gray; frontolabral apotome translucent, posteromedial and posterolateral head spots marked, pigmentation in cruciform arrangement; ventral tubercles well developed; accessory sclerite markedly flared, poorly emarginated; posterior circlet with low number of hooks (*ca* 950).

Adult female (based on specimens from the Waitakere Ranges, west Auckland). **Body**: general body colour in ethanol overall blackish-brown, when dried of grayish appearance; total length 2.0–2.4 mm. **Head**: width 0.60–0.80 mm; depth 0.40–0.52 mm; postocciput black, vestiture of sparse, short black hairs; frons blackish-brown; frons width : head width ratio 1.0 : 4.5. **Eyes**: interocular distance 0.12–0.20 mm; ommatidia diameter 0.012 mm; 35–39 rows up and across at mid-eye. **Clypeus**: width 0.17–0.20 mm; dark brown; vestiture of sparse black and pale hairs. **Antennae**: total length 0.46–0.53 mm; middle flagellomeres markedly shorter than wide; all articles dark brown. **Mouthparts**: substantial, *ca* 0.5× length of head depth; cibarial cornuae (Fig. 24) apical fluting poorly developed, but with small regular dark markings; mandibles with 22 inner teeth, increasing slightly in size towards apex; laciniae with 12 inner teeth and 17 outer teeth; maxillary palp, total length 0.51 mm, 3rd article darker brown than remainder, proportional lengths 3rd, 4th, and 5th articles 1.0 : 1.2 : 1.8, sensory vesicle ovoid, 0.5× 3rd article width, opening 0.5× vesicle width.

Thorax: length 0.66–1.04 mm; width 0.66–0.88 mm; in ethanol, postpronotal lobes concolorous with scutum; scutum evenly dark reddish-black, vestiture of sparse recumbent hairs; no vittae visible in ethanol, but when dried shows a median and 2 lateral vittae overlain with silvery pruinosity; scutellum slightly lighter medially than scutum, vestiture of a few long black hairs laterally; postnotum concolorous with scutum; pleuron lighter than scutum; pleural membrane medium brown. **Wings**: length 1.9–2.5 mm; width 0.90–1.20 mm. **Halteres**: yellowish. **Legs** (Fig. 46, 50): overall blackish-yellow, coxae blackish-brown; hind basitarsus about 6× as long as its greatest breadth, lacking row of stout setae (as found in *A. longicorne*); tarsal claws with moderately developed basal heel.

Abdomen: abdominal scale dark brown with fine pale hairs, not greatly extended; tergite II 5× wider than long, tergites III–V markedly quadratic, tergite VI 2× wider than long, dorsal vestiture of small black hairs increased in density posteriorly (Fig. 70). **Genitalia** (Fig. 90, 108): sternite VIII vestiture of coarse black hairs posterolaterally; hypogynial valves lightly pigmented with vestiture of sparse short coarse hairs and triads of microtrichia, median edges smoothly divergent, no apparent strengthening, broadly rounded posteroapically and barely extended beyond posterior edge of segment VIII; genital fork with anterior stem broad, fluted anteriorly, lateral arm with marked knee-like bend, apodeme well developed and pointed, lateral plates angular posteromedially, rounded posterolaterally; anal lobes distinctly rounded, cerci broadly rounded in lateral view, black; spermatheca ovoid, clear area at junction of duct small.

Adult male (reared specimens from Waitakere Ranges). **Body**: general colour blackish-brown; total length 1.8–2.8 mm. **Head**: width 0.66–0.80 mm; depth 0.32–0.58 mm. **Eyes**: upper ommatidia dark orange, diameter 0.018 mm, *ca* 25 across and 19 down; lower ommatidia dark orange dorsally, dark brown ventrally, diameter 0.007 mm, *ca* 33 across and 39 down. **Clypeus**: blackish-brown; vestiture of sparse fine hairs; width 0.14 mm. **Antennae**: total length 0.46 mm; flagellomeres subrectangular; all articles evenly medium brown. **Mouthparts**: poorly developed; length 0.3× head depth; mandibles untoothed, broadly tapered with apical hairs; laciniae finely tapered apically with terminal hairs; maxillary palp light brown, 0.4 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 1.1 : 1.9, sensory vesicle irregular in shape, occupying 0.33× 3rd article width, opening 0.3× vesicle width.

Thorax: length 0.7–1.1 mm; width 0.62–0.96 mm; in ethanol, scutum evenly velvety black, vestiture of fine recumbent pale hairs, when dried brassy yellow; scutellum pale with sparse long black hairs; postscutellum concolorous with scutum. **Wings**: length 1.7–2.1 mm, width 0.8–1.1 mm. **Halteres**: tan. **Legs**: (Fig. 47) light yellowish-brown, with darker brown femoral, tibial, and tarsal bases; hind basitarsus about 5× as long as its greatest breadth, lacking row of stout setae; tarsal claws partially covered by grappling pad of 18–20 hooks.

Abdomen: Dorsum dark gray. **Genitalia**: (Fig. 126). gonocoxites 1.3× longer than basal width, tapered abruptly at 1/2 length; dark brown posteriorly, pale medially, with coarse black hairs on apical 1/2; gonostyli *ca* 3.0× longer than basal width, apically with 3 substantial terminal spines; ventral plate 2.0× wider than long, with sparse vestiture of small hairs, rounded posteriorly, domed anteromedially, median keel poorly developed, basal arms substantial; median sclerite poorly developed, broad, T-shaped posteriorly; parameres poorly developed, but visible along aedeagal lateral membrane.

Pupa. Body length; male 2.6–2.7 mm, female 2.2–2.4 mm, maximum width male 1.1–1.2 mm, female 0.89–0.96 mm. **Head**: cephalic plate lacking dorsal depression; plate of male 1.3× as long as maximum width (Fig. 197, 217), female as long as wide (Fig. 198, 202); plates of both sexes lacking tuberculation but are mammillate; frontal setae absent, facial setae present, substantial, 2 epicranial setae at mid-length beneath antennal sheath (difficult to observe). **Thorax**: Dorsum lacking tubercles, but mammillate; dorsocentral setae trichoid (Fig. 238). **Gills** (Fig. 255, 268): well developed black horn with small, light-yellow basal region, directed anteroventrally, horn 2.5–3.0× as long as greatest width, margins subparallel, horn apex medium to bluntly pointed; 5 distinct grooves arrayed diagonally along dorsal surface of horn, surface scobinated (covered with coarse black points); 35–45 filaments, arising from both surfaces of horn, narrow, non-tapered, length 0.32–0.55 mm, surface annulated (Fig. 286). **Abdomen**: Grapnel hooks present on sternite IX.

Cocoon. Surface smooth, fabric closely woven, silk filaments obvious, pale brown to colourless (Fig. 178); basically slipper-shaped with low anteroventral lip, but variable depending on substrate type (fully patellate on flat surfaces, higher profiled on narrowed substrates), margins well defined, anterior aperture circular (Fig. 143, 160).

Larva. **Body** (Fig. 303): overall light gray with rare, striking variants (Fig. 304); total length 4.2–4.8 mm. **Head**: distinctly bicolorous, background pale yellow to translucent with marked dark cruciform head spots posterodorsally; males with lighter head pattern (Fig. 320) than females (Fig. 321); but variable; head length 0.68 mm, width 0.50 mm; distance between antennal bases 0.36 mm; lateral margins of head subparallel; cervical sclerites well developed and pigmented, fused to finely developed postocciput; anterior edges (labrum) of apotome distinctly pigmented; genae spotted dorsally, translucent laterally and ventrally. **Antennae** (Fig. 367): overall pale brown; total length 0.31 mm; extended well beyond labral fan stem; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.2 : 2.4; apical article markedly long, 2× as long as basal and medial articles combined; basal article 5× longer than markedly short medial article. **Labral fans**: stem translucent; *ca* 45 fine rays, length 0.60–0.67 mm, width 0.009 mm; distinct pattern of microtrichia, with microtrichia as long as ray width interspersed with *ca* 8 microtrichia decreased rapidly in length. **Postgenal cleft** (Fig. 384): small, but markedly inverted U-shaped, sclerotised posterior tentorial pit cuticle more or less continuous across cleft; heavily pigmented (tentoral pits occasionally appear as double or triple). **Postgenal bridge**: 1.5× longer than hypostoma, pale and concolorous with genae. **Hypostoma** (Fig. 403): no teeth markedly prominent, but median and lateral teeth sharp; lateral teeth slightly more prominent than median; 3 sublateral teeth with median sublateral tooth 1/2 size of other 2; 2 paralateral teeth, subequal in size; all teeth largely concealed by anterior margin of hypostoma, 2 poorly developed rounded lateral serrations; 4 or 5 hypostomal setae each side. **Mandibles** (Fig. 420): apical brushes and teeth not markedly developed, outer teeth splayed and directed anteriorly, apical tooth with roughened anterior edge; 3 subapical teeth not markedly developed, 7–9 spinous teeth variously expressed; 5 or 6 mandibular sensilla and serrations, distinct, variable; blade region long, smooth, barely convex.

Thorax: anterior prothorax light brown, remainder of thorax paler, pharate pupal gill spot with black, paddle-shaped horn; filaments curled around ventrally directed rounded apex (Fig. 255, 351).

Abdomen: evenly grayish-brown, darkening posteriorly; abdominal segments I–IV narrow, expanded smoothly at segment V and producing a slight amphora shape; distinct ventral tubercles. **Anal sclerite** (Fig. 437): median plate not markedly tapered posteriorly, crenulated laterally; anterior arms neither markedly flared nor emarginated, interarm struts narrow, slightly enlarged posteriorly, posterior arms short and substantial, tapered abruptly apically; accessory sclerite broadly flared, not markedly emarginated, narrowly joined to semicircular sclerite. **Posterior circlet**: *ca* 81 rows of 11 or 12 hooks (total *ca* 950).

Type data

australense **Schiner**, **1868**. **Lectotype**, here designated; female, condition poor; specimen is glued to a card: thorax left lateral, head, and abdomen missing, part of thorax glued separately on the card (Fig. 523), right hand basitarsus and tarsal segments 2 and 3 on microscope slide (Fig. 524). Label details (Fig. 522) "Neu Seeland [handwritten in black ink over typescript "Austria", G. Enderlein] [Auckland, Dec 1858–Jan 1859, A. Sinclair]\ Alte Sammlung", "Type" (red label), "australiensis [handwritten in faded black ink, "t" not crossed, Olga Müller according to Korschefsky in Horn & Kahle (1937: 511, Plate XVIII 51, 52)] \ Alte Sammlung", "vidit H. Zwick\ 9.1.1971" (handwritten in black ink, H. Zwick), "lectotype D. A. Craig. Jan. 2011"; and glass microscope slide mount (Fig. 524): "compared with\ Tonnoir topotypes\ JSD. 30.X.70." (handwritten in black ink directly on slide, J. S. Dugdale), "(small red circle without text)", "Austrosimulium\ australense (Schiner)\ Holotype, right hind\ basitarsus + tarsal segs\ 2+3.\ Berlese\ mountant.\ Prep. J.S. Dugdale\ Oct 30 1970" (handwritten in black ink, lower case "i"s without top dot except in "hind", red ink band on bottom of label, J. S. Dugdale), "lectotype D. A. Craig. Jan. 2011 (underside)" (NHMW). **Paralectotype**, 3 Enderlein microscope slide mounts using mica held in cardboard; 1, condition poor (Fig. 525, 526) with label details "Wilhelmia australiense (Schin. 1868)\ Neu Seeland {F} [Auckland, Dec 1858–Jan 1859, A. Sinclair]\ Type [handwritten in black ink, Enderlein]\ 2/73 [handwritten in pencil, unknown but added after early 1920s]", "paralectotype D. A. Craig. Jan. 2011" (NHMW); 2, condition excellent, with label details "Wilhelmia australensis (Schin. 1868)\ Neu Seeland. {F}\ Flügel. \Type" (handwritten in black ink, Enderlein) (Fig. 531, 532), and "Wilhelmia australensis (Schin. 1868)\ Neu Seeland. {F}\ Beine. \Type" (handwritten in black ink, Enderlein) (Fig. 533, 534), "paralectotype D. A. Craig. Jan. 2011" (ZMHU). Note: the formal assignment of *australense* to the genus *Wilhelmia* Enderlein was not until it was published by Enderlein (1930: 93), where he stated this placement was according to the type ("*W. australiensis* (Schin. 1868) Neuseeland (sec. Typ.)").

Other specimens. The Naturhistorisches Museum holds 4 specimens used in Tonnoir's (1925) redescription of *A. australense*. Given the importance of these specimens, and as Tonnoir (1925: 251) and Dumbleton (1973: 510) both note, the 3 specimens from Auckland were bred from pupae and hence the identity is impeccable, we give their full label details (see also Fig. 527–530): 1 male, left middle leg missing "Auckland\ 27 Feb. 1923\ A. Tonnoir", "Simulium\ australense\ {M} Schin" (handwritten in black ink, Tonnoir); 1 male, excellent condition. "Auckland\ 27 Feb. 1923\ A. Tonnoir", "Simulium\ australense\ {M} Schin" (handwritten in black ink, Tonnoir); 1 female, damaged; wings glued to point, antennae missing "Auckland\ 27 Feb. 1923\ A. Tonnoir", "Simulium\ australense\ {F} Schin" (handwritten in black ink, Tonnoir); 1 female, right wing slightly damaged, otherwise excellent condition "Te Aroha\ 1 Mar. 1923\ A. Tonnoir", "Simulium\ australense\ {F} Schin" (handwritten in black ink, Tonnoir) (NHMW).

***tillyardi* Tonnoir**, **1923**. **Lectotype**, here designated: "Nelson \21.12.[19]21 [A. Tonnoir]" (handwritten in black ink, Tonnoir), "{F}" (handwritten in pencil, Dumbleton); "LECTOTYPE \ Simulium Tillyardi \ Tonnoir, 1923 \ Ann. Biol. Lacustre 11: 165 \ det. T. K. Crosby & D. A. Craig 2011" (red label, line 1 typescript, remainder handwritten in black ink, Crosby) (originally placed under *australense* in NZAC without an identification label; female selected as lectotype as female *tillyardianum* have stout setae on hind basitarsus and female *australense* do not) (NZAC). **Paralectotypes**, 6: 2 specimens (originally placed under *australense* without identification label in NZAC) "Brook \6.1.[19]22 [A. Tonnoir]" (handwritten in black ink, Tonnoir); "Brook \7.1.[19]22 [A. Tonnoir]" (handwritten in black ink, Tonnoir); "{M}" (handwritten in pencil, Dumbleton) (NZAC); 3 males (originally as paratype series of *tillyardi* Tonnoir, 1925; on elbow pin (MacGillivray 1903), "Nelson N.Z. \ I.1922 \ A. Tonnoir {M}\ Bred" (date and "Bred" handwritten in black ink, "Bred" on label edge at right angle to other 3 lines, Tonnoir); "PARATYPE.\ Austrosimulium\ tillyardi n. sp.\ A. Tonnoir det." (blue label, scientific name handwritten in black ink, Tonnoir); "NZ Arthropod Collection\ {barcode}\ NZAC04022105"; other 2 with "NZAC04022107" and "NZAC04022021" (specimen lacking head and without {M} symbol); all 5 with "PARALECTOTYPE \ Simulium Tillyardi \ Tonnoir, 1923 \ Ann. Biol. Lacustre 11: 165 \ det. T. K. Crosby & D. A. Craig 2011" (blue label, line 1 typescript, remainder handwritten in black ink, Crosby) (NZAC). 1 male "Nelson \ 7.I.[19]21 [sic!, year = 1922, as Tonnoir did not arrive in New Zealand until end of November 1921 (Crosby 1976b)]" (handwritten in black ink, Tonnoir); "[blank coloured label]"; "Austrosimul. \australense {M} \ (Schin) \ A. Tonnoir det" (all but last line handwritten in black ink, Tonnoir); "Zool. Mus. \Berlin" (yellowish label) (Fig. 536); "PARALECTOTYPE \ Simulium Tillyardi \ Tonnoir, 1923 \ Ann. Biol. Lacustre 11: 165 \ det. T. K. Crosby & D. A. Craig 2011" (blue label, line 1 typescript, remainder handwritten in black ink, Crosby)(ZMHU).

The following female at CMNZ may be *tillyardi* Tonnoir, 1923, or it may be true *tillyardi* Tonnoir, 1925 based on its locality despite the date indicating it was one of Tonnoir's originally-collected specimens (we were unable re-examine this specimen as the CMNZ collection currently remains inaccessible as a result of the 2010–2011 Christchurch earthquakes). 1 female, "Maitai\ 6-1-[19]22"; "PARATYPE\ Austrosimulium\ tillyardi n. sp.\ A. Tonnoir det."; "I.282 (red)" (CMNZ).

caecutiens Walker, **1848**. About 450 females (20 in reasonable condition, most missing parts, especially antennae) in a recycled pill-box from J. H. Wood, probably placed in pill-box by Kirby about 1883 (Fig. 519–521); 3 labels beneath on glass inset "cæcutiens, *White*," and "*b*. Bay of Islands." (typescript from part lines from printed page of Walker (1848: 113)), "Simulium\ cæcutiens White.\ Zool. Erebus & \Terror." (handwritten in faded black ink, A. White according to Korschefsky in Horn & Kahle (1937: Plate XXXVIII 12 [note in Korschefsky's example label the writing on the second line after "Ceram" is not by White but by E. E. Austin according to T. Howard BMNH])). Label on top of pill-box "Simulium \Cæcutiens \Bay of \Islands \New \Zealand" (handwritten in faded black ink, Walker), on top of text scribbled out with pencil, directly on pill-box "Marton \mosquito \ [horizontal line] \trying to bite \me. 1.3.81 \.W." (handwritten in black ink, John Henry Wood [T. Howard, pers. comm. 2012]), "Austrosimulium \australense \ID & counted: ca 450. \Five retained for NZAC. \D. A. Craig. Jan. 2011." (BMNH). 4 specimens with the reproduced labels on top and bottom of pill-box (1 with additional label "*Austrosimulium \australense* (Schiner) \ Det. & Mounted \ D. A. Craig. Jan 2011 \Ex. Brit. Mus. Nat. Hist."); 2 card-point mounted, and 2 that were cleared in glycerine in pinned genitalic vials); 1 specimen in 5 sections on microscope slide, with typescript label "caecutiens, *White*,\ b. Bay of Islands.\Simulium/ caecutiens White\ Zool. Erebus &/ Terror.\ *Simulium/ Caecutiens. Bay of/\ Islands/ New / Zealand*\ *Aust. australense* (Schiner)\ Cleared, dissected, mounted\ PLVP. D. A. Craig. Jan. 2011.\ Ex BMNH. [line handwritten in black ink, D. A. Craig]" (NZAC). Sinclair drowned in the Rangitata River, 22 March 1861 (Fig. 537).

Comments on specimens

A. australense. Schiner (1868) had more than one specimen available at the time of describing the species at the Naturhistorisches Museum Wien (NHMW) ("…der nicht gut conservirten Stücke …"), but did not label any as the name-bearing type specimen. It is not known for certain who placed the red "Type" label on one specimen, but it most likely was Enderlein in the early 1920s when he borrowed the specimens from NHMW. It was usual for Enderlein to place a red "Type" label on specimens he regarded as types (Zwick 1995: 133), and Werner (2000: 228) recorded that Enderlein "attached red "type" labels to enormous numbers of specimens in the Museum für Naturkunde Diptera collection which were obviously not types, even to specimens collected years after the original collection of the species!". The label was likely to have been added before this specimen was sent by Dr Zerny (NHMW) to Tonnoir around 1923–1924, as Tonnoir (1925) recorded on page 251 that he had "been able to examine the type", and on page 214 he noted that the original description was based on "two rather defective female specimens". Enderlein wrote the word "Type" on 3 slide-mounts he made (1 in NHMW and 2 in Museum für Naturkunde, Berlin (ZMHU), which he apparently retained from the NMNW): we consider all 3 slides represent parts of 1 specimen, and none are from the "holotype". Thus we designate the specimen previously considered as the nominal "holotype" for the taxon as lectotype, and the other specimen as paralectotype.

Lectotype material in the Naturhistorisches Museum, Vienna (NHMW) is in poor condition. Tonnoir (1925: 214) wrote that the types were defective and of dubious identity — "The very short and inadequate description was made from two rather defective female specimens" — and this was the reason he used reared topotypic material for his redescription. For Dumbleton's revision, J. S. Dugdale examined the type material and partially remounted the lectotype (see above and Fig. 524), and he determined that the specimens were, with a very high probability, *A. australense* — we agree.

Further damage to the lectotype specimen appears to have occurred between the time it was examined in 1979 by Dr Heide Zwick and when received for this study in early 2011 (Fig. 523). The 2 type specimens and topotypes were received together in the same container by DAC, and the cork strip from the paralectotype cardboard mount had come free and damaged some specimens in the shipment. The unpublished notes of Dr Zwick (pers. comm. 2011) indicated that the lectotype had wings present, but these were not on the specimen when received by DAC. If remote microscopy facilities become more common in research institutes so specimens can be viewed over internet connections, it may be possible to reduce the risk of damage to important specimens by not needing to ship them to another institute (Kean *et al.* 2011).

The 4 specimens deposited in NHMW which were used in Tonnoir's (1925) redescription of *A. australense* have the generic name "*Simulium*" on their labels. This indicates that these 4 specimens were sent to NHMW with the return of Schiner's type material probably in 1924, but prior to January 1925 and publication of the new generic name *Austrosimulium* Tonnoir, 1925.

The Museum für Naturkunde, Berlin (ZMHU) holds 2 *A. australense* specimens collected by Tonnoir; label data are shown in Fig. 535 and 536. Only one is a topotype, and is in excellent condition. The other is a headless male from Nelson, dated 7.I.21 (=7. I.1922, as Tonnoir did not arrive in New Zealand until the end of November 1921 (Crosby 1976)), and is a paralectotype for the name *tillyardi* Tonnoir, 1923. As the generic name *Austrosimulium* is used on the identification labels, this indicates the specimens were sent to Enderlein after publication of his paper in January 1925 (compare with identification labels on specimens sent to NHMW above).

A. tillyardi Tonnoir, 1923. In NZAC 3 adult specimens from Tonnoir's first collections in New Zealand, with dates of Dec 1921 and Jan 1922 from Nelson and The Brook, were placed under *australense* without identification labels. We suspect Tonnoir placed them under *australense*, as Dumbleton (1973: 509–510) lists, in his remarks on *australense*, 2 of these 3 specimens as part of the "…existing material (plesiotypic—some of it topotypic) … available to Tonnoir at the time of his redescription: …". The locality labels are in Tonnoir's handwriting. We consider these are specimens that were reared through from final instar larvae collected about 2 weeks beforehand and reported in Tonnoir's (1923a, b) papers, and therefore are syntypes for this use of the name. A further 3 specimens that Tonnoir (1925) labelled as paratypes for his species *tillyardi* Tonnoir, 1925 are also now recognised as belonging to *tillyardi* Tonnoir, 1923. The headless male from Nelson dated 7.I.21 [=7.I.1922] in ZMHU Berlin is notable for being correctly labelled by Tonnoir as *Austrosimulium australense.* Tonnoir (1925) did not record his early use of *tillyardi* under *australense,* or state in his 1925 paper that his observations on cocoon spinning, mentioned on page 217, were this species: the correct identification of this specimen which Tonnoir sent to Enderlein after concluding his study is the only evidence that Tonnoir may have recognised that his 1923 use of "*tillyardi"* referred to an already-described species. We recognise these 7 specimens as forming the syntype series for the name *tillyardi*. One has been designated lectotype, with the remaining specimens becoming paralectotypes.

The 3 paralectotype specimens of *tillyardi* Tonnoir, 1923 in New Zealand collections under the name of *tillyardi* Tonnoir, 1925 were accepted without question by Dumbleton (1973: 515) and Crosby (1974: 25) as forming part of the paratype series for that species.

***Simulium* caecutiens**. Gray (1843: 181) wrote a note at the end of his article dated 15 August 1842 that stated "Since the above was written the British Museum has received … a collection of insects and shells from Dr. Sinclair…". From this accession received in 1842 White (in White & Doubleday 1843: 291) described the calliphorid *"Musca laemica*"; Dear (1986: 25) determined that the 2 specimens labelled with "42.55" were now assignable to *Calliphora stygia* (Fabricius) and *Calliphora hilli* Patton. If Sinclair had presented these caecutiens specimens to the British Museum on his return to England in 1842, as accession 42.55, then it is likely they would have been listed under "*Simulium?*" by White (in White & Doubleday 1843: 290) as was done for the 23 other insect species received from Sinclair and mentioned in this publication, rather than quoting passages from Yate (1835), Forster (1777), and Cook (1777) to support the presence of this genus.

Therefore we consider these caecutiens specimens were collected in 1844 and presented to the British Museum in 1845 as part of the accession 45.61. Sinclair arrived back in New Zealand on 23 December 1843, and within 2 weeks Governor FitzRoy prevailed upon him to take the post of Colonial Secretary and become a member of the Legislative Council (Molloy 2010). Sinclair would have travelled to the Bay of Islands during 1844 in his capacity of Colonial Secretary, as in 1844 FitzRoy was "called on to deal with New Zealand's first racial war, sparked off by the Bay of Islands chief Hone Heke. Its causes were not of FitzRoy's making, arising rather from economic failure and the diminished importance of the Far North after the removal of the government to Auckland. The first overt act of significance was the cutting down of the flagstaff on Maiki Hill above Kororareka [=Russell] on 8 July 1844" (Wards 2010). There was a peace conference held in Waimate North, one of the earliest centres of European settlement about 25 km west of Russell, in September 1844 and it is most likely Sinclair was present and quite involved; there was considerable correspondence to him as the Colonial Secretary (Daamen 1998). The overall condition of the caecutiens specimens indicates that it is unlikely they were collected while biting humans, and it is likely that they were trapped in a tent based on the high number (about 450) in the collection.

Comments on specimens examined by Enderlein

Enderlein's microscope mounts are unusual (e.g., Fig. 525). They consist of a small flat cardboard box with a cork strip along one edge to hold the square slide inside. The slide consists of 2 sheets of mica and not 2 glass coverslips as first appears. The mountant is Canada Balsam (Enderlein 1934: 279). Although the cardboard mounts are awkward to manipulate, Enderlein's slides are still eminently usable. They are, however, flexible and the 2 slips of mica easily separate.

The use of mica was common in the late 1800s and even into the early 1900s when better microscope lenses dictated use of glass coverslips (Bracegirdle 1987). It is likely that Enderlein used mica out of necessity rather than choice as it was available at ZMHU. It would have been difficult for ZMHU to justify expenditure on new glass coverslips during a period of severe purchasing restraints in Germany following World War I.

Zwick (1995: 133) noted that Enderlein mainly mounted type species of genus group names in this manner: "Of some species, essentially type species of genus group names, Enderlein mounted individual legs or wings between coverslips held in a rather large cardboard frame pinned into the collection box." Werner (2000) provided an insight as to why he kept 2 of the 3 mounts of the paralectotype in his collection at ZMHU (Fig. 531–534): they were the ones that provided the main characters on which he based his genera. Werner (2000: 229) stated that Enderlein supported his systematic conclusions using only female characters, the main ones being "... variations in wing characters, and modifications in the development of leg characters, especially the shape of the fore basitarsus, the hind tibia and the hind basitarsus and claws."

Type locality of *A. australense*

The exact type locality of *A. australense* is not known. The types were obtained when the Austro-Hungarian Naval frigate "SMS Novara" visited Auckland (21 December 1858–8 January 1859) during its highly acclaimed round-the-world expedition (1857–1859). The specimens, with a high degree of probability, were collected by A. Sinclair who had returned to New Zealand at the end of 1858, as the "Novara" largely relied on local collectors — "Sinclair in Auckland, Oxley in Nelson" (Dugdale 1988: 9). Dumbleton (1973) mentioned the specimens were probably collected while biting a human which might explain their original poor condition.

Tonnoir's *A. australense* topotype specimens

It is also not known exactly where Tonnoir obtained the specimens now recognised as topotypes, but it is most likely Nihotupu as this is the only locality given on labels in the vicinity of Auckland city for insect specimens collected by him during his 23–26 February 1923 stay (Crosby 1976b). Nihotupu also fits the description Tonnoir (1925: 213) gave for where he collected — "the Waitakerei (sic!) Ranges north of Auckland and the vicinity of that town". In 1923 there was accommodation available here associated with the building of the second major water supply dam for Auckland, the Upper Nihotupu Dam completed in 1923 (WaterCare Services Ltd 2011). Most streams in Auckland City and environs are now either piped or polluted and *A.*

australense is not commonly found. TKC notes that in the suburb of Mt Albert he is occasionally bitten in the summer period, and only found larvae once in the vicinity. Similarly, DAC has been bitten in suburbs at Mission Bay and at Te Atatu and larvae are known from trickles at the latter. Still, for the redescription here, we used material from semi-protected areas to the west of Auckland, the Waitakere Ranges (NZN93). We have now examined several hundred adult specimens from the Northland and Auckland region, and it is only *A. australense* that is attracted to humans, or to lights, even though *A. longicorne* may be present in its usual low numbers.

Material examined. Known material from Vienna (MHNW), as well as material not seen by Dumbleton (1973): the previously unknown paralectotype slides and the topotype from Berlin (ZMHU), and Walker's material in London (BMNH). In addition a large number of specimens from recent collections (Appendix 1) – from some 105 localities from the North Island, 21 from South island (including Stewart Island) — and 123 older New Zealand-wide collections, in NZAC mostly collected by Dumbleton and TKC.

Distribution (Map 3). *Austrosimulium australense* is by far the most widely distributed New Zealand simuliid. **North Island**. **ND**. Ahipara; Awarua R, NZN82 (Twin Bridges); Hatea R, NZN83 (A H Reed Kauri Park); Herekino; Houhora; Kaeo; Kaeo R, NZN99 (Waiare Road); Kaikai Beach; Kaihu R, NZN75 (SH12, near Ahikiwi); Kawaka Stm trib; Kawakawa R trib; Kohukohu (drainage channel); Kopai Stm; Mangakahia R trib; Mangamuka R, NZN80, 80a (SH1, Raiatea Forest); Manganuiowae Stm, NZN78 (Broadwood); Matariki Stm; Mirowharara Stm; Ngataki Stm; North Cape; Omahuta; Omapere; Pandora Bush stm (Spirits Bay); Peria R; Pilbrow Hill; Puketi Forest, NZN95; Puketona; Rawene (drainage channel); Tapotupotu Stm, NZN97 (Cape Reinga); Te Awhia Stm, NZN98 (SH1 bridge); Te Hapua Road, NZN96 (stm 2 km from Waitiki Landing); Trounson Kauri Park; Victoria R, NZN79 (SH1); Waiaruhe R, NZN81 (Puketona Junction); Waiharara; Waimamuku R, NZN77 (SH12, Waimamuku); Waipoua R, NZN76 (SH12), Headquarters trib; Waiokumurau Stm; Waiotemarama Stm, drainage channel; Waipu Cove, NZN100 (ditch); Wairau R (Tane Mahuta); Wekaweka Rd (drainage channel). **AK**. Araparera R, NZN73; Auckland; Bethells Beach [Te Henga]; Brookby; Cascades Stm; Fairy Falls Stm, NZN94; Glen Eden; Glen Esk Stm, NZN93; Hamiltons Gap stm; Helena Bay; Helensville; Henderson; Mahurangi R trib [Mill Stm], NZN74, 74a (Kowhai Park Scenic Reserve); Mangatangi Stm, NZN11 (Hunua Ra); Matuku Reserve; Mt Albert; Nihotupu; Omeru Falls Stm, NZN101; Orere Stm, NZN10 (bridge); Piha; Piha Stm; Silverdale; Taitaia Stm NZN9 (near Clevedon); Tamaki; Waimauku; Waipipi; Wairau R; Waitakere Ra. **CL**. Apakura Stm, NZN7 (SH26, Waiho Forest Reserve); Great Barrier Island (near school, Katherine Bay, Okiwi, Port Fitzroy); Hauturu/Little Barrier Island (Maraeroa); Hope Stm; Kauaeranga R, NZN2 (Park HQ); Ohinemuri R, NZN72 (SH2, Waikino); Tairua R, NZN3 (SH25a, Puketui Road); Thames; Umangawha Stm, NZN6 (near Colville); Waitawheta R, NZN8 (Karangahake Gorge); Waitekuri R, NZN5; Waiwawa R, NZN4. **WO**. Dixon–Waikorea Road, NZN16 (ditch); Firewood Ck, NZN12 (Ngaruawahia); Mangakahu Stm, NZN13 (Cogswell Road); Mangaora Stm, NZN15 (bridge Aotea); Mangapohue Stm, NZN19 (Natural tunnel); Mangatoa Stm, NZN20; Mapiu Stm, NZN21 (Omaru Falls); Okohua Stm; Pakoka R, NZN14; Rangitukia Stm, NZN17 (Pirongia); Waitomo Stm, NZN18 (Ruakuri Cave tunnel). **BP**. Houpoto Stm, NZN66; Lake Rotowhero stm; Maraehako Stm, NZN65; Mimiha Stm; Ohaupara Stm, NZN70; Opotiki; Taneatua; Tarawera Falls, NZN69; Tarawera R, NZN68; Tarawera R (Kawerau); Te Kaha; Te Puia; Te Rereatukahia Stm, NZN71; Torere; Waihou R; Waikare Gorge; Waimana R, NZN58, NZN67 (bridge); Waingaehe Stm, NZN56; Waiorongomai Stm; Whakatane R trib, NZN57. **TK**. Eltham (Waingongoro R trib); Heao Stm trib; Huatoki Stm; Inaha Stm; Kapoaiaia Stm; Kaupokonui Stm; Kiore; Kokowai Stm, NZN114; Mangaemiemi Stm, NZN115; Mangamawhete Stm, NZN25; Mangatoromiro Stm, NZN117; Mt Taranaki (South Hut); Otakeho Stm, NZN27; Paetahi Stm & Patea R junction, NZN113; Te Henui Stm, NZN26; Waingongoro R, NZN24; Waiongana; Waiteika Stm. **TO**. Hautapu R, NZN109; Hinemaiaia R (Hatepe); Hihitahi; Kakahi Stm trib (Owhango); Kakaho Stm, NZN22; Karioi; Mangateitei Stm, NZN120 (Ohakune); Mangawhero R trib, NZN108; Mangawhero R (upper), NZN92; Mihi; Otaratiri Stm trib, NZN112; Otaratiri Stm trib, NZN116 (Moerangi Station); Papamanuka Stm, NZN106 (SH47 bridge); Pokaka stm; Tokaanu Stm, NZN103; Tongariro R trib, NZN110 (Kaimamawa Rd); Tongariro R, NZN104 (Red Hut bridge); Waihora Stm, NZN102, 102a; Waimiha Stm trib; Waipunga R, NZN50; Wairakei; Waitahanui; Waiouru; Waitangi Stm, NZN46 (Waiouru); Whirinaki R, NZN55 (Minginui). **GB**. Aniwaniwa Stm, NZN54 (Papakorito Falls); Awatere R, NZN64 (SH35 bridge); Mangahauini R, NZN62; Mangaheia R, NZN61 (Five Bridges); Maraehara R, NZN63; Muriwai; Ruatoria; Te Araroa; Tolaga Bay; Waiharehare Bay; Wainui.. **HB**. Esk R, NZN51; Kakekino Stm, NZN45; Maraetotara R, NZN127; Ngaruroro R, NZN44; Ngaruroro R trib, NZN43; Ohiwa Stm trib, NZN41; Omahu; Ongaonga; Te Aute; Te Ngaru Stm, NZN52; Tukituki R; Tutaekuri R, NZN42; Waikare R, NZN53; Wairuru. **RI**. Hautapu R, NZN85 (SH1 bridge); Koukore Stm, NZN122 (bridge, Pipiriki); Manawatu R, NZN38 (SH2 Norsewood); Mangapurua Stm trib, NZN121 (Bridge to Nowhere); Mangateitei Stm, NZN47, NZN120 (Ohakune); Ohakune; Ohakune Lakes Reserve; Rangitikei R, NZN30 (Mangaweka); Tangarewai Stm, NZN39; Waipawa R, NZN40 (SH50). **WI**. Ongo Stm, NZN29 (SH1); Taupiri Stm, NZN28 (Atene Pa); Tutaenui Stm, NZN32, 32a, 32b (Bulls); Wanganui, NZN118 (Kaikukopu Road stm). **WN**. Abbots Ck, NZN34 (SH2); Ballance stm; Dundas Hut; Hutt R; Logan Basin; Ohau R, NZN89; Takapua Stm, NZN86 (Tawa); Tokomaru R, NZN90 (SH57); Wainuiomata R; Waitohu Stm, NZN33 (Otaki). **WA**. Akitio R, NZN128 (SH52 bridge); Dannevirke; Featherston; Hamua; Makakahi R, NZN35; Mangatora R, NZN37; Masterton; Pukeatua Stm trib, NZN129; Te Hoe Stm, NZN130; Waihi Stm. NZN36 (SH52); Waingawa. **South Island**. **SD**. Kenepuru Head stm, NZS2; Momorangi Bay stm, NZS114; Ngakuta Bay stm, NZS1; Ohinetaha Bay stm, NZS3; Te Mahia; Waikawa Bay. **NN**. Brown Ck, NZS81; Candle Ck, NZS77; Green Hills Stm, NZS99; Hira; Jones Ck, NZS74; Karamea, Baker Ck, Umere; Kohaihai R, NZS76 (Heaphy Track); Little Wanganui R, NZS79 (Te Namu); Lyell Ck, NZS82; Mangarakau Stm; Nelson; Nine Mile Rd (Westport); Pakawau; Paturau R; Pohara; Poorman Valley Stm; Rockville; Te Kuha stm; Totaranui Stm, NZS102; unmarked stm, NZS78 (near Virgin Ck, Karamea R gorge); W W Stm, NZS73 (Fairdown); Wainui R, NZS101 (Anatimo); Whareatea R (SH67). **BR**. Flowery Ck; Inangahua R, NZS67 (Rahu Saddle); Marble Hill campground stm, NZS187 (Springs Junction); Mill Ck, NZS70 (SH6 Greymouth); O'Malley Ck; Punakaiki R, NZS72 (SH6 bridge); Sawyers Ck; Tauranga Bay stm. **WD**. Jacobs R/Makawhio R; Jackson Bay; Karangarua; Kaniere R; Knights Point, NZS45; Lake Ianthe/Matahi; Mahinapua Stm; Neils Beach; Taramakau R, NZS51 (SH73); Whataroa. **MB**. Blenheim; Maungatapu Road ditch, NZS115; Nina Brook, NZS183 (Awatere Valley); Wairau R. **KA**. Kaikoura. **NC**. Culverden; Rotherham. **MC**. Bowyers Stm, NZS16; North Branch Ashburton R, NZS15 (Thompsons Track). **DN**. Evans Flat; Purakanui Falls. **SL**. Caddon Burn, NZS29; Dunsdale Stm; Fleming R; Makarewa R; Maclennan; Pounawea; Tuatapere; Tahakopa R; Tokanui; Waimeamea R, NZS30. **FD**. Alton Burn, NZS156. **Stewart Island**. Kaipipi Bay stm, NZS170; Clearwater/Freshwater R; Rakeahua R.

Ranging from North Cape (34.4089˚S), east to Great Barrier Island, and south to Stewart Island (46.8953˚S), this species appears only limited by altitude and the lack of suitable trailing vegetation in running water. Indeed, in the North Island the species could be said to be ubiquitous, and generally ranges from sea level up to 610 m a s l on the Volcanic Plateau. We have, however, obtained it in small numbers up the Mountain Road at Ohakune (NZN92) at an altitude of 920 m a s l where it occurred with *A. dugdalei.* In early December 1984 two females were collected while biting J. S. Dugdale and K. J. Fox at 1 150 m a s l at Dundas Hut, Tararua Ra, WN and another while biting TKC at the same altitude at nearby Logan Basin; it is likely these females had been blown up by wind to this altitude.

ND, AK, CL, WO, BP, TK, TO, GB, HB, RI, WI, WN, WA / SD, NN, BR, WD, MB, KA, NC, MC, DN, SL, FD, SI / —.

Austrosimulium australense appears to occur in all 13 North Island aquatic ecoregions except that of the Hauraki Plains. This absence may be the result of poor collecting, but also because of heavy agriculture and lack of suitable streams. Similarly, *A. australense* appears largely absent from the eastern section of the Wairarapa Highlands ecoregion (WA). This is probably in part because of lack of suitable running water. The region is heavily farmed on friable soil, and permanent running water tends to have high silt loads. Recent intense collecting in that area does show it to occur sporadically and at low frequency. In the eastern Gisborne area (GB), its apparent absence appears to relate more to lack of habitat—that of running water, including larger rivers, is intermittent because of the rainfall pattern. An apparent absence in the north Taranaki area (TK), while likely due to lack of collecting, may alternatively reflect habitats that are not optimal; stream and rivers tend to be deeply cut through blue mudstone (papa) and the silt load in water high. Again, recent intense collecting in that area does show it to occur sporadically and at low frequency.

For South Island aquatic ecoregions *A. australense* is absent from Northwest Nelson Forest, Central Otago, Southern Alps, and only occurs sporadically in East Coast Plains and High Country. In the Nelson region (Northwest Nelson Forest) absence of *A. australense* might be an example of competitive exclusion by *A. tillyardianum.* While both species occur together at the same locality, albeit on different substrates, in Nelson, *A. australense* is found only to the north, west, and south, not centrally: that is where *A. tillyardianum* and *A. multicorne* are found (Maps 12, 14). *Austrosimulium australense* has a propensity for lower altitudes and the central Nelson region is mountainous.

Dumbleton's distribution of *A. australense* showed an apparent gap south of Marlborough, through Canterbury, Otago and the Southland region, including Fiordland (Dumbleton 1973: 485, his fig. 2). Our more recent collections concur well with his findings, so the absence of *A. australense* from those areas is not an artifact of a lack of collecting. Absence may, in part, correlate with absence of trailing vegetation, the normal habitat, especially in braided rivers in Canterbury. The localities where we found this species in Canterbury were where tree branches trailed in the water. Dumbleton suggested terrestrial vegetation was necessary for survival of adults, but other species seem not affected by that. *Austrosimulium australense* occurs sporadically on the northern West Coast, south Southland, and a few localities on Stewart Island. The record by Hilgendorf (1918) of *A. australense* at Cass is likely a misidentification arising through *A. australense* being the only described species on mainland New Zealand at that time. Since the species is otherwise not known for the area, and its larvae are rarely found on stones, it is more likely to have been *A. multicorne* or *A. tillyardianum*. Dumbleton (1973) indicated that *A. australense* was rare on Stewart Island and that too was our experience. Cowie *et al*. (1978), however, found *A. australense* abundant in Freshwater River, in August. Chadderton (1988, 1990) probably found *A. australense* in his extensive sampling of aquatic invertebrates on Stewart Island, but did not identify simuliid material to species.

Etymology. Not mentioned in the original description by Schiner, but obviously referring to the south, as the first described simuliid species for the Australasian region.

Bionomics. *Austrosimulium australense* is the most commonly encountered simuliid in North Island, and is the main biter of humans. Dumbleton noted that eggs of *A. australense* are laid in masses on plants in the water, a typical oviposition strategy for simuliids (Crosskey 1990).

Dumbleton's ecological key for the larvae of *A. australense* can, with minor modification, still be used with confidence (see Ecological Key, p. 98). It is not necessarily the type of stream or river that determines presence of larvae or absence; rather it is presence of trailing vegetation. That may be a limiting factor for this species.

Fresh elongated leaves trailing in moderate flow (<0.90 m/s) are highly used by larvae of this species, so absence of leaves restricts their presence (Map 3). Larvae are not uncommon on detached individual broad leaves that are hung-up in flow against hard substrates and sometimes form substantial aggregations (Fig. 455). Flax (*Phormium* sp.), toetoe (*Cortaderia* sp.), tutu (*Coriaria* sp.), tussock grasses (e.g., *Festuca, Poa* spp.) and the introduced invasive lily montbretia (*Crocosmia* x *crocosmiiflora*) often support large populations, but normally only on live or recently dead leaves. Algal-clogged streams are rarely inhabited, but streams and rivers with macrophytes (e.g., *Myriophyllum* sp., *Potamogeton* sp.) will support low levels of larvae. Streams that are more torrential, with trailing vegetation absent, usually lack larvae of *A. australense*. Larvae are seldom found on stones.

Common to all substrates inhabited by larvae of this species is that the velocity is relatively low at 0.30–0.90+ m/s. Larvae are generally not found at higher velocities even on suitable substrates, and the cut-off between presence and absence can be marked. This velocity association is low for simuliid larvae (Crosskey 1990; Adler *et al*. 2004) and raises the question as to why this species is found at these moderate velocities. (Appendix 1).

A typical habitat for *A. australense* is a wide, sunlit river, with shallow, warmer water (9–26°C). Nevertheless, tolerance of immature stages for other habitats is good (Fig. 461–464). For example, streams and rivers flowing off Mount Taranaki appear to be well outside the range for *A. australense*, in that they tend to be torrential with large substrate, and larvae are almost impossible to find. Adults, however, occur in large numbers and their biting can be a nuisance (e.g., NZN114). In the North Island the majority of localities have pHs that are slightly alkaline, whereas in the South Island streams where we found *A. australense* tend to be more neutral to acidic. Also in the North Island the conductivity of streams is higher (Appendix 1). This general tolerance to an extensive range of conditions, no doubt, contributes to the wide distribution of *A. australense*.

Dumbleton (1973) said little about the number of generations per year. Scarsbrook (2000) in a review of life cycles of New Zealand aquatic invertebrates indicated that the voltinism of *A. australense* is equivocal. His comment was based on the work of Towns (1981b) who examined life cycles of aquatic invertebrates in an Auckland kauri forest stream in the Waitakere Ranges in shaded and open reaches. However, a multivoltine life cycle is suggested by the fact that in most localities where we collected, the full range of immature stages was normally present. In recent collections, denser populations of larvae were generally found in early to mid summer. Lower water levels and growth of algae appear to inhibit larvae later in the summer. During winter there is probably a slow-down in growth.

Dumbleton estimated that 80% of *A. australense* populations occurred in the absence of other simuliid species. We got a similar figure for the North Island, but in the South Island virtually all populations had other species present. In the North Island the most common associates were larvae of *A. tillyardianum,* normally taken from stones, with *A. australense* from vegetation. Rare associates were *A. dugdalei* and *A. longicorne.* In the South Island *A. tillyardianum* is also a common associate, but *A. laticorne* is too, and occasionally *A. multicorne*. Unusual associates were *A. ungulatum* larvae (NZS67, Inangahua River), and *A. stewartense* (NZS156, Stewart Island). That latter site was unusual for *A. australense*, being a heavily-shaded, brown-water stream (Fig. 464).

Remarks. As Dumbleton noted, there is little variation in structure throughout the range of *A. australense*. Immature stages are easily identified. The pupal gill is distinct and that, along with the mammillated thoracic cuticle, is definitive for pupae. Of importance is the dark cross-shaped pigmentation on the pale larval frontolabral apotome. This pigmentation also shows in earlier instar larvae and is diagnostic for immature *A. australense* larvae, and allows its separation from those of *A longicorne* and *A. multicorne,* where the heads are dark.

McLea & Lambert (1983) examined the cytogenetics of *A. australense*, but only from the North Island. They sampled 49 locations covering practically all areas and ecoregions. Coverage was, however, poor in the Waikato, Taranaki, and Wanganui areas. They showed little structural differentiation in the chromosomes, with only 10 floating inversions. Three zones of inversion polymorphisms were identified. Zone 1 populations were generally north of a line from East Cape to the Tarawera River, then south of Lake Taupo to near Wanganui. Another line between Zone 2 & 3 ran from south of Lake Taupo to near Hastings. The changes between Zone 1 & 2 in the Tarawera area were particularly abrupt. Inversions not found in Zone 1 were more evenly distributed in the other zones. They noted that Zone 1 larvae were normally found in small, slow-flowing streams winding through farmland or slower-moving regions of faster flowing streams or rivers, but that the Tarawera River population was in a large fast-flowing river. In a more detailed examination of the Tarawera area they suggested (McLea & Lambert 1985), that there might be two cryptic species in *A. australense*, and the different larval habitats between the Zones 1 and 2 was considered to be significant supporting evidence. We have found no morphological evidence to substantiate their suggestion that this represents two cryptic species, and molecular analysis of the CO1 gene also does not support it. Our sampling was, however, not extensive around Tarawera River itself, and further investigations are needed to explain the abrupt change in heterozygote inversion pairs between Zones 1 and 2 reported by McLea & Lambert (1983, 1985).

Austrosimulium australense, as a member of the *australense*-subgroup along with *A. longicorne,* is fully supported by cladistic analyses of both morphological and molecular data (Fig. 506, 509a, 509b). This is even when the pupal gills of these two species are startlingly different (*cf* Fig. 268, 269); an indication, perhaps, that gill structure should not be heavily weighted in phylogenetic analyses. It also shows that morphological change can be marked with small molecular divergence.

Within the subgroup, molecular evidence points to *A. australense* comprising 2 cryptic species: one, strictly precinctive to the South Island, the other the North Island but with occasional occurrences in the South Island. Unexpected was that *A. longicorne* is sister to the South Island clade of *A. australense* — a strong pointer that the South Island *A. australense* should, taxonomically, be a separate species. However, as yet, there is no identified morphological feature that allows discrimination. Such might be achieved by close comparison of the exemplars of North Island clades that occur in the South Island against the precinctive clade there. We leave this taxonomic situation unresolved.

While widespread in the North Island, *A. australense* has a marked gap in distribution in the mid–lower part of the South Island: almost absent from the Canterbury Plains and north Otago, occurring again along the southern edge of the South Island and on Stewart Island (Map 3). This mimics the "beech gap" known for other organisms in the South Island. This hiatus was of interest to Dumbleton and he suggested that it was related to a lack of habitats for the larvae — we concur with his suggestion.

Sampling for the molecular analysis was poor in the lower South Island (Fig. 510) and comments about distribution, from the point of view of haplotypes, are not made with confidence (see Biogeography section, p. 77). However *A. australense* from Stewart Island (NZS170) is basal to much of the North Island *A. australense*. This should be further investigated, along with material from the Catlins (NZS29), which also appears related to the North Island, but to a separate lineage from the Stewart Island haplotype (*cf* Fig. 511, 512). The two exemplars of North Island haplotypes (NZS91, NZS102) (Fig. 511, 513) in the NW of the South Island are more easily accounted for; probably colonising during Pleistocene sea level depressions when the two islands possibly were momentarily joined (Fig. 517). Of note is that all the apparent South Island exemplars of North Island lineages have poor statistical support.

Austrosimulium (*Austrosimulium*) *longicorne* Tonnoir, 1925 Slow flow black fly

Figures: female, 25, 42, 43, 51 ,71, 91, 109; male, 127; pupa and cocoon, 144, 161, 179, 203, 218, 239, 256, 269, 287; larva, 305, 306, 322, 323, 340, 352, 368, 385, 404, 421, 438; habitat, 470–474, 539, 540; Map 11.

longicorne Tonnoir, 1925: 254 (description larva, pupa, cocoon; *Austrosimulium*). Smart 1945: 499 (world catalogue). Mackerras & Mackerras 1949: 405 (occurrence). Miller 1950: 60 (listed). Gurr 1953: 81 (distribution). Dumbleton 1963b: 334 (as subgenus *Austrosimulium* (*Austrosimulium*), in *australense* group). Dumbleton 1964a: 35 (relationships, distribution). Dumbleton 1973: 511 (description female; redescription larva, pupa, cocoon; *Austrosimulium* (*Austrosimulium*)). Crosby 2006: 72 (key). Adler & Crosskey 2012: 20 (world inventory).

Diagnosis. **Female**: tarsal claw lacking basal tooth: abdominal tergites III–V wider than long, hind basitarsus with row of stout setae. **Male**: hind basitarsus with row of stout setae. **Pupa**: similar to *A. australense*, but thorax only slightly mammillated; gill not horned; common trunk short, only 2× as long as wide and not black,11–13 gill filaments long; sternites IX with grapnel hooks. **Cocoon**: slipper-shaped, less broad than *australense*, finely woven, not flared basally, opening oval. **Larva**: head pale; cephalic apotome markedly translucent, head spots poorly developed; medial article of antenna elongated; hypostomal teeth protruding; posterior hooks low in number (*ca* 880).

Adult female (based on allotype and topotype material). **Body**: in ethanol, general body bicolorous, markedly dark brown and yellow, when dried of silvery pruinose appearance; total length 2.1–2.6 mm. **Head**: width 0.73–0.78 mm; depth 0.39–0.47 mm; postocciput black, vestiture of sparse, short black hairs; frons dark brown-black; frons width : head width ratio 1.0 : 4.3. **Eyes**: interocular distance 0.16–0.17 mm; ommatidia diameter 0.015 mm; *ca* 38 rows up and across at mid-eye. **Clypeus**: width 0.15–0.17 mm; dark brown, pale medioventrally; vestiture of sparse pale hairs. **Antennae**: total length 0.47–0.53 mm; not tapered; all divisions evenly dark brown; pedicel slightly larger. **Mouthparts**: substantial, *ca* 0.8× length of head depth; cibarium cornuae broadly flared and substantially sclerotised with dark tuberculae (Fig. 25); mandibles with *ca* 29 markedly fine inner teeth, increasing in size towards apex; laciniae with 12 inner teeth and 15 outer teeth; maxillary palps, total length 0.51–0.54 mm, 3rd article darker brown than remainder, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.8 : 1.5, sensory vesicle spherical, markedly small, 0.3× 3rd article width, opening 0.3× vesicle width.

Thorax: length 1.1–1.2 mm; width 0.86 mm; in ethanol postpronotal lobes concolorous with scutum, vestiture of dense clump of fine pale hairs; scutum evenly dark brownish-black, vestiture of numerous fine pale recumbent hairs, presutellar depression with sparse longer coarse black hairs posteriorly; scutellum pale brown, vestiture of long coarse black hairs; postnotum concolorous with scutum; pleuron and plural membrane concolorous with scutum. **Wings**: length 2.4–2.7 mm; width 1.3 mm. **Halteres**: tan. **Legs** (Fig. 42): yellow and dark brown, with darker brown bases to femoral, tibial, and tarsal segments; hind basitarsus *ca* 7× as long as greatest width, with row of stout setae; tarsal claws elegantly curved with basal heel poorly developed (Fig. 51).

Abdomen (Fig. 71): abdominal scale not markedly pigmented, with fine pale hairs, not greatly extended; tergite II bowl-shaped, tergites III–V wider than long, ovoid, vestiture of fine hairs on tergite II, sparse coarse black hairs on others, increasingly so posteriorly; posterior abdomen dark brown, sternum paler. **Genitalia** (Fig. 91, 109); sternite VIII pigmented medially and along anterior and posterior edges, vestiture of sparse coarse black hairs posterolaterally; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and irregular microtrichia; median edges of hypogynial valves broadly rounded, similarly posteroapically; genital fork with anterior arm broad posteriorly, tapered smoothly to anterior nipple, slightly fluted anteriorly, lateral arms short with small knee-bend, posterolateral extension broadly rounded; anal lobes and cerci both broadly rounded in lateral view; spermatheca, clear area at junction of duct small.

Adult male (holotype and other specimens). **Body**: general colour when dried, markedly blackish-brown, in ethanol less so; total length 2.2–2.8 mm. **Head**: width 0.79–0.86 mm; depth 0.66 mm. **Eyes**: upper ommatidia dark orange, diameter 0.024 mm, *ca* 23–25 across and 27–29 down; lower ommatidia dark brown, diameter 0.014 mm, *ca* 36 across and 44 down. **Clypeus**: dark brown; width 0.15 mm; vestiture of sparse fine golden hairs. **Antennae**: total length 0.51 mm; evenly dark brown, articles subquadratic in shape. **Mouthparts**: poorly developed; length 0.33× head depth; maxillary palp 0.43 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 0.8 : 1.6, sensory vesicle irregular in shape, occupying 0.33× article width, opening 0.3× vesicle width.

Thorax: length 0.9–1.3 mm; width 0.8 mm; dry, scutum evenly dull black, vestiture of fine recumbent pale hairs, longer dark hairs in prescutellar depression; scutellum concolorous with scutum with sparse long black hairs; postnotum concolorous with scutum; depression, scutellum, and postnotum showing pollinosity under some lighting. **Wings**: length 2.4–2.5 mm, width 1.2 mm. **Halteres**: tan. **Legs** (Fig. 43): grayish-yellow, with black femoral, tibial, and tarsal bases; hind basitarsus about 5.5× as long as greatest width, with row of stout setae; tarsal claw grappling pads of *ca* 25 teeth.

Abdomen: as normal. **Genitalia** (Fig. 127): gonocoxites 2.5× longer than basal width, dark brown posteriorly, pale medially, with coarse black hairs on apical 1/2; gonostyli approximately 2.0× longer than basal width, quadratic, apical spines variable from 2–4 substantial spines, 1 usually less so; ventral plate 1.3× wider than long, broadly rounded posteriorly, membranous anteromedially, laterally angulate and substantial, vestiture of very fine hairs posterolaterally, coarser anteromedially, basal arms substantial, low rounded median keel; median sclerite poorly developed, broad, T-shaped anteriorly, difficult to observe, but junction with ventral plate distinct; parameres poorly developed.

Pupa. Body length; male 2.7–3.0 mm, female 2.3–2.6 mm. **Head**: cephalic apotome of male slightly tuberculate on upper frons (Fig. 218), that of female barely so, lacking cephalic depression (Fig. 203). Frontal setae absent; facial setae present, 1 on each side between or just above antennal bases; 2 short epicranial setae present on margin of cephalic apotome under antennal sheath at mid length (difficult to observe); ocular setae absent. **Thorax**. Dorsum; tubercles absent, cuticle slightly mammillated; setae trichoid (Fig. 239). **Gills** (Fig. 256, 269): not horned, base small *ca* 2× as long as its greatest width; not markedly dark; filaments 8–13, occasionally bifurcate, length 0.5–0.6 mm, light brown, barely tapered from base, surface pseudoannulated/ reticulated (Fig. 287). **Abdomen**. Normal; sternite IX with grapnel hooks.

Cocoon (Fig. 144, 161): slipper-shaped, not markedly flattened, edges vertical and closely fitted to pupa, lacking anterior projections, anterior opening circular, fabric thin, close-textured, but individual fibres of light brown silk obvious (Fig. 179).

Larva (based on numerous final instar specimens). **Body** (Fig. 305, 306): total length 5.3–7.0 mm, medium orangey-gray; no obvious sexual coloration. **Head**: in low-altitude populations, colour pattern normally poorly developed (Fig. 322), pale yellow and translucent, postocciput dark brown to black; length 0.69–82 mm, width 0.58–0.66 mm; distance between antennal bases 0.33–0.41 mm; lateral margins of head, markedly subparallel; anterior apotome translucent, head spot pattern not distinct, pigmentation mainly at extreme posterior of apotome; ecdysial lines barely visible, postocciput poorly developed, cervical sclerites separate, lightly coloured; high-altitude populations, head colour dark brown, ecdysial lines distinct (Fig. 323). **Antennae** (Fig. 368): total length 0.33–0.41 mm, extended just beyond apex of fan stalk; evenly light brown; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.7 : 1.9; apical narrow article *ca* 1.1× length of combined basal 2 articles, median article markedly long, *ca* 0.7× length of basal article. **Labral fans**: stalk clear; *ca* 41–46 markedly fine rays, length 0.63 mm, width 0.007 mm; indistinct pattern of microtrichia, irregular longer microtrichia as long as ray width, interspersed with *ca* 5–8 subequal microtrichia. **Postgenal cleft** (Fig. 385): broadly quadratic in shape; postgenal bridge: 1.5× longer than hypostoma, pale, concolorous with genae, elongated posteroventral muscles spots barely visible; genae with irregular grayish pigmentation; suboesophageal ganglion distinctly pigmented. **Hypostoma** (Fig. 404): median and lateral teeth sharp, prominent and subequal in length; 3 smaller sublateral teeth, medial tooth small and difficult to observe (see Dumbleton 1973: fig. 162; and Tonnoir 1925: fig. 9E); 2 paralateral teeth, outermost tooth smaller; anterior margin of hypostoma distinct, but not covering teeth, especially in Old Man Range (CO) populations; 4 or 5 poorly-developed, rounded lateral serrations, variable; 4 hypostomal setae each side. **Mandibles** (Fig. 421): outer teeth broad, well developed; apical tooth broad and substantial with anterior edge roughened, 1 subapical tooth well developed and others subequal in length to *ca* 7 spinous teeth, gap small; sensillum and serrations distinct and in 3 groups; blade region moderately long, smooth and slightly convex.

Thorax: prothorax light grayish, remainder of thorax paler, thorax wider than anterior abdomen; mature pharate pupal gill, blackish-brown, 5 filament bases visible arising from base (Fig. 340, 352).

Abdomen: anterior abdomen evenly grayish-brown, posteroventral abdomen pale; abdominal segments I–IV narrow, expanded distinctly at segment V and producing a slight amphora shape, ventral tubercles well developed. **Anal sclerite** (Fig.438): median region substantial, tapered posteriorly, interarm struts substantial and rod-like, posteroventral arms short, tapered rapidly; semicircular sclerite narrow; accessory sclerite flared, not emarginated. **Posterior circlet**: *ca* 78–85 rows, 9–12 hooks per row (total *ca* 880).

Type data. **Holotype**, male, on elbow pin (MacGillivray 1903); condition slightly dirty, greasy and collapsed, mid left leg tarsal claw absent, left and right hind tarsus absent; label details "Kaikoura N.Z.\ 24 Feb. 1922\ A. Tonnoir" ("24" handwritten in black ink, Tonnoir), "Austrosim. {M}\ longicornis\ Tonn\ Type" (handwritten in black ink, "Type" with wavy underline, Tonnoir), "NZ Arthropod Collection\ {barcode}\ NZAC04021453" (NZAC). **Paratypes** (14), pinned; 1 female, "Kaikoura N.Z.\ 24 Feb. 1922 \A. Tonnoir" ("24" handwritten in black ink, Tonnoir), "Austrosimul\ longicornis {F}\ Tonn.\ Allotype" (handwritten in black ink, "Allotype" with wavy underline, Tonnoir), "NZ Arthropod Collection\ {barcode}\ NZAC04022154" (NZAC); 3 females "Kaikoura N.Z.\ 24 Feb. 1922 \ A. Tonnoir" ("24" handwritten in black ink, Tonnoir), "PARATYPE.\ Austrosimul. {F}\ longicornis \ n. sp. \A. Tonnoir det." (blue label, scientific name handwritten in black ink, Tonnoir), "NZ Arthropod Collection \ {barcode} \ NZAC04022109", but with barcodes NZAC04022156 and NZAC04022017 (NZAC); 5 males, "Kaikoura N.Z.\ 24 Feb. 1922\ A. Tonnoir" ("24" handwritten in black ink, Tonnoir), "PARATYPE. {M}\ Austrosimul \ longicornis \ n. sp. \ A. Tonnoir det." (blue label, scientific name handwritten in black ink, Tonnoir), "NZ Arthropod Collection\ {barcode}\ NZAC04022008", but with barcodes NZAC04022023, NZAC04022025, NZAC04022152, and NZAC04022155 (NZAC). 2 males, label details "Nihotapu\ 26 Feb. 1923\ A. Tonnoir", "PARATYPE {M}\ Austrosimul.\ longicornis\ n. sp.\ A. Tonnoir det.", "I.284" (red label), and "I.285" (red label); 1 female, label details "Kaikoura N.Z.\ 24 Feb. 1922\ A. Tonnoir", "PARATYPE. {F}\ Austrosimul.\ longicornis\ n. sp.\ A. Tonnoir det.", "I.286" (red label) (CMNZ). 2 males, label details

"Kaikoura N.Z.\ 24 Feb.1922 \ A. Tonnoir", "PARATYPE {M}\ Austrosimul.\ longicornis\ n. sp. \ A. Tonnoir det." and second male "Nihotapu\ 26 Feb. 1923\ A. Tonnoir", "PARATYPE {M}\ Austrosimul.\ longicornis\ n. sp.\ A. Tonnoir det." (MONZ).

Dumbleton (1973: 512) incorrectly stated the year of the holotype to be "[19]24" instead of 1922. As well, his list of paratypes is confusing as it makes it appear that a male and a female from Nihotupu, plus 12 specimens (6 males and 6 females) from Kaikoura were deposited by Tonnoir in the Macleay Museum, Sydney. It would appear that the phrase "all in Entomology Division, Nelson" was omitted before the 3 specimens said to be in the Macleay Museum (see, for example, Dumbleton's listing for the paratypes of *tillyardianum* on page 515 in which this phrase is used). Tonnoir did not specify the number of paratypes, but only that he "… obtained a good series from pupae collected at Kaikoura …". It is likely that Tonnoir sent specimens of his species to the Macleay Museum as he studied the type of *Austrosimulium furiosum* (Skuse) at that Museum (Tonnoir 1925: 240). A list of types in the Macleay Museum, compiled in 1962 by D. E. Hahn, lists only 2 specimens from Nihotupu. Such material would have been transferred to the Australian National Insect Collection (ANIC), CSIRO in the 1970's (E. Jefferys, Macleay Museum, pers. comm. 2009). However, in the ANIC, there are 5 males and 2 female paratype specimens of *A. longicorne* only; labelled "Nihotapu\ 26 Feb. 1923\ A. Tonnoir", none from Kaikoura (C. Manchester, CSIRO, pers. comm. 2009; REGC, 2011). Given the number of paratypes (14) housed in New Zealand institutions, it is apparent that Kaikoura specimens were not deposited in the Macleay Museum.

Material examined. Type material; some 24 tubes of ethanol material in various condition in NZAC; 14 collections of recent material (Appendix 1), some of which comprised the full life cycle, including reared adults which confirmed association of mature final instar larvae, pupal, and adult stages. The paratypes deposited in Australia were examined in 2011.

Distribution (Map 11). **Three Kings Islands**. Tasman Stm. **North Island**. **ND**. Mangamuka; Omahuta; Rawene; Te Paki; Tom Bowling Bay; Waipoua R trib; Wekaweka Rd (drainage channel). **AK**. Hamiltons Gap stm; Mahurangi R trib [Mill Stm], NZN74 (Kowhai Park Scenic Reserve); Nihotupu; Tikokopu Stm. **WO**. Aotea; Pakoka R, NZN14. **TK**. Mangatoromiro Stm, NZN117. **TO**. Barryville stm; Kakahi Stm trib (Owhango); Mangatepopo Stm trib, NZN84, 84a; Mt Ruapehu, NZN119 (Blyth Track), seepage, NZN126, 126a (Silica Rapids track), seepage, NZN123, 123a (Upper Round Mt track); Mt Tongariro, NZN124 (Soda Springs seepages); Ohakune; Otaratiri Stm trib, ditch, NZN111, 111a (Moerangi Station); Pokaka stm; Waihora Stm, NZN102; Waitangi Stm, NZN46 (Waiouru). **BP**. Lake Rotowhero stm; Wairoa. **GB**. Muriwai; Wainui. **HB**. Puketapu. **WI**. Tutaenui Stm, NZN32 (Bulls); Wanganui, NZN118 (Kaikokopu Road stm). **WN**. Otaki R. **WA**. Pahiatua. **South Island**. **NN**. Buller R trib (Glenhope Scenic Reserve); Orowaiti R trib; Takaka Hill summit stm, NZS103; Whareatea R (SH67 ditch). **BR**. Tauranga Bay stm; Westport. **WD**. Waiho (Franz Josef). **MB**. Maungatapu Road near Pelorus Bridge, NZS115, 115a (ditch). **KA**. Green Burn, NZS12; Hawkswood; London Ck, NZS8. **NC**. Domett Rd (SH1); Lewis Pass; Saltwater Ck; Waipara. **MC**. Lincoln; Mt Somers stm; Okeover Stm, NZS14; Springston (drain). **CO**. Amisfield Burn; Bendigo Ck ditch; Butchers Ck headwaters, NZS39; Fraser R headwaters, NZS40, 41; Glengary Stm, NZS25; Old Man Range; Shepherds Ck; Thompsons Ck trib, NZS21.

Northernmost record: Great Island, Three Kings Islands (latitude S34.15900°); southernmost record: Old Dunstan Road, CO (latitude S45.69140°), from near sea level (NZS14) to more than 1 600 m a s l (Old Man Range). Unknown from Stewart Island. Although widely distributed throughout mainland New Zealand *A. longicorne* is not common at most sites, as it normally requires particular low-velocity, constant flow conditions.

TH / ND, AK, WO, TK, TO, GB, HB, WI, WN, WA / NN, BR, WD, MB, KA, NC, MC, CO/ —

Widely dispersed and with unusual habitat requirements for the immature stages. In the North Island, *A. longicorne* is found in the ecoregions of Northern Hill Country, Waikato Hill Country, Taupo and Volcanic Plateaus, Manawatu Plains, Central Mountains, East Arable Lowlands, and the Wairarapa Highlands. In the South Island it is found in those of the Nelson Plains, Northeast Nelson Forest, High Country, East Coast Plains, Southland Plains, Southeast Forest, and Westland Forest.

Etymology. Not given by Tonnoir (1925), but probably referring to the elongated filaments of the pupal gill which are almost as long as the pupa itself.

Bionomics. Dumbleton (1973) noted that *A. longicorne* larvae tended to be found on vegetation in smaller streams (e.g., Fig. 470) and only rarely with those of other species; occasionally with larvae of *A. australense* and once with those of *A. tillyardianum*. He noted that the habitats had a steady flow of water. Recent collections for this study confirm these observations (Appendix 1). At Tauranga Bay to the west of Westport (BR), many larvae were found in vegetation-choked small streams, where the water flow was slow at about 0.1 m/sec (TKC, 1 January 1983). This was also the situation for larvae collected on the same day in a roadside ditch near the Whareatea River to the east of Westport (BR). On the Volcanic Plateau on the slopes of Mts Ruapehu and Tongariro, large numbers of *A.*

longicorne larvae have been found in bog outlets and iron bacteria choked seepages. In the seepages the water depth was a mere 3–4 mm and velocities (measured in detail) were as low as 0.1 m/sec and never higher than 0.3 m/sec. Relevant to this is that *A. longicorne* has the lowest number of posterior circlet hooks of a New Zealand species and is found in the lowest flow streams. These findings are in full concordance with Palmer & Craig (2000) who asserted that the hook number of simuliid larvae was correlated with water velocity. For these reasons we suggest the species warrants the common name "slow flow black fly".

Austrosimulium longicorne females probably do not bite. The mouthparts overall are not well developed even though they are of substantial size compared with head depth (0.8×), which is greater than the notorious biter of Westland *A. ungulatum* (0.6×). The laciniae have a reduced number of teeth (27) in comparison with those of *A. ungulatum* (44), and similarly, the mandibles have markedly small teeth. This assertion of non-biting is further supported by the larger tergites (Fig. 71) of the female abdomen, a condition correlated with non-blood feeding.

Collection data do not give a clear indication of numbers of generations a year, still a univoltine life cycle is indicated. Two collections are of importance in this regard, both being from small roadside ditches (NZN111, NZS115, NZS115a). In November and December both localities (e.g., Fig. 472) had good flows of water and large populations of final instar larvae and pupae of *A. longicorne*. There were sparse larvae of *A. australense*. By February, NZN111 was totally dry (Fig. 473) and NZS115a almost. In the latter were a few larvae, perhaps indicative of a partial second generation. The streams on the summit of the Old Man Range (CO) arise from waterlogged soil derived from snow packs in the upper valleys (Fig. 474) and dry up by mid summer. Again, this is indicative of a univoltine life cycle. Other localities are not intermittent. The upper Waitangi Stream, west of Waiouru (NZN46), for example, has deep, steady flow and it is most unlikely to dry up, and this is also the case for the spring-fed Okeover Stream (NZS14) (Fig. 471). For the Waitangi Stream, in November 2006 there was a monospecific population of *A. longicorne*, whereas in February 2009 no simuliids of any species were recovered, again indicating univoltinism. The known water temperature of localities used by *A. longicorne* tends to be warmer, ranging from 11–20°C even at high altitude.

The recent collections from the Volcanic Plateau provide some other information on the life cycle of *A. longicorne*. The Mt Ruapehu localities (NZN123, 126) were revisited two weeks apart. Originally both had large numbers of black, middle instar larvae (Fig. 539, 540). Locality NZN126 had a water temperature of 18.2°C as against air temperature of 9.4°C, no doubt because of the shallow water and intense sun. On the second visit, there were virtually no larvae to be seen and those that were present were small. There was no indication of empty pupal exuviae. An interpretation of this observation is that perhaps the water temperatures reached a lethal threshold and the population was eliminated. For the NZN123 population, the number of larvae present was still large, and mainly still of smaller black individuals, but with a few paler mature final instar larvae. There were no pupae evident. These observations tend to indicate that larvae are slow growing under these conditions. Of note is that there were no other aquatic invertebrates obvious in the seepages. A further general observation is that bacterial films and growths of various types are commonly found in *A. longicorne* larval habitats.

The ability to survive in intermittent streams may in part account for the wide distribution of this species, including the Three Kings Islands where a few larvae have been collected only from low-flow areas.

Tonnoir (1925) recorded *A. longicorne* from vegetation in a small stream [rivulet] at Waiho, Westland, along with *A. laticorne* and *A. multicorne*. No other details were given and further *A. longicorne* have never been recovered from the immediate vicinity.

Remarks An elegant simuliid in its immature stages (Fig. 161, 305, 322), *A. longicorne* is distinct and is easily identified from other species in that the pupal gill has sparse, long filaments with virtually no base, and the larval head spot pattern is almost absent in low-altitude populations and the final instar. As both Tonnoir (1925) and Dumbleton (1973) noted this is a species widespread on both islands (Map 11). It is, however, not common and hence has been recovered from only a relatively small number of localities. It is one of the most northerly occurring simuliids on mainland New Zealand having been found at Te Paki, northern Northland; only *A. australense* is known farther north at North Cape. *A. longicorne* also occurs on Great Island, Three Kings Islands, 55 km northwest of Cape Reinga. The two immature larvae collected by G. Kuschel from there in 1970 were identified by J. S. Dugdale as *A. longicorne*. Dumbleton noted that those specimens differed from others of this species by possessing posteroventral tentorial pits, which were single, not double (illustrated as double in his Fig. 154, page 531). However, while simuliid larvae as a whole only have a single tentorial pit on each side, the appearance of two may well be a synapomorphic character of the *australense*-subgroup (*cf* Fig. 384, 385). Re-examination of the 1970 Three Kings specimens showed that the two tentorial pits, one on either side of the postgenal cleft, are normal, however, there is a tendency for them to appear as double, as illustrated by Dumbleton. Perhaps of more importance is that the antennae of these immature larvae have long median articles, diagnostic of *A. longicorne*. Newer material collected by TKC in 1999, again of earlier larval instars, is also confirmed to be *A. longicorne*.

Dumbleton (1973) noted that *A. longicorne* occurred usually without other simuliid associates, but it had been taken along with *A. australense* and *A. tillyardianum*. Our recent collections agree, but include one locality (NZS12) from the Kaikoura coast, that included *A. multicorne* larvae.

Dumbleton (1969) in a general comment on Canterbury simuliids, indicated that both *A. tillyardianum* and *A. longicorne* were found on Banks Peninsula. Crosby (1974b) felt that the record of *A. longicorne* on Banks Peninsula at Wainui (date not given, but NZAC specimens labelled 11-x-61) cited by Dumbleton (1969, 1973) was most likely incorrect, since he (Crosby) never recovered any *A. longicorne* in his intensive study of *A. tillyardianum* there. Indeed, Dumbleton's record is more likely refers to Wainui on Mahia Peninsula, GB (S39.097870°, E177.962389°), in the North Island, not Banks Peninsula, since dates of his other collections place him nearby at that time — 3 days later he collected at Tolaga Bay (14 October 1961). Stout (1969) in a general comment also mentioned only *A. tillyardianum* as occurring on Banks Peninsula.

Tonnoir maintained that *A. longicorne* larvae were identical with those of *A. multicorne*, but further material shows that this is only so in the earlier instars, where the heads of larvae of both species are evenly dark brown. That coloration is maintained in final instar larvae of *A. multicorne*, and those of high-altitude *A. longicorne,* but usually is lost in those of low-altitude where it is markedly pale (Fig. 322). An exception was a low altitude ditch by Whareatea River near Westport BR, 1 January 1983 where TKC found the final instar larvae were still dark. The longer median article of the larval antenna (Fig. 368) in *A. longicorne* always serves as a diagnostic feature even for earlier larval instars, as do the protruding hypostomal teeth.

A collection of 38 mature and near mature larvae in NZAC was extracted in August 1971 from the stomach of the Canterbury mudfish, *Neochanna burrowsius* (Phillipps, 1926) (Galaxiidae) from Mt Somers, MC, as part of the 142 specimens from 13 fish reported by Cadwallader (1975). This is one of the few confirmed records of an identified New Zealand simuliid species being eaten by a native fish species. The mudfish has been found most often in weedy drains, irrigation races, and around margins of wetlands (McDowall 1978, 2000), which is another indicator that usual habitat for *A. longicorne* is in slow-flow water where then it is able to be preyed upon by the mudfish.

Molecular evidence shows *A. longicorne* is the well supported sister species to the South Island clade of *A. australense* (Fig. 506, 510). The North Island haplotype (#10) of *Austrosimulium longicorne* is well supported and although widespread shows little genetic divergence — is this indicative of recent history? This fits 'colonist distribution' of Trewick & Wallis (2001). Molecular data from the Three Kings Islands population will be of interest. We assume these islands were colonised during one of the Pleistocene sea level depressions when there was only a narrow gap between the islands and the mainland (Fig. 516). South Island *A. longicorne* shows greater diversity, probably indicating greater age (Fig. 510). Clustering is, however, poorly supported. The lineage comprised of the high-altitude Old Man Range population (NZS41) and that of Christchurch (NZS14) near sea level, has virtually no support. With low sample numbers little more can be said about haplotype distributions for this species.

australense species-group

tillyardianum-subgroup

Austrosimulium (*Austrosimulium*) *albovelatum* Dumbleton, 1973

Figures: female, 26, 52, 72, 92, 110; male, 21, 128; pupa and cocoon, 145, 162, 180, 204, 219, 240, 257, 270, 288; larva, 307, 324, 341, 353, 369, 386, 401, 405, 422, 439; habitat, 456–458; Map 1.

albovelatum Dumbleton, 1973:524 (description pupa, cocoon, larva; *Austrosimulium* (*Austrosimulium*)). Crosby 2006: 74 (key). Adler & Crosskey 2012: 19 (world inventory).

sp. 4. Dumbleton 1964a: 36 (his Fig. 1, distribution map, pupal gill, and cocoon; *Austrosimulium*).

Diagnosis. A moderate-sized species. **Female**: hind basitarsus with row of stout setae; tarsal claw finely curved, heel poorly developed. **Male**: hind basitarsus with row of stout setae. **Pupa**: thoracic cuticle with rounded tubercles along paramedial ridge, in groups elsewhere; gill horn black and elongate, with 17–20 finely tapered filaments, abdominal sternite IX lacking grapnel hooks. **Cocoon**: slipper- to shoe-shaped, of low profile, thick white material, bunched around gill bases. **Larva**: pale; apotome markedly translucent, head spots absent, irregular gray pattern on apotome and genae, slight pigmentation posteromedially; ventral tubercles not markedly developed.

Adult female (from paratypes and topotypes). **Body**: general body colour in ethanol dark reddish brown-black, when dried with silvery pruinose appearance in some lighting; total length 2.6–3.1 mm. **Head**: width 0.64–0.72 mm; depth 0.45–0.50 mm; in ethanol postocciput black, vestiture of sparse, short black hairs; frons dark brown-black, when dry both with distinct pollinosity; frons width : head width ratio 1.0 : 3.6. **Eyes**: interocular distance 0.18–0.20 mm; ommatidia diameter 0.013 mm; *ca* 34 rows up and across at mid-eye. **Clypeus**: width 0.21–0.22 mm; dark brown laterally, pale medially; vestiture of sparse black and pale hairs. **Antennae**: length 0.53–0.54 mm; all flagellomeres pale yellowish-brown; scape and pedicel darker. **Mouthparts**: markedly well developed, 0.7–0.9× length of head depth; cibarial cornuae short and broad with faint flutings (Fig. 26); mandibles with 38 inner teeth (basally 13 of which are small); laciniae with 15 inner teeth and 19 outer teeth; maxillary palpus, total length 0.62 mm, 3rd article dark brown, remainder lighter, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.8 : 1.4, sensory vesicle spherical and small, less than 0.3× 3rd article width, opening 0.25× vesicle width.

Thorax: length 1.1–1.2 mm; width 0.88 mm; in ethanol postpronotal lobes marginally paler than scutum, more so when dried; scutum evenly dark reddish-brown, dark brown when dry, vestiture of even, shiny, recumbent hairs, prescutellar depression with a few longer hairs posteriorly, no vittae visible in ethanol, but when dried with a median and 2 lateral vittae overlain with silvery pruinosity; scutellum slightly lighter than scutum, vestiture of a few long black hairs and pale hairs laterally; postnotum concolorous with scutum; pleuron and pleural membrane concolorous with scutum. **Wings**: length 2.4–2.5 mm; width 1.3 mm. **Halteres**: colour unknown. **Legs**: yellowish-brown, with darker brown bases to femoral, tibial, and tarsal segments; hind basitarsus about 6× as long as greatest width, with row of stout setae; tarsal claws elegantly curved, heel poorly developed (Fig. 52).

Abdomen (Fig. 72): abdominal scale dark brown with fine pale hairs, poorly developed and hairs barely extended over 2nd abdominal segment; tergite II 4.5× wider than long, not bowed, tergite III 2.0× wider than long, ovoid, tergites IV–V of similar size but quadratic, tergite VI 3.0× wider than long, quadratic, vestiture of sparse fine hairs. **Genitalia** (Fig. 92, 110): sternite VIII pigmented on either side of medial line and along anterior edge, vestiture of black hairs posterolaterally; hypogynial valves lightly pigmented with central group of vestiture of sparse, small, coarse hairs and triads of microtrichia, median edges smoothly divergent, broadly rounded posteroapically, clear reinforced area anteromedially; genital fork with anterior arm narrow, finely rounded anteriorly, lateral membranous region not well developed, posterolateral extension broadly rounded posteromedially, apodeme normally developed, lateral extension angulate; in lateral view anal lobes not rounded, flattened more than most, cerci broadly rounded; spermatheca dark, clear area at junction of duct small.

Adult male (based on paratypes and reared adults). **Body**: general colour dark brownish-black; total length 3.1–3.5 mm. **Head**: width 0.85 mm; depth 0.60 mm. **Eyes**: upper ommatidia orange, diameter 0.031 mm, *ca* 24 across and down; lower ommatidia dark brown, diameter 0.014 mm, *ca* 30 across and down. **Clypeus**: markedly small, dark brown; width 0.15 mm; vestiture of very sparse fine hairs. **Antennae**: total length 0.58 mm; all divisions evenly medium brown. **Mouthparts**: poorly developed; length 0.45× head depth; mandibles insubstantial, broadly tapered with apical hairs; laciniae, finely tapered apically with terminal hairs; maxillary palp medium brown, elongate, 0.54 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 0.7 : 1.4.

Thorax: length 1.2 mm; width 0.9 mm; in ethanol, scutum evenly dark brown-black, vestiture of fine recumbent pale hairs, scutum brassy yellow when dried, longer dark hairs in prescutellar depression; scutellum concolorous with scutum with sparse long black hairs; postscutellum concolorous with scutum. **Wings**: length 2.3–2.6 mm, width 1.2 mm. **Halteres**: colour unknown. **Legs**: yellowish-brown, with darker brown femoral, tibial, and tarsal bases; hind basitarsus about 6.6× as long as greatest width; with row of stout setae, less well developed than in female; tarsal claws with grappling pad of 19–20 hooks.

Abdomen: overall dark brownish-black. **Genitalia**: (Fig. 128). Gonocoxites 1.3× longer than basal width, dark brown posteriorly, pale medially, with sparse, coarse black hairs medially, anteromedially with faint crenulations; gonostyli approximately 2.8× longer than basal width, apically with 2 substantial spines, on occasion with 3rd smaller spine; ventral plate with low median keel, sparse vestiture of coarse hairs, 1.5× wider than long, broadly cone-shaped posteriorly, angulate and poorly sclerotised laterally, flat anteromedially, basal arms fine; median sclerite poorly developed, broad, slightly expanded posteriorly; parameres more distinctly developed than most, connected to apodeme of gonocoxite.

Pupa. Body length; male 2.9–3.7 mm, female 2.2–3.1 mm. **Head**: cephalic plate of male (Fig. 219) markedly elongate, 2.5× longer than narrowest width; markedly tuberculate on upper frons, that of female (Fig. 204) tuberculate laterally only, both concave posteriorly; muscle scars paler, more so in male. Frontal setae absent; facial setae present, 1 on each side between antennal bases; 2 short epicranial setae present on margin of cephalic apotome under the antennal sheath at mid length; ocular setae absent, but trichoid sensilla variably present at that position, females only. **Thorax** (Fig. 240). Dorsum coarsely granulated; tubercles raised, circular, distinct, evenly distributed in groups of 5–7 with open centres, continuous along median ecdysial line; dorsocentral setae trichoid. **Gills** (Fig. 257, 270): horn elongate, *ca* 5× as long as wide; basally light yellow, apically black, covered with trabeculae; 17–20 filaments arising from apical 1/2 of horn, length 0.75–1.3 mm, occasional filament markedly short, or bifurcated, colour light yellowish-grey, thicker basally, tapered from mid length, surface annulated to reticulated (Fig. 288). **Abdomen**. As normal for *tillyardianum*-subgroup species, grapnel hooks absent from terminal segment.

Cocoon (Fig. 145, 162): fabric of thickened white weave, also finely alveolate (Fig. 180); low boot-shaped, not markedly flattened, close fitting; 2 dorsal ridges arising from posterior apex, oriented to pass gill bases laterally, surrounding them anterolaterally, then connected by thin sheet of fabric to 2 anteroventral projections from the ventral collar; anterodorsal edge of cocoon opening thickened and of irregular V-shape. Well defined ventrolateral edges to cocoon.

Larva (numerous final instar specimens). **Body** (Fig. 307): colour variable, but usually pale brown; colour sexual dimorphism not apparent; Kaikoura population (NZS11) markedly pale; total mean length 5.9–6.8 mm. **Head** (Fig. 324): overall bullet-shaped and markedly pale, when fully mature slightly castaneous; length 0.66–0.74 mm, width 0.54–0.55; distance between antennal bases 0.26–0.28 mm; lateral margins of head smoothly convex; apotome translucent and colourless, head spot pattern absent, with posteromedial edge of apotome light brown, reticulate light gray pigmentation anteromedially, also laterally on genae; ecdysial lines markedly rounded at maximum width, slightly sinuous, narrowest anterior of stemmata; postocciput not markedly developed, cervical sclerites not fused, not markedly pigmented. **Antennae** (Fig. 369): basal 2 articles light brown, apical article pale; total length 0.34 mm, extended well beyond apex of fan stalk; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.5 : 1.9, thin apical article *ca* 1.3× length of 2 basal articles, medial article 0.5× length of basal article. **Labral fans**: stalk translucent and relatively short; *ca* 29–33 short, fine rays (10 smaller and finer than others), length 0.56 mm, width at mid length 0.008 mm; distinct pattern of microtrichia, longer microtrichia 1.1× longer than ray width, interspersed with *ca* 8–12 smaller microtrichia. **Postgenal cleft** (Fig. 386): markedly shallow inverted U-shape, with irregular apex, posterior tentorial pit region not markedly sclerotised and pigmented. **Postgenal bridge**: 1.2× longer than hypostoma, pale, concolorous with genae, elongated posteroventral muscles spots barely visible; genae with reticulate grayish pigmentation, castaneous in fully mature specimens. **Hypostoma** (Fig. 405): median tooth prominent, lateral teeth less so; median sublateral tooth smaller; 2 paralateral teeth, lateral tooth markedly smaller; larger teeth not well concealed by anterior margin of hypostoma; occasionally teeth all directed medially as in *A. bicorne*; 4–5 rounded lateral serrations, variable; 5 (occasionally 6) hypostomal setae each side. **Mandibles** (Fig. 422): outer teeth smaller, apical and subapical teeth not substantial; *ca* 8 spinous teeth, gap absent; 2–4 sensilla and serrations, distinct; blade region short, smooth, and slightly convex. **Thorax**: wider than anterior abdomen, markedly pale dorsally, grayish-brown otherwise; mature pharate pupal gills (Fig. 341, 353) with black horn directed posteriorly at 45 degrees, visible filaments arising from horn and continued parallel before abruptly turning anteriorly, then reflexed dorsally and around — not L-shaped; filaments dark gray when mature. **Abdomen**: anterior abdomen banded grayish-brown, intersegmental regions pale, posteroventral abdomen pale; abdominal segments I–IV narrow, expanded distinctly at 5th segment producing a slight amphora shape, more brownish than gray, ventral tubercles not markedly developed; Kaikoura larvae markedly pale, light brown on posterior abdomen. **Anal sclerite** (Fig. 439): more delicately constructed than other species, median region simple, posteromedial campaniform organs distinct, anterior arms not markedly developed or flared, interarm struts substantial, ventrolateral arms finely tapered, semicircular sclerite finely developed with accessory sclerite poorly developed – variable. **Posterior circlet**: 120–123 rows of 14–18 hooks (total *ca* 1 900).

Type data. **Holotype**: in ethanol, pharate male adult with pupal cuticle and cocoon as subsidiary material; condition, pupal cuticle in 2 parts, head absent; cocoon with damage to anterior opening; all now in BEEM capsule; label details “HOLOTYPE\ Aust albovelatum\ N. Ashburton R\ 7/1/63 [“3” overwriting “0” or “8”] L.J.D” (handwritten in black ink, ?Dumbleton) (NZAC). **Paratypes**: pinned material, 5 females, on minuten pins; label details all similar and handwritten [by ?Dumbleton] “Bred. 7/1/64. LJ.D\ N. Ahsburton (sic! for “Ashburton”) R.”, “A. albivelatum (sic!)\Dum.\ PARATYPE {F}”, “NZ Arthropod Collection\ {barcode}\ NZAC04022192”, but exact use of capital and lower case letters and periods (“.”) varies with “NZAC04022243”, “NZAC04022249”, “NZAC04022326” as “Holotype” (sic!), “NZAC04022329”; 2 females on points with similar label details as above, but with “NZAC04022241”, “NZAC04022246”; 6 males on minuten pins: label details all similar and handwritten [by Dumbleton] “Bred. 7/1/64. LJD\ N. Ashburton R. {M}”, “A. albivelatum(sic!)\ Dumbleton\ PARATYPE {M}”, “NZ Arthropod Collection\ {barcode}\ NZAC04022205”, but exact use of capital and lower case letters and periods

(".") varies with "NZAC04022211", "NZAC04022212", "NZAC04022214" with "Dum." on same line as species name, "NZAC04022235" with year as "63" and abbreviation "Dum.", "NZAC04022244"; 1 male on point with label details as above, but with "NZAC04022204" with abbreviation "Dum.". Ethanol-preserved material, label details "{M} & {F} 17 pupae\ Holotypes (handwritten in pencil except "Holotype", "Holo" crossed out and replaced with "PARA" and "s" added, Dumbleton)", "A albivelatum (sic!)\ N. Ashburton R\ 7/1/63" (handwritten in pencil, Dumbleton) (NZAC).

Material examined. Type material, 4 large recent collections (Appendix 1), plus some 11 large collections by Dumbleton.

Distribution (Map 1). Not found in the North Island and of restricted distribution in the South Island. **KA**. Kowhai R, NZS11 (SH1 bridge). **MC**. Ashburton Gorge; Ashburton R North Branch (NZS120 Pudding Hill Stm, NZS121 Stour R bridge) and South Branch; Kowai R (Porters Pass); Potts R (Erewhon); Selwyn R (Glentunnel). **SC**. Forest Ck, NZS125 (Rangitata R Valley).

Northernmost record: Kaikoura Coast, SH1, Kowhai River Bridge, KA (latitude S42.41462°); southernmost record: Rangitata River, Mesopotamia, Forest Creek, SC (latitude S43.68515°), from near sea level at Kaikoura, to just over 600 m a s l at Porters Pass. The Kaikoura locality (NZS11), of indisputable *A. albovelatum* material, represents a 185 km northern extension from the range known by Dumbleton.

— / KA, MC, SC / —

In terms of aquatic ecoregions *A. albovelatum* falls into that of High Country.

Etymology. Not specifically stated by Dumbleton (1973), but no doubt in reference to the white coloration of the cocoon with its high anterior collar that enfolds the base of the gills.

Bionomics. *Austrosimulium albovelatum* is not recorded as biting, and the female abdominal tergites are more quadratic and twice as wide as those of the well known biter *A. ungulatum* (*cf* Fig. 72, 82), a strong indicator that *A. albovelatum* is autogenous.

Dumbleton noted that *A. albovelatum* appeared to have only one generation a year. All his collections were in January from the North Ashburton River (exact locations unknown) and larvae and pupae were present in vast numbers on stones. Our collection from the Stour River (NZS121) was similar, early in December and many pupae had emerged; again, all indicative of univoltinism. A collection (NZS121a) at the Stour River (November, 2011) returned few larvae, in agreement with the above.

The normal habitat of *A. albovelatum* is an open river bed with algal-free stones and a velocity range in the order of 0.80–1.00 m/s (Fig. 457–458). The Stour River Bridge locality was unusual (Fig. 456) in that it was of deep, fast water with large boulders. The immature stages occurred in large numbers in the full force of the current on the upstream sides of boulders.

Dumbleton found *A. albovelatum* occasionally associated with *A. tillyardianum*, as did we, but also *A. multicorne*. At the Pudding Hill locality (NZS120) (Fig. 457) a single pupa assignable to *A. stewartense* was recovered as well as numerous adults of *A. ungulatum*.

Remarks. With one major exception, our collections duplicated well the range given by Dumbleton, i.e., Canterbury Foothills, from Porters Pass to North Ashburton River system, with a limited altitudinal range 250–616 m a s l. The exception was unquestionable material (final instar larvae and a pupa) from the Kowhai River Bridge, Kaikoura (NZS11). The High Country aquatic ecoregion of Harding & Winterbourn (1997a, b) extends out to the coast at Kaikoura: we make this comment too in relation to distribution of *A. ungulatum*. Kowhai River is of short length, flowing rapidly off the Seaward Kaikoura Range, and the water was still relatively cool (14°C) even at entry to the sea (Appendix 1). An expectation then is that *A. albovelatum* will occur in suitable habitats between the Kowhai River and the Torlesse Range (Porter Pass).

From the small amount of data available, *A. albovelatum* appears to be associated with a narrow range of cool water, 11–14°C. An exception to that is Forest Creek, Mesopotamia (NZS125), where by mid-day in December, the temperature of water was 18.4°C. Similar to other localities of *A. albovelatum*, this creek arises from winter snow packs in the Sinclair Range, but then flows over a gravel bed in a braided fashion; it is dry at the height of summer. Material from the collection was later instar larvae and pupae and agrees well with the suggested univoltine life cycle.

This is a distinct species with unique pupal cocoon characters. On morphological characters alone, placement of *A. albovelatum* in the *tillyardianum*-subgroup is moot. Male genitalia and other structures indicate that *A. albovelatum* may have close relationship with the *ungulatum* species-group, specifically the *unicorne*-subgroup, or at least be sister to the *tillyardianum*-subgroup. Without exception *ungulatum* species-group males possess 2 spines on a narrowly tapered gonostylus (Fig. 136–142). Most of those in the *australense* species-group have 3 spines apical on an angulate gonostylus. Generally the *tillyardianum*-subgroup possess 3; however *A. dugdalei* and *A. multicorne* have 2, but the gonostylus is more angulate. *Austrosimulium albovelatum* has 2 spines (occasionally a small 3rd) and a tapered gonostylus. Males have a pronounced keel on the ventral plate, not otherwise particularly well developed in the *australense* species-group, but common in that of the *ungulatum* species-group (e.g., Fig. 128–138). For the female, *A. albovelatum* possesses a narrowed genital fork (Fig. 110), similar to that of *A. tillyardianum* (Fig. 117) and not at all similar to those of the *ungulatum* species-group in which the genital fork is broad (Fig. 118–125).

Importantly, a diagnostic character for the *ungulatum* species-group is the presence of ocular setae posterolateral on the pupal eye sheath (Fig. 196, 199). The *australense* species-group lacks any such structure in that position (Fig. 197,198, 200, 201), with the exception, however, of *A. albovelatum* that possesses there a small trichoid sensillum (Fig. 204).

Notwithstanding the above, *A. albovelatum* lacks grapnel hooks on sternite IX of the pupa in agreement with others of the *tillyardianum*-subgroup. Further, the accessory sclerite on the semicircular sclerite of *A. albovelatum* larvae is normally expanded and emarginated, as found in the *australense* species-group. In the *ungulatum* species-group this semicircular sclerite is tapered.

The cocoon of *A. albovelatum* is also at variance with others of the *tillyardianum*-subgroup in that it is of composed of thick white silk (Fig. 162) that bears a marked resemblance to the cocoon silk of *A. unicorne* (Fig. 177). The 2 dorsal ridges of *A. albovelatum* cocoons bear some resemblance to those exhibited by *A. bicorne* and *A. tonnoiri*. Anteriorly, however, those of *A. albovelatum* are directed laterally and around the gill horn.

Strict consensus morphological cladistic analysis (Fig. 505) poorly resolved the majority of the *tillyardianum*-subgroup. Majority Rule (Fig. 506) was little better, with *A. albovelatum, A. extendorum, A. stewartense* and *A. laticorne*, still unresolved. The remaining species, however, are resolved with moderate to good support.

In the molecular analysis, *A. albovelatum* is deeply embedded in the unresolved and concatenated *tillyardianum*-subgroup (see mid right Fig. 508a, 508b), and little further comment can be made. However, with no good molecular indication that this species is more closely related to the *ungulatum* species-group, could the morphological characters that indicate this be relationship reversals?

Austrosimulium (*Austrosimulium*) *alveolatum* Dumbleton, 1973 new status

Figures: female, 27, 53, 73, 93, 111; male,16, 18, 129; pupa and cocoon, 146, 163, 181, 205, 220, 241, 258, 271, 289; larva, 308, 325, 354, 370, 387, 406, 423, 440; habitat, 459, 460; Map 2.

laticorne alveolatum Dumbleton, 1973: 522 (description pupa, cocoon; *Austrosimulium* (*Austrosimulium*)). Crosby 2006:74 (key). Adler & Crosskey 2012: 20 (world inventory).

alveolatum: Death 1995: 461 (*Austrosimulium*, probable misidentification, with unsupported status change).

Diagnosis. A larger species. **Female**: 2nd antennal flagellomere wider than long; tarsal claw with well developed heel; hind basitarsus with row of stout setae; abdominal tergite II 2.5× wider than long, tergites III–V wider than long; genitalia, hypogynial valves with distinct inner edge. **Male**: row of stout setae on hind basitarsus poorly defined. **Pupa**: thoracic cuticle with spherical tubercles in open groups, with paramedial ridge; gill with black elongated horn with some 36–40 non-tapered filaments; abdominal sternite IX lacking grapnel hooks. **Cocoon**: slipper-shaped, of high profile, closely applied to pupa, fabric coarsely woven with marked alveoli, sometimes as quadratic cells with high sides. **Larva**: pale; head elongated; apotome pale, posteromedial and posterior head spots distinct; ventral tubercles not markedly developed; anal sclerite substantial, accessory sclerites flared with marked emargination.

Adult female (based on 8 reared specimens from Lake Heron). **Body**: general colour in ethanol dark brownish-black; total length 2.5–2.6 mm. **Head**: width 0.66–0.68 mm; depth 0.42–0.44 mm; postocciput black, vestiture of sparse, short black hairs; frons dark brown-black; frons width : head width ratio 1.0 : 4.5. **Eyes**: interocular distance 0.15–0.17 mm; ommatidia diameter 0.012 mm; *ca* 33 rows across and 47 down at mid-eye. **Clypeus**: dark brown, pale medioventrally; width 0.19–0.21 mm; vestiture of sparse black and pale hairs. **Antennae** (Fig. 18): total length 0.49–0.54 mm; scape and pedicel dark, flagellomeres lighter; 2nd flagellomere wider than long and shorter than remainder. **Mouthparts**: markedly bimodal in expression, from 0.50× length of head depth to some 0.65× length of head depth; cibarial cornuae not markedly sclerotised, sculpture lacking (Fig. 27); mandibles in smaller mouthparts with 30 small even inner teeth apically, 10 irregular teeth medially; laciniae with 13 inner teeth and 18 outer teeth; maxillary palp, total length 0.46 mm, 3rd article dark brown, remainder lighter, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.7 : 0.9, sensory vesicle spherical, poorly developed, <0.3× 3rd article width, opening 0.5× vesicle width.

Thorax: length 1.2–1.8 mm; width 0.81–87 mm; in ethanol, postpronotal lobes paler than scutum; scutum evenly dark reddish-brown, vestiture of sparse recumbent hairs, presutellar depression with markedly sparse longer darker hairs and no other vestiture; scutellum slightly paler than scutum, vestiture of a few long black hairs and pale hairs laterally; postnotum concolorous with scutum; pleuron and pleural membrane concolorous with scutum. **Wings**: length 2.4–2.9 mm; width 0.11–0.14 mm. **Halteres**: dark tan. **Legs**: overall yellowish-grey with darker regions at articulations; hind basitarsus 8.7× as long as its greatest width, with ventral row of stout setae; tarsal claws (Fig. 53) strongly curved with well developed heel.

Abdomen (Fig. 73): abdominal scale finely connected across midline, dark brown with fine paler hairs, not greatly extended; tergite II, darkly pigmented, except on either side of median region giving appearance of emargination, 3.5× wider than long, tergite III 2.0× as wide as long, tergite IV quadratic, tergite V marginally triangular in shape, tergite VI 2.2× as wide as long, tergite VII markedly narrowed, 4.0× as wide as long. **Genitalia** (Fig. 93, 111): Sternite VIII markedly pigmented medially along anterior edge forming distinct X-shape, vestiture of hexagonal arrays of microtrichia; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and microtrichia, median edges markedly set off from remainder of valve (but variable), lacking vestiture, smoothly concave, broadly rounded posteroapically; genital fork with anterior arm broad and evenly pigmented, lateral membranous region not extensive, lateral arms with small knee-joint, lateral apodeme cone-like, flange angulate posteriorly; anal lobes and cerci both broadly rounded in lateral view and black; spermatheca ovoid, dark, clear area at junction of duct small.

Adult male (based on numerous reared specimens from Lake Heron). **Body**: general colour black; total length 2.4–2.7 mm. **Head** (Fig. 16): width 0.81–0.82 mm; depth 0.58–0.66 mm. **Eyes**: upper ommatidia dark red, diameter 0.028 mm, *ca* 26 across and 21 down; lower ommatidia dark brown, diameter 0.011 mm, *ca* 28 across and down. **Clypeus**: dark brown; vestiture of very sparse fine hairs; width 0.15 mm. **Antennae**: total length 0.51–0.57 mm; evenly blackish-brown, 1st flagellomere elongated, *ca* 2× as long as wide, remainder subequal in size. **Mouthparts**: poorly developed; length bimodal, 0.22× and 0.33–0.47× head depth; mandibles insubstantial, broadly tapered with apical hairs; laciniae, finely tapered apically with terminal hairs; maxillary palp dark brown, length 0.51–0.53 mm, proportional lengths of 3rd, 4th, and 5th articles *ca* 1.0 : 0.7 : 1.2, sensory vesicle irregular in shape, markedly small, occupying 0.30× 3rd article width, opening 0.3× vesicle width; 3rd article markedly tubular.

Thorax: length 0.8–1.2 mm; width 0.53 mm; scutum evenly black, vestiture of fine recumbent pale hairs, prescutellar depression with sparse long black hairs; scutellum concolorous with scutum with similar long black hairs; postscutellum concolorous with scutum. **Wings**: length 2.4–3.4 mm, width 1.1–1.2 mm. **Halteres**: tan. **Legs**: dark yellow, black at articulations; hind basitarsus 5.1× as long as greatest width, row of stout setae poorly defined; tarsal claw grappling pads with *ca* 18 hooks.

Abdomen: tergites dark brown, sternites less so. Abdominal scale narrow as normal, but continuous across dorsum, hairs not markedly extended posteriorly; remaining tergites typical, occupy whole width of dorsum. **Genitalia** (Fig. 129): similar to those of *A. laticorne* (Fig. 132), gonocoxites the same; gonostyli more substantive, as are the apical spines; ventral plate with markedly low median keel, even vestiture of fine long hairs, width 1.5× length, bluntly cone-shaped posteriorly, convex anteromedially, angulate laterally and indented, basal arms finely tapered; median sclerite moderately developed, broad, T-shaped posteriorly; parameres markedly poorly developed.

Pupa (Fig. 146, 163). Body: length, male 2.3–2.7 mm, female 2.7–2.9 mm; width, male 0.89 mm, female 1.1 mm; overall colour dark brown. **Head**: cephalic plate of male 2.6× as long as wide, markedly tuberculate on upper frons (Fig. 220); that of female 1.8× as long as wide, sparsely tuberculate, if at all, and markedly concave (Fig. 205); pale muscle scars distinct, more so in male. Facial setae present, 1 on each side between antennal bases; 2 short epicranial setae present on margin of ocular sheath at antennal sheath mid length; all setae small and difficult to observe; ocular setae absent. **Thorax** (Fig. 241): dorsum coarsely tuberculate; anterodorsal edge W-shaped and markedly crenulated; tubercles spherical, distinct, in open groups of 5 or 6, forming dense trident-shaped pattern (as for *A. dugdalei* and *A. tillyardianum*, Fig. 234, 236 respectively); dorsocentral setae trichoid. **Gills** (Fig. 258, 271): horn variable, moderately elongated, *ca* 2.8–3.0× as long as greatest width; flattened, light yellow base, remainder black, narrow basally then expanded to mid length and curved smoothly to bluntly rounded apex, trabeculate basally, scobinate elsewhere, edges of horn variously notched (Fig. 258) even on same specimen; filaments 36–40, arising from both sides of broader part of horn, not from edges, narrow non-tapered, length 0.50–0.55 mm, light yellowish-brown, surface finely, distinctly annulated (Fig. 289). **Abdomen**: grapnel hooks absent from sternite IX.

Cocoon (Fig. 146, 181): fabric reticulated, variable from deep honeycomb-like cells (alveoli) with walls (0.3 mm high) arising from edges of alveoli, or with just distinct aveoli; slipper-shaped, of substantial appearance, lateral edges vertical; closely applied to pupa irrespective of substrate; pupal thorax well covered dorsally and anteriorly by higher than usual anteroventral collar, anterior opening oval.

Larva (based on topotype material and from Lake Heron). **Body** (Fig. 308): evenly pale brown, no indication of colour sexual dimorphism; total length 4.8–5.8 mm. **Head** (Fig. 325): bicolorous, pale creamy yellow to translucent with dark head spots and irregular grayish pigmentation dorsally; length 0.62–0.70 mm, width 0.52–0.58; distance between antennal bases 0.22–0.30 mm; lateral margins of head subparallel, slightly convex posteriorly; anterior apotome pale, head spot pattern marked, anteromedial spots positive brown, posteromedial spots lightly fused and darker brown, anterolateral spots pale but positive, 1st and 2nd posterolateral spots neutral; posterior edge of apotome well pigmented, continuous with posterior genae; irregular grayish pigmentation anterior of median head spots variably occurring elsewhere; ecdysial lines sinuous, narrowest anterior of stemmata, broadly rounded posteriorly; postocciput well developed with fused cervical sclerites, dark. **Antennae** (Fig. 370): basal article dark brown, medial and apical articles paler, total length 0.38 mm, extended well beyond apex of fan stem, proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.3 : 2.2, apical article 1.7× length of basal 2 articles; basal articles distinctly ovoid, medial article 0.3× length of basal article. **Labral fans**: stem light brown; 36–40 fine rays, length 0.56 mm, width 0.007 mm; distinct pattern of microtrichia with longer microtrichia 1.3× longer than ray width, separated by *ca* 12 smaller microtrichia of similar size. **Postgenal cleft** (Fig. 387): broadly inverted U-shaped, posterior tentorial pit region markedly sclerotised and pigmented, suboesophageal ganglion and ventral nerve cord markedly dark grey. **Postgenal bridge**: 1.8× longer than hypostoma, pale and concolorous with genae, elongated posteroventral muscles spots light brown; genae with irregular grayish-brown pigmentation. **Hypostoma** (Fig. 406): median and lateral teeth sharp; median tooth slightly more prominent than lateral teeth; 2 sublateral teeth subequal in size to median tooth, middle tooth 1/2 size of others; 2 paralateral teeth, outer tooth smaller; teeth not markedly concealed by anterior margin of hypostoma, lateral serrations poorly expressed if at all; 4 hypostomal setae each side. **Mandibles** (Fig. 423): outer teeth not markedly developed; apical tooth distinct, but not markedly so, as are also subapical teeth, *ca* 10 spinous teeth; sensillum and serrations not markedly developed; blade region elongated, smooth and slightly convex. **Thorax** (Fig. 354): thorax light brown, barely wider than anterior abdomen; mature pharate pupal gills with horn broad, covered in filaments directed ventrally, that then curve broadly anteriorly. **Abdomen**: anterior abdomen light brown, intersegmental regions slightly paler, posteroventral abdomen evenly pigmented; ventral tubercles distinct, but not marked. **Anal sclerite** (Fig. 440): darkly pigmented and substantial, median region tapered posteriorly; anterior arms not markedly flared, but emarginated, interarm struts substantial, posteroventral arms smoothly tapered, continued as clear cuticle between accessory sclerites and circlet of hooks; semicircular sclerite substantial with accessory sclerites well developed and emarginated. **Posterior circlet**: 97–99 rows, 15–17 hooks (total *ca* 1 560).

Type data. **Holotype**, in ethanol, pharate female adult, pupa, and cocoon; condition superb, but with slight damage on left posterior of cocoon, label details “HOLOTYPE A. laticorne\ alveolatum (cocoon)\ Porters Pass [920 m], Stone\ 4-3-[19]58)” (handwritten in black ink, ?Dumbleton) (NZAC). **Paratypes**, in ethanol, pupae and cocoons, label details as for holotype. Pharate female adult, pupal exuviae, and cocoon, label details “Barrosa Stm, 610 m.,\ 11.i.61, L. J. Dumbleton” (NZAC).

The collection from which Dumbleton chose the holotype (Porters Pass, 920 m, 4 March 1958) has a label to the effect that the type was removed. There is also a label that indicates those specimens are a “type series”, thus by definition paratypes, and they are here so regarded and now labelled as such. The status of the original paratype pupal cocoon from Barrosa Stream, 11 January 1961, designated by Dumbleton (1973) does not change.

Material examined. Holotype, paratypes, plus ethanol-stored collections in the Dumbleton material at NZAC. 5 newer collections, in particular 2 from Emily Stream, Lake Heron (NZS122, 1122a) that were extensive and provided all stages, including reared adults (Appendix 1).

Distribution (Map 2). Markedly restricted. **MC**. Lake Heron (NZS123 Emily Stm, NZS136 Gentleman Smith Stm, NZS122, 122a Olliver Stm); North Branch Ashburton R, NZS15 (Thompsons Track); Porter R; Porters Pass summit stm.

Northernmost record: Porters Pass, summit stream, MC (latitude S43.29610°); southernmost record: North Ashburton, Lake Heron, Olliver Stream (latitude S43.49474°), from 250 to about 900 m.

—/ MC / —

The restricted distribution is, with one exception, fully within the High Country aquatic ecoregion. The exception is at the western limit of the East Coast Plains ecoregion.

Etymology. Not explicitly mentioned by Dumbleton (1973), but no doubt in reference to the markedly alveolate (honeycombed) nature of the cocoon fabric.

Bionomics. Dumbleton’s collection data indicate that there might be two generations a year. He collected from the stream at the summit of Porters Pass over three years at various times. Larvae were present in December, larvae and pupae in January, and then in May, he obtained all stages and managed to rear adults. This we consider indicative of a second generation. Our recent collections do not add greatly to this scenario, except that the Emily Stream collections (NZS122, 122a) taken three weeks apart in December did show that the majority of final instar larvae noted in the first collection had pupated and many emerged by the second collection. Dumbleton, considering both *A. laticorne* and *A. alveolatum* together, was of the opinion that there was more than one generation a year. Similarly, he noted that neither *A. laticorne* nor *A. alveolatum* females were known to bite. The relatively large tergites (Fig. 73) of the female are also indicative of non-biting.

Bulk rearing of large numbers of pupae from Emily Stream (Fig. 459) showed that the sex ratio of *A. alveolatum* males to females was 1 : 1. Dumbleton (1973) noted that there was no apparent separation in the biology of *A. laticorne* and *A. alveolatum*. Both can occur in large numbers when encountered, and larvae and pupae are found on perched stones. Associated simuliids were *A. australense, multicorne*, and *tillyardianum*. In Gentleman Smith Stream (Fig. 460) *A. alveolatum* occurred at low frequency with the above species.

Remarks. Stuart & Hunter's (1995, 1998) work on cocoon spinning in simuliids and that on *A. australense* (Stuart 2002) showed cocoon-spinning behaviour to have a clear phylogenetic component. The honeycomb structure of the cocoon fabric of *A. alveolatum* is taken here as indication of specific status, still the species is closely related to *A. laticorne*. Further, the anal sclerite and semicircular sclerite of the larvae are markedly more substantial than those of *A. laticorne*, and the larval head of *A. alveolatum* is more elongate and parallel-sided (*cf* Fig. 325, 329). The cephalic apotome of *A. alveolatum* is less rounded posteriorly than that of *A. laticorne*. The larval antenna of *A. alveolatum*, while of similar proportions to that of *A. laticorne*, has more swollen basal articles (Fig. 370, 374).

While we are comfortable changing the status of *A. alveolatum* to that of full species, there is a strong likelihood that it actually comprises a complex. The basis for this assertion is that the cocoon fabric ranges from the unique hexagonal cells of the cocoon from the holotype known only from Porters Pass, to the more common, but still markedly alveolate condition, which at its less developed state approaches that of some populations of *A. laticorne.* Further, the marked bimodal size of the female mouthparts indicates a complex.

In the morphological cladistic analysis, with Majority Rule (Fig. 506), *A. alveolatum* is sister to *A. tillyardianum* and the two together sister to *A. dugdalei* + *A. multicorne*. The sister relationship with *A. tillyardianum* was unexpected given the marked difference in the pupal gills of that latter species (*cf* Fig. 271, 279), but support for the relationship is only moderate.

Molecular analysis of *A. alveolatum* places the species in unresolved relationship with *A. laticorne* and *A. tillyardianum* (see top left Fig. 508a, 508b). With the poor resolution of the *tillyardianum*-subgroup, little more can be said.

Austrosimulium (*Austrosimulium*) *dugdalei* new species

Figures: female, 20, 28, 54, 74, 94, 112; male, 130; pupa and cocoon, 147, 164, 182, 194, 206, 221, 234, 242, 272, 290; larva, 309, 326, 355, 371, 388, 407, 424, 441; habitat, 465; Map 6.

For presence in North Island, as *multicorne* Tonnoir, 1925: 254 (*Austrosimulium*). Gurr 1953: 81 (distribution). Dumbleton 1963a: 334 (as subgenus *Austrosimulium* (*Austrosimulium*), in *australense* group). Dumbleton 1964b: 35 (relationships, distribution). Dumbleton 1973: 516 (*multicorne multicorne)*. Crosby 2006: 74 (key). Adler & Crosskey 2012: 20 (world inventory).

Diagnosis. **Female**: thorax not markedly domed; tarsal claw lacking basal tooth or heel, hind basitarsus with row of stout setae; abdominal tergite II not markedly broad, tergites III–V small and rounded. **Male**: with row of stout setae on basitarsus; gonostylus markedly tapered with 2 terminal spines. **Pupa**: thoracic cuticle with rounded tubercles in groups, ungrouped anterior row marked; gill with short rounded black horn (slightly variable) with 40–55 long finely tapered filaments, some bifurcated; abdominal sternite IX lacking grapnel hooks. **Cocoon**: slipper- to shoe-shaped, of low profile, finely woven, slightly flared basally, opening ovoid with irregular edge, fabric finely woven, non-alveolate. **Larva**: overall brown; frontolabral apotome markedly brown, posteromedial and posterior head spots distinct, genae, hypostoma, and cleft areas dark brown.

Adult female (3 reared specimens). **Body**: general body colour in ethanol dark brownish-black, abdomen grayish, when dried, thorax with silvery pruinose appearance; total length 3.0 mm. **Head**: width 0.7–0.75 mm; depth 0.50–0.51 mm; postocciput black, vestiture of sparse, short black hairs; frons dark brown-black; frons width : head width ratio 1.0 : 25. **Eyes**: interocular distance 0.16–0.18 mm; ommatidia diameter 0.014 mm; *ca* 33 rows up and 36 across at mid-eye. **Clypeus**: width 0.22–0.23 mm; dark brown with pale ventromedial region; vestiture of sparse black and pale hairs. **Antennae**: length 0.5–0.6 mm; evenly medium brown. **Mouthparts**: substantial, 0.6× length of head depth; cibarial cornuae broad, markedly pigmented apically, fluting and sculpture poorly developed, medial region convex; mandibles with 33 inner teeth, increasing in size towards apex, 8 lateral teeth markedly small; laciniae with 13 inner teeth and 19 outer teeth; maxillary palp, total length 0.58 mm, 3rd article dark brown, remainder lighter, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.8 : 1.5, sensory vesicle spherical, 0.3× 3rd article width, opening 0.3× vesicle width; cibarial cornuae substantial with fine sculpting, lacking fluting, median depression broad and convex (Fig. 28).

Thorax: not markedly domed; length 1.3 mm; width 0.95 mm; in ethanol, postpronotal lobes marginally paler than scutum; scutum evenly dark brown, vestiture of even fine recumbent hairs, presutellar depression hairs few, no vittae visible in ethanol, but when dried with a median and 2 lateral vittae overlain with silvery pruinosity; scutellum pale, vestiture of a row of long black hairs and pale hairs laterally; postnotum, pleuron, and pleural membrane concolorous with scutum. **Wings**: length 3.1 mm; width 1.4 mm. **Halteres**: beige. **Legs**: bicolorous, yellowish-brown with darker brown bases to femoral, tibial, and tarsal segments; hind basitarsus about 6× as long as greatest width; with row of stout setae; tarsal claws smoothly curved with moderate basal heel (Fig. 54).

Abdomen (Fig. 74): overall grayish-brown; abdominal scale dark brown with fine pale hairs, not greatly extended; tergite II not markedly broad, tergites III–V small and rounded; vestiture of coarse dark hairs. **Genitalia** (Fig. 20, 94, 112): sternite VIII markedly medium brown medially, sharply so along anterior edge producing X-shaped mark, vestiture of coarse black hairs posterolaterally; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and triads of microtrichia; median edges of hypogynial valves ridged, slightly curved to subparallel, broadly rounded posteroapically; genital fork with anterior arm cone-shaped, slightly fluted anteriorly, posterolateral extension simple, poorly pigmented; anal lobes and cerci both broadly rounded in lateral view, black; spermatheca ovoid, clear area at junction of duct markedly small.

Adult male (holotype and 2 other reared specimens). **Body**: general colour, in ethanol, brownish-black, when dried black; total length 2.4 mm. **Head**: width 0.84 mm; depth 0.60 mm. **Eyes**: ommatidia dark reddish-orange (black when dry); upper ommatidia larger than normal, diameter 0.028 mm, *ca* 24 across and 18 down; lower ommatidia, diameter 0.011 mm, *ca* 27 across and 30 down. **Clypeus**: dark brown, pollinose under some lighting; vestiture of coarse black hairs; width 0.17 mm. **Antennae**: total length 0.50 mm; all evenly dark brown. **Mouthparts**: poorly developed; length 0.26× head depth; mandibles insubstantial, broadly tapered, tattered apically; laciniae, finely tapered apically with terminal hairs; maxillary palp medium brown, 0.5 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 0.8 : 1.5, sensory vesicle irregular in shape, occupying 0.3× 3rd article width, opening 0.3× vesicle width.

Thorax: length 0.92 mm; width 0.8 mm; scutum jet black, vestiture of sparse fine recumbent pale hairs, brassy yellow when dried; scutellum concolorous with scutum, vestiture of sparse long black hairs; scutellar depression with sparse long black hairs; postscutellum concolorous with scutum; postnotum concolorous with scutum; depression, scutellum, and postnotum showing pollinosity under some lighting; pleural regions dark grayish-brown. **Wings**: length 2.6 mm, width 1.3 mm. **Halteres**: tan. **Legs**: overall grayish-brown, with darker brown femoral, tibial, and tarsal bases; hind basitarsus 4.6× as long as its greatest width, row of stout setae poorly developed; tarsal claw grappling pads with 23 teeth.

Abdomen: basal scale markedly developed, hairs extended to segment III; dorsum blackish-brown, vestiture of long sparse golden hairs. **Genitalia** (Fig. 130): gonocoxites 1.5× longer than basal width, dark brown anteriorly, pale medially, with coarse black hairs evenly distributed except medially, where vestiture consists of arrays of microtrichia; gonostyli *ca* 2.0× longer than basal width, rapidly tapered, apically with 2 (rarely 3 on one side) substantial spines, 1 less so; ventral plate 1.8× wider than long, with low median keel, not extended to plate apex, moderately dense vestiture of fine hairs, rounded posteriorly, convex anteromedially, basal arms short but substantial; median sclerite poorly developed, broad, slightly T-shaped posteriorly (difficult to observe); parameres poorly developed.

Pupa (paratypes and others). **Body length**: male 2.8–3.2 mm, female 2.8–3.5 mm. **Head**: cephalic plate dished posteriorly, that of male markedly tuberculate on upper frons (Fig. 221), that of female tuberculate laterally, markedly concave (Fig. 206). Frontal setae absent; facial setae present, 1 on each side between antennal bases; 2 short epicranial setae on margin of ocular cuticle under antennal sheath at mid length; all difficult to observe. **Thorax** (Fig. 234, 242). Dorsum coarsely granulated; tubercles raised, circular, distinct, generally contiguous in circular groups, evenly arranged, forming ill-defined trident pattern (median line along ecdysial line, posterior transverse line, and 2 lateral, longitudinal lines arising on each end of posterior line), marked band of ungrouped tubercles vertically immediately posterior of gill base; dorsocentral setae trichoid. **Gills** (Fig. 272): horn brown basally, remainder black, length 2.2–3.0× maximum width, variable; sides slightly convex, rounded apex; filaments 43–55, originate from all over horn, markedly longer than those of *A. multicorne*, length up to 1.9 mm, width 0.018 mm basally, light yellow brown, only slightly tapered from mid-length; rarely bifurcated; surface finely annulated (Fig. 290). **Abdomen** (Fig. 194). Grapnel hooks absent from sternite IX.

Cocoon (Fig. 147, 164, 182): fabric light brown, finely woven and parchment-like with longitudinal crinkles, not alveolate; slipper-shaped, well-developed anterior lip, not close fitting, on leaves and stones may be subcircular and flattened (patellate), on grasses more elongated; anterior opening subcircular, with irregular edge over thorax; fabric may incorporate fine particles from substrate.

Larva (paratype final instars). **Body** (Fig. 309): overall brown, more grayish anteriorly; total length 5.6–6.7 mm, larger specimens probably female. **Head** (Fig. 326): variable colour ranging from extremely dark to medium brown, overall dark brown, females probably darker; pale at extreme anterior apotome, markedly dark edges at labral fan bases, darker posteriorly and ventrally (earlier instars extremely dark): length 0.76–0.80 mm, maximum width 0.68–0.72 mm; distance between antennal bases 0.40 mm; lateral margins of head smoothly convex posteriorly, converging noticeably anteriorly; head spot pattern distinct, anteromedial spots slightly negative with darker surroundings pale brown, posteromedial spots fused and dark brown positive, 1st and 2nd anterolateral spots slightly negative surrounded by fused brown pigmentation, 1st and 2nd posterolateral spots positive and fused to brownish-black posterior edge of darkly pigmented apotome, continuous with posterior genae; ecdysial lines distinct and not markedly sinuous; cervical sclerites separate from postocciput, but markedly extended anterolaterally. **Antennae** (Fig. 371): dark brown basally, pale apically; total length 0.33–0.37 mm, well extended beyond apex of fan stem; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.4 : 2.1; apical article narrow, 1.5× length of wider basal 2 articles, medial article 0.4× length of basal article. **Labral fans**: stem light brown; 29–33 fine rays, length 0.7 mm, width 0.009 mm; distinct pattern of microtrichia, longer microtrichia 1.8× longer than ray width, separated by 14–17 smaller irregular length microtrichia. **Postgenal cleft** (Fig. 388): broadly inverted U-shaped, with apex irregular, posterior tentorial pit region markedly sclerotised and pigmented. **Postgenal bridge**: 1.5× longer than hypostoma, medium brown and concolorous with genae, paler medially, elongated posteroventral muscles spots not obvious; genae with irregular darker pigmentation. **Hypostoma** (Fig. 407): median and lateral teeth sharp; lateral teeth slightly more prominent than median tooth; 2 sublateral teeth subequal in size to median tooth, middle tooth 1/2 size of others; 2 paralateral teeth, lateral tooth smaller; all teeth largely concealed by anterior margin of hypostoma, 3 or 4 poorly developed lateral serrations, variable; 5 or 6 hypostomal setae each side. **Mandibles** (Fig. 424): apical tooth distinct, as are preapical teeth; *ca* 10 spinous teeth; serration well developed, single poorly developed sensillum, but variable; blade region smoothly convex. **Thorax** (Fig. 355): light grey; mature pharate pupal gills with brown base and black horn, 10–12 filaments arising in dense formation, directed posteroventrally, to then curve broadly anteriorly; anteriorly slightly overarched by prothoracic pigmentation. **Abdomen**: evenly dark grayish-brown, darker posteriorly; ventral tubercles distinct. **Anal sclerite** (Fig. 441): median region not markedly developed, interarm struts not distinct and partially fused to median region; anterior arms flared, slightly emarginated; posterior arms short; semicircular sclerite substantial with clear cuticle evident; accessory sclerites flared and markedly emarginate. **Posterior circlet**: 100–103 rows of 15–17 hooks (total 1 500–1 750).

Type data. **Holotype**: male adult, reared, minuten pinned on pith strip, with pupal exuviae and cocoon as subsidiary material on point underneath; label details "*Austrosimulium* (*A.*) *dugdalei*\ Craig, Craig & Crosby", "HOLOTYPE [in red]{M}, NZ, NI, TO,\ SH1. Desert Rd. Trib Mangaio Strm.\ S39.31010 E175.73741. 1060m a s l\ 19-xi-2008. NZN48c. Col. D. A. Craig" (NZAC). **Paratypes** (4): 1 female adult, reared; label data as for holotype but with "PARATYPE {F}" and "3-iii-2007, NZN48b". In ethanol, 1 female pupa and cocoon plus 2 final instar larvae, label details as above, but with "PARATYPES" and circular label with faded yellow rim "Para-\type" (NZAC).

Material examined. Type material. 1 collection by Tonnoir (Ohakune; NZAC); 5 collections by Dumbleton (including 2 slide mounts) from the "Chateau", Mount Ruapehu (then as *A. multicorne*), from the Dumbleton Collection (NZAC); 15 newer collections (Appendix 1), all from TO area, or immediately adjacent (NZAC, UASM, BMNH).

Distribution (Map 6). Restricted to the Taupo area (TO), with one locality in the Rangitikei area (RI). **North Island**. **TO**. Makakikatoa Stm; Mangaio Stm, NZN48, 48a, 48b, 48c; Mangatepopo Stm, NZN107 (SH47 bridge); Mangatepopo Stm trib, NZN105; Mangatoetoenui Stm, NZN49, 49a, 49b; Mangawhero R, NZN92 (upper); Mt Ruapehu, NZN125 (Waikare Stm trib, Silica Rapids), Whakapapa; Mt Tongariro, Soda Springs seepages, NZN124 (Mangatepopo Stm); Ohakune; Pangarara Stm; Papamanuka Stm, NZN106 (SH47 bridge); Tongariro R, NZN23 (Walkway). **RI**. Hautapu R, NZN85 (SH1 bridge).

Northernmost record: Tongariro River Walkway (latitude S39.03084°); southernmost record: Hautapu River, SH1 north of Taihape (latitude S39.64218°). Altitude 481–1 289 m a s l, majority at higher altitudes.

TO, RI / — / —

The distribution falls well into the Taupo Plateau and Volcanic Plateau ecoregions. The Hautapu River record (NZN85) appears to be an outlier since only a single pupa was collected. *Austrosimulium dugdalei* might be found at higher altitudes in the Kaimanawa Mountains ranging to the NE of the Volcanic Plateau aquatic ecoregion.

Etymology. Named after John S. Dugdale, who assisted in the completion of Dumbleton's 1973 publication on New Zealand Simuliidae after Dumbleton's debilitating stroke in 1969, and whose superb illustrations we have used in this revision.

Bionomics. Tonnoir (1925), in a general comment covering *A. multicorne* as understood then, noted that pupae were present from December until March, including at Ohakune (TO). Data from Dumbleton's Chateau Tongariro material on Mount Ruapehu indicate that he reared adults at the end of February and obtained considerable larval and pupal material at the end of November. The exact whereabouts of that locality is unknown. It is possible that Dumbleton's material was from the nearby Silica Rapids where we collected large numbers from a tributary stream (NZN125). Other collections agree fully with these earlier observations and indicate a single extended generation. There may, however, be more than one depending on the conditions at any given locality.

Austrosimulium dugdalei is a higher altitude species (Appendix 1). On the Volcanic Plateau it has a narrow altitudinal range of 900–1 289 m a s l. Although it occurs in cold water (6.4°C) it seems tolerant of temperatures up to 14.5°C.

The typical habitat for immature stages of *A. dugdalei* is a cold water stream/river with good flow. Most water running off the volcanic plateau has hard rocky substrates, but this is not required by the larvae or pupae since trailing vegetation is normally inhabited — in large part tussock (Fig. 465).

There is little reason that *A. dugdalei* will not be more widespread in the volcanic region. However, with an apparent predilection for cooler water, it is unlikely to be found much farther north than the current locality south of Turangi. Nevertheless, the species might occur at altitude in the Kaweka Range to the east and Ruahine Range to the southeast. So far *A. dugdalei* has not been found on Mount Taranaki, which appears to have suitable habitats.

The 2 outlier populations with occasional specimens are the Tongariro River Walkway, just south of Turangi (altitude 500 m a s l, NZN23), and the locality just north of Taihape (altitude 481 m a s l, NZN85). Both these localities were dominated by other simuliid larvae, *A. tillyardianum* and *A. australense*, respectively. Dumbleton, when dealing with *A. dugdalei* (as *A. multicorne*), did not mention any associated species.

Remarks. The populations here described as *A. dugdalei* were originally included in *A. multicorne by* Tonnoir (1925) as the North Island lineage of that species. Neither he, nor Dumbleton. commented on differences in the thoracic tuberculation, pupal gill or cocoon from those of *A. multicorne* from the type locality, Mount Arthur (NN). The pupal gill of *A. dugdalei* is markedly different in the higher number and greater length of the filaments (Fig. 234, 272), and proportions of the basal horn. The pupal thorax of *A. dugdalei* has markedly more tubercles anteriorly than does *A. multicorne* (*cf* Fig. 242, 246). Further, the cocoon, normally patellate, differs from that of *A. multicorne*, which normally has a marked circular opening (*cf* Fig. 147, 151, 164, 169).

Collections indicate that *A. dugdalei* is univoltine — larvae occur in the spring with pupae later in the season. However, larvae have been recovered in March, perhaps indicative of more than one generation, but those collections were at higher altitude.

Austrosimulium dugdalei is sister to *A. multicorne* in the Majority Rule and Shortest Tree analyses (Fig. 506, 507) as we expected. While material was available for CO1 molecular analysis, results from that did not discriminate well between members of the *tillyardianum*-subgroup. However, placement of the *A. dugdalei* haplotype (Fig. 508, 508a mid-right side) was distant from any of the *A. multicorne* haplotypes; perhaps indicative that morphological discrimination of *A. dugdalei* as a separate species is, indeed, justified.

Austrosimulium (*Austrosimulium*) *extendorum* new species

Figures: male, 131; pupa and cocoon, 148, 165, 207, 222, 243, 273, 291; larva, 310, 327, 356, 372, 389, 408, 425, 442; habitat, 466; Map 8.

In part, *stewartense* Dumbleton, 1973: 522 (*Austrosimulium* (*A.*)).
Adler & Crosskey 2012: 20 (world inventory).

Diagnosis. **Pupa**: thoracic cuticle with groups of 4–6 rounded tubercles in a ring, paramedial ridge narrow; gill with black, elongated narrow horn with 15–20 finely-tapered filaments. **Cocoon**: ovoid, patellate, finely woven, opening circular

Adult female (single early pharate specimen). **Head**: width 0.71 mm; depth 0.47 mm; frons width: head width ratio 1.0 : 4.1. **Eyes**: interocular distance 0.17 mm; ommatidia diameter 0.016 mm. **Clypeus**: width 0.19 mm. **Antennae**: length 0.47 mm. **Mouthparts**: 0.59× length of head depth; maxillary palp, total length 0.44 mm.

Adult male (single pharate specimen). **Head**: width 0.79 mm; depth 0.55 mm. **Eyes**: upper ommatidia diameter 0.03 mm, 18–20 across and down; lower ommatidia diameter 0.02 mm, 27–28 across and down. **Clypeus**: width 0.16 mm. **Antennae**: length 0.47 mm. **Mouthparts**: 0.40× length of head depth, markedly insubstantial; maxillary palp, total length 0.38 mm.

Abdomen. **Genitalia**: (Fig. 131). gonocoxites 2.5× longer than basal width, dark brown posteriorly, pale medially, with coarse black hairs on apical 2/3, anteromedially with small crenulations; gonostyli short and broad, *ca* 1.5× longer than basal width, apically with 3 substantial spines; ventral plate with low median keel, even sparse vestiture of fine hairs, plate 2× as wide as long, broadly rounded posteriorly, smoothly convex anteromedially, basal arms well pigmented, not markedly developed; median sclerite markedly poorly developed, broad, not markedly T-shaped posteriorly; parameres poorly developed, barely obvious.

Pupa (6 specimens) (Fig. 148, 165). Body length; male 2.9–3.2 mm, female 2.3–3.1 mm. **Head**: cephalic plate, female (Fig. 207); markedly broad, 1.1× longer than narrowest width, cuticle sparsely tuberculate dorsomedially and laterally, slightly concave; no setae obvious; male (Glendhu, Fig. 222) 1.3× longer than narrowest width, well tuberculated; muscle scars distinct; slightly concave; no setae obvious. **Thorax** (Fig. 243). Dorsum not markedly tuberculate, but with 4–6 tubercles in rings; faint trident pattern, ill-defined row of tubercles well behind gill base; dorsocentral setae, trichoid, small. **Gills** (Fig. 165, 273): Total length of horn and filaments subequal to head and thorax. Gill generally directed slightly upwards and medially; horn markedly elongate, tubular, not flattened, lightly ridged, trabeculate; 8–11× as long as greatest width (at 1/3 length); base light yellow, remainder black; filaments, 25–27, maximum length 1.6 mm, *ca* 3× longer than horn, light yellow brown, finely tapered, occasionally bifurcate, surface finely annulated (Fig. 291). **Abdomen**. Grapnel hooks absent on tergite IX.

Cocoon (Fig. 148, 165): light brown in colour, fabric of fine filaments with overlay of smooth non-alveolate material; patellate (more ovoid that *A. stewartense*), anterior opening circular; marked margin around edge; pupa covered only to posterior scutum.

Larva (based on 3 immature final instars). **Body** (Fig. 310): overall medium reddish-brown; total length 4.9–5.3 mm. **Head** (Fig. 327): (older material) light medium brown; length 0.60 mm, width 0.52; distance between antennal bases 0.27 mm; lateral margins of head subparallel, not markedly convex; head spot pattern barely discernible, neutral to positive; anterior apotome with irregular grey infuscation; ecdysial lines not distinct; postocciput well developed, cervical sclerites not markedly fused. **Antennae** (Fig. 372): total length 0.42 mm, extended well beyond apex of fan stalk, basal article light brown, median article lighter; apical article pale; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.3 : 2.1; apical article 1.6× length of basal 2 articles, medial article 0.3× length of basal article. **Labral fans**: stem clear; 38–42 fine rays, length 0.62 mm, width 0.009 mm; distinct pattern of microtrichia, longer microtrichia 1.8× longer than ray width, separated by 8–12 smaller irregular length microtrichia. **Postgenal cleft** (Fig. 389): broadly inverted V-shaped, with irregular edges and apex, posterior tentorial pit region lightly sclerotised and pigmented; postocciput sclerite distinct. **Postgenal bridge**: 1.5× longer than hypostoma, pale, concolorous with genae, elongated posteroventral muscles spots not obvious; genae with irregular infuscation. **Hypostoma** (Fig. 408): teeth not markedly developed, all obscured by anterior margin of hypostoma; median and outer lateral teeth larger; 1 sublateral tooth as prominent as lateral tooth; 2 sublateral teeth markedly smaller; 2 paralateral teeth small; 3 lateral serrations, variable; 5–7 hypostomal setae each side, variable. **Mandibles** (Fig. 425): outer and preapical teeth not prominent, *ca* 13 spinous teeth; sensillum and serrations complex, on convex base; blade region straight. **Thorax** (Fig. 356): reddish-brown; immature pharate pupal gills with elongate horn; filaments directed almost vertically, before curved broadly anteriorly. **Abdomen**: evenly medium reddish-brown, distinct ventral tubercles. **Anal sclerite** (Fig. 442): anterior arms not markedly flared, median region not distinctly sculpted, markedly broadly cone-shaped, interarm struts substantial; posterolateral arms elongate; semicircular sclerite narrow, accessory sclerite not markedly emarginated. **Posterior circlet**: 104 rows of 14–17 hooks (total *ca* 1 660).

Type data. **Holotype**: pupa in BEEM capsule in ethanol, condition: excellent; label details "*Austrosimulium* (*Austro.*) *extendorum*\ HOLOTYPE, Sawyers Beach, Stewart Is.\ New Zealand S46.83215 E168.08209\ Coll. L. J. Dumbleton, 7-ii-1968?", "Holo-\ type" (round label with red rim) (NZAC). **Paratypes** (9): in BEEM capsules in ethanol, 8 pupae, some in cocoons; label details as for holotype, but with "PARATYPE" and round label "Para-\ type";. 1 microscope slide, female pupal exuviae; label details as above and "Mounted 2009, DA Craig\ PVLP" (NZAC).

Material examined. Type specimens plus pupae and larvae from the type locality, and also Big South Cape Island (NZAC).

Distribution (Map 8). Restricted to Stewart Island. **Stewart Island**. Potted Head ck (Big South Cape I.); Sawyers Beach.

Northernmost record: Sawyers Beach (latitude S46.83215°); southernmost record: Potted Head creek, Big South Cape Island, SI (latitude S47.22837°).

— / SI / —

Sites on Stewart Island fall in the ecoregions of Southeast Forest and Westland Forest.

Etymology. Named for the elongated horn of the pupal gill.

Bionomics. Little is known for *A. extendorum*, but Sawyers Beach Stream is an unusual habitat for Stewart Island and

Dumbleton so commented. Normally, most streams on the island are soft bottomed with granite sand interspersed between moderate-sized boulders, or are narrow and muddy bottomed; hence, larvae of *A. stewartense* are normally on trailing vegetation. At Sawyers Beach, however, the stream flows over cobble (Fig. 466) and Dumbleton found both *A. stewartense* and *A. extendorum* larvae on cobbles right down to high tide mark — also most unusual. We found *A. stewartense* in such situations too (Appendix 1), but not *A. extendorum*. Unusual was that the cobble consisted of a mixture of smooth andersite (fine-grained volcanic rock) and rough, coarse-grained granite. Larvae were never found on the granite. This mimics the Taramakau River, WD (NZS51), and Borland Burn, FD (NZS152), where mixed substrates also lacked larvae (of other species) on granite, but larvae were present on smooth rocks.

Remarks. Dumbleton made a collection in 1968 from Sawyers Beach, the type locality, that included *A. stewartense*, along with the material that we designate here as *A. extendorum*, but he made no comment about the mixed collection, labeling it all *A. stewartense*. Of significance there was an *A. stewartense* pupa that had spun and attached its cocoon alongside one of *A. extendorum* — the differences are marked (*cf* Fig. 165, 170).

Based on gill structure, *A. extendorum* is closely related to *A stewartense*. It can, in the main, however, be distinguished from that species by the elongate, more tubular pupal gill horn, longer filaments and larger filament numbers, and also reduced tuberculation on the female pupal head cuticle (*cf* Fig. 206, 210). Further, the cocoon tends to be more ovoid than the more circular one of *A. stewartense.*

Material for this species is sparse with only pupae from the type locality, also pupae and larvae from Big South Cape Island, off the southwest of Stewart Island, collected by Dumbleton, that we have assigned to *A. extendorum*. Attempts by DAC and REGC to obtain more material of *A. extendorum* from Sawyers Beach failed in 2008 (NZS167) and 2011 — only *A. stewartense* was present.

Similar to other members of the *tillyardianum*-subgroup, morphological analysis places *A. extendorum*, either in an unresolved relationship with *A. albovelatum*, *A. stewartense*, *A. fiordense,* and *A. laticorne* (Fig. 505), or when polytomies are removed (Fig. 507), sister to *A. stewartense*, as morphology indicates. No material was available for molecular analysis.

Dumbleton collected six pupae from Glendhu Bay, Lake Wanaka, all with elongated gill horns of the *A. extendorum* type. Thus we considered material from Glendhu to be that species. Of concern, though, was that the pupal cocoon approached the shape of *A. multicorne*. Further, the stream off Roys Peak was unlike the type locality stream at Sawyers Beach, Stewart Island. Material collected recently from Glendhu Bay (NZS180) does not completely resolve this conundrum, so we leave the taxonomic situation unchanged. However, further work may well show that the Glendhu material is an extreme variant of *A. multicorne*.

Austrosimulium (*Austrosimulium*) *fiordense* Dumbleton, 1973 new status

Figures: female, 19, 29, 55, 75, 95, 113; pupa and cocoon, 149, 166, 183, 223, 244, 274, 292; larva, 328, 373, 390, 409, 426, 443; Map 9.

multicorne fiordense Dumbleton, 1973: 518 (description pupa, *Austrosimulium* (*Austrosimulium*)). Crosby 2006: 75 (key). Adler & Crosskey 2012: 20 (world inventory).

multicorne fiordense. Dumbleton 1970: 20 (Fig. 7, distribution), *nomen nudum*.

Diagnosis. **Female**: tarsal claw lacking basal tooth, but with substantial heel; hind basitarsus with row of stout setae; abdominal tergites III–V variable, wider than long. **Male**: [unknown]. **Pupa**: as for *A. multicorne,* but lacking thoracic ornamentation; gill with black horn 5× longer than width, with *ca* 40 finely tapered filaments. **Larva**: as for *A. multicorne*.

Adult female (based on Darran Mountains material, 1977). **Body**: general body colour in ethanol reddish-brown, probably black in life; total length 2.6–3.4 mm. **Head**: width 0.68–0.73 mm; depth 0.44–0.48 mm; frons width : head width ratio 1.0 : 4.4. **Eyes**: interocular distance 0.16–0.19 mm; ommatidia diameter 0.012 mm; *ca* 33 rows across and down at mid-eye. **Clypeus**: dark brown; width 0.21–0.22 mm; vestiture of sparse black and pale hairs. **Antennae**: total length 0.41–0.50 mm; all evenly pale brown, pedicel larger than flagellomeres. **Mouthparts**: substantial, *ca* 0.5× length of head depth; cibarial cornuae not markedly pigmented, fluting minimal, medially with shallow V-shaped central depression (Fig. 29); mandibles with 28 larger fine inner teeth, plus basally *ca* 20 small-to-minute inner teeth; laciniae with 13 inner teeth and 20 outer teeth; maxillary palp, total length 0.39–0.63 mm, 3rd article dark brown and tapered, remainder lighter, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.9 : 1.5, sensory vesicle ovoid, 0.5× 3rd article width, opening 0.5× vesicle width.

Thorax: length 1.1–1.2 mm; width 0.83–0.92 mm; in ethanol, postpronotal lobes marginally paler than scutum; scutum evenly dark reddish-brown, vestiture of sparse recumbent hairs, scutellar depression with a few long black hairs posteriorly; scutellum slightly paler than scutum, vestiture of a few long black hairs and pale hairs laterally; postnotum concolorous with scutum; pleuron and pleural membrane concolorous with scutum. **Wings**: length 2.3–2.7 mm; width 1.3–1.4 mm. **Halteres**: tan. **Legs**:

yellowish-brown, with darker brown bases to femoral, tibial, and tarsal segments; hind basitarsus *ca* 6× as long as its greatest width; markedly distinct row of stouter setae (Fig. 19); tarsal claws not markedly curved, lacking basal tooth, heel substantial (Fig. 55).

Abdomen (Fig. 75): abdominal scale dark brown with fine pale hairs, not greatly extended; tergite II 3× wider than long, well emarginated anteriorly, tergites III–V semiquadratic, wider than long, tergite VI and tergite VII much wider than long, vestiture of sparse hairs. **Genitalia** (Fig. 95, 113): sternite VIII pigmented evenly, more so along anterior edge, vestiture of sparse fine black hairs posterolaterally, microtrichia in rows posteromedially; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and microtrichia; median edges of hypogynial valves smoothly concave, broadly rounded posteroapically, markedly strengthened medially; genital fork with anterior arm not markedly broad, anterior apex knobbed, posterolateral arm with knee-bend poorly developed, apodeme thumb-like, lateral plate rounded laterally, not markedly angulate medially; anal lobes and cerci both broadly rounded in lateral view, cercus not markedly developed, lobe occasionally truncated apically; spermatheca ovoid, with slight mottled pattern, clear area at junction of duct distinct.

Adult male (unknown). Most likely similar to *A. multicorne.*

Pupa (based on male neotype): **Head**: cephalic plate (Fig. 223), markedly elongate and rounded apically, 2.5× wider than narrowest width, cuticle sparsely tuberculate dorsomedially, not concave; setae not obvious. **Thorax** (Fig. 244). Dorsum lacking tubercles, mammillated, setae trichoid. **Gills** (Fig. 274): horn *ca* 4× as long as its greatest breadth; basally dark, apically black, slightly expanded at mid-length, scobinate; filament bases tightly packed on horn; filaments *ca* 40, maximum length 1.4 mm, light brown, finely tapered, surface annulated (Fig. 292). **Abdomen**: grapnel hooks absent.

Cocoon (Fig. 149, 166): shape patellate, edges strengthened; anterior opening oval and distinct; fabric coarsely woven (Fig. 183).

Larva (final instar, based on topotype slide mount). Colour unknown, however, probably brownish. **Head** (Fig. 328): bicolorous, background pale, head spots distinct, posteromedial and mediolateral spots surrounded by brown infuscation; head length 0.7 mm, width 0.5 mm; distance between antennal bases 0.35 mm; lateral head margins apparently subparallel; posterior apotome markedly dark; postocciput well developed, fused to dark cervical sclerites; ecdysial line broadly rounded posteriorly, sinuous anteriorly. **Antennae** (Fig. 373): brown basally, pale apically; proportional lengths 1st, 2nd, and 3rd articles 1.0 : 0.3 : 2.3; apical article 1.8× longer than basal 2 articles combined, medial article 0.3× as long as expanded basal article. **Labral fans**. 26+ fine rays, length 0.5 mm, width 0.009 mm; distinct pattern of microtrichia, longer microtrichia 1.8× longer than ray width, separated by 14–17 smaller microtrichia of irregular length. **Postgenal cleft** (Fig. 390): broadly inverted U-shaped, sloped sides with flattened apex, posterior tentorial pit region markedly sclerotised and pigmented. **Postgenal bridge**: 1.5× longer than postgenal cleft, pale, concolorous with genae, elongated posteroventral muscles spots light brown; genae light brown. **Hypostoma** (Fig. 409): teeth only partially obscured by ventral surface of hypostoma; median and lateral teeth distinct, 2 sublateral teeth subequal in size to median tooth, middle tooth 1/2 size of others; 2 paralateral teeth, lateral tooth smaller; smaller teeth partly concealed by anterior margin of hypostoma, 3 or 4 rounded lateral serrations, variable; 5 or 6 hypostomal setae each side. **Mandibles** (Fig. 426): outer teeth not well developed, apical tooth prominent, subapical teeth substantial, 11 spinous teeth; sensillum and serration simple; blade region smoothly convex. **Abdomen**: **anal sclerite** (Fig. 443): median plate, anterior arms, interarm struts and posterior arms substantial, but finely developed; anterior arms not markedly flared or emarginated; semicircular sclerite well developed, accessory sclerites deeply emarginated. **Posterior circlet**: 92 rows of 16 or 17 hooks (total *ca* 1 500).

Type data. **Neotype**, here designated: Male pupal exuviae and cocoon on microscope slide; label details, across top of specimens “Pupal\ Thorax\non granulate\? date Stillwater\ in alcohol” (label with 2 horizontal dotted lines; handwritten in pencil, Dumbleton), “Entomology Div., DSIR. NZ\L. J. Dumbleton Collection” (gold label), below specimen “multicorne?\pupa\ Glaisnock R.\ Te Anau\ LJD -/3/49” (handwritten in faded black ink, Dumbleton), “*Aust. (A.) fiordense*\NEOTYPE {M}\ Remounted, Craig 2009\PVLP” (typescript label, neotype in red, male symbol handwritten in black ink, D. A. Craig). The cocoon is mounted separately under its own coverslip, as are the 2 gills plus thoracic cuticle, the abdominal exuviae, and the cephalic cuticle (NZAC). Under the Code no secondary types are designated in this situation. The second specimen is not of type status; however, because of its importance, full label data for this second specimen is also given, as follows: 2nd specimen, final instar larva mounted on microscope slide; label details, above specimen “Entomology Div., DSIR. NZ\ L. J. Dumbleton Collection” (gold label), below specimen “multicorne?\ Glaisnock R.\ Larva\ LJD 3/49” (handwritten in faded black ink, Dumbleton), “*Aust.*

(A.) fiordense\ Last instar larva\ Remounted, Craig 2009\ PVLP" (typescript label, D. A. Craig). Mounted under separate cover slips are the anal sclerite, pharate pupal gills, dorsal and ventral head capsule, and mouthparts (NZAC).

Records indicate there was considerable material of *A. fiordense* collected from Fiordland and a number of tubes of material were designated paratypes (Dumbleton 1973: 518). The holotype, apparently in ethanol, was a male pupal exuviae on an *Astelia* leaf, labelled "L[ake] Marchant [FD], 12-iii-1949". This locality is at the head of Caswell Sound, on the coast, west of South West Arm, Lake Te Anau. The paratype pupa and reared male (7-iii-1948; the year provided is probably a *lapsus calami,* it is most likely 1949, when Dumbleton is known to have been in the area), also in ethanol, were from Stillwater River, which feeds Lake Marchant, immediately inland from Caswell Sound. Other immature stages were from Glaisnock River, North Fiord (Arm), Lake Te Anau. All this type material appears lost and has not been seen since designation and cannot be located in the ethanol collection, NZAC (TKC pers. obs.). The only material available from the original collections, but not designated as part of the type series, were 2 slides, one of a male pupal exuviae and the other of the head, prothorax, and anal sclerite of a final instar larva. These specimens were removed from the original slides, dissected further, remounted and used for this redescription. Since this slide material is all that remains of Dumbleton's original material, the slide of the pupal exuviae is designated here as neotype to fix the identity of the species for this human-biting species and the original type locality in the Fiordland National Park, an area which is well-visited by tourists. The labeling associated with the neotype slide is somewhat confusing in that the reference to "?date Stillwater" is not clear, but may have indicated uncertainty over the year of collection of the original Stillwater paratype specimens that may have been labelled 1948 instead of 1949.

Material examined. Neotype slide and additional specimen slide; numerous [probable] adults of *A. fiordense* from Homer Tunnel and the Darran Mountains, FD; and probable pupae from the Rangitata R Valley, near Mt Peel (SC).

Distribution (Map 9). Known from a restricted distribution in Fiordland National Park, the Catlins, and a probable population at Soup Stm, Rangitata R Valley (NZS126). **South Island**. **WD**. Robinson Ck, NZS177 (SH6). **SC**. Soup Stm, NZS126 (Rangitata R Valley). **SL**. Waikawa R trib (Tokanui). **FD**. Glaisnock R; Homer Tunnel; L Marchant; Milford Sound; Stillwater R (upper); Te Anau; Tutoko Bench (Darran Mts).

Northernmost record: Soup Ck (latitude S43.74026°), southernmost record Waikawa R trib (latitude S46.543417°), from sea level to 1100 m a s l.

— / WD, SC, SL, FD / —

The Fiordland localities are in the Southern Alps aquatic ecoregion, those of Rangitata R Valley, the High Country, and the Catlins locality falls into the Southeast Forest ecoregion.

Etymology. Named by Dumbleton (1973) for Fiordland, New Zealand, a well-known tourist destination region.

Bionomics. Virtually nothing is known about the biology of this species. Dumbleton collected final instar larvae and pupae, including pupal exuviae from the Glaisnock River, North Fiord (Arm), Lake Te Anau, and from the Stillwater River that feeds Lake Marchant, west of Lake Te Anau, Fiordland, in March 1949, which is indicative of a single generation. He noted that the pupae were on vegetation — the missing holotype pupa was on an *Astelia* leaf. Specimens occurred at low density. There was no comment on larval habitats, except they occurred in large rivers and without other simuliids. Dell (1951) commented that Dumbleton collected *A. multicorne*? (probably *A. fiordense*) at 1 219 m a s l on Saddle Hill along with those of *A. ungulatum*. Adults, identified here as *A. fiordense*, are from farther north and were taken in January 1977. Label data indicate that some bit the collector (TKC). Of note is that no adults of *A. ungulatum* were taken in those collections. Also, no immature stages that can be assigned to *A. fiordense* were taken from the Darran Mountains (see *A. tonnoiri* and *A. bicorne*); is this suggestive that *A. fiordense* adults accumulate at high altitude?

Remarks. Dumbleton described *A. fiordense* as a subspecies of *A. multicorne*, distinguishing it on the basis of mammillated pupal thoracic cuticle, as against tuberculate cuticle in the then nominate species *A. multicorne*. We have assigned the mammillate character state of the thoracic cuticle sufficient weight to warrant full specific status.

Material from Soup Stm, Rangitata R Valley is a mixture of pupae, some of which are obviously *A. multicorne* with tuberculate thoracic cuticle, but the trident pattern is not marked. Others have mammillated thoracic cuticle and we have assigned these to *A. fiordense*. The two are difficult to distinguish and, in some cases, require the cuticle to be mounted and examined at high magnification.

Identifying the female adults from the Darran Mountains, Fiordland, as *A. fiordense* was moot, but *Austrosimulium multicorne* s.s. is not recorded from the area and the adults under consideration have subtly different claw and abdominal tergite shape, so we assigned these adults to *A. fiordense,* and similarly adults from Milford Sound collected by A. M. Fallis in January 1971 to this species. More material will need to be collected from the type region and molecular confirmation will no doubt be required.

Austrosimulium fiordense is in polytomy in Strict Consensus (Fig. 505), but in Majority Rule (Fig. 506) is sister to the remainder of the *tillyardianum*-subgroup (Fig. 505, 506); this was not unexpected as it is the only member of the subgroup to lack dorsal thoracic tubercles in the pupa. No material was available for molecular analysis, but when done we expect *A. fiordense* to have a close relationship with *A. multicorne*.

Austrosimulium (*Austrosimulium*) *laticorne* Tonnoir, 1925

Figures: female, 30, 56, 76, 96, 114; male, 88,132; pupa and cocoon, 150, 167, 168, 184, 208, 224, 235, 245, 259, 275, 293; larva, 311, 329, 342, 357, 374, 391, 410, 427, 444, 501; habitat, 467–469; Map 10.

laticorne Tonnoir, 1925: 253 (description pupa, cocoon, larva; *Austrosimulium*). Pulikowsky 1929: 662 (pupal gills). Smart 1945: 499 (world catalogue). Mackerras & Mackerras 1949: 405 (general summary). Dumbleton 1963b: 334 (as subgenus *Austrosimulium* (*Austrosimulium*), in *australense* group). Dumbleton 1964a: 35 (relationships, distribution). Dumbleton 1973: 519 (redescription pupa, cocoon, larva; as subspecies *laticorne laticorne, Austrosimulium* (*Austrosimulium*)). Crosby 206: 75 (key). Adler & Crosskey 2012: 20 (world inventory).

Diagnosis. **Female**: tarsal claw with substantial heel; hind basitarsus possessing row of stout setae; abdominal tergites III–V subquadratic, hypogynial valves with acute apex. **Male**: hind basitarsus lacking definite row of stout setae; ventral plate lacking developed ventral keel. **Pupa**: thoracic cuticle with rounded granules in groups, paramedial ridge; gill with broad black horn and *ca* 40 non-tapered filaments; sternite IX lacking grapnel hooks. **Cocoon**: slipper- to shoe-shaped, of high profile, fabric alveolate with substantive anteroventral collar. **Larva**: overall pale; cephalic apotome pale, anteromedial, posteromedial, and posterior head spots distinct, genae pale; basal antennal articles short; ventral tubercles substantial.

Adult female (reared adults from NZS2). **Body**: general body colour in ethanol dark brown-black, when dried with silvery pruinose appearance; total length 2.6–2.7 mm. **Head**: broad; overall colour, including ommatidia, evenly blackish-brown; width 0.74–0.77 mm, depth 0.49–0.53 mm; frons width : head width ratio 1.0 : 3.8. **Eyes**: interocular distance 0.19–0.20 mm; ommatidia diameter 0.014 mm; *ca* 32 rows up across and 41 down at mid-eye. **Clypeus**: very dark; width 0.22–0.23 mm; vestiture of sparse black and pale hairs. **Antennae**: total length 0.45–0.55 mm; flagellomeres paler than basal segments. **Mouthparts**: substantial, 0.6× length of head depth; mandibles with 26+ inner teeth, rapidly decreased in size basally; laciniae with 12 inner teeth and 19 outer teeth; maxillary palp, total length 0.44–0.46 mm, 3rd article blackish-brown, remainder lighter, proportional lengths 3rd, 4th, and 5th articles 1.0 :0.7 : 1.1, sensory vesicle spherical, markedly small, 0.25× 3rd article width, opening 0.2× vesicle width; cibarial cornuae narrow, pigmented, sparse tubercles, central depression smoothly broad (Fig. 30).

Thorax: length 1.2 mm; width 0.90 mm; in ethanol, postpronotal lobes marginally paler than scutum; scutum evenly dark brown, vestiture of sparse recumbent hairs, prescutellar depression with a few longer darker hairs posteriorly, no vittae visible in ethanol; scutellum slightly lighter than scutum, vestiture of sparse long black hair; postnotum, pleuron, and pleural membrane concolorous with scutum. **Wings**: length 2.4–2.5 mm; width 1.2–1.3 mm. **Halteres**: tan. **Legs**: yellowish-brown, with darker brown bases to femoral, tibial, and tarsal segments; hairs short, yellowish; hind basitarsus about 7.5× as long as greatest breadth, with row of stout setae, but variable, reduced to a few in some specimens; tarsal claws (Fig. 56) lacking basal tooth, but with substantial heel.

Abdomen (Fig. 76): abdominal scale dark brown with fine pale hairs, not greatly extended; tergite II wider than long, emarginate anteriorly, tergite III ovoid, tergites IV and V quadratic, sloped laterally, increased in size posteriorly; vestiture of sparse black hairs, denser posteriorly. **Genitalia** (Fig. 96): sternite VIII pigmented medially and markedly along anterior edge, vestiture of hexagonal arrays of microtrichia; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and microtrichia; median edges of hypogynial valves strengthened and slightly concave, sharply rounded posteroapically; genital fork (Fig. 114) anterior arm not markedly broad, evenly pigmented, lateral membranous region not extensive, arms lacking marked knee-bend, lateral apodeme variably developed, triangular to blade-like, flange rounded posteriorly; anal lobes and cerci both broadly rounded in lateral view, black; spermatheca ovoid, dark, no pattern, clear area at junction of duct small.

Adult male (based on holotype, and reared adults from NZS1). **Body**: general colour in ethanol brownish-black, dried dull black; total length 2.3 mm. **Head**: width 0.82–0.84 mm; depth 0.60–0.64 mm. **Eyes**: upper ommatidia orangey brown (black when dried), diameter 0.023–0.028 mm, *ca* 21 across and 19 down, occupying much of the eye; lower ommatidia dark brown, diameter 0.014 mm, *ca* 34 across and 38 down. **Clypeus**: dark brown; 0.2× as wide as head; vestiture of very sparse fine hairs. **Antennae**: total length 0.45 mm; evenly medium brown, base of 1st flagellomere pale, apical flagellomeres tapered. **Mouthparts**: poorly developed; length 0.36× head depth; mandibles insubstantial, broadly tapered with apical hairs; laciniae, finely tapered apically with terminal hairs; maxillary palp medium brown, 0.47 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 0.75 : 1.5, sensory vesicle irregular in shape, occupying 0.33× 3rd article width, opening 0.3× vesicle width.

Thorax: length 1.1–1.2 mm; width 0.80–0.84 mm; scutum evenly dark brown-black, vestiture of fine recumbent pale hairs, brassy yellow when dried, markedly stiff, longer black hairs in prescutellar depression; scutellum concolorous with scutum with sparse long black hairs; postscutellum concolorous with scutum. **Wings**: length 2.1–2.6 mm, maximum width 1.2 mm. **Halteres**: tan. **Legs**: light brown, with darker brown femoral, tibial, and tarsal bases; hairs dark, short; hind basitarsus *ca* 5.6× greatest breadth, row of stout setae absent, but variable number (*ca* 3) of more substantive hairs present; tarsal claw grappling pads with 20 hooks.

Abdomen (Fig. 88): dorsum blackish-brown. **Genitalia** (Fig. 132): gonocoxites 2.0× longer than basal width, evenly dark brown, with coarse black hairs well distributed; gonostyli *ca* 2.5× longer than basal width, apically with 3 substantial spines, subapical spines less so; ventral plate with low median keel, even vestiture of fine long hairs, width 1.5× length, rounded posteriorly, convex anteromedially with thickening and pigmentation at angle, basal arms substantial; median sclerite moderately well developed, broad, T-shaped posteriorly; parameres poorly developed.

Pupa (Fig. 150, 167, 168). Body length; male 2.6–2.7 mm, female 2.5–3.2 mm; maximum width male 1.1 mm, female 1.1–1.3 mm. **Head**: cephalic plate of male (Fig. 224) strongly tuberculate on upper frons, 2.5× as long as wide, that of female (Fig. 208) virtually lacking tubercles, concave, as long as wide; pale muscle scars marked, more so in male; facial and epicranial setae present. **Thorax** (Fig. 235, 245): dorsum similar to *A. tillyardianum,* coarsely granulated; tubercles raised, circular, distinct, contiguous in groups, forming poorly defined trident pattern (median band along ecdysal line, posterior transverse line, and 2 lateral, longitudinal lines arising from each end of posterior line), groups of tubercles not contiguous except on trident lines, oblique transverse bands with sparse tubercles behind anterior clear area; setae trichoid. **Gills** (Fig. 259, 275, 501): variable; base small, trabeculate, light brown; horn entirely black, flattened; surface scobinated; edges of gill slightly curved on lateral edge, markedly angulate or rounded at about mid length on medial edge to produce mitten- or paddle-shaped horn, normally rounded apically, 1.5–2.5× as long as wide; laterally and apically occasionally deeply emarginate but variable, even between sides of same pupa; filaments *ca* 36–40, as long as horn, light yellowish-brown, thin and non-tapered, breadth 0.01 mm, surface distinctly annulated (Fig. 293). **Abdomen**. grapnel hooks absent from sternite IX.

Cocoon (Fig. 150, 167, 168): surface rough, fabric alveolate, long silk filaments not obvious, quite variable (Fig 184). Shape: the original description by Tonnoir (1925) was “oblong wall-pocket and of rather coarse cellular structure: always of narrow shape even when built on flat surface”, that by Dumbleton “oval, convex, close fitting with moderately high collar, pale brown fabric may be clear thin non-reticulate to reticulate”. See below in “Remarks” regarding *A. laticorne* as a complex.

Larva (based on numerous final instar larvae, NZS2). **Body** (Fig. 311): sexual dimorphism moderately developed; females larger and grayish, males smaller and yellowish; total mean length 5.4–6.0 mm. **Head** (Fig. 329): markedly bicolorous, background pale creamy yellow to translucent with dark pigmentation posteriorly and anterolaterally on apotome; length 0.62–0.73 mm, width 0.50–0.54 mm; distance between antennal bases 0.25–0.30 mm; lateral margins of head smoothly convex; anteromedial apotome translucent, head spot pattern not marked; anteromedial spots positive pale brown; posteromedial spots fused, positive, dark brown; anterolateral spots positive but pale; 1st posterolateral spots neutral; 2nd posterolateral spots distinct and embedded in dark pigmentation of posterior edge of apotome, continuous with posterior genae; ecdysial lines sinuous, narrowest anterior of stemmata; postocciput markedly pigmented medially, fused to distinct cervical sclerites. **Antennae** (Fig. 374): basal article brown, medial article lighter, apical article pale; total length 0.37 mm, not markedly extended beyond apex of fan stem; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.2 : 2.1; apical article *ca* 1.7× longer than combined basal 2 articles; medial article short, 0.2× as long as basal article. **Labral fans**: stem translucent and light brown; *ca* 44 fine rays, length 0.57 mm, width 0.009 mm; indistinct pattern of microtrichia, longer microtrichia 0.8× longer than ray width, separated by *ca* 8 irregular shorter microtrichia. **Postgenal cleft** (Fig. 391): shallowly inverted U-shaped, occasional distinct posteriorly-directed irregular or bulged projection at apex of cleft; posterior tentorial pit region well sclerotised and pigmented. **Postgenal bridge**: 1.3× longer than hypostoma, pale, lighter than genae, elongated posteroventral muscles spots very light brown but distinct; genae light brown. **Hypostoma** (Fig.410): broadly rounded, teeth all obscured by ventral margin, median tooth not prominent; sublateral teeth and paralateral teeth occasionally extended beyond anteroventral margin of hypostoma, 3 or 4 poorly developed lateral serrations; 4 or 5 hypostomal setae each side. **Mandibles** (Fig. 427): outer, apical, and subapical teeth not markedly developed; only *ca* 8 spinous teeth; sensillum and serration not markedly complex, but on raised base. **Thorax** (Fig. 357): prothorax light grayish-brown, pleurite not markedly covering pharate pupal gills, gills with small pale base, horn substantial and mitten-shaped, black, occupying most of histoblast, *ca* 12 filaments arrayed parallel on surface of horn, not coiled. **Abdomen**: anterior abdomen banded grayish-brown, posteroventral abdomen pale; narrower than thorax; abdominal segments I–IV narrowed, expanded distinctly at segment V to produce slight amphora shape; grayish-brown; distinct ventral tubercles. **Anal sclerite** (Fig. 444): median region angulate; anterodorsal arms not markedly flared, occasionally bifurcate, interarm struts broad, apically finely tapered and parallel to posterior arms, those substantial and tapered; semicircular sclerite finely developed, with accessory sclerites substantial and emarginated. **Posterior circlet**: *ca* 80–90 rows of 12–16 hooks (total *ca* 1 200).

Type data. **Holotype**: male, on elbow pin (MacGillivray 1903); condition good, albeit slightly collapsed; label details "Waiho [=Franz Josef] N. Z.\ 25 Jan. 1922\ A. Tonnoir" ("25" handwritten in black ink, Tonnoir), "Austrosimul.\ laticornis {M}\ Tonn\ Type" (handwritten in black ink, "Type" with wavy underline, Tonnoir), "NZ Arthropod Collection\ {barcode}\ NZAC04021455" (NZAC). **Paratypes**: pinned; 1 female, label details "Waiho [=Franz Josef] N.Z.\ 25 Jan. 1922\ A. Tonnoir" ("25" handwritten in black ink, Tonnoir), "Austrosimul.\ laticornis\ {F}\ allotype" (handwritten in black ink, "Allotype" with wavy underline, Tonnoir), "NZ Arthropod Collection\ {bar code}\ NZAC04022106"; 1 male, locality data as above, "PARATYPE\ Austrosimul.\ laticornis\ n. sp. {M}\A. Tonnoir det." (blue label, scientific name handwritten in black ink, Tonnoir), and as "NZAC04022098" (NZAC). 1 male, locality data as above (MONZ).

Dumbleton noted that one male paratype, collected by Tonnoir at Mount Arthur, is probably not *A. laticorne*, since that species is not known from the area. He thought it more likely to be *A. multicorne*. However, *A. laticorne* does occur in the general region (Map 10), though not yet known specifically from Mount Arthur. We did not manage to identify exactly the specimen being questioned, so cannot comment further.

Dumbleton (1973: 522) similarly noted that a male and a female collected by Tonnoir on 26 February 1923 at Nihotupu, AK, were probably *A. longicorne*. This comment is confusing since the only localities recorded for *A. laticorne* in Tonnoir (1925) were Waiho (West Coast) and the Maitai River in Nelson. However, in NZAC there are 2 Tonnoir specimens with these Nihotupu collecting data placed under *A. laticorne*, presumably by Tonnoir, in addition to 2 other Tonnoir specimens with the same collecting data that were identified and placed under *A. longicorne* by Tonnoir. The 2 specimens placed under *A. laticorne* have pinned to them a handwritten note by Dumbleton stating "longicorne {F} \ Prob. {MM}[sic!, plural] also \ No laticorne from \ North Island". The female specimen is *longicorne*, but the male appears to be *australense* since it lacks stout setae on the hind basitarsus.

Material examined. Type material, some 30 samples from the collection of Dumbleton (NZAC), and 38 recent collections (Appendix 1), comprising many hundreds of specimens of all stages, including reared adults.

Distribution (Map 10). Not known from the North Island, but ranging the full length of the South Island, though not evenly. **South Island**. **SD**. Kenepuru Head stm, NZS2, 2a; Ngakuta Bay stm, NZS1. **NN**. Aorere R, NZS97; Baker Ck; Brown Ck, NZS81; Candle Ck, NZS77; Coal Ck; Cobb R, NZS93; Cooks Ck, NZS98; Deadmans Ck; Fossil Ck, NZS96; Glenhope; Graham Stm, NZS106 (SH6); Harleys Rock (ditch); Hope R; Jones Ck, NZS74; Little Wanganui R, NZS79 (Te Namu); Lyell Ck, NZS82; Maitai R; Motupiko R, NZS89; Paturau R, NZS100; Poorman Valley Stm, NZS7; Roding R, NZS104; The Brook (Nelson City); Wainui R, NZS101 (Anatimo); West Ck; Westport. **BR**. Black Valley Stm, NZS88; Buller R (Gowanbridge, Harleys Rock); Doctor Ck, NZS83; Gowan R; Grey R, NZS69 (SH7 bridge); Hope R, NZS86 (SH6 and SH43 junction); Inangahua R, NZS68 SH7 Reefton); Porika Stm; Riordans Ck. **WD**. Karangarua; Kawhaka Ck, NZS50; L Mapourika; Mahinapuna Ck; Maimai Ck, NZS46; Taramakau R, NZS51 (SH73); Waiho (= Franz Josef); Whataroa. **MB**. Pelorus R, NZS5; Six Mile Stm bridge. **KA**. Okiwi Bay. **NC**. Hawdon R; Maruia Springs. **MK**. Fork Stm, NZS18, 18a (SH8 bridge). **CO**. Low Burn; Mataura R trib [Parawa Stm], NZS36; Taieri R. **OL**. Mossburn; Weydon Burn trib [Hamilton Ck], NZS35. **SL**. Caddon Burn, NZS29; Catlins R, NZS27; Dome Burn; Granity Stm trib, NZS159; Lumsden; Manuka Gorge; Otautau; Rock Ck; Sutton Stm; Waimeamea R, NZS30; Wairaki R, NZS31; Waitahuna; Waitati. **FD**. Alton Burn, NZS156; Lill Burn trib, NZS155.

Northernmost record; northwest Nelson, Paturau River (latitude S40.65426°); southernmost record; Southland, Otatatu (latitude S46.17780°); ranging from near sea level to *ca* 700 m a s l.

— / SD, NN, BR, WD, MB, KA, NC, MK, OL, SL, FD /—

Austrosimulium laticorne is well distributed along the Westland Forest ecoregion, and those of the Northeast Nelson Forest and Nelson Plains. It is rarely found in the High Country, but when it is, it is more commonly in the south. It also occurs in the Southland Plains ecoregion.

The exact position of the type locality (Waiho) given by Tonnoir (1925) is problematic, since it is most unlikely to have been the Waiho River itself which flows from the Franz Josef Glacier. Indeed, he noted that the type locality was a swiftly flowing small rivulet and material was on vegetation along with *A. longicorne* and *A. multicorne*. Since Tonnoir's time, the Franz Josef Glacier environs have altered considerably. In Tonnoir's time the glacier ice face was near Sentinel Rock, and while Hugh Creek was ice-covered, less than 200 m downstream, Duck Creek was open. That was, however, ice-covered by 1934 during a major advance (Sara 1974). The Waiho River itself is generally inimical to aquatic macroinvertebrates, being heavily sedimented and, not uncommonly, having floating ice. Milner *et al.* (2001), however, did recover ephemeropterans and chironomids from various reaches of the river, at low densities. No simuliids were recovered.

It is possible Tonnoir used "Waiho" as a shortened form for the then township of "Waiho Gorge", which later was renamed "Franz Josef". His labels for all the different Diptera species he collected only refer to the general locality of "Waiho", and this is how it has been recorded in the literature. Tonnoir was based in this area for 15 days from 16–30 January 1922 (Crosby 1976b), with the collection being made 9 days after arriving. On the same day (25 January) he collected the holotype of the tipulid *Gynoplistia campbelli bicornis* Alexander, 1926 and Alexander noted in the publication that the specimen was collected at an altitude of 600 feet (183 metres). On several other days Tonnoir collected many species of Mycetophilidae, which is likely to indicate he was in bush areas on those days. The type locality for *A. laticorne* was likely one of the small streams that flows off the surrounding mountains. It must be noted, however, that despite several attempts, some intensive, no *A. laticorne* material has been collected from the Waiho River and gorge area since that by Tonnoir. Material was collected by Dumbleton at nearby Lake Mapourika. The site of Tonnoir's collection may be, indeed, near Lake Mapourika where Dumbleton found *A. laticorne*.

Etymology. Not recorded in the original description by Tonnoir (1925), but no doubt in reference to the broad horn of the pupal gill.

Bionomics. Tonnoir (1925) recovered *A. laticorne* pupae from vegetation at Waiho and shingle in the Matai River, Nelson. However, Dumbleton noted that larvae and pupae of *A. laticorne* are characteristically in habitats that are almost always open to the sun, shallow, and have a substrate that consists of clean stones and boulders less than 20 cm in diameter (Fig. 467–469). Furthermore, summer temperatures are generally high. Our data agree, with a temperature range from 13–28°C (Appendix 1). Dumbleton noted that there were probably several generations annually, but there might be just a single generation from the Buller River at Lake Rotoiti outlet. The water velocity in the characteristic habitats ranges from 0.70 to 1.00 m/s, but larvae have been recovered from velocities as low as 0.30 m/s and as high as 1.40 m/s. Immature stages of *A. laticorne* are, however, also found in narrower streams with higher banks and trailing vegetation (Fig. 468). Also known to Dumbleton, while *A. laticorne* is characteristically associated with *A. tillyardianum*, it is also with *A. australense*, but more so in Westland. We now know it also occurs with *A. ungulatum* (Map 10, 16) and has occasionally been found with *A. stewartense* and *A. multicorne.*

Tonnoir (1925) noted of *A. laticorne* that he was "not certain that it bites man". Similarly, Dumbleton stated "not known to bite", in full agreement with the female's mandible that is slightly smaller and with fewer teeth than species that are blood feeding. The same reduction is found for its lacinial teeth. Also, the maxillary sensory vesicle is markedly small for an *Austrosimulium* female and the abdominal tergites are moderately large (Fig. 76), all further indications of non-blood feeding.

Remarks. Dumbleton (1973) recognised *alveolatum* as a subspecies of *laticorne*, but we elevated this subspecies to species rank (p. 117). Consequently the nominate subspecies usage introduced by Dumbleton (1973) for *A. laticorne* is no longer required.

In any one population *A. laticorne* pupal gills and cocoon are fairly consistent and over much of the species' range these are normally as shown in Fig. 259. Variants of both gill and cocoon are, however, not uncommon. The horn of the gill can be emarginate and the cocoon surface may have more deeply defined cells, approaching those of *A. alveolatum*. In Dumbleton's collection of *A. laticorne* from the Buller River outlet is one pupa that has long filaments on the gill horn, and there are similar specimens from Gowanbridge on the Buller River. He made no comment about those specimens; however, we believe it is likely that they will be shown eventually to be a separate, but closely related species to *A. laticorne.* No more material of that ilk has been collected to date.

Dumbleton included a wide range of cocoon types in his description of *A. laticorne*—from non-reticulate (lacking alveolae) to reticulate (markedly alveolate), unlike Tonnoir whose description was restricted to the reticulate form; similarly, Dumbleton included a wider range of gill forms than did Tonnoir.

It was on the basis of the unique honeycomb reticulations of the cocoon fabric and the consistently smaller gills, that we raised *A. alveolatum* to species status. Even so, within that species there is a range of cocoon fabric types from that of the holotype cocoon to cocoon fabric approaching that of *A. laticorne*. For *A. alveolatum* the gill horn is always narrower.

We are of the opinion that *A. laticorne* and *A. alveolatum* as currently recognised are both species-complexes. For example, a population at Fork Stream, Lake Tekapo (NZS18) has pupal gill horns that, while narrower than usually encountered for *A. laticorne*, are within the usual range of variation for that species. However, the cocoon is of thin winkled fabric with sparse small alveoli embedded laterally. The larvae appear to be classic *A. laticorne.* We consider the likelihood that this form is another species is high. Similar cocoons, but with classic *A. laticorne* pupal gills, occur in the Catlins (NZS27) and at Otautau (NZS159). Since analysis of mDNA of the CO1 gene does not discriminate well any of the *tillyardianum*-subgroup (Fig. 508), no further comment is made.

Austrosimulium (*Austrosimulium*) *multicorne* Tonnoir, 1925

Figures: female, 17, 31, 57, 77, 97, 115; male, 133; pupa and cocoon, 151, 169, 185, 209, 225, 246, 260, 276, 277, 294; larva, 312, 330, 343, 358, 375, 392, 411, 428, 445; habitat, 475–478; Map 12.

multicorne Tonnoir, 1925: 254 (description larva, pupa; *Austrosimulium*). Smart 1945: 499 (world catalogue). Mackerras & Mackerras 1949: 405 (occurrence). Dumbleton 1963b: 334 (as subgenus *Austrosimulium* (*Austrosimulium*), in *australense* group). Dumbleton 1964a: 35 (relationships, distribution). Dumbleton 1973: 516 (description cocoon, redescription larva, pupa; as *multicorne multicorne*, *Austrosimulium* (*Austrosimulium*)), Crosby 2006: 75 (key). Adler & Crosskey 2012: 20 (world inventory).

Not *multicorne* Tonnoir, 1925. Gurr 1953: 81 (= *A. dugdalei*).

Diagnosis. **Female**: thorax not markedly domed; tarsal claw lacking basal tooth or heel, hind basitarsus possessing row of stout setae; abdominal tergites III–V subquadratic. **Male** with row of stout setae on basitarsus. **Pupa**: thoracic cuticle with rounded granules in groups, paramedial ridge, gill of black lancet-shaped horn (variable) with 40–55 finely tapered filaments, some bifurcated; sternite IX lacking grapnel hooks. **Cocoon**: slipper- to shoe-shaped, of low profile, finely woven, lacking fenestrae, slightly flared basally, opening oval. **Larva**: pigmented; cephalic apotome markedly brown, posteromedial and posterior head spots distinct; genae, hypostoma, and cleft areas heavily dark brown.

Adult female (based on paratype and topotypes). **Body**: general body colour in ethanol dark brownish-black, abdomen grayish; when dried, thorax with silvery pruinose appearance; total length 2.7–2.9 mm. **Head**: width 0.7–0.8 mm; depth 0.45–0.51 mm; frons dark brown-black, postocciput black, vestiture of sparse, short black hairs; frons width: head width ratio 1.0 : 3.9. **Eyes**: interocular distance 0.16–0.18 mm; ommatidia diameter 0.014 mm; *ca* 33 rows up and 38 across at mid-eye. **Clypeus**: dark brown with pale ventromedial region; vestiture of sparse black and pale hairs; width 0.22–0.23 mm. **Antennae**: total length 0.5–0.6 mm; all articles medium brown. **Mouthparts** (Fig. 17): substantial, 0.6–0.7× length of head depth; cibarial cornuae substantial, sclerotised with black granulate sculpting and minor fluting (Fig. 31); mandibles with 33 inner teeth, increasing in size towards apex, 8 basal teeth markedly small; laciniae with 13 inner teeth and 19 outer teeth; maxillary palp, total length 0.58 mm, 3rd article dark brown, remainder lighter, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.8 : 1.5, sensory vesicle spherical, 0.3× 3rd article width, opening 0.3× vesicle width.

Thorax: length 1.3–1.4 mm; width 0.95–1.1 mm; in ethanol, postpronotal lobes marginally paler than scutum; scutum evenly dark brown, vestiture of even fine recumbent hairs, presutellar depression hairs few, no vittae visible in ethanol-preserved specimens, but when dried with a median and 2 lateral vittae overlain with silvery pruinosity; scutellum pale, vestiture of a row of long black hairs and pale hairs laterally; postnotum, pleuron, and pleural membrane concolorous with scutum. **Wings**: length 3.1 mm; width 0.14 mm. **Halteres**: tan. **Legs**: bicolorous, yellowish-brown with darker brown bases to femoral, tibial, and tarsal segments; hind basitarsus about 6× as long as its greatest width; with row of stout setae; tarsal claws (Fig. 57) well curved, with heel not distinctly developed.

Abdomen (Fig. 77): abdominal scale dark brown with fine pale hairs, not greatly extended; tergite II wider than long, tergites III–V subquadratic, tergite VI and tergite VII increasingly wider than long, vestiture of sparse, long dark hairs, increased posteriorly. **Genitalia** (Fig. 97): sternite VIII markedly medium brown medially, along anterior edge sharply producing X-shaped region, vestiture of coarse black hairs posterolaterally; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and triads of microtrichia; median edges of hypogynial valves strengthened, slightly curved to subparallel, broadly rounded posteroapically; genital fork (Fig.115) with anterior arm cone-shaped, slightly fluted anteriorly, posterolateral arms simple, poorly pigmented, apodeme small, lateral lobes rounded; anal lobes and cerci both broadly rounded in lateral view and black; spermatheca spherical, clear area at junction of duct distinct.

Adult male (based on holotype, plus other pinned and ethanol-preserved material). **Body**: general colour, in ethanol brownish-black, when pinned matt black; total length 2.4–2.6 mm. **Head**: width 0.84 mm; depth 0.60 mm. **Eyes**: upper ommatidia dark reddish-orange (black when dry), diameter 0.028 mm, *ca* 24 across and 18 down, markedly occupying more of eye; lower ommatidia dark brown, diameter 0.011 mm, *ca* 27 across and 30 down. **Clypeus**: dark brown, pollinose under some lighting; vestiture of coarse black hairs; width 0.12 mm. **Antennae**: total length 0.50

mm; evenly dark brown. **Mouthparts**: poorly developed; length 0.26× head depth; mandibles insubstantial, broadly tapered, tattered apically; laciniae, finely tapered apically with terminal hairs; maxillary palp medium brown, 0.5 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 0.8 : 1.5, sensory vesicle irregular in shape, occupying 0.3× 3rd article width, opening 0.3× vesicle width.

Thorax: length 0.92 mm; width 0.8 mm; in ethanol-preserved specimens scutum dull black, vestiture of sparse, fine, recumbent pale hairs, brassy yellow when dried; scutellum concolorous with scutum; vestiture of sparse long black hairs; scutellar depression with sparse long black hairs; postscutellum concolorous with scutum; postnotum concolorous with scutum; depression, postscutellum, and postnotum when dry showing pollinosity under some lighting, with 2 poorly defined vittae; pleural regions dark grayish-brown. **Wings**: length 2.6 mm, width 1.3 mm. **Halteres**: tan. **Legs**: overall grayish-brown, with darker brown femoral, tibial, and tarsal bases; hind basitarsus *ca* 4.6× as long as its greatest breadth, with row of stout setae poorly developed; tarsal claw grappling pads with 23 teeth.

Abdomen: blackish-brown; basal scale markedly developed, hairs extended to 3rd segment. **Genitalia** (Fig. 133): gonocoxites 1.5× longer than basal width, dark brown anteriorly, pale medially, with coarse black hairs evenly distributed except medially, where vestiture is of arrays of microtrichia; gonostyli approximately 2.0× longer than basal width, rapidly tapered, apically with 2 (rarely 3 on one side) substantial spines, 1 less so; ventral plate 1.8× wider than long, with low median keel, not extended to plate apex, moderately dense vestiture of fine hairs, rounded posteriorly, convex anteromedially, anterior arms well pigmented; median sclerite poorly developed, T-shaped posteriorly (difficult to observe); parameres virtually absent.

Pupa (Fig. 169). Body length; male 3.0–3.2 mm, female 2.8–3.5 mm; width, male 1.0–1.2 mm, female 1.1–1.4 mm. **Head**: female cephalic plate (Fig. 209) dished dorsally, 1.5× as long as minimum width, partially tuberculate; male cephalic plate (Fig. 225) narrow, 2.5× longer than narrowest width, sparsely tuberculate on upper frons; muscle scars pale. Frontal setae absent; facial setae present, 1 on each side between antennal bases; 2 short epicranial setae on margin of ocular cuticle under antennal sheath at mid length; all difficult to see. **Thorax** (Fig. 246). Dorsum coarsely granulated; tubercles raised, circular, distinct, contiguous in circular groups, evenly arranged, forming ill-defined trident pattern (median band along ecdysal line, posterior transverse line, and 2 lateral longitudinal lines arising from end of each posterior line); tubercles immediately posterior of gill base not marked (*cf A. dugdalei*, Fig. 242). Setae trichoid. **Gills** (Fig. 260, 276): horn brown basally, remainder black, length 4× maximum width, variable; tapered evenly to apex, or slightly expanded at mid length, sometimes slightly curved; irregularities on horn caused by filament bases; surface not noticeably scobinate; filaments *ca* 30–40, arising from apex and sides of horn, length *ca* 1.5 mm, width 0.01 mm, light yellow brown, only slightly tapered from mid length; rarely bifurcated, filament surface finely annulated (Fig. 294). **Abdomen**. Cuticle pale and membranous; grayish-brown lightly-sclerotised plates on tergite I–IV only. Grapnel hooks absent on sternite IX.

Cocoon (Fig. 151): Slipper- to shoe-shaped, well developed anterior lip, length 3.6 mm, width 2.9 mm. Orifice circular, fabric light brown, finely woven (Fig. 185); not close fitting, on leaves and stones may be subcircular and flattened, on grasses more elongated.

Larva (based on newly collected topotype and other specimens). **Body** (Fig. 312): total length 5.6–6.7 mm, larger specimens probably female; generally evenly grayish-brown. **Head** (Fig. 330): probable sexual dimorphism in colour; variable from extremely dark to medium brown, overall dark brown; paler on anterior cephalic apotome, darker posteriorly and ventrally; length 0.76–0.80 mm, width 0.64–0.68; distance between antennal bases 0.30 mm; lateral margins of head smoothly convex posteriorly, converging slightly anteriorly; head spot pattern distinct, anteromedial spots slightly negative with darker surroundings pale brown, posteromedial spots fused and dark brown positive, 1st and 2nd anterolateral spots slightly negative surrounded by fused brown pigmentation, 1st and 2nd posterolateral spots positive and fused to brownish-black posterior edge of apotome darkly pigmented, continuous with posterior genae; ecdysial lines distinct and not markedly sinuous; cervical sclerites separate from postocciput, but markedly extended anterolaterally. **Antennae** (Fig. 375): dark brown basally, lighter apically; length 0.33–0.37 mm, extended well beyond apex of fan stalk; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.4 : 2.2; apical narrow article 1.6× length of combined basal 2 articles, medial article 0.4× length of basal article. **Labral fans**: stalk light brown; *ca* 31–33 fine rays, length 0.7 mm, width 0.009 mm; distinct pattern of microtrichia, longer microtrichia 1.8× longer than ray width, interspersed with 14–17 smaller irregular length microtrichia. **Postgenal cleft** (Fig. 392): broadly inverted V-shaped, with apex rounded, posterior tentorial pit region markedly sclerotised and pigmented. **Postgenal bridge**: 1.3× longer than hypostoma, pale, concolorous with genae, elongated posteroventral muscles spots light brown; genae with irregular gray-brownish pigmentation. **Hypostoma** (Fig. 411): teeth only partially occluded by ventral lip of hypostoma; median and lateral teeth sharp; lateral teeth slightly more prominent than median tooth; 2 sublateral teeth subequal in size to median tooth, middle tooth 1/2 size of others; 2 paralateral teeth, lateral one smaller; smaller teeth partly concealed by anterior margin of hypostoma, 3 or 4 rounded lateral serrations, variable; 5 hypostomal setae per side. **Mandibles** (Fig. 428): apical tooth and preapical teeth markedly substantial, *ca* 10 spinous teeth; sensillum and serrations distinct, but not marked; blade region smoothly convex. **Thorax** (Fig. 358): in dark larvae (NZN84), prothoracic pleural sclerite markedly brown and partially covering pupal gill histoblasts; remainder of thorax lighter, sternites concolorous with prothoracic pleurite. Pharate pupal gills with yellowish base as long as black horn and *ca* 8 filaments arising, descending posteriorly to curve smoothly anteriorly and then double back again (Fig. 343, 358). **Abdomen**: anterior abdomen evenly pigmented, posterior abdomen darker brown (NZN48); distinct ventral tubercles. **Anal sclerite** (Fig. 445): median region more diffusely sclerotised than other species; anterodorsal arms normally flared, not bifurcate, ventral arms finely tapered; semicircular sclerite substantial, with accessory sclerites flared and emarginated. **Posterior circlet**: 88–107 rows (markedly variable), 14–17 hooks per row (total 1 232–1 800).

Type data. **Holotype**: male, on elbow pin (MacGillivray 1903); condition good, albeit missing right front and middle legs, label details “Mt Arthur [tableland, 4000’]\ Dec [19]21\ A. Tonnoir” (handwritten in black ink, Tonnoir), “Austrosimul.\ multicornis {M}\ Tonn.\ Type” (handwritten in black ink, “Type” with wavy underline, Tonnoir),, “NZ Arthropod Collection\ {barcode}\ NZAC04021386” (NZAC). **Paratypes** (5): 1 female, on elbow pin (MacGillivray 1903), label details “Mt Arthur\ Dec 21\ A. Tonnoir” (handwritten in black ink, Tonnoir), “Austrosimul.\ multicornis {F}\ Tonn.\ Allotype” (handwritten in black ink, “Allotype” with wavy underline, Tonnoir), “NZ Arthropod Collection\ {barcode}\ NZAC04022113”; 1 male, on elbow pin (MacGillivray 1903), label details “Mt Arthur\ Dec 21\ A. Tonnoir” (handwritten in black ink, Tonnoir), “PARATYPE. {M}\ Austrosimul.\ multicornis\ n.sp. A. Tonnoir det.” (blue label, scientific name handwritten in black ink, Tonnoir), “NZ Arthropod Collection\ {barcode}\ NZAC04022134” (NZAC). 1 male, same locality and identification label details, and “I.287” (red label) (CMNZ). 2 males, same locality and identification label details (MONZ).

Material examined. Type material; a large number of collections comprising all stages, 68 from the Dumbleton Collection in NZAC and 63 newer ones (Appendix 1), 22 slides by LJD. Note: a collection from Mount Robert, Lake Rotoiti, 14-vi-1949, by LJD, was particularly important since it contained a considerable number of reared male and female adults.

Distribution (Map 12). Widely distributed in the South Island, but not found on Stewart Island. **South Island**. **NN**. Aorere R, NZS97; Balloon Hut; Buller R trib (Glenhope Scenic Reserve); Cobb R trib, NZS94, NZS95 (runnel); Flora Stm, NZS91; Kohaihai R, NZS76 (Heaphy Track); Poorman Valley Stm, NZS116 (bridge); Salisbury Hut (Mt Arthur); Takaka Hill summit stm, NZS103a; Takaka R. **BR**. D’Urville R; Foleys Ck; Inangahua R, NZS67 (Rahu Saddle); L Rotoiti stm; Marble Hill campground stm, NZS187 (Springs Junction); Mt Robert; Rahu R, NZS66 (Springs Junction); Robert Stm, NZS87. **WD**. Fox R trib, NZS48 (Fox Glacier); Otira; Taramakau R, NZS51; Waiho (=Franz Josef); Waiho R trib, NZS141. **MB**. Boyle R, NZS64 (SH7); Dog Stm, NZS63 (SH7a); St James Walkway stm, NZS188, 189 (Lewis Pass); Tarndale; Wairau R trib [Chinamans Ck]. **KA**. Green Burn, NZS12; Hawkswood; Kowhai R trib, NZS110, NZS111; Mason R, NZS13a (SH70); Mororimu Stm, NZS10 (SH1); Ohau Stm, NZS109 (SH1); Puhi Puhi R trib, NZS108. **NC**. Arthurs Pass; Broken R (SH73); Cave Stm; Craigieburn, NZS55 (SH73); Hanmer; Jacks Pass; Lewis Pass; Maruia Springs; Mt Grey; Pahau R, NZS112 (SH7 bridge); Pegleg Ck, NZS132a (SH73 above bridge); Porter R, NZS56; Spye; Twin Ck, NZS52, NZS133a (SH73); Waimakariri R channel, NZS53 (SH73). **MC**. Acheron R, NZS131, 131b; Annat; Foggy Peak Ridge stm, SH73, NZS57, 57a, NZS134; Grasmere Stm, NZS54 (Cass); Lake Heron (Emily Stm, NZS123; Gentleman Smith Stm, NZS136; Olliver Stm, NZS122a); Mt Hutt Ski Field; Opara Stm, NZS59; Porters Pass; Pudding Hill Stm, NZS120; Ryton R; South Branch Ashburton R, NZS137; Stour R, NZS121a (bridge); Thomas R; Wainui stm, NZS58 (Banks Peninsula); Woolshed Ck, NZS138, NZS139. **SC**. Fairlie; Forest Ck, NZS125 (Rangitata R Valley); Hakataramea R; Hook R; Hurstlea; Kelceys Bush; Mt Peel; Opuha R, NZS17 (SH79); Pareora R gorge; Peel Forest; Scour Stm, NZS124; Soup Stm, NZS126 (Rangitata R Valley). **MK**. Ben Ohau; Birch Hill Stm, NZS128 (SH80); Fork Stm, NZS18, 18a; Freds Stm trib, NZS127, NZS129, NZS130 (SH80); Haldon; L Pukaki stm; Mt Cook (The Hermitage). **OL**. Cardrona R, NZS143; Fern Burn [Jack Hall stm], NZS142; Glendhu; L Howden outlet, NZS150; Mossburn; Wanaka, NZS180 (Glendhu Bay stm); Weydon Burn trib, NZS35. **CO**. Beaumont R; Cambrian; Clutha R and Kawarau R confluence (now L Dunstan); Danseys Pass; Lindis Pass; Lindis V; Mataura R trib, NZS36; Milburns Pond; Obelisk Ck irrigation ditch, NZS42; Old Man Ra top; Park Burn; Pass Burn, NZS181 (Lindis Pass summit); Roaring Meg, NZS37 (SH6); Shepherds Ck; Taieri R; Thompsons Ck, NZS22, NZS23; Tinwald Burn. **DN**. Manuka Stm; Sutton Stm; Tara Hills; Waitahuna. **SL**. Caddon Burn, NZS29; Catlins R trib; Croydon Bush; Fleming R; Owaka; Pomahaka; Tokanui. **FD**. Borland Burn, NZS152, NZS153, NZS154; Divide Ck, NZS33; Homer Tunnel; Lill Burn trib, NZS155; Upper Hollyford R.

Northernmost record: Collingwood, Aorere Valley, Aorere River, NN (latitude S40.83991°); southernmost record: Catlins, Caddon Burn, SL (latitude S46.45748°); ranging from near sea level to 1 300 m a s l. Of note are the rare specimens from Banks Peninsula.

— / NN, BR, WD, MB, KA, NC, MC, SC, MK, OL, CO, DN, SL, FD / —

As recognised at present *A. multicorne* occurs in most South Island aquatic ecoregions, but in particular that of the High Country ecoregion.

Etymology. Not given in Tonnoir's original description, but probably referring to the large number of pupal gill filaments compared with other then-known New Zealand species.

Bionomics. Dumbleton did not comment on biology of *A. multicorne*, but label data, in particular from NZAC, show larvae and pupae present in most months indicative of multiple generations. The more recent collections do not disagree with that. The immature stages are normally inhabit smaller streams (Fig. 475–478) with hard substrate, clear of algae; however, they can be found in abundance on trailing vegetation, as Tonnoir (1925) reported for the species at the type locality. Water temperatures tend to be warmer, ranging from 14 to 28°C; pH range from 6.5 to 8.7; conductivity 10–110µS/cm. Velocities tolerated tend to be higher than for other species, ranging from 0.80 to1.46 m/sec.

Remarks. Dumbleton (1973) recognised *fiordense* as a subspecies of *multicorne*, but we elevated it to species rank (p. 125). Consequently the nominate subspecies usage introduced by Dumbleton (1973) for *A. multicorne* is no longer required.

This species is markedly variable in form of the pupal gill which makes identification difficult at times (e.g., *cf.* Fig. 276, 277). Hence, for this redescription and illustrations we have used as far as possible, material from the type locality, Mount Arthur region, Balloon Hill in particular. Dumbleton commented that south of Wrights Crossing, Hakataramea River (SC) *A. multicorne* pupal gills were narrower. The difficulty is that the gill then begins to approach the shape of that of *A. stewartense*, which occurs with *A. multicorne* in southern South Island. Similar gills are found at Woolshed Creek, Mount Somers (SC).

Other notable populations are those from Kaikoura where pupae have fewer gill filaments. More importantly, the larval head is markedly similar to that of *A. tillyardianum* in showing irregular grey infuscation on a paler background. Such is also seen in larvae from the North Ashburton River, at Buicks Bridge. Normally, at such high altitude (639 m a s l) larval heads are dark.

The population at the Cardrona River (NZS142) had pupae with gills that approached those of *A. stewartense* and had fewer filaments — as low as 30; however, the cocoons did not have the well defined circular opening seen in pupae of *A. stewartense*. Further work will no doubt show this population to be an entity closely related to *A. multicorne*, but for the present, it is considered to be within the range of variation expressed by *A. multicorne*. Similarly, the population from Pudding Hill Stream, where the gill had fewer and thicker filaments and the pupal thoracic cuticle was more heavily tuberculate, may be a closely related entity.

Larvae from the Catlins, SL, also have pale larval heads and well developed spot pattern, but lack grey infuscation. Pupae indicate this material is of *A. multicorne*.

Of biogeographic importance are rare larvae and pupae of *A. multicorne* from Banks Peninsula (NZS58, NZS59, respectively 55 and 133 m a s l). This material consists of 4 final instar larvae, 2 pupae and is definitive. Crosby (1974a) in his intensive collecting, particularly concentrated at Wainui, never recovered this species. Do these specimens represent a recent invasion, or is it a matter of competitive exclusion by *A. tillyardianum*?

Further study will no doubt show that *A. multicorne* is a complex. This is indicated by the placement of *A. multicorne* haplotypes in the CO1 analysis (Fig. 508a, 508b), where they are arbitrarily grouped with other species of the *tillyardianum*-subgroup.

Austrosimulium (*Austrosimulium*) *stewartense* Dumbleton, 1973

Figures: female, 32, 58, 78, 98, 116; male, 134; pupa and cocoon, 152, 170, 186, 210, 226, 247, 261, 278, 295; larva, 313, 331, 344, 359, 376, 393, 412, 429, 446, 499; habitat, 479– 481; Map 13.

stewartense Dumbleton, 1973: 522 (description pupa, cocoon, larva; *Austrosimulium* (*Austrosimulium*)). McLellan 2003: 243. Crosby 2006: 74 (key). Adler & Crosskey 2012: 20 (world inventory).

sp. 3. Dumbleton, 1964a: 36 (Fig. 1, distribution map, pupal gill, and cocoon; *Austrosimulium*).

multicorne stewartense. Dumbleton 1970: 20 (Fig. 7, distribution), *nomen nudum*.

Diagnosis. **Female**: a smaller species; abdomen ruddy black, tergites III–IV rounded and irregular, hind basitarsus with row of stout setae. **Male**: hind basitarsus lacking row of stout setae. **Pupa**: thoracic cuticle with rounded granules in rings, paramedial ridge, gill of black elongate narrow horn with 15–23 non-tapered filaments; sternite IX lacking grapnel hooks. **Cocoon**: slipper- to patellate-shaped, finely woven, opening circular. **Larva**: pale; cephalic apotome markedly translucent, posteromedial and posterior head spots distinct, spotting on anterior of frontolabral apotome in some southern populations, often with irregular grey pattern on apotome and genae; ventral tubercles marked.

Adult female (based on paratypes and topotype material). **Body**: general body colour in ethanol dark reddish brown-black, when dried with silvery pruinose appearance; total length 2.1 mm. **Head**: width 0.62 mm; depth 0.44 mm; postocciput dark brown, vestiture of moderately dense, curved pale hairs; frons dark brown; frons width : head width ratio 1.0 : 3.8. **Eyes**: interocular distance 0.16 mm; ommatidia diameter 0.015 mm; *ca* 30 rows up and across at mid-eye. **Clypeus**: dark brown; shiny; width 0.20 mm; vestiture of sparse black and pale hairs. **Antennae**: total length 0.4 mm; all evenly pale brown; basal flagellomere slightly larger, apical flagellomere elongated. **Mouthparts**: substantial, 0.5–0.6× length of head depth; cibarial cornuae smoothly rounded apically, bearing fine transverse striae medially, not fluted (Fig. 32); mandibles with *ca* 30 small inner teeth, 3 on apex larger; laciniae with 11 inner teeth and 19 outer teeth; maxillary palp, total length 0.34 mm, 3rd article dark brown, remainder lighter, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.7 : 1.4, sensory vesicle spherical, 0.4× 3rd article width, opening 0.2× vesicle width.

Thorax: length 0.92–0.96 mm; width 0.74–0.75 mm; in ethanol postpronotal lobes marginally paler than scutum; scutum evenly dark reddish-brown, vestiture sparse, prescutellar depression bare, no vittae visible in ethanol, but when dried with a median and 2 lateral vittae overlain with silvery pruinosity; scutellum concolorous with scutum, apparently bare; postnotum concolorous with scutum; pleuron, and pleural membrane concolorous with scutum. **Wings**: length 1.9–2.3 mm; width 1.1–1.3 mm. **Halteres**: tan. **Legs**: yellowish-brown, with darker brown bases to femoral, tibial, and tarsal segments; hind basitarsus about 6× as long greatest width, with irregular row of stout setae; tarsal claws with well developed heel (Fig. 58).

Abdomen (Fig. 78): overall dark brown; tergite II markedly emarginated anteriorly, tergites III–V small and irregularly rounded; vestiture of large and small, coarse sparse hairs, more so posteriorly. **Genitalia** (Fig. 98): sternite VIII pigmented lightly medially, vestiture of sparse black hairs posterolaterally; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and microtrichia; median edges of hypogynial valves straight and slightly convergent, not strengthened, broadly rounded posteroapically; genital fork (Fig. 116) with anterior arm moderately substantive, membranous region not extensive, lateral arms lacking knee-bend, lateral flanges rounded posteriorly, apodeme relatively large and sharply pointed; in lateral view anal lobes low, cerci broadly rounded; spermatheca ovoid, slightly patterned, small clear area at junction of duct.

Adult male (based on 2 paratypes in ethanol and reared topotypes). **Body**: general colour brownish-black; total length 2.4 mm. **Head**: width 0.76–0.78 mm; depth 0.54–0.58 mm. **Eyes**: upper ommatidia orange and large, diameter 0.03 mm, *ca*_22 across and down; lower ommatidia dark brown, diameter 0.012 mm, *ca* 25 across and down. **Clypeus**: dark brown; width 0.15 mm; vestiture of sparse fine hairs. **Antennae**: total length 0.46 mm; evenly medium brown; scape noticeably broader than flagellomeres; not tapered. **Mouthparts**: poorly developed; length 0.37× head depth; mandibles insubstantial, broadly tapered with apical hairs; laciniae, finely tapered apically with terminal hairs; maxillary palp medium brown, 0.38 mm long, 3rd article densely haired, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 0.9 : 1.8, sensory vesicle irregular in shape, small, occupying 0.2× 3rd article width, opening 0.2× vesicle width.

Thorax: length 0.9–1.0 mm; width 0.69–0.72 mm; scutum evenly black, vestiture virtually absent except anteriorly and then sparse; scutellum concolorous with scutum with sparse long black hairs laterally; postscutellum concolorous with scutum. **Wings**: length 2.2 mm, width 1.1 mm. **Halteres**: light brown. **Legs**: overall brownish-black; hind basitarsus *ca* 5.3× as long as greatest breadth, lacking row of stout setae.

Abdomen: overall black. **Genitalia**: (Fig. 134). gonocoxites 2.5× longer than basal width, generally elongated, dark brown posteriorly, pale medially, with coarse black hairs on apical 2/3rd; gonostyli short and broad, robust, approximately 1.5× longer than basal width, apically with 3 substantial spines; ventral plate with moderately well developed median keel, even sparse vestiture of fine hairs, plate 2.2× wider than long, slightly peaked posteriorly, smoothly convex anteromedially, basal arms not markedly developed; median sclerite poorly developed, broad, slightly T-shaped posteriorly; parameres present but poorly developed.

Pupa (Fig. 152, 170). Body length; male 3.0–3.6 mm, female 2.8–3.4 mm. **Head**: cephalic plate of male (Fig. 226) 2.5× as long as basal width, tuberculate on posterior 1/2, slightly pointed apically; in female (Fig. 210) 1.6× as long as basal width, markedly expanded posteriorly; tuberculate apically, markedly concave, setae not obvious. **Thorax** (Fig. 247). dorsum with circular tubercles aggregated in band along median line, trident pattern not well defined, otherwise without definite pattern, but usually collected into sparse circular groups of 5–7 or more, often open; lacking linear array of individual tubercles posterior to gill base. **Gills** (Fig. 261, 278): horn elongated, *ca* 3.5–4.0× as long as its greatest width, expanded slightly at mid length, basally light yellow, apically black, finely scobinate with small elongated ridges, markedly variable, even to banana–shaped horn with more filaments and approaching *A. multicorne*, filaments arising from all surfaces of horn; filaments *ca* 20–23, length 0.65–1.0 mm (1.5× horn length), light yellow brown, non-tapered, surface annulated (Fig. 295). **Abdomen**. Grapnel hooks absent on sternite IX.

Cocoon (Fig. 170): overall light brown in colour, fabric (Fig. 186) of fine filaments with overlay of smooth non-alveolate material; slipper-shaped, but variable, from patellate on leaves (less so than in *A. australense*) to closely fitted around pupa on grass; anterior opening variable, ranging from markedly circular distinct opening with well defined margin, to more oval with pupa covered only to posterior scutum, with edge irregular, approaching *A. multicorne*.

Larva (based on topotype final instars). **Body**: sexual dimorphic colour; female (Fig. 313) evenly medium grayish-brown, head pattern more distinct, male with anterior abdomen and thorax pale, body more orangey, head pattern muted; total length 4.9–5.3 mm. **Head** (Fig. 331): two colour forms - one, probably female, markedly bicolorous, pale creamy yellow to translucent with dark head spots and surrounding infuscation, similar to *A. australense*; the other probably male, with head spots finely expressed and no infuscation; length 0.67–0.74 mm, width 0.50–0.52; distance between antennal bases 0.28–0.30 mm; lateral margins of head subparallel to slightly convex; anterior apotome translucent often with irregular infuscation, anteromedial spots positive medium brown, posteromedial spots slightly darker brown and fused, anterolateral spots positive but pale, 1st and 2nd posterolateral spots brown; posterior edge of apotome not darkly pigmented and not continuous laterally with dark posterior genae; ecdysial lines distinct and not sinuous, apotome broad posteriorly; postocciput well developed, cervical sclerites fused. **Antennae** (Fig. 376): brown basally, pale apically; total length 0.39–0.45 mm length, extended well beyond apex of fan stalk; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.2 : 2.2; apical article 1.8× length of combined basal 2 articles, median article small, *ca* 0.2× length of basal article. **Labral fans**: stem translucent; *ca* 38–44 fine rays, length 0.65 mm, width 0.007 mm; distinct pattern of microtrichia, longer microtrichia 1.2× longer than ray width, separated by *ca* 8 markedly small microtrichia. **Postgenal cleft** (Fig. 393): broadly inverted V-shaped, posterior tentorial pit region well sclerotised and extended. **Postgenal bridge**: 1.3× longer than hypostoma, lighter brown medially than genae; posteroventral muscles spots not elongated, barely visible. **Hypostoma** (Fig. 412): teeth small with median tooth slightly larger; all teeth concealed by ventral margin of hypostoma, 3 small rounded lateral serrations; 4 or 5 hypostomal setae each side. **Mandibles** (Fig. 429): outer teeth not well developed, apical tooth sharp, subapical teeth not markedly substantial; 10 or 11 well developed spinous teeth; serrations and sensilla complex; blade region short, smooth, and slightly convex. **Thorax** (Fig. 359): female (dark) prothorax grayish-brown, remainder of thorax pale grey, male (light) prothorax pale. Pharate pupal gills (Fig. 344, 359) with filaments angled posteriorly then recurved anteriorly and dorsally. **Abdomen**: female anterior abdomen banded grayish-brown, posteroventral abdomen pale; male anterior abdomen pale, remainder light brown: abdominal segments I–IV narrow, expanded distinctly at segment V producing slight amphora shape; distinct ventral tubercles. **Anal sclerite** (Fig. 446): anterior arms flared, not bifurcate, median region deeply emarginated anteriorly; interarm struts substantial, converged posteriorly, posterior arms finely developed, smoothly tapered apically; semicircular sclerite moderately substantial, accessory sclerite substantial, but not markedly emarginated. **Posterior circlet**: *ca* 90 rows of 13 or 14 hooks (total *ca* 1 200).

Type data. **Holotype**: in ethanol; pupal exuviae only; posterior abdomen and cephalic plate missing, part of antennal sheath present, majority of gill filaments broken; cocoon missing, parts now in BEEM capsule; label details "Holotype A. stewartense\ Bred ex pupae\ Mill ck Stewart Is" and on reverse of label "14-17/4/[19]59" (all but "Holotype" handwritten in pencil, Dumbleton), "Holotype {F} pupa\ + cocoon\ A. stewartense D" and on reverse of label "Mill ck Stewart Is\ coll L. J. Dumbleton\ 14-17/4/[19]59" (all but "Holotype" handwritten in pencil, Dumbleton), "Holotype {F} pupa" (all but "Holotype" handwritten in pencil, Dumbleton) (NZAC). **Paratypes** (5): in ethanol. 1 reared female, label details "Holotype [with "Holo" crossed out] {F} ex pupa \ A. stewartense" and on reverse of label "paratype" (all but "Holotype" handwritten in pencil, Dumbleton); 1 female and 3 males with associated pupal exuviae and cocoons, label details "Holotype [with "Holo" crossed out]\PARA [in pencil]", "BRED EX PUPAE\ Mill Ck. Stewart\ Is 14-17/4/[19]59" (handwritten in pencil, Dumbleton), "Aust. (A.) stewartense" (NZAC).

Material examined. Type material; some 35 collections from the Dumbleton Collection and TKC in NZAC, and 26 more recent collections (Appendix 1), comprising the full array of stages.

Distribution (Map 13). Not occurring in the North Island. Broadly distributed in the southern part of the South Island and Stewart Island. Apparently occurring also in the foothills of Mid Canterbury. **South Island**. **MC**. Camping Gully ck, NZS119; Pudding Hill Stm, NZS120. **OL**. Walker Ck, NZS34 (SH94). **CO**. Danseys Pass; Kye Burn trib, NZS24; Taieri R; Thompsons Ck, NZS22; Thompsons Ck trib, NZS21. **DN**. Bethunes Gully; Lee Stm, NZS26 (SH87 bridge); Lindsay Ck; Manuka Gorge; Silver Stm; Waitahuna; Water of Leith. **SL**. Bluff Camp Ground, NZS160; Catlins R, NZS27, trib; Croydon Bush; Evans Flat; Fleming R; Granity Stm trib, NZS159; Matai Stm, NZS28; Mossburn; Owaka; Purakaunui R; Tokanui; Waimeamea R, NZS30. **FD**. Alton Burn, NZS156; Borland Burn, NZS154; Lill Burn trib, NZS155; Papatotara Coast Rd, NZS157, NZS158. **Stewart Island**. Bush Ck; Christmas Village Hut; Duck Ck; Hicks Road stm, NZS172; Kaipipi Bay stm, NZS170, 170a; Little R trib, NZS168; Magnetic Beach stm, NZS166; Mason Bay; Mill Ck, NZS161, NZS162, NZS164; Oban, NZS169 (Kaka Retreat), NZS173 (Bay Motel); Port William; Rakeahua Hut ck; Ryans Ck outlet, NZS163; Sawyers Beach stm, NZS167, 167a; Table Hill Hut stm; Thule Bay culvert, NZS171; Vaila Voe Bay stm, NZN165, 165a, 165b. Big South Cape Island (Murderers Cove, Potted Head Ck).

Northernmost record: Rakaia River Gorge, Camping Gully creek, MC (latitude S43.52620°); southernmost: Big South Cape Island, Murderers Cove, SI (latitude S47.24439°), ranging from sea level to almost 900 m. The northernmost record may eventually be shown to be a variant of *A. multicorne*, and if this proves to be the case then the Waitaki River (latitude S44.9381°) appears to be the northern extent of *A. stewartense*.

— / MC, OL, CO, DN, SL, FD, SI / —

In the South Island, the localities fall mainly in the High Country ecoregion; a few are in that of the Southern Alps. Those in Stewart Island are in Westland Forest and Southeast Forest ecoregions.

Etymology. Named by Dumbleton (1973) after Stewart Island, the type locality.

Bionomics. Dumbleton makes little comment beyond habitat characteristics. Label data on collections indicate that larvae and pupae can be found between January and mid April, but adults are also; suggesting either an extended life cycle, or more than one generation a year. On Stewart Island recent collections in November returned all stages, indicative of an unsynchronised life cycle. In the South Island, typical habitats are smaller streams, with rock and trailing vegetation; immature stages can be on either. Only a few localities had water temperatures above 20°C, most ranged from 11 to 15°C. The pH tended to be neutral to just below, with conductivity ranging from 10 to 200 µS/cm. Velocity preference tended to be higher than for most other species, 0.90–1.20 m/s.

Habitats on Stewart Island differ from most on the South Island. Many streams run through peat and larvae are on trailing vegetation; or the streams have granite-based sand as a substrate with large moss-covered boulders, again with trailing vegetation. In both the water is brown and most streams are densely shaded (Fig. 464, 479–481). The Sawyers Beach stream (Fig. 466), also type locality for *A. extendorum*, is so far unique on Stewart Island. There, cobble extends down to the sea and larvae can be found on stones right to high tide mark — uncharacteristic for simuliids (Crainey & Post 2010). Larvae were never recovered from the rough granite cobble, only the smoother andersite. This was discussed elsewhere (p. 125).

Larvae and pupae of *A. stewartense* can occur abundantly in monospecific populations, but on occasion with those of both *A. australense* and *A. ungulatum*. Larvae of *A. stewartense* are parasitised by *Coelomycidium* (Fig. 499). The female adults of *A. stewartense* are voracious biters, and they, in concert with those of *A. ungulatum,* can be a serious nuisance at times, even indoors.

Remarks. This species is difficult to define taxonomically. Pupae of *A. stewartense,* while the main stage for diagnosis, are quite variable; larvae are less so, but are of less use. Further work may well show this species to be a complex, similar to other members of the *tillyardianum*-subgroup. Populations that need reexamination are those from the Catlins, SL (*e.g*., NZS29). Although pupae from there have been assigned to *A. multicorne*, larvae are distinctly similar to *A. stewartense*. Another population, collected by Dumbleton from Mossburn, OL, has specimens with broad pupal gills and would meet the lower range of that for *A. laticorne*, but the filament number and the cocoon indicate these specimens are assignable to *A. stewartense*.

Analysis of the CO1 gene arbitrarily groups haplotypes of *A. stewartense* with those of other species of the *tillyardianum*-subgroup (Fig 508a, 508b), similar to what occurs with *A. multicorne*. An expectation might have been to have a distinct divergence between the Stewart Island material and that of the South Island. That there is not is in agreement with the difficulty of taxonomically defining this species.

Austrosimulium (*Austrosimulium*) *tillyardianum* Dumbleton, 1973

Figures: female, frontispiece, 33, 44, 45, 59, 68, 79, 99, 117; male, 135; pupa and cocoon, 153, 171, 187, 200, 201, 211, 227, 236, 248, 262, 279, 296; larva, 314, 332, 345, 360, 377, 394, 413, 430, 447, 454; habitat, 482–485; Map 14.

tillyardi Tonnoir, 1925: 253 (description male, female, larva, pupa, cocoon, *Austrosimulium*). Pulikowsky 1929: 656 (respiratory gills). Rubtzov 1940: 117. Smart 1945: 499 (world catalogue). Mackerras & Mackerras 1948: 246; 1949: 404. Grenier 1949: 201, fig. 23 (*Simulium* (*Austrosimulium*); name *tillyardi* not used, but figure corresponds to figure given by Tonnoir 1925: 226, fig. 10F for *tillyardi*). Miller 1950: 61 (catalogue). Hennig 1950: 384. Gurr 1953: 81. Wisely 1962: 213. Dumbleton 1953: 244 (comparison with larva of *campbellense* (as *vexans*)). Peterson 1956: 500. Dumbleton 1963b: 334 (as subgenus *Austrosimulium* (*Austrosimulium*), in *australense* group). Dumbleton 1964a: 35 (relationships, distribution). Wise 1965: 208. Craig 1966: Chpt. 3, 23. Dumbleton 1969: 485. Stout 1969: 491. Dumbleton 1970: 20 (distribution). Crosby 1971: 21. Stout 1975: 442. Chubareva & Petrova 1975: 552 (salivary gland chromosomes).

tillyardianum Dumbleton, 1973: 513, replacement name for *tillyardi* Tonnoir, 1925: 253 (*Austrosimulium* (*Austrosimulium*), junior secondary homonym of *tillyardi* Tonnoir, 1923a: 165 (= *australense* Schiner, 1868: 15). Crosby 1974b: 5 (redescription all stages). Crosby 2006: 72 (key). Adler & Crosskey 2012: 20 (world inventory).

Not *tillyardianum,* species referred to is *Austrosimulium* (*A.*) *australense* (Schiner): *Simulium tillyardi* Tonnoir, 1923a: 165; 1923b: 85. Puri 1925: 301. Wu 1931: 552. Bequaert 1934: 189. Smart 1934: 236. Usova 1955: 846. Burton 1966: 48.

Diagnosis. **Female**: tarsal claw lacking basal tooth, hind basitarsus with row of stout setae: abdominal tergites III–V subquadratic. **Male**: lacking row of stout setae on hind basitarsus. **Pupa**: thoracic cuticle with rounded granules in groups, paramedial ridge, gill of short black horn with 15–20 coarse slightly tapered filaments; sternite IX lacking grapnel hooks. **Cocoon**: shoe-shaped, closely fitted to pupa, finely woven, not flared basally, anterior opening broad, 2 ill-defined dorsal longitudinal ridges. **Larva**: pale; cephalic apotome markedly translucent, posteromedial and posterior head spots distinct, irregular grey pattern on apotome and genae; ventral tubercles marked, anal sclerite substantial, semicircular sclerite substantial with accessory sclerites distinct.

Adult female (based on topotype material). **Body**: general body colour in ethanol dark reddish brown-black, when dry dull black and under some lighting showing pollinosity; total length 2.6–3.1 mm. **Head**: width 0.7–0.8 mm; depth 0.45–0.50 mm; postocciput black, vestiture of sparse, short black hairs; frons dark brown-black; frons width : head width ratio 1.0 : 4.3. **Eyes**: interocular distance 0.16–0.19 mm; ommatidia 0.013 mm in diameter; *ca* 38 rows up and across at mid-eye. **Clypeus**: dark brown; 0.22–0.24 mm wide; vestiture of sparse black and pale hairs. **Antennae**: total length 0.50–0.53 mm; evenly pale yellowish-brown. **Mouthparts**: substantial, 0.5× length of head depth; cibarial cornuae (Fig. 33) broad, substantial, with faint fluting and small black tubercles, medial depression flat; mandibles with 35 inner teeth, increasing in size towards apex; laciniae with 15 inner teeth and 20 outer teeth; maxillary palp, total length 0.55 mm, 3rd article dark brown, remainder lighter, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.7 : 1.2, sensory vesicle ovoid, 0.5× 3rd article width, opening 0.5× vesicle width.

Thorax: length 1.1–1.4 mm; width 0.96 mm; in ethanol, postpronotal lobes marginally paler than scutum; scutum evenly dark reddish-brown, vestiture of sparse recumbent hairs, presutellar depression with few longer darker hairs posteriorly, no vittae visible in ethanol, when dry a median and 2 lateral vittae overlain with silvery pruinosity show; scutellum slightly lighter than scutum, vestiture of few long black hairs and pale hairs laterally; postnotum concolorous with scutum; pleuron and pleural membrane concolorous with scutum. **Wings**: length 2.8–3.2 mm; width 1.3 mm. **Halteres**: tan. **Legs** (Fig. 44): yellowish-brown, with darker brown bases to femoral, tibial, and tarsal segments; hind basitarsus *ca* 6× as long as its greatest width, with ventral row of stouter setae; tarsal claws rapidly tapered, with massive heel (Fig. 59).

Abdomen (Fig. 79): abdominal scale dark brown with fine pale hairs, not greatly extended; tergite II markedly broad, 5× wider than long, tergite III wider than long, tergites IV–V quadratic, tergite VII and tergite VIII subequal in size to tergite II; vestiture of sparse hairs; medium brown, posterior abdomen darker, sternum paler. **Genitalia** (Fig. 99, 117): sternite VIII pigmented medially and along anterior edge, vestiture of coarse black hairs posterolaterally; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and triads of microtrichia; median edges of hypogynial valves not strengthened, smoothly divergent, broadly rounded posteroapically; genital fork with anterior arm distinct, lateral membranous areas not marked, posterolateral arm with distinct knee-bend, rounded posteromedially, apodeme coarsely cone-shaped; anal lobes and cerci both broadly rounded in lateral view and darkly pigmented; spermatheca ovoid, internal hairs moderately distinct, small clear area at junction of duct.

Adult male (holotype and reared topotypes). **Body**: general colour, dull black, under some lighting with pollinosity; total length 2.5–3.0 mm. **Head**: width 0.76–0.78 mm; depth 0.52–0.56 mm. **Eyes**: upper ommatidia blackish-red, large, 0.032 mm in diameter, *ca* 28 across and 20 down;

lower ommatidia blackish-red, 0.018 mm in diameter, *ca* 38 across and 48 down. **Clypeus**: dark brown; vestiture of very sparse fine dark hairs; 0.15 mm wide. **Antennae**: total length 0.50 mm; evenly dark brown. **Mouthparts**: poorly developed; length 0.33× head depth; mandibles insubstantial, broadly tapered with apical hairs; laciniae, finely tapered apically with terminal hairs; maxillary palp 0.42 mm long, 3rd article black, remainder gray, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 1.1 : 2.0, sensory vesicle irregular in shape, occupying 0.33× width of article, opening 0.30× width of vesicle.

Thorax: length 1.1 mm; width 0.8 mm; scutum evenly dark reddish brown-black, vestiture of fine recumbent pale hairs, brassy yellow, longer dark hairs in prescutellar depression; scutellum concolorous with scutum with sparse long black hairs; postscutellum concolorous with scutum; under some lighting all with pollinosity. **Wings**: length 2.2–2.5 mm, width 1.1 mm. **Halteres**: grayish-brown. **Legs** (Fig. 45): yellowish-brown, with darker brown femoral, tibial, and tarsal bases; hind basitarsus *ca* 6× as long as greatest breadth; lacking row of stout setae; tarsal claw grappling pads (Fig. 68) of *ca* 22 teeth.

Abdomen: abdominal scale markedly developed, hairs extended to 1/2 length of abdomen; dull blackish-brown dorsally; sternum gray and markedly pollinose. **Genitalia** (Fig. 135): gonocoxites 1.5× longer than basal width, dark brown posteriorly, pale medially, with coarse black hairs; gonostyli *ca* 2.8× longer than basal width, apically with 3 spines, 2 substantial, 1 less so; ventral plate with low median keel, sparse vestiture of coarse hairs, 1.7× wider than long, rounded posteriorly, convex anteromedially, basal arms substantial; median sclerite slightly more developed than elsewhere, broadly T-shaped posteriorly; parameres poorly developed but obvious.

Pupa (Fig. 153, 171) Body length; male 3.0–3.5 mm, female 2.5–2.7 mm. **Head** (Fig. 200, 201, 211, 227): cephalic plate of male strongly tuberculate on upper frons, that of female tuberculate laterally only, concave; paler muscle spots distinct, more so in male. Frontal setae absent; facial setae present, 1 on each side between antennal bases; 2 short epicranial setae. **Thorax** (Fig. 236, 248). Dorsum densely tuberculate, not markedly in groups, but contiguous forming marked trident-shaped pattern; setae trichoid. **Gills** (Fig. 262, 279): horn short, *ca* 2× as long as greatest width; basally light yellow, apically black, covered with trabeculae; 12–20 filaments, length 0.75–1.1 mm, light yellow brown, thick, stiff, tapered from mid length, inwardly curved; surface reticulated (Fig. 296). **Abdomen**. grapnel hooks absent from sternite IX.

Cocoon (Fig. 171, 187): fabric closely woven, finely alveolate, thin, light yellowish-brown; slipper-shaped, not markedly flattened; 2 ill-defined dorsolateral ridges arising from posterior apex and ending at anterior opening.

Larva (based on topotype final instars). **Body** (Fig. 314): colour sexual dimorphism not apparent; markedly bicolorous, pale, banded with gray; total length 5.3–5.8 mm. **Head** (Fig. 332): overall pale creamy yellow to translucent with pale head spots and grayish pigmentation anterodorsally; length 0.65–0.69 mm, width 0.55–0.59 mm; distance between antennal bases 0.28 mm; lateral margins of head smoothly convex; anterior apotome translucent, head spot pattern not marked, anteromedial spots positive pale brown, posteromedial spots fused and positive brown, anterolateral spots positive, but pale, 1st and 2nd posterolateral spots neutral; posterior edge of apotome darkly pigmented, continuous with posterior genae; usually irregular gray pigmentation lateral of median head spots and medially extended anteriorly; ecdysial lines sinuous, narrowest anterior of stemmata; postocciput not markedly pigmented, cervical sclerites appear separate, not markedly pigmented. **Antennae** (Fig. 377): dark brown basally, pale apically; total length 0.41 mm, extended well beyond apex of fan stem; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.1 : 2.4; apical narrow article long, 2.2× length of combined basal 2 articles; medial article short, 0.1× length of basal article. **Labral fans**: stem translucent; 40–45 fine rays, length 0.6 mm, width 0.004 mm; distinct pattern of microtrichia, longer microtrichia 1.2× longer than ray width, separated by *ca* 8 microtrichia rapidly decreasing in length. **Postgenal cleft** (Fig. 394): V-shaped, with broad apex, posterior tentorial pit region well sclerotised and pigmented. **Postgenal bridge**: 1.6× longer than hypostoma, pale, concolorous with genae, elongated posteroventral muscle spots light brown; genae often with irregular grayish pigmentation. **Hypostoma** (Fig. 413): median and lateral teeth sharp; lateral teeth prominent; 2 sublateral teeth subequal in size to median tooth, with middle tooth 1/2 size of others; 2 paralateral teeth, lateral tooth smaller; all teeth largely concealed by anteroventral margin of hypostoma, 3 poorly developed rounded lateral serrations, variable; 5 or 6 hypostomal setae per side. **Mandibles** (Fig. 430): outer teeth not markedly developed, apical tooth narrower and smooth, 3 subapical teeth substantial, *ca* 11 irregular spinous teeth; serration and sensillum distinct, not complex; blade region short, smooth, and slightly convex. **Thorax** (Fig. 345, 360): prothorax grayish-brown, remainder of thorax pale gray; mature pharate pupal gills distinctive, with small basal black horn and 5 or 6 dark gray, substantial filaments visible. **Abdomen**: anterior abdomen banded grayish-brown, posteroventral abdomen pale. **Anal sclerite** (Fig. 447): substantial; anterior arms flared, not bifurcate; median region well tapered; interarm struts and ventral arms substantial, the latter bluntly tapered; semicircular sclerite well developed, accessory sclerites well emarginated. **Posterior circlet**: *ca* 95–120 rows of 14–18 hooks (total *ca* 1850).

Type data. **Holotype**, male. Double pinned on minuten through acetate sheet; condition good, complete, slightly collapsed: label details "Nelson [Maitai R.] N.Z.\ vi.[19]23\ A. Tonnoir\ Bred" (date and "Bred" handwritten in black ink, "Bred" on label edge at right angle to other 3 lines, Tonnoir), "Austrosimul. {M}\ tillyardi Tonn.\ Type" (handwritten in black ink, "Type" with wavy underline, Tonnoir), "NZ Arthropod Collection\barcode \ NZACO4021451" (NZAC). **Paratypes** (8): 1 female, on elbow pin (MacGillivray 1903). "Nelson [Maitai R.] N.Z.\ vi.[19]23 \ A. Tonnoir\ Bred" (date and "Bred" handwritten in black ink, "Bred" on label edge at right angle to other 3 lines, Tonnoir), "Austrosimul \ tillyardi {F}\ Tonn.\ Allotype" (handwritten in black ink, "Allotype" with wavy underline, Tonnoir), "NZ Arthropod Collection\ {barcode}\ NZAC04022144"; 4 males, on minuten through acetate sheet, "{M}" (acetate sheet, male symbol handwritten in black ink, Tonnoir), "Nelson N.Z.\ vi.[19]23\ A. Tonnoir\ Bred" (date and "Bred" handwritten in black ink, "Bred" on label edge at right angle to other 3 lines, Tonnoir), "PARATYPE.\ Austrosimulium\ tillyardi n. sp.\ A. Tonnoir det." (blue label, lines 2 and 3 handwritten in black ink, Tonnoir), "NZ Arthropod Collection\ {barcode}\ NZAC04022020"; also with "NZAC04022114", "NZAC04022150", and "NZAC04022153" (NZAC). 2 males, "Nelson N.Z. \ vi.1923 \ A. Tonnoir", "PARATYPE.\ Austrosimulium\ tillyardi {M} n. sp.\ A. Tonnoir" (1 lacking male symbol); 1 female, label data as for males, but with {F} (MONZ). [See *A. australense*, p. 103, for 4 *tillyardi* Tonnoir, 1925 paratype specimens reassigned to *tillyardi* Tonnoir, 1923 and now paralectotypes for that name].

Material examined. All stages and reared adults. Type material; some 47 samples in Dumbleton's and TKC material in NZAC, and 113 more recent collections (Appendix 1).

Distribution (Map 14). Widely distributed on both islands, but absent from the northerly and southerly extremes of either island. Absent from Stewart Island. **North Island**. **AK**. Mangatangi Stm, NZN11 (Hunua Ra); Orere Stm, NZN10 (bridge). **CL**. Apakura Stm, NZN7 (SH26, Waiho Forest Reserve); Tairua R, NZN3 (SH25a Puketui road); Waitawheta R, NZN8 (Karangahake Gorge). **WO**. Mangatoa Stm, NZN20 (Mangatoa Scenic Reserve); Rangitukia Stm, NZN17 (Pirongia). **BP**. Maraehako Stm, NZN65; Matamata; Omaukora Stm, NZN59 (SH2 bridge); Waimana R, NZN58, NZN67 (bridge); **TO**. Hautu Prison Farm; Hinemaiaia R (Hatepe); Mangaio Stm, NZN48; Mangateitei Stm, NZN120 (Ohakune); Mangatoetoenui Stm, NZN49a, 49b; Mangawhero Stm trib, NZN108; Papamanuka Stm, NZN106 (SH47 bridge); Tongariro R, NZN23 (Walkway), NZN104 (Red Hut bridge); Waipunga R, NZN50. **GB**. Mangahauini R, NZN62; Maraehara R, NZN63; Waihuka R, NZN60 (walkway). **HB**. Esk R, NZN51; Eskdale stm; Inangatahi Stm (Puketitiri); Kakekino Stm, NZN45; Mangaonuku Stm (SH50); Ngaruroro R, NZN44; Norsewood; Ohiwa Stm trib, NZN41; Tukipo R; Tukituki R; Tutaekuri R, NZN42; Waikare R, NZN53. **WI**. Bulls; Onga Stm, NZN29 (SH1). **RI**. Hunterville; Makotuku R (Raetihi); Manawatu R, NZN38 (SH2 Norsewood); Mangateitei Stm, NZN47 (Ohakune); Mangawharariki R trib, NZN31; Rangitikei R, NZN30 (Mangaweka), NZN91 (Mokai Road); Tangarewai Stm, NZN39; Waipawa R, NZN40 (SH50). **WN**. Abbots Ck, NZN34 (SH2); Ballance stm; Pakuratahi R, NZN88 (SH2); Skerrits Ck; Takapua Stm, NZN86 (Tawa); Te Horo. **WA**. Blue Rock Stm, NZN87; Cross Ck; Makakahi R, NZN35; Mangatoro R trib, NZN37; Te Hoe Stm, NZN130. **South Island**. **SD**. Kenepuru Head stm, NZS2, 2a; Waikawa Stm, NZS107. **NN**. Brown Ck, NZS81; Buller R (Harleys Rock); Buller R trib (Glenhope Scenic Reserve); Cable Bay; Clark R; Cobb R, NZS93; Graham Stm, NZS106 (SH6); Lyell Ck, NZS82; Maitai R, NZS6, Forks; Motueka R, NZS90; Motupiko R, NZS89; Paturau R, NZS100; Poorman Valley Stm, NZS7, NZS116 (bridge); Riwaka, NZS186 (Moss Bush Scenic Reserve); Roding R, NZS104, 105; The Brook (Nelson); Wairoa R gorge. **BR**. Black Valley Stm, NZS88; Buller R, NZS85 (Gowanbridge); Doctor Ck, NZS83; D'Urville R; Grey R, NZS69 (SH7 bridge); Inangahua R, NZS68 (SH7 Reefton); Owen R, NZS84 (SH6); Porika Stm; Station Ck. **WD**. Taramakau R, NZS51. **MB**. Awatere R (Molesworth); Black Birch Stm, NZS182; Boyle R, NZS64 (SH7); Dog Stm, NZS63 (SH7a); Fuchsia Stm; Netherwood Stm, NZS184 (Waihopai Valley); Nina Brook, NZS183 (Awatere Valley); Pelorus R, NZS5; Waihopai R, NZS185; Wairau R trib (Chinamans Ck); Wakamarina R, NZS4. **KA**. Conway R, NZS118 (SH1); Green Burn, NZS12; Hundalee; Kahutara R; Kaikoura; Kekerenga R, NZS9; Kowhai R, NZS11 (SH1 bridge); London Ck, NZS8; Mason R, NZS13, 13a (SH70); Mororimu Stm, NZS10 (SH1); Ohau Stm, NZS109 (SH1); Puhi Puhi R; Puhi Puhi R trib, NZS108a. **NC**. Ashley Gorge; Ashley R, NZS61 (SH1 bridge); Cave Stm (Broken R Ski Field); Coopers Ck; Glentui R; Manson Ck; Okuku R; Pahau R, NZS62, NZS112; Spotswood; Waipara R, NZS113 (SH1 bridge); Weka Pass. **MC**. Akaroa; Bowyers Stm, NZS16; Camping Gully ck, NZS119; Cave Stm (cave exit); Coleridge Stm; Hawkins R; Kaituna R, NZS60, NZS135; Kowai Bush; Kowai R; Lake Heron (Emily Stm, NZS123; Gentleman Smith Stm, NZS136; Olliver Stm, NZS122, 122a); French Farm Bay stm; Little River; Methven; Menzies Bay; Mt

Herbert; Okeover Stm; Opara Stm, NZS59; Pudding Hill Stm, NZS120; Purau; Selwyn R; Stour R (bridge), NZS121, 121a; Wainui stm, NZS58 (Banks Peninsula); Woolshed Ck, NZS139. **SC**. North Branch Ashburton R; Opihi R (Burkes Pass); Opuha R, NZS17; Otaio R; Pareora Gorge; Peel Forest stm; Scour Stm, NZS124; Soup Stm, NZS126, 126a (Rangitata R Valley). **MK**. Ahuriri R, NZS20 (SH83); Tasman R trib, NZS19 SH80). **CO**. Clutha R (now Clyde Dam site); Gabriels Gully; Gorge Ck; Kyeburn; Lindis R, NZS44 (SH8); Manuherikia R. NZS38 (SH85); Pigroot Ck; Roaring Meg, NZS37 (SH6); Taireri R; Tent Hut stm; Thompsons Ck, NZS22; Thompsons Ck trib, NZS21.

Northernmost record: Orere Stm bridge, NZN10, AK (latitude S36.98754); southernmost record: Alexandra, Gabriels Gully, CO (latitude S45.88209°), ranging from near sea level to 1 070 m a s l. Recent collections have extended the northerly range considerably — Dumbleton recorded *A. tillyardianum* only as far north as Turangi (latitude S38.99223°).

— / AK, CL, WO, BP, TO, GB, HB, WI, RI, WN, WA/ SD, NN, BR, WD, MB, KA, NC, MC, SC, MK, CO / —

In the North Island *A. tillyardianum* occurs in all ecoregions with the exception of Mt Taranaki Forest and perhaps Hauraki Plains, but these ecoregions have been poorly collected and the latter heavily impacted by agriculture. In the South Island *A. tillyardianum* occurs more in the north and eastern ecoregions, being nearly absent from those of Westland Forest, Southern Alps, Southeast Forest, and Central Otago; it is not common in the High Country.

Etymology. Named by Tonnoir (1925) to honour R. J. Tillyard, a honorific retained by Dumbleton (1973).

Bionomics. *Austrosimulium tillyardianum* is the best understood simuliid in New Zealand. Crosby (1974a) made extensive studies of this species at Wainui, Banks Peninsula.

Under ideal conditions, larvae of *A. tillyardianum* can occur in astronomical numbers. In the Maitai River at Branford Park (NZS6b), the substrate of the river was coated with larvae and pupae, leaving little room for other macroinvertebrates. It is perhaps appropriate then that the early attempts to control New Zealand simuliids were in Nelson (see p. 32). Female *A. tillyardianum* bite and can be extremely bothersome along river valleys. They do not appear to fly great distances from running water, but see Craig & Crosby (2008) regarding gynandromorphs. Dumbleton noted that immature stages of *A. tillyardianum* were stone loving. Typical habitats are shingle-bedded streams and rivers in full sun and clear of major growths of periphyton (Fig. 482–484), but boulder substrate is not uncommon (Fig. 485). Water temperatures range from 9 to 22°C, with the majority between 13 and 18°C. The pH ranges from 6.9 to 9.9, but tends to be just alkaline. Conductivity ranges from 20 to 530 µS/cm, but mainly from 50 to 100 µS/cm. Water velocities are lower than for some other species at 0.33–0.80 m/sec, but up to 1.60 m/sec has been recorded.

Remarks. The taxonomic history of this species is relatively complex, in large part because Tonnoir confused species. See Dumbleton (1973), Crosby (1974a, b), and p. 99 for detailed accounts.

Austrosimulium tillyardianum is relatively easy to distinguish from other species on the basis of the pupal gill and lack of tuberculation on the pupal thorax.

Chubareva & Petrova (1975) examined the salivary gland chromosomes of *A. tillyardianum* (as *A. tillyardi*) that had been collected by TKC in early 1970 from his Wainui study site and supplied to Rubtsov in St. Petersburg (then Leningrad). They had little to report beyond that they considered *Austrosimulium* to be plesiomorphic, and that the chromosomes showed little similarity to those of other simuliids.

There was an expectation that the Banks Peninsula populations of *A. tillyardianum* might show morphological subspecific differences, but none were detected. The reason for such an expectation was that Banks Peninsula has a precinctive aquatic fauna — a blephariceric, *Neocurupira chiltoni* (Campbell) (Dumbleton 1963a; Craig 1969), unique for New Zealand in that it has spines on the larva, 5 species of hydrobiosid caddisflies, a stone fly (*Zelandobius wardi* McLellan), and a mayfly (*Nesameletus vulcanus* Hitchings & Staniczek) (Winterbourn 2008). Given that volcanicity of Banks Peninsula commenced in the late Tertiary (15 Mya, late Early Miocene) (Bradshaw & Soons 2008) the precinctive fauna may well represent older colonisation by aquatic macroinvertebrates than that by *A. tillyardianum*.

Molecular analysis of the CO1 gene poorly segregates haplotypes of species assigned to the *tillyardianum*-subgroup. However, for *A. tillyardianum* considerable numbers of haplotypes do group together, still, with little or no support (Fig. 508a, 508b). Certainly North Island and South Island haplotypes do not aggregate. For Banks Peninsula, with two populations analysed (NZS58, Wainui; NZS59 Okains Bay), that from Wainui appears to have two haplotypes, well separated in the analysis. On the other hand, one of those haplotypes from Wainui had 2 specimens analysed and they are clumped together, so, at some level the analysis can discriminate. Overall the molecular analysis does not detract from the assumption that *A. tillyardianum* on Banks Peninsula is a relatively recent arrival.

The sister lineage to the *tillyardianum*-subgroup is *A. tillyardianum*, NZS62 (Pahu River, Canterbury), separated from the remainder of the subgroup with high support (Fig.

508a, 508b). This is in keeping with the assumption that the origin of the *tillyardianum*-subgroup was the South Island.

ungulatum species-group

ungulatum-subgroup

Austrosimulium (*Austrosimulium*) *campbellense* Dumbleton, 1973

Figures: female, 34, 60, 80, 100, 118; male, 136; pupa and cocoon, 154, 172, 188, 228, 237, 249, 263, 280, 297; larva, 314a, 333, 346, 361, 378, 395, 414, 431, 448; habitat, 488; Map 5.

campbellense Dumbleton, 1973: 535 (description pupa, redescription larva; with female, male, and cocoon not separable from *vexans* from Auckland Is; *Austrosimulium*). Joy & Death 2000: 115 (ecological survey). Adler & Crosskey 2012: 20 (world inventory).

"sandflies": Hudson 1909: 66 (never troublesome, 1 biting).

As *vexans* Mik, 1881, for presence on Campbell I. Lamb 1909: 124 (in part, *Simulium*). Tonnoir 1925: 250 (*Austrosimulium*). Miller 1950: 61. Dumbleton 1953: 242 (description of larva). Harrison 1955: 214. Dumbleton 1963b: 334 (as subgenus *Austrosimulium* (*Austrosimulium*), in *ungulatum* group). Dumbleton 1964a: 35 (relationships, distribution). Harrison 1964: 304. Gressitt 1964: 542, 576 (wind traps). Wise 1965: 208.

Diagnosis. A large, but markedly variably-sized species. **Female**: tarsal claw with basal tooth: abdominal tergites III–IV subquadratic–rounded, vestiture of coarse black hair, hind basitarsus lacking row of stout setae. **Pupa**: thoracic cuticle with evenly distributed rounded granules, gill of black short horn with 6–9 non-tapered filaments; sternite IX possessing grapnel hooks. **Cocoon**: near *A. vexans*. **Larva**: ventral tubercles marked, anal sclerite ends tapered.

Adult female (based on older collected specimens in ethanol). **Body**: general body colour in ethanol dark brown-black, when dried with silvery pruinose appearance; total length 2.9–3.7 mm. **Head**: width 0.64–0.66 mm; depth 0.64 mm; postocciput black, vestiture of sparse, short black hairs; frons dark brown-black; frons width : head width ratio 1.0 : 4.4. **Eyes**: interocular distance 0.15–0.16 mm; ommatidia diameter 0.015 mm; *ca* 30 rows up and across at mid-eye. **Clypeus**: width 0.22–0.24 mm; dark brown; vestiture of sparse black and pale hairs. **Antennae**: length 0.48–0.59 mm; all flagellomeres dark brown, bead-like, except ovoid terminal one; pedicel subequal in size to 1st flagellomere, dark brown, as is scape. **Mouthparts**: markedly substantial, 0.9× length of head depth; cibarial cornuae narrowed and not markedly flared, ornamentation absent, median depression broad; mandibles with 27 inner teeth, 7 basal teeth markedly smaller; laciniae with 15 inner teeth and 24 outer teeth; maxillary palp, total length 0.65 mm, 3rd article markedly elongate, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.7 : 1.1, sensory vesicle, ovoid, small, 0.25× 3rd article width, opening 0.3× vesicle width; cibarium cornuae finely curved, no markings, central depression convex (Fig. 34).

Thorax: length 0.96–1.2 mm; width 0.90 mm; in ethanol, postpronotal lobes marginally paler than scutum; scutum evenly dark reddish-brown, vestiture of sparse recumbent hairs, presutellar depression with few longer darker hairs posteriorly, no vittae visible in ethanol, but when dried with median and 2 lateral vittae overlain with silvery pruinosity; scutellum slightly lighter than scutum, vestiture of few long black hairs and pale hairs laterally; postnotum concolorous with scutum; pleuron and pleural membrane concolorous with scutum. **Wings**: length 2.8–3.8 mm; width 1.4 mm. **Halteres**: white. **Legs**: yellowish-brown, with darker brown bases to femoral, tibial, and tarsal segments; hind basitarsus about 6× as long as greatest width, lacking row of stout setae; tarsal claws (Fig. 60) not markedly curved, possessing small basal tooth (claw : tooth ratio = 1 : 3.8) with indistinct basal notch, distinct inner serrations on claw.

Abdomen (Fig. 80): abdominal scale dark brown with fine dark hairs, extended only to 1/2 length of segment II; tergite II, 2.0× wider than long, markedly deep, similar to *A. vexans*, tergites III to V small and rounded, all with vestiture of sparse, black hairs. **Genitalia** (Fig. 100): sternite VIII lightly pigmented anterolaterally, vestiture of sparse black hairs posterolaterally; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and microtrichia rows; median edges of hypogynial valves strengthened anteriorly and smoothly convergent, meeting apically, broadly rounded; genital fork (Fig. 118) with anterior arm markedly broad and ill-defined, fluted anteriorly, posterolateral arms lacking knee-bend; posterolateral extension with markedly sharp apodeme, similar to *A. vexans*; anal lobes with anteromedial facet darkened with few short substantial hairs on raised bases, lobes and cerci both broadly rounded in lateral view and black; spermatheca ovoid, dark, similar to *A. dumbletoni*.

Adult male (based on mature pharate specimens). **Body**: general colour brownish-black; total length 2.5–3.0 mm. **Head**: width 0.76 mm; depth 0.52 mm. **Eyes**: upper ommatidia orange, diameter 0.032 mm, *ca*_28 across and 20 down; lower ommatidia dark brown, diameter 0.018 mm, *ca* 38 across and 48 down. **Clypeus**: dark brown; vestiture of very sparse fine hairs; width 0.15 mm. **Antennae**: total length 0.50 mm; evenly medium brown. **Mouthparts**: poorly developed; length 0.33× head depth; mandibles insubstantial, broadly tapered with apical hairs; laciniae finely tapered apically with terminal hairs; maxillary palp medium brown, 0.42 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 1.1 : 2.0, sensory vesicle irregular in shape, occupying 0.33× 3rd article width, opening 0.3× vesicle width.

Thorax: length 1.1 mm; width 0.8 mm; scutum evenly dark reddish brown-black, vestiture of fine recumbent pale hairs, scutum brassy yellow when dried; longer dark hairs in prescutellar depression; scutellum concolorous with scutum with sparse long black hairs; postscutellum concolorous with scutum. **Wings**: length 2.2–2.5 mm, width 1.1 mm. **Halteres**: colour unknown. **Legs**: light yellowish-brown, with darker brown femoral, tibial, and tarsal bases; hind basitarsus about 5.5× as long as greatest width; row of stout setae absent.

Abdomen: tergites and sternites blackish-brown, lateral areas dull black. **Genitalia** (Fig. 136): gonocoxites subequal in length to basal width, dark brown along anterior edge, pale medially, with sparse coarse black hairs, marked crenulations anteromedially; gonostyli *ca* 2.3× longer than basal width, finely tapered apically with 2 substantial spines; ventral plate with substantial medial keel, sparse vestiture of fine hairs, as wide as long, posterior apex rounded, anteromedially markedly convex, basal arms not substantial; median sclerite poorly developed, broad; parameres poorly developed, but distinct.

Pupa (Fig. 154, 172): (old ethanol specimens). Body length: male 2.3–2.5 mm, female 2.8–3.0 mm; maximum width, male 0.90, female 0.96 mm. **Head**: cephalic plate of male (Fig. 228) not concave, broad, 1.8× longer than basal width; female cephalic plate unknown; frontal, facial, and epicranial setae long; ocular setae substantial. **Thorax** (Fig. 237, 249). Dorsum evenly tuberculate, pattern absent; setae trichoid and elongate, posterior dorsocentral seta spine-like (broken in illustration). **Gills** (Fig. 237, 263, 280): black horn markedly small, small black area at base of ventral filaments and again at base of all filaments; 1 short basal filament directed anterolaterally; a dorsal group of filaments, sometimes 1 bifurcate, variable in number (3 or 4); a ventral group of 3 to 5 filaments, ventromedial filament markedly short; total filament number variable 6–9; maximum length 0.5–0.6 mm; thick, stiff, not markedly tapered, inwardly curved; surface reticulated (Fig. 297). **Abdomen**. Grapnel hooks and 2 simple setae on each side of sternite IX.

Cocoon (Fig. 154, 172, 188): fabric coarsely woven, brown, slipper-shaped, not markedly flattened, anteroventral lip well developed, pupa well covered anteriorly, 2 anterodorsal cornuae relatively short and broad, often angulate apically, not noticeably continued at junction with cocoon.

Larva (based on numerous older final instar specimens and some newer material). **Body (Fig. 314a)**: total length 4.9–6.9 mm. **Head** (Fig. 333): evenly light brown, head spots pattern barely apparent, but positive; length 0.64–0.72 mm, width 0.58–0.62 mm; distance between antennal bases 0.26–0.32 mm; lateral margins of head convex; anterior apotome clear, posterior edge of apotome pigmented medially; ecdysial lines broadly rounded posteriorly; postocciput not markedly pigmented, cervical sclerites fused to postocciput. **Antennae** (Fig. 378): clear brown basally, pale apically; total length 0.38 mm, extended well beyond apex of fan stem; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.3 : 2.1, narrow apical article relatively short at 1.6× length of combined basal 2 articles, medial article 0.3× as long as basal article; proportions variable. **Labral fans**: stalk clear; *ca* 40 fine rays, length 0.55 mm, width 0.009 mm; markedly distinct pattern of microtrichia with longer microtrichia 1.2× longer than ray width, separated by *ca* 12 rapidly decreasing in size microtrichia. **Postgenal cleft** (Fig. 395): small and with jagged depression, posterior tentoral pits elongate, markedly sclerotised and pigmented. **Postgenal bridge**: 1.5× longer than hypostoma, pale medially, darker laterally, elongated posteroventral muscles spots barely darker than background; genae light brown. **Hypostoma** (Fig. 414): median and lateral teeth subequal in length; 2 sublateral teeth subequal in size to median tooth, middle tooth 1/2 size of others; 2 paralateral teeth, lateral most smaller; all teeth largely concealed by dome-shaped anteroventral margin of hypostoma; lateral serrations absent; 7 or 8 hypostomal setae per side, variable. **Mandibles** (Fig. 431): outer teeth poorly developed, apical tooth small, but distinct; subapical teeth not substantial; *ca* 9 elongate spinous teeth; serration distinct, sensilla not, variable; blade region smooth and straight. **Thorax** (Fig. 361): overall light brown; mature pharate pupal gills L-shaped (Fig. 346), the 2 black portions of the base visible, 4 or 5 filaments visible, directed ventrally then posteriorly to loop sharply anteriorly. **Abdomen**: evenly medium brown; distinct ventral tubercles. **Anal sclerite** (Fig. 448): median region broad, short, not markedly sclerotised, anterior arms not flared, interarm struts rod-like and substantial, posterior arms straight, finely tapered; accessory sclerite absent, but occasional vestige present; semicircular sclerite normally sharply tapered, slightly expanded subapically. **Posterior circlet**: *ca* 140–150 rows of 15 or 16 hooks (total *ca* 2 200).

Type data. **Holotype**, Pupal exuviae in Canada Balsam on glass microscope slide; condition: excellent. Upper label details "Austrosimulium\ campbellense\ Dumbleton\ Pupal skin ["of" deleted]\ HOLOTYPE ({M})\ Tucker Cove. Ck.\ Campbell Is.\ L.J.D. 2.xi.[19]58" (preprinted slide label with 5 dotted horizontal lines surrounded by narrow black line boundary as a square; genus underlined, final 2 lines written below bottom boundary line of square, handwritten in black ink, Dumbleton); details of lower labels "Entomology Div., DSIR, NZ\ L.J. Dumbleton Collection" (gold label), "[N]ame A. vexans 13\[H]ost {M} in alcohol\ {M} gen. slide\[L]oc {M} PUPA\ Campbell Is\ [D]ate 2/ XI/[19]58\ [C]oll L.J. Dumbleton\[N]o Tucker Cove Ck\ [D]et. By LJD" (preprinted slide label with 7 title lines plus 1 untitled and with horizontal dots forming base of lines; "vexans" crossed out; "13" in red pencil, remaining words handwritten in blue ink (lines 1, 4, 5, and 9) or black ink (lines 2, 3, 6–8, as in top label), Dumbleton) (NZAC). **Paratypes**: 2 female adults, double pinned on minuten, Label details "Campbell Island\ J. Sorenson 1943", "Austrosimulium vexan[s] (Mik)" (crossed out, in pencil)\ Det. R.A. Harrison 1953", "Austrosimulium\ campbellense\ Dumbleton", "PARATYPE {F}", "NZ Arthropod Collection\ {barcode}\ NZAC04022263", and "NZAC04022266" NZAC). Of note are 4 other female specimens at CMNZ, 1 missing its head, and all with the same labeling as above, but not with "vexans", or with paratype label. 2 glass microscope slide mounts; slide 1, top label details "PARATYPE \Austrosimulium \campbellense \Dumbleton\ PUPAL SKIN\ Tucker Cove Ck \ Campbell Is \ LJD 2/11/[19]58" (preprinted slide label with 5 dotted horizontal lines surrounded by narrow black line boundary as a square; genus underlined, first line written above top boundary line of square, handwritten in black ink, Dumbleton), details of lower labels "Entomology Div., DSIR, NZ\ L.J. Dumbleton Collection" (gold label), "A. campbellense \A. ~~vexans~~ \Tucker Ck\ Campbell Is\ LJD 2/11[19]58 \PUPA" (preprinted slide label with 4 dotted horizontal lines, "vexans" crossed out with black ink, handwritten, with first line in black ink, rest in pencil, Dumbleton); slide 2, top label details "A. campbellense \ Dumbleton \{M} genitalia \of PARATYPE \in alcohol. \ Tucker Cove Ck \CAMPBELL IS." preprinted slide label as slide 1 top label, line 1 underlined, handwritten in black ink, Dumbleton), details of lower labels "Entomology Div., DSIR, NZ\ L.J. Dumbleton Collection" (gold label), "Austrosimulium \ campbellense \Dumbleton \{M} (ex pupa) gen \ of PARATYPE {M} \(in alc.) Tucker \ Cove Ck. 2/11/[19]58 \L.J.D. \PARATYPE" (preprinted slide label as slide 1 top label, last line below bottom margin of square and in pencil, lines 1 and 2 underlined, handwritten in black ink over underlying similar information in pencil, Dumbleton) (NZAC). 4 tubes of ethanol material, label details as follows; tube 1, "Austrosimulium \campbellense Dumbleton \{M}ex pupa" (handwritten in black ink, unknown), "Tucker Cove Ck. \Campbell Is \L.J.D. 2/XI/ [19]58" (handwritten in black ink, ?Dumbleton), "Pupal skin & \{M} genitalia of \Holotype on Slides" (handwritten in black ink, ?Dumbleton), "pupal skin of this {M}\is holotype." ("holotype" underlined, handwritten in pencil, Dumbleton), "Dumbleton collection" (NZAC printed label); tube 2 "Austrosimulium \campbellense \Dumbleton" (handwritten in pencil, Dumbleton), "Smoothwater B. \ Campbell Is \K Wise 2/3/[19]63" (handwritten in pencil, Dumbleton), "PARATYPES \2pupae \contg. {MM}" (handwritten in pencil, Dumbleton); tube 3 "Austrosimulium \campbellense \Dumbleton det LJD \PARATYPE {F}" (handwritten in pencil, Dumbleton), "DA Challies \ Nov. 1951 \Campbell Is" (handwritten in pencil, Dumbleton), "Dumbleton collection" (NZAC printed label); tube 4 "Austrosimulium \campbellense \Dumbleton" (handwritten in pencil, Dumbleton), "Tucker Cove Ck \Campbell Is \LJ.D. 2/11/[19]58" (handwritten in pencil, Dumbleton), "PARATYPE \PUPAE (2) \Contg. {MM}" (handwritten in pencil, Dumbleton), "Dumbleton collection" (NZAC printed label) (NZAC).

Material examined. Type material; substantial material by TKC in NZAC; 4 pinned female *A. campbellense* adults in NZAC originally identified as *A. vexans*; 2 listed in Harrison (1955), "Campbell Island\ J. Sorensen 1943", and 2 listed in Harrison (1964), "CAMPBELL IS.\ Lookout Bay\ Perseverence\ Harbor\ 3. II. 1963", "Sweeping", "K.A.J. Wise\Collector\BISHOP", "Austrosimulium\ vexans (Mik)\det. 1962 (sic!)\ R.A. Harrison". and "CAMPBELL I.\ Tucker Cove, 4m\ Malaise Trap\ 27.XI.-1.XII.'61", "J. L. Gressitt,\ Collector", "Austrosimulium\ vexans (Mik)\ det. 1962\ R.A. Harrison"; and 4 pinned specimens in AMNZ, 1 "Campbell Island\ J. Sorensen 1943", 3 "Austrosimulium\ vexans (Mik)\ Det. R. A. Harrison 1953", "Auckland\ Museum\ New Zealand". Male adults are not well represented, apart from pharate stages.

Distribution (Map 5). Known only from subantarctic Campbell Island. **Campbell Island**. Beeman Camp; Camp Cove Stm; Davis Point; Garden Cove Stm; LimLookout Bay Stm; Middle Cove Stm; Mt Dumas stm; Mt Honey stm; Northeast Harbour; Norton Stm; Shag Point Stm; Smoothwater Bay Stm; Tucker Cove Stm; Whalers Stm; Windlass Bay Stm.

Northernmost record Northeast Harbour (latitude S52.5222°); southernmost Shag Point stream (latitude S52.5861°); most localities of low altitude, but collected up to 220 m.

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Etymology. Named by Dumbleton (1973) for the type locality, Campbell Island.

Bionomics. Dumbleton made considerable comment about *A. campbellense* and its habitats. Campbell Island is cloudy and windswept, with a moderate annual rainfall of about 1 450 mm. Mean temperature in summer is 9.4°C and 4.5°C in winter. Frosts are few and snowfall, which can be in any month, rarely remains. The streams are deeply cut through peat and substrates are not stony except at the outlet on beaches (e.g., Fig. 488); thus larvae and pupae were taken predominately from trailing vegetation. He suggested that *A. campbellense* bred all year round; label data show larvae present for at least five months of the year.

Female adults were not abundant in Malaise traps (although these appear to have been placed some distance from suitable stream habitats) and Hudson (1909: 66) recorded only one bite. No bites were mentioned from the Meteorological Station staff, housed near Camp Creek for years. Lack of adults flying indicates they do not fly far. Given the windswept climate on Campbell Island, a reluctance to fly would be in agreement with the behaviour of adults of another subantarctic simuliid, *Crozetia crozetensis* (Womersley) (Craig *et al.* 2003) that fly little even under calm conditions. Nevertheless, over a period of 1 year 16 adults were caught in permanent nets established at Beeman Point above Perseverance Harbour; occurring in 8 of the 12 months (Gressitt 1964), again suggestive of the species being able to breed all year round. Collections by TKC, who visited Campbell Island in 1975, 1981, and 1984, recovered larvae from stones and trailing vegetation such as *Dracophyllum,* in agreement with Dumbleton. Moreover, they were collected widely in most streams where the water flow was above 0.3 m per sec, and when the *Dracophyllum* canopy overshadowed the stream they could be the most abundant species found (Crosby 1980). He also collected many flying females and some while biting. Blood feeding for the species would be indicated given the substantial mouthparts of the females and the reduced abdominal tergites (Fig. 80), similar to its close relative *A. vexans* on the Auckland Islands.

Joy & Death (2000) examined aquatic fauna of Campbell Island. They examined 20 streams, of which only eight yielded *A. campbellense,* mostly in low numbers. Their analysis is in basic agreement with previous collections of simuliids there. Larvae of *A. campbellense* tend to be found in what Joy & Death refer to as "category B habitats", which are of mid to low altitude.

Stream habitats were extensively surveyed by EOS Ecology (www.eosecology.co.nz) from Dec 2010 to Feb 2011 as part of the 50 Degree South Trust, Campbell Island Bicentennial Expedition (www.campbellisland.org.nz). In streams with fast flows and coarse substrate, simuliid larvae were in moderate abundance. Adults were observed at some localities, but only sampled with sticky traps at Tucker Stream. Samples are not yet fully processed.

However, some material that has been examined in detail, reveals that at Honey Falls stream, *Coelomycidium simulii* (or a closely related species) (e.g., Fig. 500), which is a widespread member of the order formerly known as Chytridiales (Adler *et al*. 2004), now known as a Blastocladiales, occurs at low frequency. This is a new record for this organism on Campbell Island. (see Parasitism p. 32).

Remarks. That there were Simuliidae on Campbell Island has been known now for over a century (Hudson 1909; Lamb 1909). Both early authors assumed it was *A. vexans* (Mik) of the Auckland Islands, and Lamb noted, in error, that Campbell Island was the type locality of *A. vexans*. Dumbleton (1970: 21) indicated there were 2 subantarctic island species, but he did not formally describe *A. campbellense* until 1973, from specimens he collected in November 1958 when he was able to make a brief visit on the supply ship *Holmlea* (Dumbleton family photographs). Females of *A. vexans* and *A. campbellense* are basically impossible to separate morphologically; even the genitalia only have minor difference in the hypogynial valves. Male *A. campbellense* have more substantial genitalia than those of *A. vexans* and the ventral plates differ in development of the median keel. Again, apart from these characters there is little difference between the species. Both, however, along with *A. ungulatum*, have slightly better developed parameres than other species in *Austrosimulium*. The main differences used by Dumbleton (1973) to confer species status on *A. campbellense* were embodied in the pupal gill and these reflect in the final instar larval gill spot (*cf* Fig. 361, 363). While variable, gill filament number in *A. campbellense* is lower (6–8), against the markedly variable number (6–22) for *A. vexans* and less so (9–12) for *A. ungulatum*. Filament length is markedly shorter than in the other two species. The pupal gills indicate that *A. ungulatum* and *A. vexans* are the more closely related; however, the ventral plate of *A. campbellense* and *A. ungulatum* both have similar well developed ventral keels. Larvae shed little light on relationships, except that in *A. vexans* and *A. ungulatum* the hypostomal teeth protrude more distinctly beyond the lower edge of the hypostoma. On balance, it appears that *A. ungulatum* and *A. vexans* share the most synapomorphies, and that *A. campbellense* is their sister species. Cladistic analysis of these morphological characters leaves the *ungulatum*-subgroup unresolved in Strict Consensus (Fig. 505), but in Majority Rule (Fig. 506), *A. dumbletoni* is sister to the unresolved remainder. No material was available for molecular analysis.

Given, however, the marked variability in size of larvae and antennal characteristics, pupal gill filament array and variability of the adults, a detailed molecular examination may well reveal cryptic species.

***Austrosimulium* (*Austrosimulium*) *dumbletoni* Crosby, 1976**

Figures: female, front cover, 35, 61, 81, 101, 119; male, 137; Map 7.

dumbletoni Crosby, 1976a: 17 (description female; *Austrosimulium* (*Austrosimulium*)). Tenquist & Charleston 2001: 486 (checklist of ectoparasites). McLellan 2003: 243 (list). Craig & Crosby 2008: 1 (gynandromorph). Adler & Crosskey 2012: 20 (world inventory)

Diagnosis. The largest of New Zealand simuliids, body length 2.9–4.8 mm. Darkly-pigmented species. **Female**: antenna with 1st flagellomere longer than 2nd; wings dusky, tarsal claw with basal tooth; abdominal tergites III–V small and subquadratic, hind basitarsus lacking row of stout setae. **Male** (based on gynandromorphs): hind basitarsus lacking row of stout setae.

Adult female (based on a large number of topotypes). **Body**: general body colour dark blackish-brown, with some overlying pruinosity; total length 2.9–4.8 mm. **Head**: width 0.83–0.96 mm; depth 0.59–0.64 mm; postocciput black, vestiture of sparse, short black hairs; frons dark brown-black; frons width : head width ratio 1.0 : 4.2. **Eyes**: interocular distance 0.21 mm; ommatidia diameter 0.013 mm; *ca* 42 rows up and 30 rows across at mid-eye. **Clypeus**: very dark brown, pale medioventrally; vestiture of sparse black and pale hairs; width 0.19–0.20 mm. **Antennae**: noticeably tapered, length 0.73 mm; all dark brown, 1st flagellomere *ca* 1.3× pedicel length and markedly longer than 2nd flagellomere. **Mouthparts**: substantial, 0.5–0.6× length of head depth; cibarial cornuae not markedly sclerotised, with fine cross striae and basal tubercles (Fig. 35); mandibles with 35 inner teeth, decreased in size gradually away from apex; laciniae with 15 inner and 25 outer moderately fine teeth; maxillary palp, total length 0.6 mm, 3rd article dark brown, remainder lighter, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.8 : 1.5, sensory vesicle ovoid, 0.5× 3rd article width, opening 0.5× vesicle width.

Thorax: length 1.4–1.6 mm; width 0.96–1.1 mm; in ethanol postpronotal lobes paler than scutum, scutum uniformly semi-shiny blackish-brown, sparsely covered with short, decumbent hairs; prescutellar depression with a few longer, black hairs, usually absent; scutellum concolorous with scutum, vestiture of a few long black hairs; postnotum concolorous with scutum; pleuron and pleural membrane lighter brown than scutum. **Wings**: dusky gray, length 3.4–4.2 mm; width 1.6–1.8 mm. **Halteres**: light yellowish-brown. **Legs** (Fig. 61): dark brown except for paler femoral, tibiae, and tarsal apices and all hind tarsi; hind basitarsus about 7× as long as greatest width, row of stout setae absent; tarsal claws not markedly curved, distinct serrations, basal tooth not markedly developed, basal cleft small (tooth claw ratio 1:2.8).

Abdomen (Fig. 81): abdominal scale dark with fine long hairs extended to 1/2 length of 2nd segment; tergites and sternites dark brown; tergites of variable size and shape but mainly quadratic: tergite II 3.5× as wide as long, tergites III and IV ovoid to quadratic and decreasing in size posteriorly; tergite VI dome-shaped anteriorly; vestiture markedly sparse; setae forming pleural tufts around spiracles, more so posteriorly. **Genitalia** (Fig. 101): sternite VIII pigmented laterally and anteriorly, vestiture of coarse black hairs posterolaterally; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and microtrichia; median edges of hypogynial valves strengthened and smoothly convergent apically, broadly rounded apically with apparent shallow flange; genital fork (Fig. 119) with anterior arm broad but not markedly so, apex broadly rounded, lateral membranous areas extensive, posterolateral arms with small knee-bend, lateral plate angulate medially, rounded laterally, apodeme triangular and small; anal lobes small, cerci subtruncated in lateral view, both black; spermatheca large, ovoid, dark, moderate clear area at junction of duct.

Adult male (based on 5 gynandromorphs collected in 1977). **Body**: general colour brownish-black; total length 3.7–4.8 mm. **Head**: width 1.1 mm; depth 0.72 mm. **Eyes**: upper ommatidia dark red, diameter 0.037 mm, *ca* 15–22 across and down; lower ommatidia dark brown, diameter 0.010 mm, *ca* 38 across and down. **Antennae**: total length 0.68 mm; all evenly medium brown, not markedly tapered. **Clypeus**: unknown. **Mouthparts**: unknown.

Thorax: length 1.8 mm; width 1.1 mm; scutum evenly dark reddish-brown, vestiture of fine recumbent pale hairs, brassy yellow when dried, longer dark hairs in prescutellar depression, vittae poorly visible; scutellum concolorous with scutum with sparse, long stiff black hairs; postscutellum concolorous with scutum. **Wings**: dusky; length 3.1–3.8 mm, width 1.7–1.9 mm. **Halteres**: tan. **Legs**: evenly dark brown, hind basitarsus about 6.8× as long as greatest width, row of stout setae absent; tarsal claw grappling pads of 22 teeth.

Abdomen: abdominal scale markedly dark and with long black hairs. **Genitalia**: (Fig. 137). gonocoxites 1.3× longer than basal width, dark brown, with sparse coarse black hairs, anteromedial crenulations poorly developed; gonostyli *ca* 2.1× longer than basal width, finely tapered, apically with 2 substantial spines, 1 smaller; ventral plate with well developed, but low median keel, with vestiture of coarse hairs, 1.5× wider than length, shield-shaped, slightly pointed posteromedially, anteromedial edge slightly convex, basal arms moderately developed; median sclerite poorly developed, broadly T-shaped posteriorly; parameres poorly developed, but distinct.

Pupa (unknown).

Cocoon (unknown).

Larva (unknown).

Type data. **Holotype**: female, preserved in 90% ethanol, condition: excellent, however slightly bleached; label details "H O L O T Y P E {F}\Austrosimulium \dumbletoni \Crosby" (red label, all but "HOLOTYPE" handwritten in black ink, Crosby), "NEW ZEALAND, WD. Jackson Bay\ 28 Feb 1975. S. A. Bisset. Biting\ Eudyptes p. pachyrhynchus" (handwritten in black ink, Crosby) **(**NZAC). **Paratypes** (9): 2 female adults in 90% ethanol; label details "P A R A T Y P E {FF}\ Austrosimulium\ dumbletoni\ Crosby" (blue label, all but "PARATYPE" handwritten in black ink, Crosby), "NEW ZEALAND, WD. Jackson Bay\ 28 Feb 1975. S.A. Bisset. Biting\ Eudyptes p. pachyrhynchus" (handwritten in black ink, Crosby), "Macerated, some\ parts slide-mounted [on 4 microscope slides]" (handwritten in black ink, Crosby); 4 microscope slides, all with left hand label "P A RA T Y P E {F}\Austrosimulium \dumbletoni \Crosby" (blue label, all but "PARATYPE" handwritten in black ink, Crosby), all with first 4 lines of right hand label "NEW ZEALAND, WD. \Jackson Bay 28 Feb 1975. \S.A. Bisset. Biting \Eudyptes p. pachyrhynchus", then 2 with bottom line "Head", 1 with "Leg, hind.", and 1 with "Abdominal tergites, \genitalia, hind legs" (all handwritten in black ink, Crosby). 4 females in 90% ethanol; label details "P A R A T Y P E {FF}\ Austrosimulium\ dumbletoni\ Crosby" (blue label, all but "PARATYPE" handwritten in black ink, Crosby), "NEW ZEALAND, WD. Jackson Bay\ 28 Feb 1975. S.A. Bisset. Biting\ Eudyptes p. pachyrhynchus" (handwritten in black ink, Crosby) (NZAC). Single paratypes each deposited in Australian National Insect Collection, CSIRO, Entomology, Canberra (ANIC), and the Canadian National Collection of Insects, Arachnids and Nematodes, ECORC, Agriculture & Agri-Food Canada, Ottawa (CNIC); label data as for other paratypes.

Material examined. Type material; a large number of topotype females (pinned and in ethanol), plus 5 gynandromorph males (see Craig & Crosby 2008) (NZAC).

Distribution (Map 7). Highly restricted — known only from Jackson Bay (latitude S43.97212°) and Knights Point (latitude S43.71534°), Westland. **South Island**. **WD**. Jackson Bay, NZS45; Knights Point, NZS45a.

— / WD / —

Both these localities are in the Westland Forest aquatic ecoregion.

Etymology. Named by Crosby after L. J. Dumbleton, in recognition of his work on New Zealand Simuliidae.

Bionomics. *Austrosimulium dumbletoni* females readily bite Fiordland crested penguins and engorge themselves with blood (Fallis *et al.* 1976; Crosby 1976a). The feeding sites selected are around the eyelids and beak, on the edges of the flippers, and on the legs; the flies appear not to crawl under feathers to feed. This later observation is of interest since the large basal tooth on the tarsal claws of the female and the ridges on the claw are hall-marks of bird feeding and have been assumed to allow the female to crawl along feathers (e.g., Adler *et al*. 2004).

Nothing further is known of the biology. Larvae and pupae are unknown despite considerable effort by the authors at various times to find these stages. Of importance though is that molecular analysis of CO1 gene (see Molecular Analysis section and below) shows that *A. dumbletoni* clusters with the *unicorne*-subgroup (not the *ungulatum*-subgroup), larvae of which are found at high altitudes and in cold water. A search of the upper areas of the mountain ranges east of the coast at Jackson Bay might be rewarding.

Remarks. Burrows (2005) mapped the extent of ice for the central South Island during the Otira Glaciation and for the earlier Waimaunga Glaciation (his Figs. 70, 71). For the earlier event he showed ice extending well out to sea, south of the Hokitika River, with unglaciated areas north of it. During the Otira it appears that ice extended out to sea too, but there were numerous irregular unglaciated areas. Two such of the southern areas illustrated are at Jackson Head, and Arnotts and Knights Point. These two non-glaciated regions are the only known localities for *A. dumbletoni*, suggesting that it is a refugial species, post-dating the Waimaunga Glaciation (0.28-0.22 Mya). We have suggested elsewhere that distributions of *A. alveolatum* and *A. albovelatum* are also refugial (p. 81).

Austrosimulium dumbletoni can be readily distinguished by its large size, since it is some 30% larger than any other described New Zealand species. Also, the 1st antennal flagellomere is markedly longer than the 2nd, and there are few hairs on the front of the head and on the scutum and scutellum. *A. dumbletoni* can be separated from the smaller *A. ungulatum*, the only species with which it is likely to be confused, by its uniformly dark antenna and long tarsal claw with a narrow angle between the claw and the tooth. In *A. ungulatum* the base of the 1st antennomere is pale, and the tarsal claw is shorter with a wider angle between the claw and the tooth. Distinction between *A. dumbletoni* and *A. vailavoense* is more difficult, but the former has dusky wings and much larger claw tooth, and the latter a darker, more ruddy abdomen.

As Crosby (1976a) noted it is not possible to assign *A. dumbletoni* to subgenus using the key given by Dumbleton (1973: 493). The greater length of the 1st flagellomere would place this species in the Australian subgenus *Novaustrosimulium* Dumbleton, where it would resemble most closely *A.* (*N.*) *furiosum* (Skuse) (Mackerras & Mackerras 1948: Figure 10f). However, the substantial basal tooth on the tarsal claw is characteristic of subgenus *Austrosimulium*, and Crosby (1976a) therefore considered *A. dumbletoni* should be assigned to that subgenus. The size of the tarsal claw tooth would further place *A. dumbletoni* in the *ungulatum* species-group; and because abdominal tergites III and IV are subquadratic and much narrower than tergites II or VI, morphologically it belongs in the *ungulatum*-subgroup (Dumbleton 1973).

The description of the male is based on gynandromorphs collected by TKC in 1977 and dealt with by Craig & Crosby (2008). Caveats regarding the description were discussed then. Gynandromorphs were used for description since there are no true males known for *A. dumbletoni*.

Cladistic analysis of morphological characters shows the *ungulatum*-subgroup unresolved in Strict Consensus, but in Majority Rule (Fig. 506) *A. dumbletoni* is sister to an unresolved clade of *A. campbellense* + *A. ungulatum* + *A. vexans*. Not included in the analysis was *A. vailavoense* on the basis that only adult females are known. Molecular analysis reiterates the difficulty of taxonomic assignment of *A. dumbletoni* on the basis of morphology. There (Fig. 514) *A. dumbletoni* is clustered at high support with *A. bicorne* and *A. tonnoiri*. If that is correct it gives a strong clue as to where immature stages of *A. dumbletoni* will be found — in high-altitude, cold-water habitats. The size of female adults is in close agreement, too; both other species are large, so an expectation is that larvae and pupae of *A. dumbletoni* are large and morphologically similar to those of *A. bicorne* and *A. tonnoiri*.

Austrosimulium (*Austrosimulium*) *ungulatum* Tonnoir, 1925 West Coast black fly

Figures: female, 2, 36, 48, 49, 62, 69, 89, 102, 120; male, 138; pupa and cocoon, 155, 173, 189, 196, 199, 212, 229, 250, 264, 281, 298, 538; larva, 315, 334, 347, 362, 379, 396, 402, 415, 432, 449, 500, 502, 503; habitat, 492–495; Map 16.

ungulatum Tonnoir, 1925: 250 (description female; *Austrosimulium*). Smart 1945: 499 (world catalogue). Mackerras & Mackerras 1949: 402 (occurrence). Gurr 1953: 81 (vector potential). Dumbleton 1963b: 334 (as subgenus *Austrosimulium* (*Austrosimulium*), in *ungulatum* group). Dumbleton 1964a: 35 (relationships, distribution). Dumbleton 1973: 526 (description pupa, cocoon, larva; redescription female). McLellan 2003: 243. Winterbourn 2004: 7. Crosby 2006: 72 (key). Adler & Crosskey 2012: 20 (world inventory).

Diagnosis. **Female**: base of 1st antennal flagellomere pallid; haltere white; tarsal claw with basal tooth, 0.3× as long as claw inner length from basal cleft; abdominal tergites III–V small and subquadratic; hind basitarsus lacking row of stout setae. **Male**: hind basitarsus lacking row of stout setae. **Pupa**: cephalic plate lacking ornamentation in either sex; thoracic cuticle with evenly dispersed small rounded granules; gill lacking black horn, 9–12 tapered filaments in 3 groups; sternite IX with grapnel hooks. **Cocoon**: slipper shaped, 2 long anterodorsal projections, fabric coarsely woven, pale brown. **Larva**: body markedly even in diameter along length; grayish and brown; head evenly mottled brown, medial and lateral head spots distinct; suboesophageal ganglion unpigmented; ventral tubercles marked; accessory sclerite absent, semicircular sclerite tapered apically.

Adult female (based on holotype and topotypes). **Body**: general body colour in ethanol dark brownish-black, when dried lighter, with silvery pruinose appearance in places under certain lighting; total length 2.7–3.4 mm. **Head**: width 0.64–0.68 mm; depth 0.48–0.56 mm; postocciput black, vestiture of short black hairs; frons dark brown-black; frons width: head width ratio 1.0 : 3.0. **Eyes**: interocular distance 0.16–0.19 mm; ommatidia dark red, diameter 0.013 mm; *ca* 38 rows up and across at mid-eye. **Clypeus**: brownish-black; vestiture of sparse black hairs; width 0.22–0.24 mm. **Antennae**: evenly dark brown, length 0.46–0.56 mm; base of 1st flagellomere pallid. **Mouthparts**: not markedly substantial, although long, 0.6× length of head depth; cibarial cornuae (Fig. 36) broadly developed, with arms tuberculate, fluted apically; mandibles with 24 inner teeth, basal 7 teeth small; laciniae with 15 inner teeth and 29 outer teeth; maxillary palp, total length 0.62 mm, 3rd article dark brown, remainder lighter, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.7 : 1.1, sensory vesicle ovoid, 0.5× 3rd article width, opening 0.5× vesicle width.

Thorax: length 1.1–1.4 mm; width 0.82–0.88 mm; in ethanol, postpronotal lobes paler than scutum; scutum evenly dull dark brownish-black, vestiture of sparse recumbent hairs, presutellar depression with markedly longer dark hairs posteriorly and fine pale curved hairs, no vittae visible in ethanol; scutellum concolorous with scutum, but with reddish undertones, vestiture of stiff, long black hairs and pale hairs laterally; postnotum concolorous with scutum; pleuron, and pleural membrane slightly lighter than scutum. **Wings** (Fig. 2): length 2.8–3.2 mm; width 1.2–1.4 mm. **Halteres**: white. **Legs** (Fig. 48): evenly blackish-brown, except hind basitarsus yellower; hind basitarsus about 5× as long as greatest width; lacking ventral row of stout setae; tarsal claws (Fig. 62) with tooth claw ratio 1:2.7, basal notch of tooth distinct.

Abdomen (Fig. 82): variable, dark yellowish-brown to dark brownish-black; abdominal scale dark brown with fine brown hairs, extended to 1/2 length of segment 2; tergite II 2.2× wider than long, tergites III–V small and quadratic, tergite VI domed anteriorly, 1.3× wider than long, tergite VII narrow and oval, 3× wider than long; vestiture of evenly sparse black hairs, denser posteriorly. **Genitalia** (Fig. 102, 120): near *A. campbellense* and *A. dumbletoni*; sternite VIII pigmented anteromedially; vestiture of long coarse black hairs mediolaterally; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and triads of microtrichia; median edges of hypogynial valves barely divergent, narrowly strengthened, broadly rounded apically; genital fork with anterior arm narrower than in other species, lateral membranous areas not markedly developed; posterolateral arms narrow, lacking knee-bend, flange with apodeme sharply pointed and lobe angulate medially; anal lobes and cerci both broadly rounded in lateral view and darkly pigmented; spermatheca markedly ovoid, clear area at junction of duct small.

Adult male (based on pharate material and 1 reared specimen). **Body**: general colour blackish-brownish; total length 2.5–3.0 mm. **Head**: width 0.88 mm; depth 0.64 mm. **Eyes**: upper ommatidia diameter 0.033 mm, *ca* 25 across and down; lower ommatidia diameter 0.015 mm, *ca* 38 across and down. **Clypeus**: dark brown; vestiture of markedly sparse fine hairs; width 0.16 mm. **Antennae**: total length 0.60 mm; evenly dark brown. **Mouthparts**: poorly developed; length 0.25× head depth; mandibles insubstantial, broadly tapered with apical hairs; laciniae finely tapered apically with terminal hairs; maxillary palp medium brown, 0.38 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 0.7 : 1.1, sensory vesicle irregular in shape, occupying 0.25× 3rd article width, opening 0.3× vesicle width.

Thorax: length 1.3 mm; width 0.8 mm; scutum markedly domed and evenly black, vestiture of fine recumbent pale hairs, markedly long, anteriorly-directed coarse black hairs in prescutellar depression; scutellum slightly lighter than scutum with sparse long black hairs; postscutellum concolorous with scutum. **Wings**: length 3.1 mm, width 1.5 mm. **Halteres**: white. **Legs** (Fig. 49, 69): overall brownish-black, hind basitarsus yellower; hind basitarsus about 5.5× as long as greatest width; tarsal claws with grappling pad of 23 teeth. **Abdomen** (Fig. 89): scale markedly black with long dark hairs, not shown in illustration; tergites and sternites blackish-brown. Tergites occupy whole width of dorsum. **Genitalia** (Fig. 138): gonocoxites 1.5× longer than basal width, markedly convex laterally, vestiture of sparse coarse black hair and microtrichia, anteromedial crenulations marked; gonostyli narrow, approximately 3.1× longer than basal width, apically with 2 substantial spines, 1 slightly less so; ventral plate with marked median keel, even vestiture of fine hairs, 1.3× wider than long, peaked posteriorly, flat anteromedially, basal arms narrowed and well developed anteriorly; median sclerite poorly developed, broad, T-shaped posteriorly; parameres poorly developed, barely visible.

Pupa (Fig. 155, 173, 196). Body length: 3.1–3.7 mm. **Head**: cephalic plate (Fig. 199, 212, 229) of male and female lacking granulations, but faintly corrugated. Male plate (Fig. 229) markedly rounded apically, 2× longer than basal width; female plate (Fig. 212) broad, 1.5× as long as basal width. Frontal, facial, and epicranial setae long and distinct, ocular setae present and substantial (Fig. 196). **Thorax** (Fig. 250): dorsum smooth, lacking ornamentation anterodorsally, but present as fine colourless granules posteriorly and ventrally (visible only at higher magnifications), as are hexagonal epidermal cell boundaries. Setae simple, elongate, and substantial with exception of posterior dorsocentral hair that is spine-like. **Gills** (Fig. 264, 281): lacking black-pigmented horn; filaments tapered and rigid (antlered), some bifurcated, longest nearly as long as body; common trunk short, unpigmented dorsally, black apically on venter. In lateral view filaments form 3 groups: (i) short, single unbranched filament arising dorsolaterally from near base of trunk, turning slightly caudally and becoming erect in dorsal position; (ii) apically group of 3–5 filaments lying horizontally or slightly ascending with their bases side by side, outer filament longest (as long as thorax) and inner 1 shortest and curved mesially (when 3 filaments are present the outer 2 are produced by bifurcation of a common stem and the inner filament of these 2 may branch again to produce 4 filaments, and the outer may also branch to produce 5 filaments; length of branches below bifurcation is variable); (iii) 4–6 filaments, any 1 of which may branch, arise from lateral margins and apex of ventral common trunk, which is somewhat dorsoventrally flattened; this group of filaments arises in same plane, directed forward and downward, and with outer filament longest, nearly as long as body, innermost shortest and strongly curved medially; filament next to innermost may fork at 1/2 length; ultimate terminal filament number varied from 9–12, lengths of branches and common stems variable, even on either side of pupa. Filament surface pattern (Fig. 298): imbricate-banded, i.e., bands are incomplete annuli with tapered ends. **Abdomen**: grapnel hooks and 2 simple setae present on sternite IX.

Cocoon (Fig. 189): fabric coarsely woven, but not as markedly as others of subgroup; silk brown; slipper-shaped, opening broad, circular and angled, strengthened rim laterally; distinct but low anteroventral lip, pupa well covered anteriorly; 2 elongate processes anterodorsally, 7–8× longer than basal width, not markedly continued posteriorly onto cocoon body.

Larva (numbers of mature final instars). **Body** (Fig. 315): more thickened than other species, thicker thorax and anterior abdomen; overall mottled brown, sexual dimorphism of colour not apparent; total mean length 5.3–6.0 mm. **Head** (Fig. 334): evenly mottled medium brown; length 0.65–0.67 mm, width 0.51–0.55; distance between antennal bases 0.26–0.28 mm; lateral margins of head convex posteriorly, broadly tapered anteriorly; anterior apotome translucent, head spot pattern marked, anteromedial spots darker brown, posteromedial spots partly fused and brown, anterolateral spots brown, 1st and 2nd posterolateral spots neutral; posterior edge of apotome not markedly pigmented, continuous with posterior genae; ecdysal lines broadly rounded posteriorly, straight anteriorly; postocciput markedly developed and pigmented, with cervical sclerites fused. **Antennae** (Fig. 379): brown basally, pale apically; total length 0.38 mm, extended well beyond apex of fan stalk; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.3 : 2.0; apical article *ca* 1.5× longer than combined basal 2 articles, medial article 0.3× length of basal article. **Labral fans**: stalk clear brown; *ca* 37–39 fine brown rays, length 0.6 mm, width 0.008 mm; distinct pattern of microtrichia, longer microtrichia 1.2× longer than ray width, separated by *ca* 10–12 irregular, smaller microtrichia. **Postgenal cleft** (Fig. 396): shallowly inverted V-shaped, as deep as broad, with irregular apex, posterior tentoral pit region markedly sclerotised and pigmented. **Postgenal bridge**: 1.7× longer than hypostoma, pale medially, otherwise darker than genae, elongated posteroventral muscles spots not distinct; genae with irregular brownish pigmentation; suboesophageal ganglion unpigmented (Fig. 402). **Hypostoma** (Fig. 415): lateral teeth equally prominent as median tooth; 2 sublateral teeth subequal in size to median tooth, middle tooth 1/2 size of others; 2 paralateral teeth, lateral tooth smaller; all teeth largely concealed by dome-shaped anterior margin of hypostoma, 2 or 3 poorly developed rounded lateral serrations, variable; 4 or 5 hypostomal setae per side. **Mandibles** (Fig. 432): outer, apical, and 2 subapical teeth substantial, but not well developed, *ca* 7 spinous teeth; serrations and sensilla on raised base, but small; blade region short. **Thorax** (Fig. 347, 362): prothorax grayish brick-red, remainder of thorax pale grey; mature pharate pupal gills L-shaped, 4 or 5 filaments evident basally, 1 bifurcated near base; descend ventrally before turning *ca* 45 degrees posteriorly then bluntly reflexed anteriorly and dorsally. **Abdomen**: dorsal and ventral anterior abdomen mottled grayish-brown, posteroventral abdomen pale; posterior abdomen brown dorsally; marked ventral tubercles. **Anal sclerite** (Fig. 449): heavily expressed, medial region almost completely fused to massive interarm struts; anterior arms not markedly flared, posterior arms thickened and not tapered, accessory sclerite not flared, pointed. **Posterior circlet**: *ca* 106 rows of 15 or 16 hooks (total *ca* 1 640).

Type data. **Holotype**: female adult, on elbow pin (MacGillivray 1903); condition excellent, slightly greasy, complete; label details "Reefton N.Z.\ 13 Jan. 1922\ A. Tonnoir", "Austrosimul.\ ungulatum Tonn.\ Type" (handwritten in black ink, wavy line under "Type", Tonnoir), "NZ Arthropod Collection\ {barcode}\NZAC04021449" (NZAC). **Paratypes** (9): pinned, 6 females; label details "Dun Mt 3000 ft\ 5-7 Jan. 1922\ A. Tonnoir", "PARATYPE {F}\ Austrosimul. ungulatum\ n. sp.\ A. Tonnoir det.", "NZ Arthropod Collection\ {barcode}\ NZAC04022170"; "Mt Arthur Tl\4500 ft\ 20 Dec 1921\ A. Tonnoir", "PARATYPE {F}\ Austrosimul. ungulatum\ n. sp.\ A. Tonnoir det.", "NZ Arthropod Collection\ {barcode}\ NZAC04022188"; "Mt Arthur Tl\4500 ft\ 20 Dec 1921\ A. Tonnoir", "biting", "PARATYPE {F}\ Austrosimul. ungulatum\ n. sp.\ A. Tonnoir det.", "NZ Arthropod Collection\ {barcode}\ NZAC04022215"; "Nelson N.Z.\ 30.xii.21\A. Tonnoir", "PARATYPE {F}\ Austrosimul. ungulatum\ n. sp.\ A. Tonnoir det.", "NZ Arthropod Collection\ {barcode}\ NZAC04022217"; as previous, but with "NZAC04022218"; "Lake Brunner\ 4 Feb. 1922\ A. Tonnoir", "PARATYPE {F}\ Austrosimul. ungulatum\ n. sp.\ A. Tonnoir det.", "NZ Arthropod Collection\ {barcode}\ NZAC04022222" (NZAC). 1 female, label details "Otira N.Z.\ 7 Feb. 1922\ A. Tonnoir", "PARATYPE {F}\ Austrosimul.\ ungulatum\ n. sp.\ A. Tonnoir det.", "I. 288" (red label) (CMNZ). 2 females, label details "Waiho N.Z.\ 14 Jan. 1922\ A Tonnoir", "PARATYPE {F}\ Austrosimul\ ungulatum\n. sp\ A. Tonnoir det." and "Reefton N.Z.\ 13 Jun 1922\ A. Tonnoir", "PARATYPE\ Austrosimulium\ ungulatum\{F}\ n. sp.\ A. Tonnoir det." (MONZ).

Material examined. Type specimens; some 55 collections from NZAC, and some 79 recent collections comprising the full range of stages, including reared adults (Appendix 1).

Distribution (Map 16). Not known from the North Island, widespread in the South and Stewart Islands. **South Island**. **SD**. Kenepuru Head stm, NZS2; Momorangi Bay stm, NZS114. **NN**. Aorere R, NZS97; Bainham; Baker Ck (Karamea); Brown Ck, NZS81; Candle Ck, NZS77; Cobb R, NZS93, NZS94, NZS95; Cooks Ck, NZS98; Flora Stm, NZS91; Fossil Ck, NZS96; Graham Stm, NZS106 (SH6); Heaphy Track (Karamea side); Jones Ck, NZS74; Karamea, (Umere); Kohaihai R, NZS76 (Heaphy Track); Lee R; Little Ten Mile Ck [Fuschia Ck], NZS80; Little Wanganui R, NZS79 (Te Namu); Lyell Ck, NZS82; Motupiko R, NZS89; Poorman Valley Stm, NZS7; Roding R, NZS104, NZS105; Sandel Ck, NZS75 (SH67 Karamea Bluff); Takaka Hill summit stm, NZN103a; Te Kuna; unmarked stm near Virgin Ck, Karamea gorge, NZS78; Wainui R, NZS101 (Anatimo); Wakamarina R, NZS4; Westport; Whisky Ck, NZS92 (Flora Saddle); W W Stm, NZS73 (Fairdown); Whareatea R (SH67). **BR**. Black Valley Stm, NZS88; Doctor Ck, NZS83; Hope R, NZS86 (SH6 and 63 junction); Inangahua R, NZS67 (Rahu Saddle), NZS68 (SH7 Reefton); Kumara, SH73 straight; Lewis Pass; Marble Hill Campground, NZS65; Marble Hill campground stm, NZS187 (Springs Junction); Maruia; Mill Ck, NZS70 (SH6 Greymouth); Ohikanui R (SH6 bridge); O'Malley Ck; Punakaiki R, NZS72 (SH6 bridge), Campground; Rahu R, NZS66 (Springs Junction); Reefton; Rotoroa Camping Ground; St Arnaud; Station Ck; Thirteen Mile Ck, NZS71 (SH6). **WD**. Copeland R; Franz Josef (NZS 174, Callery Gorge Track stm; Douglas Track stm, NZA176; Tatare Ck Track stm, NZS175); Franz Josef Glacier ck, NZS49, 49a; Grey R; Haast; Haast gorge; Haast Pass, NZS178 (Davis Flat Track stm); Harihari; Hunts Beach Rd; Jackson Bay, NZS45; Karangarua; Knights Point, NZS45a, 45b; Mahitahi R; Maimai Ck, NZS46; Okarito R; Ribbonwood Ck, NZS47 (SH6); Robinson Ck, NZS177 (SH6); Taramakau R, NZS51 (SH73); Waiho R trib, NZS141; Whataroa. **MB**. Black Birch Stm, NZS182; Fuchsia Stm; Hanmer Springs; Maungatapu Road, NZS115 (ditch); Six Mile Stm bridge; St James Walkway stm, NZS188, 189 (Lewis Pass). **KA**. Irongate Stm trib, NZS117; Kaikoura; Mason R, NZS13a (SH70); Mororimu Stm, NZS10 (SH1). **NC**. Arthurs Pass; Bridal Veil Falls; Cave Stm (Broken R Ski Field); Craigieburn, NZS55 (SH73); Doubtful R hut; Grasmere Stm, NZS54 (Cass); Jacks Hut; L Janet; Pegleg Ck; Porter R, NZS56 (SH73). **MC**. Acheron R, NZS131; Broken R (SH73 bridge); Foggy Peak Ridge stm, NZS57b, NZS134 (SH73); Kaituna R, NZS60; Pudding Hill Stm, NZS120; Rakaia R (Totara Point). **SC**. Mt Peel; Peel Forest; Staveley. **MK**. Birch Hill Stm; Bush Stm trib; Freds Stm trib, NZS127 (SH80); The Hermitage. **OL**. Hollyford R, NZS146 (trib), NZS147 (Gunns Camp); NZS149 (trib); Lake Hawea; Lake Howden Hut; Lake Howden outlet, NZS150; Walker Ck, NZS34 (SH94); Wanaka, NZS189 (Glendhu Bay stm); Weydon Burn trib, NZS35; Wye Ck. **CO**. Nine Mile Ck, NZS43 (SH8); Pass Burn, NZS181 (Lindis Pass summit); Roaring Meg, NZS37 (SH6); Waikaia R trib. **DN**. Bethunes Gully; Dunedin (SH1 near Sullivans Dam); Waipori. **SL**. Ajax swamp; Aurora Ck; Black Gully; Bluff, NZS160; Catlins R, NZS27, 27a; Granity Stm trib, NZS159; Mary Burn; Matai Stm, NZS28; Waimeamea R, NZS30. **FD**. Alton Burn, NZS156; Borland Burn, NZS152, NZS153; Divide Ck, NZS33; Glaisnock R; Hollyford Valley; Lake Manapouri; Milford Sound; Papatotara Coast Road, NZS157; Saddle Hill. **Stewart Island**. Christmas Village Bay stm; Christmas Village hut; Freshwater Hut stm; Hicks Road stm, NZS172; Kaipipi Bay stm, NZS170a; Lee Bay; Little R trib, NZS168; Magnetic Beach stm, NZS166; Mason Bay Hut; North Arm Hut; Oban, NZS161 (Mill Ck), NZS169 (Kaka Retreat), NZS173 (Bay Motel); Port Pegasus; Port William hut; Sawyers Beach stm; The Neck; Thule Bay culvert, NZS171; Vaila Voe Bay stm, NZS165, 165a, 165b.

Northernmost record: Aorere Valley, Bainham, Cooks Creek, NN (latitude S40.76780°); southernmost record: Stewart Island, Port Pegasus (latitude S47.17100°). Usually from sea level to 990 m a s l, but Dumbleton recorded adults from 1 200 m a s l at Saddle Hill, George Sound, FD. Adler & Crosskey (2012: 20) incorrectly list *A. ungulatum* as only occurring in the South Island.

—/ SD, NN, BR, WD, MB, KA, NC, MC, SC, MK, OL, CO, DN, SL, FD, SI /—

Austrosimulium ungulatum, with two exceptions, occurs in all South Island ecoregions, but sporadically in some. It is almost absent from the East Coast Plains, but has been collected at Kaituna, adjacent to the Banks Peninsula ecoregion, where it so far has not been collected.

Etymology. Not given by Tonnoir (1925), but most likely in reference to the toothed claw of the female.

Bionomics. *Austrosimulium ungulatum* is the notorious biting black fly of the South Island, immortalised for posterity by sculptures at Milford Sound, Fiordland, and Pukekura, Westland.

As Dumbleton noted, Tonnoir searched without success for the early stages of this species. The abundance of adults at places in the South Island suggested that they should be readily found, but they could not be located in large open streams. An early attempt by Dumbleton to find breeding sites was on a joint New Zealand–American expedition to Fiordland in 1949 (Dell 1951). No immatures were found, but Dumbleton did recover those of *A. fiordense* (as *multicorne*). The characteristic habitat was finally shown to be smaller streams under heavy shade in the forest (Fig. 492, 493). Twelve of the 14 sites in which Dumbleton found early stages were of that type and recent collections confirm this. The streams varied from trickles a few centimeters wide to those a metre wide. In most, the rocks were angular and clean of algae, but these are not the habitat of choice, and the streams were of fairly steep course and in young mountainous rather than mature topography. Dumbleton was of the general opinion that immature stages not found in such habitats were stragglers from nearby smaller hillsides streams, and this is probably the case for our finding of *A. ungulatum* in a side stream on the Waiho River bed. Cowie & Winterbourn (1979) illustrated a classic stream (Middle Bush Stream, Cass) for *A. ungulatum* where they found immatures on the mosses, *Fissidens* and *Pterygophyllum*, and also on stones. Suren & Winterbourn (1991) found that *A. ungulatum* was present only at their shaded site, a tributary of the Bealey River, and also that bryophyte fragments constituted only 2% of the gut contents. Our collections indicate that immatures of *A. ungulatum* can occur in moderate numbers in open streams, not associated with heavy shade (Fig. 494, 495), and Dumbleton had such records too. A recent collection of *A. ungulatum* from the summit of Lindis Pass (NZS181) suggests that shade is more an indicator of the cool water temperatures they require. In general, however, there is close correlation between occurrence of forest and *A. ungulatum*. Such forest is mostly *Nothofagus*, but *A. ungulatum* occurs where *Nothofagus* is absent, as on Stewart Island and central Westland. The coincidence with forested areas is strikingly shown at the eastern edge of the Canterbury foothills where the species occurs near the forest remnants, but not onto the Plains (Map 16). The two adults taken at Kaituna, Bank Peninsula (NZS60), are perhaps surprising, but the upper reaches of the Kaituna River would be ideal for immatures of this species. Since the probability of wind blown colonists is high, the question then is why is *A. ungulatum* not found commonly on Banks Peninsula?

Immatures have been found from near sea level to around 990 m a s l (Porters Pass) and Dumbleton took adults at 1 200 m a s l (Saddle Hill—exact location unknown). The relative abundance of adults in West Coast localities, especially on sea and lake beaches and on river margins, suggests that adults are long-lived with a tendency to collect in such localities. Such implies, though, that after blood feeding from sea birds or seals the females return to higher elevations for oviposition.

Dumbleton recorded steam temperatures at Arthurs Pass (920 m a s l) where they ranged from 0°C in July and August to 12°C in January, and his other records showed that the summer temperature was about the same in forested streams at lower altitudes. Our temperature data for immatures (Appendix 1) agrees, ranging from 9.5 to 17.0°C, with the majority between 11 to 15°C. Water pH ranged from 6.1 to 8.0, but tended to the acidic, in agreement with the water often being brown from humic materials derived from *Nothofagus* litter. Conductivity tended to be low, ranging from 10 to 155 µS/cm, with the majority in the 40–80 µS/cm range.

Austrosimulium ungulatum is probably multivoltine since immatures have been found in most months of the year; similarly adults in low numbers will bite even during winter. An unusual aspect of *A. ungulatum* females is that they will bite when inside a vehicle or building and will do so at night, too, an aspect recorded by Henry (1896). Larvae are parasitised by *Coelomycidium* and *Austromermis* (Fig. 500, 502, 503).

Remarks. As Dumbleton noted, the female of *A. ungulatum* can be readily distinguished from those of other species by the combination of 3 characters: toothed claw, white haltere, and pale base to the 1st flagellomere. Further, less easily observed, are the extremely small abdominal tergites (Fig. 82). Larvae placed live into 70% ethanol characteristically tightly retract their mouthparts and posterior abdomen (Fig. 315) much more than other species, making it difficult to check for the tapered accessory sclerite. The abdomen is generally more thickened than other species.

In the *ungulatum*-subgroup, for those known (*A. campbellense, A. ungulatum, A. vexans*), the anterior projections of the cocoon are subequal in length to the gills, with *A. ungulatum* having the longest (Fig. 155, 173), suggesting that these projections protect the gills.

Cladistic analysis of morphological characters shows full support for the *ungulatum*-subgroup (Fig. 506), with *A. ungulatum* sister to *A. vexans* with moderate support. This is not markedly at variance with the molecular analysis (Fig. 509, 509a, 514). Of significance here, though, is that *A. vexans* is sister to a small clade of *A. ungulatum* haplotypes that, on re-examination of the adults used, are of classic *ungulatum* morphology. Such a well-supported divergence is probably indicative of a separate species. The remainder of *A. ungulatum* haplotypes cluster into three well supported lineages, two widely distributed. This distribution shows an apparent “beech gap” for this species in Westland and is discussed elsewhere (p 000). The type locality for the species, Reefton, lies within the widespread haplotype #38 grouping (Fig. 514). Dumbleton (1973) noted variation in the number and arrangement of pupal gill filaments, but no variation amongst adults. Occasionally we have observed variation in the adults (mainly antennal coloration) and assumed this to be normal, but perhaps it is not. While it is easy to obtain adults of *A. ungulatum*, immature stages are not, but will be needed to verify the possibility of cryptic species.

Austrosimulium (*Austrosimulium*) *vailavoense* new species

Figures: female, 22, 23, 37, 63, 83, 103, 121; habitat, 479, 481; Map 18.

Diagnosis. A slightly larger than average sized species. **Female**: antenna entirely black, tapered; mouthparts markedly enlarged; 3rd article on maxillary palp elongated, tarsal claw with basal tooth small and triangular, hind basitarsus lacking row of stout setae; haltere pale tan; abdomen darker than *A. ungulatum*; abdominal tergites III–V subquadratic and less than 1/2 width of tergite II; cercus truncated apically.

Adult female (based on holotype and 5 paratypes) **Body**: general anterior body colour black, abdomen markedly paler; total length 2.9–3.4 mm. **Head**: evenly black; width

0.74 mm; depth 0.30 mm; frons width : head width ratio 1.0 : 3.5. **Eyes**: dark red; interocular distance 0.21 mm; ommatidia diameter 0.011 mm; *ca* 44 rows up and 30 across at mid-eye. **Clypeus**: width 0.19–0.22 mm; black, with slight pollinosity; vestiture of sparse, markedly-fine pale hairs. **Antennae**: evenly black; length 0.45–0.56 mm; 1st flagellomere 0.5× as long as wide, 2nd larger and quadratic, remainder of flagellomeres beadlike, noticeably tapered. **Mouthparts**: markedly substantial, 0.8× length of head depth; cibarium lacking armature, slightly convex medially, cibarial cornuae short and broad with small tubercles, flared apically, ornamentation absent (Fig. 37); mandibles with 28 inner teeth, decreased in size away from apex, plus 8 other minute teeth; laciniae with 16 inner teeth and 19 outer teeth; maxillary palp pale basally, total length 0.49 mm, 3rd article markedly elongate and black, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.8 : 1.2, sensory vesicle ovoid, 0.5× 3rd article width, opening 0.7× vesicle width.

Thorax: length 1.1–1.2 mm; width 0.79 mm; postpronotal lobes, scutum, scutellum, postnotum, pleuron, and pleural membrane all concolorous, black; scutum with vestiture of even sparse small golden hairs; scutellar depression with long fine black hairs, also on postnotum. **Wings**: slightly dusky; length 2.5–2.7 mm; width 1.5–1.6 mm. **Halteres**: white. **Legs**: all dark brown, except hind basitarsus which is yellowish; hind basitarsus lacking ventral series of stout spines, tarsal claws (Fig. 63) with small basal tooth (tooth to claw ratio 1: 3.9), thumb-shaped, with basal notch, similar to the tooth sporadically occurring in *A. unicorne*.

Abdomen (Fig. 83): in ethanol evenly mottled ruddy brown; abdominal scale black with fine tan hairs, extended full length of abdominal segment 2; tergite II 3.0× wider than long, tergites III–V quadratic, tergite VI 1.3× as wide as long; vestiture of coarse sparse hairs. **Genitalia** (Fig. 22, 23, 103, 121): sternite VIII evenly pigmented medially, dense black hairs posterolaterally; hypogynial valves with edges slightly concave medially, strengthened anteriorly, moderately sharply rounded posteriorly, well covered with microtrichia and hairs; genital fork broad and insubstantial except anteriorly, knee-bend on lateral arms broad and distinct, apodeme large, pointed but variable, posterolateral lobe markedly enlarged and smoothly rounded laterally; anal lobes coarsely haired, cerci in lateral view truncated; spermatheca darkly pigmented with internal hairs.

Adult male (unknown).

Pupa (unknown).

Larva (unknown).

Type data. **Holotype**: In ethanol, female. condition excellent; label details "*Aust.* (*A.*) *vailavoense*", "**New Zealand**, South Is., SI, Stewart\ Island, Vaila Voe Stream, S46.90284\ E168.10666, 21m a s l, 25-i-2009, Coll.\ D.A. & R.E.G Craig. NZS165", "HOLOTYPE". "Holo-\type" (round label with red rim; top and right sides trimmed) (NZAC). **Paratypes** (5): ethanol, 1 female; label details as holotype, but with "PARATYPE ". 4 females, label details "*Aust.* (*A.*) *vailavoense*", "**New Zealand**, South Is., FD, Papatotara\ Coast Road, Str. west of Rowallen Burn,\ S46.15628 E167.51268, 6m a s l, 17-i-\2009, Coll. D.A. & R.E.G. Craig. NZS157", "PARATYPE", "Para-\ type" (round label with yellow rim) (NZAC).

Material examined. Type specimens; plus 4 females from Papatotara locality (NZS157), and 1 female from Alton Burn, Tuatapere Scenic Reserve (NZS156) (Appendix 1), and 22 females from Stewart Island (NZAC).

Distribution (Map 18). **South Island**. **FD**. Alton Burn, NZS156; Papatotara Coast Rd stm, NZS157. **Stewart Island**. Christmas Village Hut; Hicks Road stm, NZS172; Kaipipi Bay stm, NZS170a; Oban, NZS173 (Bay Motel); Port William hut; Vaila Voe Bay stm, NZS165, 165a.

Northernmost record: South Island, SH99, Tuatapere Scenic Reserve, Alton Burn (latitude S46.11143°). Southernmost record: Stewart Island, Vaila Voe Bay stream (latitude S46.90284°). Low altitude, from sea level to 40 m a s l.

—/ FD, SI / —

Since all known specimens were female adults attracted to humans, it is not known if the collection sites represent the habitat of the immature stages.

The known localities are in the Southeast Forest and Southern Plain ecoregions.

Etymology. Named after the type locality stream at Vaila Voe Bay, near Oban, Stewart Island.

Bionomics. Nothing is known except that the specimens were attracted to humans and attempting to bite. The small abdominal tergites indicate blood feeding, as do the proportionally large mouthparts. The Vaila Voe Bay site (NZS 165) is a densely-bushed smaller stream (Fig. 479) typical of Stewart Island and a normal habitat for larvae of *A. stewartense*. Other adults collected at that locality and attracted to humans were *A. ungulatum* and *A. stewartense*, both common biting simuliids on Stewart Island. No immature stages assignable to *A. vailavoense* were collected, even after intense searching (NZS165a, b). The site immediately west of Rowallen Burn, Papatotara Coast Road (NZS157) was also a densely-bushed smaller stream. That of Alton Burn, Tuatapere Scenic Reserve (NZS156) was a larger stream (Fig. 481). None of the sites yielded immatures that could be assigned to *A. vailavoense.*

Remarks. Females of *A. vailavoense* are superficially similar to those of *A. vexans* in that they share completely black antennae, pale tan halteres, and truncated cerci of the genitalia. The females of *A. vailavoense* can be separated from those of *A ungulatum*, using the characters of dark antenna, pale tan haltere, darker ruddy abdomen, and markedly smaller claw tooth.

Taxonomic assignment of *A. vailavoense* involves the same problems faced by Crosby (1976a) for *A. dumbletoni*. We place *A. vailavoense* in the *ungulatum*-subgroup mainly on the basis of the toothed claw and blood-feeding behaviour.

As only the female stage is known we did not incorporate the species in the cladistic analysis. Of significance is that molecular analysis (Fig. 514) places *A. vailavoense* sister to *A. unicorne* and with high support, in what taxonomically is the *unicorne*-subgroup. The small tooth on the tarsal claw of *A. vailavoense* is markedly similar to the tooth that occasionally occurs on the claw of *A. unicorne* (*cf* Fig. 63, 67). The similar size of both species might also indicate a relationship. The immature stages of *A. vailavoense*, should provide evidence for the correct taxonomic placement. For the present we leave it in the *ungulatum*-subgroup.

***Austrosimulium* (*Austrosimulium*) *vexans* (Mik, 1881)**

Figures: female, 38, 84, 104, 122; male, 139; pupa and cocoon, 156, 174, 190, 195, 213, 230, 265, 282, 299; larva, 316, 335, 348, 363, 380, 397, 416, 433, 450; habitat, 498; Map 19.

vexans Mik, 1881: 201 (description female, illustration of wing; *Simulium*). Hutton 1902: 169 (repeats Mik's description). Hudson 1909: 64 (present at Carnley Harbour; also Lamb 1909: 124 (in part)). Tonnoir 1925: 250 (redescription female, generic placement in *Austrosimulium*). Smart 1945: 499 (world catalogue). Mackerras & Mackerras 1949: 402 (general summary). Dumbleton 1963b: 334 (as subgenus *Austrosimulium* (*Austrosimulium*), in *ungulatum* group). Dumbleton 1964a: 35 (relationships, distribution). Dumbleton 1973: 533 (female diagnostic features, description pupa, cocoon, larva). Adler & Crosskey 2012: 20 (world inventory).

"sand-flies". Ross 1847: 149 (earliest record, from 1840 diary, troublesome).

Not *vexans*, but *A. campbellense* Dumbleton, 1973. Lamb 1909: 124 (in part). Dumbleton 1953: 242. Harrison 1955: 214; 1964: 304. Gressitt 1964: 542, 576.

Diagnosis. A variably-sized species. **Female**: antenna entirely black; markedly elongated 3rd article on maxillary palp; haltere white; tarsal claw with smaller basal tooth; hind basitarsus lacking row of stout setae; abdominal tergites III–V subquadratic and 1/2 width of tergite II. **Male**: hind basitarsus lacking row of stout setae; ventral plate with marked median keel. **Pupa**: thoracic and head cuticle with evenly distributed rounded granules; gill with short horn, non-tapered filaments in groups (3 or 4 basodorsal, 6–8 apicoventral); grapnel hooks present on terminal segment. **Cocoon**: with 2 anterior cornuae; slipper-shaped, not of low profile, coarsely woven. **Larva**: evenly brown; frontolabral apotome markedly translucent, head spots indistinct; ventral tubercles marked; accessory sclerites absent; semicircular sclerite ends tapered.

Adult female (based on 2 pinned females and ethanol specimens from the 1960s). **Body**: general body colour black, when dried with sparse silvery pollinosity on thorax; total length 2.3–3.4 mm. **Head**: evenly black; width 0.71–0.80 mm; depth 0.28–0.30 mm; frons width : head width ratio 1.0 : 3.5. **Eyes**: slightly reddish; interocular distance 0.16–0.19 mm; ommatidia diameter 0.011 mm; *ca* 34 rows up and 27 across at mid-eye. **Clypeus**: black, with slight pollinosity; vestiture of sparse, markedly-fine pale hairs; width 0.19–0.22 mm. **Antennae**: evenly blackish-brown, inner pedicel and 1st flagellomere orange, length 0.45–0.54 mm; pedicel slightly narrower than 1st flagellomere. **Mouthparts**: substantial, 0.75× length of head depth; cibarial cornuae short and broad, with small tubercles and flared ends with slight scallops and striae (Fig. 38); mandibles with 22 inner teeth, decreasing in size away from apex; laciniae with 15 inner teeth and 26 outer teeth; maxillary palp evenly black, total length 0.59 mm, 3rd article markedly elongate, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.8 : 1.1, sensory vesicle ovoid, 0.5× 3rd article width, opening 0.7× times vesicle width.

Thorax: length 1.1–1.3 mm; width 0.8–0.9 mm; in ethanol (older material), postpronotal lobes, scutum, scutellum, postnotum, pleuron, and pleural membrane all concolorous blackish-brown; dried, all black, vestiture of small sparse golden scales, scutellar depression with longer fine golden hairs, black, coarse and sparse on postnotum. **Wings**: dusky; length 2.7–3.4 mm; width 1.5–1.7 mm; hyaline. **Halteres**: white. **Legs**: overall dark brown; hind basitarsus about 6.5× as long as greatest width, lacking row of stout setae, tarsal claws (Fig. 64) with basal tooth moderately small and sharp (tooth claw ratio 1:3.0).

Abdomen (Fig. 84): overall dark; abdominal scale dark brown with fine pale hairs, extended full length of segment II; tergite II 2.2× wider than long, tergites III–V quadratic, tergite VI 1.5× as wide as long; vestiture of sparse black hairs, more so posteriorly. **Genitalia** (Fig.104): sternite VIII pigmented medially and along anterior edge; hypogynial valves parallel-sided medially, strengthened and rounded posteriorly; genital fork (Fig. 122) near *A. campbellense*, insubstantial except anteriorly, posterolateral arms short, lacking knee-bend, apodeme sharply pointed, posterior lobe angular medially and laterally; anal lobes poorly developed, cerci slightly truncated apically; spermatheca slightly smaller and lighter in pigmentation than *A. campbellense*.

Adult male (based on 1 pharate specimen). **Body**: total length 2.6 mm. **Head**: width 0.79 mm; depth 0.62 mm. **Eyes**: upper ommatidia, diameter 0.033 mm, *ca* 21 across and 22 down; lower ommatidia, diameter 0.015 mm, *ca* 36 across and down. **Clypeus**: width 0.18 mm. **Antennae**: total length *ca* 0.48 mm, pedicel wider than 1st flagellomere. **Mouthparts**: poorly developed; length 0.33× head depth; maxillary palp medium brown, 0.42 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 2.4 : 1.3.

Thorax: length 1.1 mm; width 0.8 mm. **Legs**: hind basitarsus lacking row of stout setae.

Abdomen. **Genitalia** (Fig. 139). gonocoxites triangular, 1.6× longer than basal width, marked crenulations anteromedially; gonostyli narrow in ventral view, *ca* 3.2× longer than basal width, apically with 2 sharp spines, 1 smaller; ventral plate shield-shaped, 2.0× wider than length, plate cone-shaped posteriorly, slightly fluted laterally, irregular edge anteromedially, basal arms broad, median keel increased in height towards middle of plate, with sparse vestiture of fine hairs; median sclerite not observable; parameres distinct.

Pupa (Fig. 156, 174). Body length; male 2.5–2.7 mm, female 2.7–3.0 mm. maximum width for both sexes 1.0 mm. **Head**: cephalic plate of male and female evenly tuberculate, not concave; plate of female 1.5× as long as basal width, truncated apically (Fig. 213), plate in male (Fig. 230) 1.7× as long as basal width, rounded apically; frontal and facial setae present and markedly long, sometimes missing, but sockets visible, 2 epicranial setae present; ocular setae present. **Thorax** (Fig. 251): dorsum finely tuberculate, evenly distributed. Setae simple, long and obvious, sometimes broken off; posterior dorsocentral seta spine-like. **Gills** (Fig. 265, 282): horn markedly small, base pale; filaments variable, light brown and only slightly tapered; dorsal group, always of 3 filaments, 1 usually bifurcated basally; single shorter median filament; basal group with dark bases of 5–7 filaments; and shorter more ventral filament, numbers variable; maximum length 1.5 mm; surface reticulated (Fig. 299). **Abdomen** (Fig. 195): grapnel hooks present on sternite IX.

Cocoon (Fig. 190): similar to that of *A. ungulatum,* fabric filamentous, thin, brown but more coarsely woven; anterodorsal cornuae parallel-sided.

Larva (based on 30-year-old final instar specimens). **Body** (Fig. 316): overall medium brown, colour sexual dimorphism not apparent; total length 4.9–6.5 mm. **Head** (Fig. 335): overall evenly medium brown; length 0.68–0.76 mm, width 0.56–0.58 mm; distance between antennal bases 0.30–0.34 mm; lateral margins of head distinctly convex, tapered anteriorly; anterior apotome translucent, head spot pattern not marked, slightly positive; posterior edge of apotome not markedly pigmented, concolorous with remainder of head; ecdysial lines broadly curved; postocciput continuous across back of head, cervical sclerites fused to postocciput. **Antennae** (Fig. 380): medium brown basally, paler apically; length 0.33 mm, extended well beyond apex of fan stalk; proportional lengths 1st, 2nd, and 3rd articles 1.0 : 0.3 : 2.0; apical article *ca* 1.5× length of combined basal 2 articles, medial article 0.3× length of basal article. **Labral fans**: stem translucent; *ca* 28–30 fine rays, length 0.56 mm, width 0.009 mm; distinct pattern of microtrichia, longer microtrichia 1.2× longer than ray width, separated by *ca* 8 smaller irregular microtrichia. **Postgenal cleft** (Fig. 397): markedly shallow; posterior tentorial pit region extensively sclerotised and pigmented. **Postgenal bridge**: 1.7× longer than hypostoma, pale medially, darker brown laterally, elongated posteroventral muscles spots distinct. **Hypostoma** (Fig. 416): teeth all subequal in size, median and lateral teeth marginally prominent, largely concealed by dome-shaped anteroventral margin of hypostoma, 2 or 3 rounded lateral serrations, variable; 4 or 5 hypostomal setae per side. **Mandibles** (Fig. 433): outer, apical, and preapical teeth poorly developed, but curved, *ca* 7 spinous teeth; serrations and sensilla distinct, but small; blade region well developed, smooth and slightly convex. **Thorax** (Fig. 348, 363): pharate pupal gills with 5 or 6 filaments distinct, not markedly curved into L-shape. **Abdomen**: darker brown posteriorly; distinct ventral tubercles. **Anal sclerite** (Fig. 450): median region broad, slightly tapered posteriorly; anterior arms flared, not bifurcate, basal struts substantial, posterior arms relatively short; accessory sclerites poorly developed, semicircular sclerite slightly angulate but finally tapered. **Circlet of hooks**: *ca* 114 rows, 14–16 hooks (total *ca* 1700).

Type data. Although Tonnoir (1925: 250) used “type”, in the sense that it was lost according to Dr. H. Zerny (NHMW), and Dumbleton (1973: 534) used a heading “Holotype” to present collecting data, there is no indication in Mik (1881) that any of the 4 specimens on which he based his description was marked as a type; therefore they were all syntypes. Dumbleton recorded the data for one of these syntypes as follows: “{F}, Auckland I., H. Krone, 1874–75 German–Vienna Expedition (presumably near Observation Point, Terror Cove), Vienna Museum, Austria”. Tonnoir (1925) considered the material lost, which was repeated by Dumbleton (1973: 534). Nothing is listed in “Nematocera Types” (2008), Natural History Museum Vienna, Austria (NHMW), and so we also consider the syntypes are lost.

Because of lack of types, Tonnoir (1925) used 2 females from the Canterbury Museum to redescribe *A. vexans*. He stated on his p. 250 that the specimens had been collected by Captain F. W. Hutton, however, the collector is not so indicated on the specimens. Because of the importance of these specimens their data follow: Female on minuten pin on pith strip "Auck Is", then glass cover slip with legs "Revision\ A Tonnoir 1923". Female, on pin, glass coverslip with body, then glass coverslip with wings [2] "Auckland Is.\C.P. Sub-Ant.\ Exped., 1907", "Austrosimulium\ vexans Mik\ det. A. Tonnoir 1923". These are unusual mounts where the coverslips are double with a small piece of thin cardboard between the glass at one edge and all held together with Canada Balsam, and somewhat reminiscent of the Enderlein mounts of *A. australense* (e.g., Fig. 525). The cardboard piece allows the coverslips to be pinned. Tonnoir (1925) alluded to other specimens, but their whereabouts is unknown.

Dumbleton (1973: 497) indicated that a pupa had been used for a neotype designation for a species for which the type had been lost. The only species for which he listed a lost type was *vexans,* but he made no neotype designation. Presumably, the designation of a neotype was considered because there was still some doubt as to the identity of caecutiens Walker specimens, since the *Erebus* and *Terror* had visited the Auckland Islands (Dumbleton 1973: 510). However, there is now no doubt as to the identity of *vexans* and a neotype designation is not justified*,* as examination of the caecutiens Walker specimens have shown conclusively they are *australense* (p. 102).

The original syntypes described by Mik were collected during an expedition led by the astronomer Hugo Seeliger to observe the transit of Venus across the sun on 9 December 1874. A camp was set up on the bench at Terror Cove beach, Port Ross, on the NE of Auckland Island (van Roode undated). van Roode noted that the day of the transit started with rain, but the transit could be seen until shortly before last contact, when the sun was obscured by clouds again. The stream flowing by the astronomical encampment is now officially named Seeliger Creek (S50.53643°, E166.21267°; decision of New Zealand Geographical Board, 5 November 2009) and was no doubt the origin of the *A. vexans* females. A creek farther to the north has been named Krone Creek after Krone (S50.52525°, E166.22008°).

Herman Krone who collected the specimens was the official photographer of the expedition and his work was of international repute. He was also an avid naturalist and collected considerable numbers of insects while on the Auckland Islands.

Mik (1881) in his description decried that all Krone's specimens were in spirits (alcohol). It is remotely possible that these specimens are in an alcohol collection somewhere. There were apparently 4 female specimens with a note from Krone [translated]—"Our torturers on the island – the Sandflies". Thence no doubt, the specific name—*vexans*. Mik noted that *A. vexans* was similar to the European *S. hirtipes*, but did not have long leg hairs (hirtipes = hairy footed). He stated that he had examined the type of *A. australense,* noting that this was smaller and had yellower prothoracic lobes and legs. Also, he made the point that Schiner's *australense* came from the surroundings of Auckland, New Zealand, and not from the Auckland Islands as had been stated by Nowicki (1875).

Ross (1847: 149) recorded the stay of the "*Erebus*" and "*Terror*" at Port Ross 20 November–12 December 1840 as follows "Of insects we observed a great variety, and a large collection was made. The sand-flies were very troublesome during the heat of the day, and their stings painful." No simuliids appear to have been collected, or, if they were, none survived to be deposited in the British Museum with other specimens of the expedition.

Both Tonnoir (1925) and Dumbleton made the point that the type material was missing. Of interest, and in relation to that missing material, is that Krone (*in* Gourlay 1950) noted that "Representatives of all species collected by me, also single specimens, have passed into the possession of the entomological collection of the Royal Zoological Museum at Dresden". A search of Krone's material in the now Senckenberg Naturhistorische Sammlungen, Dresden, by Uwe Kallweit (pers. comm. 2010) failed to find any *A. vexans* specimens.

The specimens used by Tonnoir for his redescription appear to be of mixed provenance. Certainly the specimen dated 1907 could not have been collected by Hutton, who died in 1905 (obituary in *Nature 73*: 32–33). Indeed, that specimen was from an expedition sponsored by the then Philosophical Institute of Canterbury (now the Canterbury Branch of the Royal Society of New Zealand), that landed in the Auckland Islands, 15 November 1907. The main aim of the expedition was to extend the magnetic survey of the New Zealand region, but considerable surveying of the biota was done, although seriously interfered with by bad weather (Godley 1979). G. V. Hudson probably collected that *A. vexans* female. The undated specimen could well have been collected by Hutton, since he visited the Auckland Islands on the *Hinemoa* in 1901, during one of its regular provisioning calls to the island (Hutton 1902; Gourlay 1950).

Material examined. 2 specimens used by Tonnoir for his redescription, plus numerous specimens collected by Dumbleton in NZAC and 3 recent specimens.

Distribution (Map 19). Restricted to the Auckland Islands. **Auckland Islands**. **Enderby I**. Lake Teal stm. **Auckland I**. Deas Cove stm; Erebus Cove; Grey Duck Ck; Ranui Cove stm; Terror Cove stm; Victoria Passage; Webling Bay stm. **Adams I**. Magnetic Cove.

Northernmost record: Enderby Island, Lake Teal stream (latitude S50.49940°); southernmost record: Adams Island, Magnetic Cove (latitude S50.86600°); of low altitude.

— / —/ AU

Etymology. Basis for name not given in detail by Mik (1881), but obviously this simuliid was seriously vexatious.

Bionomics. Dumbleton noted that the adults are mostly found around the shore, although not very abundant (but see below). The immatures are found in rocky parts of streams (e.g., Fig. 498). For smaller streams this represents only the last 90 m of their course. In larger streams that have cut through the peat the whole bed carries larvae and pupae. Many larvae and pupae occur on cobble where the water flows into the sea (reminiscent of *A. extendorum* and *A. stewartense* at Sawyers Beach, Stewart Island). Dumbleton made no comment regarding life cycle, but *A. vexans* is likely multivoltine.

Remarks. Male adults are unknown from collections. The details reported here were derived from an immature pharate male; thus vestiture and sclerotisation were not observable and reconstruction of genitalia (Fig. 139) was somewhat superficial.

Females of *A. vexans* are well established as biting humans. Of relevance to this, in a historical work on the Coleoptera of the Auckland Islands, Gourlay (1950) quoted extensively from translations of Krone's notes, part of which states "… but the world of insects seems like dead except for the extremely unpleasant sandflies...". Hudson (1909) noted briefly that *Simulium vexans*, as it was then known, was very abundant around streams and "Its bites were persistent and painful". It is odd that neither Tonnoir (1925) nor Dumbleton commented on this aspect. Confirmed records of biting are by TKC and G. W. Gibbs. The substantial mouthparts and small abdominal tergites (Fig. 84) are well in agreement with blood feeding.

Cladistic analysis of morphological characters (Fig. 506) places *A. vexans* as sister to *A. ungulatum,* with moderately high support, in complete agreement with Dumbleton. Sister to those two species, again with moderate support, is *A. dumbletoni*, and this is in agreement with Crosby (1976a) who placed that species in the *ungulatum* species-group. Basal to these species is *A. campbellense*, not at variance with Dumbleton's arrangement, and together these form the *ungulatum*-subgroup.

Molecular evidence (Fig. 514) does not disagree greatly with that of morphology. With only fair support, *A. vexans* is sister to a small, well-supported segregate of what is currently recognised as *A. ungulatum*. Re-examination of those specimens (all female adults) showed no divergence from classic *A. ungulatum*—namely pale base to the antennal flagellum, white halteres, and toothed claw. Divergent at more than 4% from *A. vexans*, that segregate (haplotype #33) of *A. ungulatum* probably represents a cryptic species. Immature stages, in particular pupae, will no doubt be needed to clarify this situation.

When *A. campbellense* is subjected to molecular examination, will it be directly sister to *A. vexans*, or to its own segregate of *A. ungulatum* as is *A. vexans*?

***ungulatum* species-group**

***unicorne*-subgroup**

***Austrosimulium* (*Austrosimulium*) *bicorne* Dumbleton, 1973**

Figures: female, 39, 65, 85, 105, 123; male, 140; pupa and cocoon, 157, 175, 191, 214, 231, 252, 266, 283, 300; larva, 317, 336, 349, 364, 381, 398, 417, 434, 451; habitat, 486, 487; Map 4.

bicorne Dumbleton, 1973: 538 (description female, male, pupa, cocoon, larva; *Austrosimulium* (*Austrosimulium*)). Crosby 2006: 72 (key). Adler & Crosskey 2012: 20 (world inventory).

crosbyi Yankovsky, 1996: 113 (unnecessary substitute name, *Austrosimulium* (*Austrosimulium*)).

sp. 2. Dumbleton 1964a: 36 (Fig. 1, distribution map, pupal gill, and cocoon; *Austrosimulium*).

Diagnosis. A moderately large species. **Female**: tarsal claw with medium-sized basal tooth and notch; hind basitarsus lacking row of stout setae; abdominal tergites subquadratic, wider than long. **Male**: hind basitarsus lacking row of stout setae. **Pupa**: thoracic cuticle evenly densely covered with rounded tubercles, gill with black banana-shaped horn with *ca* 40 filaments; terminal abdominal segment with grapnel hooks. **Cocoon**: slipper- to shoe-shaped, closely applied to pupa, thick white alveolate weave, 2 narrow anterior projections continued from dorsal ridges along cocoon body, curved medioventrally apically. **Larva**: brown; cephalic apotome mottled light brown; semicircular sclerite with finely tapered dorsolateral ends.

Adult female (based on holotype and paratypes). **Body**: general body colour in ethanol dark reddish brown-black, when dried overall black with silvery pruinose appearance; total length 2.4–3.1 mm. **Head**: width 0.6–0.7 mm; depth 0.64–0.66 mm; postocciput black, vestiture of sparse, short golden hairs; frons dark brown-black, but pollinose; frons width : head width ratio 1.0 : 3.4. **Eyes**: interocular distance 0.22 mm; ommatidia diameter 0.013 mm; *ca* 38 rows up and across at mid-eye. **Clypeus**: dark brown; vestiture of very sparse pale hairs; width 0.26 mm. **Antennae**: evenly dark; total length 0.50 mm; pedicel wider and longer than remainder, flagellomeres wider than long, decreasing in width apically. **Mouthparts**: substantial, 0.5× length of head depth; cibarial cornuae, broadly rounded apically, slightly fluted (Fig. 39); mandibles with *ca* 35 inner teeth, basal ones small; laciniae with 13 inner teeth and 23 outer teeth; maxillary palp, total length 0.48 mm, dark brown, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.7 : 0.9, sensory vesicle subspherical, 0.3× 3rd article width, opening 0.5× vesicle width.

Thorax: length 1.5 mm; width 1.0 mm; in ethanol, postpronotal lobes marginally paler than scutum; when dry, scutum grayish-black, vestiture of moderately dense decumbent hairs, presutellar depression with few longer darker hairs posteriorly, no vittae visible in ethanol or when dried, but when dried with silvery pruinosity posteriorly; scutellum slightly lighter than scutum, vestiture of few long black hairs and pale hairs laterally; postnotum concolorous with scutum; pleuron and pleural membrane lighter than scutum and pollinose. **Wings**: length 3.4–4.0 mm; width 1.4–1.6 mm. **Halteres**: tan. **Legs** (Fig. 65): yellowish-brown, with darker brown bases to femoral, tibial, and tarsal segments; hind basitarsus *ca* 6.5× as long as greatest width, lacking row of stout setae; tarsal claws with well developed basal tooth (tooth claw ratio 1:2.9).

Abdomen (Fig. 85): abdominal scale with fine pale hairs, not greatly extended; tergites subrectangular, tergite II widest, tergites III and IV subquadratic. **Genitalia** (Fig. 105): sternite VIII pigmented along anterior edge, vestiture of long fine hairs posterolaterally; hypogynial valves lightly pigmented with vestiture of sparse, small hairs, microtrichia imbricated; median edges of hypogynial valves smoothly divergent, broadly rounded posteroapically, markedly reinforced medially; genital fork (Fig. 123) anterior arm broad with anterior apex knob-like, lateral arms markedly broad, knee-bend absent, posteromedial apex strengthened and angulate, posterolateral extension with rounded edge, apodeme sharply pointed; anal lobes, anterior median facet with 4 or 5 strong hairs on raised bases; lobes and cerci both broadly rounded in lateral view, with vestiture of dense fine hairs; spermatheca ovoid, clear area at junction of duct small.

Adult male (numerous mature pharate and reared specimens). **Body**: general colour dark brown-black; total length 2.6–2.8 mm. **Head**: width 0.84–1.02 mm; depth 0.57–0.76 mm. **Eyes**: upper ommatidia orange, diameter 0.036 mm, *ca* 20 across and down; lower ommatidia dark brown, diameter 0.018 mm, *ca* 38 across and down. **Clypeus**: dark brown; vestiture of extremely sparse fine hairs; width 0.1 mm. **Antennae**: evenly blackish-brown; total length 0.56 mm; not markedly tapered; pedicel wider than remainder. **Mouthparts**: poorly developed; *ca* 0.32× head depth; mandibles insubstantial, broadly tapered with apical hairs; laciniae, finely tapered apically with apical hairs; maxillary palp medium brown, 0.44 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 0.9 : 1.2, sensory vesicle irregular in shape, occupying 0.33× 3rd article width, opening 0.5× vesicle width.

Thorax: length 1.4 mm; width 1.1 mm; scutum markedly domed; evenly velvety black, vestiture of fine recumbent pale hairs, more golden than in female, few long dark hairs in prescutellar depression; scutellum concolorous with scutum with numerous long hairs; scutellum concolorous with scutum. **Wings**: length 2.6–3.2 mm, width 1.4–1.6 mm. **Halteres**: tan. **Legs**: darker yellowish-brown, with darker brown femoral, tibial, and tarsal bases; hind basitarsus about 6× as long as greatest width, lacking row of stout setae; tarsal claw grappling pads of *ca* 22 teeth. **Abdomen**: tergites and sternites blackish-brown, lateral areas dull black. **Genitalia** (Fig. 140): gonocoxites 1.6× longer than basal width, marked crenulations anteromedially; dark brown along anterior edge, vestiture of coarse black hair and microtrichia; gonostyli *ca* 0.6× as long as gonocoxites, *ca* 3.0× longer than basal width, evenly tapered with 2 substantial apical spines; ventral plate with broadly-based median keel, vestiture of fine hairs, plate 1.5× wider than long, plate broadly convex posteromedially and anteromedially, anterolateral arms not markedly developed; median sclerite poorly developed, broad, T-shaped posteriorly; parameres not markedly developed, but distinctly connected to base of dorsolateral lobe of gonocoxite.

Pupa (Fig. 157, 175). Body length; male 3.3–3.9 mm, female 3.2–3.7 mm. **Head**: cephalic plate of both female and male densely covered with small tubercles on upper frons, female plate (Fig. 214) markedly broad, 1.4× as long as basal width, that of male (Fig. 231) longer, 2.0× basal width. Frontal, facial, and epicranial setae present and prominent; ocular setae well developed. **Thorax** (Fig. 252). Dorsum evenly and densely tuberculate as for cephalic cuticle, tubercles decreased in size on wing pads and more ventrally, no obvious pattern, but slight aggregation along anterior median ecdysial line; dorsocentral setae trichoid, elongated, posterior one spine-like. **Gills** (Fig. 266, 283): horn black, slightly curved (banana-shaped), subparallel-sided, not clubbed apically as in *A. tonnoiri*; length markedly variable, 5.4–7.0× as long as width; filament insertions produce irregular outline; filaments 38–45, simple, rarely forked; filament length 0.75–1.1 mm, width 0.06 mm; not markedly tapered; surface finely annulated (Fig. 300). **Abdomen**: grapnel hooks present on sternite IX.

Cocoon (Fig. 191): fabric, thick, white, fleshy, silk threads visible, alveolate; anterior aperture circular, thickened ventral margins, low ventral collar; dorsum with 2 thickened ribs diverging from posterior end and continued over aperture as 2 long narrow cornuae, separated by distance less than basal width of each process; lateral margins of cocoon thickened.

Larva (numerous final instar specimens). **Body** (Fig. 317): overall grayish-brown, colour sexual dimorphism not apparent; total length 6.2–7.1 mm. **Head** (Fig. 336): evenly medium brown with mottled pigmentation dorsally; length 0.76 mm, width 0.66–0.68; distance between antennal bases 0.38 mm; lateral margins of head distinctly convex; anterior apotome translucent, head spot pattern not marked, spots barely present, variable, positive or negative in mature final instar larvae; posterior edge of apotome not markedly pigmented; ecdysial lines broadly curved, abruptly posteriorly; postocciput more or less continuous across back of apotome, cervical sclerites small and fused to postocciput. **Antennae** (Fig. 381): lightly brown basally, pale apically; total length 0.38 mm, not markedly extended beyond apex of fan stalk; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.4 : 2.1; apical article 1.5× as long as combined basal 2 articles, medial article 0.4× as long as basal article. **Labral fans**: stalk translucent brown; 35–38 fine rays, length 0.7 mm, width 0.009 mm; distinct pattern of microtrichia, longer microtrichia 1.1× longer than ray width, separated by 12 microtrichia that rapidly decrease in size basally. **Postgenal cleft** (Fig. 398): irregular, markedly small inverted U-shaped, posterior tentorial pit elongate, pigmented area extensive. **Postgenal bridge**: 1.5× longer than hypostoma, darker than genae; elongated posteroventral muscles spots neutral. **Hypostoma** (Fig. 417): teeth distinct, anteroventral edge of hypostoma not markedly extended; median tooth prominent beyond anteroventral edge, lateral teeth also prominent, but less so; median sublateral tooth poorly developed; paralateral teeth also small; 2 or 3 lateral serrations; 6 or 7 hypostomal setae per side. **Mandibles** (Fig. 434): outer and subapical apical teeth not well developed, apical tooth straight, not curved; *ca* 11 spinous teeth; serrations and sensilla distinct and widely separated; blade region flat. **Thorax**: Pharate pupal gill (Fig. 349, 364) L-shaped; horn distinct; up to 18 filaments visible arising from horn, filaments leaving horn ventrally then curved quickly posteriorly to form an L, then reflexed anteriorly and dorsally. **Abdomen**: evenly grayish-brown, anterior intersegmental areas paler; markedly developed and pointed ventral tubercles. **Anal sclerite** (Fig. 451): median region quadratic, campaniform sensillae posteromedially, anterior arms flared and bifurcate, interarm struts substantial and closely applied to median region, posterior arms stout, but smoothly tapered; semicircular sclerite substantial, but only thin outer band pigmented, ends finely tapered, accessory sclerites absent. **Posterior circlet**: *ca* 140 rows of 16 or 17 hooks (total *ca* 2300)—markedly more hooks than most other species.

Type data. **Holotype**: Female, double pinned, on minuten on cork strip; condition excellent, complete. “Bred {F}\ Temple Basin\ Arthur’s Pass 23.1.[19]61. L.J. Dumbleton” (all except last line handwritten in black ink, unknown); “HOLOTYPE {F}\ Austrosimulium\ bicorne\ L. J. Dumbleton\(publication name)” (label with red ink border, all lines except “L.J. Dumbleton” handwritten in black ink, unknown), “A. bicornutum\ Dumbleton\ HOLOTYPE” (short sides of label with red ink margins, handwritten in pencil, Dumbleton), “NZ Arthropod Collection\ {barcode}\ NZAC04021457” (NZAC). **Paratypes**: 5, double pinned on minuten in cork (1 in pith) strips; all with label lines as in first listed paratype, label details “Bred, 23-i-[19]61\ Temple Basin\ Arthur’s Pass\ L. J. Dumbleton” (all lines except “L.J. Dumbleton” handwritten in black ink, unknown), “PARATYPE {F}\ A. bicorne.\ L. J. Dumbleton” (all lines except “L.J. Dumbleton” handwritten in black ink, unknown), “NZ Arthropod Collection\ {barcode}\ NZAC04022090”; label details as previous, but “NZAC04022103”; “Bred, 23-i-[19]61\ Temple Basin\ Arthur’s Pass\ L. J. Dumbleton”, “PARATYPE {M}\ A. bicorne\ L. J. Dumbleton”, “NZ Arthropod Collection\ {barcode}\ NZAC04022026”; “{M} 30.1.60 isolated,\ em. in lab.\ Temple Basin\ Arthur’s Pass.\ L. J. Dumbleton”. “PARATYPE {M}\ A. bicorne\ L. J. Dumbleton”. “NZ Arthropod Collection\ {barcode}\ NZAC04022089”;. “Ex. Pupa\ Temple Basin\ Arthur’s Pass\ L. J. Dumbleton”, “PARATYPE {M}\ A. bicorne\ L. J. Dumbleton”, “NZ Arthropod Collection\ {barcode}\ NZAC04022146” (NZAC). 4 microscope slide mounts, all with form of label lines as in first slide listed, label details: “A. bicornutum\ Dumbleton\ {M} genit. of \PARATYPE” (handwritten in pencil, Dumbleton), “Entomology Div., DSIR, NZ\ L. J. Dumbleton Collection” (gold label), “Temple B\ {M}\ genitalia\ adult {M} on\ {unreadable; ?slide} on pupa\ 31/1/58” (handwritten in pencil, Dumbleton). “A. bicornutum\ Dumbleton\ Slide A1\ {F}\ PARATYPE”; “Entomology Div., DSIR, NZ\ L. J. Dumbleton Collection”, “Wings legs\palps\{F}A\ Temple B\ 3/3/58 Pupa A”. “A. bicornutum\ Dumbleton\ Slide A2\ {F}\ PARATYPE”, “Entomology Div., DSIR, NZ\ L. J. Dumbleton Collection”, “Abdomen\ spermatheca\ {F} A\ Temple B\ 3/3/58 Pupa A”. “A. bicornutum\ Dumbleton\ Slide A3\ {F}\ PARATYPE”; “Entomology Div., DSIR. NZ\ L. J. Dumbleton Collection”; “HEAD\ mandibles\ max.\ {F} A\ TEMPLE B\ 3/3/58 Pupa A” (NZAC).

Material examined. All stages, including reared adults. Type material, some 10 collections in NZAC and 8 more recent collections (Appendix 1).

Distribution (Map 4). Occurs only in the South Island, and of restricted altitudinal range. **South Island**. **WD**. Robinson Ck, NZS177 (SH6). **NC**. Otira R, NZS140 (upper). Pegleg Ck, NZS132, 132a (SH73 above bridge); Temple Basin; Twin Ck, NZS52, NZS133, 133a (SH73). **FD**. Homer Tunnel stm, NZS32, 32a (SH94).

Northernmost record: SH73, Arthurs Pass, Pegleg Creek, above bridge, NC (latitude S42.89500°); southernmost record: Takahe Valley, Te Anau, FD (latitude S45.28780°). Not found below 880 m a s l, and up to 1 800 m a s l. Dumbleton commented that he recovered a single *A. bicorne* larva at 760 m a s l, but considered it a straggler washed downstream.

Note that Dumbleton (1973: 485) has the distribution symbols for *A. unicorne* and *A. bicorne* inverted in his Figure 7a.

—/ WD, NC, FD / —

The northern localities are along the eastern edge of the Southern Alps ecoregion, the disjunct southern localities are well within those limits.

Etymology. Named by Dumbleton (1973) for the two anterior processes of the cocoon.

Bionomics. Immature stages of *A. bicorne,* along with those of *A. tonnoiri,* have specialised requirements (e.g., Fig. 486, 487). Cold water is a major one. Temperature records from Dumbleton show that at 1 550 m a s l in winter, water temperatures ranged from 3 to 4°C. Our records (Appendix 1) from summertime range from 6.1 to 9.5°C. The single record of 15°C was from water flowing down a cliff face in full sun (Fig. 491). Larvae tend to concentrate in the rubble at the base of waterfalls. This is also the position of snow packs (often avalanche derived), and larvae can be found in the stream emerging from these (Fig 490). Typical is that larvae and pupae are found on the underside of perched stones along the edge of rudimentary pools and in riffles. There must be a constant flow of water. Larvae and pupae are sparse, but often clumped on a single rock in a row of 3–5 across the current, a known strategy by simuliid larvae to enhance flow through the labral fans when particle flux in the water is low (Ciborowski & Craig 1989). The pH of water is slightly acidic, with conductivity at times below 10µS/cm, both in keeping with snow-derived water.

Dumbleton noted that in places, such as the Homer Tunnel locality, which is a series of cascades off the vertical cliff to the south of the tunnel's eastern entrance (opposite the parking lot), that the water sank into the underlying rubble within 90 m of the base of the cascade. We noticed that larvae and pupae were only found within 9 m of the base of the fall and not farther downstream (Fig. 491). Is this perhaps the shortest simuliid habitat in New Zealand? At another time, in heavy rain though, the stream extended a considerable distance and then within hours had returned to a much shorter length, making it clear that larvae and pupae are only in regions of permanent flow. We again assert here that the thickened cocoon fabric is protection from desiccation. Dumbleton suggested that there was but a single generation a year, with eggs laid in January with slow growth over the winter, with emergence in December through to March. Our recent data do not disagree. Adult females are not known to bite, but they do have substantial mouthparts and the abdominal tergites are of average size.

Dumbleton mentioned finding a single *multicorne*-like larvae with larvae of *A. bicorne,* and a single *A. bicorne* larvae with larvae of *A. ungulatum*. We have recovered immatures of *A. multicorne, A. tonnoiri,* and *A. unicorne* with those of *A. bicorne.*

Dumbleton's collection from Temple Basin (30-i-1960) contained larvae parasitised with *Coelomycidium* (?)*simulii*. He made no comment for this species, but did so for parasitised larvae of *A. unicorne* from the same general region. Parasitism is discussed elsewhere (see p. 33).

Remarks. We restrict *A. bicorne* to the segregate of the *unicorne*-subgroup that possesses the pupa and cocoon as described by Dumbleton (1973: 538); namely that the two anterior cornuae of the cocoon are elongate and narrow (Fig. 175), and the cocoon fabric is of thick white consistency that on close examination is alveolate (Fig. 191). The pupal gill is more banana-shaped and less club-shaped than populations we have segregated and named as *A. tonnoiri*. At the type locality, Temple Basin, Arthurs Pass, *A. bicorne* is common. Dumbleton (1973) assigned material from Homer Tunnel to *A. bicorne*, but much of that we place in *A. tonnoiri.* However, *A. bicorne* does occur there at moderate to low frequency. Similarly, *A. bicorne* occurs at low frequency at the Darran Mountain localities, where the majority of the material is *A. tonnoiri*. It is not possible to identify accurately the larvae collected from Takahe Valley in 1952, so until more material can be obtained from that locality they remain assigned to *A. bicorne*.

The current known distribution (Map 4) is disparate, but an expectation is that *A. bicorne* will be found at high altitudes in the Southern Alps between Arthurs Pass and Homer Tunnel.

Dumbleton (1973) in describing the male genitalia of *A. bicorne*, specifically referred to "paramedian rods (ventral sclerites), dorsad of ventral plate" and illustrated them (his Figure 224). However, re-examination of the slide material used for that illustration showed that the structures in question were, in fact, the posterolateral ends of the median sclerite. Notwithstanding that, the parameres are more developed in *A. bicorne* than generally elsewhere in New Zealand *Austrosimulium* (*cf* Fig. 135–138, 140–142) and are even more so in *A. tonnoiri* (Fig. 141). This better expression of parameres and attachment to the gonocoxa is of phylogenetic importance, since a well expressed paramere is a plesiomorphic state.

Discussed in some detail by Adler *et al*. (2004, e.g., their Fig. 28), parameres when present in Simuliidae, articulate with the basal arm of the ventral plate and the dorsomedial base of the gonocoxite. Supporting the aedeagal membrane, posteriorly the parameres can bear spines, at times markedly developed. This is the structure referred to earlier by Rubtsov (1964, 1989), as the "pleurite" (in a male of *Wilhelmia*). Well developed in *Paraustrosimulium*, the sister genus to *Austrosimulium*, and moderately so in many Australian *Austrosimulium* (DAC, pers obs.), the poor expression in New Zealand *Austrosimulium* must be considered to be a reduction and hence an apomorphic feature of that segregate of the genus. The better expression of these structures in *A. bicorne, A. tonnoiri,* and *A. unicorne* would indicate these species are more plesiomorphic New Zealand *Austrosimulium*. Placement (Fig. 509, 509a, 514) of the *unicorne*-subgroup in the CO1 mDNA analysis perhaps supports this assertion. Within that subgroup, *A. bicorne* is a complex of 3 haplotypes with good support. That the NZS133 (Arthurs Pass) haplotype is divergent from the other distant ones in the Fiordland region, perhaps indicates cryptic speciation.

Austrosimulium (*Austrosimulium*) *tonnoiri* new species

Figures: female, 40, 66, 86, 106, 124; male, 141; pupa and cocoon, 158, 176, 192, 215, 232, 253, 284, 301; larva, 318, 337, 365, 382, 399, 418, 435, 452; habitat, 489–491; Map 15.

Diagnosis. A moderately large species. **Female**: antenna overall brown; haltere, tan; tarsal claw with small basal tooth, hind basitarsus lacking row of stout setae: abdominal tergites III–V subquadratic, **Male**: overall black; hind basitarsus lacking row of stout setae; paramere moderately developed. **Pupa**: thoracic cuticle with fine evenly-dispersed hemispherical tubercles, gill horn curved club-shaped with 36–39 non-tapered filaments; posterior abdomen with grapnel hooks. **Cocoon**: of irregular shape, alveolate weave, 2 anterior projections broad and closely applied medially, no obvious ridges continued posteriorly, almost covering complete anterior of pupa; gills emerged between anterior projections and anterolateral margins of cocoon. **Larva**: evenly brown; head evenly mottled medium brown, posteromedial and posterior head spots indistinct, slightly negative; ventral tubercles marked, anal sclerite not substantial, thin semi-circular sclerite lacking flared accessory sclerites and finely tapered.

Adult female (single adult in ethanol, 1977, plus pharate adults). **Body**: general body colour in ethanol reddish-brown, total length 3.0 mm. **Head**: width 0.69 mm; depth 0.44 mm; postocciput concolorous with thorax, vestiture of sparse, short black hairs; frons concolorous; frons width : head width ratio 1.0 : 4.3. **Eyes**: interocular distance 0.16 mm; ommatidia diameter 0.010 mm; *ca* 38 rows up and across at mid-eye. **Clypeus**: concolorous with frons; vestiture of sparse black and pale hairs; width 0.19 mm. **Antennae**: medium brown; total length 0.47 mm; pedicel darker, base of 1st flagellomere pale (as in *A. ungulatum*), both those divisions longer than others, antenna not tapered. **Mouthparts**: substantial, 0.66× length of head depth; cibarial cornuae (Fig. 40) with shallow flutings apically, median depression broad and shallow; mandibles with 32 inner teeth, subequal in size, except few smaller basally; laciniae with 18 inner teeth and 25 outer teeth; maxillary palp, total length 0.47 mm, 3rd article dark brown, remainder lighter, proportional lengths 3rd, 4th, and 5th articles 1.0 : 0.7 : 1.1, sensory vesicle ovoid, 0.3× 3rd article width, opening 0.7× vesicle width.

Thorax: length 1.5 mm; width 0.87 mm; in ethanol, postpronotal lobes marginally paler than scutum; scutum evenly reddish-brown, vestiture of sparse pale recumbent hairs, presutellar depression with few longer darker hairs posteriorly, no vittae visible in alcohol; scutellum concolorous with scutum, vestiture of few long black hairs and pale hairs laterally; postnotum concolorous with scutum; pleuron and pleural membrane concolorous with scutum. **Wings**: hyaline; length 2.8 mm; width 1.4 mm. **Halteres**: tan. **Legs** (Figs. 66): light brown, with darker brown bases to femoral, tibial, and tarsal segments; hind basitarsus 6.4× as long as greatest width, lacking row of stouter setae; tarsal claws not markedly curved, with basal tooth slightly less pronounced (tooth claw ratio 1:3.4) than that of *A. ungulatum*.

Abdomen (Fig. 86): abdominal scale dark brown with fine pale hairs, not greatly extended; tergite II 3× wider than long, concave anteriorly; tergites III–V quadratic, tergite VI and tergite VII wider than long; vestiture of sparse, coarse, short black hairs. **Genitalia** (Fig. 106): sternite VIII not markedly pigmented, vestiture of coarse long black hairs posterolaterally; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and triads of microtrichia; median edges of hypogynial valves subparallel, broadly rounded posteroapically, apex strengthened; genital fork (Fig. 124) with anterior arm markedly broad, posterolateral arms short and lacking knee-bend, apodeme as small rounded cone, posterolateral extensions angulate posteromedially, broadly rounded laterally; anal lobes and cerci both narrowed in ventral view, broadly rounded in lateral view and darkly pigmented; spermatheca distinctly ovoid, clear area at junction of duct small.

Adult male (based on early and 2 mature pharate specimens). **Body**: general colour velvety black; total length 3.4 mm. **Head**: general colour black; width 1.1 mm; depth 0.70 mm. **Eyes**: upper ommatidia dark red, diameter 0.034 mm , *ca* 25 across and 22 down; lower ommatidia dark brown, diameter 0.014 mm, *ca* 40 across and 36 down. **Clypeus**: dark brown; vestiture of very sparse fine hairs; width 0.2 mm. **Antennae**: total length 0.67 mm; evenly medium brown, 1st flagellomere 2× as long as wide; antenna finely tapered. **Mouthparts**: poorly developed; length 0.35× head depth; mandibles insubstantial, broadly tapered with apical hairs; laciniae, finely tapered apically with terminal hairs; maxillary palp medium brown to black, 0.41 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 0.8 : 0.6, sensory vesicle irregular in shape, occupying 0.33× 3rd article width, opening 0.3× vesicle width.

Thorax: length 1.5 mm; width 0.96 mm; **Wings**: length 3.0 mm, width 1.5 mm. **Halteres**: tan. **Legs**: dark, long haired; hind basitarsus 7.5× as long as greatest breadth, lacking row of stout setae; tarsal claws with grappling pad of *ca* 23 teeth.

Abdomen: tergites occupy whole width of tergum, *ca* 2× wider than long, increasingly so posteriorly, vestiture of fine black hairs. **Genitalia** (Fig. 141): gonocoxites *ca* 2.0× longer than basal width, anterior edge dark brown, vestiture of coarse black hairs more or less evenly distributed, anteromedial crenulations not markedly developed; gonostyli approximately 2.5× longer than basal width, acuminate, apically with 2 spines, occasionally 3, tightly grouped; ventral plate with low median keel, vestiture of fine hairs, plate 2.0× wider than long, shallowly rounded posteriorly, flat anteromedially, with median extension, basal arms with anterior extensions not markedly developed; median sclerite more markedly developed than elsewhere in New Zealand *Austrosimulium,* broadly T-shaped posteriorly; parameres moderately well developed and attached to gonocoxite.

Pupa (Fig. 158, 176) (numerous topotype specimens). **Body**: male, length 3.3–3.6 mm, female, length 3.5–3.8 mm. **Head**: cephalic plate of male and female finely tuberculate overall except on muscle scars, tubercles extended onto antennal sheaths and ventrally onto frontal area and ocular cuticle; female plate (Fig. 215) markedly broad and short, 1.3× longer than basal width, apically truncated, male plate (Fig. 232) 1.9× as long as basal width; frontal setae not apparent, facial and epicranial setae present; ocular setae present, finely developed. **Thorax** (Fig. 253): dorsum finely tuberculate in ill-defined hexagonal pattern, covering most cuticle but becoming finer laterally and towards the wing pads; dorsocentral setae trichoid. **Gills** (Fig. 284): horn curved and expanded from mid length, club-shaped; length 0.36–0.45 mm, *ca* 4× longer than mid-width; basally light yellow, apically dark brown to black; finely scobinate; filaments 36–39, length 1.0–1.4 mm, light brown, fine, non-tapered, arising from mid-length of horn, surface finely annulated (Fig. 301). **Abdomen**: tergite IX with grapnel hooks.

Cocoon (Fig. 176, 192): variable, irregular shape, alveolate, 2 poorly defined anterodorsal projections extended beyond pupa, typically curved ventrally to cover anterior of pupa, appear co-joined, but they are not; projections not obviously continued posteriorly along cocoon. Fabric alveolate with silk threads not markedly obvious.

Larva (topotype final instars). **Body** (Fig. 318): prothorax medium brown, remainder of thorax paler, abdomen evenly brown, darkening posteriorly; total length 6.0–6.7 mm. **Head** (Fig. 337): evenly medium brown; length 0.74–0.80 mm, width 0.67–0.70 mm; distance between antennal bases 0.32–39 mm; overall shape narrowed anteriorly, lateral margins of head convex, more so posteriorly; anterior apotome translucent, head spot pattern poorly developed, slightly negative, covered by mottled pigmentation; posterior edge of apotome narrowly pigmented; ecdysial lines broadly divergent and rounded posteriorly; postocciput fine, but continuous across posterior apotome, cervical sclerites fused. **Antennae** (Fig. 382): brown basally, pale apically; total length 0.4 mm; not extended much beyond labral fan stem; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.2 : 2.5; apical article 2.1× length of wider combined basal 2 articles, medial article small, 0.2× as long as basal article. **Labral fans**: stalk relatively short, light brown, 40–46 fine rays, length 0.74–0.79 mm, width 0.010 mm at mid length; distinct pattern of microtrichia, longer microtrichia 1.0× longer than ray width, separated by *ca* 10 smaller microtrichia. **Postgenal cleft** (Fig. 399): small and inverted V-shaped, posterior tentorial pit markedly elongate, well sclerotised and pigmented. **Postgenal bridge**: 1.8× longer than hypostoma, pale medially, darker laterally, elongated posteroventral muscles spots pale and indistinct. **Hypostoma** (Fig. 418): teeth not markedly obscured by anteroventral edge of hypostoma, median and lateral teeth prominent, subequal in length; 2 or 3 rounded lateral serrations, variable; 5 or 6 hypostomal setae each side. **Mandibles** (Fig. 435): outer and subapical teeth markedly poorly developed, apical tooth substantial, but short, 7 or 8 short spinous teeth; serrations and sensilla widely separated; blade region elongated, smooth and straight. **Thorax** (Fig. 365): mature pharate pupal gill similar to *A. bicorne*, but fewer filaments obvious and L-shape not as accentuated. **Abdomen**: anterior abdomen banded grayish-brown, posteroventral abdomen pale; thorax wider than anterior abdomen, abdominal segments I–IV narrow, expanded distinctly at 5th segment producing a slight amphora shape; markedly developed ventral tubercles. **Anal sclerite** (Fig. 452): median region broad and crenulated laterally, slightly tapered posteriorly; anterior arms neither markedly flared, nor bifurcate, interarm struts narrow and rod-like, only slightly angled posteromedially, posterior arms smoothly tapered; semicircular sclerite thin, ends finely tapered. **Posterior circlet**: *ca* 136 rows of 17 or 18 hooks (total *ca* 2380).

Type data. **Holotype**: in ethanol, pharate female adult in pupa and cocoon; label details "HOLOTYPE *Austrosimulium tonnoiri*", "New Zealand, South Is., OL, SH94\ Homer Tunnel, left stream, upper\ Hollyford River, S44.76580 E167.98969,\ 920mabs 24-i-2007. Coll. D.A. & R.E.G.\ Craig NZS32" (NZAC). **Paratypes** (13): pinned, 2 males on minuten; specimen "b" with head and genitalia in vial on the pin; label details "Homer\ saddle\ 3700'\ 26-1-46\ R. Forster". "PARATYPE "a"(or "b")*Austrosimulium tonnoiri*" (MONZ); ethanol, 2 pharate male adults in pupa and cocoon; label details "PARATYPE *Austrosimulium tonnoiri*", "New Zealand FD Darran Mts\ Tutoko Bench, Mahere Basin 1350m\ stream 1–2 m wide\ 10 Jan 1977 T K Crosby" (NZAC); 3 pharate female adults in pupa and cocoon, label details "PARATYPE *Austrosimulium tonnoiri*", "Simonin Crk, Upper Pyke River,\ 24-i-1975, J. S. Dugdale. \Under perched stones"; 6 final instar larvae, label details "PARATYPE *Austrosimulium tonnoiri*", "New Zealand FD Darran Mts\ Tutoko Bench, Middle Gully 1150 m stream\ 1 m wide, base of waterfall\ 13 Jan 1977 T K Crosby" (NZAC).

Material examined. Type material, and 7 more recent collections (Appendix 1). Pupae were not reared since they cannot be removed from the rock substrate without damage.

Distribution (Map 15). So far known mainly from the Hollyford Valley region of Fiordland, with one more southerly record. **South Island**. **OL**. Pass Ck bridge, NZS151 (Routeburn Track); Simonin Stm. **FD**. Borland Burn, NZS152; Divide Ck, NZS148 (Routeburn Track); Gertrude Valley stm, NZS145; Homer Saddle; Homer Tunnel stm, NZS32, 32a (SH94); Homer Tunnel, NZS144 (Cleddau R South Branch); Red Stm; Tutoko Bench (Darran Mts).

Northernmost record; Upper Pyke River, Simonin Creek, OL (latitude S44.34301°); southernmost record: Borland Pass, upper south branch, Borland Burn, FD (latitude S45.74690°); altitude 660–1300 m a s l.

— / OL, FD / —

Almost all localities fall within the Southern Alps ecoregion. An expectation is that the species will be widespread in the southern part of this ecoregion.

Etymology. Named after André L. Tonnoir for his original work on Australasian Simuliidae.

Bionomics. The life cycle is probably similar to that of *A. bicorne*. Immatures, however, occur in streams with more rocky substrate (Fig. 489–491) than do those of *A. bicorne*. Cold pure water is, again, a requirement. It is unknown how the two male adults were taken by Forster in 1946 on the Homer Saddle; possibly they were light trapped since simuliid males are almost impossible to obtain by netting, but a few can be attracted to lights at night.

Associated simuliids: immature stages of *A. bicorne, A. multicorne*, and *A. ungulatum*; adults of *A. fiordense*.

Remarks. *Austrosimulium tonnoiri* material was considered by Dumbleton as merely a variant of *A. bicorne*. However, with new material, it is here deemed a new species, on the basis of the distinct cocoon (*cf* Fig. 156, 157 and 175, 176), coupled with gill and male genitalia characters. It is closely related to *A. bicorne* and it is not possible to easily separate larvae of the two species. Males of *A. bicorne* and *A. tonnoiri* show minor character differences in the shape of the ventral plate and tip of the gonostylus. Molecular analysis of the CO1 gene places *A. tonnoiri* in the same clade as *A. bicorne,* as morphology indicates, but that clade unexpectedly includes *A. dumbletoni* (Fig. 514).

Do females of *A. tonnoiri* bite? In the collections from the Darran Mountains, Fiordland, 1977, is a substantial collection of approximately 50 adult female simuliids attracted to TKC, of which the label data indicate some were attempting to bite. Of these adults, only one is identifiable as *A. tonnoiri*; the remainder being *A. fiordense,* indicating that *A. tonnoiri* is not attracted to humans in any major way. The small size of abdominal tergites of *A. tonnoiri* females, however, indicates that like those of the *ungulatum* species-group *A. tonnoiri* probably could feed on birds: the mouthparts are substantial enough for that.

As also noted for *A. bicorne*, the male paramere of *A. tonnoiri* is better developed than in other New Zealand *Austrosimulium*. This suggests that these species are plesiomorphic for this segregate, an assertion borne out by the molecular evidence (Fig. 509a, 509b, 514).

Austrosimulium (*Austrosimulium*) *unicorne* Dumbleton, 1973

Figures: female, 41, 67, 87, 107, 125; male, 142; pupa and cocoon, 159, 177, 193, 216, 233, 254, 267, 285, 302; larva, 319, 338, 350, 366, 383, 400, 419, 436, 453; habitat, 496, 497; Map 17.

unicorne Dumbleton, 1973: 543 (description female, male, pupa, cocoon, larva; *Austrosimulium* (*Austrosimulium*)). Crosby 2006: 72 (key). Adler & Crosskey 2012: 20 (world inventory).

sp. 1. Dumbleton 1964a: 36 (Fig. 1, distribution map, pupal gill, and cocoon; *Austrosimulium*).

Diagnosis. Relatively large species. **Female**: antenna brown; haltere white; tarsal claw normally lacking basal tooth, but with heel; abdominal tergites III–V broader than long, hind basitarsus lacking row of stout setae. **Male**: hind basitarsus lacking row of stout setae. **Pupa**: thoracic cuticle finely tuberculate; gill with minute horn and *ca* 40 non-tapered filaments projected in rosette; terminal abdominal segment with grapnel hooks. **Cocoon**: slipper- to shoe-shaped, closely applied to pupa; thick white in structure, with single anterior projection overhanging anterior opening, with gills protruding anterolaterally. **Larva**: pale; semicircular sclerite with finely tapered accessory sclerite.

Adult female (based on holotype and material from Freds Creek, Mount Cook). **Body**: general body colour in ethanol dark reddish brown-black, when dried yellowish-black with silvery pruinosity; total length 2.5–3.1 mm. **Head**: width 0.74–0.80 mm; depth 0.48–0.58 mm; postocciput black, vestiture of sparse, short black hairs; frons blackish-brown, markedly pollinose; frons width : head width ratio 1.0 : 4.2. **Eyes**: interocular distance 0.17–0.20 mm, broader than usual; ommatidia diameter 0.012 mm; *ca* 31 rows up and across at mid-eye. **Clypeus**: dark brown; vestiture of sparse black and pale hairs; width 0.22–0.24 mm. **Antennae**: total length 0.60–0.70 mm; scape and pedicel darker than flagellomeres, all flagellomeres evenly brown; pedicel larger than flagellomeres and trapezoid, 1st flagellomere square; other flagellomeres not markedly tapered towards tip. **Mouthparts**: poorly developed, 0.4× length of head depth; cibarial cornuae not markedly developed, lacking apical flutings or other sculpting, median depression broad (Fig. 41); mandibles lacking outer teeth, 38 inner teeth, increasing in size towards apex, 12 basally and markedly small; laciniae with 10 inner teeth and 18 outer teeth; maxillary palp, total length 0.62 mm, 3rd article medium brown, remainder lighter, only expanded apically, proportional lengths 3rd, 4th, and 5th articles 1.0 : 1.1 : 1.3, 5th article occasionally noticeably short, sensory vesicle ovoid, 0.35× 3rd article width, opening 0.3× vesicle width.

Thorax: length 1.2–1.5 mm; width 0.96 mm; postpronotal lobes marginally paler than scutum; scutum evenly dull blackish-brown, vestiture of sparse small recumbent hairs, presutellar depression with few longer darker hairs posterolaterally, no vittae visible in ethanol, but when dried and under some lighting, with median and 2 lateral vittae overlain with silvery pruinosity; scutellum slightly lighter than scutum, vestiture of a few long black hairs and pale hairs laterally; postnotum concolorous with scutum; pleuron and pleural membrane lighter than scutum. **Wings**: hyaline; length 3.0–3.2 mm; width 1.5–1.7 mm. **Halteres**: white. **Legs**: light grayish-yellow, with darker brown bases to femoral, tibial, and tarsal segments; hind basitarsus about 6× as long as its greatest breadth; lacking ventral series of stout setae; tarsal claws (Fig. 67) shallowly tapered without basal tooth, but with slight development of heel (small tooth occasionally on one claw; tooth claw ratio 1:6).

Abdomen (Fig. 87): abdominal scale dark brown with sparse fine hairs, not greatly extended posteriorly; tergites uniquely broad for female, similar to male, tergites II–VI subequal in width, tergite II 3× wider than long, not markedly emarginate anteriorly; tergites III and IV quadratic, 2× as wide as long; tergite V shallowly rounded anteriorly, 2.5× wider than long; tergite VI similarly shaped, 3.2× wider than long; vestiture of sparse hairs, denser on posterior tergites. **Genitalia** (Fig. 107): sternite VIII lightly pigmented along anterior edge, vestiture of coarse black hairs posterolaterally; hypogynial valves lightly pigmented with vestiture of sparse small coarse hairs and triads of microtrichia, median edges slightly reinforced anteriorly as narrowed clear edge, edges smoothly convergent posteriorly, broadly rounded posteroapically; genital fork (Fig. 125) with anterior arm broad and poorly defined, fluted anteriorly, posterolateral arms broad and lack knee-bend; apodeme sharp and not markedly developed, posterolateral plate rounded; in lateral view anal lobes with small basal lobe and cercus truncated apically, both densely hirsute and dark; spermatheca with slight patterning, no clear area at duct junction.

Adult male (based on pharate specimens and pinned paratypes). **Body**: general colour dark brown-black; total length 4.6 mm. **Head**: width 0.94 mm; depth 0.68 mm. **Eyes**: upper ommatidia orange, diameter 0.032 mm, *ca* 24 across and down; lower ommatidia dark brown, diameter 0.015 mm, *ca* 27 across and down. **Clypeus**: dark brown; vestiture of very sparse fine hairs; width 0.19 mm. **Antennae**: total length 0.56 mm; evenly medium brown. **Mouthparts**: poorly developed; length 0.35× head depth; mandibles insubstantial, broadly tapered with apical hairs; laciniae, finely tapered apically with terminal hairs; maxillary palp medium brown, 0.48 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0 : 1.1 : 1.6, sensory vesicle irregular in shape, occupying 0.33× 3rd article width, opening 0.3× vesicle width.

Thorax: length 1.4–1.6 mm; width 0.7–0.9 mm; scutum markedly domed, evenly dark brownish-black, vestiture of fine recumbent pale hairs and brassy yellow when dried, longer pale hairs in prescutellar depression; scutellum concolorous with scutum with sparse long hairs; postscutellum concolorous with scutum. **Wings**: length 2.6–2.9 mm, width 1.3–1.4 mm. **Halteres**: white. **Legs**: medium yellowish brown, with darker brown femoral, tibial, and tarsal bases; hind basitarsus about 8× as long as greatest breadth; lacking row of stout setae; tarsal claw grappling pads of 22 teeth.

Abdomen: tergites and sternites blackish brown, pleural areas dull black. Tergites occupy whole width of dorsum. **Genitalia** (Fig. 142, reconstructed from pharate specimens): gonocoxites 1.6× longer than basal width, with anteromedial crenulations; gonostylus subequal in length to gonocoxite, elongate, *ca* 3.0× longer than basal width, tapered smoothly, apically with 2 substantial spines; ventral plate with markedly developed median keel, even vestiture of hairs, plate 2.0× wider than long, broadly rounded posteriorly, weakly convex anteromedially, basal arms substantial; median sclerite poorly developed, broad, T-shaped posteriorly; parameres poorly developed, but distinctly connected to the gonocoxite apodeme; aedeagal membrane apparently bare.

Pupa (Fig. 159, 177, 216, 233). Body length, male 2.8–4.6 mm; female 3.1–3.3 mm. **Head**: cephalic plate not concave; male with upper frons tuberculate, female evenly tuberculate; cephalic plate of female broad and short, 1.4× longer than basal width; male 1.8× longer than basal width; frontal, facial, and epicranial setae present, not always apparent; pair of postorbital spines present, not markedly developed. **Thorax** (Fig. 254): dorsum with evenly arrayed tubercles, denser anteriorly, faded to absent posteriorly; setae spine-like posteriorly. **Gills** (Fig. 267, 285): base and horn subequal in size; base yellow, horn black; total length of both *ca* 0.2 mm, horn slightly tapered and bluntly rounded, trabeculae in base small and regularly arranged, filament insertions produce irregular edge of horn; filament number *ca* 40, 1.1–1.4 mm in length, non-tapered, arising evenly over base and arrayed in brush pattern, surface pattern finely annulated (Fig. 302). **Abdomen**: sternite IX with grapnel hooks.

Cocoon (Fig. 177, 193): fabric, thick white and fleshy, not alveolate as in *A. bicorne* and *A. tonnoiri*. Single median thick anterior projection, continued posteriorly as median rib along cocoon; edges of opening thickened.

Larva (numerous topotype final instars). **Body** (Fig. 319): overall colour banded gray; total length 6–7 mm. **Head** (Fig. 338): evenly mottled brown, head spots variable, occasionally in cruciform pattern, normally barely visible; length 0.78 mm, width 0.62; distance between antennal bases 0.38 mm; lateral margins of head subparallel, smoothly convex; posterior edge of apotome not markedly pigmented; ecdysial lines not sinuous, narrowest posterior of antennal bases; postocciput not markedly developed, but fused to cervical sclerites. **Antennae** (Fig. 383): medium brown basally, pale apically; total length 0.39 mm; extended well beyond apex of fan stem; proportional lengths 1st , 2nd, and 3rd articles 1.0 : 0.6 : 2.1; apical article 1.3× as long as combined basal 2 articles; medial article markedly long, 0.6× as long as basal article. Distance between antennal bases 0.3 mm. **Labral fans**: stem translucent; *ca* 40 fine rays, length 0.7 mm, width 0.007 mm; distinct pattern of microtrichia, longer microtrichia 1.2× longer than ray width, separated by 12–14 rapidly decreasing microtrichia but variable. **Postgenal cleft** (Fig. 400): shallow, broadly rounded, posterior tentorial pit region finely sclerotised and pigmented. **Postgenal bridge**: 2.0× longer than postgenal cleft, pale, concolorous with genae, elongated posteroventral muscle spots neutral. **Hypostoma** (Fig. 419): teeth not markedly developed, generally obscured by anteroventral edge of hypostoma, median and lateral teeth sharp; lateral teeth slightly more prominent than median tooth; 2 sublateral teeth subequal in size to median tooth, middle sublateral tooth 1/2 size of others; 2 small paralateral teeth; lateral serrations absent, 5 or 6 hypostomal setae per side. **Mandibles** (Fig. 436): outer and preapical teeth not markedly developed, apical tooth elongated and slim; *ca* 7 spinous teeth; serrations and sensilla numerous, distinct, on irregular raised base; blade region elongate, smooth, and slightly convex. **Thorax** (Fig. 366): prothorax pale gray, remainder of thorax paler, pupal gill histoblasts (Fig. 350), L-shaped with short black horn, filaments descending ventrally (farther than *bicorne*), then curved posteriorly, and then recurved with filament tips ended anterior at horn apex. **Abdomen**: anterior abdomen banded grayish-brown, posteroventral abdomen evenly grayish-brown; markedly developed thumb-like ventral tubercles. **Anal sclerite** (Fig. 453): median region slightly tapered posteriorly, sparse campaniform sensilla posteriorly; anterior arms flared, not markedly bifurcate, interarm struts short and substantial, posterior arms substantial, finely tapered; semicircular sclerite insubstantial with ends finely tapered, but obvious, with underlying clear cuticle. **Circlet of hooks**: *ca* 140 rows, 16 hooks per row (total hooks *ca* 2 240).

Type data. **Holotype**: double pinned on minuten on cork strip; condition excellent, slightly collapsed, complete; label details “Bred 23.1.[19]61\ Otira River\ Arthurs Pass\ L. J. Dumbleton” (all but final line handwritten in black ink, unknown), “HOLOTYPE {F}\ Austrosimulium\ unicorne\ L.J. Dumbleton” (short sides of label with red ink margin, all but final line handwritten in black ink, unknown), “HOLOTYPE {F}\ Austrosimulium\ unicornutum.\ L. J. Dumbleton” (short sides of label with red ink margin, all but final line handwritten in black ink, unknown), “N.Z. Arthropod Collection\ {barcode}\ NZAC04021445” (NZAC). **Paratypes**: pinned, 6 males double pinned on minuten in cork strips; label details “Bred 23.1.[19]61\ Otira River\ Arthurs Pass.\ L. J. Dumbleton”, “PARATYPE {M}\ A. unicorne\ L. J. Dumbleton”, “N.Z. Arthropod Collection\ {barcode}\ NZAC04022172” (“L. J. Dumbleton” as typescript, collecting and identification information handwritten in black ink with some variable punctuation, unknown), other male paratypes with barcodes "NZAC04022173", "NZAC04022174", "NZAC04022197", "NZAC04022220", and "NZAC04022221"; 3 females, as above, but with "{F}" and barcodes "NZAC04022213", "NZAC04022216", and "NZAC04022245" (NZAC). Ethanol specimens; 3 reared females and parts of pupal exuviae and cocoons, label details "A. unicornutum\ PARATYPES" (handwritten in pencil, Dumbleton), "Mt Cook\ 4/11/[19]57" (handwritten in pencil, Dumbleton), "Aust. (A.) unicorne", "Dumbleton Collection"; 1 reared male, label details "A. unicornutum {M}\ genitalia mounted\ PARATYPE" (handwritten in pencil, Dumbleton), "Aust. (A.) unicorne", "Dumbleton Collection" (note: no locality label). Female, two males and two females extracted from pupae. "Black Birch Ck, Mt Cook\ 4.ii.[19]57, [L. J. Dumbleton]", "Dumbleton Collection]" (NZAC). 3 microscope slides, label details, all with gold label "Entomology Div., DSIR, NZ\ L.J. Dumbleton Collection"; and all with handwritten in pencil by Dumbleton "A. unicornutum\ Dumbleton\ {M}\ PARATYPE\ Otira R\ 30/1/[19]60 LJD"; "A. unicornutum\ Dumbleton\ {M}\genitalia\ PARATYPE"; and "A. unicornutum\ {F}\ PARATYPE\ Mt Cook\ 4/11/[19]57" (NZAC).

Material examined. All stages, including reared adults. Type specimens; some 15 collections from the Dumbleton and TKC material in NZAC, and 4 recent collections (Appendix 1).

Distribution (Map 17). So far known only from the middle portion of the Southern Alps and, in the main, from high altitude. **South Island**. **WD**. Haast Pass, NZS179 (Fish R); Robinson Ck, NZS177 (SH6). **NC**. Pegleg Ck, NZS132, 132a (SH73 above bridge). **MC**. Havelock R; Mt Hutt; Otira R, NZS140 (upper); Rangitata R. **MK**. Birch Hill Stm, NZS128 (SH80); Freds Stm; Glentanner; Hoophorn Stm; Sawyer Stm. **OL**. Makarora R.

Northernmost record: SH73, Otira River, NC (latitude S42.82890°); southernmost record: SH80, Aoraki/Mount Cook, Birch Hill Stream, MK (latitude S43.79896°). Found only above 760 m a s l, with few exceptions (e.g., NZS177).

Dumbleton (1973: 485) has the distribution symbols for *A. unicorne* and *A. bicorne* inverted in his Figure 7a.

—/ WD, NC, MC, MK, OL / —

There are 2 further Dumbleton collections in NZAC of which we question the accuracy of the label information, as these localities are not typical of the higher altitude, cold-water habitats the species inhabits: Lawyer Creek at Lake Kaniere, WD (20 m a s l), and Lake Hawea, OL (350 m a s l). We consider the Kaniere locality is the more suspect of the two. Unknown for both collections is the exact location, or temperature of the water at the time of collection, so we do not include these localities in the distribution. The specialised habitat requirements for *A. unicorne* immature stages are discussed below.

Apart from the Lake Kaniere locality, all others fall mainly along the eastern edge of the Southern Alps ecoregion in junction with that of the High Country.

Etymology. Named by Dumbleton (1973) for the single anteromedial process on the pupal cocoon.

Bionomics. Similar to other high-altitude species, such as *A. bicorne* and *A. tonnoiri*, a single generation a year is indicated for *A. unicorne*. Larvae and pupae were collected by Dumbleton in mid-October (Bush Stream), and up until mid-December when smaller larvae were plentiful. Pupae and adults were abundant in January and February. He suggested, however, there may be more than one generation per year, noting that there was no evidence of winter diapause, and larvae of *A. unicorne* (like those of *A. bicorne*) probably passed the winter without cessation of growth. Immatures of *A unicorne* are found in relatively large open streams (Fig. 496, 497) below permanent snowfields and hanging glaciers, but not in rivers that carry much "rock flour" from the larger valley glaciers. Typical streams have steep courses, boulders that are large and rounded, free of algal growth, and water clear and cold. Indeed, known temperatures range from only 6.1 to 9.4°C in December and water conductivity is below 30µS/cm (Appendix 1). In winter and summer most streams of this type disappear into the substrate a short distance from their source.

Label data on one of Dumbleton's microscope slide mounts of a female *A. unicorne* have the notation "blood feeding". But, while the tergites of that female are well displayed (Fig. 87), they are uniquely broad for a female, indeed the equal of those normally exhibited by males (e.g., Fig. 88), and well indicative of non-blood feeding. A further indication that *A. unicorne* is not normally a blood feeder is that the female mouthparts are poorly developed by *Austrosimulium* standards. This label notation is the only record of *A. unicorne* biting and Dumbleton made no mention of it in his 1973 publication.

Immatures of *A. unicorne* have habitat requirements similar to those of *A. bicorne* and *A. tonnoiri* in that larvae and pupae are not present on the upper surface of stones, but rather on the undersurfaces of suspended large stones, or between and underneath stones with good water flow. Cocoons are often aggregated in numbers in these places, but the density is not great. Dumbleton noted that *A. unicorne* usually occurred in monospecific populations, but that he had obtained immatures of *A. ungulatum* and *A. multicorne* as well. We also obtained those of *A. bicorne*.

Dumbleton (1973) felt that such occurrence on the undersides of stones gave some protection from the abrasive action of coarse sand carried by streams during their frequent freshes, and that similarly cocoon thickness gave added protection. This may well be so, simuliid larvae try to avoid ultraviolet (UV) radiation, either by escaping it, or being more pigmented (Donahue & Schindler 1998; Craig & Currie 1999). Given that the members of the *unicorne*-subgroup tend to occur in localities of higher altitude, UV avoidance is perhaps a better explanation for the usual habitats of the immatures. This also relates to their paler colour — unusual for high-altitude simuliids. Dumbleton (1973) further suggested that the thick white cocoons of *A. unicorne* and *A. bicorne* gave protection from cold water temperatures. We are, however, of the opinion that the thick cocoons are protection against desiccation given the rapidly changing water levels in these habitats.

A few larvae from Otira R. (NZS140) were parasitised by *Coelomycidium* (?)*simulii* (see p. 33).

Remarks. *Austrosimulium unicorne* is an unusual member of the *ungulatum* species-group, lacking for the most part the tooth on the adult female tarsal claw. Occurrence of that character is sporadic, as Dumbleton so noted and we illustrate here (e.g., Fig. 67). We interpret this, phylogenetically, as a loss. Larvae of *A. unicorne*, otherwise unremarkable, have amongst the highest number of hooks in the circlet on the posterior proleg. The number of hooks correlates with velocity of water (Palmer & Craig 2000), but we know nothing of the velocity of flow under the perched stones habitat. We assumed it to be high. Larvae have a long medial article to the antenna (Fig. 383), much more so than those of *A. bicorne* and *A. tonnoiri* (Fig. 381, 382). The above is in agreement with the molecular analysis (Fig. 514) that indicates the latter two species are sister in a separate clade and distinct from *A. unicorne*. Overall, the *unicorne*-subgroup erected by Dumbleton (1973) is well supported, but is indicated as sister to all New Zealand *Austrosimulium*, not sister to just the *ungulatum*-subgroup.

The sharp delimitation in altitudinal range of *A. unicorne*, immatures of which are rarely found below 760 m a s l, may involve two aspects of the habitats. Cold water is well indicated as a requirement. Mosley (1982) provided a regression equation using latitude and altitude that fitted more than 30% of known mean temperature data of New Zealand rivers. Application of the regression to our data gives good agreement to recorded temperatures. However, on the Southern Alps where greywacke is the underpinning rock, erosion of the river profile is rapid. Upper steep reaches (Fig. 487) tend to consist of large boulders remaining from deglaciation flows with sizable stones forming pools with ill-formed edges. This arrangement is the result of bed transport of different sized substrate (Frey & Church 2009). Although subjected to flooding from snow melt and rainfall, there is considerable stability via the large boulders. These provide a habitat to an array of high-altitude, cold-water macroinvertebrates, including Blephariceridae (Winterbourn 2008; Craig 1969). But, downstream of this (*ca* 700 m a s l) and rapidly, the rivers change to a depositional character with smaller substrate and begin to braid — much less stable and the macroinvertebrate fauna is much less abundant. Calculations following Mosely (1982) indicate little change in temperature with such a small change in altitude, so it is unlikely the sharp altitudinal limit to *A. unicorne* is one of temperature. Rather it is the perched stones on the lip of pools above the braided section of streams that provide habitat for *A. unicorne* immatures, and which occur mainly above 760 m a s l. Be that as it may, a recent collection of *A. unicorne* from the Haast Pass region (NZS177) was at a distinctly lower altitude of 471 m a s l. Water temperature was, however, merely 6.1°C. Calculations following Mosely (1982) indicate that the mean annual temperature for that locality would be in the region of 10°C, somewhat higher than presently known for this species. It does, however, suggest that there would be but a single generation during the colder period of the year. This assertion could be tested at the Haast Pass locality.

Cladistic analysis (Fig. 507) of morphological characters is in agreement with Dumbleton's placement of *A. unicorne*. Now with *A. tonnoiri* recognised as a full species, *A. unicorne* is sister to *A. bicorne* + *A. tonnoiri*, together constituting the *unicorne*-subgroup, sister to the *ungulatum*-subgroup. This arrangement based on morphological characters is slightly at variance with the CO1 mDNA analysis (Fig. 509, 509a, 514). There the *unicorne* subgroup is sister to all New Zealand *Austrosimulium* and thus would constitute its own species-group. Further, that group contains the new species *A. vailavoense* which together with *A. unicorne* is sister to a clade comprised of *A. bicorne* + *A. dumbletoni* + *A. tonnoiri*. This placement of *A. dumbletoni* is at variance with that by Crosby (1976a) who placed it in the *ungulatum*-subgroup.

The placement of, and deep divergence between haplotypes of this clade indicate that these species are older members of New Zealand's simuliid fauna. However, because of lack of immatures for some of the species involved, we do not change the current taxonomic arrangement of the *ungulatum* species-group.

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Appendix 1 Numerical listing of D. A. Craig & R. E. G. Craig collection localities in New Zealand with hydrological parameters, according to prefixes NZN (North Island) and NZS (South and Stewart Islands), October 2006–February 2012. AC = area code; ER = aquatic ecoregion; Alt. = altitude; Cond. = conductivity. Stages collected: A =adults; RA = adults reared; L = larvae; P = pupae. Species: albov. = albovelatum; alveo. = alveolatum; aust. = australense; lat. = laticorne; long. = longicorne; mult. = multicorne; stew. = stewartense; till. = tillyardianum; ung. = ungulatum.

Collection Number	AC	ER	Locality name	Latitude	Longitude	Alt. m.a.s.l.	Date	Time h	Air C	Water C	pH	Cond. µS/cm	Velocity m/s	Stages collected and species
North Island														
NZN1 [not used]														
NZN2	CL	CP	Kauaeranga R (Park HQ)	S37.12409	E175.62761	53	14-Oct-2006	17:15	-	-	8.4	60	0.62	L, P, RA (aust.)
NZN3	CL	CP	Tairua R (SH25a, Puketui Road)	S37.09622	E175.74121	15	15-Oct-2006	10:50	16.7	15.8	8.4	55	-	L, P, RA (aust.); L, P (till.)
NZN4	CL	CP	Waiwawa R	S36.94584	E175.66999	33	15-Oct-2006	16:15	18.3	16.6	8.2	60	0.63	L, P, RA (aust.)
NZN5	CL	CP	Waitekuri R	S36.75830	E175.57892	31	16-Oct-2006	12:30	16.1	15.2	7.4	110	0.63	L, P, RA (aust.)
NZN6	CL	CP	Umangawha Stm (near Colville)	S36.65778	E175.48694	28	16-Oct-2006	13:12	12.9	15.3	7.3	115	0.50-0.76	L, P, RA (aust.)
NZN7	CL	CP	Apakura Stm (SH26, Waiho Forest Reserve)	S37.21765	E175.66613	75	17-Oct-2006	10:02	10.1	11.3	7.4	55	0.38-0.44	L, P, RA (aust.); L (till.)
NZN8	CL	CP	Waitawheta R (Karangahake Gorge)	S37.43193	E175.74093	72	17-Oct-2006	8:52	18.1	14.7	7.3	60	0.38-0.54	L, P, RA (aust.); L (till.)
NZN9	AK	NH	Taitaia Stm (near Clevedon)	S36.99066	E175.02994	50	22-Oct-2006	12:30	18.7	16.5	9.0	150	0.24-0.31	L, P, RA (aust.)
NZN10	AK	NH	Orere Stm (bridge)	S36.98754	E175.18852	80	22-Oct-2006	14:00	20.8	16.4	9.0	80	0.44	L, P, RA (aust.); L, P, RA (till.)
NZN11	AK	NH	Mangatangi Stm (Hunua Ra)	S37.12773	E175.22469	120	22-Oct-2006	15:35	17.6	14.4	8.1	60	0.54-0.60	L (aust.); L (till.)
NZN12	WO	WO	Firewood Ck (Ngaruawahia)	S37.68486	E175.12373	85	28-Oct-2006	12:00	16.1	13.4	7.1	80	0.88-0.94	L (aust.)
NZN13	WO	WO	Mangaokahu Stm (Cogswell Road)	S37.80062	E175.03608	80	28-Oct-2006	13:53	17.6	14.2	6.6	90	0.30-0.44	L (aust.)
NZN14	WO	WO	Pakoka R	S37.90853	E174.89668	200	29-Oct-2006	14:00	16.0	13.8	7.1	90	0.44	L, P, RA (aust.); L (long.)
NZN15	WO	WO	Mangaora Stm (bridge Aotea)	S37.99557	E174.88895	60	29-Oct-2006	12:33	15.3	14.0	7.1	111	0.30-0.44	L (aust.)
NZN16	WO	WO	Dixon-Waikorea Road (ditch)	S37.57604	E174.88521	60	30-Oct-2006	11:53	17.8	16.8	7.4	100	0.76	L (aust.)
NZN17	WO	WO	Rangitukia Stm (Pirongia)	S37.94495	E175.12288	136	4-Nov-2006	14:00	20.0	13.9	7.7	60	0.33-0.44	L (aust.); L (till.)
NZN18	WO	WO	Waitomo Stm (Ruakuri Cave tunnel)	S38.26522	E175.07961	78	5-Nov-2006	10:00	14.1	12.0	7.8	150	0.31-0.44	L (aust.)
NZN19	WO	WO	Mangapohue Stm (Natural tunnel)	S38.26134	E174.89937	140	5-Nov-2006	11:48	18.1	11.8	7.6	160	-	L, P, RA (aust.)
NZN20	WO	WO	Mangatoa Stm (Mangatoa Scenic Reserve)	S38.43547	E174.70197	100	5-Nov-2006	14:29	17.6	13.0	7.4	70	-	L, P, RA (aust.); L (till.)
NZN21	WO	WO	Mapiu Stm (Omaru Falls)	S38.52493	E175.15828	290	6-Nov-2006	14:00	16.5	14.4	7.6	70	0.31-0.44	L, A (aust.)
NZN22	TO	BP	Kakaho Stm	S38.56621	E175.71751	503	7-Nov-2006	10:17	18.8	10.8	7.7	30	0.31-0.45	L (aust.)
NZN23	TO	TO	Tongariro R (Walkway)	S39.03443	E175.81982	414	7-Nov-2006	15:00	16.4	12.4	7.4	70	0.31-0.46	P, RA (dugdalei); L, P, RA (till.)
NZN24	TK	MA	Waingongoro R	S39.35992	E174.22772	360	10-Nov-2006	13:30	12.5	9.1	7.1	40	-	L (aust.)
NZN25	TK	MA	Mangamawhete Stm	S39.25077	E174.21209	364	10-Nov-2006	16:30	13.3	13.2	7.1	40	-	L (aust.)
NZN26	TK	MA	Te Henui Stm	S39.07597	E174.09345	30	11-Nov-2006	15:35	16.6	14.9	6.9	70	0.44	L, P, RA (aust.)
NZN27	TK	MA	Otakeho Stm	S39.43510	E174.06009	256	12-Nov-2006	13:00	14.8	12.4	6.8	80	-	L (aust.)
NZN28	WI	WO	Taupiri Stm (Atene Pa)	S39.72062	E175.14962	45	13-Nov-2006	14:00	19.7	16.5	6.9	150	-	L, P, RA (aust.)
NZN29	WI	MA	Ongo Stm (SH1)	S39.96440	E175.52495	220	14-Nov-2006	10:20	19.0	16.3	7.2	110	0.62-0.70	L, P, RA (aust.); L (till.)
NZN30	RI	MA	Rangitikei R (Mangaweka)	S39.80991	E175.80797	247	14-Nov-2006	12:00	21.9	14.0	6.6	70	0.31-0.44	L (aust.); L (till.)
NZN31	RI	CM	Mangawhararíki R trib	S39.84056	E175.89137	387	14-Nov-2006	13:00	-	-	-	-	-	L (till.)
NZN32	WI	MA	Tutaenui Stm (Bulls)	S40.18893	E175.35623	35	15-Nov-2006	9:30	20.4	18.4	7.1	200	0.44-0.76	L, P, RA (aust.); L, P (long.)
NZN32a	WI	MA	Tutaenui Stm (Bulls)	S40.18893	E175.35623	31	1-Mar-2007	10:03	22.8	20.9	7.4	380	-	L (aust.)
NZN32b	WI	MA	Tutaenui Stm (Bulls)	S40.18893	E175.35623	31	28-Nov-2008	14:34	25.6	26.3	7.8	350	-	L, P (aust.)
NZN33	WN	MA	Waitohu Stm (Otaki)	S40.76582	E175.19295	75	15-Nov-2006	14:00	19.0	12.9	6.9	70	-	A (aust.)
NZN34	WN	EA	Abbots Ck (SH2)	S41.10598	E175.29318	105	16-Nov-2006	10:00	18.7	12.4	7.1	65	0.44-0.76	L (aust.); L (till.)
NZN35	WA	EA	Makakahi R	S40.70399	E175.65811	271	16-Nov-2006	15:37	21.2	13.8	7.1	30	1.6	L, P, RA (aust.); L, P (till.)
NZN36	WA	WA	Waihi Stm (SH52)	S40.43691	E176.29528	65	17-Nov-2006	12:30	22.4	20.3	10.0	170	0.44-0.76	L (aust.)
NZN37	WA	WA	Mangatora R trib	S40.27074	E176.21983	64	17-Nov-2006	14:00	20.4	19.1	9.9	240	0.44-0.80	L (aust.); L, P (till.)
NZN38	RI	EA	Manawatu R (SH2 Norsewood)	S40.05450	E176.24163	298	18-Nov-2006	10:00	22.4	16.4	-	60	0.70-0.90	L, P (aust.); L, P (till.)
NZN39	RI	EA	Tangarewai Stm	S39.96573	E176.28390	317	18-Nov-2006	13:00	19.7	17.0	7.7	60	0.90-1.00	L, P (aust.); L, P, RA (till.)
NZN40	RI	EA	Waipawa R (SH50)	S39.86441	E176.44602	217	18-Nov-2006	15:30	20.1	16.9	7.6	70	0.60+	L, P (aust.); L, P (till.)
NZN41	HB	EA	Ohiwa Stm trib	S39.55383	E176.69506	44	19-Nov-2006	10:00	18.5	16.3	7.9	530	-	L (aust.); L (till.)
NZN42	HB	EH	Tutaekuri R	S39.37091	E176.43907	350	19-Nov-2006	12:00	20.8	13.8	7.9	70	-	L (aust.); L, P, A (till.)
NZN43	HB	VP	Ngaruroro R trib	S39.38531	E176.33168	481	19-Nov-2006	14:00	19.8	12.3	7.9	250	0.40-0.60	L (aust.)
NZN44	HB	VP	Ngaruroro R	S39.38544	E176.33090	480	19-Nov-2006	14:30	24.1	11.7	7.8	30	-	L (aust.); L (till.)

NZN45	HB	VP	Kakekino Stm	S39.40693	E176.30383	501	19-Nov-2006	15:45	19.8	15.2	7.6	70	-	L (aust.); L (till.)
NZN46	TO	VP	Waitangi Stm (Waiouru)	S39.46986	E175.64320	735	20-Nov-2006	10:47	15.5	11.2	7.5	140	-	L (aust.); L (long.)
NZN47	RI	VP	Mangateitei Stm (Ohakune)	S39.41973	E175.40312	607	20-Nov-2006	13:30	16.7	11.9	7.5	40	-	L (aust.); L (till.)
NZN48	TO	VP	Mangaio Stm	S39.31007	E175.73737	1070	20-Nov-2006	16:00	14.8	9.6	6.5	20	0.60-0.80	L, P, RA (dugdalei); L (till.)
NZN48a	TO	VP	Mangaio Stm	S39.31007	E175.73737	1070	21-Nov-2006	9:00	12.4	6.4	-	-	-	L, P, RA (dugdalei)
NZN48b	TO	VP	Mangaio Stm	S39.31007	E175.73737	1075	3-Mar-2007	12:26	16.9	14.5	7.4	30	-	L, P, RA (dugdalei)
NZN48c	TO	VP	Mangaio Stm	S39.31007	E175.73737	1075	19-Nov-2008	10:41	13.1	7.6	7.6	30	-	L (dugdalei)
NZN49	TO	VP	Mangatoetoenui Stm	S39.23428	E175.73170	972	21-Nov-2006	11:37	20.4	9.8	7.2	70	-	L (dugdalei)
NZN49a	TO	VP	Mangatoetoenui Stm	S39.23445	E175.73138	978	3-Mar-2007	13:02	20.8	13.3	7.7	110	-	L (dugdalei); L (?till.)
NZN49b	TO	VP	Mangatoetoenui Stm	S39.23493	E175.73102	977	19-Nov-2008	13:12	14.9	10.9	7.6	80	-	L (dugdalei); L (till.)
NZN50	TO	TP	Waipunga R	S39.01520	E176.55575	466	22-Nov-2006	12:15	24.2	11.0	7.0	30	0.44-0.62	L, P (aust.); L, P, RA (till.)
NZN51	HB	EA	Esk R	S39.35749	E176.81408	38	22-Nov-2006	14:10	20.8	19.7	8.1	260	0.40-0.60	L, A (aust.); L, P, A (till.)
NZN52	HB	EA	Te Ngaru Stm	S39.31250	E176.88431	50	23-Nov-2006	10:30	20.3	13.6	6.7	280	-	L, P (aust.)
NZN53	HB	EA	Waikare R	S39.12884	E176.99706	31	23-Nov-2006	12:00	25.4	19.7	8.3	290	-	L, P, RA (aust.); L (till.)
NZN54	GB	EA	Aniwaniwa Stm (Papakorito Falls)	S38.74084	E177.17623	650	24-Nov-2006	14:00	22.3	13.5	8.1	90	-	L, P (aust.)
NZN55	TO	TO	Whirinaki R (Minginui)	S38.70350	E176.69630	644	25-Nov-2006	12:00	15.0	11.3	7.7	50	-	P (aust.)
NZN56	BP	BP	Waingaehe Stm	S38.12236	E176.30829	299	26-Nov-2006	9:00	15.3	15.2	7.6	100	-	L, P (aust.)
NZN57	BP	BP	Whakatane R trib	S38.01235	E176.94786	13	30-Nov-2006	10:30	17.9	16.2	7.1	80	-	L, P, RA (aust.)
NZN58	BP	BP	Waimana R	S38.10667	E177.04245	26	30-Nov-2006	11:30	18.5	15.7	7.1	60	-	L (aust.); L (till.)
NZN59	BP	TO	Omaukora Stm (SH2 bridge)	S38.27139	E177.33901	125	1-Dec-2006	10:30	13.7	12.9	7.4	50	-	L (till.)
NZN60	GB	EH	Waihuka R (walkway)	S38.47037	E177.66680	146	1-Dec-2006	12:30	20.7	19.0	7.8	280	0.44-1.00	L, P, RA (till.)
NZN61	GB	EH	Mangaheia R (Five Bridges)	S38.32588	E178.16092	72	2-Dec-2006	12:30	14.0	17.0	8.1	420	0.76	L, P (aust.)
NZN62	GB	EH	Mangahauini R	S38.10974	E178.29097	62	2-Dec-2006	16:30	13.0	15.8	8.1	300	-	L (aust.); L (till.)
NZN63	GB	EH	Maraehara R	S37.73071	E178.35936	58	3-Dec-2006	10:00	20.5	16.3	7.6	450	-	L (aust.); L (till.)
NZN64	GB	EH	Awatere R (SH35 bridge)	S37.67459	E178.34813	22	3-Dec-2006	11:01	20.3	17.0	7.6	140	0.62	L (aust.)
NZN65	BP	TP	Maraehako Stm	S37.67423	E177.80238	2	3-Dec-2006	15:15	22.7	21.3	7.8	90	-	L, P (aust.); P (till.)
NZN66	BP	TO	Houpoto Stm	S37.86862	E177.60206	5	4-Dec-2006	10:23	20.3	15.1	6.9	70	-	L, P, A (aust.)
NZN67	BP	BP	Waimana R (bridge)	S38.13506	E177.06362	41	4-Dec-2006	13:30	23.3	18.5	6.9	50	-	L, P (aust.); L, P (till.)
NZN68	BP	TO	Tarawera R	S38.12421	E176.65687	52	5-Dec-2006	10:30	20.9	16.7	7.0	200	-	L, P (aust.)
NZN69	BP	TO	Tarawera Falls	S38.16277	E176.51988	58	5-Dec-2006	12:10	20.7	16.7	6.9	360	-	L (aust.)
NZN70	BP	BP	Ohaupara Stm	S37.96038	E176.16962	58	6-Dec-2006	10:30	13.6	11.7	6.9	40	-	L, P (aust.)
NZN71	BP	CP	Te Rereatukahia Stm	S37.58763	E175.88224	78	6-Dec-2006	15:30	20.0	18.0	7.3	50	-	L, P, RA (aust.)
NZN72	CL	CP	Ohinemuri R (SH2, Waikino)	S37.41264	E175.77238	97	7-Dec-2006	10:00	19.6	18.7	7.1	200	-	L (aust.)
NZN73	AK	NH	Araparera R	S36.46584	E174.54236	48	16-Dec-2006	10:30	21.6	18.5	8.1	160	-	L (aust.)
NZN74	AK	NH	Mahurangi R trib [Mill Stm], Kowhai Park Scenic Reserve	S36.39610	E174.66026	44	16-Dec-2006	13:47	18.8	14.7	8.1	210	-	L, P (aust.); L (long.)
NZN74a	AK	NH	Mahurangi R trib [Mill Stm], Kowhai Park Scenic Reserve	S36.39348	E174.65613	30	2-Nov-2008	14:27	17.4	15.3	8.5	160	-	L (aust.)
NZN75	ND	NH	Kaihu R (SH12, near Ahikiwi)	S35.79952	E173.73430	30	17-Dec-2006	13:30	23.7	19.6	7.3	90	-	L, P (aust.)
NZN76	ND	NH	Waipoua R (SH12)	S35.65220	E173.55898	89	17-Dec-2006	17:15	22.3	17.7	7.5	75	-	L, P, A (aust.)
NZN77	ND	NH	Waimamuku R (SH12, Waimamuku)	S35.55773	E173.48094	53	18-Dec-2006	11:30	20.8	18.3	7.2	90	-	L, P (aust.)
NZN78	ND	NH	Manganuiowae Stm (Broadwood)	S35.26040	E173.39170	85	18-Dec-2006	15:30	25.3	21.7	7.4	120	-	L, P, A (aust.)
NZN79	ND	NH	Victoria R (SH1)	S35.14681	E173.40745	78	19-Dec-2006	10:30	19.4	18.1	7.1	130	-	L, P (aust.)
NZN80	ND	NH	Mangamuka R (SH1, Raiatea Forest)	S35.19342	E173.48076	86	19-Dec-2006	11:15	20.0	17.5	7.1	170	-	L, P (aust.)
NZN80a	ND	NH	Mangamuka R (SH1, Raiatea Forest)	S35.19417	E173.48203	75	3-Nov-2008	15:57	20.4	14.6	8.0	110	0.88	L, A (aust.)
NZN81	ND	NH	Waiaruhe R (Puketona Junction)	S35.30223	E173.96090	63	19-Dec-2006	15:20	22.9	21.5	7.1	110	-	L, P (aust.)
NZN82	ND	NH	Awarua R (Twin Bridges)	S35.62318	E173.84572	62	19-Dec-2006	17:04	22.2	20.8	7.3	140	-	L, P (aust.)
NZN83	ND	NH	Hatea R (A H Reed Kauri Park)	S35.69005	E174.33678	42	20-Dec-2006	10:41	19.4	19.3	7.1	210	-	L, P (aust.)
NZN84	TO	VP	Mangatepopo Stm trib	S39.14087	E175.57286	1075	18-Dec-2006	10:30	10.1	9.2	8.8	10	-	L (long.)
NZN84a	TO	VP	Mangatepopo Stm trib	S39.14087	E175.57286	1075	4-Mar-2011	9:30	16.9	14.5	7.4	30	-	L (long.)
NZN85	RI	VP	Hautapu R (SH1 bridge)	S39.64259	E175.76771	481	28-Dec-2006	14:00	19.0	15.5	8.4	110	-	L, P (aust.); P (dugdalei)
NZN86	WN	MA	Takapua Stm (Tawa)	S41.17762	E174.84563	73	26-Feb-2007	16:24	22.3	20.3	8.4	150	-	L, P (aust.); P (till.)
NZN87	WA	WA	Blue Rock Stm	S41.33495	E175.38744	261	27-Feb-2007	13:30	23.9	19.9	7.6	130	-	L (till.)
NZN88	WN	CM	Pakuratahi R (SH2)	S41.07972	E175.20171	198	27-Feb-2007	16:07	24.5	22.2	7.7	80	-	L (till.)

Collection Number	AC	ER	Locality name	Latitude	Longitude	Alt. m.a.s.l.	Date	Time h	Air C	Water C	pH	Cond. µS/cm	Velocity m/s	Stages collected and species
NZN89	WN	CM	Ohau R.	S40.67106	E175.24103	21	28-Feb-2007	12:07	23.0	21.5	7.4	75	0.40-0.50	L (aust.)
NZN90	WN	CM	Tokomaru R (SH57)	S40.57875	E175.48870	294	28-Feb-2007	14:23	20.5	17.2	7.5	70	-	L (aust.)
NZN91	RI	CM	Rangitikei R (Mokai Road)	S39.70362	E175.97165	360	2-Mar-2007	11:30	22.9	19.6	7.7	130	0.30-0.90	L, A (till.)
NZN92	TO	VP	Mangawhero R (upper)	S39.35749	E175.47224	906	2-Mar-2007	16:20	16.8	13.2	7.0	40	-	L (aust.); L (dugdalei)
NZN93	AK	NH	Glen Esk Stm	S36.95215	E174.48406	19	21-Mar-2007	10:00	18.8	16.0	7.7	195	-	L (aust.)
NZN94	AK	NH	Fairy Falls Stm	S36.91482	E174.55513	218	21-Mar-2007	14:09	17.6	14.6	8.1	90	-	L (aust.)
NZN95	ND	NH	Puketi Forest	S35.27687	E173.68309	19	3-Nov-2008	10:04	21.5	16.5	8.1	100	0.63	L, A (aust.)
NZN96	ND	NH	Te Hapua Road (stm 2 km from Waitiki Landing)	S34.50733	E172.85158	17	4-Nov-2008	11:00	22.2	16.3	7.5	210	0.6	L, P (aust.)
NZN97	ND	NH	Tapotupotu Stm (Cape Reinga)	S34.44425	E172.72318	3.5	4-Nov-2008	9:30	15.6	15.2	7.6	260	0.38-0.72	L (aust.)
NZN98	ND	NH	Te Awhia Stm (SH1 bridge)	S34.70803	E173.03409	18	4-Nov-2008	12:29	20.8	17.3	7.2	200	0.54-0.62	L (aust.)
NZN99	ND	NH	Kaeo R (Waiare Road)	S35.11702	E173.79854	13	7-Nov-2008	12:31	21.4	16.9	7.6	100	0.35-0.54	L, P, A (aust.)
NZN100	ND	NH	Waipu Cove (ditch)	S36.03062	E174.50858	9	9-Nov-2008	13:27	19.1	17.5	7.6	160	-	L (aust.)
NZN101	AK	NH	Omeru Falls Stm	S36.55738	E174.47513	13	9-Nov-2008	18:34	20.3	15.8	9.0	160	0.66	L (aust.)
NZN102	TO	BP	Waihora Stm	S38.63753	E175.72357	505	13-Nov-2008	13:55	28.0	14.1	8.9	30	-	L, P (aust.); -?? (long.)
NZN102a	TO	BP	Waihora Stm	S38.63753	E175.72357	505	14-Nov-2008	18:43	23.4	12.9	8.7	30	0.63-0.83	L, P (aust.)
NZN103	TO	BP	Tokaanu Stm	S38.96859	E175.76622	356	14-Nov-2008	9:45	22.7	15.2	8.6	80	0.54	L, P (aust.)
NZN104	TO	BP	Tongariro R (Red Hut bridge)	S39.03279	E175.81676	426	14-Nov-2008	12:32	25.0	15.2	8.0	80	-	L (aust.); L (till.)
NZN105	TO	VP	Mangatepopo Stm trib.	S39.14655	E175.58372	1134	15-Nov-2008	12:53	21.1	13.0	8.0	310	-	L, P (dugdalei)
NZN106	TO	VP	Papamanuka Stm (SH47 bridge)	S39.12563	E175.52280	872	16-Nov-2008	11:00	15.0	13.4	7.3	10	0.63	L (aust.); L (dugdalei); L, P, RA (till.)
NZN107	TO	VP	Mangatepopo Stm trib (SH47 bridge)	S39.07144	E175.56316	762	16-Nov-2008	12:53	18.4	12.9	7.3	170	<1.25	L (dugdalei)
NZN108	TO	VP	Mangawhero R trib.	S39.41351	E175.40382	579	17-Nov-2008	13:15	15.8	14.1	7.1	100	0.44-0.77	L (aust.); P (till.)
NZN109	TO	VP	Hautapu R.	S39.54343	E175.68419	778	18-Nov-2008	13:09	11.2	13.6	7.4	130	0.44-0.70	L, P (aust.)
NZN110	TO	VP	Tongariro R trib (Kaimanawa Road)	S39.15424	E175.82301	721	20-Nov-2008	10:30	-	-	-	-	-	A (aust.)
NZN111	TO	VP	Otaratiri Stm trib, ditch (Moerangi Station)	S38.94495	E175.59873	610	21-Nov-2008	8:37	14.4	13.6	7.4	50	-	L (long.)
NZN111a	TO	VP	Otaratiri Stm trib, ditch (Moerangi Station)	S38.94496	E175.59879	606	2-Feb-2012	8:47	15.6	15.2	6.9	3015-20		L (long.)
NZN112	TO	VP	Otaratiri Stm trib	S38.94680	E175.59158	606	21-Nov-2008	9:29	15.6	9.7	7.7	30	-	L (aust.)
NZN113	TK	MA	Paetahi Stm & Patea R junction	S39.34222	E174.27747	303	22-Nov-2008	9:35	14.9	11.7	7.6	70	0.44-0.70	L (aust.)
NZN114	TK	MT	Kokowai Stm	S39.25019	E174.09627	680	23-Nov-2008	13:15	-	-	-	-	-	A (aust.)
NZN115	TK	MA	Mangaemiemi Stm	S39.05037	E174.12742	13	26-Nov-2008	12:54	22.1	17.6	8.2	180	0.62	L, P (aust.)
NZN116	TO	TP	Otaratiri Stm trib (Moerangi Station)	S38.94522	E175.59867	606	12-Feb-2009	8:37	23.9	14.9	7.4	45	0	L, P (aust.)
NZN117	TK	VP	Mangatoromiro Stm	S39.42783	E174.49580	102	10-Jan-2012	11:31	20.1	19.4	7.3	30	0.8	L, P (long.); L, P (aust.)
NZN118	WI	VP	Wanganui (Kaikokopu Road stm)	S39.89826	E175.03725	39	13-Jan-2012	14.3118.519.5			7.6	250	0.76	L, P (long.); L, P (aust.)
NZN119	TO	VP	Mt Ruapehu (Blyth Track, Rotokawa)	S39.33234	E175.50533	1258	16-Jan-2012	13:09	13.0	12.3	7.2	10	-	L, P (long.)
NZN120	TO	VP	Mangateitei Stm (Ohakune)	S39.41822	E175.39793	576	17-Jan-2012	14:01	18.2	13.3	6.8	30	0.83	L, P (aust.); L, P (till.)
NZN121	RI	WO	Mangapurua Stm trib (Bridge to Nowhere)	S39.27268	E174.97259	94	18-Jan-2012	12:30	21.2	14.8	7.2	60	-	L (aust.)
NZN122	RI	WO	Kaukore Stm (bridge, Pipiriki)	S39.48030	E175.04550	32	19-Jan-2012	11:54	17.2	14.1	7.3	90	0.88	L (aust.)
NZN123	TO	VP	Mt Ruapehu seepage (Upper Round Mt track)	S39.23638	E175.53329	1469	20-Jan-2012	2:32	11.1	9.5	7.4	10	0.3	L (long.)
NZN123a	TO	VP	Mt Ruapehu seepage (Upper Round Mt track)	S39.23638	E175.53329	1469	5-Feb-2012	11:01	12.5	10.4	6.8	10	0.05-0.30	L (long.)
NZN124	TO	VP	Mt Tongariro, Soda Springs seepages (Mangatepopo Stm)	S39.13948	E175.62691	1375	21-Jan-2012	12:30	16.0	12	-	-	-	L (long.)
NZN125	TO	VP	Mt Ruapehu, Waikare Stm trib (Silica Rapids)	S39.22013	E175.53175	1289	23-Jan-2012	11:45	6.6	10.6	6.8	100	-	L (long.); L (dugdalei)
NZN126	TO	VP	Mt Ruapehu seepage (Silica Rapids track)	S39.21618	E175.53043	1237	23-Jan-2012	12:17	9.4	18.2	7.4	160	-	L (long.)
NZN126a	TO	VP	Mt Ruapehu seepage (Silica Rapids track)	S39.21618	E175.53043	1237	4-Feb-2012	11:30	13.2	15.6	7.8	200	-	L (long.)
NZN127	HB	EL	Maraetotara R	S39.74195	E176.95139	87	26-Jan-2012	11:30	25.2	17.8	7.4	200	0.99	L (aust.)
NZN128	WA	WA	Akitio R (SH52 bridge)	S40.41029	E176.32172	58	27-Jan-2012	12:51	11.8	15.1	7.7	190	0.76	L, P (till.)
NZN129	WA	WA	Pukeatua Stm trib	S40.86086	E176.17419	40	30-Jan-2012	9:58	18.4	12.9	7.4	260	0.35	L (aust.)
NZN130	WA	WA	Te Hoe Stm	S40.71759	E175.95245	214	30-Jan-2012	11:29	19.4	12.9	7.4	90	0.76	L, P (aust.); L (till.)

South Island

NZS1	SD	NE	Ngakuta Bay stm	S41.27440	E173.96304	1	29-Dec-2006	16:00	17.8	16.1	8.5	40	0.30-0.40+	L, P, RA (aust.); L, P, RA (lat.)
NZS2	SD	NE	Kenepuru Head stm	S41.16583	E174.12406	10	30-Dec-2006	13:00	17.8	14.7	7.8	30	0.40-1.00	L, P, RA (aust.); L, P, RA (lat.); L, P, RA (till.); A (ung.)
NZS2a	SD	NE	Kenepuru Head stm	S41.16583	E174.12406	10	31-Dec-2006	12:30	15.3	13.4	7.4	40	0.40-1.00	L (lat.); L, P (till.)
NZS3	SD	NE	Ohinetaha Bay stm	S41.22914	E173.92055	5	30-Dec-2006	15:00	16.8	13.7	7.9	80	-	L, P (aust.)
NZS4	MB	NE	Wakamarina R	S41.35821	E173.62038	40	1-Jan-2007	11:36	17.3	14.6	7.3	30	-	L, A (till.)
NZS5	MB	NE	Pelorus R	S41.29987	E173.57859	24	1-Jan-2007	12:37	15.6	16.9	7.5	50	-	L, P (lat.); L, P (till.)
NZS6	NN	NP	Maitai R	S41.27394	E173.30561	35	2-Jan-2007	13:48	17.3	16.5	7.7	110	-	L, P (lat.); L, P, RA (till.)
NZS7	NN	NP	Poorman Valley Stm	S41.31686	E173.24836	73	3-Jan-2007	15:30	18.0	17.4	7.8	100	-	L, P (lat.); L, P, A (till.); A (ung.)
NZS8	KA	MP	London Ck	S41.82272	E174.16390	21	14-Jan-2007	12:15	24.9	20.0	7.3	220	0.25	L (long.); L, P (till.)
NZS9	KA	HC	Kekerenga R	S42.00428	E174.00911	8	14-Jan-2007	14:40	24.8	17.9	8.0	270	0.70-0.90	L, P (till.)
NZS10	KA	HC	Mororimu Stm (SH1)	S42.21698	E173.86707	7	14-Jan-2007	16:00	18.1	15.5	8.1	60	-	L, P (mult.); L, P, A (till.); A (ung.)
NZS11	KA	HC	Kowhai R (SH1 bridge)	S42.41462	E173.63216	9	15-Jan-2007	10:00	18.6	14.8	8.1	90	0.88-1.00	L, P (albov.); L, P (till.)
NZS12	KA	HC	Green Burn	S42.39443	E173.40114	273	15-Jan-2007	11:30	24.6	16.3	7.8	90	-	L (long.); L, P (mult.); L, P (till.)
NZS13	KA	HC	Mason R (SH70)	S42.50510	E173.16721	437	15-Jan-2007	13:38	26.0	21.1	8.0	80	1.25	L (till.)
NZS13a	KA	HC	Mason R (SH70)	S42.50507	E173.16708	433	15-Oct-2008	10:36	17.9	10.2	7.2	90	-	L (mult.); L (till.); A (ung.)
NZS14	MC	EC	Okeover Stm	S43.52314	E172.58622	22	17-Jan-2007	13:10	16.6	13.6	6.9	110	-	L (long.)
NZS15	MC	EC	North Branch Ashburton R (Thompsons Track)	S43.73253	E171.59078	250	18-Jan-2007	11:00	19.6	15.5	7.0	40	-	P (alveo.); L (aust.)
NZS16	MC	EC	Bowyers Stm	S43.73527	E171.53548	261	18-Jan-2007	12:00	20.3	13.6	7.0	40	0.70-0.90	L, P (aust.); L (till.)
NZS17	SC	HC	Opuha R (SH79)	S44.08039	E170.97881	248	18-Jan-2007	15:00	22.0	18.8	7.4	20	1.25	P (mult.); L, P (till.)
NZS18	MK	HC	Fork Stm (SH8 bridge)	S44.00064	E170.41161	748	19-Jan-2007	10:05	21.0	11.6	8.0	10	-	L, P (lat.); L, P (mult.)
NZS18a	MK	HC	Fork Stm (SH8 bridge)	S43.99959	E170.41194	760	23-Nov-2011	15:32	19.3	13.2	6.9	10	-	L (mult.); cocoon (lat.)
NZS19	MK	HC	Tasman R trib (SH80)	S43.85198	E170.11399	575	19-Jan-2007	13:00	24.0	18.1	7.0	30	0.80-1.00	L, P (till.)
NZS20	MK	HC	Ahuriri R (SH83)	S44.46859	E169.98616	414	19-Jan-2007	16:00	28.0	22.2	7.7	20	1.1	L, P (till.)
NZS21	CO	HC	Thompsons Ck trib	S44.97391	E170.52174	413	20-Jan-2007	11:00	16.5	14.5	7.1	90	-	P (long.); L, P (stew.); L (till.)
NZS22	CO	HC	Thompsons Ck	S44.95600	E170.48056	353	20-Jan-2007	12:00	16.5	14.5	6.9	30	0.90-1.10	L, P (mult.); L, P (stew.); L, P (till.)
NZS23	CO	HC	Thompsons Ck	S44.94774	E170.40334	584	20-Jan-2007	12:45	18.2	15.7	7.2	60	-	L (mult.)
NZS24	CO	HC	Kye Burn trib	S44.95646	E170.35158	764	20-Jan-2007	14:05	16.7	12.1	7.1	20	1.2	L, P (stew.)
NZS25	CO	HC	Glengary Stm	S45.69140	E170.00186	449	21-Jan-2007	10:00	16.5	14.8	6.9	90	-	- (long.)
NZS26	DN	HC	Lee Stm (SH87 bridge)	S45.80048	E170.12809	330	21-Jan-2007	11:00	13.0	15.3	6.9	40	-	L (stew.)
NZS27	SL	SL	Catlins R	S46.45572	E169.48007	85	21-Jan-2007	16:30	14.9	14.5	7.1	65	-	L, P (lat.); L, P, RA (stew.); L, A (ung.)
NZS27a	SL	SL	Catlins R	S46.45572	E169.48007	85	22-Jan-2007	10:00	-	-	-	-	-	L (ung.)
NZS28	SL	SE	Matai Stm (falls)	S46.50318	E169.48869	151	22-Jan-2007	10:45	15.8	12.7	7.0	80	-	L, P (stew.); L (ung.)
NZS29	SL	SE	Caddon Burn	S46.45748	E169.08877	131	22-Jan-2007	15:36	22.7	15.0	7.1	80	-	L, P (aust.); L (lat.); L (mult.)
NZS30	SL	HC	Waimeamea R	S46.25898	E167.73851	26	23-Jan-2007	10:00	16.2	13.0	6.7	80	-	A (aust.); L, P (lat.); L, P, RA (stew.); A (ung.)
NZS31	SL	HC	Wairaki R	S45.93467	E167.70512	88	23-Jan-2007	14:30	19.0	18.2	6.9	80	-	L, P (lat.)
NZS32	FD	SA	Homer Tunnel stm (SH94)	S44.76580	E167.98969	882	24-Jan-2007	12:30	16.4	15.0	6.9	<10	-	L, P (bicorne); L, P (tonnoiri)
NZS32a	FD	SA	Homer Tunnel stm (SH94)	S44.76587	E167.98969	882	5-Jan-2009	13:00	9.1	6.5	-	<10	-	P (bicorne); L, P (tonnoiri)
NZS33	FD	SA	Divide Ck	S44.80442	E168.11256	300	24-Jan-2007	15:05	17.4	11.1	6.7	30		L, P (mult.); L, P, A (ung.)
NZS34	OL	HC	Walker Ck (SH94)	S45.10146	E167.96719	276	24-Jan-2007	17:50	23.6	15.3	6.8	40	-	L, P (stew.); P, A (ung.)
NZS35	OL	HC	Weydon Burn trib [Hamilton Ck]	S45.56556	E168.0700	424	25-Jan-2007	13:30	16.1	17.0	6.4	40	-	L (lat.); L (mult.); L, A (ung.)
NZS36	CO	HC	Mataura R trib [Parawa Stm]	S45.54439	E168.53186	273	25-Jan-2007	15:00	16.4	11.8	6.4	30	-	L, P, RA (lat.); L, P (mult.)
NZS37	CO	CO	Roaring Meg (SH6)	S45.00055	E169.07075	249	26-Jan-2007	10:30	13.7	11.9	6.6	50	-	L, P (mult.); (till.); A (ung.)
NZS38	CO	CO	Manuherikia R (SH85)	S45.24561	E169.40571	155	26-Jan-2007	14:30	19.9	20.3	6.8	60	0.80-1.00	L, P (till.)
NZS39	CO	CO	Butchers Ck headwaters	S45.34363	E169.22985	1373	26-Jan-2007	10:00	11.3	11.1	6.7	20	-	L (long.)
NZS40	CO	CO	Fraser R.headwaters	S45.31887	E169.19748	1610	26-Jan-2007	11:00	11.7	10.6	6.7	10	0.8	L (long.)
NZS41	CO	EA	Fraser R headwaters	S45.35496	E169.20728	1605	27-Jan-2007	12:47	16.7	13.4	6.7	<10	-	L, P (long.)
NZS42	CO	CO	Obelisk Ck irrigation ditch	S45.34150	E169.28629	507	27-Jan-2007	15:33	24.7	17.3	6.9	20	-	L, P (mult.)
NZS43	CO	CO	Nine Mile Ck (SH8)	S45.08722	E169.27061	210	28-Jan-2007	10:38	18.5	11.6	6.4	130	-	A (ung.)
NZS44	CO	CO	Lindis R (SH8)	S44.88054	E169.35429	225	28-Jan-2007	11:36	20.5	13.6	6.5	50	1.10-1.20	(till.)
NZS45	WD	WD	Jackson Bay	S43.97212	E168.61392	15	29-Jan-2007	11:30	-	-	-	-	-	A (dumbletoni); A (ung.)
NZS45a	WD	WD	Knights Point	S43.71534	E169.22536	126	29-Jan-2007	15:40	-	-	-	-	-	A (aust.); A (dumbletoni); A (ung.)

Collection Number	AC	ER	Locality name	Latitude	Longitude	Alt. m.a.s.l.	Date	Time h	Air C	Water C	pH	Cond. µS/cm	Velocity m/s	Stages collected and species
NZS45b	WD	WD	Knights Point	S43.71534	E169.22536	126	21-Nov-2011	12:00	-	-	-	-	-	A (ung.)
NZS46	WD	SA	Maimai Ck	S43.57311	E169.79755	38	30-Jan-2007	9:28	16.4	13.8	6.1	20	-	L, P (lat.); L, A (ung.)
NZS47	WD	SA	Ribbonwood Ck (SH6)	S43.48880	E169.97733	132	30-Jan-2007	10:40	14.6	10.1	-	-	-	L (ung.)
NZS48	WD	SA	Fox R trib (Fox Glacier)	S43.49004	E170.03666	233	30-Jan-2007	12:04	12.3	7.3	6.3	110	-	L (mult.)
NZS49	WD	WD	Franz Josef Glacier ck	S43.42008	E170.16996	221	30-Jan-2007	14:15	16.0	11.3	6.5	50	-	L, P (ung.)
NZS49a	WD	WD	Franz Josef Glacier ck	S43.42008	E170.16996	221	1-Jan-2009	9:58	15.6	10.8	-	60	-	L, P (ung.)
NZS50	WD	WD	Kawhaka Ck	S42.72852	E171.16219	159	31-Jan-2007	12:00	14.2	12.1	7.4	20	-	L (lat.)
NZS51	WD	SA	Taramakau R (SH73)	S42.74009	E171.51152	157	31-Jan-2007	15:06	13.2	10.9	7.2	40	0.80-1.20	L, P (lat.); L (aust.); L (mult.); L (till.); A (ung.)
NZS52	NC	SA	Twin Ck (SH73)	S42.90961	E171.57412	1330	1-Feb-2007	11:00	12.4	8.3	6.9	10	-	P (bicorne); L (mult.)
NZS53	NC	HC	Waimakariri R channel (SH73)	S43.02036	E171.60675	623	2-Feb-2007	9:40	12.3	11.4	7.5	30	-	L (mult.)
NZS54	NC	HC	Grasmere Stm (Cass)	S43.03541	E171.75811	576	2-Feb-2007	11:30	15.6	13.1	6.9	40	-	P (mult.); A (ung.)
NZS55	NC	HC	Craigieburn (SH73)	S43.13790	E171.75743	690	2-Feb-2007	12:11	17.1	11.0	6.9	30	1.13	L, P (mult.); A (ung.)
NZS56	NC	HC	Porter R (SH73)	S43.27776	E171.66375	912	2-Feb-2007	14:50	13.1	9.5	7.1	20	-	L, P (mult.); L (ung.)
NZS57	NC	HC	Foggy Peak Ridge stm (SH73)	S43.29359	E171.72443	867	2-Feb-2007	16:03	13.7	10.1	7.0	30	-	L (mult.)
NZS57a	NC	HC	Foggy Peak Ridge stm (SH73)	S43.29664	E171.74129	952	2-Feb-2007	16:31	-	-	-	-	-	L (mult.)
NZS57b	MC	HC	Foggy Peak Ridge stm (SH73)	S43.29544	E171.74098	955	25-Nov-2011	12:45	21.7	8.9	6.8	10	-	L, P (mult.); L, P (ung.)
NZS58	MC	BP	Wainui stm (Banks Peninsula)	S43.81013	E172.89372	55	4-Feb-2007	11:13	16.5	12.1	6.5	90	-	L (mult.); L (till.)
NZS59	MC	BP	Opara Stm	S43.72596	E173.00143	113	4-Feb-2007	12:38	19.1	15.1	6.8	110	-	L, P (mult.); L. P (till.)
NZS60	MC	BP	Kaituna R	S43.74265	E172.68663	30	4-Feb-2007	16:30	19.5	16.5	7.1	100	0.60-0.80	L, P (till.); A (ung.)
NZS61	NC	EC	Ashley R (SH1 bridge)	S43.27691	E172.68919	10	6-Feb-2007	10:31	18.8	17.5	6.6	70	-	L. P (till.)
NZS62	NC	EC	Pahau R (SH7 bridge)	S42.79754	E172.82897	182	6-Feb-2007	12:00	20.6	18.6	6.9	80	1.00-1.20	L. P (till.)
NZS63	MB	HC	Dog Stm (SH7a)	S42.52772	E172.83291	356	6-Feb-2007	14:30	23.5	16.4	7.3	70	0.60-0.80	L (mult.); P (till.)
NZS64	MB	HC	Boyle R (SH7)	S42.51598	E172.38922	589	6-Feb-2007	16:15	26.7	18.7	7.5	50	0.75-0.90	P (mult.); L. P (till.)
NZS65	BR	HC	Marble Hill Campground	S42.34993	E172.22298	522	6-Feb-2007	18:00	-	-	-	-	-	A (ung.)
NZS66	BR	WD	Rahu R (Springs Junction)	S42.33929	E172.15599	457	7-Feb-2007	9:30	15.6	11.4	6.6	20	-	L (mult.); L, P (ung.)
NZS67	BR	WD	Inangahua R (Rahu Saddle)	S42.30365	E172.10300	638	7-Feb-2007	11:12	17.7	11.2	6.6	20	-	L (aust.); L (mult.); L (ung.)
NZS68	BR	WD	Inangahua R (SH7 Reefton)	S42.12076	E171.86412	188	7-Feb-2007	13:30	26.7	20.1	6.8	30	-	L (lat.); P, A (till.); A (ung.)
NZS69	BR	WD	Grey R (SH7 bridge)	S42.28880	E171.67273	99	7-Feb-2007	15:06	28.2	21.5	7.1	40	-	L, P (lat.); L (till.)
NZS70	BR	WD	Mill Ck (SH6 Greymouth)	S42.48846	E171.18018	10	8-Feb-2007	9:30	22.1	16.4	6.5	70	-	L, A (aust.); A (ung.)
NZS71	BR	NW	Thirteen Mile Ck (SH6)	S42.30731	E171.28365	10	8-Feb-2007	13:30	-	-	-	-	-	L, A (ung.)
NZS72	BR	WD	Punakaiki R (SH6 bridge)	S42.12495	E171.33294	10	8-Feb-2007	14:30	-	-	-	-	-	A (aust.); A (ung.)
NZS73	NN	WD	W W Stm (Fairdown)	S41.73389	E171.74327	19	9-Feb-2007	10:07	20.5	15.4	6.5	35	-	L, P, RA (aust.); A (ung.)
NZS74	NN	WD	Jones Ck	S41.66662	E171.81023	13	9-Feb-2007	10:47	21.5	15.6	6.4	60	0.70-0.75	A (aust.); L (lat.); A (ung.)
NZS75	NN	WD	Sandel Ck (SH67 Karamea Bluff)	S41.51805	E172.02477	400	9-Feb-2007	12:00	-	-	-	-	-	L, A (ung.)
NZS76	NN	WD	Kohaihai R (Heaphy Track)	S41.10850	E172.10777	16	9-Feb-2007	15:00	22.5	17.3	7.1	40	-	A (aust.); L (mult.); A (ung.)
NZS77	NN	WD	Candle Ck	S41.15262	E172.10673	14	9-Feb-2007	16:40	25.0	23.2	7.0	110	-	L (aust.); L (lat.); A (ung.)
NZS78	NN	WD	unmarked stm (near Virgin Ck, Karamea R gorge).	S41.24755	E172.21533	28	10-Feb-2007	10:30	16.5	14.2	6.6	40	-	L (aust.); A (ung.)
NZS79	NN	WD	Little Wanganui R (Te Namu)	S41.37559	E172.10310	12	10-Feb-2007	12:16	21.9	17.3	6.4	50	-	L (aust.); L (lat.); A (ung.)
NZS80	NN	NW	Little Ten Mile Ck [Fuschia Ck]	S41.83577	E171.68443	45	11-Feb-2007	10:04	16.7	14.1	6.4	40	-	L, A (ung.)
NZS81	NN	NW	Brown Ck	S41.88485	E171.92355	70	11-Feb-2007	12:00	19.1	16.8	6.5	20	-	L, P (aust.); L, P (lat.); L (till.); A (ung.)
NZS82	NN	NW	Lyell Ck	S41.79536	E172.04998	86	11-Feb-2007	13:50	20.6	15.0	6.5	40	-	L, P (aust.); L, P (lat.); L (till.); A (ung.)
NZS83	BR	NP	Doctor Ck	S41.74760	E172.39467	206	12-Feb-2007	22:45	21.6	19.5	6.5	90	-	P (lat.); L, P (till.); A (ung.)
NZS84	BR	NP	Owen R (SH6)	S41.68418	E172.45396	246	12-Feb-2007	11:44	22.4	20.4	7.2	120	-	L, P, A (till.)
NZS85	BR		Buller R (Gowanbridge)	S41.71208	E172.56052	330	12-Feb-2007	12:30	16.6	18.1	7.4	20	-	L (till.)
NZS86	BR	NP	Hope R (SH6 and 63 junction)	S41.69285	E172.61832	353	12-Feb-2007	14:40	17.3	16.8	6.6	30	-	L, P (lat.); A (ung.)
NZS87	BR	NP	Robert Stm	S41.82747	E172.82117	842	13-Feb-2007	11:40	13.7	11.3	6.2	50	-	L, P (mult.)
NZS88	BR	NP	Black Valley Stm	S41.80097	E172.85258	647	13-Feb-2007	13:45	15.5	14.3	6.3	30	-	A (ung.)
NZS89	NN	NP	Motupiko R	S41.61327	E172.79314	334	14-Feb-2007	11:10	22.0	18.8	6.4	40	-	P (lat.); L, P (till.); A (ung.)
NZS90	NN	NP	Motueka R	S41.28931	E172.80903	89	14-Feb-2007	13:45	21.9	19.8	7.0	70	-	L, P (till.)
NZS91	NN	NP	Flora Stm	S41.18216	E172.73069	910	14-Feb-2007	16:20	14.0	9.7	6.4	90	-	L, A (mult.); L, P, A (ung.)

NZS92	NN	NP	Whisky Ck (Flora Saddle)	S41.18872	E172.74378	985	14-Feb-2007	17:12	17.3	9.5	6.4	80	-	L (ung.)
NZS93	NN	NP	Cobb R	S41.12882	E172.61388	826	15-Feb-2007	14:14	19.9	16.2	6.6	60	1.1	L, P (lat.); L, P (till.); A (ung.)
NZS94	NN	NW	Cobb R trib	S41.12604	E172.60221	857	15-Feb-2007	15:47	17.4	12.8	6.6	70	-	L (mult.); L, P, A (ung.)
NZS95	NN	NW	Cobb R trib, runnel	S41.12267	E172.60026	841	15-Feb-2007	16:36	21.3	9.3	6.8	80	-	(mult.); L (ung.)
NZS96	NN	NW	Fossil Ck	S40.84712	E172.44877	112	16-Feb-2007	16:14	19.7	15.2	7.7	10	-	L, P (lat.); L, P, A (ung.)
NZS97	NN	NW	Aorere R	S40.83991	E172.45228	115	17-Feb-2007	10:08	19.5	14.0	7.6	20	-	L, P (lat.); P (mult.); A (ung.)
NZS98	NN	WD	Cooks Ck	S40.76780	E172.55944	55	17-Feb-2007	11:00	23.0	17.0	7.8	50	-	L, P (lat.); A (ung.)
NZS99	NN	WD	Green Hills Stm	S40.51286	E172.65201	8	17-Feb-2007	14:39	19.0	18.4	7.6	140	0.60-0.70	L, P (aust.)
NZS100	NN	WD	Paturau R	S40.65426	E172.45720	8	18-Feb-2007	12:15	20.7	18.2	8.0	50	0.35-0.40	L, P (lat.); L, P (till.)
NZS101	NN	NP	Wainui R (Anatimo)	S40.83613	E172.93750	10	19-Feb-2007	13:17	22.4	16.0	8.4	50	-	L, P (aust.); L, P (lat.); A (ung.)
NZS102	NN	NP	Totaranui Stm	S40.82201	E172.99995	3	19-Feb-2007	15:14	28.4	16.6	7.9	40	-	L, P (aust.)
NZS103	NN	NP	Takaka Hill summit stm	S41.03215	E172.86527	790	20-Feb-2007	14:00	18.8	13.5	8.4	150	-	L (long.)
NZS103a	NN	NP	Takaka Hill summit stm	S41.03220	E172.86536	804	29-Nov-2011	11:25	8.8	8.6	6.7	40	0.20-0.30	L (ung.); L (mult.); L (?albov.)
NZS104	NN	NE	Roding R (upper)	S41.36021	E173.29276	256	21-Feb-2007	13:17	22.8	17.4	8.9	140	-	P (lat.); L, P (till.); A (ung.)
NZS105	NN	NE	Roding R	S41.36808	E173.2400	155	21-Feb-2007	17:03	25.3	24.6	8.9	140	-	L, P, A (till.); A (ung.)
NZS106	NN	NE	Graham Stm (SH6)	S41.18433	E173.48661	94	24-Feb-2007	13:20	21.4	17.5	8.1	150	-	L, P (lat.); L, P (till.); A (ung.)
NZS107	SD	NE	Waikawa Stm	S41.27358	E174.03323	12	25-Feb-2007	21:30	16.3	15.6	8.0	60	-	L, P (till.)
NZS108	KA	SA	Puhi Puhi R trib	S42.24994	E173.75130	246	13-Oct-2008	14:30	17.0	12.3	8.7	110	-	L, P (mult.)
NZS108a	KA	SA	Puhi Puhi R trib	S42.24994	E173.75130	246	6-Dec-2008	10:43	15.6	12.5	-	110	-	L (till.)
NZS109	KA	SA	Ohau Stm (SH1)	S42.24377	E173.82927	21	13-Oct-2008	13:40	12.4	9.3	7.7	120	-	L (mult.); L (till.)
NZS110	KA	HC	Kowhai R trib	S42.33664	E173.55217	237	14-Oct-2008	11:00	16.1	10.1	7.7	160	-	A (mult.)
NZS111	KA	HC	Kowhai R trib	S42.33602	E173.55360	240	14-Oct-2008	12:00	14.1	8.8	7.5	90	-	A (mult.)
NZS112	NC	EC	Pahau R (SH7 bridge)	S42.79761	E172.82874	177	15-Oct-2008	12:23	19.0	15.4	7.6	80	0.63-1.10	L (mult.); L, P (till.)
NZS113	NC	EC	Waipara R (SH1 bridge)	S43.06932	E172.75395	78	15-Oct-2008	13:30	21.8	16.6	8.4	220	0.78-0.88	L, P (till.)
NZS114	SD	NE	Momorangi Bay stm	S41.27153	E173.94145	5	30-Nov-2008	17:29	20.8	16.7	8.0	80	-	L, P (aust.); A (ung.)
NZS115	MB	NE	Maungatapu Road near Pelorus Bridge (ditch)	S41.31188	E173.49544	70	1-Dec-2008	15:20	23.1	14.5	8.1	50	0.6	L (aust.); L, P, RA (long.); A (ung.)
NZS115a	MB	NE	Maungatapu Road near Pelorus Bridge (ditch)	S41.31188	E173.49544	70	8-Feb-2009	15:31	30.1	14.1	-	60	-	L (long.)
NZS116	NN	NP	Poorman Valley Stm (bridge)	S41.31278	E173.24101	36	3-Dec-2008	16:39	22.5	19.1	-	100	0.7	L (mult.); L (till.)
NZS117	KA	SA	Irongate Stm trib	S42.24187	E173.78619	253	6-Dec-2008	15:03	13.8	11.6	-	250	-	L, P (ung.)
NZS118	KA	HC	Conway R (SH1)	S42.59902	E173.41679	20	7-Dec-2008	11:00	21.5	21.3	-	250	0.45+	L, P (till.)
NZS119	MC	HC	Camping Gully ck	S43.52669	E171.67268	278	8-Dec-2008	14:00	23.1	14.9	-	90	1.08	L, P (stew.); L, P (till.)
NZS120	MC	HC	Pudding Hill Stm	S43.57772	E171.52826	497	8-Dec-2008	15:14	18.1	12.1	-	50	-	L, P (albov.); P (mult.); L (stew.); L, P (till.); A (ung.)
NZS121	MC	HC	Stour R (bridge)	S43.64607	E171.27010	504	9-Dec-2008	10:35	12.4	11.7	-	50	0.98	L, P, RA (albov.); L, P (till.)
NZS121a	MC	HC	Stour R (bridge)	S43.64607	E171.27010	504	25-Nov-2011	9:30	19.6	10.3	6.7	30	1	L P (till.); L (mult.)
NZS122	MC	HC	Lake Heron (Olliver Stm)	S43.49474	E171.15659	708	9-Dec-2008	12:00	13.1	10.9	-	10	1.17	L, P, RA (alveo.); L, P (till.)
NZS122a	MC	HC	Lake Heron (Olliver Stm)	S43.49474	E171.15659	708	28-Dec-2008	10:30	20.4	11.6	-	10	-	L, P, RA (alveo.); L, P (mult.); L, P (till.)
NZS123	MC	HC	Lake Heron (Emily Stm)	S43.55796	E171.19330	644	9-Dec-2008	15:23	14.4	13.2	-	70	0.88	L, P (alveo.); P (mult.); L, P (till.)
NZS124	SC	HC	Scour Stm (Rangitata R Valley)	S43.65104	E170.91016	478	10-Dec-2008	11:00	20.0	15.0	-	20	1.46	L (mult.); L (till.)
NZS125	SC	HC	Forest Ck (Rangitata R Valley)	S43.68515	E170.95885	476	10-Dec-2008	11:25	21.8	18.4	-	20	-	L, P (albov.); L, P (mult.)
NZS126	SC	HC	Soup Ck (Rangitata R Valley)	S43.74028	E171.12442	436	10-Dec-2008	13:57	22.0	21.0	-	90	-	L, P (fiordense); L, P (mult.); L, P (till.)
NZS126a	SC	HC	Soup Ck (Rangitata R Valley)	S43.74028	E171.12442	444	24-Nov-2011	15:30	20.8	13.5	7	70	0.76	L, P (mult.); L (till.)
NZS127	MK	HC	Freds Stm trib (SH80)	S43.82879	E170.09256	664	11-Dec-2008	12:26	19.5	10.5	-	20	-	L, P (mult.); A (ung.)
NZS128	MK	HC	Birch Hill Stm (SH80)	S43.79896	E170.09120	779	12-Dec-2008	13:00	10.8	7.2	-	30	-	L (mult.); L (unicorne)
NZS129	MK	HC	Freds Stm trib (SH80)	S43.83521	E170.08682	844	13-Dec-2008	11:30	16.1	9.9	-	50	-	L, P (mult.)
NZS130	MK	HC	Freds Stm trib (SH80)	S43.83664	E170.08979	852	13-Dec-2008	12:35	15.6	9.6	-	20	-	L, P (mult.)
NZS131	MC	HC	Acheron R	S43.32874	E171.67484	795	14-Dec-2008	12:17	16.8	10.5	-	40	0.76	L, P (mult.); A (ung.)
NZS131b	MC	HC	Acheron R	S43.32872	E171.67482	801	25-Nov-2011	12:09	20.6	9.2	6.9	20	1.3	L, P (mult.)
NZS132	NC	SA	Pegleg Ck (SH73 above bridge)	S42.89500	E171.56091	846	14-Dec-2008	15:55	17.6	8.4	-	30	-	L, P (bicorne); L (unicorne)
NZS132a	NC	SA	Pegleg Ck (SH73 above bridge)	S42.89500	E171.56091	846	29-Dec-2008	11:47	18.1	9.4	-	30	-	L, P (bicorne); P (mult.); L, P (unicorne)
NZS133	NC	SA	Twin Ck (SH73)	S42.90994	E171.57713	1385	15-Dec-2008	11:12	8.7	6.3	-	20	-	L, P (bicorne)

Collection Number	AC	ER	Locality name	Latitude	Longitude	Alt. m.a.s.l.	Date	Time h	Air C	Water C	pH	Cond. µS/cm	Velocity m/s	Stages collected and species
NZS133a	NC	SA	Twin Ck (SH73)	S42.90994	E171.57713	1385	30-Dec-2008	11:00	14.8	9.5	-	25	-	L, P, R (bicorne); P, RA (mult.)
NZS134	MC	HC	Foggy Peak Ridge stm (SH73)	S43.29364	E171.74205	993	16-Dec-2008	12:23	20.0	8.9	-	20	-	L, P (mult.); L (ung.)
NZS135	MC	BP	Kaituna R (upper)	S43.71798	E172.74806	214	18-Dec-2008	11:24	13.0	10.8	-	65	-	L (till.)
NZS136	MC	HC	Lake Heron (Gentleman Smith Stm)	S43.53728	E171.18435	706	28-Dec-2008	11:00	23.0	15.5	-	50	-	L, P (alveo.); P, A (mult.); P (till.)
NZS137	MC	HC	South Branch Ashburton R	S43.58335	E171.16104	639	28-Dec-2008	12:46	22.3	13.6	-	20	-	L (mult.)
NZS138	MC	HC	Woolshed Ck	S43.62668	E171.30031	571	28-Dec-2008	13:30	28.0	11.1	-	10	-	(mult.)
NZS139	MC	HC	Woolshed Ck	S43.62489	E171.30392	582	28-Dec-2008	14:30	26.4	16.1	-	20	-	L, P (mult.); L (till.)
NZS140	MC	SA	Otira R (upper)	S42.89613	E171.53532	1083	29-Dec-2008	14:23	21.1	6.1	-	10	-	P (bicorne); L (unicorne)
NZS141	WD	SA	Waiho R trib	S43.42964	E170.16971	232	1-Jan-2009	15:42	16.7	11.1	-	60	-	L (mult.); P (ung.)
NZS142	OL	HC	Fern Burn [Jack Hall stm]	S44.66958	E169.00343	303	3-Jan-2009	10:05	13.5	10.9	-	80	0.98	L, P (mult.)
NZS143	OL	HC	Cardrona R	S44.95271	E168.95876	759	3-Jan-2009	11:32	11.8	10.1	-	50	1.25	L, P, RA (mult.)
NZS144	FD	SA	Homer Tunnel (Cleddau R South Branch)	S44.76345	E167.97026	740	10-Jan-2009	11:00	11.7	9.6	-	<10	-	P (tonnoiri)
NZS145	FD	SA	Gertrude Valley stm	S44.75717	E168.01944	885	10-Jan-2009	14:00	17.4	9.1	-	<10	-	L, P (tonnoiri)
NZS146	OL	SA	Hollyford R (trib)	S44.66138	E168.12634	110	13-Jan-2009	12:34	17.1	10.0	-	120	-	L, P (ung.)
NZS147	OL	SA	Hollyford R (Gunns Camp)	S44.76083	E168.13936	147	14-Jan-2009	9:30	-	-	-	-	-	A (ung.)
NZS148	FD	SA	Divide Ck Routeburn Track)	S44.81597	E168.11928	582	13-Jan-2009	10:30	11.3	8.6	-	30	-	L, P (tonnoiri)
NZS149	OL	SA	Hollyford R (trib)	S44.81079	E168.12692	777	13-Jan-2009	11:48	16.5	9.3	-	120	-	L (ung.)
NZS150	OL	SA	L Howden outlet	S44.81573	E168.13534	683	13-Jan-2009	12:30	17.9	14.8	-	80	-	L, P, A (mult.); A (ung.)
NZS151	FD	SA	Pass Ck bridge (Routeburn Track)	S44.81531	E168.13826	693	13-Jan-2009	13:30	15.5	8.6	-	<10	-	L, P (tonnoiri)
NZS152	FD	SA	Borland Burn	S45.74703	E167.38639	954	14-Jan-2009	14:23	15.3	9.1	-	10	-	L, A (mult.); P (tonnoiri); L, A (ung.)
NZS153	FD	SA	Borland Burn	S45.73658	E167.41534	748	14-Jan-2009	16:30	18.6	14.1	-	10	-	L (mult.); A (ung.)
NZS154	FD	SA	Borland Burn	S45.73317	E167.40755	750	16-Jan-2009	11:38	17.3	12.4	-	10	-	P (mult.); L, P (stew.)
NZS155	FD	HC	Lill Burn trib	S45.99939	E167.64885	73	17-Jan-2009	10:30	15.5	12.7	-	125	-	L, P (lat.); P (mult.); L, P (stew.)
NZS156	FD	HC	Alton Burn	S46.11143	E167.68390	40	17-Jan-2009	11:20	17.2	14.9	-	120	0.88	L (lat.); L (stew.); A (ung.); L (vailavoense)
NZS157	FD	HC	Papatotara Coast Rd stm	S46.15628	E167.51268	6	17-Jan-2009	13:37	18.1	13.7	-	90	-	L, P (stew.); A (ung.); L, P (vailavoense)
NZS158	FD	HC	Papatotara Coast Rd gutter	S46.15168	E167.48538	8	17-Jan-2009	14:53	19.6	15.1	-	200	-	L, P (stew.)
NZS159	SL	HC	Granity Stm trib	S46.17780	E167.91415	136	18-Jan-2009	12:15	13.2	10.5	-	60	-	P (lat.); L (stew.); L, A (ung.)
NZS160	SL	SL	Bluff Camp Ground	S46.60412	E168.35098	12	22-Jan-2009	10:00	-	-	-	-	-	A (stew.); A (ung.)
NZS174	WD	WD	Franz Josef (Callery Gorge Track stm)	S43.39502	E170.18797	269	19-Nov-2011	12:30	12.7	10	7.3	60	0.6	L, A (ung.)
NZS175	WD	WD	Franz Josef (Tatare Ck Track stm)	S43.38783	E170.18619	163	19-Nov-2011	14:05	14.8	10.5	7.3	10	-	L (ung.)
NZS176	WD	WD	Franz Josef (Douglas Track stm)	S43.41956	E170.17984	209	20-Nov-2011	11:00	9.6	9.6	7.4	<10	0.88	L (ung.)
NZS177	WD	WD	Robinson Ck (SH6)	S44.08159	E169.37296	471	22-Nov-2011	10:30	8.5	6.1	7.3	<10	-	L, P (unicorne); L (bicorne); A (fiordense)
NZS178	WD	WD	Haast Pass (Davis Flat Track stm)	S44.11381	E169.34329	491	22-Nov-2011	12:00	8.3	7.6	6.8	10	-	L, P (ung.)
NZS179	WD	WD	Haast Pass (Fish R) [Broderick Stm]	S44.11187	E169.33271	572	22-Nov-2011	13:00	9.8	8.2	6.9	10	1.08	L, P (unicorne)
NZS180	OL	HC	Wanaka (Glendhu Bay stm)	S44.67382	E169.02496	326	23-Nov-2011	10:30	17.5	9.6	7.3	90	-	L, P, A (ung.); L, P (mult.)
NZS181	CO	HC	Pass Burn (Lindis Pass summit)	S44.57922	E169.61269	780	23-Nov-2011	13:05	16.1	10.1	6.9	30	1.4	L, P, A (mult.); P (ung.)
NZS182	MB	MP	Black Birch Stm	S41.71968	E173.89124	166	26-Nov-2011	13:46	17.3	13.1	6.9	120	-	L, P, A (till.); A (ung.)
NZS183	MB	MP	Nina Brook (Awatere Valley)	S41.66857	E173.99692	90	26-Nov-2011	15:41	13.1	13.1	6.9	120	-	L, P (aust.); P (till.)
NZS184	MB	MP	Netherwood Stm (Waihopai Valley)	S41.70472	E173.48473	353	27-Nov-2011	11:00	21.0	14.8	7.1	60	0.4	L, P, A (till.)
NZS185	MB	MP	Waihopai R	S41.66129	E173.57173	286	27-Nov-2011	11:34	20.0	15.6	6.6	20	<0.80	L, P, A (till.)
NZS186	NN	NP?	Riwaka (Moss Bush Scenic Reserve)	S41.04832	E172.92395	48	30-Nov-2011	10:56	21.6	14.1	7.3	80	0.70-0.80	L (till.)
NZS187	BR	NP?	Marble Hill campground stm (Springs Junction)	S42.34768	E172.22437	459	2-Dec-2011	16:30	20.3	14.3	6.8	10	-	L (aust.); L (mult.); A (ung.)
NZS188	MB	HC	St James Walkway stm (Lewis Pass)	S42.52197	E172.40768	644	3-Dec-2011	11:30	18.7	9.6	6.7	20	0.7	L (ung.), L (mult.)
NZS189	MB	HC	St James Walkway stm (Lewis Pass)	S42.51912	E172.41524	675	3-Dec-2011	12:59	19.3	13	6.7	<10	0.55	L, P (ung.); L, P (mult.)

Stewart Island

NZS161	SI	SE	Mill Ck (Oban/Halfmoon Bay)	S46.89374	E168.10719	21	22-Jan-2009	15:37	17.8	11.6	-	90	-	L (stew.); A (ung.)
NZS162	SI	SE	Mill Ck (Oban/Halfmoon Bay)	S46.89259	E168.09979	79	23-Jan-2009	10:41	14.1	11.0	-	100	-	L (stew.)
NZS163	SI	SE	Ryans Ck outlet	S46.90168	E168.09068	9	23-Jan-2009	12:44	16.8	11.8	-	130	-	L, P, RA (stew.)
NZS164	SI	SE	Mill Ck (Oban/Halfmoon Bay)	S46.89469	E168.11293	17	24-Jan-2009	11:10	19.6	12.3	-	110	-	L, P (stew.)
NZS165	SI	SE	Vaila Voe Bay stm	S46.90284	E168.10666	21	25-Jan-2009	11:13	16.6	12.9	-	155	-	L (stew.); A (ung.); A (vailavoense)
NZS165a	SI	SE	Vaila Voe Bay stm	S46.90268	E168.10683	20	8-Nov-2011	11:13	10.9	9.6	6.8	80	-	L, P, A (stew.); A (ung.); A (vailavoense)
NZS165b	SI	SE	Vaila Voe Bay stm	S46.90268	E168.10683	20	10-Nov-2011	10:15	10.4	8.9	7.4	60	-	L, P, A (stew.); A (ung.)
NZS166	SI	SE	Magnetic Beach stm	S46.83937	E168.07977	41	26-Jan-2009	11:08	16.0	12.0	-	130	-	L, P (stew.); A (ung.)
NZS167	SI	SE	Sawyers Beach stm	S46.83215	E168.08209	1	26-Jan-2009	12:21	19.3	12.7	-	130	-	L, P, RA (stew.)
NZS167a	SI	SE	Sawyers Beach stm	S46.83218	E168.08203	1	12-Nov-2011	9:06	13.1	9.1	6.6	70	0.30-0.40	L, P, RA (stew.)
NZS168	SI	SE	Little R trib	S46.86249	E168.10915	11	26-Jan-2009	16:00	17.8	12.4	-	130	-	L, P, RA (stew.); A (ung.)
NZS169	SI	SE	Oban/Halfmoon Bay (Kaka Retreat)	S46.89637	E168.12726	34	28-Jan-2009	15:00	-	-	-	-	-	A (stew.); A (ung.)
NZS170	SI	SE	Kaipipi Bay stm	S46.89537	E168.06371	34	30-Jan-2009	12:39	12.4	11.4	-	110	-	L, P, RA (aust.); L, P, RA (stew.)
NZS170a	SI	SE	Kaipipi Bay stm (Gallons Mill stm)	S46.89523	E168.06378	20	14-Nov-2011	12:06	14.6	8	6.4	10	0.20-0.30	L, P, RA (stew.); A (ung.); A (vailavoense)
NZS171	SI	SE	Thule Bay culvert	S46.90292	E168.11856	2	10-Nov-2011	12:08	12.9	9.6	7.3	90	-	L, P, A (stew.); A (ung.)
NZS172	SI	SE	Hicks Road stm	S46.88675	E168.12001	44	11-Nov-2011	11:33	13.2	9.5	7.3	70	-	L, P, RA (stew.); A (ung.); A (vailavoense)
NZS173	SI	SE	Oban/Halfmoon Bay (Bay Motel)	S46.89861	E168.12584	20	11-Nov-2011	14:00	-	-	-	-	-	A (ung.); A (stew.); A (vailavoense)

Appendix 2. Geographic coordinates of main localities in degrees and minutes; Craig & Craig collection locality numbers (Appendix 1) are prefixed with NZN or NZS. Coordinates have been rounded to the nearest minute. The two-letter area codes follow Crosby *et al*. (1976, 1998).

Abbots Ck (SH2), NZN34, WN	41°06’S 175°18’E
Acheron R, NZS131, 131b, MC	43°20’S 171°40’E
Adams Island, Magnetic Cove, AU	50°52’S 166°01’E
Ahipara, ND	35°10’S 173°09’E
Ahuriri R (SH83), NZS20, MK	44°28‘S 169°59’E
Ajax swamp, SL	46°26’S 169°18’E
Akaroa, MC	43°48’S 172°58’E
Akitio R (SH52 bridge), NZN128, WA	40°25’S 176°19’E
Alton Burn, NZS156, FD	46°07’S 167°41’E
Amisfield Burn, CO	44°56’S 169°16’E
Aniwaniwa Stm (Papakorito Falls), NZN54, GB	38°44’S 177°11’E
Annat, MC	43°22’S 171°60’E
Aorere R, NZS97, NN	40°50’S 172°27’E
Aotea, WO	38°01’S 174°49’E
Apakura Stm (SH26, Waiho Forest Reserve), NZN7, CL	37°13’S 175°40’E
Araparera R, NZN73, AK	36°28’S 174°33’E
Arthurs Pass (Bridal Veil Falls track), NC	42°56’S 171°34’E
Arthurs Pass (Jacks Hut), NC	42°55’S 171°34’E
Arthurs Pass, NC	42°54’S 171°34’E
Ashburton Gorge (bridge), MC	43°38’S 171°12’E
Ashley Gorge, NC	43°14’S 172°14’E
Ashley R (SH1 bridge), NZS61, NC	43°17’S 172°41’E
Auckland Island, AU	50°41’S 166°07’E
Aurora Ck, SL	46°30’S 169°27’E
Awarua R (Twin Bridges), NZN82, ND	35°37’S 173°51’E
Awatere R (SH35 bridge), NZN64, GB	37°40’S 178°21’E
Awatere R Valley (Molesworth), MB	42°05’S 173°16’E

Bainham, NN	40°46’S 172°34’E
Baker Ck (Karamea), NN	41°15’S 172°08’E
Ballance stm, WN	40°24’S 175°46’E
Balloon Hut (Mt Arthur), NN	41°10’S 172°37’E
Barryville stm, TO	38°29’S 175°34’E
Beaumont R, CO	45°49’S 169°32’E
Beeman Camp shore, CA	52°33’S 169°09’E
Ben Ohau, MK	44°15’S 169°54’E
Bendigo Ck (ditch), CO	44°56’S 169°21’E
Bethells Beach (Te Henga), AK	36°53’S 174°27’E
Bethunes Gully, DN	45°50’S 170°33’E
Big South Cape Island (Murderers Cove), SI	47°15’S 167°25’E
Big South Cape Island (Potted Head Ck), SI	47°14’S 167°25’E
Birch Hill Stm (SH80), NZS128, MK	43°48’S 170°05’E
Black Birch Stm, NZS182, MB	41°43’S 173°53’E
Black Gully (Tapanui), SL	45°54’S 169°21’E
Black Valley Stm, NZS88, BR	41°48’S 172°51’E
Blenheim, MB	41°31’S 173°57’E
Blue Rock Stm, NZN87, WA	41°20’S 175°23’E
Bluff Camp Ground, NZS160, SL	46°36’S 168°21’E
Borland Burn, NZS152, FD	45°45’S 167°23’E
Borland Burn, NZS153, FD	45°44’S 167°25’E
Borland Burn, NZS154, FD	45°44’S 167°24’E
Bowyers Stm, NZS16, MC	43°44’S 171°32’E
Boyle R (SH7), NZS64, MB	42°31’S 172°23’E
Broadwood, ND	35°15’S 173°23’E
Brookby, AK	37°00’S 175°00’E
Broken R (SH73 bridge), MC	43°12’S 171°44’E
Brown Ck, NZS81, NN	41°53’S 171°55’E
Buller R (bridge), WD	41°46’S 171°36’E
Buller R (Gowanbridge), NZS85, BR	41°43’S 172°34’E
Buller R (Harleys Rock), BR	41°42’S 172°39’E
Buller R trib (Glenhope Scenic Reserve), NN	41°42’S 172°38’E
Bulls, WI	40°10’S 175°23’E
Bush Ck trib, MK	43°52’S 170°06’E
Butchers Ck headwaters, NZS39, CO	45°21’S 169°14’E

Cable Bay, NN	41°10’S 173°25’E
Caddon Burn, NZS29, SL	46°27’S 169°05’E
Cambrians, CO	44°54’S 169°45’E
Camp Cove stm, CA	52°33’S 169°08’E
Campbell Island, CA	52°33’S 169°09’E
Camping Gully ck, NZS119, MC	43°32’S 171°40’E
Candle Ck, NZS77, NN	41°09’S 172°06’E
Cardrona R, NZS143, OL	44°57’S 168°58’E
Cascades Stm, AK	36°53’S 174°31’E
Catlins R trib, SL	46°20’S 169°19’E
Catlins R, NZS27, 27a, SL	46°27’S 169°29’E
Cave Stm (Broken R Ski Field), NC	43°09’S 171°44’E
Cave Stm (cave exit), MC	43°12’S 171°45’E
Christmas Village Bay stm, SI	46°45’S 167°59’E
Christmas Village Hut, SI	46°45’S 167°59’E
Clarke R (Hope Saddle), NN	41°37’S 172°44’E
Clutha R (now Clyde Dam site), CO	45°10’S 169°18’E
Clutha R, Kawarau R confluence (now L Dunstan), CO	45°03’S 169°13’E
Coal Ck, NN	41°49’S 171°38’E
Cobb R trib, NZS94, NN	41°08’S 172°36’E
Cobb R trib, runnel, NZS95, NN	41°07’S 172°36’E
Cobb R, NZS93, NN	41°08’S 172°37’E
Coleridge Stm, MC	43°20’S 171°36’E
Conway R (SH1), NZS118, KA	42°36’S 173°25’E
Cooks Ck, NZS98, NN	40°46’S 172°34’E
Coopers Creek, NC	43°17’S 172°06’E
Copland R (Welcome Flat), WD	43°38’S 169°58’E
Coromandel, CL	37°08’S 175°33’E
Craigieburn (SH73), NZS55, NC	43°08’S 171°45’E
Cross Ck (L Wairarapa), WA	41°10’S 175°15’E
Croydon Bush (Gore), SL	46°04’S 168°53’E
Culverden, NC	42°47’S 172°51’E

Dannevirke, WA	40°13’S 176°07’E
Danseys Pass, CO	44°57’S 170°22’E
Davis Point, CA	52°33’S 169°14’E
Deadmans Ck, NN	41°45’S 171°41’E
Deas Cove Stm, AU	50°31’S 166°13’E
Deep Stm trib (Tent Hut), CO	45°40’S 169°52’E
Divide Ck (Routeburn Track), NZS148, FD	44°49’S 168°07’E
Divide Ck, NZS33, FD	44°48’S 168°07’E
Dixon-Waikorea Road (ditch), NZN16, WO	37°35’S 174°53’E
Doctor Ck, NZS83, BR	41°45’S 172°24’E
Dog Stm (SH7a), NZS63, MB	42°32’S 172°50’E

Dome Burn, SL	45°45’S 168°49’E
Doubtful R hut, NC	42°32’S 172°17’E
Duck Ck (Mason Bay), SI	46°56’S 167°47’E
Dundas Hut, WN	40°43’S 175°28’E
Dunedin Motorway (SH1), DN	45°49’S 170°31’E
Dunsdale Stm, SL	46°11’S 168°36’E
Dunsdale, SL	46°07’S 168°37’E
D’Urville R (L Rotoroa), BR	41°55’S 172°39’E
Eltham (Waingongoro R trib), TK	39°25’S 174°14’E
Enderby Island (Teal L outlet), AU	50°30’S 166°17’E
Enderby Island, AU	50°30’S 166°17’E
Esk R, NZN51, HB	39°21’S 176°49’E
Eskdale stm, HB	39°24’S 176°49’E
Evans Flat, DN	45°54’S 169°38’E
Fairlie, SC	44°06’S 170°49’E
Fairy Falls Stm, NZN94, AK	36°55’S 174°33’E
Featherston, WA	41°07’S 175°20’E
Fern Burn [Jack Hall stm], NZS142, OL	44°40’S 169°00’E
Firewood Ck (Ngaruawahia), NZN12, WO	37°41’S 175°07’E
Fleming R, SL	46°35’S 169°25’E
Flora Stm, NZS91, NN	41°11’S 172°44’E
Flowery Ck, BR	42°40’S 171°03’E
Foggy Peak Ridge stm (SH73), NZS134, MC	43°18’S 171°45’E
Foggy Peak Ridge stm (SH73), NZS57, 57a, 57b, NC	43°18’S 171°43’E
Foleys Ck, BR	42°24’S 172°24’E
Forest Ck (Rangitata R Valley), NZS125, SC	43°41’S 170°58’E
Fork Stm (SH8 bridge), NZS18, 18a, MK	44°00’S 170°25’E
Fossil Ck, NZS96, NN	40°51’S 172°27’E
Fox R trib (Fox Glacier), NZS48, WD	43°29’S 170°02’E
Franz Josef (Callery Gorge Track stm), NZS174, WD	43°24’S 170°11’E
Franz Josef (Douglas Track stm), NZS176, WD	43°25’S 170°11’E
Franz Josef (Tatare Ck Track stm), NZS175, WD	43°23’S 170°11’E
Franz Josef Glacier ck, NZS49, 49a, WD	43°25’S 170°10’E
Fraser R headwater, NZS40, CO	45°19’S 169°12’E
Fraser R headwaters, NZS41, CO	45°21’S 169°12’E
Freds Stm trib (SH80), NZS127, MK	43°50’S 170°06’E
Freds Stm trib (SH80), NZS129, 130, MK	43°50’S 170°05’E
French Farm Bay stm, MC	43°47’S 172°54’E
Freshwater Hut, SI	46°52’S 167°55’E
Fuchsia Stm, MB	41°42’S 173°11’E
Gabriels Gully, CO	45°54’S 169°41’E
Garden Cove stm, CA	52°34’S 169°09’E
Gertrude Valley stm, NZS145, FD	44°45’S 168°01’E
Glaisnock R, FD	44°59’S 167°41’E
Glen Eden, AK	36°55’S 174°39’E
Glen Esk Stm, NZN93, AK	36°57’S 174°29’E
Glendhu Bay (L Wanaka), OL	44°41’S 169°02’E
Glengary Stm, NZS25, CO	45°41’S 170°00’E
Glenhope (SH6), NN	41°39’S 172°39’E
Glentanner, MK	43°55’S 170°07’E
Glentui R, NC	43°13’S 172°16’E
Gorge Ck, CO	45°23’S 169°16’E
Graham Stm (SH6), NZS106, NN	41°11’S 173°29’E
Granity Stm trib, NZS159, SL	46°11’S 167°55’E
Grasmere Stm (Cass), NZS54, NC	43°02’S 171°45’E
Great Barrier Island, CL	36°11’S 175°24’E
Great Barrier Island, Katherine Bay, CL	36°07’S 175°22’E
Great Barrier Island, Okiwi, CL	36°09’S 175°24’E
Great Barrier Island, Port Fitzroy, CL	36°10’S 175°22’E
Green Burn, NZS12, KA	42°24’S 173°24’E
Green Hills Stm, NZS99, NN	40°31’S 172°39’E
Grey Duck Ck, AU	50°34’S 166°10’E
Grey R (SH7 bridge), NZS69, BR	42°17’S 171°40’E
Haast (gorge), WD	44°02’S 169°23’E
Haast Pass (Davis Flat Track stm), NZS178, WD	44°07’S 169°21’E
Haast Pass (Fish R) [Broderick Stm], NZS179, WD	44°07’S 169°20’E
Haast, WD	43°53’S 169°02’E
Hakataramea R (Wrights Crossing), SC	44°40’S 170°36’E
Haldon, MK	44°21’S 170°16’E
Hamiltons Gap stm, AK	37°08’S 174°34’E
Hamner, NC	42°31’S 172°50’E
Hamua, WA	40°34’S 175°45’E
Hanmer Springs, MB	42°32’S 172°50’E
Harihari, WD	43°09’S 170°33’E
Harleys Rock (ditch), NN	41°42’S 172°39’E
Hatea R (A H Reed Kauri Park), NZN83, ND	35°41’S 174°20’E
Hautapu R (SH1 bridge), NZN85, RI	39°39’S 175°46’E
Hautapu R, NZN109, TO	39°33’S 175°41’E
Hautu Prison Camp, TO	38°60’S 175°51’E
Hauturu/Little Barrier Island (Maraeroa), CL	36°13’S 175°03’E
Havelock R (between Totara Point & Big Fan Ck), MC	43°26’S 170°43’E
Hawdon R, NC	42°59’S 171°45’E
Hawkins R (Sheffield), MC	43°24’S 172°01’E
Hawkswood, KA	42°40’S 173°19’E
Heao Stm trib, TK	38°57’S 174°57’E
Heaphy Track (Karamea), NN	41°01’S 172°07’E
Helena Bay, AK	35°26’S 174°21’E
Helensville, AK	36°41’S 174°27’E
Henderson, AK	36°53’S 174°38’E
Herekino, ND	35°16’S 173°13’E
Hicks Road stm, NZS172, SI	46°53’S 168°07’E
Hihitahi, RI	39°34’S 175°42’E
Hinemaiaia R (Hatepe), TO	38°51’S 176°01’E
Hira, NN	41°13’S 173°23’E
Hollyford R (Gunns Camp), NZS147, OL	44°46’S 168°08’E
Hollyford R (SH94), FD	44°47’S 168°01’E
Hollyford R (trib), NZS146, OL	44°40’S 168°08’E
Hollyford R (trib), NZS149, OL	44°49’S 168°08’E
Homer Saddle, FD	44°46’S 167°59’E
Homer Tunnel (Cleddau R South Branch), NZS144, FD	44°46’S 167°58’E
Homer Tunnel stm (SH94), NZS32, 32a, OL	44°46’S 167°59’E
Homer Tunnel, FD	44°46’S 167°59’E
Hook R, SC	44°40’S 171°02’E
Hoophorn Stm, MK	43°46’S 170°06’E
Hope R (SH6 and 63 junction), NZS86, BR	41°42’S 172°37’E
Hope R (SH6), NN	41°21’S 173°09’E

Hope Stm, CL	36°34’S 175°24’E
Houhora, ND	34°48’S 173°06’E
Houpoto Stm, NZN66, BP	37°52’S 177°36’E
Huatoki Stm, TK	39°07’S 174°04’E
Hunterville, RI	39°56’S 175°34’E
Hunts Beach Rd, WD	43°33’S 169°41’E
Hurstlea farm (Meyers Pass Road), SC	44°39’S 170°41’E
Hutt R, WN	41°07’S 175°03’E
Inaha Stm, TK	39°34’S 174°10’E
Inangahua R (Rahu Saddle), NZS67, BR	42°18’S 172°06’E
Inangahua R (SH7 Reefton), NZS68, BR	42°07’S 171°52’E
Inangatahi Stm (Puketitiri), HB	39°17’S 176°32’E
Irongate Stm trib, NZS117, KA	42°15’S 173°47’E
Jacks Pass, NC	42°28’S 172°50’E
Jackson Bay stm, WD	43°58’S 168°37’E
Jackson Bay, NZS45, WD	43°58’S 168°37’E
Jacobs R (Makawhio R.), WD	43°34’S 169°41’E
Jones Ck, NZS74, NN	41°40’S 171°49’E
Kaeo R (Waiare Road), NZN99, ND	35°07’S 173°48’E
Kaeo, ND	35°06’S 173°47’E
Kahutara R (Inland Kaikoura Route), KA	42°23’S 173°27’E
Kaihu R (SH12, near Ahikiwi), NZN75, ND	35°48’S 173°44’E
Kaikai Beach, ND	35°35’S 173°25’E
Kaikoura, KA	42°25’S 173°41’E
Kaipipi Bay stm (Gallons Mill stm), NZS170, 170a, SI	46°54’S 168°04’E
Kaituna R (upper), NZS135, MC	43°43’S 172°45’E
Kaituna R, NZS60, MC	43°45’S 172°41’E
Kakahi Stm trib (Owhango), TO	38°59’S 175°22’E
Kakaho Stm, NZN22, TO	38°34’S 175°43’E
Kakekino Stm, NZN45, HB	39°24’S 176°18’E
Kaniere R, WD	42°45’S 171°03’E
Kapoaiaia Stm, TK	39°17’S 173°54’E
Karamea, NN	41°15’S 172°07’E
Karangarua, WD	43°32’S 169°50’E
Karioi, TO	39°27’S 175°30’E
Kauaeranga R (Park HQ), NZN2, CL	37°07’S 175°38’E
Kaukore Stm (bridge, Pipiriki), NZN122, RI	39°29’S 175°03’E
Kaupokonui Stm, TK	39°33’S 174°04’E
Kawaka Stm trib, ND	35°33’S 173°50’E
Kawakawa R trib, ND	35°23’S 174°05’E
Kawerau, BP	38°05’S 176°43’E
Kawhaka Ck, NZS50, WD	42°44’S 171°10’E
Kekerenga R, NZS9, KA	42°00’S 174°01’E
Kekerengu, KA	42°00’S 173°60’E
Kelceys Bush, SC	44°42’S 170°58’E
Kenepuru Head stm, NZS2, 2a, SD	41°10’S 174°07’E
Kiore, TK	39°14’S 174°32’E
Knights Point, NZS45a, 45b, WD	43°43’S 169°14’E
Kohaihai R (Heaphy Track), NZS76, NN	41°07’S 172°06’E
Kohukohu, ND	35°22’S 173°32’E
Kokowai Stm, NZN114, TK	39°15’S 174°06’E
Kopai Stm, ND	35°39’S 173°35’E
Kowai Bush (Springfield), MC	43°18’S 171°55’E
Kowai R (SH73), MC	43°19’S 171°46’E
Kowhai R (SH1 bridge), NZS11, KA	42°25’S 173°38’E
Kowhai R trib, NZS110, 111, KA	42°20’S 173°33’E
Kumara (SH73 straight) BR	42°37’S 171°10’E
Kye Burn trib, NZS24, CO	44°57’S 170°21’E
Kyeburn (SH85), CO	45°09’S 170°16’E
L Hawea (Beachmere Camp), OL	44°37’S 169°16’E
L Heron (Emily Stm), NZS123, MC	43°33’S 171°12’E
L Heron (Gentleman Smith Stm), NZS136, MC	43°32’S 171°11’E
L Heron (Olliver Stm), NZS122, 122a, MC	43°30’S 171°09’E
L Howden outlet, NZS150, OL	44°49’S 168°08’E
L Ianthe (Matahi), WD	43°03’S 170°37’E
L Janet (Mt Grey), NC	43°08’S 172°33’E
L Manapouri, FD	45°34’S 167°37’E
L Mapourika, WD	43°19’S 170°12’E
L Marchant, FD	45°03’S 167°20’E
L Pukaki stm, MK	43°58’S 170°10’E
L Rotoiti (Mt Robert ski club hut stm), NN	41°51’S 172°48’E
L Rotoiti stm, BR	41°50’S 172°51’E
L Rotowhero stm, BP	38°19’S 176°22’E
L Wahapo, WD	43°15’S 170°16’E
L Wakatipu (near Wye Ck), OL	45°08’S 168°45’E
Lawyer Ck, WD	42°53’S 171°03’E
Lee Bay, SI	46°52’S 168°07’E
Lee R (Brightwater), NN	41°26’S 173°09’E
Lee Stm (SH87 bridge), NZS26, DN	45°48’S 170°08’E
Lewis Pass, BR	42°23’S 172°24’E
Lill Burn trib, NZS155, FD	45°60’S 167°39’E
Lincoln, MC	43°38’S 172°29’E
Lindis Pass, CO	44°35’S 169°38’E
Lindis R (SH8), NZS44, CO	44°53’S 169°21’E
Lindis Valley (Long Acre), CO	44°46’S 169°31’E
Lindsay Ck (Bethunes Gully), DN	45°50’S 170°33’E
Little R trib, NZS168, SI	46°52’S 168°07’E
Little River, MC	43°46’S 172°48’E
Little Ten Mile Ck [Fuschia Ck], NZS80, NN	41°50’S 171°41’E
Little Wanganui R (Te Namu), NZS79, NN	41°23’S 172°06’E
Logan Basin, WN	40°43’S 175°27’E
London Ck, NZS8, KA	41°49’S 174°10’E
Lookout Bay stm, CA	52°32’S 169°10’E
Low Burn, CO	44°60’S 169°12’E
Lumsden, SL	45°44’S 168°26’E
Lyell Ck, NZS82, NN	41°48’S 172°03’E
Maclennan, SL	46°32’S 169°28’E
Magnetic Beach stm, NZS166, SI	46°50’S 168°05’E
Mahinapua Ck, WD	42°45’S 170°56’E
Mahitahi R, WD	43°36’S 169°35’E
Mahurangi R trib [Mill Stm], Kowhai Park Scenic Reserve, NZN74, 74a, AK	36°24’S 174°40’E
Maimai Ck, NZS46, WD	43°34’S 169°48’E
Maitai R fork, NN	41°17’S 173°22’E
Maitai R, NZS6, NN	41°16’S 173°18’E
Makakahi R, NZN35, WA	40°42’S 175°39’E
Makakikatoa Stm, TO	39°23’S 175°40’E
Makarewa R, SL	46°12’S 168°31’E
Makarora R (SH6), FD	44°08’S 169°20’E
Makotuku R (Raetihi), RI	39°25’S 175°17’E
Manawatu R (SH2 Norsewood), NZN38, RI	40°03’S 176°14’E

Mangaemiemi Stm, NZN115, TK	39°03’S 174°08’E
Mangahauini R, NZN62, GB	38°07’S 178°17’E
Mangaheia R (Five Bridges), NZN61, GB	38°20’S 178°10’E
Mangaio Stm, NZN48, 48a, 48b, 48c, TO	39°19’S 175°44’E
Mangakahia R trib, ND	35°36’S 173°43’E
Mangamawhete Stm, NZN25, TK	39°15’S 174°13’E
Mangamuka R (SH1, Raiatea Forest), NZN80, 80a, ND	35°12’S 173°29’E
Mangamuka, ND	35°14’S 173°33’E
Manganuiowae Stm (Broadwood), NZN78, ND	35°16’S 173°24’E
Mangaokahu Stm (Cogswell Road), NZN13, WO	37°48’S 175°02’E
Mangaonuku Stm (SH50), HB	39°43’S 176°30’E
Mangaora Stm (bridge Aotea), NZN15, WO	37°60’S 174°53’E
Mangapohue Stm (Natural tunnel), NZN19, WO	38°16’S 174°54’E
Mangapurua Stm trib (Bridge to Nowhere), NZN121, RI	39°16’S 174°58’E
Mangarakau Stm, NN	40°38’S 172°33’E
Mangatangi Stm (Hunua Ra), NZN11, AK	37°08’S 175°13’E
Mangateitei Stm (Ohakune), NZN47, 120, TO	39°25’S 175°24’E
Mangatepopo Stm trib (SH47 bridge), NZN107, TO	39°04’S 175°34’E
Mangatepopo Stm trib, NZN105, TO	39°09’S 175°35’E
Mangatepopo Stm trib, NZN84, 84a, TO	39°08’S 175°34’E
Mangatoa Stm (Mangatoa Scenic Reserve), NZN20, WO	38°26’S 174°42’E
Mangatoetoenui Stm, NZN49, 49a, 49b, TO	39°14’S 175°44’E
Mangatora R trib, NZN37, WA	40°16’S 176°13’E
Mangatoromiro Stm, NZN117, TK	39°26’S 174°30’E
Mangawhararariki R trib, NZN31, RI	39°50’S 175°53’E
Mangawhero R (upper), NZN92, TO	39°21’S 175°28’E
Mangawhero R trib, NZN108, TO	39°25’S 175°24’E
Manson Ck, NC	43°08’S 171°46’E
Manuherikia R (SH85), NZS38, CO	45°15’S 169°24’E
Manuka Gorge (SH8), DN	46°02’S 169°48’E
Manuka Gorge, SL	46°04’S 169°49’E
Mapiu Stm (Omaru Falls), NZN21, WO	38°31’S 175°09’E
Maraehako Stm, NZN65, BP	37°40’S 177°48’E
Maraehara R, NZN63, GB	37°44’S 178°22’E
Maraetotara R, NZN127, HB	39°45’S 176°57’E
Marble Hill campground stm (Springs Junction), NZS65, 187, BR	42°21’S 172°13’E
Maruia Cascade stm (SH65), BR	41°52’S 172°15’E
Maruia Springs, NC	42°23’S 172°20’E
Maruia stm (SH65), BR	42°11’S 172°13’E
Mary Burn, SL	46°28’S 169°12’E
Mason Bay Hut, SI	46°56’S 167°47’E
Mason Bay, SI	46°56’S 167°48’E
Mason R (SH70), NZS13, 13a, KA	42°30’S 173°10’E
Masterton, WA	40°58’S 175°40’E
Matai Stm (falls), NZS28, SL	46°30’S 169°29’E
Matamata, WO	37°48’S 175°46’E
Matariki Stm, ND	35°30’S 173°25’E
Mataura R (Gore), SL	46°04’S 168°56’E
Mataura R trib [Parawa Stm], NZS36, CO	45°33’S 168°32’E
Matuku Reserve, AK	36°52’S 174°29’E
Maungatapu Road near Pelorus Bridge (ditch), NZS115, 115a, MB	41°19’S 173°30’E
Menzies Bay, MC	43°39’S 172°58’E
Methven, MC	43°37’S 171°42’E
Middle Cove stm, CA	52°33’S 169°05’E
Mihi, TO	38°29’S 176°17’E
Milburns Pond (Victoria Dam), CO	45°53’S 169°40’E
Milford Sound, FD	44°40’S 167°56’E
Mill Ck (Oban), NZS161, 162, SI	46°54’S 168°06’E
Mill Ck (Oban), NZS164, SI	46°54’S 168°07’E
Mill Ck (SH6 Greymouth), NZS70, BR	42°29’S 171°11’E
Mimiha Stm, BP	37°53’S 176°42’E
Mirowharara Stm, ND	35°40’S 173°34’E
Momorangi Bay stm, NZS114, SD	41°16’S 173°56’E
Mororimu Stm (SH1), NZS10, KA	42°13’S 173°52’E
Morrinsville, WO	37°39’S 175°31’E
Mossburn, SL	45°40’S 168°13’E
Motueka R, NZS90, NN	41°17’S 172°49’E
Motupiko R, NZS89, NN	41°37’S 172°48’E
Mount Peel, SC	43°52’S 171°10’E
Mt Cook (Godley Hut), MK	43°29’S 170°31’E
Mt Dumas stm, CA	52°34’S 169°06’E
Mt Herbert, MC	43°42’S 172°44’E
Mt Honey stm, CA	52°34’S 169°11’E
Mt Hutt ski field (water supply), MC	43°30’S 171°32’E
Mt Hutt ski field road, MC	43°32’S 171°33’E
Mt Ruapehu (Blyth Track, Rotokawa), NZN119, TO	39°20’S 175°30’E
Mt Ruapehu seepage (Silica Rapids track), NZN126, 126a, TO	39°13’S 175°32’E
Mt Ruapehu seepage (Upper Round Mt track), NZN123, 123a, TO	39°14’S 175°32’E
Mt Ruapehu, Waikare Stm trib (Silica Rapids), NZN125, TO	39°13’S 175°32’E
Mt Somers stm, MC	43°40’S 171°23’E
Mt Taranaki (South Hut), TK	39°20’S 174°04’E
Mt Tongariro, Soda Springs seepages (Mangatepopo Stm), NZN124, TO	39°08’S 175°38’E
Muriwai (SH2), GB	38°45’S 177°55’E
Neils Beach stm (Jackson Bay), WD	43°60’S 168°39’E
Neils Beach, WD	43°60’S 168°40’E
Netherwood Stm (Waihopai Valley), NZS184, MB	41°42’S 173°29’E
Ngakuta Bay stm, NZS1, SD	41°16’S 173°58’E
Ngaruroro R trib, NZN43, HB	39°23’S 176°20’E
Ngaruroro R, NZN44, HB	39°23’S 176°20’E
Ngataki Stm, ND	34°44’S 173°03’E
Nihotupu, AK	36°57’S 174°35’E
Nina Brook (Awatere Valley), NZS183, MB	41°40’S 173°60’E
Nine Mile Ck (SH8), NZS43, CO	45°05’S 169°16’E
North Arm Hut, SI	46°53’S 168°01’E
North Branch Ashburton R (Thompsons Track), NZS15, MC	43°44’S 171°35’E
North Cape, ND	34°24’S 173°01’E
Northeast Harbour, CA	52°31’S 169°11’E
Norton Stm, CA	52°33’S 169°04’E
Oban (Bay Motel), NZS173, SI	46°54’S 168°08’E

Oban (hotel), SI	46°54’S 168°08’E
Oban (Kaka Retreat), NZS169, SI	46°54’S 168°08’E
Obelisk Ck irrigation ditch, NZS42, CO	45°20’S 169°17’E
Ohakune Lakes Reserve, RI	39°26’S 175°23’E
Ohakune, RI	39°25’S 175°24’E
Ohinetaha Bay stm, NZS3, SD	41°14’S 173°55’E
Ohau R, NZN89, WN	40°40’S 175°14’E
Ohau Stm (SH1), NZS109, KA	42°15’S 173°50’E
Ohaupara Stm, NZN70, BP	37°58’S 176°10’E
Ohikanui R (SH6 bridge), BR	41°51’S 171°43’E
Ohinemuri R (SH2, Waikino), NZN72, CL	37°25’S 175°46’E
Ohiwa Stm trib, NZN41, HB	39°33’S 176°42’E
Okarito R, WD	43°13’S 170°10’E
Okeover Stm, NZS14, MC	43°31’S 172°35’E
Okiwi Bay (SH1), KA	42°13’S 173°52’E
Okohua Stm, WO	38°18’S 175°03’E
Okuku R, NC	43°03’S 172°21’E
Old Man Range (top), CO	45°19’S 169°12’E
Old Man Range, CO	45°19’S 169°12’E
Omahu (SH50), HB	39°35’S 176°45’E
Omahuta, ND	35°14’S 173°38’E
O’Malley Ck, BR	41°50’S 171°33’E
Omapere, ND	35°32’S 173°23’E
Omaukora Stm (SH2 bridge), NZN59, BP	38°16’S 177°20’E
Omeru Falls Stm, NZN101, AK	36°33’S 174°29’E
Ongaonga, HB	39°55’S 176°25’E
Ongo Stm (SH1), NZN29, WI	39°58’S 175°31’E
Opara Stm, NZS59, MC	43°44’S 173°00’E
Opihi R (Burkes Pass), SC	44°02’S 170°42’E
Opotiki, BP	38°00’S 177°18’E
Opuha R (SH79), NZS17, SC	44°05’S 170°59’E
Orere Stm (bridge), NZN10, AK	36°59’S 175°11’E
Orowaiti R trib, NN	41°48’S 171°38’E
Otaio R, SC	44°33’S 171°11’E
Otakeho Stm, NZN27, TK	39°26’S 174°04’E
Otaki R (Otaki Forks), WN	40°52’S 175°14’E
Otaratiri Stm trib (Moerangi Station), NZN116, TO	39°57’S 175°36’E
Otaratiri Stm trib, ditch (Moerangi Station), NZN111, 111a, TO	38°57’S 175°36’E
Otaratiri Stm trib, NZN112, TO	38°57’S 175°35’E
Otautau, SL	46°09’S 168°00’E
Otira R (SH73), NC	42°50’S 171°34’E
Otira R (upper), NZS140, MC	42°54’S 171°32’E
Otira, WD	42°50’S 171°34’E
Owaka, SL	46°26’S 169°39’E
Owen R (SH6), NZS84, BR	41°41’S 172°27’E

Paetahi Stm & Patea R junction, NZN113, TK	39°21’S 174°17’E
Pahau R (SH7 bridge), NZS62, 112, NC	42°48’S 172°50’E
Pahiatua, WN	40°27’S 175°50’E
Pakawau-Puponga, NN	40°33’S 172°42’E
Pakoka R, NZN14, WO	37°55’S 174°54’E
Pakuratahi R (SH2), NZN88, WN	41°05’S 175°12’E
Pandora Bush stm, ND	34°27’S 172°46’E
Pangarara Stm, TO	39°12’S 175°45’E
Papamanuka Stm (SH47 bridge), NZN106, TO	39°08’S 175°31’E
Papatotara Coast Rd gutter, NZS158, FD	46°09’S 167°29’E
Papatotara Coast Rd stm, NZS157, FD	46°09’S 167°31’E
Pareora Gorge, SC	44°24’S 171°01’E
Pareora R Gorge, SC	44°40’S 171°02’E
Park Burn, CO	44°57’S 169°15’E
Pass Burn (Lindis Pass summit), NZS181, CO	44°35’S 169°37’E
Pass Burn, CO	44°35’S 169°38’E
Pass Ck bridge (Routeburn Track), NZS151, FD	44°49’S 168°08’E
Paturau R, NZS100, NN	40°39’S 172°27’E
Peel Forest stm, SC	43°53’S 171°16’E
Peel Forest, SC	43°54’S 171°14’E
Pegleg Ck (SH73 above bridge), NZS132, 132a, NC	42°54’S 171°34’E
Pelorus R, NZS5, MB	41°18’S 173°35’E
Peria R, ND	35°07’S 173°29’E
Pigroot Ck (SH85), CO	45°12’S 170°26’E
Piha Stm, AK	36°57’S 174°30’E
Piha, AK	36°57’S 174°28’E
Pilbrow Hill, ND	36°04’S 174°25’E
Pohara, NN	40°50’S 172°53’E
Pokaka stm, TO	39°17’S 175°23’E
Pomahaka Railway Station, SL	46°01’S 169°14’E
Poorman Valley Stm (bridge), NZS116, NN	41°19’S 173°14’E
Poorman Valley Stm, NZS7, NN	41°19’S 173°15’E
Porika Stm, BR	41°46’S 172°40’E
Port Pegasus, SI	47°10’S 167°42’E
Port William, SI	46°50’S 168°05’E
Porter R (SH73), NZS56, NC	43°17’S 171°40’E
Porters Pass summit stm, MC	43°18’S 171°44’E
Porters Pass, MC	43°18’S 171°44’E
Potts R (Erewhon), MC	43°35’S 170°56’E
Pounawea, SL	46°28’S 169°41’E
Pudding Hill Stm, NZS120, MC	43°35’S 171°32’E
Puhi Puhi R trib, NZS108, 108a, KA	42°15’S 173°45’E
Pukeatua Stm trib, NZN129, WA	40°52’S 176°10’E
Puketapu, HB	39°31’S 176°48’E
Puketi Forest, NZN95, ND	35°17’S 173°41’E
Puketona, ND	35°18’S 173°58’E
Punakaiki Campground, BR	42°07’S 171°20’E
Punakaiki R (SH6 bridge), NZS72, BR	42°07’S 171°20’E
Purakanui Fall’S DN	45°47’S 170°37’E
Purakaunui R, SL	46°31’S 169°34’E
Purau, MC	43°39’S 172°45’E

Rahu R (Springs Junction), NZS66, BR	42°20’S 172°09’E
Rakaia R (Totara Point), MC	43°17’S 171°04’E
Rakeahua Hut ck, SI	46°59’S 167°53’E
Rakeahua R, SI	46°59’S 167°52’E
Rangitikei R (Mangaweka), NZN30, RI	39°49’S 175°48’E
Rangitikei R (Mokai Road), NZN91, RI	39°42’S 175°58’E
Rangitukia Stm (Pirongia), NZN17, WO	37°57’S 175°07’E
Ranui Cove, AU	50°32’S 166°16’E
Rawene, ND	35°26’S 173°30’E
Red Stm (Little Red Hill), FD	44°22’S 168°17’E
Reefton, BR	42°07’S 171°52’E
Ribbonwood Ck (SH6), NZS47, WD	43°29’S 169°59’E
Riordans Ck, BR	42°27’S 172°24’E
Riwaka (Moss Bush Scenic Reserve), NZS186, NN	41°03’S 172°55’E
Roaring Meg (SH6), NZS37, CO	45°00’S 169°04’E

Robert Stm, NZS87, BR	41°50’S 172°49’E
Robinson Ck (SH6), NZS177, WD	44°05’S 169°22’E
Rock Ck, SL	45°31’S 170°07’E
Rockville (Collingwood), NN	40°44’S 172°38’E
Roding R (upper), NZS104, NN	41°22’S 173°18’E
Roding R, NZS105, NN	41°22’S 173°14’E
Rotherham, NC	42°42’S 172°56’E
Rotoroa Camping Ground, BR	41°48’S 172°36’E
Ruatoria, GB	37°53’S 178°19’E
Ryans Ck outlet, NZS163, SI	46°54’S 168°05’E
Ryton R (L Coleridge), MC	43°17’S 171°33’E

Saddle Hill (George Sound), FD	44°60’S 167°25’E
Salisbury Hut (Mt Arthur), NN	41°11’S 172°39’E
Saltwater Creek, NC	43°15’S 172°41’E
Sandel Ck (SH67 Karamea Bluff), NZS75, NN	41°31’S 172°01’E
Sawyer Stm (SH80), MK	43°46’S 170°07’E
Sawyers Beach stm, NZS167, 167a, SI	46°50’S 168°05’E
Sawyers Beach, SI	46°50’S 168°05’E
Sawyers Ck, BR	42°38’S 171°04’E
Scour Stm (Rangitata R Valley), NZS124, SC	43°39’S 170°55’E
Selwyn R (Glentunnel), MC	43°29’S 171°56’E
Selwyn R (Springston), MC	43°42’S 172°25’E
Shag Point stm, CA	52°35’S 169°13’E
Shepherds Ck, CO	45°08’S 169°09’E
Silver Stm, DN	45°51’S 170°23’E
Silverdale, AK	36°37’S 174°40’E
Simonin Stm, FD	44°21’S 168°20’E
Six Mile Stm bridge, MB	41°44’S 173°02’E
Skerrits Ck, WN	41°17’S 174°58’E
Smoothwater Bay stm, CA	52°32’S 169°14’E
Snowy Ck (Headlong Peak), OL	44°32’S 168°38’E
Soup Ck (Rangitata R Valley), NZS126, 126a, SC	43°44’S 171°07’E
South Bay (SH1), KA	42°25’S 173°40’E
South Branch Ashburton R, NZS137, MC	43°35’S 171°10’E
Spotswood, NC	42°44’S 173°16’E
Springbank, MC	43°18’S 172°26’E
Springston (drain), MC	43°41’S 172°25’E
Spy R, NC	42°59’S 172°54’E
St Arnaud, BR	41°48’S 172°51’E
St James Walkway stm (Lewis Pass), NZS188, MB	42°31’S 172°24’E
St James Walkway stm (Lewis Pass), NZS189, MB	42°31’S 172°25’E
Station Ck, BR	41°42’S 172°41’E
Staveley, SC	43°39’S 171°25’E
Stillwater R (L Marchant), FD	45°02’S 167°28’E
Stour R (bridge), NZS121, 121a, MC	43°39’S 171°16’E
Sutton Stm (SH87), DN	45°36’S 170°06’E

Table Hill Hut stm, SI	47°00’S 167°51’E
Tahakopa R, SL	46°30’S 169°19’E
Taieri R (Patearoa), CO	45°16’S 169°59’E
Taieri R (Ranfurly), CO	45°12’S 170°06’E
Tairua R (SH25a, Puketui Road), NZN3, CL	37°06’S 175°44’E
Taitaia Stm (near Clevedon), NZN9, AK	36°59’S 175°02’E
Takahe Valley, FD	45°17’S 167°40’E
Takaka Hill summit stm, NZS103, 103a, NN	41°02’S 172°52’E
Takaka R, NN	41°01’S 172°49’E
Takapua Stm (Tawa), NZN86, WN	41°11’S 174°51’E
Taneatua, BP	38°04’S 176°60’E
Tangarewai Stm, NZN39, RI	39°58’S 176°17’E
Tapotupotu Stm (Cape Reinga), NZN97, ND	34°27’S 172°43’E
Tara Hills, DN	45°49’S 170°21’E
Taramakau R (SH73), NZS51, WD	42°44’S 171°31’E
Tarawera Falls, NZN69, BP	38°10’S 176°31’E
Tarawera R (Kawerau), BP	38°06’S 176°43’E
Tarawera R, NZN68, BP	38°07’S 176°39’E
Tarere, GB	38°38’S 177°58’E
Tarndale (Molesworth), MB	42°10’S 172°56’E
Tasman R trib (SH80), NZS19, MK	43°51’S 170°07’E
Tasman Stm (Great Island), TH	34°10’S 172°09’E
Taupiri Stm (Atene Pa), NZN28, WI	39°43’S 175°09’E
Tauranga Bay stm, BR	41°47’S 171°28’E
Te Araroa, GB	37°38’S 178°21’E
Te Aute (SH2), HB	39°48’S 176°41’E
Te Awhia Stm (SH1 bridge), NZN98, ND	34°42’S 173°02’E
Te Hapua Road (stm 2 km from Waitiki Landing), NZN96, ND	34°30’S 172°51’E
Te Henui Stm, NZN26, TK	39°05’S 174°06’E
Te Hoe Stm, NZN130, WA	40°43’S 175°57’E
Te Horo, WN	40°48’S 175°07’E
Te Kaha, BP	37°44’S 177°41’E
Te Kuha stm, NN	41°50’S 171°39’E
Te Mahia (Kenepuru Sound), SD	41°13’S 173°58’E
Te Ngaru Stm, NZN52, HB	39°19’S 176°53’E
Te Paki, ND	34°30’S 172°48’E
Te Puia, BP	38°06’S 177°02’E
Te Rereatukahia Stm, NZN71, BP	37°35’S 175°53’E
Temple Basin, NC	42°55’S 171°35’E
The Brook, NN	41°18’S 173°18’E
The Hermitage, MK	43°44’S 170°06’E
The Neck, SI	46°56’S 168°10’E
Thirteen Mile Ck (SH6), NZS71, BR	42°18’S 171°17’E
Thomas R, MC	43°13’S 171°43’E
Thompsons Ck trib, NZS21, CO	44°58’S 170°31’E
Thompsons Ck, NZS22, CO	44°57’S 170°29’E
Thompsons Ck, NZS23, CO	44°57’S 170°24’E
Thule Bay culvert, NZS171, SI	46°54’S 168°07’E
Thule Bay, SI	46°54’S 168°07’E
Tikokopu Stm (Helensville), AK	36°43’S 174°30’E
Tinwald Burn, CO	44°55’S 169°17’E
Tokaanu Stm, NZN103, TO	38°58’S 175°46’E
Tokanui, SL	46°34’S 168°57’E
Tokomaru R (SH57), NZN90, WN	40°35’S 175°29’E
Tokoroa, WO	38°13’S 175°51’E
Tolaga Bay, GB	38°22’S 178°17’E
Tom Bowling Bay, ND	34°26’S 172°58’E
Tongariro R (Red Hut bridge), NZN104, TO	39°02’S 175°49’E
Tongariro R (Walkway), NZN23, TO	39°02’S 175°49’E
Tongariro R trib (Kaimanawa Road), NZN110, TO	39°09’S 175°49’E
Torere, BP	37°57’S 177°29’E
Tormore, NC	42°54’S 173°08’E
Totoranui Stm, NZS102, NN	40°49’S 172°60’E
Trounson Kauri Park, ND	35°43’S 173°38’E
Tuatapere, SL	46°08’S 167°41’E

Tucker Cove, CA	52°33’S 169°09’E
Tukipo R, HB	39°58’S 176°29’E
Tukituki R (SH2), HB	39°59’S 176°33’E
Tukituki R (SH50), HB	39°56’S 176°25’E
Tumbledown Bay (bridge), MC	43°51’S 172°46’E
Tutaekuri R, NZN42, HB	39°22’S 176°26’E
Tutaenui Stm (Bulls), NZN32, 32a, 32b, WI	40°11’S 175°21’E
Tutoko Bench (Darran Mts camp), FD	44°38’S 168°00’E
Tutoko Bench (Darran Mts), FD	44°38’S 168°00’E
Tutoko Bench (Darran Mts, camp basin), FD	44°38’S 167°01’E
Tutoko Bench (Darran Mts, Mahere Basin), FD	44°38’S 168°01’E
Tutoko Bench (Darran Mts, middle gully), FD	44°38’S 168°00’E
Twin Ck (SH73), NZS52, 133, 133a, NC	42°55’S 171°35’E

Umangawha Stm (near Colville), NZN6, CL	36°39’S 175°29’E
Umere (Karamea), NN	41°16’S 172°10’E
unmarked stm (near Virgin Ck, Karamea R gorge), NZS78, NN	41°15’S 172°13’E

Vaila Voe Bay stm, NZS165, 165a, 165b, SI	46°54’S 168°06’E
Victoria Passage, AU	50°50’S 165°55’E
Victoria R (SH1), NZN79, ND	35°09’S 173°24’E

W W Stm (Fairdown), NZS73, NN	41°44’S 171°45’E
Waiaruhe R (Puketona Junction), NZN81, ND	35°18’S 173°58’E
Waiharara, ND	34°57’S 173°11’E
Waiharehare, GB	38°31’S 178°17’E
Waihi Stm (SH52), NZN36, WA	40°26’S 176°18’E
Waiho (Franz Josef), WD	43°23’S 170°11’E
Waiho R trib, NZS141, WD	43°26’S 170°10’E
Waihopai R, NZS185, MB	41°40’S 173°34’E
Waihora Stm, NZN102, 102a, TO	38°38’S 175°43’E
Waihou R (Te Aroha), BP	37°32’S 175°43’E
Waihuka R (walkway), NZN60, GB	38°28’S 177°40’E
Waikaia R trib (Piano Flat), CO	45°34’S 169°00’E
Waikare R, NZN53, HB	39°08’S 176°60’E
Waikawa Bay (Picton), SD	41°17’S 174°02’E
Waikawa R trib (Tokanui), SL	46°33’S 169°06’E
Waikawa Stm, NZS107, SD	41°16’S 174°02’E
Waimakariri R channel (SH73), NZS53, NC	43°01’S 171°36’E
Waimamaku, ND	36°14’S 174°02’E
Waimamuku R (SH12, Waimamuku), NZN77, ND	35°33’S 173°29’E
Waimana R (bridge), NZN67, BP	38°08’S 177°04’E
Waimana R, NZN58, BP	38°06’S 177°03’E
Waimauku, AK	36°47’S 174°28’E
Waimeamea R, NZS30, SL	46°16’S 167°44’E
Waimiha Stm trib, TO	38°30’S 175°33’E
Waingaehe Stm, NZN56, BP	38°07’S 176°18’E
Waingawa, WA	40°58’S 175°35’E
Waingongoro R, NZN24, TK	39°22’S 174°14’E
Wainui (Mahia Peninsula), GB	39°06’S 177°58’E
Wainui R (Anatimo), NZS101, NN	40°50’S 172°56’E
Wainui stm (Banks Peninsula), NZS58, MC	43°49’S 172°54’E
Wainuiomata, WN	41°16’S 174°57’E
Waiokumurau Stm, ND	35°39’S 173°41’E
Waiongana, TK	39°07’S 174°13’E
Waiorongomai Stm, BP	37°34’S 175°45’E
Waiotemarama (SH12 drainage channel), ND	35°34’S 173°25’E
Waiotemarama Stm, ND	35°33’S 173°26’E
Waiouru, TO	39°29’S 175°40’E
Waipara R (Amberley), NC	43°08’S 172°47’E
Waipara R (SH1 bridge), NZS113, NC	43°04’S 172°45’E
Waipara, NC	43°03’S 172°46’E
Waipawa R (SH50), NZN40, RI	39°52’S 176°27’E
Waipori, DN	45°56’S 170°06’E
Waipoua R (SH12), NZN76, ND	35°39’S 173°34’E
Waipoua R Headquarters trib, ND	35°39’S 173°34’E
Waipoua R, ND	35°39’S 173°33’E
Waipu Cove (ditch)., NZN100, ND	36°02’S 174°31’E
Waipunga R, NZN50, TO	39°01’S 176°33’E
Wairakei, TO	38°38’S 176°06’E
Wairaki R, NZS31, SL	45°56’S 167°42’E
Wairau R (Tane Mahuta), ND	35°36’S 173°32’E
Wairau R trib (Chinamans Ck), MB	41°43’S 173°06’E
Wairau R, AK	36°06’S 174°22’E
Wairau R, MB	41°29’S 173°47’E
Wairoa R Gorge (top forks), NN	41°29’S 173°05’E
Wairuru, HB	39°56’S 176°44’E
Waitahanui, TO	38°47’S 176°05’E
Waitahuna (SH8), DN	46°07’S 169°35’E
Waitahuna, SL	45°60’S 169°46’E
Waitakere, AK	36°51’S 174°32’E
Waitangi Stm (Waiouru), NZN46, TO	39°28’S 175°39’E
Waitati, DN	45°45’S 170°35’E
Waitawheta R (Karangahake Gorge), NZN8, CL	37°26’S 175°44’E
Waiteika Stm, TK	39°27’S 173°54’E
Waitekuri R, NZN5, CL	36°45’S 175°35’E
Waitohu Stm (Otaki), NZN33, WN	40°46’S 175°12’E
Waitomo Stm (Ruakuri Cave tunnel), NZN18, WO	38°16’S 175°05’E
Waitomo Stm, WO	38°16’S 175°05’E
Waiwawa R, NZN4, CL	36°57’S 175°40’E
Wakamarina R, NZS4, MB	41°21’S 173°37’E
Walker Ck (SH94), NZS34, OL	45°06’S 167°58’E
Wanaka (Glendhu Bay stm), NZS180, OL	44°40’S 169°01’E
Wanganui (Kaikokopu Road stm), NZN118, WI	39°54’S 175°02’E
Waters of Leith, DN	45°50’S 170°30’E
Webling Bay, AU	50°33’S 166°15’E
Weka Pass, NC	43°00’S 172°42’E
Wekaweka Rd (drainage channel), ND	35°34’S 173°33’E
West Ck, NN	41°49’S 171°39’E
Westport (Nine Mile Road, end), NN	41°50’S 171°39’E
Westport, NN	41°45’S 171°36’E
Weydon Burn trib [Hamilton Ck], NZS35, OL	45°34’S 168°04’E
Whakapapa (Mt Ruapehu), TO	39°13’S 175°33’E
Whakatane R trib, NZN57, BP	38°01’S 176°57’E
Whalers Stm, CA	52°33’S 169°05’E
Whareatea R (SH67 ditch), NN	41°44’S 171°44’E
Whareatea R (SH67), NN	41°44’S 171°44’E
Whataroa, WD	43°16’S 170°22’E
Whirinaki R (Minginui), NZN55, TO	38°42’S 176°42’E
Whisky Ck (Flora Saddle), NZS92, NN	41°11’S 172°45’E
Windlass Bay stm, CA	52°32’S 169°08’E
Woolshed Ck, NZS138, 139, MC	43°38’S 171°18’E

Appendix 3. BOLD (Barcode of Life Data Systems) accession numbers for *Austrosimulium* specimens used in molecular analyses.

Craig Number	Sample Identification	Field Number	Identification
NZN2	ACBZsimNZN2	simNZN2	australense
NZN3	ACBZsimNZN3A	simNZN3A	australense
NZN3	ACBZsimNZN3B	simNZN3B	tillyardianum
NZN4	ACBZsimNZN4	simNZN4	australense
NZN5	ACBZsimNZN5	simNZN5	australense
NZN6	ACBZsimNZN6	simNZN6	australense
NZN7	ACBZsimNZN7A	simNZN7A	australense
NZN7	ACBZsimNZN7B	simNZN7B	tillyardianum
NZN8	ACBZsimNZN8A	simNZN8A	australense
NZN8	ACBZsimNZN8B	simNZN8B	tillyardianum
NZN9	ACBZsimNZN9	simNZN9	australense
NZN10	ACBZsimNZN10A	simNZN10A	australense
NZN10	ACBZsimNZN10B	simNZN10B	tillyardianum
NZN11	ACBZsimNZN11A	simNZN11A	australense
NZN11	ACBZsimNZN11B	simNZN11B	tillyardianum
NZN12	ACBZsimNZN12	simNZN12	australense
NZN13	ACBZsimNZN13	simNZN13	australense
NZN13	ACBZsimNZN13B	simNZN13B	tillyardianum
NZN14	ACBZsimNZN14A	simNZN14A	australense
NZN14	ACBZsimNZN14B	simNZN14B	longicorne
NZN15	ACBZsimNZN15	simNZN15	australense
NZN17	ACBZsimNZN17A	simNZN17A	australense
NZN17	ACBZsimNZN17B	simNZN17B	australense
NZN19	ACBZsimNZN19	simNZN19	australense
NZN20	ACBZsimNZN20A	simNZN20A	australense
NZN20	ACBZsimNZN20B	simNZN20B	tillyardianum
NZN21	ACBZsimNZN21	simNZN21	australense
NZN22	ACBZsimNZN22	simNZN22	australense
NZN23	ACBZsimNZN23A	simNZN23A	dugdalei
NZN23	ACBZsimNZN23B	simNZN23B	tillyardianum
NZN23	ACBZsimNZN23	simNZN23	tillyardianum
NZN24	ACBZsimNZN24	simNZN24	australense
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NZN32	ACBZsimNZN32B	simNZN32B	longicorne
NZN32a	ACBZsimNZN32aA	simNZN32aA	australense
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NZN37	ACBZsimNZN37A	simNZN37A	australense
NZN37	ACBZsimNZN37B	simNZN37B	tillyardianum
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NZN42	ACBZsimNZN42	simNZN42	tillyardianum
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NZN45	ACBZsimNZN45	simNZN45	tillyardianum
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NZN47	ACBZsimNZN47B	simNZN47B	tillyardianum
NZN48	ACBZsimNZN48A	simNZN48B	dugdalei
NZN48	ACBZsimNZN48B	simNZN48B	tillyardianum
NZN48b	ACBZsimNZN48bA	simNZN48bA	multicorne
NZN48b	ACBZsimNZN48bB	simNZN48bB	australense
NZN49	ACBZsimNZN49A	simNZN49A	dugdalei
NZN49a	ACBZsimNZN49aA	simNZN49aA	dugdalei
NZN49a	ACBZsimNZN49aB	simNZN49aB	tillyardianum
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NZN61	ACBZsimNZN61B	simNZN61B	australense
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NZN84	ACBZsimNZN84A	simNZN84A	longicorne
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NZS1	ACBZsimNZS1A	simNZS1A	australense
NZS1	ACBZsimNZS1B	simNZS1B	laticorne
NZS2	ACBZsimNZS2A	simNZS2A	australense
NZS2	ACBZsimNZS2B	simNZS2B	laticorne
NZS2	ACBZsimNZS2C	simNZS2C	tillyardianum
NZS2a	ACBZsimNZS2aA	simNZS2aA	tillyardianum
NZS2a	ACBZsimNZS2aB	simNZS2aB	laticorne
NZS3	ACBZsimNZS3A	simNZS3A	australense
NZS4	ACBZsimNZS4A	simNZS4A	tillyardianum
NZS4	ACBZsimNZS4B	simNZS4B	ungulatum
NZS4	ACBZsimNZS4C	simNZS4C	tillyardianum
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NZS5	ACBZsimNZS5B	simNZS5B	australense
NZS5	ACBZsimNZS5C	simNZS5C	laticorne
NZS5	ACBZsimNZS5D	simNZS5D	laticorne
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NZS5	ACBZsimNZS5F	simNZS5F	tillyardianum
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NZS7	ACBZsimNZS7A	simNZS7A	tillyardianum
NZS8	ACBZsimNZS8A	simNZS8A	longicorne
NZS9	ACBZsimNZS9A	simNZS9A	tillyardianum
NZS10	ACBZsimNZS10A	simNZS10A	tillyardianum
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NZS13	ACBZsimNZS13A	simNZS13A	tillyardianum
NZS14	ACBZsimNZS14A	simNZS14A	longicorne
NZS15	ACBZsimNZS15A	simNZS15A	australense
NZS16	ACBZsimNZS16A	simNZS16A	australense
NZS16	ACBZsimNZS16B	simNZS16B	tillyardianum
NZS17	ACBZsimNZS17A	simNZS17A	tillyardianum
NZS18	ACBZsimNZS18A	simNZS18A	laticorne
NZS19	ACBZsimNZS19A	simNZS19A	tillyardianum
NZS20	ACBZsimNZS20A	simNZS20A	tillyardianum
NZS21	ACBZsimNZS21A	simNZS21A	tillyardianum
NZS21	ACBZsimNZS21B	simNZS21B	longicorne
NZS21	ACBZsimNZS21C	simNZS21C	stewartense
NZS22	ACBZsimNZS22A	simNZS22A	tillyardianum
NZS22	ACBZsimNZS22B	simNZS22B	stewartense
NZS22	ACBZsimNZS22C	simNZS22C	stewartense
NZS24	ACBZsimNZS24A	simNZS24A	stewartense
NZS25	ACBZsimNZS25A	simNZS25A	longicorne
NZS27	ACBZsimNZS27A	simNZS27A	laticorne
NZS27	ACBZsimNZS27B	simNZS27B	ungulatum
NZS28	ACBZsimNZS28A	simNZS28A	stewartense
NZS28	ACBZsimNZS28B	simNZS28B	ungulatum
NZS29	ACBZsimNZS29A	simNZS29A	australense
NZS29	ACBZsimNZS29B	simNZS29B	laticorne
NZS29	ACBZsimNZS29C	simNZS29C	multicorne
NZS30	ACBZsimNZS30A	simNZS30A	stewartense
NZS30	ACBZsimNZS30B	simNZS30B	laticorne
NZS30	ACBZsimNZS30C	simNZS30C	ungulatum
NZS30	ACBZsimNZS30D	simNZS30D	ungulatum
NZS30	ACBZsimNZS30E	simNZS30E	australense
NZS31	ACBZsimNZS31A	simNZS31A	laticorne
NZS32	ACBZsimNZS32A	simNZS32A	bicorne
NZS32	ACBZsimNZS32B	simNZS32B	bicorne
NZS32	ACBZsimNZS32C	simNZS32C	bicorne
NZS33	ACBZsimNZS33A	simNZS33A	ungulatum
NZS34	ACBZsimNZS34A	simNZS34A	stewartense
NZS34	ACBZsimNZS34B	simNZS34B	ungulatum
NZS35	ACBZsimNZS35A	simNZS35A	stewartense
NZS35	ACBZsimNZS35B	simNZS35B	ungulatum
NZS35	ACBZsimNZS35C	simNZS35C	laticorne
NZS35	ACBZsimNZS35D	simNZS35D	tillyardianum
NZS36	ACBZsimNZS36A	simNZS36A	laticorne
NZS37	ACBZsimNZS37A	simNZS37A	ungulatum
NZS37	ACBZsimNZS37B	simNZS37B	tillyardianum

NZS38	ACBZsimNZS38A	simNZS38A	tillyardianum
NZS39	ACBZsimNZS39A	simNZS39A	longicorne
NZS41	ACBZsimNZS41A	simNZS41A	longicorne
NZS42	ACBZsimNZS42A	simNZS42A	multicorne
NZS44	ACBZsimNZS44A	simNZS44A	tillyardianum
NZS45	ACBZsimNZS45A	simNZS45A	dumbletoni
NZS45	ACBZsimNZS45B	simNZS45B	ungulatum
NZS45a	ACBZsimNZS45aA	simNZS45aA	dumbletoni
NZS45a	ACBZsimNZS45aB	simNZS45aB	ungulatum
NZS46	ACBZsimNZS46A	simNZS46A	laticorne
NZS46	ACBZsimNZS46B	simNZS46B	ungulatum
NZS47	ACBZsimNZS47A	simNZS47A	ungulatum
NZS49	ACBZsimNZS49A	simNZS49A	ungulatum
NZS50	ACBZsimNZS50A	simNZS50A	australense
NZS50	ACBZsimNZS50B	simNZS50B	laticorne
NZS51	ACBZsimNZS51A	simNZS51A	tillyardianum
NZS51	ACBZsimNZS51B	simNZS51B	tillyardianum
NZS51	ACBZsimNZS51C	simNZS51C	laticorne
NZS51	ACBZsimNZS51D	simNZS51D	australense
NZS51	ACBZsimNZS51E	simNZS51E	ungulatum
NZS52	ACBZsimNZS52A	simNZS52A	multicorne
NZS53	ACBZsimNZS53A	simNZS53A	multicorne
NZS54	ACBZsimNZS54A	simNZS54A	ungulatum
NZS54	ACBZsimNZS54B	simNZS54B	australense
NZS55	ACBZsimNZS55A	simNZS55A	ungulatum
NZS55	ACBZsimNZS55B	simNZS55B	multicorne
NZS56	ACBZsimNZS56A	simNZS56A	ungulatum
NZS56	ACBZsimNZS56(1)	simNZS56(1)	stewartense
NZS56	ACBZsimNZS56(2)	simNZS56(2)	multicorne
NZS56	ACBZsimNZS56(3)	simNZS56(3)	multicorne
NZS57a	ACBZsimNZS57aA	simNZS57aA	multicorne
NZS57a	ACBZsimNZS57aB	simNZS57aB	multicorne
NZS58	ACBZsimNZS58A	simNZS58A	tillyardianum
NZS58	ACBZsimNZS58B	simNZS58B	tillyardianum
NZS58	ACBZsimNZS58C	simNZS58C	tillyardianum
NZS59	ACBZsimNZS59A	simNZS59A	tillyardianum
NZS59	ACBZsimNZS59B	simNZS59B	multicorne
NZS60	ACBZsimNZS60A	simNZS60A	tillyardianum
NZS61	ACBZsimNZS61A	simNZS61A	tillyardianum
NZS62	ACBZsimNZS62	simNZS62	tillyardianum
NZS63	ACBZsimNZS63A	simNZS63A	tillyardianum
NZS63	ACBZsimNZS63B	simNZS63B	multicorne
NZS63	ACBZsimNZS63C	simNZS63C	multicorne
NZS64	ACBZsimNZS64A	simNZS64A	tillyardianum
NZS64	ACBZsimNZS64B	simNZS64B	ungulatum
NZS65	ACBZsimNZS65	simNZS65	ungulatum
NZS66	ACBZsimNZS66A	simNZS66A	ungulatum
NZS66	ACBZsimNZS66B	simNZS66B	multicorne
NZS66	ACBZsimNZS66C	simNZS66C	multicorne
NZS67	ACBZsimNZS67A	simNZS67A	australense
NZS67	ACBZsimNZS67B	simNZS67B	ungulatum
NZS67	ACBZsimNZS67C	simNZS67C	multicorne
NZS67	ACBZsimNZS67D	simNZS67D	multicorne
NZS68	ACBZsimNZS68A	simNZS68A	australense
NZS68	ACBZsimNZS68B	simNZS68B	tillyardianum
NZS68	ACBZsimNZS68C	simNZS68C	laticorne
NZS68	ACBZsimNZS68D	simNZS68D	laticorne
NZS68	ACBZsimNZS68E	simNZS68E	ungulatum
NZS69	ACBZsimNZS69A	simNZS69A	tillyardianum
NZS69	ACBZsimNZS69B	simNZS69B	laticorne
NZS70	ACBZsimNZS70A	simNZS70A	australense
NZS70	ACBZsimNZS70B	simNZS70B	australense
NZS70	ACBZsimNZS70C	simNZS70C	ungulatum
NZS71	ACBZsimNZS71	simNZS71	ungulatum
NZS72	ACBZsimNZS72A	simNZS72A	ungulatum
NZS72	ACBZsimNZS72B	simNZS72B	australense
NZS73	ACBZsimNZS73A	simNZS73A	ungulatum
NZS73	ACBZsimNZS73B	simNZS73B	australense
NZS74	ACBZsimNZS74A	simNZS74A	ungulatum
NZS74	ACBZsimNZS74B	simNZS74B	laticorne
NZS74	ACBZsimNZS74C	simNZS74C	australense
NZS75	ACBZsimNZS75	simNZS75	ungulatum
NZS76	ACBZsimNZS76A	simNZS76A	ungulatum
NZS76	ACBZsimNZS76B	simNZS76B	ungulatum
NZS77	ACBZsimNZS77A	simNZS77A	australense
NZS77	ACBZsimNZS77B	simNZS77B	laticorne
NZS77	ACBZsimNZS77C	simNZS77C	ungulatum
NZS77	ACBZsimNZS77D	simNZS77D	laticorne
NZS78	ACBZsimNZS78A	simNZS78A	australense
NZS78	ACBZsimNZS78B	simNZS78B	ungulatum
NZS78	ACBZsimNZS78C	simNZS78C	ungulatum
NZS79	ACBZsimNZS79A	simNZS79A	australense
NZS79	ACBZsimNZS79B	simNZS79B	laticorne
NZS79	ACBZsimNZS79C	simNZS79C	ungulatum
NZS79	ACBZsimNZS79D	simNZS79D	ungulatum
NZS80	ACBZsimNZS80A	simNZS80A	ungulatum
NZS80	ACBZsimNZS80B	simNZS80B	ungulatum
NZS81	ACBZsimNZS81A	simNZS81A	australense
NZS81	ACBZsimNZS81B	simNZS81B	tillyardianum
NZS81	ACBZsimNZS81C	simNZS81C	laticorne
NZS81	ACBZsimNZS81D	simNZS81D	ungulatum
NZS82	ACBZsimNZS82A	simNZS82A	tillyardianum
NZS82	ACBZsimNZS82B	simNZS82B	tillyardianum
NZS82	ACBZsimNZS82C	simNZS82C	ungulatum
NZS82	ACBZsimNZS82D	simNZS82D	australense
NZS82	ACBZsimNZS82E	simNZS82E	ungulatum
NZS83	ACBZsimNZS83A	simNZS83A	tillyardianum
NZS83	ACBZsimNZS83B	simNZS83B	laticorne
NZS83	ACBZsimNZS83C	simNZS83C	ungulatum
NZS83	ACBZsimNZS83D	simNZS83D	tillyardianum
NZS84	ACBZsimNZS84A	simNZS84A	tillyardianum
NZS84	ACBZsimNZS84B	simNZS84B	tillyardianum
NZS84	ACBZsimNZS84C	simNZS84C	tillyardianum
NZS84	ACBZsimNZS84D	simNZS84D	tillyardianum
NZS84	ACBZsimNZS84E	simNZS84E	tillyardianum
NZS84	ACBZsimNZS84F	simNZS84F	tillyardianum
NZS86	ACBZsimNZS86A	simNZS86A	australense
NZS86	ACBZsimNZS86B	simNZS86B	laticorne
NZS86	ACBZsimNZS86C	simNZS86C	laticorne
NZS86	ACBZsimNZS86D	simNZS86D	ungulatum
NZS87	ACBZsimNZS87A	simNZS87A	multicorne
NZS87	ACBZsimNZS87B	simNZS87B	multicorne
NZS88	ACBZsimNZS88A	simNZS88A	laticorne
NZS88	ACBZsimNZS88B	simNZS88B	laticorne
NZS88	ACBZsimNZS88C	simNZS88C	tillyardianum
NZS89	ACBZsimNZS89A	simNZS89A	tillyardianum

NZS89	ACBZsimNZS89B	simNZS89B	laticorne
NZS89	ACBZsimNZS89C	simNZS89C	ungulatum
NZS89	ACBZsimNZS89D	simNZS89D	australense
NZS90	ACBZsimNZS90	simNZS90	tillyardianum
NZS91	ACBZsimNZS91A	simNZS91A	ungulatum
NZS91	ACBZsimNZS91B	simNZS91B	multicorne
NZS91	ACBZsimNZS91C	simNZS91C	multicorne
NZS93	ACBZsimNZS93A	simNZS93A	tillyardianum
NZS93	ACBZsimNZS93B	simNZS93B	laticorne
NZS93	ACBZsimNZS93C	simNZS93C	laticorne
NZS93	ACBZsimNZS93D	simNZS93D	ungulatum
NZS93	ACBZsimNZS93E	simNZS93E	ungulatum
NZS94	ACBZsimNZS94A	simNZS94A	ungulatum
NZS94	ACBZsimNZS94B	simNZS94B	multicorne
NZS96	ACBZsimNZS96A	simNZS96A	laticorne
NZS96	ACBZsimNZS96B	simNZS96B	ungulatum
NZS97	ACBZsimNZS97A	simNZS97A	laticorne
NZS98	ACBZsimNZS98A	simNZS98A	laticorne
NZS99	ACBZsimNZS99A	simNZS99A	australense
NZS99	ACBZsimNZS99B	simNZS99B	australense
NZS99	ACBZsimNZS99C	simNZS99C	australense
NZS100	ACBZsimNZS100	simNZS100	laticorne
NZS101	ACBZsimNZS101A	simNZS101A	australense
NZS101	ACBZsimNZS101B	simNZS101B	laticorne
NZS101	ACBZsimNZS101C	simNZS101C	ungulatum
NZS102	ACBZsimNZS102A	simNZS102A	australense
NZS102	ACBZsimNZS102B	simNZS102B	australense
NZS103	ACBZsimNZS103	simNZS103	longicorne
NZS104	ACBZsimNZS104A	simNZS104A	tillyardianum
NZS104	ACBZsimNZS104B	simNZS104B	laticorne
NZS104	ACBZsimNZS104C	simNZS104C	ungulatum
NZS104	ACBZsimNZS104D	simNZS104D	tillyardianum
NZS105	ACBZsimNZS105A	simNZS105A	tillyardianum
NZS106	ACBZsimNZS106A	simNZS106A	tillyardianum
NZS106	ACBZsimNZS106B	simNZS106B	laticorne
NZS106	ACBZsimNZS106C	simNZS106C	ungulatum
NZS107	ACBZsimNZS107	simNZS107	tillyardianum
NZS121	ACBZsimNZS121	simNZS121	albovelatum
NZS122a	ACBZsimNZS122a	simNZS122a	alveolatum
NZS132	ACBZsimNZS132	simNZS132	unicorne
NZS133	ACBZsimNZS133	simNZS133	bicorne
NZS145	ACBZsimNZS145	simNZS145	tonnoiri
NZS157a	ACBZsimNZS157a	simNZS157a	ungulatum
NZS157a	ACBZsimNZS157b	simNZS157b	vailavoense
NZS162	ACBZsimNZS162	simNZS162	stewartense
NZS165	ACBZsimNZS165	simNZS165	vailavoense
NZS170a	ACBZsimNZS170a	simNZS170a	ungulatum
NZS170b	ACBZsimNZS170b	simNZS170b	ungulatum
Auck.Is.	ACBZsimAUEn	simAuck.Is.	vexans

ILLUSTRATIONS

Fig. **1** Habitus of female of *Austrosimulium* (*Austrosimulium*) *australense* (modified from 1989 original by D. W. Helmore; scale bar = 0.5 mm).

Fig. **2–5** Wing venation and pupal structure, New Zealand *Austrosimulium*: (2) *A. ungulatum* female, left wing, showing general venation, Manapouri; (3) *A. australense* female, showing basal wing venation; (4) *A. australense*, dorsal view of female pupa, showing gills, thorax, and abdomen; (5) *A. australense,* posterior view of pupal abdomen, showing terminal spines and grapnel hooks. (Fig. 2, 3, 5 modified from originals by J. S. Dugdale (in Dumbleton 1973), Fig. 4 modified from 1989 original by D. W. Helmore; scale bars for Fig. 2 & 4 = 0.5 mm, others not to scale). (veins—A = anal, C = costa, CuA = anterior cubital, CuP = posterior cubitus, hm = humeral, M = median, R = radial, Rs = radial sector, Sc = subcosta).

Fig. 6–14 Larval structures of *Austrosimulium australense*: (6) right lateral view of final instar larva; (7) single labral fan ray, and (7a) detail of ray microtrichia; (8) ventral view of head; (9) anterior view of head; (10) dorsal view of head; (11) dorsal view of posterior proleg and anal sclerite; (12) right lateral view of posterior proleg and anal sclerite (arrow indicates single hook); (13) hypostoma; (14) mandible. (Not to scale. Modified from originals in Dumbleton (1973)).

Fig. 15–19 (left) Adult structures of New Zealand *Austrosimulium* species: (15) head of female *A. australense*, showing the dichoptic condition and the uniform facet size of ommatidia, NZN93; (16) head of male *A. alveolatum*, showing holoptic condition and the larger, dorsal ommatidial facets, NZS122; (17) mouthparts of female *A. multicorne*, Balloon Hut; (18) antenna of adult male *A. alveolatum,* numbers indicate flagellomeres, NZS122; (19) leg of female *A. fiordense* showing calcipala and pedisulcus, Darran Mountains, FD (scale bar, Fig. 15, 16 = 0.1 mm; Fig. 17, 18 = 0.05 mm; Fig. 19 = 0.025 mm). (arrowheads = stout basitarsal setae).

Fig. 20–23 (above) Genitalia: (20) female *A. dugdalei*, NZN23; (21) male *A. albovelatum*, NZS121, cleared and stained in Chlorazol Black; (22) female *A. vailavoense*, hypogynial valves; (23) female *A. vailavoense*, anal lobe and cercus in lateral view, NZS165 (scale bars, Fig. 20, 21 = 0.05 mm. Fig. 22, 23 = 0.02 mm).

Fig. **24–41** Adult female cibaria: Fig. 24, 25, *australense*-subgroup: (24) *A. australense;* (25) *A. longicorne.* Fig. 26–32. *tillyardianum*-subgroup: (26) *A. albovelatum*; (27) *A. alveolatum*; (28) *A. dugdalei;* (29) *A. fiordense*; (30) *A. laticorne*; (31) *A. multicorne*; (32) *A. stewartense* (scale bar = 0.05 mm).

Adult female cibaria: *tillyardianum*-subgroup (cont.): Fig. 33. *A. tillyardianum*. Fig. 34–38. *ungulatum*-subgroup: (34) *A. campbellense*, (35) *A. dumbletoni*, (36) *A. ungulatum*, (37). *A. vailavoense*, (38) *A. vexans*. Fig. 39–41 *unicorne*-subgroup: (39) *A. bicorne*, (40) *A. tonnoiri*, (41) *A. unicorne* (scale bar = 0.05 mm).

Fig. **42–49** Apical end of hind basitarsus of New Zealand *Austrosimulium*, showing distribution of stout setae, arrow heads indicate setae: Fig. 42–47 *australense* species-group: (42) female *A. longicorne,* NZN111; (43) male *A. longicorne,* NZN111; (44) female *A. tillyardianum*, NZS58; (45) male *A. tillyardianum*, NZS58; (46) female *A. australense*, NZN93; (47) male *A. australense*, NZN93. Fig. 48, 49 *ungulatum* species-group: (48) female *A. ungulatum,* NZS165; (49) male *A. ungulatum*, NZS91 (scale bar = 0.05 mm).

Fig. **50–67** Tarsal claws of female *Austrosimulium*: Fig. 50, 51, *australense*-subgroup: (50) *A. australense,* NZN93*;* (51) *A. longicorne*, NZN111. Fig. 52–57, *tillyardianum*-subgroup: (52) *A. albovelatum,* NZS121; (53) *A. alveolatum*, NZS122; (54) *A. dugdalei,* NZN23; (55) *A. fiordense*, Darran Mountains; (56) *A. laticorne,* NZS2; (57) *A. multicorne,* Balloon Hut (scale bar = 0.02 mm).

(Left) Tarsal claws of female *Austrosimulium, tillyardianum*-subgroup (cont.): (58) *A. stewartense*, NZS162; (59) *A. tillyardianum*, NZS58. Fig. 60–64, *ungulatum*-subgroup: (60) *A. campbellense*; (61) *A. dumbletoni*, NZS45; (62) *A. ungulatum*, NZS68; (63) *A. vailavoense*, NZS165; (64) *A. vexans*. Fig. 65–67, *unicorne*-subgroup: (65) *A. bicorne,* NZS133 (scale bar = 0.02 mm).

(Above) Tarsal claws of female *Austrosimulium*, *unicorne*-subgroup (cont.): (66) *A. tonnoiri*, NZS32; (67) *A. unicorne*, Hawea (arrow indicates small basal tooth). **Fig**. **68**, **69** Male claws, *australense* and *ungulatum* species-groups respectively: (68). *A. tillyardianum,* NZS58; (69) *A. ungulatum*, NZS91 (scale bar = 0.02 mm).

Fig. **70–85** Tergites of female *Austrosimulium*: Fig. 70, 71 *australense*-subgroup: (70) *A. australense*, NZN25a; (71) *A. longicorne*, NZS8. Fig. 72–79 *tillyardianum*-subgroup: (72) *A. albovelatum*, North Ashburton River; (73) *A. alveolatum*, NZS 122; (74) *A. dugdalei,* NZN48; (75) *A. fiordense*, Darran Mountains (scale bar = 0.2 mm).

Tergites of female *Austrosimulium, tillyardianum*-subgroup (cont.): (76) *A. laticorne*, NZS2; (77) *A. multicorne,* Balloon Hut; (78) *A. stewartense*, NZS170; (79) *A. tillyardianum*, NZS6. Fig. 80–84 *ungulatum*-subgroup: (80) *A. campbellense;* (81) *A. dumbletoni,* NZS45 (scale bars = 0.2 mm).

Tergites of *Austrosimulium, ungulatum*-subgroup (cont.): (82) *A. ungulatum*, NZS68; (83) *A. vailavoense*, NZS165; (84) *A. vexans*, Auckland Is. Fig. 85–87 *unicorne*-subgroup: (85) *A. bicorne,* NZS133a; (86) *A. tonnoiri*, Darran Mountains; (87) *A. unicorne,* Temple Basin. **Fig**. **88**, **89** Tergites of males: (88) *A. laticorne*, NZS2; (89) *A. ungulatum,* NZS91 (scale bar = 0.2 mm).

Fig. **90–107** Genitalia of female *Austrosimulium*: Fig. 90, 91 *australense*-subgroup: (90) *A. australense*, Nihotupu, Waitakere Ranges, Tonnoir 1923; (91) *A. longicorne*, NZS115. Fig. 92–99 *tillyardianum*-subgroup: (92) *A. albovelatum*, NZS121; (93) *A. alveolatum*, NZS122a; (94) *A. dugdalei*, NZN48; (95) *A. fiordense*, Darran Mountains; (96) *A. laticorne*, NZS2; (97) *A. multicorne*, Balloon Hut; (98) *A. stewartense*, NZS170 (scale bars = 0.05 mm).

Genitalia of female *Austrosimulium*, *tillyardianum*-subgroup (cont.): (99) *A. tillyardianum*, NZS58. Fig. 100–104 *ungulatum*-subgroup: (100) *A. campbellense*, Campbell Island; (101) *A. dumbletoni*, NZS45; (102) *A. ungulatum*, NZS68; (103) *A. vailavoense*, NZS165; (104) *A. vexans*, Auckland Islands. Fig. 105–107 *unicorne*-subgroup: (105) *A. bicorne*, NZS133a; (106) *A. tonnoiri*, NZS32a; (107) *A. unicorne*, Temple Basin (scale bar = 0.05 mm).

Fig. **108–125** Genital forks of *Austrosimulium:* Fig. 108, 109 *australense*-subgroup: (108) *A. australense*, NZS58. (109) *A. longicorne*, NZS115. Fig. 110–117 *tillyardianum*-subgroup: (110) *A. albovelatum*, NZS121; (111) *A. alveolatum*, NZS122a; (112) *A. dugdalei*, NZN48; (113) *A. fiordense*, Darran Mountains. (scale bars = 0.02 mm).

Genital forks of *Austrosimulium, tillyardianum*-subgroup (cont.): (114) *A. laticorne*, NZS2. (115) *A. multicorne*, Balloon Hut; (116) *A. stewartense*, NZS170; (117) *A. tillyardianum*, NZS58. Fig. 118–122 *ungulatum*-subgroup: (118) *A. campbellense*, Campbell Island; (119) *A. dumbletoni*, NZS45 (scale bars = 0.02 mm).

ungulatum-subgroup (cont.): (120) *A. ungulatum*, NZS68; (121) *A. vailavoense*, NZS165; (122) *A. vexans*, Auckland Islands. Fig. 123–125 *unicorne*-subgroup: (123) *A. bicorne*, NZS133a; (124) *A. tonnoiri*, NZS32; (125) *A. unicorne*, Temple Basin (scale bars = 0.02 mm).

Fig. **126–142 (left)** Genitalia of male *Austrosimulium*: inserts, (below) posterior view of ventral plate; (right) left lateral view of ventral plate: Fig. 126, 127 *australense*-subgroup: (126) *A. australense*, NZN93; (127) *A. longicorne*, Tormore. Fig. 128–135 *tillyardianum*-subgroup: (128) *A. albovelatum*, NZS121; (129) *A. alveolatum*, NZS122; (130) *A. dugdalei*, NZN48b; (131) *A. extendorum*, Sawyers Beach; (132) *A. laticorne*, NZS2; (133) *A. multicorne*, Balloon Hut; (134) *A. stewartense*, paratype, Mill Creek, Stewart Island (scale bar = 0.05 mm).

(Above) Genitalia of male *Austrosimulium, tillyardianum*-subgroup (cont.): (135) *A. tillyardianum*, NZS58. Fig. 136–139 *ungulatum*-subgroup: (136) *A. campbellense*, Campbell Island; (137) *A. dumbletoni*, Jackson Bay, based on gynandromorph; (138) *A. ungulatum*, Peel Forest; (139) *A. vexans*, Auckland Island, early pharate specimen. Fig. 140–142 *unicorne*-subgroup: (140) *A. bicorne*, Temple Basin; (141) *A. tonnoiri*, NZS32a; (142) *A. unicorne*, Temple Basin (scale bar = 0.05 mm).

Fig. **143–159** Generalised shapes of cocoons of New Zealand *Austrosimulium,* based mainly on Dumbleton (1973): Fig. 143,144 *australense*-subgroup: (143) *A. australense*; (144) *A. longicorne*. Fig. 145–153 *tillyardianum*-subgroup: (145) *A. albovelatum*; (146) *A. alveolatum*; (147) *A. dugdalei*; (148) *A. extendorum*; (149) *A. fiordense*; (150) *A. laticorne*; (151) *A. multicorne*; (152) *A. stewartense*; (153) *A. tillyardianum*. Fig. 154–156 *ungulatum*-subgroup: (154) *A. campbellense*; (155) *A. ungulatum*; (156) *A. vexans*. Fig. 157–159 *unicorne*-subgroup: (157) *A. bicorne*; (158) *A. tonnoiri*; (159) *A. unicorne* (not to scale).

Fig. **160–177** Pupae and cocoons of New Zealand *Austrosimulium*: Fig. 160,161 *australense*-subgroup: (160) *A. australense*, Great Barrier Island; (161) *A. longicorne*, NZS14. Fig. 162–171 *tillyardianum*-subgroup: (162) *A. albovelatum*, NZS120; (163) *A. alveolatum*, holotype, Porters Pass; (164) *A. dugdalei*, NZN48; (165) *A. extendorum*, Sawyers Beach (scale bar = 0.5 mm).

Pupae and cocoons of New Zealand *Austrosimulium*, *tillyardianum*-subgroup (cont.): (166) *A. fiordense* cocoon, neotype, Glaisnock River; (167) *A. laticorne*, NZS2; (168) *A. laticorne* variant, NZS86; (169) *A. multicorne*, NZS154; (170) *A. stewartense*, narrower form, NZS165; (171) *A. tillyardianum*, NZS89 (scale bar = 0.5 mm).

Pupae and cocoons of New Zealand *Austrosimulium*: Fig. 172–174 *ungulatum*-subgroup: (172) *A. campbellense*, Campbell Island; (173) *A. ungulatum*, NZS49; (174) *A. vexans*, Auckland Islands. Fig. 175–177 *unicorne*-subgroup: (175) *A. bicorne*, Temple Basin; (176) *A. tonnoiri*, NZS 32; (177) *A. unicorne*, NZS132a (scale bar = 0.5 mm).

Fig. **178–193** Cocoon fabric of New Zealand *Austrosimulium:* Fig. 178,179 *australense*-subgroup: (178) *A. australense*, NZN30; (179) *A. longicorne*, NZS8. Fig. 180–187 *tillyardianum*-subgroup: (180) *A. albovelatum*, NZS120; (181) *A. alveolatum*, Porters Pass; (182) *A. dugdalei*, NZN48; (183) *A. fiordense*, neotype, Glaisnock River (scale bar = 0.1 mm).

Cocoon fabric of New Zealand *Austrosimulium*, *tillyardianum*-subgroup (cont.): (184) *A. laticorne*, NZS2; (185) *A. multicorne*, Balloon Hut; (186) *A. stewartense*, NZS168; (187) *A. tillyardianum,* NZS89 (scale bar = 0.1 mm).

Cocoon fabric of New Zealand *Austrosimulium*: Fig. 188, 189 *ungulatum*-subgroup: (188) *A. campbellense*, Campbell Island; (189) *A. ungulatum*, NZS49; (190) *A. vexans*, Auckland Islands. Fig. 191–193 *unicorne*-subgroup: (191) *A. bicorne*, NZS32; (192) *A. tonnoiri*, NZS32a; (193) *A. unicorne*, NZS132 (scale bar = 0.1 mm).

Fig. **194–196** Pupal structures of New Zealand *Austrosimulium*: (194) *A. dugdalei*, ventral view of exuviae from pupal abdomen showing hooks and spines, NZN48; (195) *A. vexans*, exuviae of pupal segment IX showing terminal spines and grapnel hooks, Auckland Islands; (196) *A. ungulatum*, anterior view of pharate male adult head showing ocular setae on pupal cuticle, NZS91 (scale bar, Fig. 194 = 0.2 mm; Fig. 195 = 0.05 mm; Fig. 196 = 0.2 mm).

Fig. **197–201** Outlines of pupal head exuviae of New Zealand *Austrosimulium* showing differences between males and females, and arrangement of sensillae (setae and spines): (197) *A. australense*, male; (198) *A. australense*, female; (199) *A. ungulatum*, female; (200) *A. tillyardianum*, male; (201) *A. tillyardianum*, female (not to scale, adapted from Dumbleton (1973)).

Fig. **202–216** Pupal head exuviae of female *Austrosimulium*: Fig. 202, 203 *australense*-subgroup: (202) *A. australense*, NZN93; (203) *A. longicorne*, NZS115. Fig. 204–211 *tillyardianum*-subgroup: (204) *A. albovelatum*, NZS121; (205) *A. alveolatum*, Porters Pass; (206) *A. dugdalei*, NZN48; (207) *A. extendorum*, Sawyers Beach (scale bar = 0.2 mm).

(Above) Pupal head exuviae of female *Austrosimulium*, *tillyardianum*-subgroup (cont.): (208) *A. laticorne*, NZS68; (209) *A. multicorne*, Balloon Hut; (210) *A. stewartense*, NZS163; (211) *A. tillyardianum*, NZS6 (scale bar = 0.2 mm).

(Right) Pupal head exuviae of female *Austrosimulium*, Fig. 212, 213 *ungulatum*-subgroup: (212) *A. ungulatum*, NZS91; (213) *A. vexans*, Auckland Islands. Fig. 214–216 *unicorne*-subgroup: (214) *A. bicorne*, NZS133a; (215) *A. tonnoiri*, NZS32; (216) *A. unicorne*, Temple Basin (scale bar = 0.2 mm).

Fig. **217–233** Pupal head exuviae of male *Austrosimulium*: Fig. 217, 218 *australense*-subgroup: (217) *A. australense*, NZN93; (218) *A. longicorne*, NZS115. Fig. 219–227 *tillyardianum*-subgroup: (219) *A. albovelatum*, NZS121; (220) *A. alveolatum*, NZS121; (221) *A. dugdalei*, NZN48; (222) *A. extendorum*, Sawyers Beach (scale bar = 0.2 mm).

Pupal head exuviae of male *Austrosimulium*, *tillyardianum*-subgroup (cont.): (223) *A. fiordense*, neotype, Glaisnock River; (224) *A. laticorne*, NZS68; (225) *A. multicorne*, Balloon Hut; (226) *A. stewartense*, paratype, Sawyers Beach; (227) *A. tillyardianum*, NZS6 (scale bar = 0.2 mm).

(Left) Pupal head exuviae of male *Austrosimulium,* Fig. 228–230 *ungulatum*-subgroup: (228) *A. campbellense*, paratype, Campbell Island; (229) *A. ungulatum*, NZS91; (230) *A. vexans*, Auckland Islands. Fig. 231–233 *unicorne*-subgroup: (231) *A. bicorne*, NZS133a; (232) *A. tonnoiri*, NZS32; (233) *A. unicorne*, NZS132a (scale bar = 0.2 mm).

Fig. **234–237 (above)** Pupal gills and thorax of some *Austrosimulium* species, dorsal views: Fig. 234–236 *australense* species-group: (234) *A. dugdalei*, NZN48; (235) *A. laticorne*, NZS2; (236) *A. tillyardianum*, NZS6. Fig. 237 *ungulatum* species-group: (237) *A. campbellense*, Campbell Island (scale bar = 0.2 mm).

Fig. **238–254** Lateral views of pupal thorax and gill base of *Austrosimulium* species: Fig. 238, 239 *australense*-subgroup: (238) *A. australense*, NZN93; (239) *A. longicorne*, NZS12. Fig. 240–247 *tillyardianum*-subgroup: (240) *A. albovelatum*, NZS121; (241) *A. alveolatum*, Porters Pass; (242) *A. dugdalei*, NZN48; (243) *A. extendorum*, Sawyers Beach (scale bar = 0.1 mm).

Lateral views of pupal thorax and gill base of *Austrosimulium* species, *tillyardianum*-subgroup (cont.): (244) *A. fiordense*, neotype, Glaisnock River; (245) *A. laticorne*, NZS68; (246) *A. multicorne*, Balloon Hut; (247) *A. stewartense*, NZS170; (248) *A. tillyardianum*, NZS6 (scale bar = 0.1 mm).

Lateral views of pupal thorax and gill base of *Austrosimulium* species, *ungulatum*-subgroup: (249) *A. campbellense*, Campbell Island; (250) *A. ungulatum*, NZS91; (251) *A. vexans*, Auckland Islands. Fig. 252–254 *unicorne*-subgroup: (252) *A. bicorne*, NZS133a; (253) *A. tonnoiri*, Darran Mountains; (254) *A. unicorne*, NZS132a (scale bar = 0.1 mm).

Fig. **255–267** Generalised outlines of gill structure for some *Austrosimulium* species, Fig. 255, 256 *australense*-subgroup: (255) *A. australense*; (256) *A. longicorne*. Fig. 257–262 *tillyardianum*-subgroup: (257) *A. albovelatum*; (258) *A. alveolatum*; (259) *A. laticorne*; (260) *A. multicorne*; (261) *A. stewartense*; (262) *A. tillyardianum* (not to scale; inserts show horn variation; adapted from Dumbleton (1973)).

Generalised outlines of gill structure for some *Austrosimulium* species: Fig. 263–265 *ungulatum*-subgroup: (263) *A. campbellense*; (264) *A. ungulatum*; (265) *A. vexans*. Fig. 266–278 *unicorne*-subgroup: (266) *A. bicorne*; (267) *A. unicorne* (not to scale; adapted from Dumbleton (1973)).

Fig. **268–285** Right lateral views of pupal gills of *Austrosimulium* species: Fig. 268, 269 *australense*-subgroup: (268) *A. australense*, NZN93; (269) *A. longicorne*, Tormore. Fig. 270–279 *tillyardianum*-subgroup: (270) *A. albovelatum*, NZS121; (271) *A. alveolatum*, Porters Pass; (272) *A. dugdalei*, NZN48; (273) *A. extendorum*, shorter variant, Sawyers Beach (scale bar = 0.1 mm).

Right lateral views of pupal gills of *Austrosimulium* species, *tillyardianum*-subgroup (cont.): (274) *A. fiordense*, neotype, Glaisnock River; (275) *A. laticorne*, NZS1; (276) *A. multicorne*, Balloon Hut; (277) *A. multicorne*, variant, NZS18; (278) *A. stewartense*, Freshwater Beach; (279) *A. tillyardianum*, NZS58 (scale bar = 0.1 mm).

Right lateral views of pupal gills of *Austrosimulium* species: Fig. 280–283 *ungulatum*-subgroup: (280) *A. campbellense,* Campbell Island; (281) *A. ungulatum*, NZS49; (282) *A. vexans*, Auckland Islands. Fig. 283–285 *unicorne*-subgroup: (283) *A. bicorne*, NZS133; (284) *A. tonnoiri*, NZS32; (285) *A. unicorne*, NZS132a (scale bar = 0.1 mm).

Fig. **286–302** Pupal gill filament structure of *Austrosimulium* species: Fig. 286, 287 *australense*-subgroup: (286) *A. australense*, NZN93; (287) *A. longicorne*, NZS12. Fig. 288–296 *tillyardianum*-subgroup: (288) *A. albovelatum*, L. J. Dumbleton; (289) *A. alveolatum*, NZS122; (290) *A. dugdalei*, NZN48; (291) *A. extendorum*, Sawyers Beach (scale bar = 0.02 mm).

Pupal gill filament structure of *Austrosimulium* species, *tillyardianum*-subgroup (cont.): (292) *A. fiordense*, neotype, Glaisnock River; (293) *A. laticorne*, NZS2; (294) *A. multicorne*, Balloon Hut; (295) *A. stewartense*, NZS170; (296) *A. tillyardianum*, NZS58 (scale bar = 0.02 mm).

Pupal gill filament structure of *Austrosimulium* species: Fig. 297–299 *ungulatum*-subgroup: (297) *A. campbellense*, Campbell Island; (298) *A. ungulatum*, NZS49; (299) *A. vexans*, Auckland Islands. Fig. 300–302 *unicorne*-subgroup: (300) *A. bicorne*, NZS133; (301) *A. tonnoiri*, NZS32; (302) *A. unicorne*, NZS132a (scale bar = 0.02 mm).

Fig. **303–319** Habitus of final instar larvae of *Austrosimulium* species, left lateral view, Fig. 303–306 *australense*-subgroup: (303) *A. australense*, typical, NZS70; (304) *A. australense*, variant, NZN75; (305) *A. longicorne*, medium altitude, NZN46; (306) *A longicorne*, higher altitude, NZS41 (scale bar = 0.5 mm).

Habitus of final instar larvae of *Austrosimulium* species, left lateral view: Fig. 307–314 *tillyardianum*-subgroup: (307) *A. albovelatum*, NZS121; (308) *A. alveolatum*, NZS57a; (309) *A. dugdalei*, NZN48a; (310) *A. extendorum*, Sawyers Beach (scale bar = 0.5 mm).

Habitus of final instar larvae of *Austrosimulium* species, left lateral view, *tillyardianum*-subgroup (cont.): (311) *A. laticorne*, NZS2; (312) *A. multicorne*, NZS56; (313) *A. stewartense*, NZS164; (314) *A. tillyardianum*, NZS58 (scale bar = 0.5 mm).

Habitus of final instar larvae of *Austrosimulium* species, left lateral view: Fig. 314a, 315, 316 *ungulatum*-subgroup: (314a) *A. campbellense*, Campbell Island; (315) *A. ungulatum*, NZS27; (316) *A. vexans*, Auckland Island.

Habitus of final instar larvae of *Austrosimulium* species, left lateral view: Fig. 317–319 *unicorne*-subgroup: (317) *A. bicorne*, NZS133; (318) *A. tonnoiri*, NZS32a; (319) *A. unicorne*, NZS132 (scale bar = 0.5 mm).

Fig. **320–338**. Heads of final instar larvae of *Austrosimulium* species, dorsal view: Fig 320–323 *australense*-subgroup: (320) *A. australense*, male, Glen Esk; (321) *A. australense*, female, Glen Esk; (322) *A. longicorne*, low altitude, NZN46; (323) *A. longicorne*, high altitude, NZS41. Fig. 324, 325 *tillyardianum*-subgroup: (324) *A. albovelatum*, NZS121; (325) *A. alveolatum*, Porters Pass (scale bar = 0.2 mm).

Heads of final instar larvae of *Austrosimulium* species, dorsal view, *tillyardianum*-subgroup (cont.): (326) *A. dugdalei*, NZN48a; (327) *A. extendorum*, Sawyers Beach; (328) *A. fiordense*, microscope slide mount, Glaisnock River; (329) *A. laticorne*, NZS2; (330) *A. multicorne*, Old Man Range; (331) *A. stewartense*, NZS164 (scale bar = 0.2 mm).

Heads of final instar larvae of *Austrosimulium* species, dorsal view, *tillyardianum*-subgroup (cont.): (332) *A. tillyardianum*, NZS20. Fig. 333–335 *ungulatum*-subgroup: (333) *A. campbellense*, Campbell Island; (334) *A. ungulatum*, NZS91; (335) *A. vexans*, Auckland Islands. (scale bar = 0.2 mm).

Heads of final instar larvae of *Austrosimulium*, dorsal view: Fig. 336–338 *unicorne*-subgroup: (336) *A. bicorne*, NZS133; (337) *A. tonnoiri*, NZS145; (338) *A. unicorne*, NZS132 (scale bar = 0.2 mm).

Fig. **339–350 (above)** General shape of mature pharate pupal gills in final instar larvae of *Austrosimulium*: Fig. 339, 340 *australense*-subgroup: (339) *A. australense*; (340) *A. longicorne*. Fig. 341–345 *tillyardianum*-subgroup: (341) *A. albovelatum*; (342) *A. laticorne*; (343) *A. multicorne*; (344) *A. stewartense*; (345) *A. tillyardianum*. Fig. 346–348 *ungulatum*-subgroup: (346) *A. campbellense*; (347) *A. ungulatum*; (348) *A. vexans*. Fig. 349, 350 *unicorne*-subgroup: (349) *A. bicorne*; (350) *A. unicorne* (not to scale; adapted from Dumbleton (1973)).

Fig. **351–366 (right)** Habitus of mature pharate pupal gills in final instar larvae of *Austrosimulium*: Fig. 351, 352 *australense*-subgroup: (351) *A. australense*, NZS1; (352) *A. longicorne*, NZN32. Fig. 353–360 *tillyardianum*-subgroup: (353) *A. albovelatum*, NZS11; (354) *A. alveolatum*, NZS122; (355) *A. dugdalei*, NZN48; (356) *A. extendorum*, Sawyers Beach (scale bar = 0.2 mm).

(Above) Habitus of mature pharate pupal gills in final instar larvae of *Austrosimulium*: *tillyardianum*-subgroup (cont.): (357) *A. laticorne*, NZS46; (358) *A. multicorne*, Old Man Range; (359) *A. stewartense*, NZS61; (360) *A. tillyardianum*, NZS20. (scale bar = 0.2 mm).

(Right) Habitus of mature pharate pupal gills in final instar larvae of *Austrosimulium,* Fig. 361–363 *ungulatum*-subgroup: (361) *A. campbellense*, Campbell Island; (362) *A. ungulatum*, NZS27; (363) *A. vexans*, Auckland Islands. Fig. 364–366 *unicorne*-subgroup: (364) *A. bicorne*, NZS133; (365) *A. tonnoiri*, NZS32a; (366) *A. unicorne*, NZS132 (scale bar = 0.2 mm).

Fig. **367–383 (left)** Antennae of final instar larvae of New Zealand *Austrosimulium*: Fig. 367, 368 *australense*-subgroup (arrows indicate junction between basal and medial articles): (367) *A. australense*, Glen Esk; (368) *A. longicorne*, NZN111. Fig. 369–377 *tillyardianum*-subgroup: (369) *A. albovelatum*, NZS121; (370) *A. alveolatum*, Porters Pass; (371) *A. dugdalei*, NZN48; (372) *A. extendorum*, Sawyers Beach (scale bar = 0.05 mm).

(Above) Antennae of final instar larvae of New Zealand *Austrosimulium*, *tillyardianum*-subgroup (cont.): (373) *A. fiordense*, Glaisnock River; (374) *A. laticorne*, NZS2; (375) *A. multicorne*, Balloon Hut; (376) *A. stewartense*, Freshwater Creek; (377) *A. tillyardianum*, NZS20 (scale bar = 0.05 mm).

Antennae of final instar larvae of New Zealand *Austrosimulium*: Fig. 378–380 *ungulatum*-subgroup: (378) *A. campbellense*, Campbell Island; (379) *A. ungulatum*, NZS91; (380) *A. vexans*, Auckland Islands. Fig. 381–383 *unicorne*-subgroup: (381) *A. bicorne*, NZS133; (382) *A. tonnoiri*, NZS32; (383) *A. unicorne*, NZS132 (scale bar = 0.05 mm).

Fig. **384–400** Postgenal cleft, postgenal bridge, and hypostoma of final instar larvae of *Austrosimulium*: Fig. 384, 385 *australense*-subgroup: (384) *A. australense*, NZN93; (385) *A. longicorne*, NZN111. Fig. 386–394 *tillyardianum*-subgroup: (386) *A. albovelatum*, NZS121; (387) *A. alveolatum*, Porters Pass; (388) *A. dugdalei*, NZN48; (389) *A. extendorum*, Sawyers Beach (scale bar = 0.1 mm).

Postgenal cleft, postgenal bridge, and hypostoma of final instar larvae of *Austrosimulium*, *tillyardianum*-subgroup (cont.): (390) *A. fiordense*, Glaisnock River; (391) *A. laticorne*, NZS1; (392) *A. multicorne*, Balloon Hut; (393) *A. stewartense*, NZS61; (394) *A. tillyardianum*, NZS6 (scale bar = 0.1 mm).

Postgenal cleft, postgenal bridge, and hypostoma of final instar larvae of *Austrosimulium*, Fig. 395–397 *ungulatum*-subgroup: (395) *A. campbellense*, Campbell Island; (396) *A. ungulatum*, NZS91; (397) *A. vexans*, Auckland Islands. Fig. 398–400 *unicorne*-subgroup: (398) *A. bicorne*, NZS133; (399) *A. tonnoiri*, NZS32; (400) *A. unicorne*, NZS132 (scale bar = 0.1 mm).

Fig. **401–402** Ventral view of final instar larval head of *Austrosimulium* showing suboesophageal ganglia: *australense* species-group: (401) *A. albovelatum*, NZS121; note pigmented ganglion. *ungulatum* species-group: (402) *A. ungulatum*, NZS91; ganglion unpigmented (scale bar = 0.1 mm).

Fig. **403–419** Hypostomata of final instar larvae of *Austrosimulium*: Fig. 403, 404 *australense*-subgroup: (403) *A. australense*, NZN93; (404) *A. longicorne*, NZS115. Fig. 404–413 *tillyardianum*-subgroup: (405) *A. albovelatum*, NZS121; (406) *A. alveolatum*, Barrosa Creek; (407) *A. dugdalei*, NZN48; (408) *A. extendorum*, Sawyers Beach (scale bar = 0.025 mm).

Hypostomata of final instar larvae of *Austrosimulium*, *tillyardianum*-subgroup (cont.): (409) *A. fiordense*, Glaisnock River; (410) *A. laticorne,* NZS1; (411) *A. multicorne*, Balloon Hut; (412) *A. stewartense*, Freshwater Creek; (413) *A. tillyardianum*, Maitai River (Tonnoir) (scale bar = 0.025 mm).

Hypostomata of final instar larvae of *Austrosimulium*, Fig. 414–416 *ungulatum*-subgroup: (414) *A. campbellense*, Campbell Island; (415) *A. ungulatum*, NZS49; (416) *A. vexans*, Auckland Islands. Fig. 417–419 *unicorne*-subgroup: (417) *A. bicorne*, NZS133; (418) *A. tonnoiri*, NZS32; (419) *A. unicorne*, NZS132 (scale bar = 0.025 mm).

Fig. **420–436** Mandible apices of final instar larvae of *Austrosimulium*: Fig. 420, 421 *australense*-subgroup: (420) *A. australense*, NZN93; (421) *A. longicorne*, NZN32. Fig. 422–430 *tillyardianum*-subgroup: (422) *A. albovelatum*, NZS121; (423) *A. alveolatum*, NZS57a; (424) *A. dugdalei*, NZN48b; (425) *A. extendorum*, Sawyers Beach (scale bar = 0.02 mm).

Mandible apices of final instar larvae of *Austrosimulium*, *tillyardianum*-subgroup (cont.): (426) *A. fiordense*, Glaisnock River; (427) *A. laticorne*, NZS1; (428) *A. multicorne*, Balloon Hut; (429) *A. stewartense*, NZS164; (430) *A. tillyardianum*, NZS58 (scale bar = 0.02 mm).

Mandible apices of final instar larvae of *Austrosimulium*, Fig. 431–433 *ungulatum*-subgroup: (431) *A. campbellense*, Campbell Island; (432) *A. ungulatum*, NZS27; (433) *A. vexans*, Auckland Islands. Fig. 434–436 *unicorne*-subgroup: (434) *A. bicorne*, Dumbleton specimen; (435) *A. tonnoiri*, NZS32a; (436) *A. unicorne*, NZS132 (scale bar = 0.02 mm).

Fig. **437–453** Anal sclerites of final instar larvae of *Austrosimulium*, Fig. 437, 438 *australense*-subgroup: (437) *A. australense*, NZN93; (438) *A. longicorne*, NZN32. Fig. 439–447 *tillyardianum*-subgroup: (439) *A. albovelatum*, NZS121; (440) *A. alveolatum*, NZS57a; (441) *A. dugdalei*, NZN48b; (442) *A. extendorum*, Sawyers Beach (scale bar = 0.1 mm).

Anal sclerites of final instar larvae of *Austrosimulium*, *tillyardianum*-subgroup (cont.): (443) *A. fiordense*, Glaisnock River; (444) *A. laticorne*, NZS1; (445) *A. multicorne*, Balloon Hut; (446) *A. stewartense*, Fern Gulley; (447) *A. tillyardianum*, NZS6 (scale bar = 0.1 mm).

Anal sclerites of final instar larvae of *Austrosimulium*, Fig. 448–450 *ungulatum*-subgroup: (448) *A. campbellense*, Campbell Island, Dumbleton; arrow indicates rudimentary development of accessory sclerite; (449) *A. ungulatum*, NZS27; (450) *A. vexans*, Auckland Islands. Fig. 451–453 *unicorne*-subgroup: (451) *A. bicorne*, NZS133; (452) *A. tonnoiri*, Darran Mountains; (453) *A. unicorne*, NZS32; arrow indicates lack of accessory sclerite (scale bar = 0.1 mm).

Fig. **454–455** Larvae of *Austrosimulium* in situ, arrows indicate direction of water flow, arrowheads indicate pupae: (454) *A. tillyardianum*, NZS2; (455) *A. australense*, NZS74a.

Fig. **456–498** Typical habitats for immature stages of New Zealand *Austrosimulium*: Fig. 456–485 *australense* species-group: Fig. 456–458 *A. albovelatum*: (456) Stour River, NZS121; (457) Pudding Hill Stream, NZS121; (458) Forest Stream, Mesopotamia, NZS125. Fig. 459, 460 *A. alveolatum*: (459) Emily Stream, Lake Heron, NZS123; (460) Gentleman Smith Stream, Lake Heron, NZS136. Fig. 461 *A. australense*: (461) Kowhai Park, stream, Warkworth, NZN74a.

Typical habitats for immature stages of New Zealand *Austrosimulium*, *australense* species-group (cont.): Fig. 462–464 *A. australense*: (462) Mangamuka River, NZN80a; (463) Kaeo River, NZN99; (464) Kaipipi Stream, Stewart Island, NZS170. Fig. 465 *A. dugdalei*: (465) Mangaio Stream, Desert Road, NZN48b. Fig. 466 *A. extendorum:* (466). Sawyers Beach, Stewart Island, NZS167, arrow indicates position of larvae. Fig. 467 *A. laticorne*: (467) Kenepuru Head stream, NZS2.

Typical habitats for immature stages of New Zealand *Austrosimulium*, *australense* species-group (cont.): Fig. 468–469 *A. laticorne*: (468) tributary to Lill Burn, NZS155; (469) Granity Creek, NZS159. Fig. 470–474 *A. longicorne*: (470) Kowhai Park, stream, Warkworth, NZN74; (471) Okeover Stream, NZS14; (472) Moerangi Station ditch, November, NZN111; (473) Moerangi Station ditch, February.

Typical habitats for immature stages of New Zealand *Austrosimulium*, *australense* species-group (cont.): Fig. 474 *A. longicorne*: (474) headwater Frazer River, Old Man Range, NZS40. Fig. 475–478 *A. multicorne*: (475) upper Acheron River, NZS131; (476) Lake Howden outlet, NZS150; (477) Scour Stream, Rangitata Valley, NZS124; (478) Soup Creek, Rangitata Valley, NZS126. Fig. 479–481 *A. stewartense*: (479) Vaila Voe Bay stream, Stewart Island, NZS165.

Typical habitats for immature stages of New Zealand *Austrosimulium*, *australense* species-group (cont.): Fig. 480, 481 *A. stewartense*: (480) Mill Creek, Stewart Island, NZS162; (481) Alton Burn, Tuatapere, NZS156. Fig. 482–485 *A. tillyardianum*: (482) Rangitikei River, Mokai Canyon, NZN91; (483) Kowhai River, Kaikoura, NZS11; (484) Maitai River, NZS6; (485) Wainui stream, Banks Peninsula, NZS58.

(Above) Typical habitats for immature stages of New Zealand *Austrosimulium*, *ungulatum* species-group: Fig. 486, 487 *A. bicorne*: (486) Upper Twin Creek, Temple Basin, NZS133a; (487) Upper Otira River, NZS140. Fig. 488 *A. campbellense*: (488) Tucker Stream, Tucker Cove, Campbell Island (L. J. Dumbleton 1958). Fig. 489–491 *A. tonnoiri*: (489) Pass Creek, Routeburn, NZS151; (490) Snow cave stream, Homer Tunnel; (491) Homer Tunnel cascade, NZS32.

(Right) Typical habitats for immature stages of New Zealand *Austrosimulium*, *ungulatum* species-group (cont.): Fig. 492–495 *A. ungulatum*: (492) Flora Hut Stream, NZS91; (493), Blue Duck Scenic Reserve stream, Kaikoura, NZS117; (494) Ribbonwood Creek, Franz Josef, NZS49; (495) Trident Falls Stream, Waiho River bed, NZS141. Fig. 496, 497 *A. unicorne*: (496) Birch Hill Stream, Mount Cook, NZS128; (497) Pegleg Creek, Arthurs Pass, NZS132. Fig 498 *A. vexans*: (498) Teal Lake outlet stream, Enderby Island, Auckland Islands (L. J. Dumbleton 1963).

Fig. **499–504**. Parasitoids of *Austrosimulium* larvae: Fig. 499–502 Blastocladiales: (499) *Coelomycidium* (?)*simulii*, head of larval *A. stewartense,* NZS159; (500) *Coelomycidium* (?)*simulii*, posterior abdomen, *A. ungulatum*, NZS134; (501) deformed pharate pupal gill, final instar larva, *A. laticorne*, infected with *Coelomycidium* (?)*simulii*, NZS165; (502) deformed pharate pupal gill, final instar larva, *A. ungulatum*, infected with *Coelomycidium* (?)*simulii*, NZS134. Fig. 503 Nematoda: (503) *Austromermis namis* in final instar larva, *A. ungulatum*, Porters Pass. Fig. 504 (?)Thelohaniidae: (504) (?)*Thelohania*, final instar larva *A. tonnoiri*, NZS32 (scale bar, Fig. 499–503 = 0.2 mm; Fig. 504 = 0.005 mm).

Fig. **505** Strict Consensus tree (TL 99) of 10680 equally parsimonious trees (EPTs) showing the most parsimonious relationships for *Austrosimulium*.

Fig. **506 (left)** 50% Majority Rule Consensus tree (TL 99) from 815 EPTs after successive weight heuristic analysis, showing a hypothesis of relationships for *Austrosimulium.* Bootstrap branch support is indicated.

Fig. **507 (above)** Shortest tree possible with polytomies resolved (MacClade™) showing a hypothesis of species relationship for New Zealand representatives of *Austrosimulium*; arranged after Dumbleton (1973). Independent evidence from distribution and general habitat requirements of larvae is indicated. Three Kings Islands (TH), Stewart Island (SI), Campbell Island (CA), Auckland Islands (AU), South America (SA), Australia (Aust.), high altitude (HA), cold water (CW), cool/temperate (CT), temperate (TP), warm (WM), small streams (SS), large streams/rivers (LS), shaded (SD), open/sunlit (OS), vegetation (VG), hard substrate (HS). Half squares indicate occasional occurrence.

Fig. **508a** Neighbour joining tree of mDNA gene CO1 (800 bp) for the *tillyardianum*-subgroup of *Austrosimulium* species. Species names in full. Homogenous haplotype groups have been collapsed. South Island localities indicated by blue, North Island by yellow.

Fig. **508b** Neighbour joining tree of mDNA gene CO1 (800 bp) for the *tillyardianum*-subgroup of *Austrosimulium* species. Species names grouped. Homogenous haplotype groups have been collapsed. South Island localities indicated by blue, North Island by yellow.

Fig. **509a**. Neighbour joining tree of mDNA gene CO1 (800 bp) for the *australense*-subgroup and *ungulatum* species-group of *Austrosimulium* (continued from Fig. 508). Species names in full. Homogenous haplotype groups have been collapsed. South Island localities are indicated by blue, Auckland Islands in purple.

Fig. **509b** Neighbour joining tree of mDNA gene CO1 (800 bp) for the *australense*-subgroup and *ungulatum* species-group of *Austrosimulium* (continued from Fig. 508a). Species names grouped. Homogenous haplotype groups have been collapsed. South Island localities indicated by blue, North Island by yellow, Auckland Islands by purple.

Fig. 510 Neighbour joining tree and distribution of haplotypes for mDNA gene CO1 (800 bp) of the South Island clade of *A. australense* and for *A. longicorne*.

Fig. 511 Neighbour joining tree and distribution of haplotypes for mDNA gene CO1 (800 bp) of part of the North Island clade of *A. australense* (continued Fig. 512, 513).

Fig. 512 Neighbour joining and distribution of haplotypes for mDNA gene CO1 (800 bp) of part of the North Island clade of *A. australense* (continued from Fig. 511; continued Fig. 513).

Fig. **513** Neighbour joining tree and distribution of haplotypes for mDNA gene CO1 (800 bp) of part of the North Island clade of *A. australense* (continued from Fig. 511, 512).

Fig. **514** Neighbour joining tree of mDNA gene CO1 (800 bp) for South Island and Auckland Islands *ungulatum*- and *unicorne*-subgroups of *Austrosimulium*.

Fig. **515** Sea levels during the last 250 000 years BP in relation to possible exposure of Foveaux Strait and Farewell Rise (Cook Strait) during glacial and interglacial periods. Fine solid line = sea level curve, adapted from Thompson & Goldstein (2006). Fine dotted line = sea level estimates from Huybrecht (2002).

Fig. **516** Possible extent of land, illustrated by light stippling, between northern North Island and the Three Kings Islands at maximum sea level depression (-135 m) during the Otira Glaciation. The approximate contour was estimated from known contours and spot depths; adapted from hydrographic maps, Land Information New Zealand.

Fig. **517** Cook Strait showing bathymetric contours pertinent to connection of the South and North Islands during the last ice age (Otira Glaciation). Sea level depression was at maximum -135m and possible extent of land illustrated by light stippling. The approximate contour was estimated from known contours and spot depths; others were derived from hydrographic maps of both Land Information New Zealand and the National Aquatic Biodiversity Information System (NABIS) of the Ministry for Primary Industries, New Zealand.

Fig. **518** Bathymetry of Stewart Island, Auckland Islands, and Campbell Island showing possible extent of land, illustrated by light stippling, at maximum sea level depression (-135 m) during the Otira Glaciation. The approximate contour was estimated from known contours and spot depths; adapted from hydrographic maps of both Land Information New Zealand and, the National Aquatic Biodiversity Information System (NABIS), of the Ministry for Primary Industries, New Zealand. The position of the Great South Basin was adapted from Cook *et al*. (1999).

Fig. **519–526 (left)** New Zealand specimens collected 1844–1859. Fig. 519–521 'Simulium caecutiens' (= *Austrosimulium australense*) material in pill box in BMNH labelled from Bay of Islands, *Erebus* & *Terror*: (519) top view; (520) contents, some 450 badly damaged female adults; (521) bottom view. Fig. 522–526 *Austrosimulium australense*: (522) labels from lectotype, in NHMW; (523) lectotype, female adult, in NHMW; head, wings, most legs, and abdomen absent, postscutellum and abdominal scale mounted separately on the card; (524) slide of hind leg of lectotype mounted by J. S. Dugdale, 1970, in NHMW; (525) paralectotype, female adult, Enderlein preparation — small cardboard 'box' containing Canada Balsam mount between mica slips, in NHMW; (526) paralectotype, higher magnification of female wing, mid leg, parts of thorax, and hind leg, Canada Balsam mount between mica slips, in NHMW (scale bar Fig. 519–522 = 5.0 mm; Fig. 522, 523 = 0.5 mm; Fig. 524–526 = 1.0 mm).

Fig. **527–536 (above)** Labels associated with *Austrosimulium australense* specimens examined by Tonnoir and Enderlein: Fig. 527–530 Tonnoir labels in NHMW: (527, 528) topotype males; (529) topotype female; (530) female specimen, not a topotype. Fig. 531–534 Enderlein specimen preparation and labels in ZMHU: (531, 532) paralectotype, female wing (Flügel), in small cardboard 'box' containing Canada Balsam mount between mica slips; (533) paralectotype female legs (Beine), fore (v)-, mid (m)-, and hind legs (h); (534) higher magnification of female legs. Fig. 535, 536 Tonnoir labels in ZMHU: (535) topotype, female; (536) male specimen, not a topotype (scale bar Fig. 527–530, 535–536 = 2 mm; Fig. 531, 533 = 10 mm; Fig. 532 = 0.5 mm).

Fig. **537** Doug and Ruth Craig at the grave of Dr Andrew Sinclair (43.630406°S, 170.910712°E), who collected the first extant *Austrosimulium* specimens. Sinclair drowned in the Rangitata River near Mesopotamia Station on 22 March 1861 (Department of Conservation 2011). Mount Sinclair is in the background and a strong Norwester wind is blowing (24 November 2011).

Fig. **538** *Austrosimulium ungulatum* pupa on a grass seedhead.

Fig. **539 (right)**, **540 (below)** *Austrosimulium longicorne* in a high altitude, slow-flowing, seepage on an iron bacteria film at Silica Rapids, Mt Ruapehu, NZN126, 23 January 2012 (arrow indicates direction of flow, scale bar = 4.0 mm).

Maps 1–19 Collection localities for New Zealand *Austrosimulium* species. Open circles = Craig & Craig collections 2006–2012 (Appendix 1). The 2-letter codes and their aquatic ecoregions are provided on Map 20 and p. 38.

Map 5 Collection localities *Austrosimulium campbellense*

Map 19 Collection localities *Austrosimulium vexans*

TAXONOMIC INDEX

This index covers the nominal taxa mentioned in the text, regardless of their current status in taxonomy. Taxa in **bold** indicate those described in this monograph. Page numbers in **bold** indicate main monograph entries, numbers in *italic* indicate an illustration or diagram. The letter "**k**" after a page indicates an identification key; "**m**", a distribution map.

Area codes for collecting localities from mainland New Zealand, North Island (from Walker, A. K.; Crosby, T. K. 1988. The preparation and curation of insects. *New Zealand DSIR Information Series 163*).

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Nematoda

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NGĀ PĀNUI

Kua whakatūria tēnei huinga pukapuka hei whakahauhau i ngā tohunga whai mātauranga kia whakaputa i ngā kōrero poto, engari he whaikiko tonu, e pā ana ki ngā aitanga pepeke o Aotearoa. He tōtika tonu te āhua o ngā tuhituhi, engari ko te tino whāinga, kia mārama te marea ki ngā tohu tautuhi o ia ngārara, o ia ngārara, me te roanga atu o ngā kōrero mō tēnā, mō tēnā.

He titiro whāiti tā tēnei pukapuka ki ngā mea noho whenua, kāore he tuarā; i pēnei ai i te mea kei te mōhio whānuitia ngā mea whai tuarā, ā, ko ngā mea noho moana, koirā te tino kaupapa o te huinga pukapuka *NIWA Biodiversity Memoirs.*

Ka āhei te tangata ki te **whakauru tuhituhinga** mehemea kei a ia ngā tohungatanga me ngā rauemi e tutuki pai ai tana mahi. Heoi anō, e wātea ana te Kohinga Angawaho o Aotearoa hei āta tirotiro mā te tangata mehemea he āwhina kei reira.

Me whāki te kaituhi i ōna whakaaro ki tētahi o te Kāhui Ārahi Whakarōpūtanga Tuarā-Kore, ki te Ētita rānei i mua i te tīmatanga, ā, mā rātou a ia e ārahi mō te wāhi ki tana tuhinga.

Ko te hunga pīrangi **hoko pukapuka**, me tuhi ki *Fauna of N.Z.*, Manaaki Whenua Press, Manaaki Whenua, Pouaka Poutāpeta 40, Lincoln 8152, Aotearoa.