Diversity and biogeography of the New Zealand species of the genus *Pseudolycoriella* (Sciaridae: Diptera)

Dissertation

zur Erlangung des
Doktorgrades der Naturwissenschaften (Dr. rer. nat.)

der

Naturwissenschaftlichen Fakultät I
– Biowissenschaften –
der Martin-Luther-Universität
Halle-Wittenberg,

vorgelegt

von Herrn Arne Köhler
geb. am 16.11.1981 in Berlin

Gutachter: Prof. Dr. Thomas Schmitt, Müncheberg
Prof. Dr. Gerald B. Moritz, Halle (Saale)
Prof. Dr. Matthias Jentzsch, Dresden

Verteidigung: 28. November 2024

Abstract

The Black Fungus Gnats of New Zealand have only been taxonomically analysed in two major studies to date. Nevertheless, many undiscovered species are still to be expected, especially on the less anthropogenically modified South Island. The cosmopolitan genus *Pseudolycoriella* MENZEL & MOHRIG, 1998, of which five species were previously known from New Zealand, was used as an exemplary study. In combination with a new inventory of the species, the biogeography of the New Zealand representatives of the genus is also discussed. The taxonomic analysis was based on the imaginal morphology of the males as well as three molecular markers—two mitochondrial genes and one nuclear gene. The gene sequences obtained were also used for biogeographical analyses.

The species inventory was expanded to 36, with 30 species being newly described. A junior synonym was found for one species. The species can be grouped into four species complexes, whereby the phylogenetically youngest complex can be categorised as a separate species group and placed among the eight existing species groups of the provisional genus classification. The three other species complexes form a purely New Zealand monophylum, which is classified in the *Pseudolycoriella bruckii* species group. As a result of the description of the new species, the already existing imbalance in the distribution of species among the various zoogeographical regions is further weighted in favour of Australasia. A revision of the genus is urgently needed to replace the inadequate system of species groups and to clarify the question of the zoogeographical origin of the genus.

For four selected species, the distribution of different haplotypes was used to recognise intraspecific distribution patterns in New Zealand. This proved the usefulness of the genus for the clarification of biogeographical questions. Two species show a northern centre of genetic diversity. Above the species level, at least 13 dispersal events were detected across the strait separating the two main islands. Of these, nine were directed southwards and one northwards. For three dispersal events, no direction of dispersal could be ascertained. From this it was concluded that North Island is the centre of radiation of the genus on New Zealand. This is interpreted as a consequence of the Pleistocene glaciation cycles.

The initial colonisation of New Zealand by this genus occurred in three independent events, presumably in the late Miocene, in the late Pliocene and at the Pliocene/Pleistocene boundary. An Australian origin for the most recent colonisation event is likely and is considered most plausible for the two older ones.

Zusammenfassung

Die Trauermücken Neuseelands wurden bisher nur von zwei größeren Studien taxonomisch bearbeitet. Dennoch sind noch viele unentdeckte Arten, vor allem auf der weniger vom Menschen beeinflussten Südinsel, zu erwarten. Exemplarisch wurde die kosmopolitische Gattung *Pseudolycoriella* MENZEL & MOHRIG, 1998, von der bisher fünf Arten von Neuseeland bekannt waren, bearbeitet. Neben einer reinen Inventarisierung der Arten wird auch die Biogeographie der neuseeländischen Vertreter der Gattung erörtert. Die taxonomische Untersuchung erfolgte auf Basis der Imaginalmorphologie der Männchen sowie von drei molekularen Markern, zwei mitochondrieller Gene und einem Kerngen. Die gewonnen Gensequenzen wurden auch für biogeographische Analysen genutzt.

Das Arteninventar wurde auf 36 erweitert, wobei 30 Arten neu beschrieben wurden. Für eine Art wurde ein jüngeres Synonym festgestellt. Die Arten lassen sich in vier Artkomplexe gliedern, wobei der phylogenetisch jüngste Komplex sich als Artenruppen zu den bestehenden acht Artengruppen der provisorischen Gattungssystematik einreihen lässt. Die drei anderen Artkomplexe bilden ein rein neuseeländisches Monophylum, das sich in die *Pseudolycoriella bruckii*-Artengruppe einordnet. Mit den neuen Arten verstärkt sich das bereits bestehende Ungleichgewicht in der Verteilung der Arten auf die verschiedenen zoogeographischen Regionen weiter zugunsten der Australis. Eine Revision der Gattung ist dringend angeraten, um zum einen das unzureichende System der Artengruppen zu ersetzen und die Frage nach dem zoogeographischen Ursprung der Gattung zu klären.

Bei vier ausgewählten Arten wurden an Hand der Verteilung von verschiedenen Haplotypen intraspezifische Verbreitungsmuster in Neuseeland erkannt und die Nutzbarkeit der Gattung für die Klärung biogeographischer Fragestellungen demonstriert. Bei zwei Arten zeigt sich ein nördlicher Schwerpunkt der genetischen Vielfalt. Oberhalb der Artebene wurden mindestens 13 Ausbreitungsereignisse über die die beiden Hauptinseln trennende Meerenge festgestellt. Von diesen waren neun nach Süd und eine nach Nord gerichtet. Für drei Ausbreitungsereignisse ließ sich keine Ausbreitungsrichtung ableiten. Daraus wurde geschlussfolgert, dass die Nordinsel das Radiationszentrum der Gattung auf Neuseeland ist. Dieses wird als Folge der pleistozänen Vergletscherungszyklen interpretiert.

Die ursprüngliche Kolonialisierung Neuseelands durch die Gattung erfolgte dreimal unabhängig und vermutlich im späten Miozän, im späten Pliozän sowie an der Plio-/Pleistozän-Grenze. Ein australischer Ursprung für das jüngste Kolonisierungsereignis ist wahrscheinlich und für die beiden älteren zu vermuten.

Preface and copyright statement

Due to the cumulative nature of this thesis, i. e. several articles on one topic are presented together, the reference section (chapter 7) covers chapters 1, 2 and 6. Chapters 3 to 5, i. e. the articles already published, each have a separate reference section at the end of the respective chapter. Furthermore, the numbering of the figures in this work is not standardised. Chapters 3 to 5 have their own consecutive numbering, which is based on the author guidelines of the respective journals. When figures from these chapters are cited, the figure number and the chapter concerned are given together to make navigation easier for the reader. The previously unpublished figures in chapters 2 and 6 are numbered with Roman numerals.

KÖHLER and SCHMITT (2023) provided an extensive electronical supplement. Adding this supplement would have exceeded the scope of this work, but it can be accessed under https://doi.org/10.6084/m9.figshare.24517117. For easier access, a QR code can be found on page 126.

1 Introduction

1.1 General

Biogeography is the scientific discipline that describes the distribution of taxa around the globe and aims to reveal the underlying patterns and processes. It arose as an independent branch of science in the course of the great expeditions of the 19th century. Thus, the names of outstanding explorers such as Alexander VON HUMBOLDT (1769–1859), Charles DARWIN (1809–1882), and Alfred Russel WALLACE (1823–1913) are inseparably linked with the blossoming of this discipline (SCHMITT 2020). At the end of the last century, the utilisation of molecular biological methods was the next significant milestone in this discipline. It was now possible to recognise differences in populations that have not (yet) manifested themselves phenotypically. Biogeographical processes that took place in shorter periods of time could now also be analysed. HEWITT (1996), for instance, was able to reconstruct the postglacial expansion across Europe of the grasshopper *Chorthippus parallelus* (ZETTERSTEDT, 1821) based on the haplotype distribution of different populations.

Given the genesis of this branch of science, which is strongly characterised by voyages across the oceans, it is not surprising that the composition of the flora and fauna of remote archipelagos and islands has always attracted particular attention. Island biogeography has thus become a special branch of this discipline (SCHMITT 2020). From this perspective, a very famous group of islands in the southern hemisphere is New Zealand. It gained fame far beyond biologists, as it harbours/harboured living fossils and iconic endemics. Well-known examples are extinct giant wingless birds (†Dinornithiformes; Moas), ancient lizards otherwise only known from the fossil record [*Sphenodon punctatus* (GRAY, 1842); Tuatara], sandpipers with asymmetrically bent beaks (*Anarhynchus frontalis* QUOY & GAIMARD, 1830; Wrybill), giant crickets (*Deinacrida* spp.; Giant Wētā), etc. Not to forget the national symbol of New Zealand—the famous Kiwi (*Apteryx* spp.). Actually, these are five species of flightless birds with stubby wings and nostrils at the tip of their beaks, an adaptation to a hedgehog-like lifestyle. Besides these widely known extraordinary species, exceptional taxa are found also among the two-winged flies (Diptera): Rangomaramidae, an endemic gnat family with five species, belonging to the Sciaroidea; the New Zealand bat fly (*Mystacinobia zelandica* HOLLOWAY, 1976), which parasitises New Zealand bats and is so highly derived that it is placed in a family of its own—the Mystacinobiidae; or the famous "glow-worm" *Arachnocampa luminosa* (SKUSE, 1891), whose predatory, bioluminescent larvae are a boon to the New Zealand tourism industry.

A rather unspectacular part of the dipterous fauna of New Zealand are the Sciaridae. These gnats—colloquially known as Black Fungus Gnats—belong to the suborder Nematocera, which along with other midges and gnats includes black flies (Simuliidae), crane flies (Tipuloidea), and mosquitos (Culicidae). Among these, the Sciaridae are placed together with the families Bolitophilidae, Cecidomyiidae, Diadocidiidae, Ditomyiidae, Keroplatidae, Mycetophilidae, Rangomaramidae in the superfamily Sciaroidea. The Sciaridae, with currently about 3000 known species (VILKAMAA et al. 2023), are one of most species-rich families in the superfamily. Due to their uniform habitus—a brief description of their morphology is given in chapter 1.3—they did not excite the interest of many dipterists. As evidence for this persistent neglect, the sciaridologists like to cite the legendary comment by Ignaz R. SCHINER (1813–1873), published in the preface to the monograph on these gnats by his friend Johannes WINNERTZ (1800–1890): "Die Sciarinen sind monoton in ihren Farben, monoton in ihrem Betragen, monoton in ihrem Habitus, monoton in allen Richtungen und Beziehungen, sie zeigen nichts Markirtes, nichts Charakteristisches... [The sciarines are monotonous in their colours, monotonous in their behaviour, monotonous in their habitus, monotonous in all directions and relationships, they show nothing distinctive, nothing characteristic...]" (WINNERTZ 1867). It is therefore not surprising that a large number of sciarid species still await discovery and scientific description. For instance, SAVAGE et al. (2019) found that the number of barcode index numbers [BINs—automatically assigned operational taxonomic units (OTUs), i. e. potential species (RATNASINGHAM & HEBERT 2013)] recorded for Canada exceeded the number of described sciarid species by a factor of 22 (129 known species compared with 2863 BINs). Furthermore, this underestimation varies between the zoogeographic realms, whereby the Palaearctic fauna is the best-studied (MENZEL & MOHRIG 2000). The reason for this is that the most important and influential experts in this field come from Europe. In contrast, the Sciaridae in the south-west Pacific region of Australasia and in Australia itself are regarded as "orphaned taxa" (AUSTIN et al. 2004, BICKEL 2009), which are extremely abundant but poorly studied.

On the other hand, SCHINER also emphasised the great ecological importance of Sciaridae: "Die Sciaren sind aber im Haushalte der Natur von grosser Wichtigkeit... Die Gartenerde ist selten leer von Sciaren-Lärvchen... [However, sciarids are of great importance in nature's household... The garden soil is rarely empty of sciarid larvae]" (WINNERTZ 1867). As they occur at high abundances (BRAUNS 1954) and feed on plant litter, decaying wood or plant tissue (SHIN et al. 2013), they play a major role as decomposers in the upper soil layers. Some species like *Lycoriella ingenua* (DUFOUR, 1839) or *Bradysia impatiens* (JOHANNSEN, 1912) honour the vernacular name of the family by being fungivore, as listed for example by BROADLEY et al. (2018) or KATUMANYANE et al. (2020). In this context, it is interesting to note that TRINCA et al. (2023) discovered that *Pseudolycoriella hygida* (SAUAIA & ALVES, 1968)—a neotropical species belonging to the genus studied in this thesis—utilises carbohydrate-active enzymes in the saliva for degrading plant and fungal cell wall polysaccharides. Accordingly, the adaptation to plant or fungal tissues allowed some species to emerge as economic pests in agricultural production, which is why these pest species are an exception to the long-standing scientific neglect of the family and have received more attention (MENZEL & MOHRIG 2000, BROADLEY et al. 2018).

The Sciaridae have also attracted the interest of geneticists, as they have some peculiarities in their inheritance. For instance, sciarid flies undergo chromosome diminution at several states of their life cycle: at male meiosis I, during early cleavages and in germ cell development (Metz 1938, Goday & Esteban 2001). Due to the modified male meiosis, a sperm cell contains a diploid maternal gonosome, while an egg cell has whether a maternal or a paternal haploid gonosome. The zygote therefore contains three gonosomes and during the early cleavages one or two of them are eliminated, which leads to sex-determination of the embryo (Metz 1938). A maternally inherited factor is responsible for ensuring that the offspring of a female have the same sex. Another genetic peculiarity of Sciaridae are germline-restricted chromosomes, which are also found in the dipteran families of Cecidomyiidae and Chironomidae (Hodson & Ross 2021).

However, our understanding of the biogeography of Black Fungus Gnats remains a blind spot, as these globally distributed gnats have not been subjected to any major biogeographic analysis. Only brief biogeographic remarks are found in some taxonomic revisions, e. g. Mohrig and Jaschhof (1999), Menzel and Mohrig (2000), etc.

Accordingly, it seems to be fruitful to analyse a taxonomically poorly accessible group, which is also distributed in a region that has been shaped by many geological processes and thus exhibits many interesting biogeographical patterns.

1.2 New Zealand's Geographic History

In the course of the Mesozoic [252–66 Ma; stratigraphic dates according to Raine et al. (2015)], the supercontinent Pangaea broke up into Laurasia in the North and Gondwana in the South. Gondwana also fragmented into several parts, which continuously drifted apart. The fragments that already resembled the shape of today's continents were Africa, Antarctica, Australia, India, South America, and Zealandia. The latter covers an area that is now more than 90 % submerged, and only the Chatham Islands, New Caledonia, New Zealand, and several smaller islands are above sea level. However, because this area consists of continental crust, it can be argued that it should be recognised as a continent (Mortimer et al. 2017).

After its isolation from Australia ca. 82 million years ago (Wallis & Trewick 2009), Zealandia remained a plaything of various geological forces. From the Palaeocene (66.0–56.0 Ma), Zealandia was inundated, with a flood peak during the Oligocene (33.9–23.0 Ma). There has been an intense debate about the extent to which the area of present-day New Zealand was flooded. After reviewing estimated emergence dates of New Zealand taxa, Wallis and Jorge (2018) concluded that there is no disjunction between emergence dates before and after this inundation. A complete submergence of New Zealand is therefore highly unlikely to have occurred. Another geological peculiarity of New Zealand that still has an impact today is that the landmass lies on two tectonic plates that are bounded by an active subduction zone. This plate boundary between the Australian and the Pacific plate came into existence during the Eocene (56.0–33.9 Ma) (Ballance 2009). The landmasses of what are nowadays North Island and the western part of South Island are positioned on the Australian plate, while the eastern part of South Island is located on the Pacific plate. The anti-clockwise movement of the Pacific plate led to the collision of these two plates and the formation of an interjacent transform fault about 25 million years ago. The sideways-movement along this fault piled up enormous amounts of material which formed the Southern Alps approximately five million years ago (Coates & Cox 2002). Since then, this high alpine mountain range has been a solid barrier between the eastern and western parts of South Island, which results, for example, in very different climates on each side. As a typical feature of high alpine mountain ranges, the Southern Alps harbour glaciers which acted as a nucleus for the extensive glaciation during the Pleistocene (2.6–0.0 Ma). The periodic glacial cycles of this epoch affected New Zealand in several ways. Large areas, especially of South Island, were devastated by the advancing ice sheets, forcing populations into small refugia or to extinction. Interglacial warming and glacier retreat allowed the recolonization of the previously depopulated areas. A very famous botanical example is the distribution of the southern beeches (*Nothofagus* spp., Nothofagaceae) across South Island. All five species exhibit a distribution gap—the so called "beech gap"—in central South Island (Wardle 1963, Rawlence et al. 2021), where postglacial colonisation has not occurred. Such oscillations of population size and distribution in the course of displacement into small-scale refugia naturally leads to effects on population genetics (Hewitt 1996). Another phenomenon in New Zealand related to the glacial cycles of the Pleistocene is repeated marine regressions that led to the formation of land bridges between the two major islands (Bunce et al. 2009, Trewick & Bland 2012). This allowed for the first time an easy exchange between the previously isolated terrestrial faunas (Bunce et al. 2009).

The sequence of glacial and interglacial periods, with their respective New Zealand names, is given by Barrell (2011). The last glacial maximum in New Zealand occurred between 31 and 29 ka (Williams et al. 2015).

Beside the aforementioned "beech gap" on South Island, biogeographic boundaries have also been discovered on North Island. The first recognised boundary was the later so-called Taupo Line, proposed by Wardle (1963) on the basis of plant distribution. This border runs East-West through the middle of North Island at approximately 39° S. Sea-strait flooding, tectonic uplift, volcanism and glacial cycles have been discussed as causes of the dichotomy (Ellis et al. 2015). In recent years the validity of the Taupo line has however been questioned, and either amended or replaced by other postulated boundaries, e. g. Northland line, Kauri line, and Cockayne's line (Ellis et al. 2015, Painting et al. 2017).

In addition to the geological factors that have affected the distribution of organisms, the significance of the recent climatic zones of New Zealand should not be underestimated. According to Troll and Paffen (1964), New Zealand is characterised by three different climate zones: The northern three quarters of North Island belong to a temperate subtropical zone with a permanently humid climate, while South Island belongs to a temperate zone that is strongly oceanic west of the Southern Alps and more temperate east of this meteorological divide.

1.3 Morphological characterisation of Sciaridae with special emphasis on the genus *Pseudolycoriella*

Typically, Sciaridae are small to minute flies with a uniform habitus (fig. Ia) that makes the members of the family easy to recognise. Their body length generally spans 0.7–8.0 mm whereby species up to 15 mm occur rarely (Menzel & Smith 2017). The vernacular name—Black Fungus Gnats—refers to their unspectacular black to brown body colour. The round head bears the large compound eyes which are connected with an eye bridge dorsal to the antennal bases (fig. 7 in chapter 4). Three ocelli are present. The long antennae consist of 16 segments—scape, pedicel, and a 14-segmented flagellum. In the taxonomy of sciarids, the length and width of the fourth segment of the flagellum, e. g. the sixth antennomere, is measured and thus used as standard for comparing species (fig. 1–5 in chapter 4). The mouthparts correspond to the typical ground plan of Diptera: labrum, hypopharynx, maxilla, and labium with attached labella. Adjected to the maxilla is the three-segmented maxillary palp, whose first segment bears species-typical sensilla and several long setae (fig. 6–7 in chapter 2). In *Pseudolycoriella*, the sensilla are arranged in a simple patch lacking the surrounding margin found in other sciarid genera. Prefrons and clypeus—head sclerites basal to the labrum—bulge outwards and the mouthparts are slightly elongated to form a small proboscis (fig. Ia & fig. 7 in chapter 2). Such pronounced proboscides are atypical for Sciaridae, but also occur in a few other genera, e. g. in *Rhynchosciara* Rübsaamen, 1894 or—to the greatest extent—in *Eugnoriste* Coquillett, 1896.

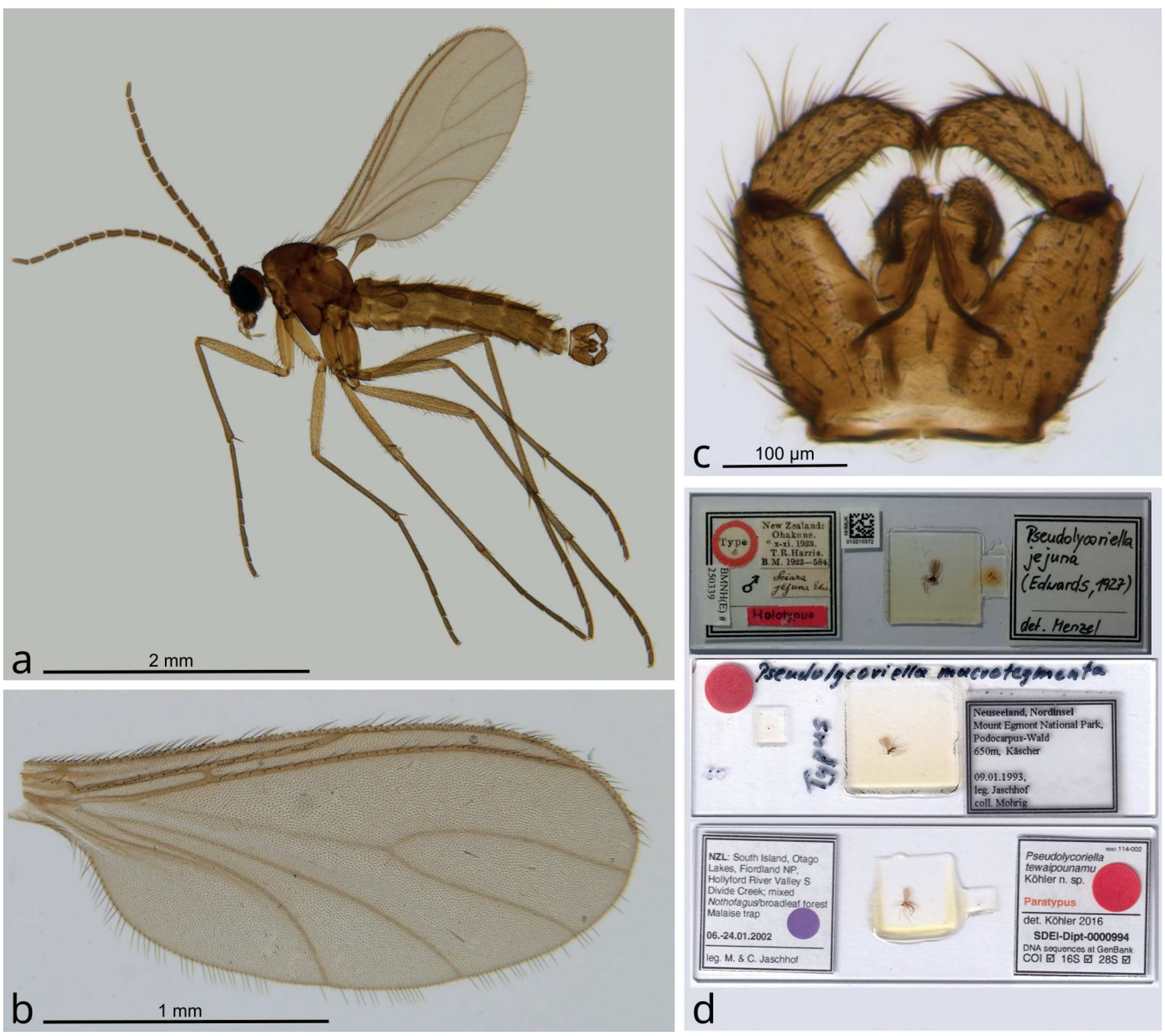

Figure I: a) Habitus of a paratype of *Pseudolycoriella tewaipounamu* Köhler, 2019, lateral view, the originally separated hypopygium is graphically added. **b)** Wing of same specimen, lateral view. **c)** Hypopygium, ventral view. **d)** Slides with type specimens: Holotype of *Pseudolycoriella jejuna* (Edwards, 1927); holotype of *P. macrotegmenta* Mohrig, 1999, and a paratype of *P. tewaipounamu* Köhler, 2019.

Of the thoracic appendages, the wings have very characteristic venation, by which the Sciaridae can be easily recognised: the median vein (M) bifurcates into an anterior (M_1) and posterior branch (M_2), and resembles a pitchfork with two tines (fig. Ib and fig. 9 in chapter 4). The tibial organ located anteriomedially on the fore tibia is of taxonomic value. It consists of a group of setae in a special arrangement and serves most probably for cleaning the antennae. *Pseudolycoriella* has a tibial organ with setae arranged in a single, not strictly linear row, surrounded by a more or less strongly developed margin (fig. 5B in chapter 3 & fig. 8 in chapter 4).

The claws on the tarsi of Sciaridae can be armed with teeth. Toothed claws are a typical characteristic of *Pseudolycoriella*, and they can be of enormous size, for instance in the *P. triacanthula* group (Mohrig 2013).

The most important structure for species delimitation in Sciaridae is the male copulatory organ attached on the posterior tip of the abdomen (fig. Ia). It is reduced in complexity compared to other fly families (fig. Ic). The basal structures are the gonocoxites to which the gonostyli are hinged. The gonostyli grasp the female abdomen during copulation (MacDonald et al. 1977), and vary species-typically in size, shape, setae armament, etc. Medioventrally on the gonocoxites is the actual copulatory organ—the so called tegmen (fig. 22–24 in chapter 4)—which transfers the spermatophore into the female's genital opening during copulation. In *Pseudolycoriella*, the tegmen is often equipped with lateral or medial structures, as for example in *P. bruckii* (Winnertz, 1867). There, the tegmen has two medio-posterior horn-like structures (Menzel & Mohrig 2000). The gonostyli of ***Pseudolycoriella*** possess several subapical strong spines, which stand out from surrounding setosity. In most species, their number varies between one and five, with two spines being most commonly present. These spines are rarely completely reduced. An apical tooth—a distinct hook-shaped, strongly sclerotised structure that occurs in many sciarid genera—is absent. An important diagnostic character of the male genital of *Pseudolycoriella* is a long whip-lash hair on the apical third of the gonostylus (fig. 22 in chapter 4). In some species, this whip-lash hair can be lost secondarily—as in the *Pseudolycoriella quadrispinosa* species group described by Mohrig (2013)—or even be doubled or tripled (see fig. 54 in chapter 4). Such a whip-lash hair also occurs in other genera, but the combination of its position on the apical half of the gonostylus with the absence of a gonostylar tooth is only found in *Pseudolycoriella* and *Eugnoriste*.

Female genitalia form a simple ovipositor and are weakly sclerotised (Menzel & Mohrig 2000). Accordingly, they do not show prominent structures, and therefore the taxonomy and systematics of the Sciaridae are currently still based exclusively on males.

1.4 Systematics of *Pseudolycoriella*

The genus *Pseudolycoriella* was erected by Menzel and Mohrig (1998) to accommodate species which formerly had been mistakenly assigned to the subgenus *Lycoriella* (*Hemineurina*). Menzel and Mohrig (2000) proposed three species groups for this new genus in order to collate morphologically similar species. These are the *P. bruckii* group, the *P. morenae* group, and the *P. horribilis* group. The *P. bruckii* group, which contains the largest number of species, is characterised by toothed claws, the absence of lobes on the inner base of the gonocoxites, and gonostyli without any tooth and with up to five spines. Currently, 41 of a total of 134 species are assigned to this species group (Tab. I). The two species forming the *P. morenae* group bear conspicuous lobes with bristles on the inner gonocoxites and the claws have no teeth. *Pseudolycoriella horribilis* (Edwards, 1931), currently the only member of the eponymous species group, shows a remarkable truncated tooth on the gonostylus.

Later, five more species groups were added, because new species did not fit into the three initial groups. First, Mohrig et al. (2004) introduced the *P. torva* group and the *P. aculeacea* group for species from the Caribbean. Species of the *P. torva* group have a reduced tibial organ containing only a weakly developed batch of bristles. Species of the *P. aculeacera* group are characterised by a large, ovoid gonostylus, a larger number of spines, and a tegmen without any structuration. In a study on the Sciaridae of Papua New Guinea, Mohrig (2013) established three additional species groups: the *P. longicostalis* group, the *P. triacanthula* group, and the *P. quadrispinosa* group. Members of the *P. longicostalis* group have deep sensorial pits on the antennomeres. Species assigned to the *P. triacanthula* group have three or more spines on the gonostylus, short antennomeres with a conspicuous grid structure, and claws with strong teeth. The *P. quadrispinosa* group is characterised by a reduction or a complete loss of the whip-lash hair and having more than two spines.

Heller (2012) proposed *Ostroverkhovana* Komarova, 2002 as the first subgenus of *Pseudolycoriella*, to accommodate *P. borealis* (Komarova, 2002), *P. lobosa* (Pettey, 1918), *P. nodulosa* (Mohrig & Krivosheina, 1985) and *P. villabonensis* Heller, 2012. However, Mohrig and Kauschke (2019) disagreed with this hypothesis and argued that the proposed characters are not sufficient for this assumption. The character similarity between *Pseudolycoriella* and *Eugnoriste*, e. g. the elongated mouthparts and the similar structure of the gonostylus, had led some researchers to speculate about congenerity (Heller 2012, Vilkamaa et al. 2012). Menzel and Mohrig (2000) recognized a sister relationship between *Pseudolycoriella* and the fossil genus †*Protolycoriella* Mohrig & Röschmann, 1995, which was described from Miocene amber inclusions (Röschmann & Mohrig 1995).

Table 1: Species of *Pseudolycoriella* sorted by species groups. Abbreviations: AFT–Afrotropic, AUS–Australasia, NEA–Nearctic, NEO–Neotropic, ORI–Oriental, PAL–Palaearctic.

Species group	Species	Distribution	Source of group assignment
P. aculeacera group	*P. aculeacera* Mohrig & Rulik, 2004	NEO	Mohrig et al. (2004)
	P. chlorothoracica Mohrig & Kauschke, 2019	NEA	Menzel et al. (2019)
	P. ovistyla Mohrig & Rulik, 2004	NEO	Mohrig et al. (2004)
	P. rotundostyla Mohrig & Rulik, 2004	NEO	Mohrig et al. (2004)
	P. rubroalata Mohrig, Kauschke & Broadley, 2018	AUS	Menzel et al. (2019)
	P. subovistyla Mohrig & Rulik, 2004	NEO	Mohrig et al. (2004)
	P. virgata Mohrig & Rulik, 2004	NEO	Mohrig et al. (2004)
P. bruckii group	*P. acicula* Vilkamaa, Hippa & Mohrig, 2012	AUS	Menzel et al. (2019)
	P. bispina Mohrig, 1999	AUS	Menzel et al. (2019)
	P. bisulca Vilkamaa, Hippa & Mohrig, 2012	AUS	Menzel et al. (2019)
	P. brevialata Mohrig & Kauschke, 2019	NEA	Menzel et al. (2019)
	P. breviantennata (Mohrig & Mamaev, 1983)	PAL	Menzel & Mohrig (2000)
	P. breviseta Mohrig, 1999	AUS	Menzel et al. (2019)
	P. bruckii (Winnertz, 1867)	PAL	Menzel & Mohrig (2000)
	P. brunnea (Bukowski & Lengersdorf, 1936)	PAL	Menzel & Mohrig (2000)
	P. campanulata (Frey, 1945)	PAL	Menzel & Mohrig (2000)
	P. capillosa Vilkamaa, Hippa & Mohrig, 2012	AUS	Menzel et al. (2019)
	P. compacta Heller, 2000	PAL	Heller (2000)
	P. dissonata (Mohrig & Mamaev, 1982)	PAL	Menzel & Mohrig (2000)
	P. flavipila Mohrig & Kauschke, 2019	NEA	Menzel et al. (2019)
	P. florentissima Mohrig & Rulik, 2004	NEO	Menzel et al. (2019)
	P. fuscivenosa Mohrig & Rulik, 2004	NEO	Menzel et al. (2019)
	P. fuscovenosa Mohrig, Kauschke & Broadley, 2020	AUS	Mohrig et al. (2020)
	P. hartmanni (Menzel & Mohrig, 1991)	PAL	Menzel & Mohrig (2000)
	P. hispana (Lengersdorf, 1957)	PAL	Menzel & Mohrig (2000)
	P. indocera Mohrig & Rulik, 2004	AFT	Menzel et al. (2019)
	P. japonensis (Mohrig & Menzel, 1992)	PAL	Menzel & Mohrig (2000)
	P. koreensis (Mohrig & Menzel, 1992)	PAL	Menzel & Mohrig (2000)
	P. latiflagellata Vilkamaa, Hippa & Mohrig, 2012	AUS	Menzel et al. (2019)
	P. latostylata Mohrig, Kauschke & Broadley, 2018	AUS	Menzel et al. (2019)
	P. martita Rudzinski, Baumjohann & Wolff, 2016	NEO	Rudzinski et al. (2016)
	P. monticula (Mohrig & Menzel, 1992)	PAL	Menzel & Mohrig (2000)
	P. paludum (Frey, 1948)	PAL	Menzel & Mohrig (2000)
	P. rigua (Menzel & Mohrig, 1991)	PAL	Menzel & Mohrig (2000)
	P. secura Mohrig, Kauschke & Broadley, 2020	AUS	Mohrig et al. (2020)
	P. setigera (Hardy, 1960)	AUS	Menzel & Smith (2009)
	P. simplex Vilkamaa, Hippa & Mohrig, 2012	AUS	Menzel et al. (2019)
	P. subbruckii (Mohrig & Hövemeyer, 1992)	PAL	Menzel & Mohrig (2000)
	P. submonticula (Mohrig & Mamaev, 1990)	PAL	Menzel & Mohrig (2000)
	P. tenebrioalata Mohrig, 2013	AUS	Mohrig (2013)
	P. tenuis Vilkamaa, Hippa & Mohrig, 2012	AUS	Menzel et al. (2019)
	P. tribulosa Vilkamaa, Hippa & Mohrig, 2012	AUS	Menzel et al. (2019)
	P. trispicata Vilkamaa, Hippa & Mohrig, 2012	AUS	Menzel et al. (2019)
	P. tumidior Vilkamaa, Hippa & Mohrig, 2012	AUS	Menzel et al. (2019)
	P. unispina (Mohrig & Krivosheina, 1983)	NEA	Menzel & Mohrig (2000)
	P. unispinata Mohrig, Kauschke & Broadley, 2020	AUS	Mohrig et al. (2020)
	P. villosa Vilkamaa, Hippa & Mohrig, 2012	AUS	Menzel et al. (2019)
	P. zealandica (Edwards, 1927)	AUS	Mohrig & Jaschhof (1999)
P. horribilis group	*P. horribilis* (Edwards, 1931)	AUS, ORI, PAL	Menzel & Mohrig (2000)
P. longicostalis group	*P. angustoantennata* Mohrig, Kauschke & Broadley, 2020	AUS	Mohrig et al. (2020)
	P. attrita Mohrig, 2013	AUS	Mohrig (2013)
	P. breviradiata Mohrig, Kauschke & Broadley, 2020	AUS	Mohrig et al. (2020)
	P. densispina Mohrig, 2013	AUS	Mohrig (2013)
	P. espinosa Mohrig, 2013	AUS	Mohrig (2013)
	P. espinula Mohrig, 2013	AUS	Mohrig (2013)
	P. longicostalis Mohrig, 2013	AUS	Mohrig (2013)
	P. paucispina Mohrig, 2013	AUS	Mohrig (2013)
	P. paucispinata Mohrig, Kauschke & Broadley, 2020	AUS	Mohrig et al. (2020)
	P. sinoupalpa Mohrig, 2013	AUS	Mohrig (2013)
P. morenae group	*P. morenae* (Strobl, 1900)	PAL	Menzel & Mohrig (2000)
	P. semialata (Edwards, 1913)	PAL	Menzel & Mohrig (2000)

Table I: Continued

Species group	Species	Distribution	Source of group assignment
P. quadrispinosa group	*P. bitorquia* Mohrig, 2013	AUS	Mohrig (2013)
	P. macrotrichata Mohrig, 2013	AUS	Mohrig (2013)
	P. microphalli Mohrig, 2013	AUS	Mohrig (2013)
	P. microtrichata Mohrig, 2013	AUS	Mohrig (2013)
	P. perspicua Mohrig, 2013	AUS	Mohrig (2013)
	P. praecipua Mohrig, 2013	AUS	Mohrig (2013)
	P. quadrispinosa Mohrig, 2013	AUS	Mohrig (2013)
	P. snellingi Mohrig, 2013	AUS	Mohrig (2013)
	P. tenebriocoxa Mohrig, 2013	AUS	Mohrig (2013)
P. torva group	*P. barbata* Mohrig & Rulik, 2004	NEO	Menzel et al. (2019)
	P. pulla Mohrig & Rulik, 2004	NEO	Menzel et al. (2019)
	P. torva Mohrig & Rulik, 2004	NEO	Menzel et al. (2019)
P. triacanthula group	*P. cavatiostyla* Mohrig, 2013	AUS	Mohrig (2013)
	P. commoda Mohrig, 2013	AUS	Mohrig (2013)
	P. consectaria Mohrig, Kauschke & Broadley, 2020	AUS	Mohrig et al. (2020)
	P. fortunata Mohrig, 2013	AUS	Mohrig (2013)
	P. globostylata Mohrig, Kauschke & Broadley, 2020	AUS	Mohrig et al. (2020)
	P. notanda Mohrig, Kauschke & Broadley, 2020	AUS	Mohrig et al. (2020)
	P. skusei Mohrig, Kauschke & Broadley, 2016	AUS	Menzel et al. (2019)
	P. triacanthula Mohrig, 2013	AUS	Mohrig (2013)
	P. vestita Mohrig, 2013	AUS	Mohrig (2013)
unplaced	*P. abrevicaudata* (Yang, Zhang & Yang, 1993)	ORI, PAL	
	P. anguistifurca (Alam, 1988)	ORI	
	P. basisetosa Mohrig & Kauschke, 2019	AUS	
	P. bifasciculata (Rudzinski, 1997)	AFT	
	P. borealis (Komarova, 2002)	PAL	
	P. cavatica (Skuse, 1888)	AUS	
	P. coecoalata Mohrig, 2003	NEO	
	P. curvimedia Mohrig & Rulik, 2004	NEO	
	P. curviseta Mohrig, 2003	NEO	
	P. defluviata Rudzinski, 2003	AFT	
	P. deformata Rudzinski, 2003	AFT	
	P. enigmatica Vilkamaa, Hippa & Heller, 2013	PAL	
	P. fascistylata (Alam, 1988)	ORI	
	P. ferocia Mohrig, 2003	NEO	
	P. fuscorubroides Mohrig & Blasco-Zumeta, 1996	PAL	
	P. hygida (Sauaia & Alves, 1968)	NEO	
	P. ignobilis (Skuse, 1888)	AUS	
	P. inexplorata Rudzinski, 2003	AFT	
	P. jejuna (Edwards, 1927)	AUS	
	P. jucunda (Johannsen, 1912)	NEA	
	P. kumasiensis (Rudzinski, 1997)	AFT	
	P. lobosa (Pettey, 1918)	NEA	
	P. longisetosa Mohrig & Kauschke, 2019	NEA	
	P. macrotegmenta Mohrig, 1999	AUS	
	P. mecocteniuni (Zhang & Yang, 1990)	PAL	
	P. meinacusi (Lane, 1959)	NEO	
	P. microcteniuni (Yang & Zhang, 1987)	AFT, PAL	
	P. neotropica (Lane, 1959)	NEO	
	P. nigrofemoralis Mohrig, Kauschke & Broadley, 2019	AUS	
	P. nocturna Mohrig & Kauschke, 2019	NEA	
	P. nodulosa (Mohrig & Krivosheina, 1985)	PAL	
	P. pallidula Vilkamaa, Hippa & Mohrig, 2012	AUS	
	P. pammela (Edwards, 1928)	ORI	
	P. parilis (Johannsen, 1912)	NEA, NEO	
	P. parilongiculmi (Alam, 1988)	ORI	
	P. patronata Rudzinski, 2003	AFT	
	P. planiforceps (Steffan, 1971)	NEA, NEO	
	P. pollicis (Pettey, 1918)	NEA	
	P. ponapensis (Steffan, 1969)	AUS	
	P. pristinata Rudzinski, 2003	AFT	
	P. pseudoparvula (Alam, 1988)	ORI	

Table I: Continued

Species group	Species	Distribution	Source of group assignment
	P. pugionata Rudzinski, 2003	AFT	
	P. sabroskyi (Steffan, 1969)	AUS	
	P. senticosa Vilkamaa, Hippa & Mohrig, 2012	AUS	
	P. sexspinosa (Alam, 1988)	ORI	
	P. spicata Vilkamaa, Hippa & Mohrig, 2012	AUS	
unplaced	*P. subjucunda* Mohrig & Kauschke, 2019	NEA	
	P. subvetula Rudzinski, 2000	PAL	
	P. sylviae (Steffan, 1969)	AUS	
	P. tenebriosa Mohrig & Rulik, 1999	PAL	
	P. trivialis (Johannsen, 1912)	NEA	
	P. villabonensis Heller, 2012	PAL	

1.5 Research history of New Zealand Sciaridae

Only two major taxonomic studies have so far dealt with the sciarid fauna of New Zealand. In the first half of the 20th century, Tonnoir and Edwards (1927) examined the fungus gnats (Mycetophilidae) of the island country and listed 20 native—mostly newly described—species of Black Fungus Gnats, which were regarded as a subfamily of the Mycetophilidae at this time. Seventeen of those species were assigned to the genus *Sciara* Meigen, 1803, according to the former taxonomic state of knowledge. The three remaining species were placed in *Scythropochroa* Enderlein, 1911, or the newly erected genera *Ohakunea* Edwards, 1927 and *Neophnyxia* Tonnoir & Edwards, 1927. The modern assignment to genera was done by Menzel and Mohrig (2000), who placed two species in *Corynoptera* Winnertz, 1867; six species in *Ctenosciara* Tuomikoski, 1960; two in *Pseudolycoriella* Menzel & Mohrig, 1998; one in *Scatopsciara* Edwards, 1927; and one in *Zygoneura* Meigen, 1830. The remaining species were recognised as synonyms (Mohrig & Jaschhof 1999), excluded from the Sciaridae (Jaschhof & Hippa 2003), or left unrevised due to missing type material (Mohrig & Jaschhof 1999). Based on this preliminary taxonomic work, Mohrig and Jaschhof (1999) added 40 newly described species to the species list of New Zealand. This tripling of the number of species indicated that many species were probably still undiscovered—especially when keeping in mind that the authors had only gnat material from the more anthropogenically influenced North Island at their disposal. Thus, at the start of the new millennium, the definitely known sciarid fauna of New Zealand comprised 53 species. After *Corynoptera* and *Ctenosciara*, *Pseudolycoriella* was the third most species-rich genus. Five species—*Pseudolycoriella bispina* Mohrig, 1999; *P. breviseta* Mohrig, 1999; *P. jejuna* (Edwards, 1927); *P. macrotegmenta* Mohrig, 1999; and *P. zealandica* (Edwards, 1927)—were assigned to it.

In addition to these two major taxonomic studies, the Sciaridae of New Zealand have also been the subject of two smaller studies, one on the life history traits of selected species (Wisely 1959) and the other on regional distributions (Davies 1988).

1.6 Research questions and hypotheses

The research history and existing results pointed towards a rather open field for intensive research. A fundamental question is whether the regional species diversity of Sciaridae in New Zealand, especially that of *Pseudolycoriella*, is completely recorded. Is it possible to expand the known species inventory of Sciaridae by a significant proportion? Mohrig and Jaschhof (1999) were able to rediscover nine of the 17 species described by Tonnoir and Edwards (1927) which are considered valid today. This fact together with the taxonomic classifications and changes proposed by Menzel and Mohrig (2000) led these authors to the conclusion that the basic structure of the composition of New Zealand's sciarid fauna is known. However, the limitation of the study by Mohrig and Jaschhof (1999) to material originating from North Island gives reason to think that this statement was premature. It is quite likely that the larger and not so strongly anthropogenically affected South Island still hides a remarkable proportion of undiscovered species or even unknown taxa of higher rank.

As noted in the general introduction, as well as this fundamental question about the regional diversity of Sciaridae, their biogeography is also of interest. As always, when it comes to organisms from New Zealand, the question of the origin of these taxa arises. A crucial point, however, is whether the Sciaridae are at all suitable for answering this question. For the Palaearctic, Menzel and Mohrig (2000) stated that a surprisingly homogenous fauna without endemics existed, except for a few highly specialised species. The authors cited both active migration and passive drift due to air currents as reasons for this homogeneity. Correspondingly, Mohrig et al. (1997) stated that they did not find taxa endemic to the Canary Islands. Although they were able to describe two species new to science, they argued that later discoveries of these two species in neighbouring regions are to be expected. Thus, they characterised the sciarids of the Canary Islands as typical faunistic elements of the Mediterranean. Nevertheless, in two common species—*Corynoptera fatigans* (Johannsen, 1912) and *Scatopsciara edwardsi* Freeman, 1983—they observed a quantitative shift of characters caused by an "island effect".

Even in the Hawaiian Islands, only seven out of 22 species were found that do not occur anywhere else in the world (MOHRIG et al. 2019). For instance, one species described from there—*Bradysia bishopi* STEFFAN, 1973—proved to be widespread in the Southern Hemisphere (American Samoa, Australia, Fiji, French Polynesia, Galápagos Islands, New Caledonia, Papua New Guinea, Seychelles Islands, Thailand, Western Samoa) and even in the Caribbean (Puerto Rico) (KÖHLER & MENZEL 2013, BROADLEY et al. 2019). Such an island-dominated distribution is also known for *P. cavatica* (SKUSE, 1888), found in Australia, Hawaii, New Caledonia, Seychelles, Tristan da Cunha, and South Africa (BROADLEY et al. 2016, BOLD 2019, MOHRIG et al. 2019). In the light of such findings, it is unlikely that Sciaridae could serve as a proxy for revealing general biogeographical patterns. Nevertheless, MOHRIG and JASCHHOF (1999) discussed the zoogeography of New Zealand's Black Fungus Gnats. They argued that the sciarids of New Zealand are not of the same age, and belong to two "faunal layers". Whereby, they classified the genus *Pseudolycoriella* as belonging to phylogenetically older faunal elements. Because related species exist in Micronesia, Japan, Korea, and the Central Palaearctic, they further recognised a faunal exchange across a land bridge between Melanesia and Indomalaya at the end of the Mesozoic and at the beginning of the Eocene. Will it be possible to validate this hypothesis? Can endemic monophyletic groups be recognised? Is it possible to hypothesise about their age and their arrival to New Zealand? How are they distributed across New Zealand? Did the dynamic geological history leave traces in their distribution within New Zealand, or do the Sciaridae have a homogeneous distribution across the archipelago?

2 Material and methods

2.1 Origin of specimens

The present study is based on sample material from 126 different collection sites across New Zealand (fig. II). The intensity of the investigation of the individual sites varies greatly and ranges from one-time encounters with sweep nets to systematic Malaise-trapping. Most of the material examined is from a survey undertaken 2001–2002 by Catrin and Mathias JASCHHOF (Färjestaden, Sweden) of all three major islands of New Zealand, i. e. including Steward Island. The focus of their field trip was several fly families which, like the Sciaridae, belong to the superfamily Sciaroidea (JASCHHOF & Didham 2002, JASCHHOF & JASCHHOF 2003a, 2003b, 2004, JASCHHOF 2004). These are in detail the—so called wood midges—Cecidomyiidae and Lestremiinae, and the then newly discovered Rangomaramidae (JASCHHOF & DIDHAM 2002). Continuing the pioneering work of MOHRIG and JASCHHOF (1999), they also collected Sciaridae. Due to the habitat requirements of the Sciaroidea (VOCKEROTH 1981, SØLI et al. 2000), the focus of collecting was on forest habitats. The pasture and tussock communities in the east of South Island were therefore not sampled (fig. II). Also, Fiordland National Park in the southwest of South Island is not accessible and therefore could not be surveyed.

Catrin and Mathias JASCHHOF also examined some New Zealand insect collections in order to add material from further localities. This material originated from A. E. BROOKES, the Department of Conservation St. Arnaud, T. R. HARRIS, John HUTCHESON, Peter Malcom JOHNS, Uwe KALLWEIT, Roderick P. MACFARLANE, and Andreas STARK. A second batch of sciarid material, collected more recently on North Island, was kindly provided by Peter A. MADDISON (Katikati, New Zealand). For redescription and comparison with potential new species, the holotypes of *P. jejuna* and *P. zealandica* were loaned from the Natural History Museum London, United Kingdom (BMNH). The material on which the study of MOHRIG and JASCHHOF (1999) was based was also available. Collection material from Tasmania (Australia) was also provided by Catrin and Mathias JASCHHOF. It was trapped as part of a Malaise trap project at the Warra Long-term Ecological Research Site (BASHFORD et al. 2001). Specimens designated as types of newly described species, as well as other material, are deposited as described in chapters 3 and 4.

2.2 Preparation and morphological analysis

The collected sciarids were stored in 70 % ethanol and deposited at the collection of the Senckenberg German Entomological Institute (SDEI). The preparation procedure followed the protocol of MENZEL and MOHRIG (2000). In brief, the transfer of the specimens from ethanol into Canada balsam on glass slides for microscopy was carried out with an alcohol series, followed by a bath in creosote. A crucial point before mounting the specimens on slides was the separation of the hypopygium from the abdomen, to allow a ventral view of this taxonomically important organ (fig. Ic). This manipulation was done with two micropins under a dissection microscope with magnification up to 40 ×. The hypopygium is covered by a separate cover slip on the same slide as the remaining parts of the specimen (fig. Id). The slides were then labelled with locality labels and placed in a heating chamber at 35 °C for two to three weeks to dry the Canada balsam. Morphological examination was undertaken with an Olympus BX50 microscope. To ensure that drawings are true to scale, the microscope was equipped with an Olympus U-DA drawing tube. The resulting pencil sketches were digitised and edited using the software Adobe Illustrator CS6. More detailed information on preparation and morphological analysis are given in chapter 4.

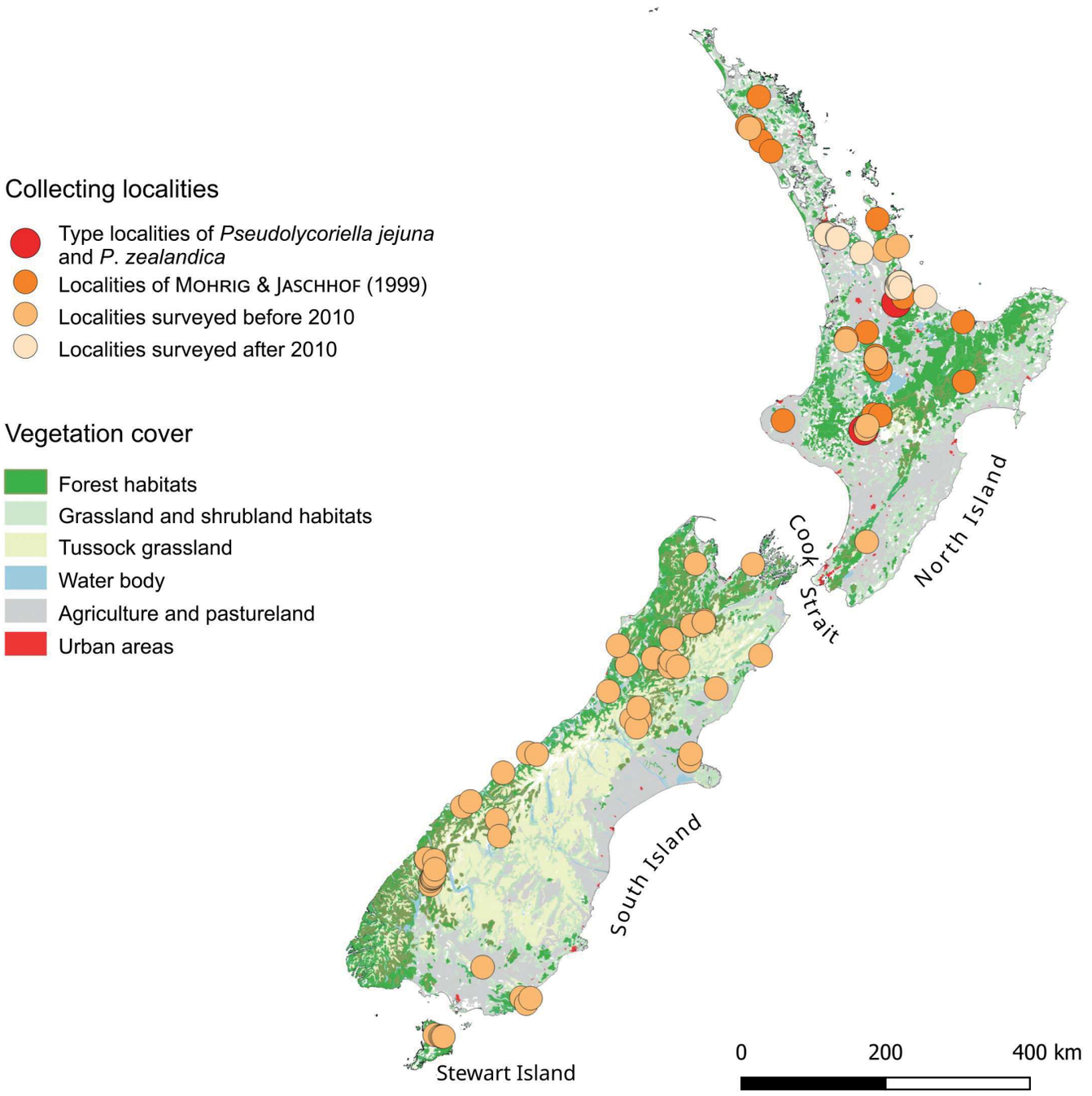

Figure II: Simplified vegetation cover of New Zealand according to Landcare Research (2015) and collection localities of Sciaridae used in this study. Data reproduced with the permission of Landcare Research New Zealand Limited.

2.3 Molecular analysis

The first phylogenetic work on sciarids was conducted by Shin et al. (2013). These authors used the mitochondrial genes COI and 16S, and the nuclear ribosomal genes 18S and 28S. This balance of more quickly evolving mitochondrial genes and more conservative nuclear ones is advantageous, because different time spans can be considered (Schmitt 2020).

To allow a comparison with their results and an integration of their data in the present study, this gene selection was adopted for this thesis. However, the amplification of the 18S gene with a length of approximately 1970 base pairs could not be reliably reproduced with the available material, which is probably due to the fact that the samples were stored for too long under suboptimal conditions, e. g. at room temperature. Details on DNA extraction, PCR settings, primer used, se-

quencing procedure, and analysing software are given in the materials and methods section in chapter 4. All obtained sequences were uploaded to GenBank (Sayers et al. 2019). A list of all GenBank accession numbers is published in the electronical supplement of Köhler and Schmitt (2023) and is available under: https://doi.org/10.6084/m9.figshare.24517117.

The obtained sequences of these three markers were used for several purposes: primary to underpin species delimitation, further elucidate the phylogeny [software IQ-TREE 1.6.1; Nguyen et al. (2015)], to obtain the ancestral distribution of each most recent common ancestor [software RASP 4.2; Yu et al. (2019)] and finally to obtain divergence time estimations [multilocus sequence data package *BEAST from the program BEAST 2.6.0; Bouckaert et al. (2019)]. Details of the procedure for the Bayesian approach with *BEAST and the analysis of the ancestral distribution patterns are given in the materials and methods section in chapter 5.

NEW ZEALAND ENTOMOLOGIST, 2016
http://dx.doi.org/10.1080/00779962.2016.1153233

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Additions to the New Zealand fauna of black fungus gnats (Diptera: Sciaridae), with descriptions of six new species

A. Köhler and W. Mohrig

Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany

ABSTRACT

The sciarid fauna of New Zealand is not well known and only two major studies have dealt with this group. The present study is based on material from the later of the two studies as well as new material. Six species are recognised as new to science and are here described: *Bradysia novaeseelandiae* sp. nov., *Corynoptera aggregata* sp. nov., *Corynoptera catrinjaschhofae* sp. nov., *Ctenosciara etorutao* sp. nov., *Pseudolycoriella frederickedwardsi* sp. nov. and *Pseudolycoriella tonnoiri* sp. nov. *Bradysia novaeseelandiae* sp. nov. is the first *Bradysia* species described from New Zealand. The Holarctic species *Bradysia pallipes* and *Corynoptera fatigans* are recorded from New Zealand for the first time.

http://zoobank.org/urn:lsid:zoobank.org:pub:7E1F0507-8740-41C7-BCB9-84910D8EBC65

ARTICLE HISTORY
Received 3 July 2015
Accepted 17 December 2015

KEYWORDS
Bradysia; *Corynoptera*; *Ctenosciara*; introduced species; new records; *Pseudolycoriella*; Sciaroidea

Introduction

Black fungus gnats, Sciaridae, are a family of Bibionomorpha found abundantly, worldwide, in all kinds of terrestrial habitats (although chiefly in mesic forests). Outside Europe, the sciarid faunas are especially poorly worked taxonomically, with the Australasian Region being no exception (Bickel 2009; Yeates et al. 2009). Even so, due to its outstanding zoogeographical importance, the New Zealand Sciaridae fauna has been studied to some extent. The first publication dealing with this family was by Hutton (1881) who described a new species, *Sciara rufescens* Hutton, 1881 (nec *Sciara rufescens* Zetterstedt, 1852), which is now known as *Sciara neorufescens* Miller, 1950. The first more detailed study of New Zealand fungus gnats – Mycetophilidae including the Sciarinae, i.e. Edwards (1925) – was published by Tonnoir and Edwards (1927). They described 17 species as new to science, most of them assigned to the genus *Sciara* Meigen, 1803, following the taxonomic practice at the time. Seventy years later, Mohrig and Jaschhof (1999) addressed the sciarids in New Zealand for a second time, with a modern taxonomic framework for Sciaridae (Menzel & Mohrig 2000). Based on a study of both Edwards' types and fresh specimens collected by Catrin and Mathias Jaschhof on the North Island, Mohrig and Jaschhof (1999) redescribed nine of Edwards' species and described 40 new species. They assigned the New Zealand sciarids to the genera *Corynoptera* Winnertz, 1867 (with four different species groups); *Cratyna* Winnertz, 1867; *Ctenosciara* Tuomikoski, 1960; *Epidapus* Haliday, 1851; *Neophnyxia* Tonnoir & Edwards, 1927; *Pseudolycoriella* Menzel & Mohrig, 1998; *Scatopsciara* Edwards, 1927; *Scythropochroa* Enderlein, 1911; and *Zygoneura* Meigen, 1930. Also, these authors noted, to their astonishment, the near-absence in New Zealand of *Bradysia* Winnertz, 1867, a genus of otherwise worldwide distribution. They referred to just two females of the *Bradysia pallipes* group of species, which they provisionally identified as *Bradysia pallipes* (Fabricius, 1787), introduced from the Holarctic realm.

CONTACT A. Köhler arne.koehler@senckenberg.de

In the course of an ongoing project addressing the taxonomy of the Sciaridae of the Australasian region (A. Köhler, unpublished data), we examined previously unused specimens that the Jaschhofs had collected from the North Island. As shown here, this material contained six species new to science and a number of faunal records that increase our knowledge of the distribution of Sciaridae species in New Zealand.

Material and methods

Most of the specimens that we studied were collected by Catrin and Mathias Jaschhof at different sites in the North Island of New Zealand from November 1992 to January 1993 (see Mohrig & Jaschhof 1999 for a list of collecting sites). Additional material examined was obtained during another collecting campaign by the same collectors (with occasional collaborators) on both North and South Islands in 2002–2003 (collecting permit granted by the Department of Conservation #9900/143/3/04). Other specimens were given to us by the Jaschhofs, but were obtained by New Zealand collectors, namely Raphael K. Didham and his research group, John Hutchinson and Peter M. Johns. Adult sciarids were caught either by sweep net or Malaise trap. Specimens were mounted in Canada balsam on microscope slides following the procedure described by Mohrig and Jaschhof (1999). The slide mounts are deposited in the insect collections of the New Zealand Arthropod Collection, Auckland, New Zealand (NZAC); Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI); Finnish Museum of Natural History, Helsinki, Finland (UZMH); and Werner Mohrig's private collection of world Sciaridae, Poseritz, Germany (PWMP). Specimens presumably belonging to *Ctenosciara rufulenta* (Edwards, 1927) were excluded from the present study, because *Ct. rufulenta* is likely to comprise a complex of several cryptic species (A. Köhler, unpublished data).

Morphological examination and preparation of line-drawings were undertaken with an Olympus BX-50 microscope fitted with an Olympus U-DA drawing tube. The final illustrations were produced digitally, following the instructions in Coleman (2003, 2009) and Bober and Riehl (2014). Collection locality maps were compiled using the GIS-software QGIS 2.8 Wien. The morphological terminology used here follows Mohrig et al. (2013). The length of a flagellomere is the total length, i.e. flagellomere body plus neck.

Descriptions of new species

Bradysia novaeseelandiae Köhler & Mohrig sp. nov.

(Figure 1A–D, Map 1)

Material examined. Holotype: ♂, New Zealand, North Island, White Pine Bush, 3 km southwest of Whakatane/Bay of Plenty, 26 December 1992, leg. M. Jaschhof (NZAC).

Description. Male. Head: Head capsule brown. Eye bridge three facets wide. Antennae brown; scape and pedicel slightly paler than flagellum; necks of flagellomeres bicoloured; fourth flagellomere 3.8 times longer than wide (Figure 1A), surface slightly rough, covered with sensilla and hairs, sensilla of two different lengths, long sensilla sparser than short ones, hairs sparsely arranged. Maxillary palp poorly visible in the only specimen available for study, presumably three-segmented. *Thorax:* Pale brown. Posterior pronotum bare. Anterior pronotum with two hairs. Episternum 1 with four hairs. Mesonotum with four long hairs laterally, several shorter hairs elsewhere. Scutellum with two strong bristles and several minor hairs. Katepisternum 1.3 times longer than high. *Wing:* Length 1.5 mm, width/length ratio 0.37. Membrane transparent, without macrotrichia, anal area inconspicuous. Posterior veins usually distinct, m-stem weak; r-m and bM without macrotrichia; R, R_1 and R_5 with only dorsal macrotrichia; R_1 short, 0.43 times as long as R; c/w ratio 0.78; r-m as long as bM. Halteres pale brown; shaft as long as head. *Legs:* Yellow. Vestiture of fore and mid tibiae includes several long, outwardly oriented hairs. Hind tibia on distal half with posterodorsal row of spines. Tibial organ

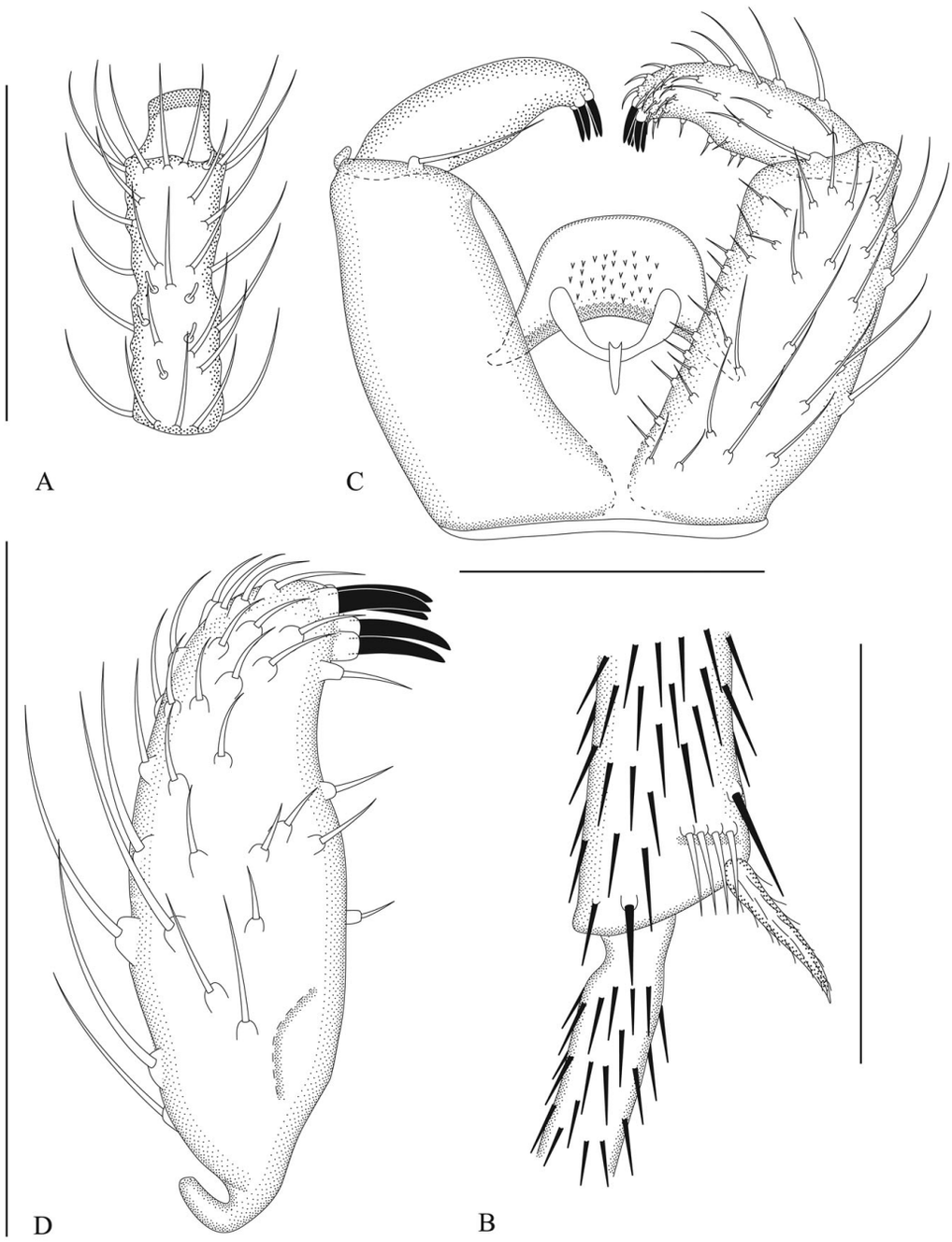
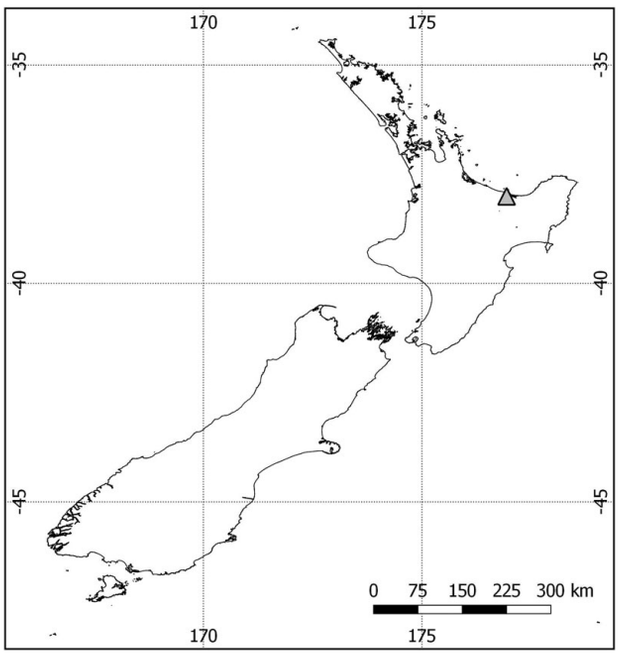


Figure 1. *Bradysia novaeseelandiae* Köhler & Mohrig sp. nov. **A,** Fourth flagellomere. **B,** Tibial organ of fore leg. **C,** Hypopygium. **D,** Gonostylus. Scale bars = 0.1 mm.

with short comb-like row of four bristles (Figure 1B). Tibial spurs equal in length. Claws without teeth. *Abdomen:* Same colour as thorax. *Hypopygium:* Gonocoxites (Figure 1C) wider than long, not fused basally, with fine long hairs, ventral, inner-side of gonocoxites V-shaped. Gonostylus (Figure 1D) 3.1 times longer than wide, elongated, with slight impression ventrally on apical third, five inwardly oriented spines apically. Tegmen (Figure 1C) trapezoidal, wider than high, membranous apically, basal apodemes strongly sclerotised, minute teeth triangular, scattered over large area. Ejaculatory apodeme (Figure 1C) short, with a membranous semi-circular base. *Body size:* 1.5 mm.
Female: Unknown.

Etymology. The species epithet, *novaeseelandiae*, refers to the fact that this is the first *Bradysia* species described from New Zealand.



Map 1. Collection localities of *Bradysia novaeseelandiae* Köhler & Mohrig sp. nov.

Discussion. This new species is classified in the *Bradysia hilaris* group of species, based on the presence of bicoloured flagellomere necks and toothless claws. Outside the Palaearctic region this group is widely distributed throughout the islands in the southwest Pacific (Vilkamaa et al. 2012; Mohrig in press). The characters mentioned above distinguish *Br. novaeseelandiae* from species classified in the *Br. fungicola* group that have similar gonostyli, e.g. *Br. melina* Vilkamaa et al. 2012. This New Caledonian species also differs in having a shorter fourth flagellomere (length/width ratio 2.2 versus 3.8). Among the species of the *Br. hilaris* group, *Br. novaeseelandiae* is similar to *Br. seticornis* Vilkamaa et al., 2012 in the shape of the gonostylus and the number of apical spines. However, in *Br. seticornis* the gonostylus has one spine a little isolated from the group of apical spines, and the tibial organ comprises a longer row of bristles.

Corynoptera aggregata Köhler & Mohrig sp. nov.

(Figure 2A–D, Map 2)

Material examined. Holotype: ♂, New Zealand, North Island Coromandel Range, 5 km east of Coromandel, *Podocarpus* secondary wood with tree ferns, 28 December 1992, leg. M. Jaschhof (NZAC). Paratypes: 1♂, North Island, Hauhungaroa Range, 5 km southwest of Tihoi; *Podocarpus* wood with ground ferns, 21 December 1992, leg. M. Jaschhof (PWMP). 1♂, North Island, Urewera National Park, Huiarau Range 30 km southeast of Murupara; *Podocarpus-Nothofagus* wood, altitude 600–1000 m; sweep net, 23 December 1992, leg. M. Jaschhof (PWMP). 1♂, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992, leg. M. Jaschhof (PWMP). 5♂♂, South Island, Buller, Ahaura, Granville State Forest, *Nothofagus truncata* forest, 170–250 m, December 1994, leg. J. Hutcheson (2♂♂ NZAC, 2♂♂ SDEI, 1♂ UZMH). 6♂♂, South Island, Nelson, Kahurangi NP, Takaka River Valley (Cobb Dam Road), 450–800 m, 31 August to 7 October 2001, leg. M. & C. Jaschhof (3♂♂ NZAC, 2♂♂ SDEI, 1♂ UZMH). 1♂, South Island, Buller, Maruia Forest, Shenandoah Saddle, *Nothofagus* forest, 500 m, 9 October to 3 November 2001, leg. M. & C. Jaschhof (SDEI). 1♂, same locality as previous, 3–25 November 2001, leg. M. & C. Jaschhof (SDEI). 1♂, South Island, Buller, Lewis Pass; tussock grassland at beech forest edge, 850 m, 26 November to 25 December 2001, leg. M. & C. Jaschhof (SDEI). 1♂, North Island, Tararua Forest Park, Blue Range Hut Track 10 km southwest of Mount Bruce, mixed

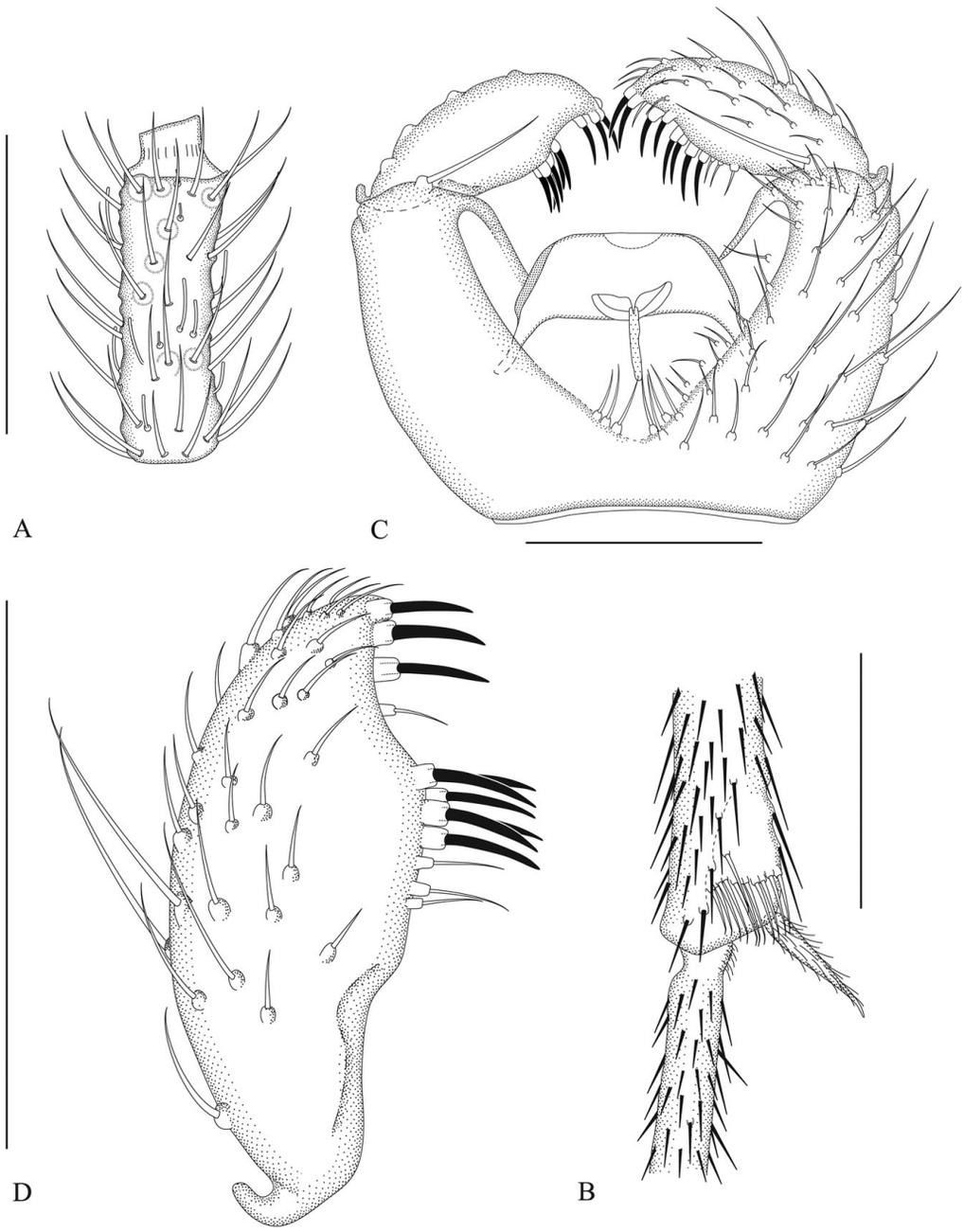
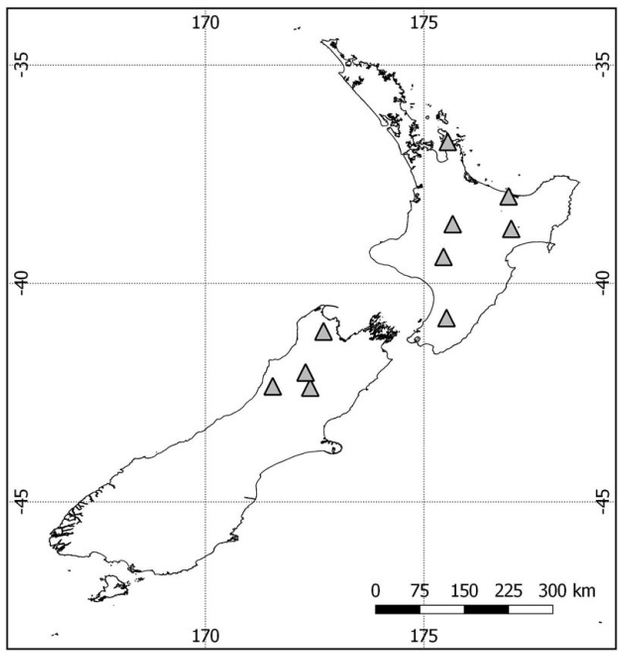


Figure 2. *Corynoptera aggregata* Köhler & Mohrig sp. nov. **A,** Fourth flagellomere. **B,** Tibial organ of fore leg. **C,** Hypopygium. **D,** Gonostylus. Scale bars = 0.1 mm.

Nothofagus/podocarp/broadleaf forest, 2 February 2002, leg. M. & C. Jaschhof (SDEI). 1♂, North Island, Taupo, Tongariro NP, Mangawhero River Valley 3 km northeast of Ohakune, 690 m; mixed podocarp/broadleaf forest, 26 November to 28 December 2002, M. & C. Jaschhof & U. Kallweit (SDEI).

Descriptions. Male. Head: Head capsule brown. Eye bridge two or three facets wide. Antennae unicolorous brown; fourth flagellomere 3.4–3.9 times as long as wide (Figure 2A); flagellomeres with hairs and sensilla of two different lengths, small ones with a hook-like shape and pale coronas and long ones, which extend parallel to the flagellomere; hairs of the antennal segments are strong and sparsely arranged, with conspicuous coronas. Maxillary palp pale; palpomeres not elongated, nearly equal in size; palpomere 1 mostly with one bristle (seven of the 21 specimens with two bristles and one paratype with three bristles); palpomere 2 with one longer outer bristle. *Thorax:* Brown. Posterior pronotum bare. Anterior pronotum with two to five hairs. Episternum 1 with 5–14 hairs.



Map 2. Collection localities of *Corynoptera aggregata* Köhler & Mohrig sp. nov.

Mesonotum with four or five strong laterals. Scutellum with two strong bristles and several minor hairs. Katepisternum approximately 1.2 times longer than high. *Wing:* Length 1.6–2.5 mm; width/length ratio 0.4. Membrane transparent, without macrotrichia, anal area inconspicuous; veins usually distinct, m-stem weak; r-m and all posterior veins bare; bM exceptionally with one to three fine hairs on the apex; R, R_1 and R_5 only with dorsal macrotrichia; R_1/R ratio 0.55–0.81; c/w ratio 0.61–0.70; r-m as long as bM. Halteres pale brown; shaft 1.5 times longer than head. *Legs:* Yellow. Coxal bristles long and dark. Vestiture of fore tibia sometimes includes longer hairs. Tibial organ with a row of bristles which are not strictly linearly arranged; clearly wider than half of tibial apex width (Figure 2B). Inner tibial spurs slightly weaker than outer ones. Posterodorsal row of spines inconspicuous, comprises apical half of hind tibia. Claws with fine teeth. *Abdomen:* Same colour as thorax. *Hypopygium:* Gonocoxites (Figure 2C) wider than long, with fine long hairs; ventral, inner-side of gonocoxites with two groups of three or four bristles; bristles of each group converge towards the other group. Gonostylus (Figure 2D) 2.0–2.6 times longer than wide, elongated with medial swelling and slight emargination apically; gonostylar spines arranged in two groups with a single spine between; the apical group comprising two or three spines and the subapical one four to nine (mostly five or six) spines. Tegmen (Figure 2C) very broad, trapezoidal with strongly sclerotised lateral edges; basal apodemes strong and long. Area of teeth not visible. Ejaculatory apodeme (Figure 2C) long with a broad basal part. *Body size:* 1.7 to 2.4 mm.
Female: Unknown.

Etymology. The species epithet, *aggregata*, means clustered, joined together, and refers to the similarity of the new species to *Corynoptera semiaggregata* Mohrig, 1999.

Discussion. Corynoptera aggregata is very similar to *C. semiaggregata*. Mohrig has already illustrated the gonostylus and the base of the hypopygium of *C. aggregata* in his description of *C. semiaggregata* (fig. 34b, d in Mohrig & Jaschhof 1999], but he did not make corresponding comments in the written description. The arrangement of these figures together with figures showing the same organs of 'true' *C. semiaggregata* (fig. 34a, c in Mohrig & Jaschhof 1999) suggest that *C. aggregata* falls within the range of variability of *C. semiaggregata*. The rediscovered material that we examined strongly supported the existence of two distinct species. *Corynoptera aggregata* is distinguished from *C. semiaggregata* by a different arrangement of the bristles at the base of the hypopygium.

While *C. semiaggregata* possesses a single group of sparse bristles (Figure 7A), *C. aggregata* displays two separate groups of a few bristles with a convergent arrangement. The shape of the gonostylus of these species also differs: more slender and curved in *C. semiaggregata* (Figure 7B) and more stout in *C. aggregata*. Furthermore, the subapical group of spines of *C. aggregata* is positioned more towards the apex of the gonostylus than in *C. semiaggregata*. The tegmen of *C. aggregata* is trapezoidal, in contrast to the rectangular tegmen with convex lateral edges of *C. semiaggregata*. The area of teeth of *C. semiaggregata* is clearly visible, unlike in *C. aggregata*. *Corynoptera aggregata* belongs to the *Corynoptera basisetosa* group. Due to its bipartite group of bristles at the base of the hypopygium, *C. aggregata* cannot be confused with another species of this species group.

Corynoptera catrinjaschhofae Köhler & Mohrig sp. nov.

(Figure 3A–D, Map 3)

Material examined. Holotype: ♂, New Zealand: North Island, Egmont National Park, East Egmont, 9 Jaunary 1993, leg. M. Jaschhof (NZAC). Paratype: ♂ South Island, Southland, Catlins, Purakaunui Scenic Reserve, 6 December 2002, leg. M. Jaschhof (SDEI).

Description. Male. Head: Head capsule brown. Eye bridge three or four facets wide. Antennae unicolorous brown; fourth flagellomere 3.0–3.1 times longer than wide (Figure 3A); flagellomeres with sensilla of two different lengths, small ones with a hook-like shape and pale coronas, and long ones that extend parallel to the axis of the flagellomeres; hairs of the flagellomeres densely arranged. Maxillary palp pale; palpomeres not elongate; palpomere 2 is the shortest; palpomere 1 with one bristle and a patch of sensilla; palpomere 2 with one longer outer bristle and several minor ones. *Thorax:* Brown, unicolorous with head. Posterior pronotum bare. Anterior pronotum with one long hair located on the posterior edge, and one or two minor hairs. Episternum 1 with two or three hairs. Mesonotum with five strong and some weaker laterals and a row of medial dorsocentrals. Scutellum with two strong bristles and several minor hairs. Katepisternum 1.4 times longer than high. *Wing:* Length 2.4–2.5 mm; width/length ratio 0.35–0.36. Membrane transparent, without macrotrichia on its surface and the posterior veins; anal area not striking; veins distinct, only m-stem weak; r-m and bM without macrotrichia, although the paratype bears one bristle on the middle of r-m; R, R_1 and R_5 with macrotrichia only dorsally; R_1/R ratio 0.58–0.62; c/w ratio 0.73–0.77; r-m/bM ratio 1.4–1.7. Halteres pale brown; shaft approximately 1.5 times longer than head. *Legs:* Yellow. Coxal bristles dark. Fore, mid and hind tibia without longer bristles within vestiture; comb-like row on tibial organ not strictly at the same level, wider than half of tibial apex width (Figure 3B). All tibial spurs equal. Posterodorsal row of spines on hind tibia weakly developed, comprising apical third of hind tibia. Claws with fine teeth. *Abdomen:* Brown, paler than thorax. Hairs fine and dense. *Hypopygium:* Same colour as abdomen. Gonocoxites (Figure 3C) wider than long, with fine middle-sized hairs; ventral, inner-side of gonocoxites brightened and with short hairs, V-shaped and without a basal lobe of bristles. Gonostylus (Figure 3D) 2.6 times longer than wide, lemon-shaped with a flattened inner side; armed with a nearly right-angled apical tooth. The apical half of the inner side of the gonostylus comprises 9 to 15 small spines. One spine is located beside the apical tooth and therefore not easy to recognise. Tegmen (Figure 3C) trapezoidal with a membranous apex, lateral edges more sclerotised, basal apodemes strong and short. Area of teeth minute, with approximately 20 broad, triangular teeth. Ejaculatory apodeme (Figure 3C) long and thin with a well-developed basal part. *Body size:* 1.9 to 2.0 mm.

Female: Unknown.

Etymology. The new species is named after Catrin Jaschhof, to honour her contribution to Sciaroidea research.

Discussion. The single bristle on three-segmented maxillary palp, the tibial organ with an irregular row of bristles, the bare posterior veins and the fine teeth on the claws place this new species in one of

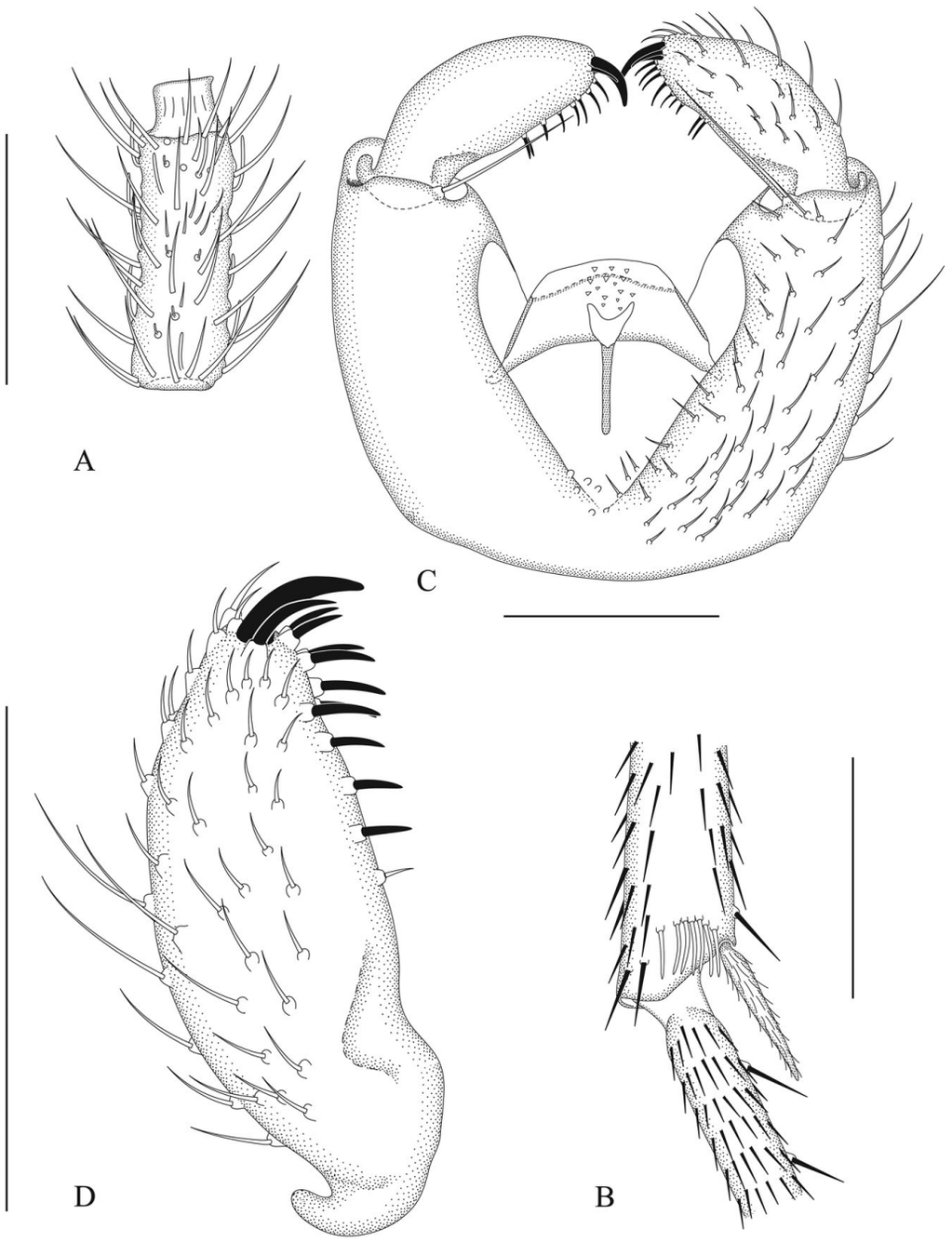
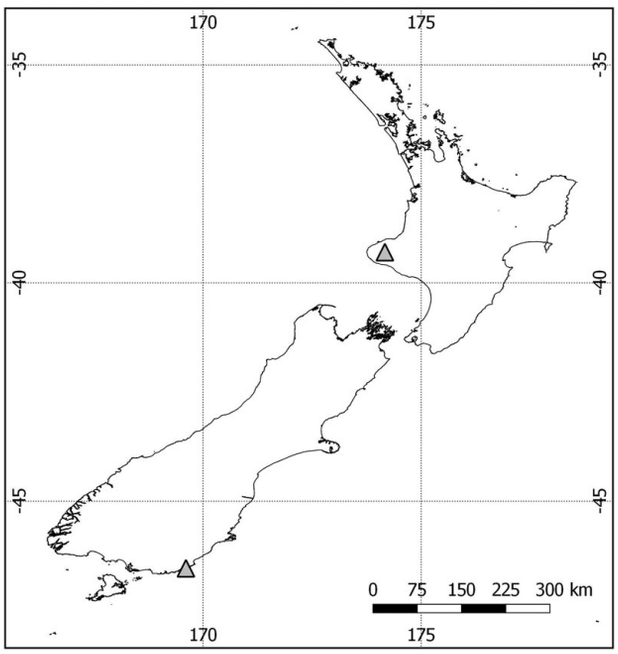


Figure 3. *Corynoptera catrinjaschhofae* Köhler & Mohrig sp. nov. **A,** Fourth flagellomere. **B,** Tibial organ of fore leg. **C,** Hypopygium. **D,** Gonostylus. Scale bars = 0.1 mm.

the New Zealand groups of *Corynoptera*. Further, the presence of an apical tooth and lack of an apical excavation on the gonostylus lead to a classification to the *Corynoptera ancylospina* group. Among this species group *C. catrinjaschhofae* is unique because of its small and numerous spines on the gonostylus. Nevertheless, the shape of the gonostylus of *C. catrinjaschhofae* is reminiscent of those of *C. coronospina* Mohrig, 1999 and *C. propriospina* Mohrig, 1999. *Corynoptera coronospina* differs in having a wider tegmen, an inner side of the gonocoxites that is wide open and studded with several striking setae. *Corynoptera propriospina* has an apically rounded tegmen and a rather narrow gonostylus.



Map 3. Collection localities of *Corynoptera catrinjaschhofae* Köhler & Mohrig sp. nov.

Ctenosciara etorutao Köhler sp. nov.

(Figure 4A–F, Map 4)

Material examined. Holotype: ♂, New Zealand, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992; leg. M. Jaschhof (NZAC). Paratypes: 9♂♂, same data as holotype (1♂ SDEI, 1♂ UZMH, 7♂♂ PWMP). 10♂♂, North Island, Coromandel, Wharekawa Redwood Picnic Area near Opoutere; redwood plantation with pines and tree ferns, 9 February 2002, leg. M. Jaschhof (3♂♂ NZAC, 5♂♂ SDEI, 1♂ UZMH, 1♂ PWMP).

Description. Male. Head: Head capsule brown. Eye bridge three to four facets wide. Antennae unicolorous brown; fourth flagellomere 2.5–3.6 times longer than wide (Figure 4A); flagellomeres with sensilla of two different lengths, small ones with a hook-like shape and pale coronas and long ones, which extend parallel to the segment; hairs on the flagellomeres densely arranged. Maxillary palp very pale; palpomeres 1 and 3 both longer than segment 2; palpomere 1 with two or three bristles (except one specimen that bears just one bristle) and a patch of fine sensilla. *Thorax:* Brown, without any contrast to head and abdomen. Posterior pronotum bare. Anterior pronotum with one strong hair located on the posterior edge, and up to three fine ones. Episternum 1 with two to seven hairs. Mesonotum with a row of stronger dorsocentrals, first strong dorsocentral near the anterior edge of the Mesonotum; five or six long and several weaker laterals. Scutellum with four strong bristles and several hairs. Katepisternum slightly longer than high. *Wing* (Figure 4D): Length 1.5–2.0 mm; width/length ratio 0.35–0.43. Membrane transparent, without macrotrichia; anal area not striking; veins distinct except weak m-stem; m_1, m_2, CuA_1 with macrotrichia; CuA_2 and r-m without macrotrichia, bM with one to four macrotrichia (one specimen exceptionally with a bare bM on one wing); R and R_1 with dorsal macrotrichia only; apical part of R_5 with ventral and dorsal macrotrichia; R_1/R ratio 0.58–0.86; c/w ratio 0.62–0.68; r-m and bM equal in length. Halteres yellow; head approximately as long as shaft. *Legs:* Yellow. Coxal bristles pale. Fore-, mid and hind tibia with some longer hairs within vestiture; tibial organ on fore tibia (Figure 4B) with a comb-like row of bristles, seldom discontinuous (3 of 20 specimens, Figure 4C) wider than half of tibial apex width. All tibial spurs long; spurs of mid tibia and hind tibia longer than spurs on fore tibia. A posterodorsal

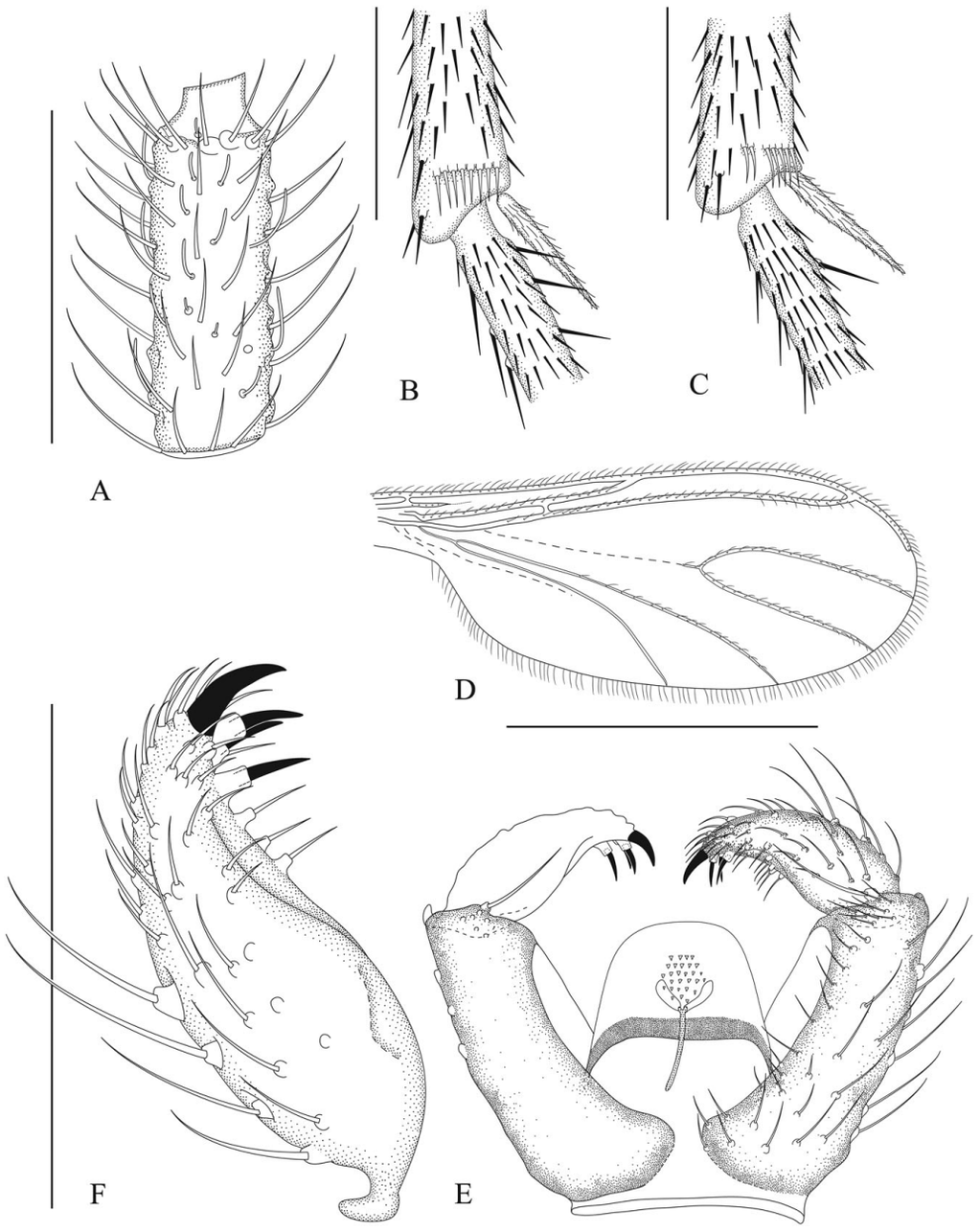
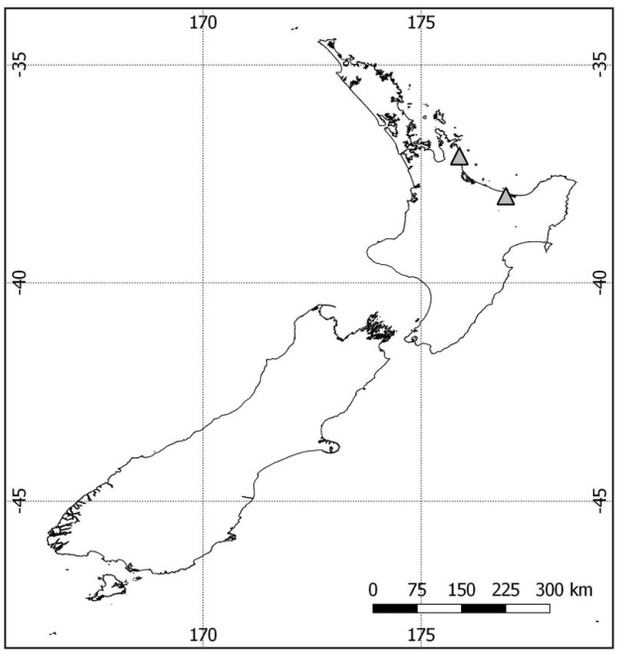


Figure 4. *Ctenosciara etorutao* Köhler sp. nov. **A,** Fourth flagellomere. **B,** Tibial organ of fore leg, variation without gap in the row of bristles. **C,** Tibial organ of fore leg, variation with a gap in the row of bristles. **D,** Wing. **E,** Hypopygium. **F,** Gonostylus. Scale bars = 0.1 mm.

row of strong spines along two-thirds of the hind tibia, these spines as long as tibial width. Claws with one strong tooth and one minor (not always visible). *Abdomen:* Brown, same colour as thorax, with dark hairs. *Hypopygium:* As brown as abdomen. Gonocoxites (Figure 4E) wider than long, with a normal setosity. Ventral, inner-side of gonocoxites not fused. Shape of gonocoxal inner-side U- or V-shaped. Gonostylus (Figure 4F) 2.3 to 2.8 times longer than wide, apically curved inwards and basally swollen (shape of gonostylus like a 'bent drop'); the apex with a tooth and three subapical strong spines, which are not as long as the tooth; two of them are situated ventrally and one more dorsally. A group of fine bristles is located basally of the spines. Tegmen (Figure 4E) typical for *Ctenosciara* spp., trapezoidal, with long and sclerotised basal apodemes. Area of teeth large, with numerous strong, triangular teeth. Ejaculatory apodeme (Figure 4E) long and thin. Basal part of ejaculatory apodeme slightly visible. *Body size:* 1.6 to 2.6 mm.
Female: Unknown.



Map 4. Collection localities of *Ctenosciara etorutao* Köhler sp. nov.

Etymology. The epithet is formed from the Māori words *e toru tao*. *Toru* means three and *tao* javelin, referring to the three spines on the gonostylus.

Discussion. The shape of the gonostylus and the number of apical spines characterise this new species very well. Only three species of *Ctenosciara* are known with just three spines on the gonostylus – *Ctenosciara crinita* Vilkaama, Hippa & Mohrig, 2012; *Ctenosciara exilis* Vilkaama et al., 2012; and *Ctenosciara cracens* Vilkaama et al., 2012 from New Caledonia. *Ctenosciara crinita* has a thicker gonostylus, a very short apical tooth and a very different shape of gonocoxites. Therefore it cannot be confused with *Ct. etorutao*. *Ctenosciara exilis* bears three or four apical spines, but they are arranged in two distinct groups. Furthermore, the shape of the gonostylus and the vestiture of posterior veins differ from the new species. *Ctenosciara cracens*, which has three spines in some specimen and sometimes a bare CuA_2, has a gonostylus that is straight or slightly curved and not swollen at the base.

Pseudolycoriella frederickedwardsi Köhler sp. nov.

(Figure 5A–D, Map 5)

Material examined. Holotype: ♂, New Zealand, North Island, Taupo, Tongariro NP, Mangawhero River Valley 3 km northeast Ohakune, 690 m, mixed podocarp/broadleaf forest, 26 November to 28 December 2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC). Paratypes: 1♂, North Island, Urewera National Park, Huiarau Range 30 km southeast of Murupara, *Podocarpus-Nothofagus* wood, altitude 600–1000 m, 23 December 1992, leg. M. Jaschhof (PWMP). 5 ♂♂, same locality as holotype (1♂ NZAC, 3♂♂ SDEI, 1♂ UZMH).

Description. Male. Head: Head capsule brown. Eye bridge two or three facets wide. Antennae light brown, without any contrast between scape and pedicel and the flagellum; fourth flagellomere 2.9–3.2 times longer than wide (Figure 5A), necks of flagellomeres well differentiated; surface of flagellomeres rough with deep pits, sensilla of two different lengths visible; hairs on the flagellomere sparsely distributed and slightly longer than flagellomeres' width, inserted in small impressions. Maxillary palp pale with three palpomeres, first and third nearly of the same length, second one shortest, first

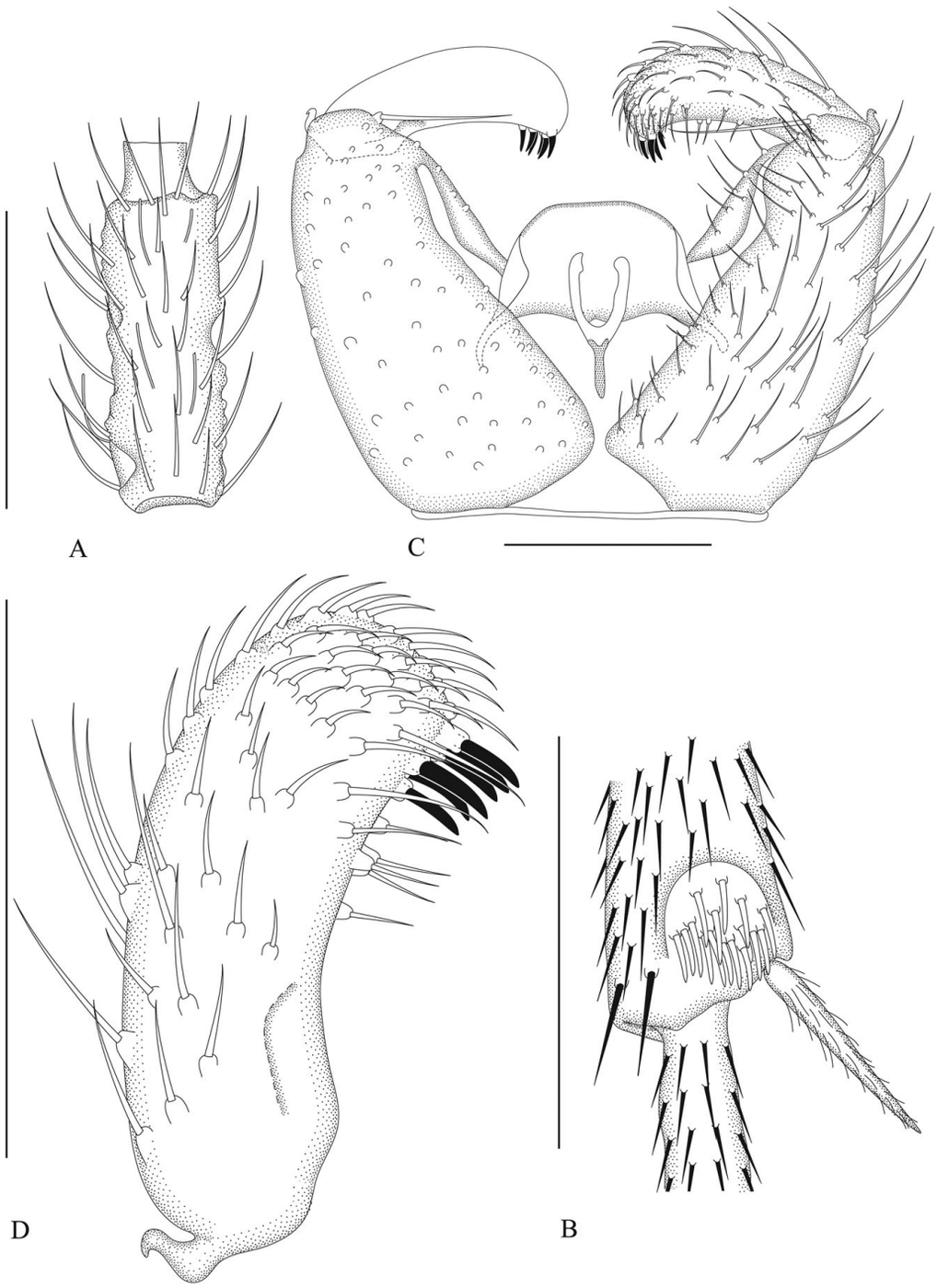
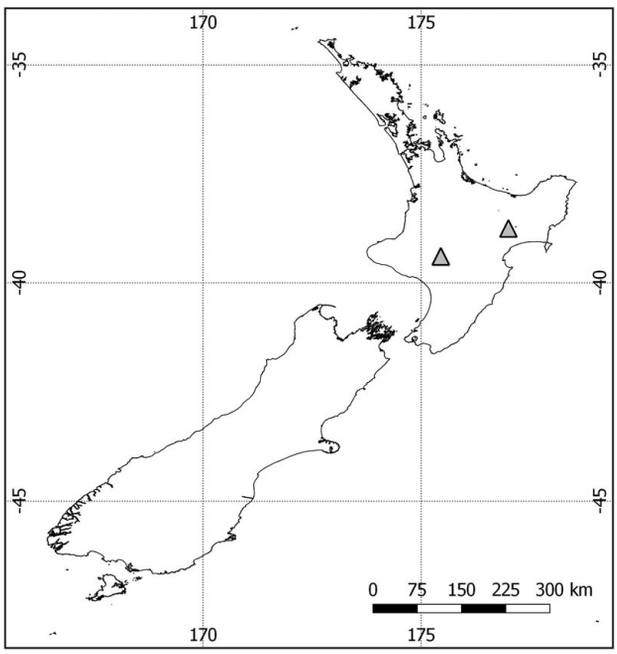


Figure 5. *Pseudolycoriella fredericked wardsi* Köhler sp. nov. **A,** Fourth flagellomere. **B,** Tibial organ of fore leg. **C,** Hypopygium. **D,** Gonostylus. Scale bars = 0.1 mm.

palpomere with several bristles; second palpomere with one longer outer bristle. Clypeus and prefrons bulging outwards. *Thorax:* Pale brown. Posterior pronotum bare. Anterior pronotum with four to six hairs. Episternum 1 with six to nine hairs. Mesonotum with four long laterals and several small ones. Scutellum with two strong bristles and several hairs. Katepisternum nearly as long as high. *Wing:* Length 2.1–2.4 mm; width/length ratio 0.35–0.38. Membrane transparent and without macrotrichia, anal area minor developed; all posterior veins distinct; r-m and bM without macrotrichia; apical half of R_5 with one to seven additional macrotrichia on the ventral side; R_1 short, 0.59–0.72 times as long as R; c/w ratio 0.63–0.69; r-m slightly longer than bM. Halteres pale brown; shaft longer than head. *Legs:* Yellowish brown. Tibial organ surrounded by a circular border and wider than half width of tibial apex; bristles of tibial organ arranged in an irregular row (Figure 5B). Mid tibia with



Map 5. Collection localities of *Pseudolycoriella frederickedwardsi* Köhler sp. nov.

some strong bristles located anteroventrally and posteroventrally, these bristles are as long as tibia is wide. Hind tibia with a dorsal row of strong spines and additional strong spines on the ventral and posterior sides, only the basal one-fifth of the hind tibia not armed with strong spines. All tibial spurs equal in length. Claws with one strong tooth followed by a few minor teeth. *Abdomen:* Pale brown, as thorax. *Hypopygium:* Gonocoxites (Figure 5C) wider than long, inner side of gonocoxites with short hairs, outer side with long hairs; ventral, inner side of gonocoxites V-shaped and basally not fused. Gonostylus (Figure 5D) 2.8–3.6 times longer than wide and curved; apical half thicker than basal one; apex with five or six spines among dense vestiture; one to three subapical whip-lash hairs. Tegmen (Figure 5C) large with recurved lateral edges; basal apodemes strong. Area of teeth not visible. Ejaculatory apodeme (Figure 5C) strong; base like an elongated horseshoe. *Body size:* 1.8–2.2 mm.
Female: Unknown.

Etymology. The new species is named in honour of the dipterist Frederick Wallace Edwards (1888–1940).

Discussion. Pseudolycoriella frederickedwardsi is similar to three other *Pseudolycoriella* species from New Zealand – *Pseudolycoriella breviseta* Mohrig, 1999, *Pseudolycoriella macrotegmenta* Mohrig, 1999 and *Pseudolycoriella tonnoiri* sp. nov. These *Pseudolycoriella* species share gonostyli with more than three apical spines and a small number of whip-lash hairs, which are not as long as in the remaining three *Pseudolycoriella* species from New Zealand [*Pseudolycoriella bispina* Mohrig, 1999; *Pseudolycoriella jejuna* (Edwards, 1927) and *Pseudolycoriella zealandica* (Edwards, 1927)]. Especially the shape of the gonostylus of *P. frederickedwardsi* and *P. breviseta* is very similar. Nevertheless *P. frederickedwardsi* can be distinguished by the recurved lateral edges of its tegmen that lacks any lateral teeth or projection. Furthermore *P. frederickedwardsi* has the longest flagellomeres (length/width ratio ≥ 2.9) of all the four similar species. The species groups erected by Mohrig (2013) for *Pseudolycoriella* species from Papua New Guinea could not be applied for *P. frederickedwardsi* very well. Due to its greater number of spines on the gonostylus and its non-elongated tegmen *P. frederickedwardsi* could be placed in the *Pseudolycoriella triacanthula* group, but the shape of the gonostylus and the antennae are contradictory.

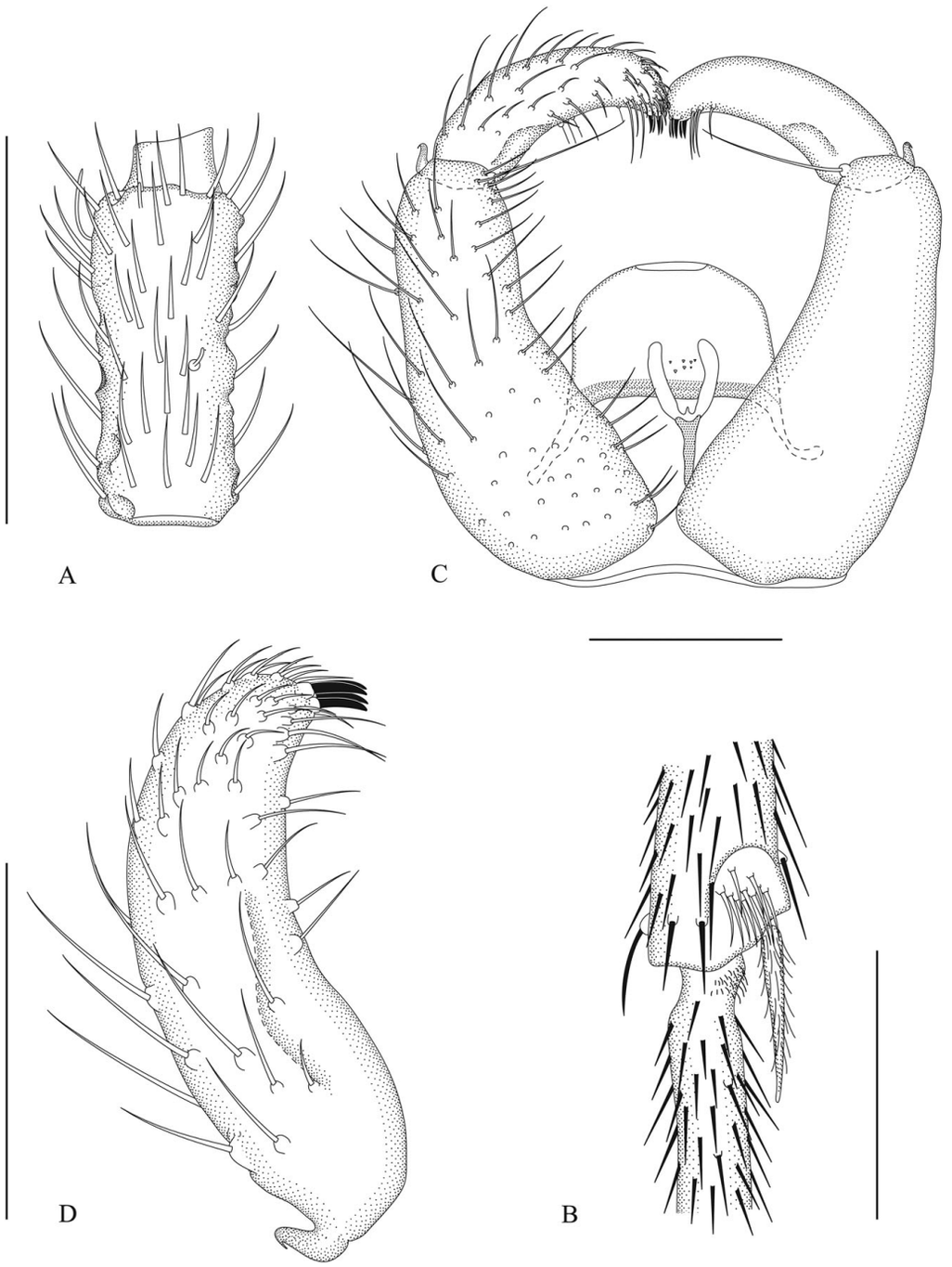
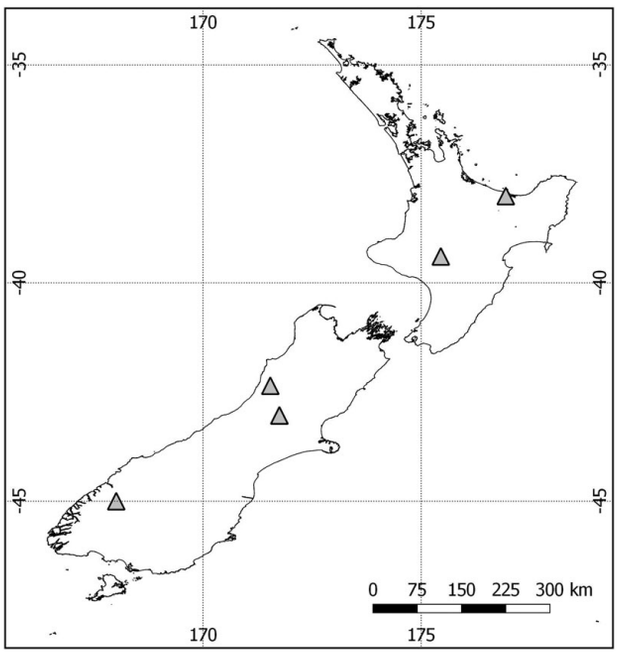


Figure 6. *Pseudolycoriella tonnoiri* Köhler sp. nov. **A,** Fourth flagellomere. **B,** Tibial organ of fore leg. **C,** Hypopygium. **D,** Gonostylus. Scale bars = 0.1 mm.

Pseudolycoriella tonnoiri Köhler sp. nov.

(Figure 6A–D, Map 6)

Material examined. Holotype: ♂, New Zealand: South Island, Otago Lakes, Fiordland NP, Eglinton River Valley, Deer Flat; *Nothofagus* forest, 1–20 December 2002, leg. M. & C. Jaschhof & U. Kallweit. (NZAC). Paratypes: 2♂♂, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992, leg. M. Jaschhof (1♂ SDEI, 1♂ PWMP). 1♂, South Island, Buller, Ahaura, Granville State Forest; *Nothofagus truncata* forest, 170–250 m, December 1994, leg. J. Hutcheson (SDEI). 1♂, South Island, Mid Canterbury, Cass, Middle Bush, *Nothofagus solandri* forest, 30 May 1998, leg. P.M. Johns (SDEI). 1♂, same locality as previous, 10 December 1998, leg. P.M. Johns (SDEI). 10♂♂, North Island, Taupo, Tongariro NP, Mangawhero River Valley

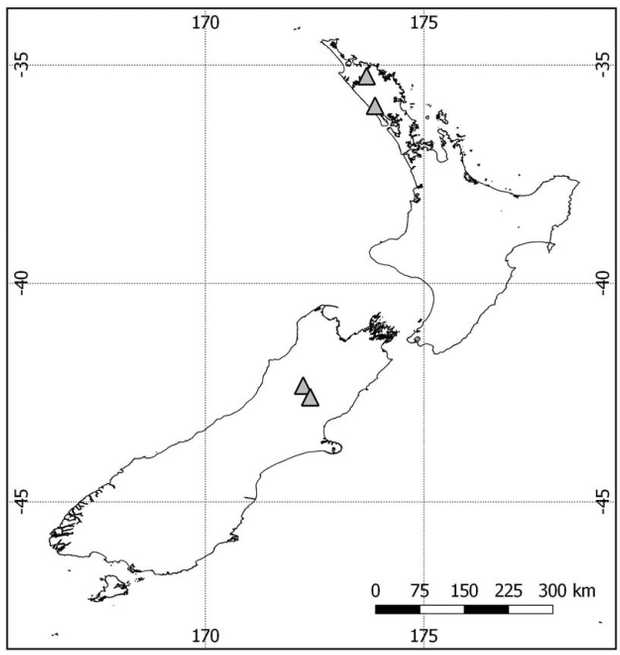


Map 6. Collection localities of *Pseudolycoriella tonnoiri* Köhler sp. nov.

3 km northeast Ohakune, 690 m, mixed podocarp/broadleaf forest, 26 November to 28 December 2002, leg. M. & C. Jaschhof & U. Kallweit (2♂♂ NZAC, 6♂♂ SDEI, 1♂ UZMH, 1♂ PWMP).

Description. Male. Head: Brown. Eye bridge two or three facets wide. Antennae light brown, scape and pedicel concolorous with flagellum; fourth flagellomere 2.2–2.8 times longer than wide (Figure 6A), necks of flagellomeres well differentiated; flagellomeres with deep grooves that give them a rough surface, two types of sensilla present, small and short with a pale corona and longer ones; hairs on the flagellomeres sparsely arranged and slightly shorter than flagellomeres' width. Maxillary palp pale with three palpomeres, first and third of same length, second one shortest, palpomere 1 with three bristles; second palpomere with one longer outer bristle. Clypeus and prefrons bulging outwards. *Thorax:* Pale brown. Posterior pronotum bare. Anterior pronotum with five long and fine hairs. Episternum 1 with four hairs. Mesonotum with three slightly longer laterals and many smaller ones. Scutellum with two strong bristles and several hairs. Katepisternum 1.2 times longer than high. *Wing:* Length 1.8–2.2 mm; width/length ratio 0.3–0.4. Membrane transparent and without macrotrichia, anal area slightly developed; all posterior veins distinct; r-m and bM without macrotrichia; apical half of R_5 with macrotrichia on both sides, basal half just with dorsal ones; R_1 short, just 0.45–0.63 times as long as R; c/w ratio 0.71–0.78; r-m as long as bM. Halteres pale brown; shaft as long as head. *Legs:* Pale brown. Tibial organ small, less than half as wide as tibial apex, consisting of a short row of bristles surrounded by a circular border (Figure 6B). Mid tibia with some strong ventral bristles, which are as long as tibia diameter. Hind tibia with a dorsal and a ventral row of strong spines, the dorsal one located in the apical half and ventral one more in the middle of the tibia. All tibial spurs equal in length. Claws with two teeth. *Abdomen:* Same colour as thorax. *Hypopygium:* Gonocoxites (Figure 6C) wider than long, with long hairs; ventral, inner-side of gonocoxites V-shaped and basally not fused. Gonostylus (Figure 6D) 2.7–3.4 longer than wide, curved, apex with four to seven spines among a dense vestiture, three subapical whip-lash hairs. Tegmen (Figure 6C) large and nearly quadrangular, basal apodemes strong. Area of teeth with a few tiny teeth. Ejaculatory apodeme (Figure 6C) strong with a large horseshoe-shaped base. *Body size:* 1.7–2.3 mm.
Female: Unknown.

Etymology. The new species is named after the dipterist André Léon Tonnoir (1885–1940).



Map 7. Collection localities of *Bradysia pallipes* (Fabricius, 1787).

Discussion. Like *P. frederickedwardsi*, discussed above, *P. tonnoiri* is reminiscent of *P. breviseta* and *P. macrotegmenta*. *Pseudolycoriella tonnoiri* can be distinguished from similar species by the shape of the tegmen. Only *P. tonnoiri* has a more or less quadrangular tegmen without any striking features, whereas the tegmen of *P. breviseta* bears some prominent lateral projections and that of *P. macrotegmenta* is toothed laterally. The tegmen of *P. frederickedwardsi* has lateral edges which are recurved ventrally. *Pseudolycoriella tonnoiri* does not fit without contradiction in the *Pseudolycoriella triacanthula* group erected by Mohrig (2013).

New faunistic records

Bradysia pallipes (Fabricius, 1787)

(Map 7)

1 ♀, New Zealand, North Island, Dargaville, Kauri (*Agathis australis*) wood with tree ferns, 30 December 1992. M. Jaschhof (PWMP). 1♀, North Island, Puketi Forest, Waipapa River Valley, mixed secondary wood of Kauri (*Agathis australis*) and *Podocarpus* with tree ferns, 1–2 January 1993. M. Jaschhof (PWMP). 1♀, South Island, Buller, Lake Daniells, track 5 km east of Spring Junction, mixed red/silver beach forest, 24 December 2001. A. Stark (SDEI). 1♂, South Island, Buller, Hope River, 'Windy Point', 18 December 2000, R.K. Didham & R. Ewers (SDEI). 1♂, same locality as previous, 19 December 2000, R.K. Didham & R. Ewers (SDEI).

Remarks. Mohrig and Jaschhof's (1999) assumption that two females that obviously belong to the *Bradysia pallipes* group would belong to *Br. pallipes* [= *Br. brunnipes* (Meigen, 1804)] can be confirmed here by our finding of two males of the same species. According to Mohrig et al. (2013), *Br. pallipes* is Holarctic in distribution, so its occurrence in New Zealand is presumably due to introduction rather than indicating a cosmopolitan distribution pattern.

Corynoptera cowanorum Mohrig, 1999

5 ♂♂, New Zealand, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992, leg. M. Jaschhof (1♂ UZMH, 4♂♂ PWMP).

Corynoptera densospica Mohrig, 1999

5 ♂♂, New Zealand, North Island, Urewera National Park, Huiarau Range 30 km southeast of Murupara, *Podocarpus-Nothofagus* wood, altitude 600–1000 m, 23 December 1992, leg. M. Jaschhof (1♂ UZMH, 4♂♂ PWMP).

Corynoptera didymistyla Mohrig, 1999

1 ♂, New Zealand, North Island, Urewera National Park, Huiarau Range 30 km southeast of Murupara, *Podocarpus-Nothofagus* wood, altitude 600–1000 m, 23 December 1992, leg. M. Jaschhof (PWMP).

Corynoptera dividospica Mohrig, 1999

1 ♂, New Zealand, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992, leg. M. Jaschhof (PWMP).

Corynoptera expressospina Mohrig, 1999

1 ♂, New Zealand, North Island, Urewera National Park, Huiarau Range 30 km southeast of Murupara, *Podocarpus-Nothofagus* wood, altitude 600–1000 m, 23 December 1992, leg. M. Jaschhof (PWMP).

Corynoptera fatigans (Johannsen, 1912)

1 ♂, New Zealand, North Island, Dargaville, Kauri (*Agathis australis*) wood with tree ferns, 30 December 1992, leg. M. Jaschhof (PWMP).

Remarks. This is the first record of this species for New Zealand. *Corynoptera fatigans* (= *Corynoptera perpusilla* Winnertz, 1867) is a common and widespread species in the Holarctic region (Hippa et al. 2010; Mohrig et al. 2013) and can be found in a variety of habitats, e.g. broad-leaved forests, grasslands, wetlands, gardens (Menzel et al. 2006). Due to these undemanding ecological requirements on its habitat and its wide distribution in the Holarctic, *C. fatigans* can be considered to be an introduced species. Mohrig (2004) already mentioned that *C. fatigans* has been introduced to New Caledonia.

Corynoptera filispica Mohrig, 1999

61 ♂♂, New Zealand, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992, leg. M. Jaschhof (20♂♂ NZAC, 37♂♂ SDEI, 2♂♂ UZMH, 2♂♂ PWMP).

Remarks. All specimens examined in the present study have five spines on the gonostylus instead of six as noted by Mohrig & Jaschhof (1999).

Corynoptera fuscispica Mohrig, 1999

1 ♂, New Zealand, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992, leg. M. Jaschhof (PWMP).

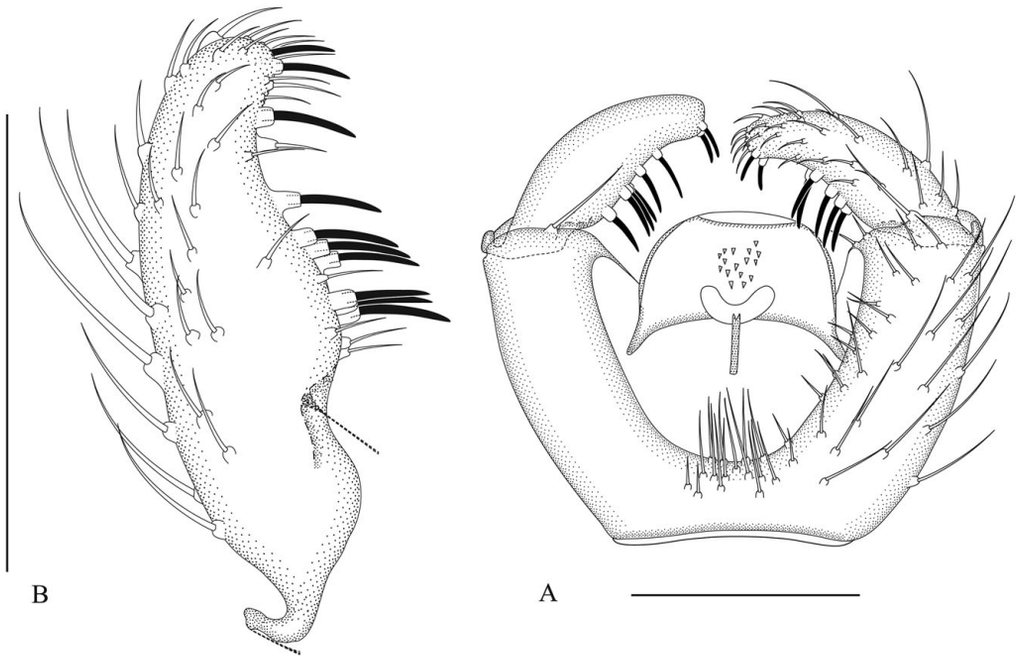


Figure 7. *Corynoptera semiaggregata* Mohrig, 1999. **A,** Hypopygium. **B,** Gonostylus. Scale bars = 0.1 mm.

Corynoptera microsetosa Mohrig, 1999

1 ♂, New Zealand, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992, leg. M. Jaschhof (PWMP).

Corynoptera nigrotegminis Mohrig, 1999

1 ♂, New Zealand, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992, leg. M. Jaschhof (PWMP).

Corynoptera semiaggregata Mohrig, 1999

(Figure 7A–B)

1 ♂, New Zealand, South Island, Westland NP, southeast of Gillespies Beach, mixed podocarp forest, 19 October 2001, leg. M. Jaschhof (SDEI).

Corynoptera tapleyi (Edwards, 1927)

4 ♂♂, New Zealand, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992, leg. M. Jaschhof (PWMP).

Corynoptera variospina Mohrig, 1999

9 ♂♂, New Zealand, North Island, Urewera National Park, Huiarau Range 30 km southeast of Murupara, *Podocarpus-Nothofagus* wood, altitude 600–1000 m, 23 December 1992, leg. M. Jaschhof (2♂♂ SDEI, 7♂♂ PWMP). 1♂, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992, leg. M. Jaschhof (PWMP).

Pseudolycoriella jejuna (Edwards, 1927)

1 ♂, New Zealand, North Island, White Pine Bush 3 km southwest of Whakatane/Bay of Plenty, *Podocarpus* wood, 26 December 1992, leg. M. Jaschhof (PWMP).

Acknowledgements

The authors thank Catrin and Mathias Jaschhof (Färjestaden, Sweden) for donating the specimens that we studied; Mathias Jaschhof and Frank Menzel (Müncheberg, Germany) for reading and commenting on an earlier draft of the manuscript; Andrew Liston (Müncheberg) for improving the language; and Pekka Vilkamaa (Helsinki, Finland) and an anonymous reviewer for valuable comments. The senior author acknowledges the kind support of Charles Oliver Coleman (Berlin, Germany) who gave him an introduction to the techniques of digital drawing.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Zootaxa 4707 (1): 001–069
https://www.mapress.com/j/zt/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4707.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:3C00FB35-708D-4FF0-94C2-B15BD2A1F37A

ZOOTAXA

4707

The genus *Pseudolycoriella* Menzel & Mohrig, 1998 (Diptera, Sciaridae) in New Zealand

ARNE KÖHLER
Senckenberg Deutsches Entomologisches Institut, Eberswalder Straße 90, D-15374 Müncheberg, Germany.
E-mail: arne.koehler@senckenberg.de

Magnolia Press
Auckland, New Zealand

Accepted by K. Heller: 4 Oct. 2019; published: 12 Dec. 2019

ARNE KÖHLER

The genus *Pseudolycoriella* Menzel & Mohrig, 1998 (Diptera, Sciaridae) in New Zealand

(*Zootaxa* 4707)

69 pp.; 30 cm.

12 Dec. 2019

ISBN 978-1-77670-827-7 (paperback)

ISBN 978-1-77670-828-4 (Online edition)

FIRST PUBLISHED IN 2019 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: magnolia@mapress.com

https://www.mapress.com/j/zt

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of Contents

Abstract

In the course of the present study 28 species of the genus *Pseudolycoriella* Menzel & Mohrig, 1998 from New Zealand were described as new to science: *Pseudolycoriella aotearoa* **sp. n.**, *Psl. dagae* **sp. n.**, *Psl. dentitegmenta* **sp. n.**, *Psl. fiordlandia* **sp. n.**, *Psl. gonotegmenta* **sp. n.**, *Psl. hauta* **sp. n.**, *Psl. huttoni* **sp. n.**, *Psl. jaschhofi* **sp. n.**, *Psl. jejunella* **sp. n.**, *Psl. kaikoura* **sp. n.**, *Psl. maddisoni* **sp. n.**, *Psl. mahanga* **sp. n.**, *Psl. nahenahe* **sp. n.**, *Psl. orite* **sp. n.**, *Psl. plicitegmenta* **sp. n.**, *Psl. porehu* **sp. n.**, *Psl. porotaka* **sp. n.**, *Psl. puhihi* **sp. n.**, *Psl. raki* **sp. n.**, *Psl. robustotegmenta* **sp. n.**, *Psl. subtilitegmenta* **sp. n.**, *Psl. sudhausi* **sp. n.**, *Psl. teo* **sp. n.**, *Psl. tewaipounamu* **sp. n.**, *Psl. tuakana* **sp. n.**, *Psl.*

wernermohrigi **sp. n.**, *Psl. whakahara* **sp. n.**, and *Psl. whena* **sp. n.** *Pseudolycoriella cavatica* (Skuse, 1888), a widely distributed species, was recorded from New Zealand for the first time, and recognised as a senior synonym of *Spathobdella setigera* Hardy, 1960 **syn. n.** Apart from *Psl. kaikoura* and *Psl. cavatica* all New Zealand *Pseudolycoriella* species group in four different clusters: the *Psl. bispina* complex, the *Psl. jejuna* complex, the *Psl. macrotegmenta* complex, and the *Psl. zealandica* complex. The monophyly of those four species complexes was confirmed by a genetic analysis based on two mitochondrial genes (COI and 16S) and one nuclear gene (28S). A key to the species is given.

Key words: 16S, 28S, Australasian region, COI, DNA sequencing, key, morphology, new species, new synonym, systematics, taxonomy

Introduction

Menzel & Mohrig (1998) recognised the morphological unity of several sciarid species which were previously scattered within the genera *Sciara* Meigen, *Corynoptera* Winnertz, and *Lycoriella* Frey. Accordingly, they transferred those species to the newly erected genus *Pseudolycoriella* Menzel & Mohrig. The two authors stated that the following apomorphic characters demonstrate the monophyly of the new genus: one whip-lash hair on the apical third of the gonostylus, claws with teeth, and a tibial organ consisting of a dense row of bristles without a basal ridge. The monophyly of the genus *Pseudolycoriella* was later verified by a genetic analysis by Shin *et al*. (2013). Since 1998 several new species have been described and assigned to this genus. As of May 2019, *Pseudolycoriella* comprised 132 species (Menzel, personal communication). Several authors have stated that *Pseudolycoriella* is probably one of the most species-rich genera of the Sciaridae (e.g. Menzel & Mohrig 2000; Rudzinski *et al*. 2016). Species of this genus are found in all biogeographic realms, but with different levels of diversity. Only a small proportion of all known species is found in the Palaearctic realm (Menzel & Mohrig 2000), while the southern hemisphere is much more diverse (e.g. Vilkamaa *et al*. 2012; Mohrig 2013).

The intrageneric systematics of *Pseudolycoriella* is still in its infancy. Menzel & Mohrig (2000) established three species groups—*Psl. bruckii* group, *Psl. horribilis* group, and *Psl. morenae* group—mainly to allow an easier use of identification keys, and thus implemented a first provisional system of *Pseudolycoriella*. *Pseudolycoriella horribilis* (Edwards), the only member of the *Psl. horribilis* species group, is characterized by the presence of a truncated tooth on the gonostylus that is not homologous with the gonostylar tooth of other sciarid taxa (Menzel & Mohrig 2000). The two species of the *Psl. morenae* group possess conspicuous lobes with bristles on the inner gonocoxites and lack any teeth on the claws. Menzel & Mohrig (2000) placed the remaining 17 species known at that time in the *Psl. bruckii* group, which comprises the majority of all species. The following diagnostic characters were given for this group: toothed claws, absence of lobes on the inner base of the gonocoxites, the absence of a tooth on the gonostylus, and up to five spines on the gonostylus (rarely without any spines). Later Mohrig (2013) amplified the provisional system by adding three further species groups to accomodate newly described *Pseudolycoriella* species from Papua New Guinea. These groups are the *Psl. longicostalis* group, the *Psl. quadrispinosa* group, and the *Psl. triacanthula* group. The *Psl. longicostalis* group comprises tiny species with deep sensory pits on the flagellomeres, a gonostylus with two spines (sometimes reduced), a tegmen without any secondary structures, and a conspicuous row of longitudinal bristles on the hind tibia. However, the delimitation between this group and the *Psl. bruckii* group remained vague. The *Psl. quadrispinosa* group is characterised by the presence of more than two spines on the gonostylus and a gradual reduction of the whip-lash hair. The species of the *Psl. triacanthula* group are relatively large and bear three or more robust spines on the gonostylus. The attempt to apply this species group concept to the New Zealand species *Psl. frederickedwardsi* Köhler, and *Psl. tonnoiri* Köhler failed, and Köhler & Mohrig (2016) did not propose a new provisional species group to accomodate them. The first valid intrageneric taxon of *Pseudolycoriella* was established by Heller (2012), who changed the former genus *Ostroverkhovana* Komarova into a subgenus of *Pseudolycoriella*. However, Mohrig & Kauschke (2019) disagreed with Heller (2012) and included *Ostroverkhovana* in *Pseudolycoriella* without distinguishing any subgenera. A possible congenericity of *Pseudolycoriella* and *Eugnoriste* Coquillett is still to be investigated (Vilkamaa *et al*. 2012).

The sciarids of New Zealand have attracted little attention by previous workers. Only two major studies (Tonnoir & Edwards 1927; Mohrig & Jaschhof 1999) and a few minor ones (Hutton 1881; Wisely 1959; Davies 1988; Köhler & Mohrig 2016) dealt with this dipteran family. A total of 54 sciarid species are known from New Zealand, seven of which belong to *Pseudolycoriella*.

Materials and methods

Collecting and depository. The majority of the sciarid flies examined were obtained as bycatch from a survey of New Zealand Cecidomyiidae by Catrin and Mathias Jaschhof between 2001 and 2002 (Jaschhof & Jaschhof 2003a, 2003b, 2004; collecting permit #9900/143/3/04 issued by the Department of Conservation, New Zealand). Another important part of the material was collected by Peter A. Maddison between 2014 and 2016. Only a small number of examined specimens was caught by other entomologists. Most specimens were collected with Malaise traps, aspirators, or sweep nets. Rather rarely, light traps, pitfall traps, and pan traps were used. Additionally, historic type material was borrowed from the relevant collections. The studied material is deposited in the following scientific collections: the Natural History Museum, London, United Kingdom (BMNH); the Centre for Biodiversity Genomics, Guelph, Canada (CBG); the New Zealand Arthropod Collection, Auckland, New Zealand (NZAC); the private collection of Werner Mohrig, Poseritz, Germany (PWMP); the Senckenberg Deutsches Entomologisches Institut, Müncheberg Germany (SDEI); and the Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland (UZMH).

Morphology. All sciarids were stored in 70% ethanol after they were collected. Prior to examination, the specimens were mounted in Canada balsam on glass slides following the instructions of Mohrig & Jaschhof (1999), and Menzel & Mohrig (2000). Accordingly, on each slide the hypopygium is mounted with the ventral side up, separated from the rest of the body, which lies on its right lateral side. Therefore the lengths of both these separated body parts have to be added, to obtain the total body length. The right wing was also separated and covered by a cover slip. For some specimens belonging to morphologically challenging species tergite IX was dissected from the remaining hypopygium to allow a better view of the tegmen. Morphological examination was conducted with an Olympus BX50 Microscope fitted with an Olympus U-DA drawing tube. The drawings were digitised using the software Adobe Illustrator CS6 according to Coleman (2003, 2009). Scanning electron microscope (SEM) images of details of the male genitalia of a species of the *Psl. jejuna* complex were obtained. One specimen was dehydrated sequentially with ethanol (70–98%) and acetone (100%), then critical-point dried, glued on a micro pin, and sputtered with gold. The images were taken with a SEM JSM-6060LV (JEOL) at an acceleration voltage of 8–12 kV.

The general terminology and the application of taxonomically important measurements follow Menzel & Mohrig (2000) (Fig. 22). The length of the fourth flagellomere, which is necessary for the length-width ratio, represents the whole length i.e. the combined lengths of the flagellomere's body and the flagellomere's neck. The width of the fourth flagellomere was measured at the widest part, mostly at the apex of the flagellomere's body. The notation of the wing veins follows Hippa *et al*. (2010) (Fig. 9) and the use of the terms anterior portion of gonocoxal apodeme, posterior portion of gonocoxal apodeme, and parameral apodeme derives from Jaschhof & Jaschhof (2009) (Fig. 11). For specimens of the *Psl. bispina* and the *Psl. jejuna* complex the term lateral lobes (e.g. *ll* in Fig. 22) is used. This term is only used for descriptive purposes and should not be misinterpreted as a statement about homology. Where larger series of type specimens were available, a sample of at least ten specimens was measured using a micrometre. Specimens that could not be reliably determined to species level were not included in the type series, but are included as additional material. The order in which the species are treated is more or less arbitrary, although an attempt has been made to group closely related species together for easier comparison.

Molecular analysis. All specimens that underwent a molecular analysis are labelled with a unique number, consisting of the prefix "SDEI-Dipt-" and a seven-digit number. DNA was extracted with the E.Z.N.A.® Tissue DNA Kit (Omega Bio-tek Inc.), following the manufacturer's instructions. To obtain a greater amount of DNA from old material, which had usually been stored for longer periods under poor conditions, the first extraction step—the tissue lysis—was prolonged overnight. Additionally, whole specimens were used in the lysis procedure instead of some individual body parts. Attempts were made to obtain sequences of the mitochondrial genes COI and 16S, and the nuclear gene 28S via polymerase chain reactions (PCR) following Shin *et al*. (2013). In this phylogenetic study the nuclear gene 18S was also sequenced. However, the 18S gene could not be reliably obtained from the mostly older material which was available. In general, the primer pair LCO_1490 and HCO_2198 was used for COI amplifying (Folmer *et al*. 1994). If those primers did not show sufficient results, the primers LepF1 and LepR1 (Hebert *et al*. 2004), or LCO_1490 and HCO_2198 in combination with the internal primers sym-C1-J-1718 (Simon *et al*. 1994) and C1-N1760 (Prous *et al*. 2011) were used. The length of the COI sequence is 658 base pairs (bp). For the 16S sequence the primers 16SAR-L and 16SBR-H (Palumbi *et al*. 1991) were used. Due to a high percentage of failures in comparison to the other markers, an alternative primer set was designed. The new primers Psl_16S_for

and Psl_16S_rev bind within the 16S region and therefore yield a shorter sequence than the primer pair 16SAR-L and 16SBR-H. The length of the 16S sequence is 538 bp. A part of the nuclear 28S sequence was obtained using the four primers 28S A, 28S-rD7b1, 28S-rD5b, and 28S-Rd48a (Friedrich & Tautz 1997; Whiting *et al*. 1997) as done by Shin *et al*. (2013). Furthermore, the primers 28SF2 and 28SB2 (Boevé *et al*. 2013) were used to get an additional part of the 28S gene, which is located upstream (i.e., at the 5' end of the coding strand) of the former 28S locus. Both sequences overlap in the nuclear genome and can therefore be easily pasted together to yield a sequence of 1,857 bp. All used primers, their annealing temperature and the the number of PCR cyles are listed in Table 1. PCR products were purified with Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase (Life Technologies, Darmstadt, Germany) and sent to Macrogen Europe (Amsterdam, The Netherlands) for Sanger sequencing. The primers from each PCR were also used for sequencing. The software Geneious 11.0.5 was used to assamble the resulting ab1-files provided by Macrogen and aligned with the online software MAFFT version 7 (https://mafft.cbrc.jp/alignment/software/; Katoh *et al*. 2002; Katoh & Standley 2013; Katoh *et al*. 2017). The sequences used for the phylogenetic analyses were uploaded to GenBank (https://www.ncbi.nlm.nih.gov/genbank/). The accession numbers are listed in Table 2. Residual DNA extracts are deposited in the SDEI.

The pairwise p-distances (uncorrected) for the genes COI and 28S were calculated with the software MEGA7 (Kumar *et al*. 2016) for each species. The maximal intraspecific p-distances between all available sequences of a species and the lowest p-distance to another species ("nearest neighbour") are given in each species account. Due to a future analysis, not all COI sequences used for the calculation of the p-distances are yet available online.

All three genes were used for the phylogenetic analysis. Each gene was aligned separately using default settings and afterwards concatenated using the software FASconCAT-G v1.04 (Kück & Longo 2014). The phylogenetic analysis was carried out with the software IQ-TREE 1.6.1 (Nguyen *et al*. 2015) using the implemented tool Modelfinder (Kalyaanamoorthy *et al*. 2017) for an automatic model selection. The statistical validation of the phylogenetic tree was undertaken using the ultrafast bootstrap approximation [UFBoot] (Minh *et al*. 2013; Hoang *et al*. 2018). For the UFBoot estimation 1,000 replicates were deployed. As outgroup, two species of Diadocidiidae (Diptera, Sciaroidea) and one species of Scatopsidae (Diptera, Scatopsoidea) were used (see Table 2). The scatopsid species—*Coboldia* sp.—was used to root the phylogenetic tree.

Key to the males of New Zealand *Pseudolycoriella* species

1. Gonostylus with one or two obvious spines . . . . . *Psl. bruckii* group, 2
- Gonostylus with more than two small spines . . . . . *Psl. macrotegmenta* complex, 26
2. Gonostylus with two spines 3
- Gonostylus with one spine 11
3. Wing length greater than 2.4 mm; length of gonocoxites more than 200 µm 4
- Wing length less than 2.4 mm; length of gonocoxites 200 µm or less 5
4. Base of the ejaculatory apodeme horseshoe-shaped . . . . . *Psl. zealandica* (Edwards)
- Base of the ejaculatory apodeme elongate and slender . . . . . *Psl. aotearoa* **sp. n.**
5. Fourth flagellomere less than twice as long as wide . . . . . *Psl. cavatica* (Skuse)
- Fourth flagellomere more than twice as long as wide . . . . . *Psl. bispina* complex, 6
6. Fourth flagellomere less than three times as long as wide, with dense setae (Fig. 5) . . . . . *Psl. puhihi* **sp. n.**
- Fourth flagellomere at least three times as long as wide, with sparsely scattered setae (e.g. Fig. 4) 7
7. Wings slender, anal area weakly developed 8
- Wings of normal shape, anal area well developed 9
8. Wing length less than 2.2 mm; c/w ratio greater than 0.65 . . . . . *Psl. orite* **sp. n.**
- Wing length 2.2 mm or more; c/w ratio less than 0.65 . . . . . *Psl. porehu* **sp. n.**
9. Base of the ejaculatory apodeme lyre-shaped; apex of tegmen surrounded by a sclerotized margin (Figs 14 & 18); body length more than 1.8 mm, gonocoxites of normal length 10
- Base of the ejaculatory apodeme u-shaped; apex of tegmen with membranous area (Fig. 15), body length less than 1.8 mm, gonocoxites short . . . . . *Psl. teo* **sp. n.**
10. Apex of R_5 with macrotrichia only on ventral side; hind tibia with ten or more robust bristles in a longitudinal row . . . . . *Psl. bispina* Mohrig
- Apex of R_5 with macrotrichia on both sides; hind tibia with less than ten robust bristles in a longitudinal row . . . . . *Psl. mahanga* **sp. n.**
11. Fourth flagellomere less than twice as long as wide; tegmen apically roundish (Fig. 11) . . . . . *Psl. kaikoura* **sp. n.**
- Fourth flagellomere more than twice as long as wide; tegmen with a pronounced apex (*at* in Fig. 22) . . . . . *Psl. jejuna* complex, 12
12. Scape and pedicel bright yellowish, contrasting strongly with the brown flagellomeres 13

- Scape and pedicel pale brown, contrasting slightly with flagellomeres. 17
13. Body length less than 2.5 mm 14
- Body length greater than 2.5 mm 15
14. Fourth antennal flagellomere at least 2.8 times longer than broad; gonostylus more than 2.8 times longer than broad; wing length less than 2.2 mm (ca. 1.9–2.1 mm) . . . . . *Psl. whena* **sp. n.**
- Fourth antennal flagellomere less than 2.8 times longer than broad; gonostylus less than 2.8 times longer than broad; wing length 2.2 mm . . . . . *Psl. nahenahe* **sp. n.**
15. Ejaculatory apodeme slender (Fig. 39); fourth antennal flagellomere less than 2.6 times as long as broad . *Psl. porotaka* **sp. n.**
- Ejaculatory apodeme broad (Fig. 42); fourth antennal flagellomere at least 2.6 times longer than broad 16
16. Gonostylus more than 2.8 times as long as broad; inner base of gonostylus with a conspicuous angle (*ba* in Fig. 42) . . . . . *Psl. dagae* **sp. n.**
- Gonostylus less than 2.8 times as long as broad; inner base of gonostylus without or only with a minor angle (Fig. 41) . . . . . *Psl. raki* **sp. n.**
17. Ratio R_1/R less than 0.80 18
- Ratio R_1/R greater than or equal to 0.80. 22
18. Mesonotum with long and dense setae; 5–6 bristles on the scutellum. . . . . *Psl. hauta* **sp. n.**
- Mesonotum with normal setosity; 2–4 bristles on the scutellum 19
19. Fourth antennal flagellomere less than 2.8 times longer than broad 20
- Fourth antennal flagellomere more than 2.8 times longer than broad . . . . . *Psl. sudhausi* **sp. n.**
20. Small species; wing length less than 2.5 mm; gonostylus slender. . . . . *Psl. jejunella* **sp. n.**
- Larger species; wing length greater than 2.5 mm. . . . . *Psl. maddisoni* **sp. n.**
22. Apical cavity on gonostylus prominent and extensively bare, without microtrichia (Figs 20 & 22). 23
- Apical cavity on gonostylus absent or inconspicuous, or with microtrichia 24
23. Wing length greater than 3.0 mm . . . . . *Psl. whakahara* **sp. n.**
- Wing length less than 3.0 mm . . . . . *Psl. tewaipounamu* **sp. n.**
24. Ejaculatory apodeme slender (Figs 37 & 39). . . . . *Psl. sudhausi* **sp. n.**
- Ejaculatory apodeme broad (e.g. Fig. 41) 25
25. Apical spine on the gonostylus short, not protruding from the surrounding setae (Figs 30–31); mid tibia without robust bristles among the vestiture. . . . . *Psl. tuakana* **sp. n.**
- Apical spine on the gonostylus slightly longer, protruding from the surrounding setae (Figs 25–26); mid tibia with robust bristles among the vestiture . . . . . *Psl. jejuna* (Edwards)
26. Tegmen laterally with small teeth (*lt* in Fig. 52) 31
- Tegmen laterally without small teeth 27
27. Tegmen basolaterally with robust projections (Fig. 59), apex of gonostylus broad. . . . . *Psl. breviseta* Mohrig
- Tegmen basolaterally without projections, apex of gonostylus not broader than base 28
28. Tegmen large with lateral ledges (Fig. 55); gonostylus strongly curved . . . . . *Psl. fiordlandia* **sp. n.**
- Tegmen of normal proportions; gonostylus elongated 29
29. Tegmen with a medial, hood-like structure (Fig. 56); gonostylus longer, usually more than 3.5 times as long as wide. . . . . *Psl. jaschhofi* **sp. n.**
- Tegmen without a medial structure; gonostylus shorter, usually less than 3.5 times as long as wide 30
30. Tegmen with recurved lateral edges; fourth flagellomere more than 2.8 times as long as broad . *Psl. frederickedwardsi* Köhler
- Tegmen without lateral structures; fourth flagellomere equal to or less than 2.8 times as long as broad . . . *Psl. tonnoiri* Köhler
31. Tegmen with teeth laterally and apically (Fig. 60). . . . . *Psl. dentitegmenta* **sp. n.**
- Tegmen with lateral teeth only 32
32. Tegmen with dorsal structures (*ds* in Fig. 52); spines on gonostylus more transversely oriented. 33
- Tegmen without dorsal structures; gonostylus bulging apically, spines more longitudinally orientated. . . . . *Psl. macrotegmenta* Mohrig
33. Base of vein M longer than M-fork; sclerotized margin of tegmen very broad; tegmen with dorsal structures strongly developed, reaching apex of tegmen. . . . . *Psl. robustotegmenta* **sp. n.**
- Base of M vein shorter than M-fork; sclerotized margin of tegmen narrower; dorsal structures mostly not reaching apex of tegmen (except in *Psl. wernermohrigi*) 34
34. Margin of tegmen narrowly sclerotized; gonostylus apically tapered . . . . . *Psl. subtilitegmenta* **sp. n.**
- Margin of tegmen broadly sclerotized; gonostylus apically not tapered 35
35. Ejaculatory apodeme long (Fig. 50); sclerotized edge of tegmen apically closed. . . . . *Psl. wernermohrigi* **sp. n.**
- Ejaculatory apodeme short (e.g. Fig. 51); sclerotized edge of tegmen apically closed or interrupted. 36
36. Base of ejaculatory apodeme v-shaped; ratio R_1/R mostly greater than 0.65 . . . . . *Psl. gonotegmenta* **sp. n.**
- Base of ejaculatory apodeme u-shaped; ratio R_1/R less than 0.65 37
37. Gonostylus more than 3.0 times as long as broad; sclerotized edge of tegmen apically interrupted; ratio R_1/R less than 0.55 . . . . . *Psl. plicitegmenta* **sp. n.**
- Gonostylus less than 3.0 times as long as broad; sclerotized edge of tegmen apically closed; ratio R_1/R greater than 0.55 . . . . . *Psl. huttoni* **sp. n.**

TABLE 1. List of primers used for PCR.

Locus	Primer	Direction F/R (i)	Primer sequence (5' to 3')	Annealing temperature	PCR cycles	Reference
COI	LCO_1490	F	GGTCAACAAATCATAAAGATATTGG	49°C	38	Folmer *et al.* (1994)
COI	HCO_2198	R	TAAACTTCAGGGTGACCAAAAAATCA	49°C	38	Folmer *et al.* (1994)
COI	LepF1	F	ATTCAACCAATCATAAAGATATTGG	49°C	38	Hebert *et al.* (2004)
COI	LepR1	R	TAAACTTCAGGGTGACCAAAAAATCA	49°C	38	Hebert *et al.* (2004)
COI	sym-C1-J-1718	F (i)	GGAGGATTTGGAAAYTGAYTAGTWCC	49°C	38	Simon *et al.* (1994)
COI	C1-N1760	R (i)	GGTARAAATCARAATCTTATATTAT	49°C	38	Prous *et al.* (2011)
16S	16SAR-L	F	CGCCTGTTTATCAAAAACAT	49°C	38	Palumbi *et al.* (1991)
16S	16SBR-H	R	CCGGTCTGAACTCAGATCACGT	49°C	38	Palumbi *et al.* (1991)
16S	Psl_16S_for	F (i)	GTACAAAGGTAGCATAATCRTT	53°C	38	present study
16S	Psl_16S_rev	R (i)	AATCCAAMATSGAGGTCGCAA	53°C	38	present study
28S	28S A	F	GACCCGTCTTGAAACACGGA	49°C	40	Whiting *et al.* (1997)
28S	28S-rD7b1	R	GACTTCCCTTACCTACAT	49°C	40	Friedrich & Tautz (1997); Whiting *et al.* (1997)
28S	28S-Rd48a	F (i)	ACCTATTCTCAAACTTTAAATGG	49°C	40	Whiting *et al.* (1997)
28S	28S-rD5b	R (i)	CCACAGCGCCAGTTCTGCTTAC	49°C	40	Whiting *et al.* (1997)
28S	28SF2	F	CACGAGCCGATAGCGAACAAG	54°C	40	Boevé *et al.* (2013)
28S	28SB2	R	CCAAGGCCTCTAATCATTCGC	54°C	40	Boevé *et al.* (2013

TABLE 2. List of sequenced specimens used in this study with GenBank accession numbers or BOLD link.

Species	Family	Country	Sample number	GenBank Accession Number			Reference
				COI	16S	28S	
Diadocidia ferruginosa	Diadocidiidae	Slovakia	SJ1	KC435634	KC435562	KC435598	Ševčík *et al*. (2013)
Diadocidia spinosula	Diadocidiidae	Slovakia	JSSJ7	KJ136800	KJ136737	KJ136773	Ševčík *et al*. (2014)
Coboldia sp.	Scatopsidae	China	905	JQ613854	JQ613854	JQ613758	Shin *et al*. (2013)
Corynoptera sp. bs9	Sciaridae	New Zealand	SDEI-Dipt-0000853	MK906346	MK906438	MK906528	
Ctenosciara etorutao	Sciaridae	New Zealand	SDEI-Dipt-0001305	MK906386	MK906481	MK906571	
Pseudolycoriella aotearoa	Sciaridae	New Zealand	SDEI-Dipt-0000997	MK906359	MK906451	MK906541	
Psl. bispina	Sciaridae	New Zealand	SDEI-Dipt-0000946	MK906352	MK906444	MK906534	
Psl. bispina	Sciaridae	New Zealand	SDEI-Dipt-0000974	MK906355	MK906447	MK906537	
Psl. bispina	Sciaridae	New Zealand	SDEI-Dipt-0001251	MK906384	MK906479	MK906569	
Psl. bispina	Sciaridae	New Zealand	SDEI-Dipt-0001518	MK906399	MK906497	MK906587	
Psl. bispina	Sciaridae	New Zealand	SDEI-Dipt-0001522	MK906401	MK906499	MK906589	
Psl. cavatica	Sciaridae	New Zealand	SDEI-Dipt-0001085	MK906405	MK906455	MK906545	
Psl. cavatica	Sciaridae	New Zealand	SDEI-Dipt-0001411	MK906395	MK906490	MK906580	
Psl. dagae	Sciaridae	New Zealand	SDEI-Dipt-0000628	MK906330	MK906421	MK906511	
Psl. dagae	Sciaridae	New Zealand	SDEI-Dipt-0000655	MK906331	MK906422	MK906512	
Psl. frederickedwardsi	Sciaridae	New Zealand	SDEI-Dipt-0000756	MK906339	MK906431	MK906521	
Psl. frederickedwardsi	Sciaridae	New Zealand	SDEI-Dipt-0000772	MK906341	MK906433	MK906523	
Psl. frederickedwardsi	Sciaridae	New Zealand	SDEI-Dipt-0001224	MK906374	MK906468	MK906558	
Psl. frederickedwardsi	Sciaridae	New Zealand	SDEI-Dipt-0001237	MK906379	MK906474	MK906564	
Psl. frederickedwardsi	Sciaridae	New Zealand	SDEI-Dipt-0001247	MK906382	MK906477	MK906567	
Psl. gonotegmenta	Sciaridae	New Zealand	SDEI-Dipt-0000977	MK906356	MK906448	MK906538	
Psl. hauta	Sciaridae	New Zealand	SDEI-Dipt-0000506	MK906322	MK906412	MK906502	
Psl. horribilis	Sciaridae	Korea	074	JQ613788	JQ613887	JQ613691	Shin *et al*. (2013)
Psl. huttoni	Sciaridae	New Zealand	SDEI-Dipt-0000621	MK906327	MK906418	MK906508	
Psl. jaschhofi	Sciaridae	New Zealand	SDEI-Dipt-0001511	MK906409	MK906494	MK906584	
Psl. jaschhofi	Sciaridae	New Zealand	SDEI-Dipt-0001513	MK906410	MK906495	MK906585	
Psl. jaschhofi	Sciaridae	New Zealand	SDEI-Dipt-0001514	MK906398	MK906496	MK906586	

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TABLE 2. (Continued)

Species	Family	Country	Sample number	GenBank Accession Number			Reference
				COI	16S	28S	
Psl. jejuna	Sciaridae	New Zealand	SDEI-Dipt-0000603	MK906326	MK906416	MK906506	
Psl. jejuna	Sciaridae	New Zealand	SDEI-Dipt-0000617	MK906403	MK906417	MK906507	
Psl. jejuna	Sciaridae	New Zealand	SDEI-Dipt-0000744	MK906404	MK906428	MK906518	
Psl. jejuna	Sciaridae	New Zealand	SDEI-Dipt-0000773	MK906342	MK906434	MK906524	
Psl. jejuna	Sciaridae	New Zealand	SDEI-Dipt-0000829	MK906344	MK906436	MK906526	
Psl. jejuna	Sciaridae	New Zealand	SDEI-Dipt-0001193	MK906371	MK906464	MK906554	
Psl. jejuna	Sciaridae	New Zealand	SDEI-Dipt-0001195	MK906406	MK906466	MK906556	
Psl. jejuna	Sciaridae	New Zealand	SDEI-Dipt-0001339	MK906390	MK906485	MK906575	
Psl. jejuna	Sciaridae	New Zealand	SDEI-Dipt-0001347	MK906391	MK906486	MK906576	
Psl. jejunella	Sciaridae	New Zealand	SDEI-Dipt-0000935	MK906351	MK906443	MK906533	
Psl. kaikoura	Sciaridae	New Zealand	SDEI-Dipt-0000500	MK906321	MK906411	MK906501	
Psl. macrotegmenta	Sciaridae	New Zealand	SDEI-Dipt-0000757	MK906340	MK906432	MK906522	
Psl. maddisoni	Sciaridae	New Zealand	SDEI-Dipt-0000627	MK906329	MK906420	MK906510	
Psl. maddisoni	Sciaridae	New Zealand	SDEI-Dipt-0000664	MK906332	MK906423	MK906513	
Psl. mahanga	Sciaridae	New Zealand	SDEI-Dipt-0000595	MK906324	MK906414	MK906504	
Psl. mahanga	Sciaridae	New Zealand	SDEI-Dipt-0001008	MK906362	MK906454	MK906544	
Psl. orite	Sciaridae	New Zealand	SDEI-Dipt-0000863	MK906347	MK906439	MK906529	
Psl. plicitegmenta	Sciaridae	New Zealand	SDEI-Dipt-0001153	MK906366	MK906459	MK906549	
Psl. plicitegmenta	Sciaridae	New Zealand	SDEI-Dipt-0001158	MK906367	MK906460	MK906550	
Psl. porotaka	Sciaridae	New Zealand	SDEI-Dipt-0001225	MK906375	MK906469	MK906559	
Psl. porotaka	Sciaridae	New Zealand	SDEI-Dipt-0001250	MK906383	MK906478	MK906568	
Psl. puhihi	Sciaridae	New Zealand	SDEI-Dipt-0001005	MK906361	MK906453	MK906543	
Psl. puhihi	Sciaridae	New Zealand	SDEI-Dipt-0001422	MK906396	MK906491	MK906581	
Psl. raki	Sciaridae	New Zealand	SDEI-Dipt-0000834	MK906345	MK906437	MK906527	
Psl. robustotegmenta	Sciaridae	New Zealand	SDEI-Dipt-0001358	MK906392	MK906487	MK906577	
Psl. robustotegmenta	Sciaridae	New Zealand	SDEI-Dipt-0001371	MK906393	MK906488	MK906578	

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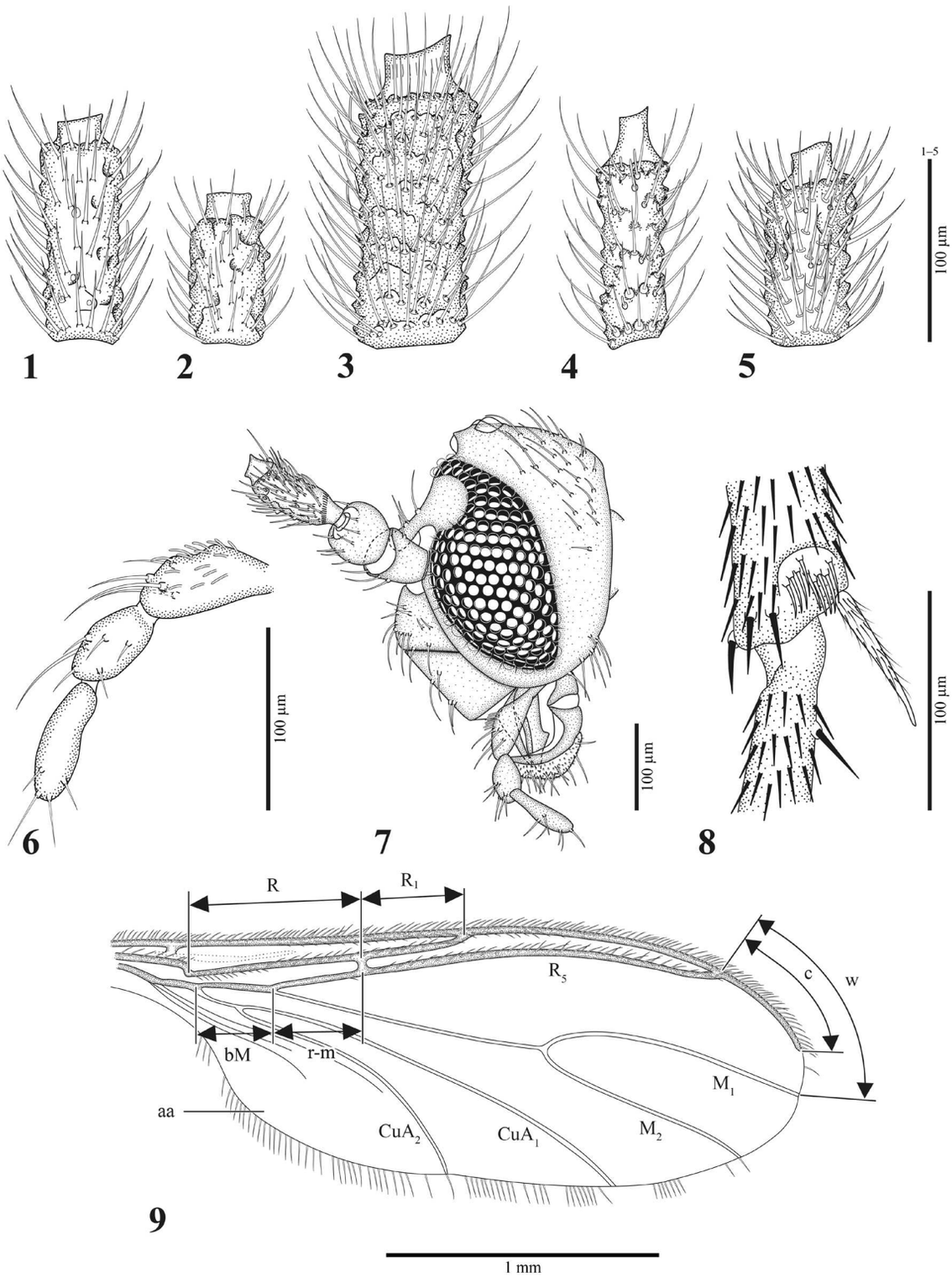
TABLE 2. (Continued)

Species	Family	Country	Sample number	GenBank Accession Number			Reference
				COI	16S	28S	
Psl. sp. 1 SS-2012	Sciaridae	Korea	586	JQ613816	JQ613916	JQ613720	Shin *et al*. (2013)
Psl. sp. 2 SS-2012	Sciaridae	Korea	640	JQ613823	JQ613923	JQ613727	Shin *et al*. (2013)
Psl. sp. I	Sciaridae	New Zealand	BIOUG14863-H041	see BOLD (2019b)	n/a	n/a	BOLD (2019b)
Psl. sp. I	Sciaridae	New Zealand	BIOUG15289-H10	see BOLD (2019b)	n/a	n/a	BOLD (2019b)
Psl. sp. I	Sciaridae	New Zealand	BIOUG15552-D06	see BOLD (2019b)	n/a	n/a	BOLD (2019b)
Psl. sp. I	Sciaridae	New Zealand	BIOUG15560-H06	see BOLD (2019b)	n/a	n/a	BOLD (2019b)
Psl. sp. II	Sciaridae	New Zealand	SDEI-Dipt-0000745	MK906337	MK906429	MK906519	
Psl. sp. SS-2012	Sciaridae	China	084	JQ613789	JQ613888	JQ613692	Shin *et al*. (2013)
Psl. subtilitegmenta	Sciaridae	New Zealand	SDEI-Dipt-0001151	MK906364	MK906457	MK906547	
Psl. sudhausi	Sciaridae	New Zealand	SDEI-Dipt-0000885	MK906348	MK906440	MK906530	
Psl. sudhausi	Sciaridae	New Zealand	SDEI-Dipt-0001167	MK906368	MK906461	MK906551	
Psl. sudhausi	Sciaridae	New Zealand	SDEI-Dipt-0001170	MK906369	MK906462	MK906552	
Psl. sudhausi	Sciaridae	New Zealand	SDEI-Dipt-0001175	MK906370	MK906463	MK906553	
Psl. sudhausi	Sciaridae	New Zealand	SDEI-Dipt-0001459	MK906397	MK906493	MK906583	
Psl. teo	Sciaridae	New Zealand	SDEI-Dipt-0001528	MK906402	MK906500	MK906590	
Psl. tewaipounamu	Sciaridae	New Zealand	SDEI-Dipt-0000513	MK906323	MK906413	MK906503	
Psl. tewaipounamu	Sciaridae	New Zealand	SDEI-Dipt-0000752	MK906338	MK906430	MK906520	
Psl. tewaipounamu	Sciaridae	New Zealand	SDEI-Dipt-0000907	MK906350	MK906442	MK906532	
Psl. tewaipounamu	Sciaridae	New Zealand	SDEI-Dipt-0000956	MK906353	MK906445	MK906535	
Psl. tewaipounamu	Sciaridae	New Zealand	SDEI-Dipt-0000960	MK906354	MK906446	MK906536	
Psl. tewaipounamu	Sciaridae	New Zealand	SDEI-Dipt-0000994	MK906358	MK906450	MK906540	
Psl. tonnoiri	Sciaridae	New Zealand	SDEI-Dipt-0000597	MK906325	MK906415	MK906505	
Psl. tonnoiri	Sciaridae	New Zealand	SDEI-Dipt-0000980	MK906357	MK906449	MK906539	
Psl. tonnoiri	Sciaridae	New Zealand	SDEI-Dipt-0001140	MK906363	MK906456	MK906546	
Psl. tonnoiri	Sciaridae	New Zealand	SDEI-Dipt-0001152	MK906365	MK906458	MK906548	
Psl. tuakana	Sciaridae	New Zealand	SDEI-Dipt-0001194	MK906372	MK906465	MK906555	

.....continued on the next page

TABLE 2. (Continued)

Species	Family	Country	Sample number	GenBank Accession Number			Reference
				COI	16S	28S	
Psl. tuakana	Sciaridae	New Zealand	SDEI-Dipt-0001337	MK906389	MK906484	MK906574	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0000665	MK906333	MK906424	MK906514	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0000670	MK906334	MK906425	MK906515	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0000674	MK906335	MK906426	MK906516	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0001223	MK906373	MK906467	MK906557	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0001227	MK906376	MK906470	MK906560	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0001234	MK906378	MK906472	MK906562	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0001235	MK906407	MK906473	MK906563	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0001238	MK906380	MK906475	MK906565	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0001245	MK906381	MK906476	MK906566	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0001270	MK906385	MK906480	MK906570	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0001334	MK906387	MK906482	MK906572	
Psl. wernermohrigi	Sciaridae	New Zealand	SDEI-Dipt-0001373	MK906394	MK906489	MK906579	
Psl. cf. *wernermohrigi*	Sciaridae	New Zealand	SDEI-Dipt-0000681	MK906336	MK906427	MK906517	
Psl. cf. *wernermohrigi*	Sciaridae	New Zealand	SDEI-Dipt-0001232	MK906377	MK906471	MK906561	
Psl. whakahara	Sciaridae	New Zealand	SDEI-Dipt-0001439	MK906408	MK906492	MK906582	
Psl. whena	Sciaridae	New Zealand	SDEI-Dipt-0001336	MK906388	MK906483	MK906573	
Psl. zealandica	Sciaridae	New Zealand	SDEI-Dipt-0000623	MK906328	MK906419	MK906509	
Psl. zealandica	Sciaridae	New Zealand	SDEI-Dipt-0000886	MK906349	MK906441	MK906531	
Psl. zealandica	Sciaridae	New Zealand	SDEI-Dipt-0000998	MK906360	MK906452	MK906542	
Zygoneura contractans	Sciaridae	New Zealand	SDEI-Dipt-0000826	MK906343	MK906435	MK906525	



FIGURES 1–9. Various body parts of *Pseudolycoriella* spp., in lateral view. **1.** *Pseudolycoriella dagae* **sp. n.**, fourth flagellomere. **2.** *Pseudolycoriella jejunella* **sp. n.**, fourth flagellomere. **3.** *Pseudolycoriella aotearoa* **sp. n.**, fourth flagellomere. **4.** *Pseudolycoriella bispina* Mohrig, fourth flagellomere. **5.** *Pseudolycoriella puhihi* **sp. n.**, fourth flagellomere. **6.** *Pseudolycoriella jejunella* **sp. n.**, palp. **7.** *Pseudolycoriella robustotegmenta* **sp. n.**, head. **8.** *Pseudolycoriella jejunella* **sp. n.**, tibial organ. **9.** *Pseudolycoriella hauta* **sp. n.**, wing. Abbreviations: aa = anal area; bM = base of the medial vein; c = distance between intersection of vein R_5 and radial vein and the end of costal vein; CuA_1/CuA_2 = first and second branch of the anterior branch of the cubital vein; M_1/M_2 = first and second branch of the medial vein ("M-fork"); R = radial vein; R_1/R_5 = first and fifth branch of the radial vein; r-m = crossvein between radial and median veins; w = distance between intersection of vein R_5 and radial vein and intersection of vein M_1 and wing margin.

Species account

Pseudolycoriella cavatica (Skuse, 1888)

(Fig. 10)

Synonyms.
Sciara familiaris Skuse, 1888
Sciara festiva Skuse, 1888
Spathobdella setigera Hardy, 1960 **syn. n.**

Literature. *Sciara cavatica* Skuse, 1888; *S. familiaris* Skuse, 1888 & *S. festiva* Skuse, 1888: Skuse (1888): 687–690.—*Pseudolycoriella cavatica* (Skuse, 1888): Broadley *et al*. (2016): 437, 439–441, Fig. 23 A–D & Fig. 24 A–B.—*Spathobdella setigera* Hardy, 1960: Hardy (1960): 234, Fig. 80 a–c.—*Bradysia setigera* (Hardy, 1960): Steffan (1973): 356.—Leblanc *et al*. (2009): 1455.—*Pseudolycoriella setigera* (Hardy, 1960): Menzel & Heller (2007): 223.—Menzel & Smith (2009): 41–43, Figs 1.45–47.—Köhler & Menzel (2013): 69.—Menzel *et al*. (2013): 292–293, Figs 22–23.—Menzel & Smith (2017): 21, Fig. 82.—Mohrig *et al*. (2019): 426–427, Fig. 17 A–E.—Sciaridae indet.: BOLD (2019a).

Material studied. 1♂ New Zealand: North Island, Auckland, Manurewa, Mill Road, pitfall trap, 03–13.02.2015, leg. P.A. Maddison (SDEI, SDEI-Dipt-0001281). 2♂♂ same locality as previous, 14–27.02.2015 (NZAC, SDEI-Dipt-0001283; SDEI, SDEI-Dipt-0001255). 9♂♂ North Island, Western Bay of Plenty, Katikati, 140 Wharawhara Road, bush area, pitfall trap, 14.02–05.03.2015, leg. P.A. Maddison (4x NZAC; 5x SDEI, SDEI-Dipt-0001411). 1♂ same locality as previous, 14.02–05.03.2015, Malaise trap, leg. P.A. Maddison (NZAC, SDEI-Dipt-0001085). 2♀♀ North Island, Western Bay of Plenty, Katikati, 140 Wharawhara Road, kiwifruit block, Malaise trap, 14.02–05.03.2015, leg. P.A. Maddison (all SDEI, SDEI-Dipt-0001443 & SDEI-Dipt-0001458). 3♂♂ North Island, Western Bay of Plenty, Katikati, Te Mania catchment, Malaise trap, 19.09–27.10.2016, leg. P.A. Maddison (1x NZAC, SDEI-Dipt-0001231; 2x SDEI, SDEI-Dipt-0001229 & SDEI-Dipt-0001368). 1♂ North Island, Western Bay of Plenty, Katikati, Uretara, mangrove area, Malaise trap, 04.09–22.10.2016, leg. P.A. Maddison (SDEI, SDEI-Dipt-0001377). 2♀♀ North Island, Western Bay of Plenty, Katikati, 17 Francis Drive, Malaise trap, 14.02–05.03.2015, leg. P.A. Maddison (NZAC, SDEI-Dipt-0001298; SDEI, SDEI-Dipt-0001297). 2♂♂ South Island, Buller, Ahaura, Granville State Forest, altitude 170–250 m, *Nothofagus truncata* forest, Malaise trap, 01.12.1994, leg. J. Hutcheson (all SDEI). 1♂ South Island, Christchurch, Halswell quarry, light trap and pan trap, 26.02.2004, leg. R.P. Macfarlane (UZMH).

Description. See Menzel & Smith (2009) and Broadley *et al*. (2016).

Genetic distances. All 16 investigated COI sequences are identical and do not show any pairwise distance. Among the New Zealand species, the nearest neighbour is *Pseudolycoriella teo*, diverging by a minimum of 8.85%. No differences between two conspecific 28S sequences were found. The nearest neighbours are *Psl. horribilis* and an undescribed species from Korea (*Psl.* sp. 1 SS-2012). Both p-distances are 0.75%.

Distribution. Australia (New South Wales and Western Australia [BOLD 2019a]); Hawaii, New Caledonia, Seychelles, Tristan da Cunha, and South Africa (BOLD 2019a). New to New Zealand.

Remarks. The COI-barcode of *Psl. cavatica* is also recorded on the Barcode of Life Data System (BOLD 2019a). There it is listed under the BIN BOLD:ABW3602. All these new records fit well into the already known distribution pattern of this species, which comprises Australia and islands south of the Tropic of Cancer. The frequent occurrence of *Psl. cavatica* in pitfall traps suggests an epigean ecology as already noted by Menzel & Smith (2009).

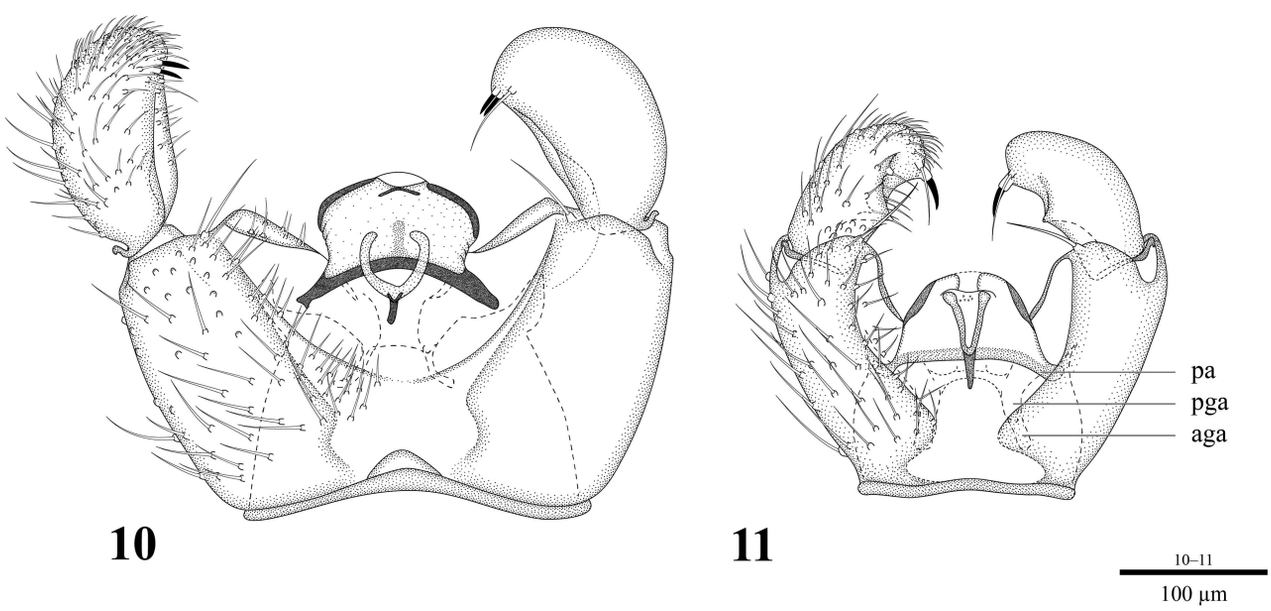
Pseudolycoriella kaikoura sp. n.

(Fig. 11)
urn:lsid:zoobank.org:act:F587D109-BD83-490F-921F-E515D4356B80

Material studied. *Holotype male.* New Zealand, South Island, Kaikoura, Waiau, Pillona, altitude 400 m, *Kunzea ericoides* over water supply seepage, Malaise trap, 26.12.2000–12.01.2001, leg. P.M. Johns (NZAC, SDEI-Dipt-0000500). *Paratype*. 1♂ same locality and same date as holotype (SDEI, SDEI-Dipt-0000501).

Description. *Male*. **Head.** Head capsule brown. Eye bridge two to three facets wide. Antennae light brown,

without any contrast between scape, pedicel and flagellum; fourth flagellomere 1.8–1.9 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough with deep pits, sensilla of two different lengths; setae on the flagellomere as long as flagellomere width. Maxillary palp pale with three palpomeres, first one longest, second and third short and of same length, first palpomere with two to four bristles; patch of sensilla on first palpomere not conspicuous. Prefrons and clypeus bulging. **Thorax** pale brown. Posterior pronotum bare. Anterior pronotum with three to five setae. Episternum 1 with four to seven setae. Mesonotum with three long lateral bristles and several small ones. Scutellum with four robust bristles and several smaller setae. Katepisternum as long as high, distal part slightly darker than proximal part. **Wing.** Length 2.0 mm; width/length ratio 0.35. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct; r-m and bM without macrotrichia; R_5 with macrotrichia on dorsal side only (the paratype bears two additional macrotrichia at ventral side of R_5 apex); R_1 approximately 0.7–0.8 times as long as R; c/w ratio 0.7; r-m as long as bM. Haltere brownish; with a short shaft; head of haltere longer than shaft. **Legs** yellowish brown. Tibial organ surrounded by a circular border and as wide as half width of tibial apex; bristles of tibial organ arranged in an irregular row. Front tibia with one robust bristle among vestiture. Mid tibia with one slightly robust bristle. Hind tibia with a posteriodorsal row of eight robust bristles, comprising apical two-thirds of tibia, additional robust bristles on the ventral and posterior sides. All tibial spurs equal in length. Claws with teeth. **Abdomen** pale brown, slightly paler than thorax. **Hypopygium** (Fig. 11)**.** Gonocoxites wider than long, inner side of gonocoxites with short setae, outer side with long hairs; ventral, inner side of gonocoxites v-shaped and basally widely separated; apicolaterally strongly incised. Gonostylus two times longer than wide; with a prominent edge in the middle of the inner side, one spine and one long whip-lash hair subapically, apex with a dense vestiture of robust setae. Tegmen apical roundish, lateral parts sclerotized; parameral apodeme very robust. Area of teeth with approximately ten tiny teeth. Ejaculatory apodeme short and dark; base distinct, v-shaped. Posterior portion of gonocoxal apodeme long, brown, widely separated, and medially connected. Anterior portion of gonocoxal apodeme long and dark brown.



FIGURES 10–11. *Pseudolycoriella bruckii* group, hypopygia. **10.** *Pseudolycoriella cavatica* (Skuse). **11.** *Pseudolycoriella kaikoura* **sp. n.** Abbreviations: aga = anterior portion of gonocoxal apodeme; pa = parameral apodeme; pga = posterior portion of gonocoxal apodeme.

Body size: 2.0 mm.

Female. Unknown.

Genetic distances. Only one specimen was successfully sequenced. The nearest neighbour is *Psl*. sp. I, diverging by a minimum of 4.86%. For the 28S sequence the nearest neighbour is *Psl*. *horribilis*, diverging by a minimum of 0.25%.

Etymology. The newly described species is named after the Kaikoura peninsula, where both specimens were caught.

Distribution. New Zealand.

Discussion. The reduction to one gonostylar spine—as in this new species—is an infrequent character state among the species of *Pseudolycoriella*. Outside of New Zealand only a few species are known to have such a reduction: *Pseudolycoriella curviseta* Mohrig, *Psl. defluviata* Rudzinski, *Psl. japonensis* (Mohrig & Menzel), *Psl. patronata* Rudzinski, *Psl. pollicis* (Pettey) [for this species Mohrig *et al*. (2013) stated two narrow subequal spines, while Mohrig & Kauschke (2019) only gave one spine], *Psl. pugionata* Rudzinski, *Psl. microcteniuni* (Yang & Zhang), *Psl. morenae* (Strobl), *Psl. pendleburyi* (Edwards), *Psl. semialata* (Edwards), and *Psl. subbruckii* (Mohrig & Hövemeyer). None of these species has a prominent edge in the middle of the inner side of the gonostylus. Therefore, confusion with *Psl. kaikoura* can be excluded. Among the New Zealand representatives of the genus the species of the *Psl. jejuna* complex also bear only one spine on the gonostylus. Nevertheless, *Psl. kaikoura* can easily be distinguished from them by its uniquely shaped gonostylus and its different tegmen structure. *Pseudolycoriella kaikoura* can be assigned to the *Psl. bruckii* group.

Pseudolycoriella sp. I

Literature. *Pseudolycoriella* indet.: BOLD (2019b).

Barcoded material. 1♀ New Zealand: North Island, Waikato, Hamilton, altitude 39 m, Malaise trap, 05.06.2012, leg. I. Hogg (CBG, BIOUG14863-H041). 1♀ same locality as previous, Malaise trap, 19.11.2012, leg. I. Hogg (CBG, BIOUG15289-H10). 1♀ same locality as previous, Malaise trap, 11.03.2013, leg. I. Hogg (CBG, BIOUG15552-D06). 1♀ same locality as previous, Malaise trap, 08.04.2013, leg. I. Hogg (CBG, BIOUG15560-H06).

Genetic distances. The maximum p-distance between all four available COI sequences is 0.17%. The nearest neighbour is *Psl. kaikoura*, diverging by a minimum of 4.86%. No 28S sequence data are available.

Discussion. The COI barcodes of *Psl.* sp. I are registered on the Barcode of Life Data System under the BIN: BOLD:ACP1302 (BOLD 2019b). The p-distance of 4.86% towards the nearest neighbour suggests the existence of a further unknown species. Nevertheless, it was judged premature to prepare a formal description because no males are available and the lack of knowledge about the taxonomy of the females of *Pseudolycoriella* does not allow solid conclusions to be made on species delimitation.

Pseudolycoriella zealandica complex

The *Pseudolycoriella zealandica* complex consists of probably three species—*Pseudolycoriella zealandica*, *Psl. aotearoa*, and the undescribed *Psl.* sp. II. Individuals have a relatively large body, and thus the largest New Zealand *Pseudolycoriella* specimens can be found in this complex. The males of the described species are characterized by two gonostylar spines, and the trapezoid tegmen with a broad hood-like structure (*hs* in Fig. 12). Their phylogenetic relationship is shown in Figure 61.

Discussion. The *Psl. zealandica* complex can be assigned to the *Psl. bruckii* group without any contradictions. It is not possible to state which morphological characters might be regarded as autapomorphies of this complex, because the undescribed species is located basally in the clade of the *Psl. zealandica* complex. Therefore, conclusions about the ground plan of the *Psl. zealandica* complex are not possible. It can only be stated that this complex comprises the largest species of *Pseudolycoriella* in New Zealand. Nevertheless, the monophyly is clearly indicated by genetic data.

Pseudolycoriella zealandica (Edwards, 1927)
(Fig. 12)

Literature. *Sciara zealandica* Edwards, 1927: Tonnoir & Edwards (1927): 796, Fig. 180.—Miller (1950): 57.—Davies (1988): 13.—Steffan (1989): 151.—*Pseudolycoriella zealandica* (Edwards, 1927): Mohrig & Jaschhof (1999): 37, Fig. 18 a–g.—Menzel & Mohrig (2000): 715–716.—Rudzinski (2000): 183.—Macfarlane *et al*. (2010): 441

Material studied. *Holotype male*. New Zealand: North Island, Waikato, Okauia, Matamata, 18.11.1922, leg. A.E.

Brookes (BMNH, BMNH(E)250341). *Previously published material*: 7♂♂ North Island, Taupo, Hauhungaroa Range, 5 km southwest of Tihoi, *Podocarpus* wood with ground ferns, sweep net, 21.12.1992, leg. M. Jaschhof (6x PWMP; 1x SDEI). *New records*: 22♂♂ North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, 690 m, mixed podocarp/broadleaf forest, Malaise trap, 26.11–28.12.2002, leg. M. & C. Jaschhof & U. Kallweit (7x NZAC, SDEI-Dipt-0000622, SDEI-Dipt-0000624, SDEI-Dipt-0000998, SDEI-Dipt-0001002, SDEI-Dipt-0001243 & SDEI-Dipt-0001246; 15x SDEI, SDEI-Dipt-0000623, SDEI-Dipt-0001001, SDEI-Dipt-0001239, SDEI-Dipt-0001242, SDEI-Dipt-0001244, SDEI-Dipt-0001248, SDEI-Dipt-0001254, SDEI-Dipt-0001538, SDEI-Dipt-0001539, SDEI-Dipt-0001540, SDEI-Dipt-0001541 & SDEI-Dipt-0001542). 1♀ same locality as prevoius, sweep net, 03–04.02.2002, leg. M. Jaschhof (SDEI, SDEI-Dipt-0000783). 9♂♂, 2♀♀ South Island, Selwyn, Cass, Middle Bush, *Nothofagus solandri* forest, stream site, Malaise trap, 09.04.1998, leg. P.M. Johns (4x NZAC, SDEI-Dipt-0001166, SDEI-Dipt-0001176, SDEI-Dipt-0001186 & SDEI-Dipt-0001189; 7x SDEI, SDEI-Dipt-0001168, SDEI-Dipt-0001183 [♀], SDEI-Dipt-0001185, SDEI-Dipt-0001187, SDEI-Dipt-0001188, SDEI-Dipt-0001190 & SDEI-Dipt-0001191 [♀]). 1♂, 1♀ same locality as previous, 11.04.1998, leg. P.M. Johns (all SDEI, SDEI-Dipt-0001163 [♂] & SDEI-Dipt-0001162 [♀]). 21♂♂ South Island, Southland, Fiordland, Fiordland NP, Hollyford River Valley, Moraine Creek Track, mixed podocarp/*Nothofagus* forest, Malaise trap, 05–24.01.2002, leg M. & C. Jaschhof (8x NZAC, SDEI-Dipt-0000883, SDEI-Dipt-0001544, SDEI-Dipt-0001546, SDEI-Dipt-0001548, SDEI-Dipt-0001551, SDEI-Dipt-0001554, SDEI-Dipt-0001557 & SDEI-Dipt-0001559; 13x SDEI, SDEI-Dipt-0000882, SDEI-Dipt-0000884, SDEI-Dipt-0000886, SDEI-Dipt-0001543, SDEI-Dipt-0001545, SDEI-Dipt-0001547, SDEI-Dipt-0001549, SDEI-Dipt-0001550, SDEI-Dipt-0001552, SDEI-Dipt-0001553, SDEI-Dipt-0001555, SDEI-Dipt-0001556 & SDEI-Dipt-0001558). 1♂ South Island, Southland, Otago Lakes, Fiordland NP, Hollyford River Valley S Divide Creek, mixed *Nothofagus*/broadleaf forest, Malaise trap, 06–24.01.2002, leg. M. & C. Jaschhof (SDEI).

Redescription. *Male*. **Head.** Head capsule brown. Eye bridge four facets wide, two to three facets at margin. Scape and pedicel slightly paler than the flagellomeres; fourth flagellomere 2.3–3.2 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough, sensillae of two different lengths, small ones and longer, curved sensilla; setae on the flagellomere dense and as long as flagellomere width, slightly curved. Maxillary palp long and three-segmented, first palpomere longest, second one shortest; first palpomere with an inconspicuous patch of sensilla and five to eight long bristles, one of these bristles longer and more robust, located on the outer side of the first palpomere. Prefrons and clypeus bulging. **Thorax** brown, paler than head; some specimens with small brightened parts anteriorly and posteriorly. Posterior pronotum bare. Anterior pronotum with four to eight setae. Episternum 1 with five to 14 setae. Mesonotum with five to nine robust lateral bristles; row of dorsocentral bristles well developed. Scutellum with five to eight robust bristles and several minor setae. Katepisternum slightly longer than high. **Wing.** Length 2.4–2.9 mm; width/length ratio 0.35–0.39. Membrane smoky and without macrotrichia, anal area present; all posterior veins distinct, stem of M weakest, apical half of R_5 with macrotrichia on ventral and dorsal side; r-m and bM bare, exceptionally r-m with one seta; R_1 0.7–0.9 times as long as R; c/w ratio 0.73–0.82; r-m 0.6–1.0 as long as bM. Haltere short and sooty brown; knob as long as shaft. **Legs** pale, yellowish brown. Tibial organ surrounded by a circular border and wider than half width of tibial apex; tibial organ consists of a transverse row of bristles. Fore and mid tibia without robust bristles among vestiture. Hind tibia with two to seven robust bristles arranged in a longitudinal, posteriodorsal row. All tibial spurs equal in length. Claws with robust teeth, arranged in decreasing size. **Abdomen** brown, slightly paler than thorax, with dark setae. **Hypopygium** (Fig. 12)**.** Gonocoxite wider than long, inner side of gonocoxites with a membranous area scattered with short pale setae, outer side with long setae; ventral, inner side of gonocoxites basally not fused. Gonostylus bean shaped, 2.1–2.8 times longer than wide, apically with a large inner cavity without any microtrichia, two robust spines and one long whip-lash hair present. Tegmen trapezoid with a strongly sclerotized base, parameral apodeme short and robust; medially with a broad hood-like structure (*hs* in Fig. 12) laterally flanked by a group of small teeth (not expressed in all specimens, 19 of 30 specimens from the North island and six of 33 from the South Island are without this character). Area of teeth consists of many small teeth. Ejaculatory apodeme dark, short and broad; base of ejaculatory apodeme long, basally widely fused, horseshoe-shaped. Posterior portion of gonocoxal apodeme medium sized and brown. Anterior portion of gonocoxal apodeme long and dark brown.

Body size: 2.1–3.8 mm.

Female. Tonnoir & Edwards (1927) designated two female paratypes of *Psl. zealandica*. The metadata of one of those (BMNH(E)250343) are available online from the Natural History Museum (2014). However, those types are not included in the present study. Some descriptive information is given by Tonnoir & Edwards (1927) and by Menzel & Mohrig (2000).

Genetic distances. The maximum p-distance between all 17 available COI sequences is 2.43%. The nearest neighbour is *Psl. teo*, diverging by a minimum of 10.63%. All three available conspecific 28S sequences are identical and show no differences to the sequences of *Psl. zealandica* and *Psl.* sp. II.

Remarks. All previous studies containing descriptions of the morphology of *Psl. zealandica* (Tonnoir & Edwards 1927; Mohrig & Jaschhof 1999; Menzel & Mohrig 2000) did not mention the groups of additional lateral teeth on both sides of the median structure on the tegmen (Fig. 12). In fact, the holotype does not have this unique feature, and even among the material available to Mohrig & Jaschhof (1999), this feature is rarely present. The quality of the preparation also influences whether the teeth are easy to observe or not. Removal of tergite IX increases the possibility of observing teeth. In addition, specimens from New Zealand's South Island—examined in the present study for the first time—have a higher expression rate of this character and a larger number of teeth, when present. The presence of these lateral teeth is not homogenously distributed across both populations (chi-square test of homogeneity, $\chi^2 \approx 13.38$, $\alpha < 0.005$).

Pseudolycoriella aotearoa sp. n.

(Figs 3 & 13)
urn:lsid:zoobank.org:act:02F615B4-A7CB-4F4C-8736-1D568B686260

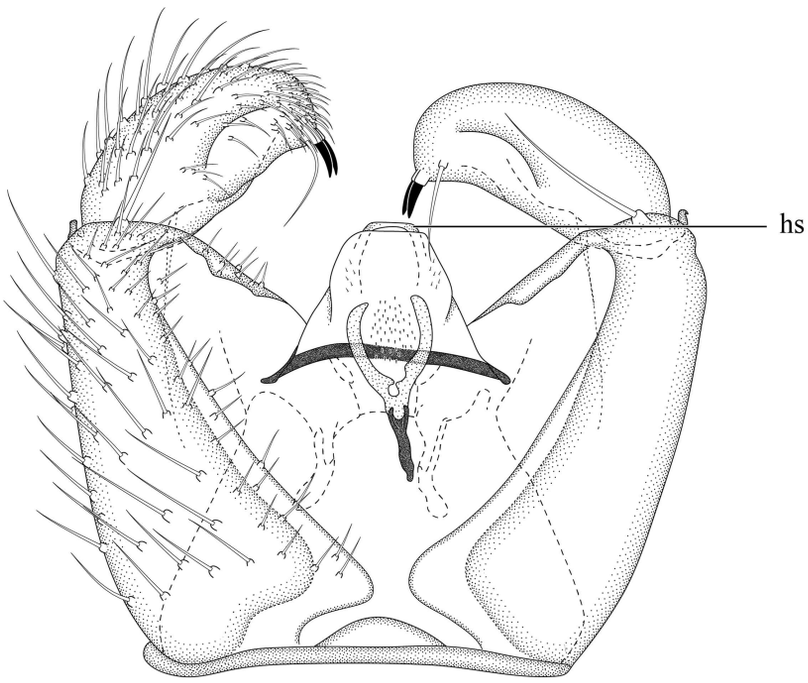
Literature. *Pseudolycoriella zealandica* (Edwards, 1927): Mohrig & Jaschhof (1999): 37 [misidentification].

Material studied. *Holotype male*. New Zealand: North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, mixed podocarp/broadleaf forest, Malaise trap, 26.11–28.12.2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC, SDEI-Dipt-0000997). *Paratypes*: 11♂♂ same date and same locality as holotype (4x NZAC, SDEI-Dipt-0001000; 7x SDEI, SDEI-Dipt-0000625, SDEI-Dipt-0000758, SDEI-Dipt-0000978 & SDEI-Dipt-0000999). 2♂♂ North Island, Taupo, Hauhungaroa Range, 5 km southwest of Tihoi, *Podocarpus* wood with ground ferns, sweep net, 21.12.1992, leg. M. Jaschhof (all PWMP [previously misidentified, published as *Psl. zealandica* in Mohrig & Jaschhof (1999)]).

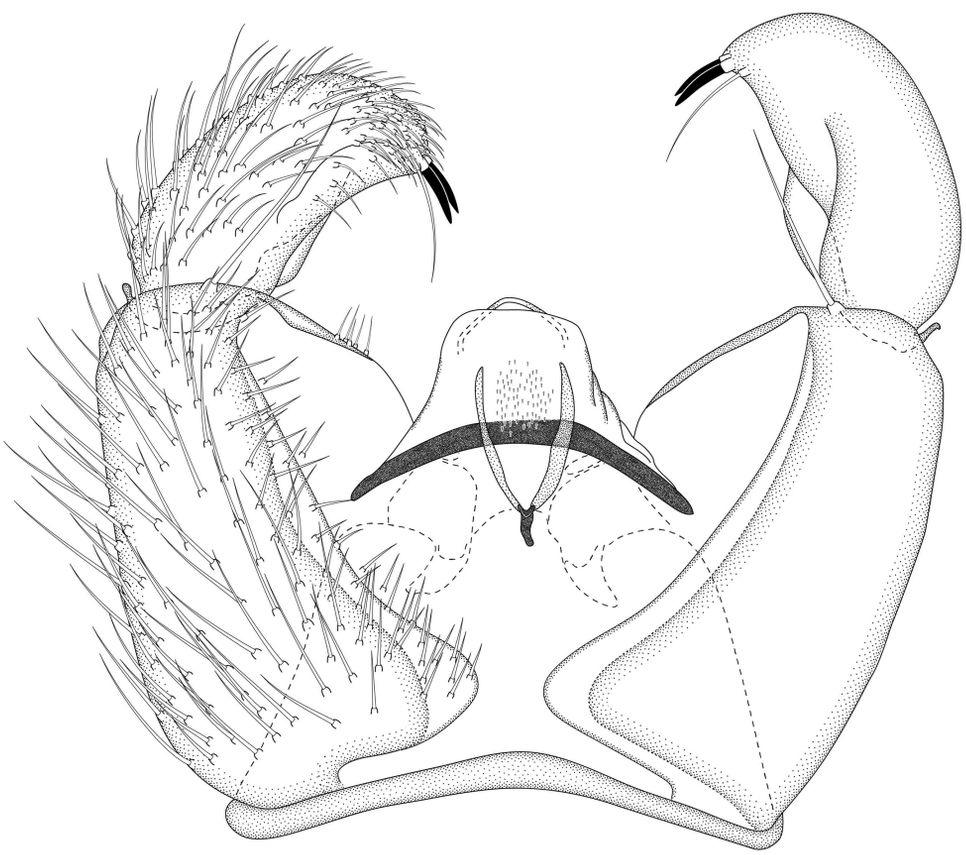
Description. *Male*. **Head.** Head capsule brown. Eye bridge four facets wide, two to three facets at margin. Scape and pedicel slightly paler than the flagellomeres; fourth flagellomere (Fig. 3) 2.3–2.6 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough, sensilla of two different lengths, small ones and longer, curved sensilla; setae on the flagellomere dense and as long as flagellomere width, slightly curved. Maxillary palp long and three-segmented, first palpomere longest, second one shortest; first palpomere with an inconspicuous patch of sensilla and four to eight long bristles, one of these bristles longer and more robust, located on the outer side. Prefrons and clypeus bulging. **Thorax** brown, paler than head; some specimens with small anterior and posterior brightened parts. Posterior pronotum bare. Anterior pronotum with seven to eleven setae. Episternum 1 with four to eleven setae. Mesonotum with six to eleven robust lateral bristles; row of dorsocentral bristles well developed. Scutellum with six to nine robust bristles and several minor setae. Katepisternum slightly longer than high. **Wing.** Length 2.6–3.3 mm; width/length ratio 0.34–0.38. Membrane smoky and without macrotrichia, anal area present; all posterior veins distinct, stem of M weakest, apical half of R_5 with macrotrichia on ventral and dorsal side; bM bare, r-m bare or with up to two setae; R_1 0.8–1.0 times as long as R; c/w ratio 0.70–0.81; r-m 0.7–0.8 as long as bM. Haltere short and sooty brown; knob as long as shaft, or slightly longer than shaft. **Legs** pale brown. Tibial organ surrounded by a circular border and wider than half width of tibial apex; tibial organ consists of a transverse row of bristles. Fore and mid tibia without robust bristles among vestiture. Hind tibia with two to seven robust bristles organised in a longitudinal, posteriodorsal row. All tibial spurs equal in length. Claws with robust teeth, arranged in decreasing size. **Abdomen** brown, slightly paler than thorax, with dark setae. **Hypopygium** (Fig. 13)**.** Gonocoxites wider than long, inner side of gonocoxites with a membranous area scattered with short pale setae, outer side with long setae; ventral, inner side of gonocoxites basally not fused. Gonostylus bean shaped, 2.1–2.4 times longer than wide, apically with a large inner cavity without any microtrichia, two robust spines and one long whip-lash hair present. Tegmen trapezoid with a strongly sclerotized base, parameral apodeme short and robust; medially with a broad hood-like structure. Area of teeth consists of many small teeth. Ejaculatory apodeme dark, short and narrow; base of ejaculatory apodeme long and narrow. Posterior portion of gonocoxal apodeme medium sized and brown. Anterior portion of gonocoxal apodeme short, comma-shaped, and dark brown.

Body size: 3.2–4.4 mm.

Female. Unknown.



12



13

12–13

100 µm

FIGURES 12–13. *Pseudolycoriella zealandica* complex, hypopygia. **12.** *Pseudolycoriella zealandica* (Edwards). **13.** *Pseudolycoriella aotearoa* **sp. n.** Abbreviation: hs = hood-like structure.

Genetic distances. The maximum p-distance between all six available COI sequences is 0.76%. The nearest neighbour is *Psl*. *zealandica*, diverging by a minimum of 12.21%. One successfully obtained 28S sequence is identical to those of *Psl*. *zealandica* and *Psl*. sp. II.

Etymology. *Aotearoa* is the Māori word for New Zealand and was chosen as an epithet for the newly described species to underline the close phylogenetic relationship to *Psl*. *zealandica*.

Distribution. New Zealand.

Discussion. *Pseudolycoriella aoteraoa* is the sister species of *Psl*. *zealandica*, and therefore morphologically very similar. However, in general *Psl*. *aoteraoa* has a larger a body size and a greater wing length. The discrimination of both species, relying on these characters only, is not sufficient, because both ranges show overlaps. The lengths of the gonostyli of both species do not show identical values, but are very close together (170–200 µm *vs*. 210–230 µm). A more reliable character is the structure of the base of the ejaculatory apodeme. *Pseudolycoriella aoteraoa* has a base consisting of two long and slender branches while *Psl*. *zealandica* has broader and widely connected branches. Further, the tegmen shows differences. The basal width of the tegmen is wider in *Psl*. *aoteraoa* and the middle hood-like structure is also broader. Lateral teeth on the tegmen as found in some specimens of *Psl*. *zealandica* are absent in *Psl*. *aotearoa*.

Due to its large body size *Psl*. *aotearoa* also resembles *Psl*. *skusei* Mohrig, Kauschke & Broadley and *Psl*. *tenebrioalata* Mohrig. Nevertheless, the structure of the hypopygia differs significantly. *Pseudolycoriella skusei* has an elongated gonostylus with a sharp apical bend and more spines and more whip-lash hairs than *Psl*. *aotearoa* (Mohrig *et al*. 2016). *Pseudolycoriella tenebrioalata* shows a similar gonostylar shape and a similar arrangement of spines. However, the tegmen structure and the ejaculatory apodeme differ fundamentally (Mohrig 2013). *Pseudolycoriella tenebrioalata* has a tegmen that is just slightly tapered towards the apex, and the ejaculatory apodeme is very short. Furthermore *Psl*. *tenebrioalata* does not have a border on its tibial organ, and its claws lack any teeth (Mohrig 2013).

Pseudolycoriella sp. II

Material studied. 1♀, New Zealand: South Island, Canterbury, Selwyn, Cass, Middle Bush, 17.11.1998, Malaise trap, leg. P.M. Johns (SDEI, SDEI-Dipt-0000745).

Genetic distances. The nearest neighbour of the COI-sequence of *Psl*. sp. II is *Psl*. *orite*, diverging by a minimum of 10.89%. The one successfully sequenced 28S sequence is identical to those of *Psl*. *zealandica* and *Psl*. *aotearoa*.

Discussion. The molecular analysis of the female specimen SDEI-Dipt-0000745 revealed an isolated cluster for all three genetic markers, and consequently a well separated cluster in the consensus tree shown in Figure 61. Therefore, the presence of a new and undescribed species is very likely, but without conspecific male specimens a reasonable description allowing meaningful comparisons with other *Pseudolycoriella* species is not possible.

Pseudolycoriella bispina complex

The following six species form the *Psl*. *bispina* complex. Common to them is a small body size, and presence of lateral lobes on the tegmen. The phylogeny of this complex is depicted in Figure 61.

Discussion. This complex can be assigned to the *Psl*. *bruckii* group. Nevertheless, due to its small body size and the two spines on the gonostylus the species of the *Psl*. *bispina* complex resemble the *Psl*. *longicostalis* group from Papua New Guinea (Mohrig 2013). Furthermore, some of those species share the very robust bristles arranged in a posteriodorsal row on the hind tibia. However, the two apicolateral lobes on the tegmen of *Psl*. *bispina* and the other species of this complex cannot be found in the *Psl*. *longicostalis* group. As an additional character Mohrig (2013) emphasised that these species have very robust bristles in the posteriodorsal row on the hind tibia, which could also be found in the *Psl*. *bispina* complex, except in *Psl*. *mahanga*. Nevertheless, all these species are not assigned to the *Psl*. *longicostalis* group. The key characteristics like the conspicuous row of robust bristles on the hind tibia surely result from convergent miniaturisations of two independent stem species with a typical *Psl*. *bruckii* group habitus.

Conspicuous apicolateral lobes can be found in other *Pseudolycoriella* species: for instance, *Psl*. *commoda*

Mohrig (*Pseudolycoriella triacanthula* group; Mohrig 2013), and *Psl*. *microphalli* Mohrig and *Psl*. *bitorquia* Mohrig (*Psl*. *quadrispinosa* group; Mohrig 2013). A confusion of those three species with *Psl*. *bispina* and its close relatives is not expected, because all of the Papua New Guinea species have three gonostylar spines and remarkable dorsal teeth on the claws. Among the New Zealand species, *Psl*. *cavatica*, *Psl*. *kaikoura*, and the species of the *Psl*. *jejuna* complex have similar lateral lobes on the tegmen, but these species differ either by the reduction of the number of gonostylar spines or the shape of the gonostylus together with stout flagellomeres. Although the monophyly of the *Psl*. *bispina* complex is highly supported by genetic data, no unequivocal apomorphic characters could be identified.

Pseudolycoriella bispina **Mohrig, 1999**

(Figs 4 & 14)

Literature. *Pseudolycoriella bispina* Mohrig, 1999: Mohrig & Jaschhof (1999): 40–41, Fig. 20 a–g.—Macfarlane *et al*. (2010): 441.

Material studied. *Holotype male*. New Zealand: North Island, Wairoa, Urewera National Park, Huiarau Range 30 km southeast of Murupara, altitude 600–1,000 m, *Podocarpus-Nothofagus* wood, sweep net, 23.12.1992, leg. M. Jaschhof (PWMP). *Paratype*. 1♂ same locality and same date as holotype (PWMP). *New records*: 1♂ North Island, Thames-Coromandel, Coromandel, Kirikiri Saddle, Kaitarakiri Track, secondary mixed podocarp/broadleaf forest, sweep net, 09.02.2002, leg. M. Jaschhof (SDEI). 1♂ North Island, Western Bay of Plenty, Katikati, 140 Wharawhara Road, bush area, pitfall trap, 14.02–05.03.2015, leg. P.A. Maddison (SDEI, SDEI-Dipt-0001418). 1♂ North Island, Western Bay of Plenty, Katikati, 449 Lund Road, Malaise trap, 25.07–08.08.2016, leg. P.A. Maddison (SDEI, SDEI-Dipt-0001251). 3♂♂ North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, mixed podocarp/broadleaf forest, sweep net, 03–04.02.2002, leg. M. Jaschhof (2x NZAC, SDEI-Dipt-0000946 & SDEI-Dipt-0001526; 1x SDEI, SDEI-Dipt-0001522). 6♂♂ North Island, Taupo, Pureora Forest Park, Waipapa Reserve, altitude 600 m, mixed podocarp/broadleaf forest, sweep net, 04–05.02.2002, leg. M. Jaschhof (3x NZAC, SDEI-Dipt-0000974, SDEI-Dipt-0000975 & SDEI-Dipt-0001516; 3x SDEI, SDEI-Dipt-0000844, SDEI-Dipt-0001517 & SDEI-Dipt-0001518). 1♂ same locality as previous, sweep net, 24–25.11.2002 leg. M. Jaschhof (SDEI).

Redescription. *Male*. **Head.** Head capsule brown. Eye bridge three facets wide, two facets at margin. Scape and pedicel slightly paler than the flagellomeres; fourth flagellomere 3.1–3.4 times longer than wide (Fig. 4); necks of flagellomeres well differentiated; surface of flagellomeres rough, sparsely scattered with long setae arising from slight elevations, setae 1.5 times as long as flagellomere width; sensilla of two different lengths present, small ones and longer, curved sensilla. Maxillary palp long and three-segmented, first palpomere usually as long as third, second one shortest; first palpomere with an inconspicuous patch of sensilla and two to five bristles, one of these bristles longer and more robust, located on the outer side. Prefrons and clypeus bulging. **Thorax** brown, paler than head. Posterior pronotum bare. Anterior pronotum with three to five setae. Episternum 1 with three to eight setae. Mesonotum with four to five robust lateral bristles; row of dorsocentral bristles well developed. Scutellum with four robust bristles and several minor setae. Katepisternum slightly longer than high. **Wing.** Length 1.7–2.1 mm; width/length ratio 0.35–0.39. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, stem of M weakest, R_5 without macrotrichia on ventral side; bM and r-m bare; R_1 0.6–0.8 times as long as R; c/w ratio 0.61–0.72; r-m 0.7–0.9 as long as bM. Haltere short; knob as long as shaft. **Legs** pale, trochanter slightly darkened. Tibial organ surrounded by a circular border and wider than half width of tibial apex; tibial organ consists of an irregular transverse row of bristles and some bristles above the row. Fore tibia without robust bristles among the vestiture. Mid tibia mostly without robust bristles, exceptionally four specimens with one bristle among vestiture. Hind tibia with ten to 16 very robust bristles arranged in a longitudinal, posteriodorsal row; on posterior side of hind tibia one to six robust bristles among the vestiture. All tibial spurs equal in length. Claws with robust teeth, arranged in decreasing size. **Abdomen** brown with dark setae. **Hypopygium** (Fig. 14)**.** Gonocoxites wider than long, inner side of gonocoxites basally widely separated. Gonostylus short, and curved, 1.9–2.4 times longer than wide, apically with a large inner cavity, dorsal inner margin also apically constricted; two robust spines present, the dorsal one located on a basal lobe and unusually straight; one long whip-lash hair is located on the ventral apex of the gonostylus. Tegmen broader than long, apicolaterally with two strongly sclerotized lobes, apex roundish

and surrounded by a thin sclerotized margin, only exceptionally with a small membranous area; parameral apodeme short and robust. Area of teeth consists of nine to 20 small teeth. Ejaculatory apodeme dark, of medium length and narrow; base of ejaculatory apodeme pale, lyre-shaped e.g. broadly fused basally with two medium long branches. Posterior portion of gonocoxal apodeme of medium size and brown, medially connected by a slender bridge. Anterior portion of gonocoxal apodeme long and broad.

Body size: 1.9–2.5 mm.

Female. Unknown.

Genetic distances. The maximum p-distance between all nine available COI sequences is 3.07%. The nearest neighbour is *Psl*. *mahanga*, diverging by a minimum of 7.14%. The maximum p-distance between all five available 28S sequences is 0.12%. The nearest neighbour is *Psl*. *mahanga*, diverging by a minimum of 0.06%.

Distribution. New Zealand.

Remarks. One paratype of *Psl*. *bispina*, deposited in the NZAC, was not investigated in the present study and its species affiliation has not been revised. Nevertheless, it has to be mentioned, that it is labelled with another locality than published in Mohrig & Jaschhof (1999). According to New Zealand Arthropod Collection (2019) the collection data are: one paratype, North Island, Taupo, Hauhungaroa Range, 5 km SW Tihoi, podocarp forest, sweep net, 21.12.1992, leg. Jaschhof (NZAC, NZAC02016076).

Pseudolycoriella teo sp. n.

(Fig. 15)

urn:lsid:zoobank.org:act:NomenclaturalActs/5CAAD136-9980-4B4D-8536-B0A7034BFD41

Material studied. *Holotype male*. New Zealand: Taupo, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, 690 m, mixed podocarp/broadleaf forest; sweep net, 03–04.02.2002, leg. M. Jaschhof (NZAC, SDEI-Dipt-0001528).

Description. *Male*. **Head.** Head capsule brown. Eye bridge three facets wide, two facets at margin. Scape, pedicel and flagellomeres concolourous; fourth flagellomere 3.3 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres slightly rough without deep pits, sparsely scattered with long setae, which are 1.5 times as long as flagellomere width; small sensilla and longer, curved sensilla present. Maxillary palp three-segmented; palpomeres inappropriately prepared in the holotype; first palpomere with four bristles, one of these bristles longer and more robust. Prefrons and clypeus slightly bulging. **Thorax** brown, paler than head, central parts brighter. Posterior pronotum bare. Anterior pronotum with two setae. Episternum 1 with five setae. Mesonotum with four robust lateral bristles; row of dorsocentral bristles present. Scutellum with four sockets, which formerly contained robust bristles. Katepisternum longer than high. **Wing.** Length 1.9 mm; width/length ratio 0.36. Membrane transparent and without macrotrichia, anal area well developed; all posterior veins distinct, stem of M weakest, R_5 only with macrotrichia on the dorsal side; bM bare and r-m bare; R_1 0.6 times as long as R; c/w ratio 0.59; r-m 0.9 as long as bM. Haltere short; knob as long as shaft. **Legs** pale. Tibial organ surrounded by a circular border and as long as half width of tibial apex; tibial organ consists of an irregular transverse row of bristles. Fore and mid tibia without robust bristles among vestiture. Hind tibia with seven very robust bristles arranged in a longitudinal, posteriodorsal row; on posterior side of hind tibia two robust bristles among vestiture. All tibial spurs equal in length. Claws strongly toothed. **Abdomen** concolourous with thorax. **Hypopygium** (Fig. 15)**.** Gonocoxites wider than long, inner side of gonocoxites basally not fused. Gonostylus short, bean-shaped and only with a very slight curvation, 2.3 times longer than wide, apex rounded and with a small inner cavity; two robust spines present, not inserting on basal lobes; one whip-lash hair present on the ventral apex of the gonostylus. Tegmen broader than long, apicolaterally with two not very broad, strongly sclerotized lobes, apex membranous; parameral apodeme short and robust. Area of teeth consisting of approximately 15 small teeth. Ejaculatory apodeme brown, medium long and broad; base of ejaculatory apodeme delicate. Posterior portion of gonocoxal apodeme medium sized and brown. Anterior portion of gonocoxal apodeme long and broad.

Body size: 1.7 mm.

Female. Unknown.

Genetic distances. Because there is only a single specimen, no intraspecific distance is calculable. The nearest neighbour is *Psl*. *jaschhofi*, diverging by a minimum of 4.92%. For the 28S sequence the nearest neighbour is *Psl*. *mahanga*, diverging by a minimum of 0.13%.

Etymology. The Māori adjective *teo* means small and was therefore deemed to be a suitable name for one of the smallest New Zealand *Pseudolycoriella* species.

Distribution. New Zealand.

Discussion. *Pseudolycoriella teo* has the smallest body size of the six species of *Psl*. *bispina* complex. Nevertheless, some specimens of *Psl*. *orite* have similarly small body sizes. In fact, this species is very similar to *Psl*. *teo*. The best distinguishing characters for *Psl*. *teo* are the shorter length of the gonocoxites and the very round apex of the gonostylus, which also has a small inconspicuous apical cavity.

***Pseudolycoriella puhihi* sp. n.**

(Figs 5 & 16)

urn:lsid:zoobank.org:act:NomenclaturalActs/0C3972BD-BD5F-4A83-A049-03D6FC42CCB7

Material studied. *Holotype male*. New Zealand: North Island, Taupo, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, 690 m, mixed podocarp/broadleaf forest, by sweep net, 03–04.02.2002, leg. M. Jaschhof (NZAC, SDEI-Dipt-0001523). *Paratypes*. 2♂♂ North Island, Bay of Plenty, Katikati, 140 Wharawhara Road, bush area, pitfall traps, 14.02–05.03.2015, leg. P.A. Maddison (NZAC; SDEI, SDEI-Dipt-0001420); 2♂♂ North Island, Bay of Plenty, Katikati, 140 Wharawhara Road, bush area, Malaise trap, 14.02–05.03.2015, leg. P.A. Maddison (NZAC, SDEI-Dipt-0001005 [without hypopygium]; SDEI, SDEI-Dipt-0001422). 1♂ North Island, Taupo, Hauhungaroa Range, 5 km southwest of Tihoi, *Podocarpus* wood with ground ferns, sweep net, 21.12.1992, leg. M. Jaschhof (PWMP [previously misidentified, published as *Psl*. *bispina* in Mohrig & Jaschhof (1999); incorrect collection locality published in Mohrig & Jaschhof (1999), slide with the printed label: "Neuseeland, Nordinsel / Hauhungaroa Range, / Tihoi / Podocarpus-Wald / 21.12.1992 Käscher / leg. Jaschhof / coll. Mohrig"]).

Description. *Male*. **Head.** Head capsule brown. Eye bridge three facets wide, two facets at margin. Scape and pedicel usually concolourous with flagellomeres, rarely with a slightly paler pedicel; fourth flagellomere 2.3–2.5 times longer than wide (Fig. 5); necks of flagellomeres well differentiated; surface of flagellomeres rough with deep pits, densely scattered with long setae, which are as long as flagellomere width; small sensilla and longer, curved sensilla present. Maxillary palp three-segmented, first palpomere mostly as long as third, second one shortest, first palpomere with three to five bristles, one of these bristles longer and more robust. Prefrons and clypeus slightly bulging. **Thorax** brown, paler than head, central parts brighter. Posterior pronotum bare. Anterior pronotum with three to seven setae. Episternum 1 with five to seven setae. Mesonotum with four to five robust lateral bristles; row of dorsocentral bristles present. Scutellum with four robust bristles and several minor setae. Katepisternum slightly longer than high. **Wing.** Length 1.5–1.8 mm; width/length ratio 0.36–0.39. Membrane transparent and without macrotrichia, anal area well developed; all posterior veins distinct, stem of M weakest, apex of R_5 with up to five additional setae on the ventral side; bM and r-m bare; R_1 0.6–0.7 times as long as R; c/w ratio 0.65–0.71; r-m 0.9–1.2 as long as bM. Haltere short; knob as long as shaft. **Legs** pale. Tibial organ surrounded by a circular border and as long as half width of tibial apex; tibial organ consists of an irregular transverse row of bristles. Fore tibia without robust bristles among vestiture. Mid tibia with one to two bristles among vestiture. Hind tibia with eight to ten robust bristles organised in a longitudinal, posteriodorsal row; on posterior side of hind tibia one to four robust bristles among vestiture. All tibial spurs equal in length. Claws strongly toothed. **Abdomen** concolourous with thorax. **Hypopygium** (Fig. 16)**.** Gonocoxites wider than long, inner side of gonocoxites not fused basally. Gonostylus short, bean-shaped, and slightly curved, 1.9–2.2 times longer than wide, inner median edge strongly concave, apex blunt and with an inner cavity; two robust spines present, not inserted on basal lobes; one whip-lash hair present on the ventral apex of the gonostylus; on inner median site with conspicuous tendon insertion (*ti* in Fig. 16). Tegmen broader than long, apicolaterally with two not very broad, strongly sclerotized lobes, apex with a membranous edge; parameral apodeme short and robust. Area of teeth consists of approximately 15 small teeth. Ejaculatory apodeme brown, of medium length and narrow; base of ejaculatory apodeme delicate with thin branches. Posterior portion of gonocoxal apodeme of medium size and brown. Anterior portion of gonocoxal apodeme long and narrow.

Body size: 1.8–2.2 mm.

Female. Unknown.

Genetic distances. The maximum p-distance between all four available COI sequences is 4.44%. The nearest neighbour is *Psl*. *orite*, diverging by a minimum of 7.54%. Both available 28S sequences are identical and show no differences to a sequence of *Psl*. *orite*.

Etymology. *Pūhihi* is the Māori word for antenna. The epithet refers to the distinctive flagellomeres compared to the other species closely related to *Psl. bispina*.

Distribution. New Zealand.

Discussion. Among the species of the *Psl. bispina* complex, *Psl. puhihi* is the only one where the length to width ratio of the fourth flagellomere is less than three. This ratio results from the greater width of the flagellomeres (Fig. 5). In addition, the flagellomeres are much more densely setose than in the other five species of this species complex. Furthermore, the length of the wing is shorter than in most other species around *Psl. bispina* (≤ 1.8 mm). The only exception that was examined is one specimen of *Psl. bispina* (SDEI-Dipt-0001418), which also had a short wing length (< 1.8 mm).

Pseudolycoriella orite sp. n.

(Fig. 17)

urn:lsid:zoobank.org:act:FB195DA5-5D08-4CE0-990C-111633F9F7E1

Material studied. *Holotype male*. New Zealand: North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, mixed podocarp/broadleaf forest, sweep net, 03–04.02.2002, leg. M. Jaschhof (NZAC, SDEI-Dipt-0000863). *Paratypes*: 8♂♂ same locality and same date as holotype (3x NZAC, SDEI-Dipt-0001519, SDEI-Dipt-0001527 & SDEI-Dipt-0001529; 5x SDEI, SDEI-Dipt-0001520, SDEI-Dipt-0001521, SDEI-Dipt-0001524, SDEI-Dipt-0001525 & SDEI-Dipt-0001533). 1♂ North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 7 km NE Ohakune, mixed *Nothofagus*/podocarp forest, sweep net, 03.02.2002, leg. M. Jaschhof (SDEI). 3♂♂ North Island, Masterton, Tararua Forest Park, Blue Range Hut Track 10 km SW Mt. Bruce, mixed *Nothofagus*/podocarp/broadleaf forest, sweep net, 02.02.2002, leg. M. Jaschhof (2x NZAC; 1x SDEI).

Description. *Male*. **Head.** Head capsule brown. Eye bridge three facets wide, two facets at margin. Scape and pedicel concolourous with flagellomeres; fourth flagellomere 3.0–3.6 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough with deep pits, sparsely scattered with long setae, which are 1.5 times as long as flagellomere width; small sensilla and longer, curved sensilla present. Maxillary palp three-segmented, first palpomere mostly as long as third, second one shortest, first palpomere with two to four bristles, one of these bristles longer and more robust. Prefrons and clypeus slightly bulging. **Thorax** brown, paler than head, central parts brighter. Posterior pronotum bare. Anterior pronotum with two to four setae. Episternum 1 with three to six setae. Mesonotum with four robust lateral bristles; row of dorsocentral bristles present. Scutellum with four robust bristles and several minor setae. Katepisternum longer than high. **Wing.** Length 1.8–2.2 mm; width/length ratio 0.34–0.36. Membrane transparent and without macrotrichia, anal area weakly developed; all posterior veins distinct, stem of M weakest, R_5 only with setae on the dorsal side; bM and r-m bare; R_1 0.5–0.7 times as long as R; c/w ratio 0.66–0.70; r-m 0.5–1.0 as long as bM. Haltere short; shaft slightly longer than knob. **Legs** pale. Tibial organ surrounded by a circular border and as long as half of the width of the tibial apex; tibial organ consists of an irregular transverse row of bristles. Fore tibia without robust bristles among vestiture. Mid tibia mostly with one bristle among vestiture. Hind tibia with eight to nine very robust bristles arranged in a longitudinal, posteriodorsal row; on posterior side of hind tibia one to three robust bristles among vestiture. All tibial spurs equal in length. Claws strongly toothed. **Abdomen** concolourous with thorax. **Hypopygium** (Fig. 17)**.** Gonocoxites wider than long, inner side of gonocoxites not fused basally. Gonostylus short, bean-shaped, and slightly curved, 2.0–2.3 times longer than wide, on inner median side with a clearly developed tendon insertion, apex blunt and with a large apical cavity; two robust spines present, dorsal spine on a small basal lobe; one whip-lash hair present on the ventral apex of the gonostylus. Tegmen broader than long, apicolaterally with two long, strongly sclerotized lobes, apex with a small membranous edge; parameral apodeme robust, short to medium long. Area of teeth with six to twelve small teeth. Ejaculatory apodeme brown, medium long and broad; base of ejaculatory apodeme delicate with two thin branches. Posterior portion of gonocoxal apodeme medium sized and brown. Anterior portion of gonocoxal apodeme long and broad.

Body size: 1.8–2.1 mm.

Female. Unknown.

Genetic distances. The maximum p-distance between all six available COI sequences is 0.39%. The nearest neighbour is *Psl. jaschhofi*, diverging by a minimum of 6.35%. The p-distance between both available 28S sequences is 0.12%. One of those sequences is identical to one sequence of *Psl. puhihi*.

Etymology. In Māori the word *ōrite* means being equal or being similar. The epithet indicates the morphologi-

cal similarity of the newly described species to its sibling species.

Distribution. New Zealand.

Discussion. It is not easy to distinguish this new species from its relatives within the *Psl. bispina* complex. However, *Psl. bispina* and *Psl. mahanga* show diagnostic differences in the apical edge of the tegmen (fully sclerotized *vs*. membranous) and the base of the ejaculatory apodeme (lyre-shaped *vs*. narrow and bifurcated along the whole length). *Pseudolycoriella puhihi* can be distinguished by the shorter and wider fourth flagellomere and the more clearly developed tendon insertion of the gonostylus adductor. *Pseudolycoriella teo* has shorter gonocoxites and gonostyli, and a lower c/w ratio (0.59 *vs*. ≥ 0.66). The new species and *Psl. porehu* are the most similar species of this complex. Of all members, both species have the narrowest wings, and therefore the lowest ratio of width to length of wings and the least developed anal area. In order to distinguish between these species, the body size must be taken into account. On average, *Psl. porehu* has a larger body size, but there is some overlap with *Psl. orite*. However, the wing length is always less than 2.2 mm in *Psl. orite*, and greater than or equal to 2.2 mm in *Psl. porehu*. The c/w ratio also differs: it is less than 0.65 in *Psl. porehu* and greater than 0.65 in *Psl. orite*. Further minor distinguishing characters are found in the robust bristles among the vestiture of the tibiae: on the mid tibia *Psl. orite* bears one (or no) robust bristle while *Psl. porehu* has three to five bristles; on the hind tibia the longitudinal, posteriodorsal row contains three to six bristles in *Psl. porehu* and eight to nine bristles in *Psl. orite*. Unfortunately, for *Psl. porehu* no genetic data are available, which could be used to verify this morphological species delimitation.

***Pseudolycoriella mahanga* sp. n.**

(Fig. 18)

urn:lsid:zoobank.org:act:14AD5BCD-06F0-4CBC-BB21-8E519C072047

Material studied. *Holotype male*. New Zealand: South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, opposite Gladehouse Track, *Nothofagus* forest, Malaise trap, 01–21.12.2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC, SDEI-Dipt-0001008). *Paratypes*: 15♂♂ South Island, Westland, 5 km SW Arawhata, mixed *Nothofagus*/podocarp forest, aspirator, 20.10.2001, leg. M. Jaschhof (7x NZAC; 8x SDEI). 1♂ South Island, Queenstown Lakes, Otago Lakes, Mt Aspiring NP, Makarora River Valley near Cameron Creek Track, mixed *Nothofagus*/broadleaf forest, sweep net, 18–19.12.2002, leg. M. Jaschhof (SDEI, SDEI-Dipt-0000595). 2♂♂ South Island, Southland, Fiordland, Fiordland NP, 3 km E Milford Sound, mixed podocarp/broadleaf forest, Malaise trap, 01–21.12.2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC; SDEI). 1♂ same locality as previous, sweep net, 21.12.2002, leg. M. Jaschhof (NZAC). 1♂ South Island, Southland, Fiordland, Fiordland NP, 4 km E Milford Sound, mixed broadleaf/*Nothofagus* forest, sweep net, 07.01.2002, leg. M. Jaschhof (NZAC; SDEI-Dipt-0000904). 1♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, opposite Earl Mountain Tracks, *Nothofagus* forest, Malaise trap, 05–24.01.2002, leg. M. & C. Jaschhof (SDEI, SDEI-Dipt-0000849). *Additional material*: 5♂♂ South Island, Kaikoura, Blue Duck Reserve, altitude 300–400 m, mixed podocarp/*Nothofagus solandri* forest, sweep net, 29.11.2001, leg. M. Jaschhof; U. Kallweit & A. Stark (SDEI).

Description. *Male*. **Head.** Head capsule brown. Eye bridge three facets wide, two facets at margin. Scape and pedicel concolourous with flagellomeres; fourth flagellomere 3.0–3.5 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough, sparsely scattered with long setae arising from slight elevations, setae 1.5 times as long as flagellomere width; sensilla of two different lengths present, small ones and longer, curved sensilla. Maxillary palp long and three-segmented, first palpomere slightly longer than third, second one shortest; first palpomere with an inconspicuous patch of sensilla and two to five bristles, one of these bristles longer and more robust, located on the outer side. Prefrons and clypeus bulging. **Thorax** brown, central parts brightened. Posterior pronotum bare. Anterior pronotum with three to seven setae. Episternum 1 with five to ten setae. Mesonotum with four to six robust lateral bristles; row of dorsocentral bristles well developed. Scutellum with four robust bristles (exceptionally five) and several minor setae. Katepisternum as long as high, or slightly longer than high. **Wing.** Length 2.0–2.4 mm; width/length ratio 0.35–0.42. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, stem of M weakest, apical quarter to apical third of R_5 with macrotrichia on both sides; bM and r-m bare; R_1 0.6–1.0 times as long as R; c/w ratio 0.66–0.76 (specimens from Kaikoura show a c/w ratio from 0.53–0.60); r-m 0.7–1.1 as long as bM (specimens from Kaikoura 0.9–1.5). Haltere short; knob as long as shaft. **Legs** pale brown, trochanter slightly darkened. Tibial organ surrounded by a circular border and wider than half width of tibial apex; tibial organ consists of an irregular transverse row of bristles and some bristles above

the row. Fore tibia without robust bristles among vestiture. Mid tibia without or exceptionally with one robust bristle among vestiture. Hind tibia with three to nine robust bristles organised in a longitudinal, posteriodorsal row; on posterior side of hind tibia one to three robust bristles among vestiture. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** brown with dark setae. **Hypopygium** (Fig. 18)**.** Gonocoxites wider than long, basal inner side of gonocoxites widely separated. Gonostylus short, curved, and hunchbacked, 1.7–2.3 times longer than wide, apically with a large inner cavity; two robust spines present, the dorsal one located on a basal lobe; one long whiplash hair is located on the ventral apex of the gonostylus. Tegmen wider than long, apicolaterally with two strongly sclerotized lobes, apex roundish and surrounded by a strongly sclerotized margin, only exceptionally with a small membranous area; parameral apodeme short and robust. Area of teeth consists of 15 to 30 small teeth. Ejaculatory apodeme dark, broad, and short to medium long; base of ejaculatory apodeme pale, lyre-shaped, branches of base of ejaculatory apodeme of different width. Posterior portion of gonocoxal apodeme medium sized and brown. Anterior portion of gonocoxal apodeme long and broad.

Body size: 1.9–2.7 mm.

Female. Unknown.

Genetic distances. The maximum p-distance between the two available COI sequences is 1.14%. The nearest neighbour is *Psl. bispina*, diverging by a minimum of 7.14%. Both available 28S sequences are identical. The nearest neighbour is *Psl. bispina*, diverging by a minimum of 0.06%.

Etymology. The Māori word *māhanga*—meaning twin or twins—was selected as the epithet, to illustrate that the new described species is one of the sibling species around *Psl. bispina*.

Distribution. New Zealand.

Discussion. Of all species of this complex, only *Psl. mahanga* and *Psl. bispina* have in common a lyre-shaped base of the ejaculatory apodeme and a strongly sclerotized apex of the tegmen. *Pseudolycoriella mahanga* can be distinguished from *Psl. bispina* by the setosity of vein R_5. In *Psl. mahanga* macrotrichia are located on both the ventral and dorsal sides, whereas in *Psl. bispina* they occur only on the dorsal side. On the hind tibia *Psl. mahanga* has a less developed longitudinal row of robust bristles. Their number does not exceed nine and they are also smaller than in *Psl. bispina*.

Five males originating from the Blue Duck Reserve in the Kaikoura District differ significantly in c/w ratio from remaining specimens (0.53–0.60 *vs*. 0.66–0.76). Also, the r-m/bM ratio is slightly higher in some specimens from Kaikoura (0.7–1.1 *vs*. 0.9–1.5). Genetic data on this population are not available and no further morphological differences have been found, so it was decided not to describe a further new species. Because of this uncertainty, these specimens were not assigned to the type series of *Psl. mahanga*.

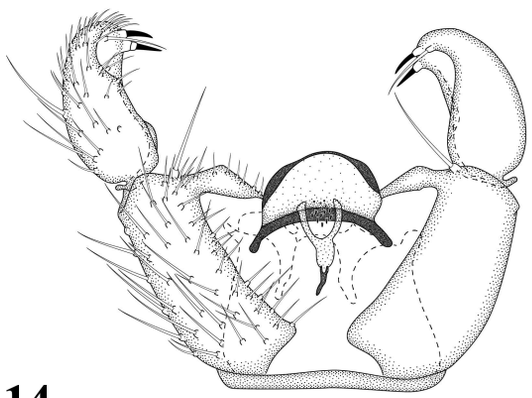
Pseudolycoriella porehu sp. n.

(Fig. 19)

urn:lsid:zoobank.org:act:NomenclaturalActs/0B09BE48-A529-4737-B03E-CF2ED15CFAF9

Material studied. *Holotype male*. New Zealand: South Island, Clutha, Catlins, Purakaunui Scenic Reserve, mixed podocarp/broadleaf/*Nothofagus* forest, sweep net, 03.01.2002, leg. M. Jaschhof (NZAC, SDEI-Dipt-0001394). *Paratypes*: 4♂♂ same locality and same date as holotype (1x NZAC; 3x SDEI, SDEI-Dipt-0001485).

Description. *Male*. **Head.** Head capsule brown. Eye bridge three facets wide, two facets at margin. Scape and pedicel concolourous or slightly paler than flagellomeres; fourth flagellomere 3.3–3.9 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough, sparsely scattered with long setae arising from slight elevations, setae 1.5 times as long as flagellomere width; sensilla of two different lengths present, small ones and longer, curved sensilla. Maxillary palp long and three-segmented, first palpomere as long as third, second one shortest; first palpomere with an inconspicuous patch of sensilla and two to three bristles, one of these longer and more robust, located on the outer side. Prefrons and clypeus bulging. **Thorax** pale brown to brown, central parts brighter. Posterior pronotum bare. Anterior pronotum with three to five setae. Episternum 1 with four to seven setae. Mesonotum with five to six robust lateral bristles; row of dorsocentral bristles well developed. Scutellum with four robust bristles and several minor setae. Katepisternum as long as high, or slightly longer than high. **Wing.** Length 2.2–2.3 mm; width/length ratio 0.33–0.36. Membrane transparent and without macrotrichia, anal area weakly developed; all posterior veins distinct, stem of M weakest, apical fifth to apical third of R_5 with macrotrichia on ventral and dorsal side; bM and r-m bare; R_1 0.6–0.7 times as long as R; c/w ratio 0.52–0.61; r-m 0.7–0.9 as long as bM. Haltere short; knob as long as shaft. **Legs** pale brown, trochanter slightly darkened. Tibial organ surrounded by a



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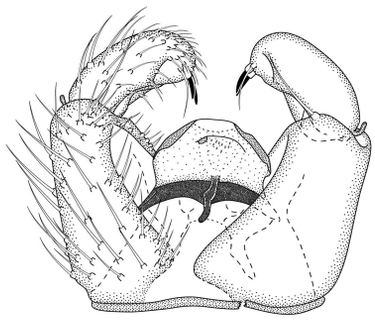

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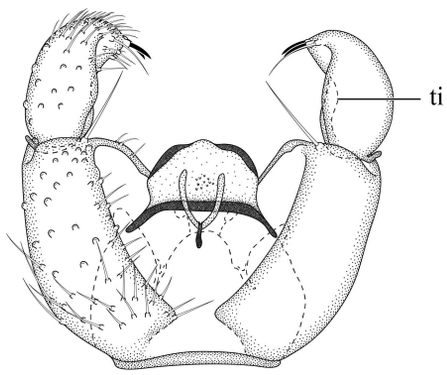

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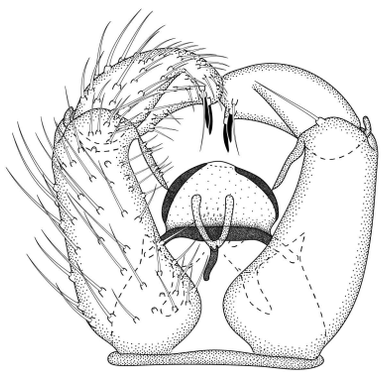

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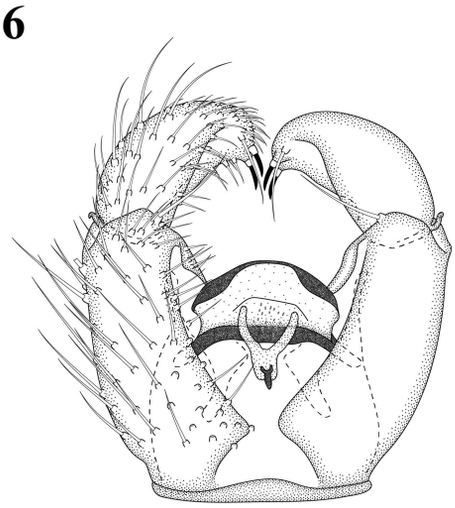

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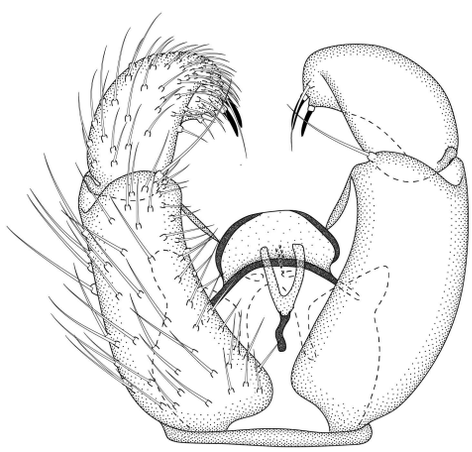


19

14–19

100 µm

FIGURES 14–19. *Pseudolycoriella bispina* complex, hypopygia. **14.** *Pseudolycoriella bispina* Mohrig. **15.** *Pseudolycoriella teo* **sp. n. 16.** *Pseudolycoriella puhihi* **sp. n. 17.** *Pseudolycoriella orite* **sp. n. 18.** *Pseudolycoriella mahanga* **sp. n. 19.** *Pseudolycoriella porehu* **sp. n.** Abbreviation: ti = insertion of the tendon of the gonostylus adductor.

circular border and wider than half width of tibial apex; tibial organ consists of a patch of several robust bristles arranged in a transverse band. Fore tibia without robust bristles among vestiture. Mid tibia with three to five robust bristles among vestiture, located anterioventrally and posterioventrally. Hind tibia with four to seven robust bristles organised in a longitudinal, posteriodorsal row; on posterior side of hind tibia five to six robust bristles among vestiture. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** brown with dark setae. **Hypopygium** (Fig. 19)**.** Gonocoxites wider than long, basal inner side of gonocoxites widely separated. Gonostylus short, broad, and slightly curved; 2.0–2.3 times longer than wide, apex blunt with an inner cavity; two robust spines present, the dorsal one located on a basal lobe; one long whip-lash hair is located on the ventral apex of the gonostylus. Tegmen broader than long, apicolaterally with two strongly sclerotized lobes, apex roundish with a small membranous edge; parameral apodeme robust and short to medium long. Area of teeth with ten to 15 small teeth. Ejaculatory apodeme dark, broad, and of medium length; base of ejaculatory apodeme pale, branches broad and basally connected. Posterior portion of gonocoxal apodeme medium sized and brown. Anterior portion of gonocoxal apodeme long and broad.

Body size: 1.9–2.5 mm.

Female. Unknown.

Genetic distances. No genetic information available.

Etymology. *Porehu* is a Māori modifier and means mysterious. It was chosen as the epithet because the taxonomic rank of these specimens remained unclear to the author for a long time.

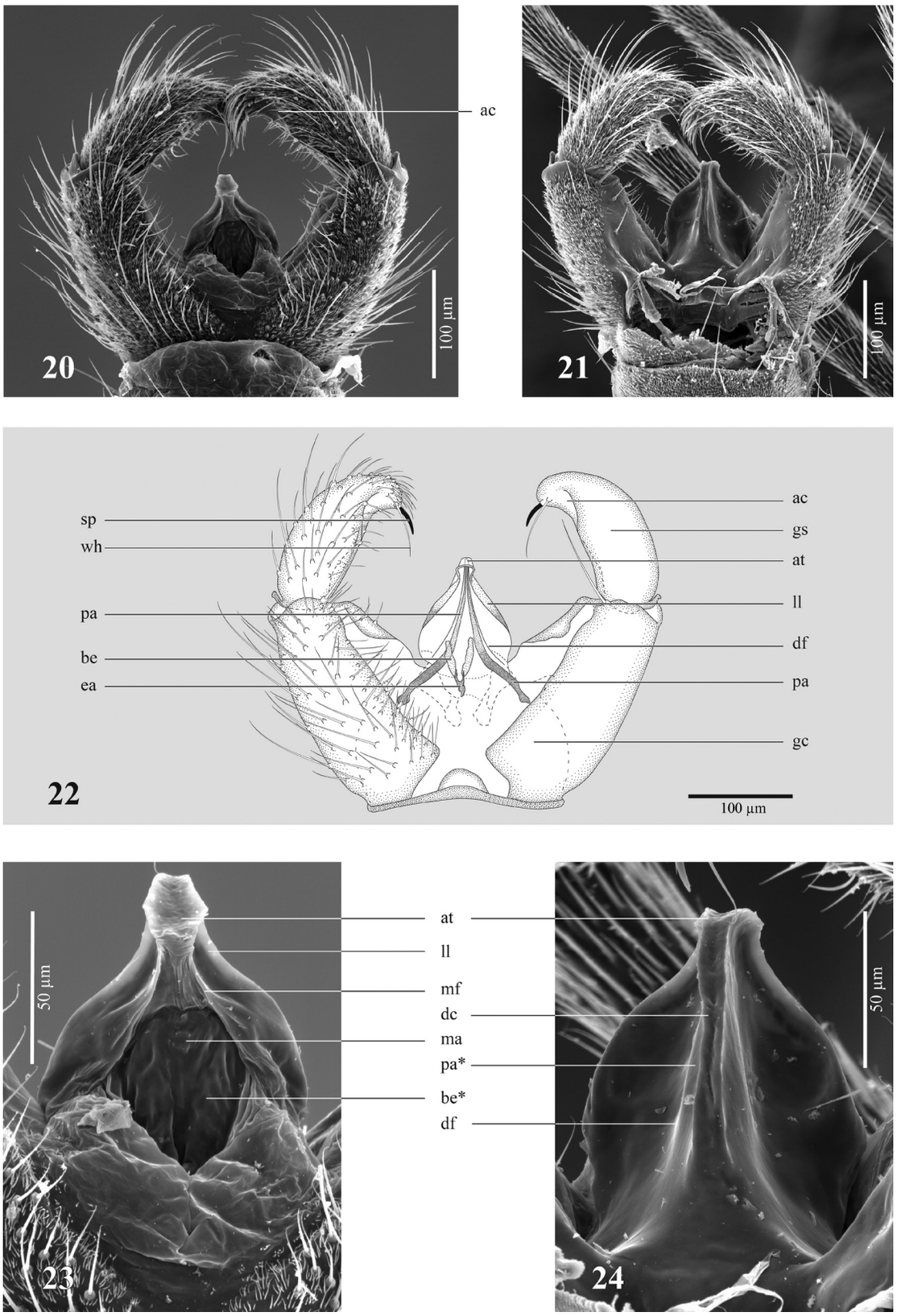
Distribution. New Zealand.

Discussion. See discussion paragraph for *Psl. orite*.

***Pseudolycoriella jejuna* complex**

The *Psl. jejuna* complex is a group of thirteen closely related and cryptic species. These species share a complex and synapomorph structure of their hypopygia. In Figures 20–22 a hypopygium of *Psl. tewaipounamu* is depicted. The gonostylus (*gs*) is elongated and curved with an inwardly bent apex. The apex possesses one spine (*sp*) and a whip-lash hair (*wh*) and—in most species—on the inward part a cavity (*ac*). The tegmen is highly derivative compared with the tegmen of typical sciarids. Its general shape is onion-shaped: more or less roundish with an apical contraction (*at*). Adjacent to the apical contraction the tegmen has two lateral lobes (*ll*) on the ventral side, which can easily be observed in light microscopy. In the middle of the ventral side of the tegmen a membranous area (*ma*) bordered by two median folds (*mf*) can easily be observed by using scanning electron microscopy. In light microscopy these delicate structures are hardly visible. At this membranous area a bulge of the base of the ejaculatory apodeme (*be*) can be observed. An area of teeth is absent. In light microscopy, the parameral apodemes (*pa*) do not fuse medially. Instead they are stretched to the apex of the tegmen and form the apical contraction (*at*). On the dorsal side of the tegmen the parameral apodemes protrude and form a dorsal carina (*dc*). This carina is bent around the apex and ends subapically on the ventral side of the tegmen. The bulges of the parameral apodemes are accompanied by a dorsal fold (*df*), which can also be observed in light microscopy. The phylogeny of this complex is shown in Figure 61.

Discussion. The species of the *Psl. jejuna* complex can be assigned to the *Psl. bruckii* group. The monophyly of this complex is strongly supported by genetics and can also be demonstrated by some autapomorphic morphological characters such as the extraordinary tegmen, the reduction of the number of gonostylar spines, and the secondary absence of an area of teeth. Due to this unique character set, all species of the *Psl. jejuna* complex can easily be recognized. Only *Psl. fuscorubroides* (Mohrig & Blasco-Zumeta) from Spain has a similar tegmen (Mohrig & Blasco-Zumeta 1996). It also possesses a dorsal carina that derives from the parameral apodemes. However, there are differences: the parameral apodemes are fused and not separated by a gap, as in the *Psl. jejuna* complex, and the carina in *Psl. fuscorubroides* arises vertically in the middle base of the tegmen. Furthermore, *Psl. fuscorubroides* possesses a large area of conspicous teeth (Mohrig & Blasco-Zumeta 1996). Several other structures of the hypopygium are also disimilar. For instance, the gonostylus of *Psl. fuscorubroides* is armed with two short spines and has a conspicuous lobe on the dorsal margin and therefore differs significantly from the gonostyli of the *Psl. jejuna* complex. It is not clear whether the dorsal carina of the tegmen is a convergent or a homologous character. Maybe *Psl. fuscorubroides* is closely related to the *Psl. jejuna* complex, but it certainly does not belong to the crown group of the *Psl. jejuna* complex, since the absence of an area of teeth can be regarded as a synapomorpy of the New Zealand *Psl.*



FIGURES 20–24. *Pseudolycoriella jejuna* complex, *Pseudolycoriella tewaipounamu* **sp. n.**, details of hypopygium. **20.** Hypopygium, ventral. **21.** Hypopygium, dorsal, tergite IX removed. **22.** Hypopygium, ventral. **23.** Tegmen, ventral. **24.** Tegmen, dorsal. Abbreviations: ac = apical cavity; at = apex of tegmen; be = base of ejaculatory apodeme; be* = base of ejaculatory apodeme covered by the membranous area; dc = dorsal carina; df = dorsal fold; ea = ejaculatory apodeme; gc = gonocoxite; gs = gonostylus; ll = lateral lobe; ma = membranous area; mf = median fold; pa = parameral apodeme; pa* = parameral apodeme covered by integument; sp = gonostylar spine; wh = whip-lash hair.

jejuna complex members. In other words, the hypothesis of a monophyly of the New Zealand representatives of the *Psl*. *jejuna* complex cannot be rejected.

The occurrence of two atavisms among the specimens of the *Psl*. *jejuna* complex confirms the above character polarisation regarding the single gonostylar tooth and the absence of the area of teeth. One paratype of *Psl*. *dagae* has two spines on the left gonostylus while the right one only bears one. This atavistic state is unique among all 233 investigated specimens belonging to the *Psl*. *jejuna* complex and indicates that the species of the *Psl*. *jejuna* complex derivate from an ancestor that bears two spines at the gonostylus, like the extant species of the *Psl*. *bispina* complex or the *Psl*. *zealandica* complex. The second detected atavism occured in two paratypes of *Psl*. *whena*, where an area of the teeth is present, although to a varying degree—one paratype shows only five tiny teeth, the other twelve.

Pseudolycoriella jejuna **(Edwards, 1927)**

(Figs 25–29)

Literature. *Sciara jejuna* Edwards, 1927: Tonnoir & Edwards (1927): 796, Fig. 181.—Miller (1950): 57.—Steffan (1989): 150.—*Pseudolycoriella jejuna* (Edwards, 1927): Mohrig & Jaschhof (1999): 37–39, Fig. 19 a–g.—Menzel & Mohrig (2000): 715.—Rudzinski (2000): 183.—Macfarlane *et al*. (2010): 441.

Material studied. *Holotype male*. New Zealand: North Island, Manawatu-Wanganui, Ohakune, Oct.-Nov. 1923, leg. T.R. Harris (BMNH, BMNH(E)250339). *Previously published material*: 1♂ North Island, Far North, Waipoua Forest, 45 km northwest of Dargaville, old Kauri-*Podocarpus* wood, sweep net, 31.12.1992, leg. M. Jaschhof (PWMP). 2♂♂ North Island, Taupo, Hauhungaroa Range, 5 km southwest of Tihoi, *Podocarpus* wood with ground ferns, sweep net, 21.12.1992, leg. M. Jaschhof (PWMP; SDEI [Slide with the handwritten label: "Neuseeland: Nordins. / Pureora Forest / Kescher, Podocarpus / 21.12.92 / leg. Jaschhof". The locality information is obviously incorrect, because the sample locality and the date do not correspond with locality information in Mohrig & Jaschhof (1999).]). 2♂♂ North Island, Wairoa, Urewera National Park, Huiarau Range 30 km southeast of Murupara, altitude 600–1,000 m, *Podocarpus-Nothofagus* wood, sweep net, 23.12.1992, leg. M. Jaschhof (all PWMP). 1♂ North Island, Stratford, Mount Egmont National Park, East Egmont, altitude 650 m, *Podocarpus* wood with rotten wood and a dense layer of herbs, sweep net, 09.01.1993, leg. M. Jaschhof (PWMP). *New records*: 3♂♂ North Island, Taupo, Pureora Forest, Select Loop Road, 500 m, mixed mature podocarp forest, Malaise trap, 15.07–23.08.2001, leg. M. & C. Jaschhof (SDEI, SDEI-Dipt-0000579, SDEI-Dipt-0000583 & SDEI-Dipt-0000588). 1♂ North Island, Taupo, Pureora Forest Park, Waipapa Reserve, altitude 600 m, mixed podocarp/broadleaf forest, sweep net, 24–25.11.2002, leg. M. Jaschhof (SDEI). 2♂♂ North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, mixed podocarp/broadleaf forest, sweep net, 03–04.02.2002, leg. M. Jaschhof (NZAC, SDEI-Dipt-0000773; SDEI, SDEI-Dipt-0000829). 8♂♂ same locality as previous, Malaise trap, 26.11–28.12.2002, leg. M. & C. Jaschhof & U. Kallweit (3x NZAC SDEI-Dipt-0000744 & SDEI-Dipt-0001195 & SDEI-Dipt-0001347; 5x SDEI, SDEI-Dipt-0000603, SDEI-Dipt-0000617, SDEI-Dipt-0001193 & SDEI-Dipt-0001339). 2♂♂ same locality as previous, sweep net, 26.11.2002, leg. M. Jaschhof (NZAC; SDEI).

Redescription. *Male*. **Head.** Head capsule brown. Eye bridge three facets wide, two facets at margin. Scape and pedicel mostly slightly paler than the flagellomeres; fourth flagellomere 2.7–3.3 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough with deep pits, sensilla of two different lengths, small ones and longer, curved sensilla; setae on the flagellomere as long as flagellomere width, slightly curved. Maxillary palp long and three-segmented, first palpomere longest, second one shortest; first palpomere with an inconspicuous patch of sensilla and three to five long bristles (exceptionally two), one bristle longer and more robust, located on the outer side. Prefrons and clypeus bulging. **Thorax** brown, paler than head; some specimens with lateral brightened areas. Posterior pronotum bare. Anterior pronotum with two to six setae. Episternum 1 with four to eight setae. Mesonotum with four to six robust lateral bristles; row of dorsocentral bristles well developed; anteriorly on the mesonotum two to seven (median four) small arcostichal setae (Figs 28–29). Scutellum with four robust bristles (the inner ones longer than the outer two) and several minor setae. Katepisternum as long as high. **Wing.** Length 2.3–3.1 mm; width/length ratio 0.35–0.40. Membrane transparent, slightly shaded and without macrotrichia, anal area present; all posterior veins distinct, except faint stem of M, apical one-fifth to half of R_5 with macrotrichia on ventral and dorsal side; bM and r-m bare, exceptionally three specimens bearing one setae on r-m (in two cases only

on one wing), R_1 0.8–1.2 times as long as R; c/w ratio 0.75–0.82; r-m 0.8–1.4 as long as bM (the holotype has an extraordinarily short r-m on the right wing, resulting in a r-m/bM ratio of 2.1). Haltere long and sooty brown; shaft longer than knob. **Legs** pale brown, paler than thorax, mid and hind coxae slightly darker than front coxae. Tibial organ surrounded by a circular border and as broad as half of the width of the tibial apex; tibial organ consists of an irregular row of bristles. Front tibia without robust bristles among the vestiture (exceptionally one specimen with one bristle among the vestiture). Mid tibia with one to three robust bristles among the vestiture (one specimen without robust bristles among vestiture). Posteriodorsal row of bristles inconspicuous, consisting of three to six bristles. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** brown, slightly paler than thorax, with long, dark setae. **Hypopygium** (Fig. 25)**.** Gonocoxites wider than long, inner side of gonocoxites with medium sized setae, outer side with long setae; ventral, inner side of gonocoxites not fused basally. Gonostylus elongate and curved, 2.4–3.1 times longer than wide, apex differentiated, apex width varies between slender and broad (compare Figs 25 & 26), inner side of gonostylus concave and scattered with microtrichia; apex with one long spine and one whiplash hair. Tegmen of the typical ground plan of the *Psl. jejuna* complex, mostly onion-shaped (in some specimens more elongated), apical contraction broad; dorsal folds present; parameral apodeme basally strongly sclerotized, medially connected, posterior branches of the parameral apodemes nearly parallel. Area of teeth absent. Ejaculatory apodeme dark, broad, and long; base of ejaculatory apodeme very delicate, long, and slender (one specimen shows an exceptionally broad base [Fig. 27]). Posterior portion of gonocoxal apodeme medium sized and brown, medially fused. Anterior portion of gonocoxal apodeme long and dark brown.

Body size: 2.5–3.3 mm.

Female. A female paratype (BMNH(E)250340, BMNH) was designated by Tonnoir & Edwards (1927) and described by Menzel & Mohrig (2000). This type is not included in the present study.

Genetic distances. The maximum p-distance between all eight available COI sequences is 2.75%. The nearest neighbour is *Psl. teo*, diverging by a minimum of 7.55%. All ten available 28S sequences are identical. The nearest neighbour is *Psl. dagae*, diverging by a minimum of 0.75%.

Distribution. New Zealand.

Remarks. Although Menzel & Mohrig (2000) gave an accurate redescription of *Psl. jejuna*, some details have to be amended. These authors stated that *Psl. jejuna* possesses an area of teeth twice as high as broad, with long single-pointed teeth (Menzel & Mohrig, 2000). This could not be verified because an area of teeth could not be observed in the holotype or in any other investigated specimen. Just two paratypes of another species of this complex—*Psl. whena*—show an atavistic area of teeth (see discussion of *Psl. jejuna* complex). Moreover, Menzel & Mohrig (2000) gave a lower value for the body length of *Psl. jejuna* than measured in the present study (2.2 mm *vs*. 2.5–3.3 mm). Maybe this is a result of measuring the shrunken holotype without taking the length of the hypopygium into account. The holotype of *Psl. jejuna* has an extraordinary ratio of the length of the wing vein r-m and bM. On the right wing the r-m/bM ratio is 2.1 and on the left wing 1.8. The r-m/bM ratio of the newly examined specimens ranges from 0.8 to 1.4.

Pseudolycoriella tuakana **sp. n.**

(Figs 30–34)

urn:lsid:zoobank.org:act:NomenclaturalActs/9392599F-A28F-4DCC-B7AF-C558BCBCFCEB

Material studied. *Holotype male*. New Zealand: North Island, Manawatu-Wanganui, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, mixed podocarp/broadleaf forest, Malaise trap, 26.11–28.12.2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC, SDEI-Dipt-0001194). *Paratype*. 1♂ same locality and same date as holotype (SDEI, SDEI-Dipt-0001337).

Description. *Male*. **Head.** Head capsule brown. Eye bridge three facets wide, two facets at margin. Scape and pedicel slightly paler than the flagellomeres; fourth flagellomere 2.8–2.9 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough with deep pits, sensilla of two different lengths, small ones and longer, curved sensilla; setae on the flagellomere as long as flagellomere width, slightly curved. Maxillary palp long and three-segmented, first palpomere longest, second one shortest; first palpomere with an inconspicuous patch of sensilla and two to four long bristles, one of these bristles longer and more robust, located on the outer side. Prefrons and clypeus bulging. **Thorax** brown, concolourous with head; laterally extensively brighter. Posterior pronotum bare. Anterior pronotum with five setae. Episternum 1 with three to four setae. Mesonotum with four to five robust lateral

bristles; row of dorsocentral bristles well developed; anteriorly on the mesonotum a patch of nine closely arranged arcostichal setae (Figs 33–34). Scutellum with three to four robust bristles and several minor setae. Katepisternum as long as high. **Wing.** Length 2.7–2.9 mm; width/length ratio 0.39–0.40. Membrane transparent, slightly shaded and without macrotrichia, anal area present; all posterior veins distinct, except faint stem of M, apical third of R_5 with macrotrichia on ventral and dorsal side; bM and r-m bare (the paratype bears on the right wing setae on r-m), R_1 1.0–1.1 times as long as R; c/w ratio 0.77–0.80; r-m 1.1–1.3 as long as bM. Haltere long and sooty brown; shaft longer than knob. **Legs** pale brown, mid and hind coxae slightly darker than fore coxae. Tibial organ surrounded by a circular border and slightly narrower than half width of tibial apex; tibial organ consists of an irregular row of bristles. Front tibia without robust bristles among the vestiture (the holotype bears on the left tibia one bristle among vestiture). Mid tibia without bristles among vestiture. Posteriodorsal row of bristles very inconspicuous, consisting of two to three bristles. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** brown, slightly paler than thorax, with long, dark setae. **Hypopygium** (Fig. 30)**.** Gonocoxites wider than long, inner side of gonocoxites with medium sized setae, outer side with long setae; ventral, inner side of gonocoxites basally not fused. Gonostylus elongate and curved, 2.9–3.0 times longer than wide, apex slightly differentiated, inner side of gonostylus concave and with scattered microtrichia; apex with one medium-sized spine that is only slightly longer than the surrounding setae (Figs 30 & 31); one whip-lash hair present. Tegmen of the typical ground plan of the *Psl. jejuna* complex, onion-shaped but elongated, apical contraction broad; dorsal folds well developed; parameral apodemes basally strongly sclerotized, median connected, posterior branches of the parameral apodemes nearly parallel and close. Area of teeth absent. Ejaculatory apodeme dark, broad, and short; base of ejaculatory apodeme very delicate, long, and broad. Posterior portion of gonocoxal apodeme medium sized and brown, medially joined. Anterior portion of gonocoxal apodeme of medium length and dark brown.

Body size: 3.0–3.2 mm.

Female. Unknown.

Genetic distances. Both available COI sequences are identical and do not show any p-distance. The nearest neighbour is *Psl. dagae*, diverging by a minimum of 5.93%. Both available 28S sequences are identical. The nearest neighbour is *Psl. dagae*, diverging by a minimum of 0.11%.

Etymology. The Māori word *tuakana* means elder brother or elder sister. Thus, the epithet refers to the close relationship of the new species to *Psl. jejuna*.

Distribution. New Zealand.

Discussion. Superficially *Psl. tuakana* is identical to *Psl. jejuna* and they would be regarded as conspecific, if the genetic analysis did not show a considerable difference between the species (Fig. 61). Given that both type specimens of *Psl. tuakana* originated from the same collection locality as *Psl. jejuna* the existence of one single species with two distinct genetic variants is highly unlikely. A subsequent closer examination revealed some slight morphological differences. Nevertheless, these have to be interpreted carefully in the light of the small number of specimens of *Psl. tuakana*, which does not enable a robust statistical analysis. *Pseudolycoriella tuakana* does not have any bristles among the vestiture on the mid tibia; while 21 out of 22 specimens of *Psl. jejuna* bear one to two (exceptionally three) bristles on the mid tibia. The spine on the gonostylus is shorter in *Psl. tuakana* (Fig. 35a) and therefore does not protrude from the surrounding setae as in *Psl. jejuna*. Another difference is the longer ejaculatory apodeme in *Psl. jejuna* (Fig. 35c). Nevertheless, there are exceptions: one specimen of *Psl. jejuna* (SDEI-Dipt-0000588) has an aberrant short ejaculatory apodeme (Fig. 27). The following weaker differences have more auxiliary character. The number of arcostichal bristles on the mesonotum differs between the species. *Pseudolycoriella jejuna* has two to seven arcostichal bristles while *Psl. tuakana* has nine (Figs 28, 29, 33, 34 & 36). The length to width ratio of the gonostylus of both species might show different median values, but a huge overlap has to be considered (Fig. 35b). Additionally, the tegmen of most *Psl. jejuna* specimens is more rounded while the tegmen of *Psl. tuakana* is more tapered.

Pseudolycoriella dagae **sp. n.**

(Figs 1 & 42)
urn:lsid:zoobank.org:act:8C8A28A2-ADE2-4D2F-9D16-01A2A4F788F2

Literature. *Pseudolycoriella jejuna* (Edwards, 1927): Mohrig & Jaschhof (1999): 37 [misidentification].

Material studied. *Holotype male*. New Zealand: North Island, Western Bay of Plenty, Katikati, 449 Lund Road, Malaise trap, 25.07–08.08.2016, leg. P.A. Maddison (NZAC, SDEI-Dipt-0000679). *Paratypes*. 3♂♂ same locality

and same date as holotype (1x NZAC, SDEI-Dipt-0001249; 2x SDEI, SDEI-Dipt-0000628 & SDEI-Dipt-0000655). 1♂ North Island, Western Bay of Plenty, Katikati, Te Mania catchment, Malaise trap, 19.09–27.10.2016, leg. P.A. Maddison (NZAC, SDEI-Dipt-0001367). 1♂ North Island, Wairoa, Urewera National Park, Huiarau Range 30 km southeast of Murupara, altitude 600–1,000 m, *Podocarpus-Nothofagus* wood, sweep net, 23.12.1992, leg. M. Jaschhof (SDEI [previously misidentified, published as *Psl. jejuna* in Mohrig & Jaschhof 1999]). 1♂ South Island, Kaikoura, Blue Duck Reserve, altitude 300–400 m, mixed podocarp-*Nothofagus solandri* forest, Malaise trap, 12.05–09.06.2001, leg M. & C. Jaschhof (SDEI).

Description. *Male*. **Head.** Head capsule brown. Eye bridge three to four facets wide. Scape and pedicel yellow, strongly contrasting with the dark brown flagellomeres; fourth flagellomere (Fig. 1) 2.8–3.3 times longer than wide; necks of flagellomeres well differentiated and pale; surface of flagellomeres rough with deep pits, sensilla of two different lengths, small ones and longer, curved sensilla; setae on the flagellomere longer than flagellomere width, slightly curved. Maxillary palp long and three-segmented, first and third palpomeres of equal length, second one shortest, oval; first palpomere with long sensilla and two to five long bristles, one bristle longer and more robust, located on the outer side. Prefrons and clypeus bulging. **Thorax** as brown as head, lateral and frontal parts brightened. Posterior pronotum bare. Anterior pronotum with two to three setae. Episternum 1 with four to ten setae. Mesonotum with five to seven robust lateral bristles. Scutellum with three to four robust bristles and several minor setae. Katepisternum as long as high. **Wing.** Length 2.5–3.1 mm; width/length ratio 0.38–0.40. Membrane transparent, slightly shaded and without macrotrichia, anal area present; all posterior veins distinct, except faint stem of M, apical 40–67% of R_5 with macrotrichia on ventral and dorsal side (exceptionally: one paratype with macrotrichia only on the dorsal side); bM bare, the holotype and two paratypes bear one seta on r-m, the remaining three paratypes with a bare r-m; R_1 0.7–1.0 times as long as R; c/w ratio 0.70–0.74; r-m 1.0–1.4 as long as bM. Haltere long and sooty brown; head of haltere longer than shaft. **Legs** pale brown, paler than thorax, mid and hind coxae slightly darker than front coxae. Tibial organ surrounded by a circular border and slightly wider than half width of tibial apex; tibial organ consists of an irregular row of bristles. Front tibia without robust bristles among vestiture. Mid tibia with one to three robust bristles among vestiture. Posteriodorsal row of bristles inconspicuous. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** brown, slightly paler than thorax, with long, dark setae. **Hypopygium** (Fig. 42)**.** Gonocoxites wider than long, inner side of gonocoxites with medium sized setae, outer side with long setae; ventral, inner side of gonocoxites basally separated. Gonostylus elongated and curved, 2.8–3.2 times longer than wide, apex not well differentiated, inner side strongly concave, apical cavity with some microtrichia, remaining inner side with several microtrichia, one spine (exceptionally one paratype [SDEI-Dipt-0000655] with two gonostylar spines on the right gonostylus) and one whip-lash hair present, inner base of gonostylus with a conspicuous angle (*ba* in Fig. 42). Tegmen of the typical ground plan of the *Psl. jejuna* complex, onion-shaped, apical contraction broad; dorsal folds present; parameral apodemes basally strongly sclerotized, median connected. Area of teeth absent. Ejaculatory apodeme dark, broad, and long; base of ejaculatory apodeme pale, long, in some specimens y-shaped. Posterior portion of gonocoxal apodeme medium sized and brown, medial joined. Anterior portion of gonocoxal apodeme long and dark brown.

Body size: 2.5–3.2 mm.

Female. Unknown.

Genetic distances. All five available COI sequences are identical and do not show any pairwise distance. The nearest neighbour is *Psl. tuakana*, diverging by a minimum of 5.93%. The p-distance between both available 28S sequences is 0.06%. The nearest neighbour is *Psl. tuakana*, diverging by a minimum of 0.11%.

Etymology. The epithet *dagae* is an anagram of the German abbreviation of the *German Society of general and applied Entomology* (*DGaaE*).

Distribution. New Zealand.

Discussion. *Pseudolycoriella dagae* is one of three species of this complex which have a yellowish scape and pedicel strongly contrasting with a dark flagellum. Another of those—*Psl. porotaka*—has a much shorter length/width ratio of the fourth flagellomere (2.3–2.4 *vs*. 2.8–3.3 in *Psl. dagae*) and a much narrower ejaculatory apodeme. The remaining species—*Psl. raki*—can be distinguished by a more slender gonostylus shape, which manifests itself in a larger length to width ratio of the gonostylus (2.8–3.2 *vs*. 2.4–2.6 in *Psl. dagae*). In practice, however, discrimination between these two species can be as challenging as in *Psl. jejuna* and *Psl. tuakana*. In particular, preparations in which the gonostylus has not been mounted in a perfect ventral view can lead to misidentifications. A helpful additional character is a bulging basal angle at the inner base of gonostylus, which is well developed in *Psl. dagae* (Fig. 42) and absent or less conspicuous in *Psl. raki*. With respect to the wing, there are two other slight differences:

Psl. *dagae* has macrotricha on both the dorsal and ventral side for more than the apical half of vein R_5, while in *Psl*. *raki* this double-sided setosity is limited to a maximum of the apical two-fifths of R_5. The c/w ratio of *Psl*. *dagae* is equal to or less than 0.74, while in *Psl*. *raki* it is equal to or greater than 0.74. Another slight difference, which should be treated with caution: the antepronotum of *Psl*. *dagae* bears 2–3 setae while that of *Psl*. *raki* bears 3–8 setae. One paratype of *Psl*. *dagae* has two gonostylar spines on the right gonostylus, which is regarded as an atavism (see *Psl*. *jejuna* complex discussion).

Pseudolycoriella raki **sp. n.**

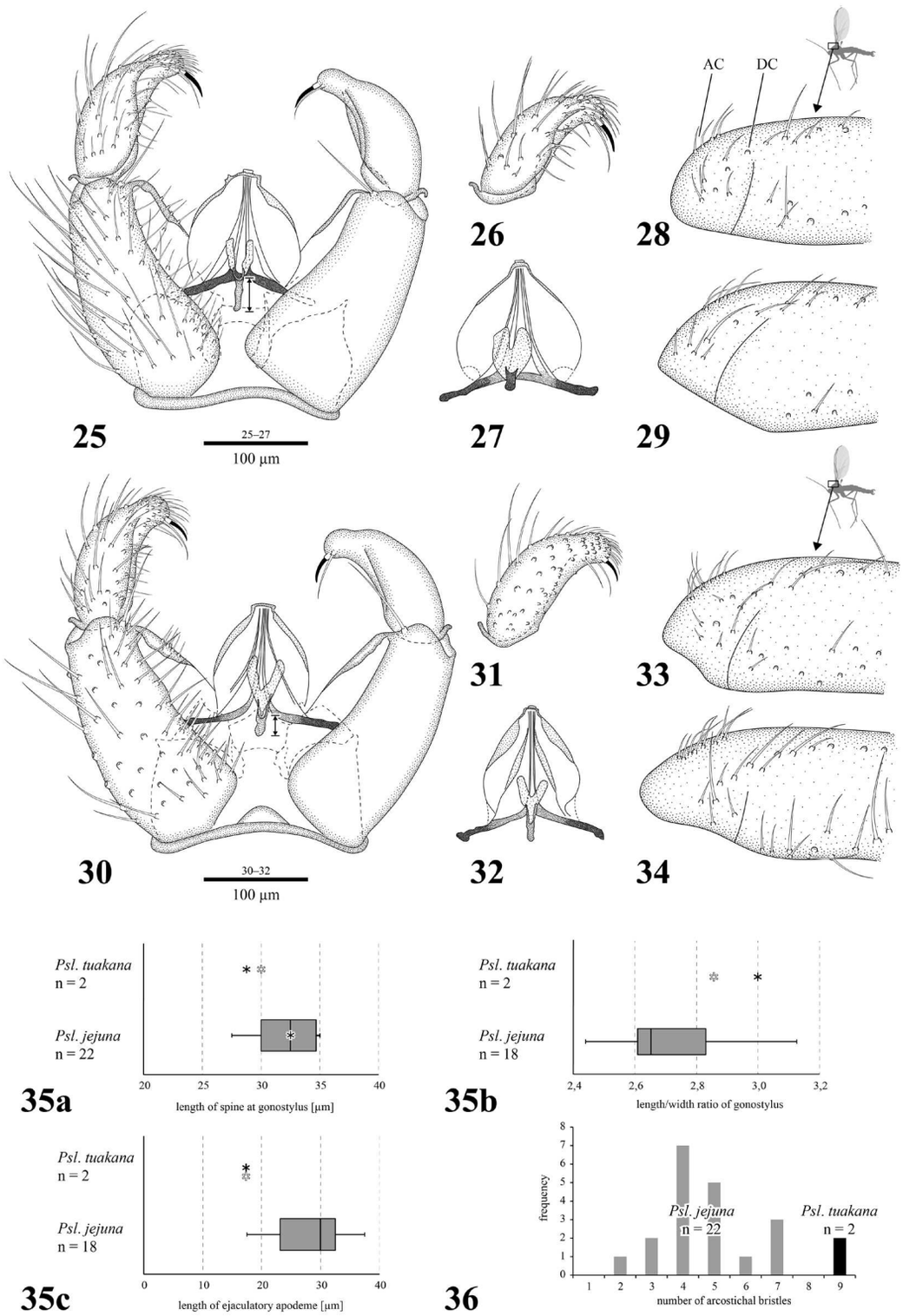
(Fig. 41)

urn:lsid:zoobank.org:act:NomenclaturalActs/01500E3C-735A-400F-968D-3B3E1F4A14C9

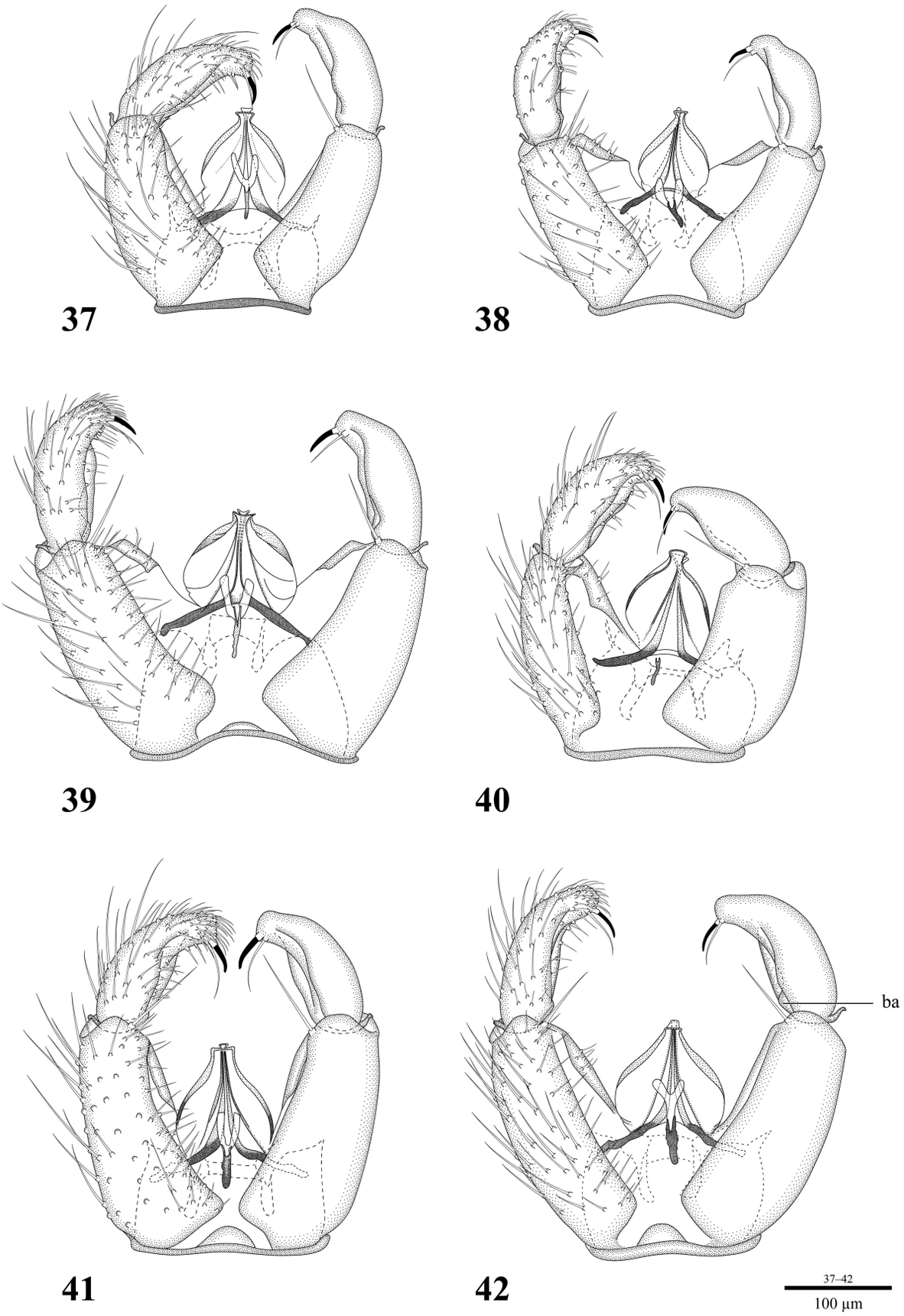
Literature. *Pseudolycoriella jejuna* (Edwards, 1927): Mohrig & Jaschhof (1999): 37 [misidentification].—Köhler & Mohrig (2016): 108 [misidentification].

Material studied. *Holotype male*. New Zealand: North Island, Far North, Waipoua Forest, alongside Highway 12, altitude 300 m, mixed mature Kauri/podocarp forest, Malaise trap, 24.07–17.08.2001, leg. M. & C. Jaschhof (NZAC, SDEI-Dipt-0000834). *Paratypes*. 3♂♂ same locality and same date as holotype (1x NZAC; 2x SDEI). 1♂ North Island, Far North, Puketi Forest, Waipapa River Valley, mixed secondary wood of Kauri and *Podocarpus* with tree fern, sweep net, 01–02.01.1993, leg. M Jaschhof (PWMP [previously misidentified, published as *Psl*. *jejuna* in Mohrig & Jaschhof 1999]). 1♂ North Island, Thames-Coromandel, Coromandel Range, 5 km east of Coromandel, dense *Podocarpus* secondary wood with tree ferns, sweep net, 28.12.1992, leg. M. Jaschhof (PWMP [previously misidentified, published as *Psl*. *jejuna* in Mohrig & Jaschhof (1999)]). 1♂ North Island, Whakatane-Distrikt, White Pine Bush 3 km southwest of Whakatane, *Podocarpus* wood, sweep net, 26.12.1992, leg. M. Jaschhof (PWMP [previously misidentified, published as *Psl*. *jejuna* in Köhler & Mohrig 2016]).

Description. *Male*. **Head.** Head capsule brown. Eye bridge three to four facets wide. Scape and pedicel bright yellow, strongly contrasting with the brown flagellum; fourth flagellomere 2.6–3.4 times longer than wide; necks of flagellomeres well differentiated, paler than body of flagellomeres, flagellomere necks at antenna apex show distal dark rings; surface of flagellomeres rough with deep pits, sensilla of two different lengths, small ones and longer, curved sensilla; setae on the flagellomere longer than the flagellomere width, slightly curved, arising from small elevations; apical flagellomeres very rough with prominent elevations. Maxillary palp very long and three-segmented, first or third palpomere longest, second one shortest; first palpomere with long sensilla and four to five long bristles, one bristle longer and more robust, located on the outer side. Prefrons and clypeus bulging. **Thorax** pale brown, slightly paler than head, with some indistinct lateral brightening. Posterior pronotum bare. Anterior pronotum with three to eight setae. Episternum 1 with two to eight setae. Mesonotum with four to five robust lateral bristles. Scutellum with three to four robust bristles and several minor setae. Katepisternum as long as high. **Wing.** Length 2.2–2.9 mm; width/length ratio 0.38–0.41. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, except faint stem of M, apical fifth to two-fifths of R_5 with macrotrichia on ventral and dorsal side; bM and r-m bare; R_1 0.8–1.0 times as long as R; c/w ratio 0.74–0.79; r-m 0.8–1.2 as long as bM. Haltere brownish; head of haltere slightly longer than shaft. **Legs** yellowish pale brown, paler than thorax. Tibial organ surrounded by a circular border and wider than half of the width of the tibial apex; tibial organ consists of an irregular row of bristles. Fore tibia with one robust bristle among the vestiture, or without. Mid tibia with one to three robust bristles among the vestiture. Posteriodorsal row of seven to eleven bristles occupies half to two-thirds of the apex of the tibia. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** concolourous with thorax, with long, dark setae. **Hypopygium** (Fig. 41)**.** Gonocoxites wider than long, inner side of gonocoxites with small setae, outer side with long setae; ventral, inner side of gonocoxites basally separated. Gonostylus curved and slender, 2.4–2.6 times longer than wide, apex not clearly separated, apical end broad, blunt, on ventral side with a huge apical cavity scattered with few microtrichia, one spine and one whip-lash hair present, inner base of gonostylus without or only with a minor angle. Tegmen of the typical ground plan of the *Psl*. *jejuna* complex, onion-shaped but more elongated than in *Psl*. *jejuna*; dorsal folds present; parameral apodeme basally strongly sclerotized, distal branches forming a triangle. Area of teeth absent. Ejaculatory apodeme dark, broad and long; base of ejaculatory apodeme delicate, long, u-shaped. Posterior portion of gonocoxal apodeme medium sized and brown, joined medially. Anterior portion of gonocoxal apodeme long and dark brown, widely separated.



FIGURES 25–36. *Pseudolycoriella jejuna* complex, *Pseudolycoriella jejuna* (Edwards) and *Pseudolycoriella tuakana* **sp. n.** **25**. *Psl. jejuna* (SDEI-Dipt-0000583), hypopygium. **26**. *Psl. jejuna* (SDEI-Dipt-0000603), gonostylus. **27**. *Psl. jejuna* (SDEI-Dipt-0000583), tegmen with aberrant ejaculatory apodeme. **28.** *Psl. jejuna* (SDEI-Dipt-0000603), mesonotum. **29.** *Psl. jejuna* holotype, mesonotum. **30.** *Psl. tuakana* holotype, hypopygium. **31.** *Psl. tuakana* paratype, gonostylus. **32.** *Psl. tuakana* paratype, tegmen. **33.** *Psl. tuakana* holotype, mesonotum (lateral view). **34.** *Psl. tuakana* paratype, mesonotum (lateral view). **35a.** Comparison of the length of gonostylar spine of both species; values for holotypes are indicated by black asterisks. **35b.** Comparison of the length-width ratio of gonostylus of both species; values for holotypes are indicated by black asterisks. **35c.** Comparison of the length of ejaculatory apodeme of both species; values for holotypes are indicated by black asterisks. **36.** Histogram of arcostichal bristles of both species. Abbreviations: AC = arcostichal bristles; DC = dorsocentral bristles.



FIGURES 37–42. *Pseudolycoriella jejuna* complex, hypopygia. **37.** *Pseudolycoriella sudhausi* **sp. n. 38.** *Pseudolycoriella whena* **sp. n. 39.** *Pseudolycoriella porotaka* **sp. n. 40.** *Pseudolycoriella nahenahe* **sp. n. 41.** *Pseudolycoriella raki* **sp. n. 42.** *Pseudolycoriella dagae* **sp. n.** Abbreviation: ba = basal angle.

Body size: 2.3–2.9 mm.

Female. Unknown.

Genetic distances. Only one specimen was successfully sequenced. For the COI sequence, the nearest neighbour is *Psl*. *tuakana*, diverging by a minimum of 8.42%. For the 28S sequence the nearest neighbour is also *Psl*. *tuakana*, diverging by a minimum of 0.44%.

Etymology. *Raki* is the Māori word for northern.

Distribution. New Zealand.

Discussion. See discussion paragraph for *Psl*. *dagae*.

***Pseudolycoriella hauta* sp. n.**

(Figs 9 & 44)

urn:lsid:zoobank.org:act:0B34C8C6-9E06-40BA-8731-229742E97203

Material studied. *Holotype male*. New Zealand: South Island, Clutha, Catlins, Purakaunui Scenic Reserve, mixed podocarp/broadleaf/*Nothofagus* forest, Malaise trap, 27.01–05.03.2002, leg. M. & C. Jaschhof (NZAC, SDEI-Dipt-0001134). *Paratypes*. 3♂♂ same locality and same date as holotype (1x NZAC, SDEI-Dipt-0001137; 2x SDEI, SDEI-Dipt-0000506 & SDEI-Dipt-0001142).

Description. *Male*. **Head.** Head capsule dark brown, laterally with several longer setae among the normal setosity. Eye bridge three to four facets wide. Scape and pedicel slightly paler brown than the flagellum; fourth flagellomere 2.5–2.8 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough with deep pits, sensilla of two different lengths, small ones and longer, curved sensilla; setae on the flagellomere longer than flagellomere width, curved. Maxillary palp long and three-segmented, first palpomere is the longest, second one shortest; first palpomere with long sensilla and two to six long bristles, one bristle longer and more robust, located on the outer side. Prefrons and clypeus bulging. **Thorax** brown, mesonotum slightly darker. Posterior pronotum bare. Anterior pronotum with five to seven long and middle-sized setae. Episternum 1 with seven to nine long and medium sized setae. Mesonotum with six to seven robust lateral bristles. Scutellum with five to six robust bristles and several minor setae. Long dorsocentral bristles forming a complete row on the mesonotum. Katepisternum as long as high. **Wing** (Fig. 9)**.** Length 2.6–2.8 mm; width/length ratio 0.33–0.39. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, apical 33–50% of R_5 with macrotrichia on ventral and dorsal side; bM bare, r-m with 1–3 macrotrichia (exceptionally r-m on one wing of one paratype bare); R_1 0.6–0.7 times as long as R; c/w ratio 0.70–0.75; r-m 0.7–0.9 as long as bM. Haltere brownish; head of haltere slightly longer than shaft. **Legs** brown, coxae as brown as thorax. Tibial organ surrounded by a circular border and as wide as half width of tibial apex; tibial organ consists of more than ten bristles arranged in an irregular row. Front tibia without robust bristle among vestiture. Mid tibia with one or two slightly robust bristles among vestiture. Posteriodorsal row of five to eight bristles mainly on middle of hind tibia. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** brown, paler than thorax, with long, dark setae. **Hypopygium** (Fig. 44)**.** Gonocoxites wider than long, inner side of gonocoxites with short setae, outer side with long setae; ventral, inner side of gonocoxites basally separated. Gonostylus slender, 2.7–3.3 times longer than wide, apical third curved inward, not distinctly delimited; inner side concave; apical cavity long and remaining inner side without microtrichia, ventral margin distinct; one spine present, located at the apex; long whip-lash hair present. Tegmen of the typical ground plan of the *Psl*. *jejuna* complex, with an acuminate basic shape; dorsal folds present; parameral apodemes basally strongly sclerotized, medially connected. Area of teeth absent. Ejaculatory apodeme short and dark, base of ejaculatory apodeme pale brown. Posterior portion of gonocoxal apodeme medium sized and brown, joined medially. Anterior portion of gonocoxal apodeme of medium-length and dark brown.

Body size: 2.7–3.2 mm.

Female. Unknown.

Genetic distances. All four available COI sequences are identical and do not show any pairwise distance. The nearest neighbour is *Psl*. *tewaipounamu*, diverging by a minimum of 8.68%. The nearest neighbour of the only available 28S sequence is *Psl*. *tewaipounamu*, diverging by a minimum of 0.17%.

Etymology. *Hauta* is the Māori word for south. The name for this new species reflects the southern distribution of this species.

Distribution. New Zealand.

Discussion. Among the species of the *Psl. jejuna* complex examined during this study, *Psl. hauta* has the most developed setosity on the mesonotum, the anterior pronotum, the episternum 1, and the scutellum. Furthermore, the shape of the gonostylus is unique and allows a clear delimitation from the other species of the complex. The spine on the gonostylus lies at the inner angle of the gonostylus apex and is more apically located than in all the other species. Another distinguishing feature is the prominent ventral margin. Due to the more concave inner side of the gonostylus the ventral margin is more obvious than in the related species.

***Pseudolycoriella jejunella* sp. n.**

(Figs 2, 6, 8 & 46)

urn:lsid:zoobank.org:act:06EB5442-74EE-4676-A0C1-2CC6F04C7EF9

Material studied. *Holotype male*. New Zealand: South Island, Southland, Fiordland, Fiordland NP, Hollyford River Valley, Moraine Creek Track, mixed podocarp/*Nothofagus* forest, Malaise trap, 05–24.01.2002, M. & C. Jaschhof (NZAC, SDEI-Dipt-0000880). *Paratypes*. 1♂ same locality and same date as holotype (SDEI, SDEI-Dipt-0000935). 1♂ South Island, Southland, Otago Lakes, Fiordland NP, Hollyford River Valley S Divide Creek, mixed *Nothofagus*/broadleaf forest, Malaise trap, 06–24.01.2002, M. & C. Jaschhof (SDEI).

Description. *Male*. **Head.** Head capsule brown, concolourous with thorax. Eye bridge one to three facets wide. Scape and pedicel not paler brown than the flagellum; fourth flagellomere (Fig. 2) 1.9–2.3 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough with deep pits, sensilla of two different lengths, small ones and longer, curved sensilla; setae on the flagellomere as long as flagellomere width, slightly curved. Maxillary palp (Fig. 6) short and three-segmented, first palpomere is the longest, third one shortest, first palpomere with long sensilla and three to four long bristles, one bristle longer and more robust, located on the outer side. Prefrons and clypeus bulging. **Thorax** brown, mesonotum slightly darker. Posterior pronotum bare. Anterior pronotum with four setae. Episternum 1 with five setae. Mesonotum with five robust lateral bristles. Scutellum with two robust bristles and several minor setae. Katepisternum as long as high. **Wing.** Length 2.0–2.1 mm; width/length ratio 0.38–0.41. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, stem of M weak; apical 33–40% of R_5 with macrotrichia on ventral and dorsal side; r-m and bM without macrotrichia; R_1 approximately 0.6–0.7 times as long as R; c/w ratio 0.7; r-m 1.2–1.8 as long as bM. Haltere brownish; head of haltere as long as shaft. **Legs** brownish, coxae as brown as thorax. Tibial organ surrounded by a circular border and as wide as half width of tibial apex; tibial organ (Fig. 8) consists of approximately eight bristles arranged in an irregular row. Front tibia without robust bristles among the vestiture. Mid tibia with one or two slightly robust bristles. Posteriodorsal row of bristles on hind tibia present but inconspicuous. All tibial spurs equal in length. Claws with five robust teeth. **Abdomen** brown, concolourous with thorax; with long, dark setae. **Hypopygium** (Fig. 46)**.** Gonocoxites wider than long, inner side of gonocoxites with short setae, outer side with long setae; ventral, inner side of gonocoxites basally separated. Gonostylus slender, 3.0–3.4 times longer than wide; apical fourth kinked inwards, apical cavity present, but inconspicuous, scattered with some microtrichia; one spine present, located subapically, medium long whip-lash hair present. Tegmen of the typical ground plan of the *Psl. jejuna* complex, with an acuminate basic shape; the dorsal folds strikingly developed; parameral apodemes basally strongly sclerotized. Area of teeth absent. Ejaculatory apodeme short and dark, base of ejaculatory apodeme not visible. Posterior portion of gonocoxal apodeme medium sized and brown, joined medially. Anterior portion of gonocoxal apodeme short and dark brown.

Body size: 1.9–2.5 mm.

Female. Unknown.

Genetic distances. Both available COI sequences are identical and do not show any distance. The nearest neighbour is *Psl. maddisoni*, diverging by a minimum of 10.79%. The nearest neighbour of the single available 28S sequence is *Psl. whakahara*, diverging by a minimum of 0.24%.

Etymology. The epithet *jejunella* is the diminutive of *jejuna*, and refers to the smallness of the new species compared with *Psl. jejuna*.

Distribution. New Zealand.

Discussion. By its small body and wing length *Psl. jejunella* can be easily separated from most other species of this complex. Only specimens of *Psl. whena* and small specimens of *Psl. sudhausi* are similarly small. In addition, the structure of the gonostylus is unique in this complex. With a gonostylar index of 3.0–3.4, the gonostylus of *Psl.*

jejunella is more slender than in most other species. Only some individuals of *Psl*. *dagae* and *Psl*. *hauta* lie in this range. Furthermore, the gonostylus appears more tubular and does not show the typical cavity on the inner basal side, and the spine on the gonostylus is more subapically located than in other species.

Pseudolycoriella maddisoni **sp. n.**

(Fig. 47)
urn:lsid:zoobank.org:act:FB0BF871-1F03-4675-AF10-AFC8DCB8C269

Material studied. *Holotype male*. New Zealand: North Island, Western Bay of Plenty, Katikati, 449 Lund Road, Malaise trap, 25.07–08.08.2016, leg. P.A. Maddison (NZAC, SDEI-Dipt-0000627). *Paratypes*. 2♂♂ North Island, Western Bay of Plenty, Katikati, Te Mania catchment, Malaise trap, 19.09–27.10.2016, leg. P.A. Maddison (SDEI, SDEI-Dipt-0000664 & SDEI-Dipt-0001369).

Description. *Male*. **Head.** Head capsule brown, slightly darker than thorax. Eye bridge two to three facets wide. Scape and pedicel pale brown, slightly paler than the flagellum; fourth flagellomere 2.7 times longer than wide (flagella are missing in both paratypes); necks of flagellomeres well differentiated, bright; surface of flagellomeres rough with deep pits, sensilla of two different lengths, small ones and longer, curved sensilla; setae on the flagellomere as long as flagellomere width, slightly curved. Maxillary palp long and three-segmented, first palpomere is the longest, second is shortest, first palpomere with long sensilla and four to six long bristles, one bristle longer and more robust, located on the outer side. Prefrons and clypeus bulging. **Thorax** dark brown. Posterior pronotum bare. Anterior pronotum with four to six setae. Episternum 1 with four to seven setae. Mesonotum with four to five robust lateral bristles. Scutellum with two to three robust bristles and several minor setae. Katepisternum as long as high. **Wing.** Length 2.5–2.7 mm; width/length ratio 0.38–0.42. Membrane transparent, slightly shaded and without macrotrichia, anal area present; all posterior veins distinct, stem of M weak; apical 40–50% of R_5 with macrotrichia on both ventral and dorsal sides; r-m and bM without macrotrichia; R_1 0.7 times as long as R; c/w ratio 0.74–0.80; r-m 0.7–0.8 as long as bM. Haltere brownish; head of haltere as long as shaft. **Legs** brownish, slightly paler than thorax. Tibial organ surrounded by a circular border and as wide as half width of tibial apex; tibial organ arranged in an irregular row. Front tibia without or with one robust bristle among vestiture. Mid tibia with one or two slightly robust bristles. Posteriodorsal row of bristles extending two-thirds of apical tibia length. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** pale brown, paler than thorax; with long, dark setae. **Hypopygium** (Fig. 47)**.** Gonocoxites wider than long, inner side of gonocoxites with several medium sized setae, outer side with long setae; ventral, inner side of gonocoxites basally separated. Gonostylus swollen, 2.4–2.5 times longer than wide; apex well differentiated, bent inwards, apical cavity conspicuous without microtrichia; one spine on the gonostylus, located subapically, and one long whip-lash hair. Tegmen of the typical ground plan of the *Psl*. *jejuna* complex, onion-shaped and roundish; the dorsal folds strikingly developed; parameral apodemes basally strongly sclerotized, apically broad. Area of teeth absent. Ejaculatory apodeme short and dark; base of ejaculatory apodeme pale yellow, v-shaped. Posterior portion of gonocoxal apodeme of medium size and brown, medially joined. Anterior portion of gonocoxal apodeme medium long and dark brown.

Body size: 2.6–2.9 mm.

Female. Unknown.

Genetic distances. All three available COI sequences are identical and do not show any pairwise distance. The nearest neighbour is *Psl*. *tewaipounamu*, diverging by a minimum of 5.84%. Both available 28S sequences are identical. The nearest neighbour is *Psl*. *tewaipounamu*, diverging by a minimum of 0.17%.

Etymology. This new species is named after Peter A. Maddison to acknowledge his valuable collection work.

Distribution. New Zealand.

Discussion. Among all species of the *Psl*. *jejuna* complex *Psl*. *maddisoni* and *Psl*. *whakahara* have the broadest gonostyli. However due to the hunchbacked shape of the gonostylus *Psl*. *maddisoni* is easy to identify.

Pseudolycoriella tewaipounamu **sp. n.**

(Figs 20–24, 43)
urn:lsid:zoobank.org:act:NomenclaturalActs/CC9D30E2-C277-42B6-9BB0-257662D26B46

Material studied. *Holotype male*. New Zealand: South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, Deer Flat, *Nothofagus* forest, Malaise trap, 01–20.12.2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC, SDEI-Dipt-0000956). *Paratypes*: 6♂♂, same date and same locality as holotype (2x NZAC, SDEI-Dipt-0000952; 4x SDEI, SDEI-Dipt-0000964). 4♂♂ same locality as holotype, Malaise trap, 04–24.01.2002, leg. M. & C. Jaschhof (2x NZAC; 2x SDEI). 4♂♂ South Island, Buller, 5 km W Maruia Springs, mixed *Nothofagus* forest, Malaise trap, 26.11–25.12.2001, leg. M. & C. Jaschhof (2x NZAC, SDEI-Dipt-0000988; 2x SDEI, SDEI-Dipt-0000942 & SDEI-Dipt-0000973). 35♂♂, South Island, Buller, Ahaura, Granville State Forest, altitude 170–250 m, *Nothofagus truncata* forest, Malaise trap, 01.12.1994, leg. D. Hutcheson (17x NZAC, 18x SDEI). 7♂♂ South Island, Buller, Maruia Forest, Shenandoah Saddle, altitude 500 m, *Nothofagus* forest, Malaise trap, 09.10–03.11.2001, leg. M. & C. Jaschhof (3x NZAC, SDEI-Dipt-0000788, SDEI-Dipt-0000960 & SDEI-Dipt-0001179; 4x SDEI, SDEI-Dipt-0000752, SDEI-Dipt-0000787, SDEI-Dipt-0001180 & SDEI-Dipt-0001181). 3♂♂ same locality as previous, Malaise trap, 03–25.11.2001, leg. M. & C. Jaschhof (1x NZAC, SDEI-Dipt-0001045; 2x SDEI, SDEI-Dipt-0001038 & SDEI-Dipt-0001044). 1♂ same locality as previous, sweep net, 25.12.2001, leg. M.Jaschhof (SDEI). 2♂♂ South Island, Buller, Paparoa NP, 5 km E Punakaiki, Inland Pack Track, mixed podocarp/*Nothofagus* forest, Malaise trap, 30.09–05.11.2001, leg. M. & C. Jaschhof (NZAC; SDEI). 4♂♂ South Island, Buller, Rahu Scenic Reserve, 12 km NW Springs Junction, altitude 550 m, mixed *Nothofagus*/podocarp forest, Malaise trap, 27.11–25.12.2001, leg. M. & C. Jaschhof (2x NZAC, SDEI-Dipt-0001481 & SDEI-Dipt-0001490; 2x SDEI, SDEI-Dipt-0001492 & SDEI-Dipt-0001493). 1♂ South Island, Westland, Waiatoto, Kahikatea swamp forest, Malaise trap, 16.10–20.11.2001, M. & C. Jaschhof (SDEI). 1♂ South Island, Westland, Westland NP, SE Gillespies Beach, mixed podocarp forest, Malaise trap, 14.10–21.11.2001, leg. M. & C. Jaschhof (SDEI, SDEI-Dipt-0001028). 3♂♂ South Island, Queenstown Lakes, Otago Lakes, Mt Aspiring NP, Makarora River Valley near Cameron Creek Track, mixed *Nothofagus*/broadleaf forest, sweep net, 18–19.12.2002, leg. M. Jaschhof (1x NZAC, SDEI-Dipt-0000513; 2x SDEI, SDEI-Dipt-0001506). 2♂♂ South Island, Southland, Fiordland, Fiordland NP, Lake Gunn, *Nothofagus* forest, sweep net, 08.01.2002, leg. M. Jaschhof (NZAC; SDEI). 1♂ same locality as previous, Malaise trap, 01–21.12.2002, leg. M. & C. Jaschhof & U. Kallweit (SDEI). 2♂♂ South Island, Southland, Fiordland, Fiordland NP, 3 km E Milford Sound, mixed podocarp/broadleaf forest, Malaise trap, 01–21.12.2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC; SDEI). 1♂ same locality as previous, sweep net, 21.12.2002, leg. M. Jaschhof (SDEI). 8♂♂ South Island, Southland, Fiordland, Fiordland NP, Hollyford River Valley, Moraine Creek Track, mixed podocarp/*Nothofagus* forest, Malaise trap, 05–24.01.2002, leg. M. & C. Jaschhof (4x NZAC, SDEI-Dipt-0000910, SDEI-Dipt-0000927, SDEI-Dipt-0000928 & SDEI-Dipt-0000934; 4x SDEI, SDEI-Dipt-0000879, SDEI-Dipt-0000881, SDEI-Dipt-0000907 & SDEI-Dipt-0000924). 7♂♂ South Island, Southland, Otago Lakes, Fiordland NP, Hollyford River Valley S Divide Creek, mixed *Nothofagus*/broadleaf forest, Malaise trap, 06–24.01.2002, leg. M. & C. Jaschhof (3x NZAC; 4x SDEI, SDEI-Dipt-0000994). 1♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, opposite Earl Mountain Tracks, *Nothofagus* forest, Malaise trap, 05–24.01.2002, leg. M. & C. Jaschhof (SDEI, SDEI-Dipt-0000871). 3♂♂ same locality as previous, Malaise trap, 01–21.12.2002, M. & C. Jaschhof & U. Kallweit (1x NZAC; 2x SDEI). 7♂♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, 2 km N entrance Earl Mountain Tracks, *Nothofagus* forest, Malaise trap, 01–21.12.2002, leg. M. & C. Jaschhof & U. Kallweit (3x NZAC, SDEI-Dipt-0001169 & SDEI-Dipt-0001173; 4x SDEI, SDEI-Dipt-0001165, SDEI-Dipt-0001172 & SDEI-Dipt-0001174). 2♂♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, 2 km N entrance Gladehouse Track, *Nothofagus* forest, Malaise trap 01–20.12.2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC, SDEI-Dipt-0001206; SDEI, SDEI-Dipt-0001143). 7♂♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, opposite Gladehouse Track, *Nothofagus* forest, Malaise trap, 01–21.12.2002, leg. M. & C. Jaschhof & U. Kallweit (4x NZAC, SDEI-Dipt-0001006, SDEI-Dipt-0001014 & SDEI-Dipt-0001016; 3x SDEI, SDEI-Dipt-0001012, SDEI-Dipt-0001017 & SDEI-Dipt-0001025). 5♂♂ same locality as previous, sweep net, 03–04.12.2002, leg. M. Jaschhof (2x NZAC; 3x SDEI). 1♂ South Island, Clutha, Catlins, Purakaunui Scenic Reserve, mixed podocarp/broadleaf/*Nothofagus* forest, sweep net, 03.01.2002, leg. M. Jaschhof (SDEI, SDEI-Dipt-0001484). 3♂♂ same locality as previous, Malaise trap, 27.01–05.03.2002, leg. M. & C. Jaschhof (1x NZAC, SDEI-Dipt-0001139; 2x SDEI, SDEI-Dipt-0001132 & SDEI-Dipt-0001156). 4♂♂ South Island, Clutha, Catlins Coastal Rain Forest Park, Catlins River Valley, silver beech forest, Malaise trap, 27.01–05.03.2002, leg. M. & C. Jaschhof (2x NZAC, SDEI-Dipt-0000614 & SDEI-Dipt-0000801; 2x SDEI, SDEI-Dipt-0000804 & SDEI-Dipt-0000814). ***Additional material:*** 1♂, SEM-object, same date and same locality as holotype (SDEI, SDEI-Dipt-0000968).

Description. *Male*. **Head.** Head capsule brown. Eye bridge two to three facets wide. Scape and pedicel mostly

slightly paler brown than the flagellum, or as brown as flagellum; fourth flagellomere 2.5–3.3 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough with deep pits, sensilla of two different lengths, longer sensilla robust and curved; setae on the flagellomere slightly shorter than flagellomere width, slightly curved. Maxillary palp long and pale containing three palpomeres, first one longest, third shortest, first palpomere with four to five long bristles; sensilla on first palpomere long. Prefrons and clypeus bulging. **Thorax**. lateral side yellowish brown, mesonotum and metanotum brownish. Posterior pronotum bare. Anterior pronotum with two to four setae. Episternum 1 with four to seven setae. Mesonotum with five to seven robust lateral bristles. Scutellum with three to four robust bristles and several smaller setae. Katepisternum as long as high, distal part slightly darker than proximal part. **Wing.** Length 2.3–2.7 mm; width/length ratio 0.35–0.41. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, stem of M weak; apical half to apical third of R_5 with macrotrichia on both sides; exceptionally in one specimen (SDEI-Dipt-0001156) three macrotrichia on M_1 on left wing and one macrotricha on the right M_1; r-m and bM without macrotrichia (exceptionally one macrotrichium on r-m on one wing of one specimen [SDEI-Dipt-0001490]); R_1 approximately 0.9–1.3 times as long as R; c/w ratio 0.6–0.8; r-m 1.1–1.3 as long as bM. Haltere brownish; head of haltere as long as shaft. **Legs** pale brown, much brighter than thorax. Tibial organ surrounded by a circular border and as wide as half of the width of the tibial apex; tibial organ consists of approximately ten bristles arranged in an irregular row. Front tibia without or with one robust bristle among the vestiture. Mid tibia with one or two slightly robust bristles. Hind tibia with a posteriodorsal row of robust bristles, comprising 50–66% of apical part of tibia, several longer additional bristles on the ventral side. All tibial spurs equal in length. Claws with five robust teeth. **Abdomen** pale brown, slightly paler than thorax; with long, dark setae. **Hypopygium** (Figs 20–24 & 43)**.** Gonocoxites wider than long, inner side of gonocoxites with short setae, outer side with long setae; ventral, inner side of gonocoxites widely separated basally. Gonostylus 2.2–2.7 times longer than wide; basal part broad, dorsal margin slightly stretched; apical part large, curved inwards with an apical cavity without microtrichia (Fig. 20); subapically one spine and one long whip-lash hair. Tegmen (Fig. 23) with typical structure of the *Psl. jejuna* complex, parameral apodemes strongly sclerotized up to the apex of the tegmen. Area of teeth absent. Ejaculatory apodeme short and dark, with a distinct base; base pale bown and slender. Posterior portion of gonocoxal apodeme medium sized, brown, and medially connected. Anterior portion of gonocoxal apodeme short and dark brown.

Body size: 2.7–3.5 mm.

Female. Unknown.

Genetic distances. The maximum p-distance between all 48 available COI sequences is 2.28%. The nearest neighbour is *Psl. whakahara*, diverging by a minimum of 3.51%. All six available 28S sequences are identical and do not show differences to *Psl. whakahara*.

Etymology. *Te Waipounamu* is the Māori name for the South Island of New Zealand. The epithet of the new species refers to the restricted distribution of this species.

Distribution. New Zealand.

Discussion. *Pseudolycoriella tewaipounamu* is one of the larger species of the *Psl. jejuna* complex. Some specimens reach a body size similar to that of *Psl. whakahara*, but never have a similarly large wing length. Furthermore, *Psl. tewaipounamu* shows a well-developed apical cavity on the gonostylus, without any microtrichia. The tegmen of this species has strongly sclerotized parameral apodemes, which are darkly coloured up to the apex of the tegmen. In nearly all other species only the proximal branches of these parameral apodemes are strongly sclerotized. Only *Psl. whakahara* has dark coloured distal branches like *Psl. tewaipounamu*, but they are always darker in *Psl. tewaipounamu*.

Pseudolycoriella whakahara sp. n.

(Fig. 45)

urn:lsid:zoobank.org:act:NomenclaturalActs/2227602E-6F96-471F-BED4-CAEB57B55893

Material studied. *Holotype male*. New Zealand: South Island, Tasman, Kahurangi NP, Takaka River Valley (Cobb Dam Road), altitude 450–800 m, mixed podocarp/broadleaf forest, Malaise trap, 31.08–07.10.2001, leg. M. & C. Jaschhof (NZAC, SDEI-Dipt-0001439). *Paratypes*. 2♂♂ same locality and same date as holotype (all SDEI, SDEI-Dipt-0001386 and a second specimen in poor condition).

Description. *Male*. **Head.** Head capsule brown. Eye bridge two to three facets wide. Scape and pedicel pale

brown, slightly paler than the flagellum. Fourth flagellomere 3.5 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough, with deep pits, sensilla of two different lengths, setae on the flagellomere robust, longer than flagellomere width, slightly curved. Maxillary palp long and pale, consisting of three palpomeres, first one longest, second shortest, first palpomere with four bristles, one of them more robust; sensilla on first palpomere present. Prefrons and clypeus bulging. **Thorax** pale brown. Posterior pronotum bare. Anterior pronotum with three to four setae. Episternum 1 with five to nine setae. Mesonotum with five to six robust lateral bristles. Scutellum with four to six robust bristles and several smaller setae. Katepisternum as long as high. **Wing.** Length 3.1–3.2 mm; width/length ratio 0.32–0.39. Membrane slightly shaded and without macrotrichia, anal area present; all posterior veins distinct, stem of M weak; apical 50% to 60% of R_5 with macrotrichia on both sides; R_1 0.9–1.0 times as long as R; c/w ratio 0.75–0.77; r-m 0.6–0.7 as long as bM. Haltere brownish; head of haltere shorter than shaft. **Legs** pale brown, brighter than thorax. Tibial organ surrounded by a circular border and as wide as half width of tibial apex; bristles of tibial organ arranged in an irregular row. Front tibia without robust bristle among the vestiture; mid tibia with two robust bristles among the vestiture; hind tibia with an inconspicuous posteriodorsal row of longer setae, two to three robust bristles in the middle of this row. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** slightly paler than thorax; with long, dark setae. **Hypopygium** (Fig. 45)**.** Gonocoxites wider than long, inner side of gonocoxites with medium sized setae, outer side with long setae; ventral, inner side of gonocoxites widely separated basally. Gonostylus 2.2–2.5 times longer than wide; broad, slightly tumid in the middle, apical part not strikingly set off; apical cavity conspicuous, whole inner side without microtrichia; subapically one spine and one long whip-lash hair. Tegmen of the typical ground plan of the *Psl. jejuna* complex; the dorsal folds strikingly developed; parameral apodemes strongly sclerotized basally, moderately sclerotized apically. Area of teeth absent. Ejaculatory apodeme short and strongly sclerotized, base of ejaculatory apodeme delicate, broad, longer than remaining ejaculatory apodeme. Posterior portion of gonocoxal apodeme of medium size and brown, joined medially. Anterior portion of gonocoxal apodeme of medium length and dark brown.

Body size: 3.4–3.8 mm.

Female. Unknown.

Genetic distances. Only one specimen was successfully sequenced. The nearest neighbour is *Psl. tewaipounamu*, diverging by a minimum of 3.51%. For the 28S sequence the nearest neighbours are *Psl. sudhausi* and *Psl. tewaipounamu*.

Etymology. *Whakahara* is the Māori modifier for large or giant. It was chosen as the epithet to reflect the large size of the new species.

Distribution. New Zealand.

Discussion. With a body size of more than 3.4 mm, *Psl. whakahara* is the largest species of the *Psl. jejuna* complex and thus nearly unmistakable. There is a small overlap with larger specimens of *Psl. tewaipounamu*. Nevertheless, such specimens can be separated by comparing wing lengths. The wing of *Psl. tewaipounamu* never reaches in the length of the wing of *Psl. whakahara* (2.3–2.7 mm *vs*. 3.1–3.2 mm, respectively). Some specimens of *Psl. dagae* also has a wing length which reaches the lower span of *Psl. whakahara*, but the former species can be separated by the more slender and concave gonostylus.

***Pseudolycoriella sudhausi* sp. n.**

(Fig. 37

urn:lsid:zoobank.org:act:NomenclaturalActs/427BBF3C-2DDD-44CA-B7BF-76C0B15212BA)

Material studied. *Holotype male*. New Zealand: Stewart Island, Southland, Kaipipi Bay 3 km W Halfmoon Bay, mixed broadleaf/podocarp forest, sweep net, 07.03.2002, leg. M. Jaschhof (NZAC, SDEI-Dipt-0001090). *Paratypes*. 1♂ same locality and same date as holotype (SDEI, SDEI-Dipt-0001093). 2♂♂ South Island, Westland, Waiatoto; Kahikatea swamp forest, Malaise trap, 16.10–20.11.2001, leg. M. & C. Jaschhof (all SDEI). 2♂♂ South Island, Westland, Westland NP, Lake Matheson, mixed podocarp forest, exhauster, 22.10.2001, leg. M. Jaschhof (NZAC; SDEI). 2♂♂ South Island, Westland, Westland NP, SE Gillespies Beach, mixed podocarp forest, exhauster, 19.10.2001, leg. M. Jaschhof (NZAC; SDEI). 3♂♂ South Island, Southland, Fiordland, Fiordland NP, Hollyford River Valley, Moraine Creek Track, mixed podocarp/*Nothofagus* forest, Malaise trap, 05–24.01.2002, leg. M. & C. Jaschhof (2x NZAC, SDEI-Dipt-0000885 & SDEI-Dipt-0000922; 1x SDEI, SDEI-Dipt-0000929). 6♂♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, 2 km N entrance Earl Mountain Tracks,

Nothofagus forest, Malaise trap, 01–21.12.2002, leg. M. & C. Jaschhof & U. Kallweit (3x NZAC, SDEI-Dipt-0001167 & SDEI-Dipt-0001175; 3x SDEI, SDEI-Dipt-0001170 & SDEI-Dipt-0001459). 6♂♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, 2 km N entrance Gladehouse Track, *Nothofagus* forest, Malaise trap, 01–20.12.2002, leg. M. & C. Jaschhof & U. Kallweit (2x NZAC, SDEI-Dipt-0001147 & SDEI-Dipt-0001148; 4x SDEI, SDEI-Dipt-0001146, SDEI-Dipt-0001149 & SDEI-Dipt-0001177). 2♂♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, opposite Gladehouse Track, *Nothofagus* forest, sweep net, 03–04.12.2002, leg. M. Jaschhof (NZAC; SDEI). 4♂♂ same locality as previous, Malaise trap, 01–21.12.2002, leg. M. & C. Jaschhof & U. Kallweit (3x NZAC, SDEI-Dipt-0001009, SDEI-Dipt-0001013 & SDEI-Dipt-0001015; 1x SDEI, SDEI-Dipt-0001011). 1♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, Deer Flat, *Nothofagus* forest, Malaise trap, 04–24.01.2002, leg. M. & J. Jaschhof (SDEI). 1♂ same locality as previous, Malaise trap, 01–20.12.2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC). 1♂ Stewart Island, Southland, Rakiura Track between Kaipipi Bay and Sawdust Bay, mixed podocarp/broadleaf forest, sweep net, 07.03.2002, leg. M. Jaschhof (NZAC). 6♂♂ Stewart Island, Southland, Rakiura Track between Sawdust Bay and North Arm Hut, mixed podocarp/broadleaf forest, sweep net, 08.03.2002, leg. M. Jaschhof (2x NZAC; 4x SDEI, SDEI-Dipt-0001071 & SDEI-Dipt-0001116). 5♂♂ Stewart Island, Southland, Freshwater Landing Hut, mixed podocarp/manuka/broadleaf forest, sweep net, 12.03.2002, leg. M. Jaschhof (3x NZAC; 2x SDEI). *Additional material*. 1♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, opposite Earl Mountain Tracks, *Nothofagus* forest, Malaise trap, 01.12–21.12.2002, leg. M. & C. Jaschhof & U. Kallweit (SDEI; specimen in poor condition).

Description. *Male*. **Head.** Head capsule brown. Eye bridge two to three facets wide. Scape and pedicel slightly paler brown than the flagellum; fourth flagellomere 2.9–3.5 times longer than wide; necks of flagellomeres well differentiated, length of necks increase towards the antennal apex; surface of flagellomeres rough with deep pits, sensilla of two different lengths, small ones and longer, curved sensilla; setae on the flagellomere longer than the flagellomere width, slightly curved. Maxillary palp long and three-segmented, first palpomere is the longest one, second one shortest; first palpomere with long sensilla and two to four long bristles, one bristle longer and more robust, located on the outer side of the first palpomere. Prefrons and clypeus bulging. **Thorax** pale brown, mesonotum slightly darker. Posterior pronotum bare. Anterior pronotum with four to five setae. Episternum 1 with three to seven setae. Mesonotum with four to five robust lateral bristles. Scutellum with three to four robust bristles and several minor setae. Dorsocentral bristles forming a complete row on the mesonotum, anterior ones smaller. Katepisternum as long as high. **Wing.** Length 2.2–2.8 mm; width/length ratio 0.37–0.41. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, except faint stem of M, apical 33–50% of R_5 with macrotrichia on ventral and dorsal side; bM and r-m bare (except one paratype [SDEI-Dipt-0000922] with one macrotricha on r-m on one wing); R_1 0.6–0.9 times as long as R; c/w ratio 0.76–0.81; r-m 0.9–1.3 as long as bM. Haltere brownish; shaft of haltere longer than head. **Legs** pale brown, slightly paler than thorax, occasionally mid and hind coxae concolourous with thorax. Tibial organ surrounded by a circular border and slightly wider than half of the width of the tibial apex; tibial organ consists of an irregular row of bristles. Front tibia without robust bristles among the vestiture (occasionally one bristle). Mid tibia with one slightly robust bristle among vestiture, or bristle missing. Posteriodorsal row of bristles inconspicuous, one to four weak bristles. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** concolourous with thorax, with long, dark setae. **Hypopygium** (Fig. 37)**.** Gonocoxites wider than long, inner side of gonocoxites with medium sized setae, outer side with long setae; ventral, inner side of gonocoxites basally separated. Gonostylus elongate, 2.6–3.1 times longer than wide, apex globular and slightly curved inwards, inner side slightly tumid, apical cavity small without microtrichia, remaining inner side scattered with microtrichia, one spine and one whip-lash hair present. Tegmen of the typical ground plan of the *Psl. jejuna* complex, onion-shaped but elongated; dorsal folds present; parameral apodemes basally strongly sclerotized, medially connected, distal branches close and nearly parallel. Area of teeth absent. Ejaculatory apodeme pale, narrow and long, proximal end slightly thickened and slightly darkened; base of ejaculatory apodeme delicate, narrow and long. Posterior portion of gonocoxal apodeme medium sized and brown, joined medially. Anterior portion of gonocoxal apodeme long and dark brown, nearly reaching the proximal end of the hypopygium.

Body size: 2.3–2.8 mm.

Female. Unknown.

Genetic distances. The maximum p-distance between all 19 available COI sequences is 1.37%. The nearest neighbour is *Psl. whena*, diverging by a minimum of 5.02%. All five available 28S sequences are identical and do not show differences to sequences of *Psl. porotaka* and *Psl. whena*. One of those sequences is also identical to the

sequence of *Psl. whakahara*. The reason for this is that both sequences are fragmentary and only share a middle part of about 480 bp in the alignment.

Etymology. The new species is named after the phylogenetic biologist Prof. Dr Walter Sudhaus.

Distribution. New Zealand.

Discussion. *Pseudolycoriella sudhausi* and the species *Psl. nahenahe*, *Psl. whena*, and *Psl. porotaka* have in common a much narrower ejaculatory apodeme than the remaining species of the *Psl. jejuna* complex. Of these species, *Psl. sudhausi* and *Psl. whena* have a width/length ratio of the fourth flagellomere greater than 2.8. *Pseudolycoriella sudhausi* can be distinguished from *Psl. whena* by the wing length (2.2–2.8 mm *vs*. 1.9–2.1 mm, respectively). The body size also differs, but shows a small range of overlap at 2.3 mm. *Pseudolycoriella whena* has a comparatively smaller tegmen, a shorter gonostylus, and a shorter anterior portion of gonocoxal apodeme than *Psl. sudhausi*.

***Pseudolycoriella whena* sp. n.**

(Fig. 38)

urn:lsid:zoobank.org:act:73E8E6FC-CF31-4DD9-9751-C8653FAFE299

Material studied. *Holotype male*. New Zealand: North Island, Western Bay of Plenty, Katikati, Te Mania catchment, Malaise trap, 19.09–27.10.2016, leg. P.A. Maddison (NZAC, SDEI-Dipt-0001336). *Paratypes*. 6♂♂ South Island, Marlborough, Marlborough Sounds, Okiwi Bay, Moncrieff Scenic Reserve, mixed *Nothofagus*/podocarp forest, sweep net, 24.12.2001, leg. M. Jaschhof (3x NZAC, SDEI-Dipt-0001118; 3x SDEI, SDEI-Dipt-0001100 & SDEI-Dipt-0001127).

Description. *Male*. **Head.** Head capsule brown. Eye bridge two to three, exceptionally four, facets wide, two at margin. Scape and pedicel mostly paler, contrasting with the brown flagellum. Fourth flagellomere 2.8–3.2 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough with deep pits, sensilla of two different lengths, setae on the flagellomere robust, longer than flagellomere width, slightly curved. Maxillary palp of medium length and pale, consisting of three palpomeres, first one longest, second shortest, first palpomere with two to three bristles, one of them longer and more robust, located on the outer side; sensilla on first palpomere long. Prefrons and clypeus bulging. **Thorax** pale brown, mesonotum slightly darker. Posterior pronotum bare. Anterior pronotum with two to four setae. Episternum 1 with four to seven setae. Mesonotum with two to four robust lateral bristles. Scutellum with four robust bristles and several smaller setae. Dorsocentral bristles forming a complete row on the mesonotum, anterior ones smaller. Katepisternum as long as high. **Wings** of the holotype damaged. Length 1.9–2.1 mm; width/length ratio 0.37–0.41. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, except faint stem of M, apical 33–40% of R_5 with macrotrichia on ventral and dorsal side (except two paratypes which each bear only one macrotrichium on the ventral side of R_5); bM and r-m without macrotrichia; R_1 0.6–0.7 times as long as R; c/w ratio 0.72–0.78; r-m 1.0–1.5 as long as bM. Haltere brownish; head of haltere shorter than shaft. **Legs** pale brown, slightly brighter than thorax. Tibial organ surrounded by a circular border and as wide as or even smaller than half the width of the tibial apex; tibial organ consists of an irregular row of bristles. Fore tibia without robust bristles among the vestiture (two paratypes with only one bristle on one side). Mid tibia with none to two slightly robust bristles among the vestiture. Posteriodorsal row of bristles inconspicuous, four to nine weak bristles. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** pale brown, as thorax; with long, dark setae. **Hypopygium** (Fig. 38)**.** Gonocoxites wider than long, inner side of gonocoxites with short setae, outer side with long setae; ventral, inner side of gonocoxites widely separated basally. Gonostylus 2.8–3.1 times longer than wide; elongate and curved, apical part slightly curved inwards, inner side slightly tumid, apical cavity small with scattered macrotrichia; subapically one spine and one long whip-lash hair present. Tegmen of the typical ground plan of the *Psl. jejuna* complex, with an acuminate basic shape; the dorsal folds strikingly developed; parameral apodemes basally strongly sclerotized, medially fused. Area of teeth absent, exceptionally two paratypes (SDEI-Dipt-0001100 & SDEI-Dipt-0001127) with small aggregations of five and twelve tiny teeth, respectively. Ejaculatory apodeme long and of medium thickness, base of ejaculatory apodeme very delicate, short, and u-shaped. Posterior portion of gonocoxal apodeme medium sized and brown, joined medially. Anterior portion of gonocoxal apodeme long and dark brown.

Body size: 1.8–2.3 mm.

Female. Unknown.

Genetic distances. DNA was successfully isolated from only one specimen. The nearest neighbour is *Psl. sudhausi*, diverging by a minimum of 5.02%. The available 28S sequence is identical to those of *Psl. porotaka* and *Psl. sudhausi*.

Etymology. The Māori word for dwarf—*whena*—was chosen as epithet, to highlight the minute body size of the new species.

Distribution. New Zealand.

Discussion. With a body size of up to 2.3 mm, *Psl. whena* together with *Psl. jejunella*, *Psl. nahenahe*, and *Psl. sudhausi* belongs to the smaller species of this species complex. *Pseudolycoriella whena* can be distinguished from *Psl. jejunella* and *Psl. nahenahe* by the longer fourth flagellomere (> 2.8 *vs*. < 2.5). *Pseudolycoriella jejunella* also differs significantly in the shape of the gonostylus. For the distinction of *Psl. whena* and *Psl. sudhausi* see discussion paragraph for *Psl. sudhausi*.

In two paratypes of *Psl. whena* atavistic remains of the area of the teeth are present (see *Psl. jejuna* complex discussion).

***Pseudolycoriella porotaka* sp. n.**

(Fig. 39)

urn:lsid:zoobank.org:act:NomenclaturalActs/EC053068-0F35-494E-9F41-4A28247CA143

Material studied. *Holotype male*. New Zealand: North Island, Bay of Plenty, Katikati, Te Mania catchment, Malaise trap, 19.09–27.10.2016, leg. P.A. Maddison (NZAC, SDEI-Dipt-0001225). *Paratype*. 1♂ North Island, Bay of Plenty, Katikati, 449 Lund Road, Malaise trap, 25.07–08.08.2016, leg. P.A. Maddison (SDEI, SDEI-Dipt-0001250).

Description. *Male*. **Head.** Head capsule brown. Eye bridge three facets wide. Scape and pedicel much paler than the brown flagellomeres; fourth flagellomere 2.3–2.4 times longer than wide; necks of flagellomeres well differentiated, paler than body of flagellomeres; surface of flagellomeres rough with deep pits, sensilla of two different lengths, small ones and longer, curved sensilla; densely arranged setae on the flagellomere shorter than flagellomere width, slightly curved, arising from small elevations. Maxillary palp very long and three-segmented, first palpomere longest, second one shortest; first palpomere with an inconspicuous patch of sensilla and four long bristles, one of which is longer and more robust, located on the outer side of the first palpomere. Prefrons and clypeus bulging. **Thorax** brown, laterally brighter. Posterior pronotum bare. Anterior pronotum with three to five setae. Episternum 1 with seven to nine setae. Mesonotum with five robust lateral bristles. Scutellum with four robust bristles and several minor setae. Katepisternum slightly longer than high. **Wing.** Length 2.7–2.8 mm; width/length ratio 0.36–0.37. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, except faint stem of M, apical half to three-fifths of R_5 with macrotrichia on both ventral and dorsal sides; bM and r-m bare; R_1 0.8–0.9 times as long as R; c/w ratio 0.77–0.78; r-m as long as bM. Haltere brownish; head of haltere slightly longer than shaft. **Legs** yellowish pale brown, paler than thorax; coxae pale brown. Tibial organ surrounded by a circular border and as wide as half of the width of the tibial apex; tibial organ consists of an irregular row of bristles. Front tibia without robust bristles among the vestiture. Mid tibia without (holotype) or with two (paratype) robust bristles among the vestiture. Posteriodorsal row of bristles inconspicuous, extending along two-thirds of tibia apex. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** concolourous with long, dark setae. **Hypopygium** (Fig. 39)**.** Gonocoxites wider than long, inner side of gonocoxites with small setae, outer side with long setae; ventral, inner side of gonocoxites not fused basally. Gonostylus elongate, slightly tumid in the middle, with a dorsal edge, 2.7–2.9 times longer than wide; apex moderately separated, slightly bent, apical end broad, blunt, on ventral side with a apical cavity without microtrichia, one spine and one whip-lash hair present. Tegmen of the typical ground plan of the *Psl. jejuna* complex, of very rounded shape; dorsal folds present; parameral apodemes basally strongly sclerotized, medially fused, distal branches very parallel and close. Area of teeth absent. Ejaculatory apodeme pale brown, slender, and long; base very delicate, long, and u-shaped. Posterior portion of gonocoxal apodeme medium sized and brown, joined medially. Anterior portion of gonocoxal apodeme short and dark brown.

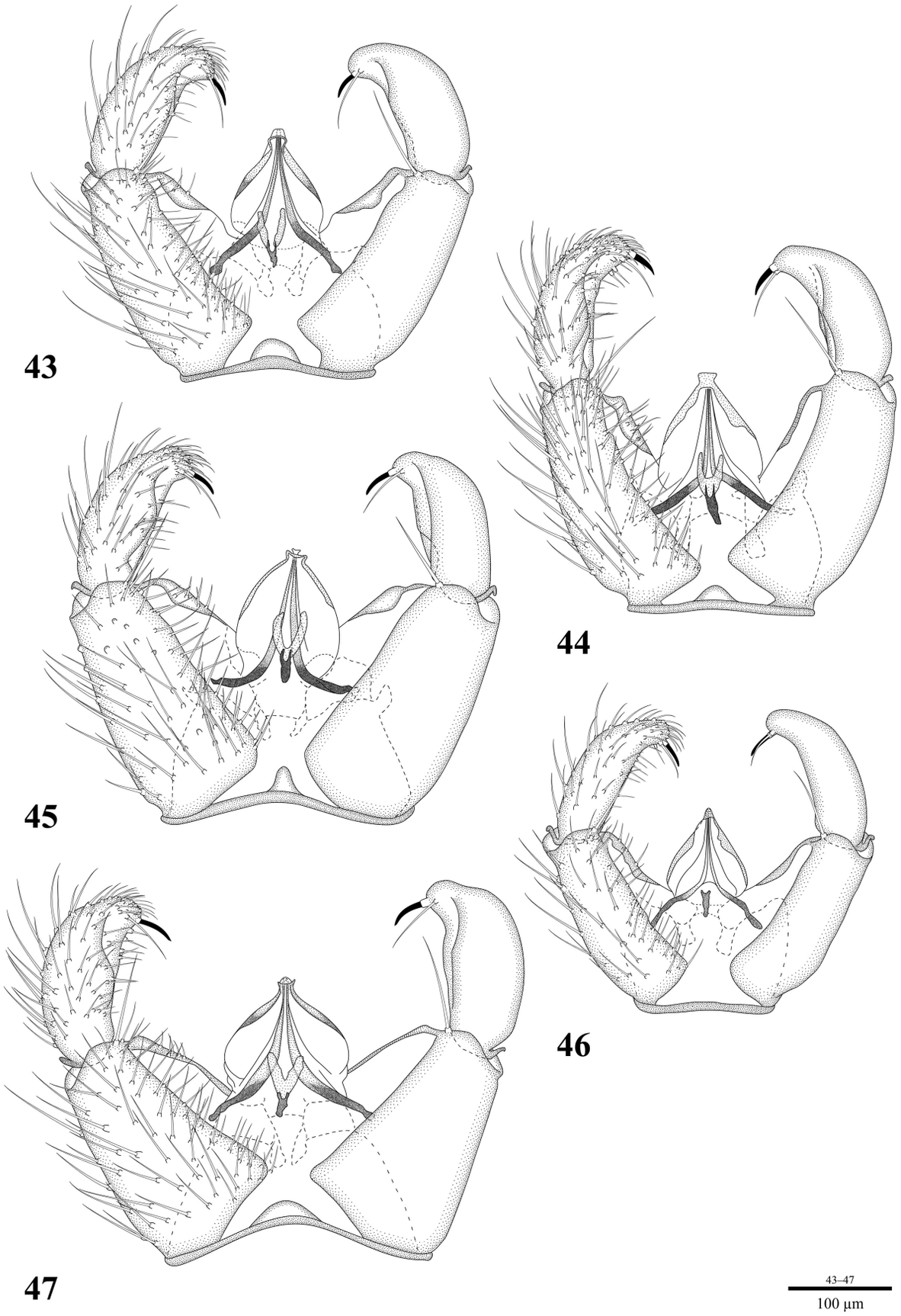
Body size: 2.9–3.1 mm.

Female. Unknown.

Genetic distances. Both available COI sequences show a p-distance of 1.16%. The nearest neighbour is *Psl. whena*, diverging by a minimum of 9.30%. Both available 28S sequences are identical and do not show differences to the sequences of *Psl. sudhausi* and *Psl. whena*.

Etymology. *Porotaka* is a Māori word which means round or circular. The epithet refers to the roundish shape of the tegmen.

Distribution. New Zealand.



FIGURES 43–47. *Pseudolycoriella jejuna* complex, hypopygia. **43.** *Pseudolycoriella tewaipounamu* **sp. n. 44.** *Pseudolycoriella hauta* **sp. n. 45.** *Pseudolycoriella whakahara* **sp. n. 46.** *Pseudolycoriella jejunella* **sp. n. 47.** *Pseudolycoriella maddisoni* **sp. n.**

Discussion. *Pseudolycoriella porotaka* can be distinguished from all other species of the *Psl. jejuna* complex by the combination of a very rounded tegmen and a low width/length ratio of the fourth flagellomere. In addition, this species has flagellomeres with shorter and denser setae compared to the other species. Like *Psl. nahenahe*, *Psl. sudhausi*, and *Psl. whena, Psl. porotaka* has a narrow ejaculatory apodeme.

Pseudolycoriella nahenahe sp. n.

(Fig. 40)
urn:lsid:zoobank.org:act:B0518863-0580-4308-B7E2-61F10B824DB8

Material studied. *Holotype male*. New Zealand: Coromandel, Wharekawa Redwood Picnic Area near Opoutere, redwood plantation with pines and tree fern, sweep net, 09.02.2002, leg. M. Jaschhof (NZAC).

Description. *Male*. **Head.** Head capsule brown. Eye bridge four facets wide, two facets at margin. Scape and pedicel pale, contrasting with the brown flagellum; fourth flagellomere 2.5 times longer than wide; necks of flagellomeres well differentiated; surface of flagellomeres rough with deep pits, sensilla of two different lengths, small ones and longer, curved sensilla; setae as long as a flagellomere's width, slightly curved. Maxillary palp long and three-segmented, first palpomere is the longest, the second shortest; first palpomere with long sensilla and three long bristles. Prefrons and clypeus bulging. **Thorax** brown, with frontal and lateral pale brown patches. Posterior pronotum bare. Anterior pronotum with three setae. Episternum 1 with six setae. Mesonotum with five robust lateral bristles. Scutellum with four robust bristles and several minor setae. Longer and shorter dorsocentral bristles forming a complete row on the mesonotum. Katepisternum as long as high. **Wing.** Length 2.2 mm; width/length ratio 0.37. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, except faint stem of M, apical two-thirds of R_5 with macrotrichia on ventral and dorsal side; bM and r-m bare; R_1 0.7 times as long as R; c/w ratio 0.71; r-m 1.2 as long as bM. Haltere brownish; shaft of haltere slightly longer than knob. **Legs** pale brown, slightly paler than thorax, mid and hind coxae concolourous with thorax. Tibial organ surrounded by a circular border and slightly wider than half of the width of the tibial apex; tibial organ consists of an irregular row of bristles. Front tibia without robust bristles among the vestiture. Mid tibia with one robust bristle among vestiture. Posteriodorsal row of bristles inconspicuous, consisting of three to five bristles. All tibial spurs equal in length. Claws with robust teeth. **Abdomen** concolourous with thorax, with long, dark setae. **Hypopygium.** (Fig. 40) Gonocoxites wider than long, inner side of gonocoxites with medium sized setae, outer side with long setae; ventral, inner side of gonocoxites basally separated. Gonostylus elongated, 2.6 times longer than wide, apex globular and slightly curved inwards, inner side tumid, apical cavity small; one spine and one whip-lash hair present. Tegmen of the typical ground plan of the *Psl. jejuna* complex, onion-shaped but elongated; parameral apodeme basally strongly sclerotized, medially connected. Area of teeth absent. Ejaculatory apodeme pale, narrow and short; base of ejaculatory apodeme not present. Posterior portion of gonocoxal apodeme long and brown, medially joined by a slender bridge. Anterior portion of gonocoxal apodeme long and dark brown.

Body size: 2.2 mm.

Female. Unknown.

Genetic distances. No genetic data available.

Etymology. The Māori adjective *nahenahe*—meaning being separate, alone etc.—was chosen as epithet, indicating that only one specimen of this newly described species was available.

Distribution. New Zealand.

Discussion. Due to the slender ejaculatory apodeme and the tumid gonostylus *Psl. nahenahe* is similar to *Psl. sudhausi*, *Psl. porotaka*, and *Psl. whena*. Among these species *Psl. nahenahe* can be distinguished by a combination of a small body size (2.2 mm) and a low length-width index of the fourth flagellomere. Both *Pseudolycoriella sudhausi* and *Psl. whena* have a fourth flagellomere with a length-width index greater than 2.8, while *Psl. porotaka* has a similar low index of the fourth flagellomere, but has a body size of more than 2.8 mm.

Pseudolycoriella macrotegmenta complex

Thirteen of the species examined during this study have a very similar hypopygia structure. The number of gonostylar spines, ranging from four to ten, is greater than in most other *Pseudolycoriella* species. The length of those spines is also reduced. Consequently, the spines are very difficult to distinguish from the surrounding setae at the

apex of the gonostylus. The apical whip-lash hair is also mostly reduced in length, and in several species two or even three hairs are present. The tegmen possesses a variety of unique characters. Some species bear teeth on the lateral margin of the tegmen (*lt* in Fig. 52). In the most derived state these teeth cover the whole apicolateral part of the tegmen (Fig. 60). On the dorsal side of the tegmen of some species there are creases arising from the outer base and converging towards the apex. These dorsal structures (*ds* in Fig. 52) can vary in length and number. The phylogeny of the *Psl*. *macrotegmenta* complex is shown in Figure 61.

Discussion. An assignment of this assemblage of species to one of the existing species groups of *Pseudolycoriella* was not possible, as already mentioned by Köhler & Mohrig (2016) for *Psl*. *frederickedwardsi* and *Psl*. *tonnoiri*. With the bulging prefrons and clypeus, and the ground plan of the tibial organ this species complex is undoubtedly part of the genus *Pseudolycoriella*. The increase in the number of gonostylar spines and the reduction of the length and the multiplication of the whip-lash hair can be considered to be morphological evidence for the monophyly of the *Psl*. *macrotegmenta* complex. The result of the molecular analysis also strongly supports the monophyly (Fig. 61). With the numerous gonostylar spines and the reduction of the length of the whip-lash hair the *Psl*. *macrotegmenta* complex resembles the *Psl*. *quadrispinosa* group from Papua New Guinea (Mohrig 2013). However, in the *Psl*. *quadrispinosa* group the gonostylar spines are easily distinguishable from the surrounding setae and the whip-lash hair is lost, except in *Psl*. *bitorquia* Mohrig where a small whip-lash hair persists. In the *Psl*. *macrotegmenta* complex the spines are not as easy to distinguish from the surrounding setae and the whip-lash hair is never completely reduced, only shortened. Further, several species of the *Psl*. *macrotegmenta* complex possess two or three whip-lash hairs. Thus, the gonostylar spines and the whip-lash hair(s) do not necessarily share the same taxonomic value and it is likely that their appearance is a result of convergence. Another similar species is *Psl*. *curvimedia* Mohrig & Rulik—a species recorded from the Dominican Republic. It also has a similar pattern of spines on the gonostylus. However, there are other characters that differ significantly from those in the *Psl*. *macrotegmenta* complex and therefore do not support integration into the *Psl*. *macrotegmenta* complex. The flagellomeres of *Psl*. *curvimedia* have a rather smooth surface (Mohrig *et al*. 2004), while those of the species of *Psl*. *macrotegmenta* complex are rough with deep pits. Also, the wing venation of *Psl*. *curvimedia* is very aberrant in comparison to representatives of the *Psl*. *macrotegmenta* complex. *Pseudolycoriella curvimedia* shows a very short R_1 that only comprises a fourth of R, a very unusual M-fork, and a nearly rectangularly bent CuA_2. Furthermore, the gonocoxites of *Psl*. *curvimedia* are fused ventrally, while they are widely separated in the *Psl*. *macrotegmenta* complex. Another similar species is the Australian *Psl*. *rubroalata* Mohrig, Kauschke & Broadley, which also bears eight to ten short spines (Mohrig *et al*. 2018), but shows none of the characters on the tegmen that occur in the New Zealand *Psl*. *macrotegmenta* complex. However, without an accurate examination, preferably incorporating genetic analyses, a well-founded conclusion about the relationship of the *Psl*. *quadrispinosa* group, *Psl*. *curvimedia*, and *Psl*. *rubroalata* to the species of the *Psl*. *macrotegmenta* complex is not possible. Until such an examination, it remains unclear whether these species belong to the *Psl*. *macrotegmenta* complex or whether the similar patterns of gonostylar spines are a result of convergence. Nevertheless, it can be stated that surely these species do not belong to the New Zealand crown group of the *Psl*. *macrotegmenta* complex. The combination of an increased number of reduced (i.e. thinner) spines and flagellomeres with a pitted surface can be held to be a synapomorphy for the New Zealand members of this complex. Apart from the morphological considerations noted above, the very small genetic distances between the New Zealand representatives of this complex indicate a more recent radiation of these species.

Pseudolycoriella macrotegmenta Mohrig, 1999

(Fig. 48)

Literature. *Pseudolycoriella macrotegmenta* Mohrig, 1999: Mohrig & Jaschhof (1999): 41–43, Fig. 22 a–f.—Macfarlane *et al*. (2010): 441.

Material studied. *Holotype male*. New Zealand: North Island, Stratford, Mount Egmont National Park, East Egmont, altitude 650 m, *Podocarpus* wood with rotten wood and a dense layer of herbs, sweep net, 09.01.1993, leg. M. Jaschhof (PWMP). *New records*. 1♂ North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, mixed podocarp/broadleaf forest, sweep net, 03–04.02.2002, leg. M. Jaschhof (SDEI, SDEI-Dipt-0000859). 2♂♂ same locality as previous, Malaise trap, 26.11–28.12.2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC; SDEI, SDEI-Dipt-0000757).

Redescription. *Male*. **Head** brown; eye bridge three facets wide; lateral border of eye bridge two facets wide. Scape and pedicel brown, concolourous with flagellomeres; fourth flagellomere 2.9–3.6 times as long as wide; necks of flagellomeres differentiated; surface of flagellomeres rough with deep pits; sensilla of two different lengths present; setae fine and curved, approximately as long as flagellomere width. Prefrons and clypeus bulging. Maxillary palp three-segmented; first palpomere longest, second palpomere shortest; first palpomere with four bristles and a patch of sensilla. **Thorax** brown, laterally a brighter yellowish-brown. Posterior pronotum bare. Anterior pronotum with five to six bristles. Episternum 1 with seven to eleven bristles. Mesonotum with five to six robust lateral bristles and several longer bristles among the dorsocentrals. Frontal part of mesonotum with a few arcostichal bristles. Scutellum with four robust and some shorter bristles. Katepisternum as long as high. **Wing**. Length 2.4–2.5 mm; width/length ratio 0.36–0.38. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct and without macrotrichia; apical quarter to two-thirds of R_5 with additional macrotrichia ventrally; bM and r-m bare, exceptionally one specimen with one seta on r-m on one wing; R_1 short, 0.50–0.67 times as long as R; M-fork longer than stem of M; c/w ratio 0.70–0.74; r-m/bM ratio 0.8–1.1. Haltere pale brown. **Legs** pale brown; trochanter darker. Fore tibia with none or one to two bristles among the vestiture. Tibial organ comprising more than half of tibial apex, consisting of a patch of bristles surrounded by a robust circular border. Mid tibia with two to four anterioventral and two to three posterioventral robust bristles among the vestiture. Hind tibia with several very robust bristles on anterioventral, posterior and posterioventral sides and a longitudinal row of robust bristles, which comprises two thirds to three quarters of the tibia length. Basal tarsomere of all legs with conspicuous robust bristles. All tibial spurs equal in length. Claws with one robust and three minor teeth. **Abdomen** brown like the thorax or slightly paler, with dark bristles. **Hypopygium** (Fig. 48) brown. Gonocoxites wider than long; basally not fused, without a basal lobe of bristles. Gonostylus slender, slightly curved inwards, 2.7–3.0 times longer than wide; thickest part in the middle, apically with dense setae and a group of approximately six small spines, spines more or less longitudinally directed; subapically with one short whip-lash hair, which is two times as long as the apical spines. Tegmen wider than long and sclerotized, base very strongly sclerotized with short and robust parameral apodeme; lateral margin of tegmen with a sclerotized edge, which bears several small teeth on middle third; apex straight, sclerotisation widely interrupted; dorsal structures absent. Area of teeth consists of more than 20 conspicuous teeth. Ejaculatory apodeme short, broad, and very dark, with a long, broad base. Posterior portion of gonocoxal apodeme broad and brown. Anterior portion of gonocoxal apodeme small, roundish, darker than posterior portion.

Body size: 1.8–2.4 mm.

Female. Unknown.

Genetic distances. Both available COI sequences are identical and do not show any distance. The nearest neighbour is *Psl. wernermohrigi*, diverging by a minimum of 1.84%. The one available 28S sequence is identical to those of *Psl. frederickedwardsi*, *Psl. huttoni*, *Psl. jaschhofi*, *Psl. plicitegmenta*, *Psl. robustotegmenta*, *Psl. subtilitegmenta*, *Psl. tonnoiri*, and *Psl. wernermohrigi*.

Distribution. New Zealand.

Discussion. *Pseudolycoriella macrotegmenta* belongs to those species of the *Psl. macrotegmenta* complex which bear lateral teeth on the tegmen. Among these species *Psl. macrotegmenta* is the only species that lacks the dorsal structures on the tegmen and has a gonostylus with a subapical lobe on the inner side.

The author of *Psl. macrotegmenta* had a wide concept of this species. Accordingly, the paratype series contained two other species: three specimens of *Psl. wernermohrigi* and one specimen of *Psl. frederickedwardsi*. The fifth paratype which is deposited in the NZAC (NZAC02016074) was not studied and remains unrevised. This broad concept of *Psl. macrotegmenta* led to an inaccuracy in the original description. Mohrig & Jaschhof (1999) gave a length to width ratio of the fourth flagellomere of 2.4, which is much shorter than the value of 2.9–3.6 revealed by the present study.

Pseudolycoriella plicitegmenta sp. n.

(Fig. 49)

urn:lsid:zoobank.org:act:NomenclaturalActs/256F08AF-B9EB-40A7-8D03-E59A5DF412F0

Material studied. *Holotype male*. New Zealand: South Island, Clutha, Catlins, Purakaunui Scenic Reserve, mixed podocarp/broadleaf/*Nothofagus* forest, Malaise trap, 27.01–05.03.2002, leg. M. & C. Jaschhof (NZAC, SDEI-Dipt-0001158). *Paratypes*. 4♂♂ same locality and same date as holotype (2x NZAC, SDEI-Dipt-0000560 & SDEI-Dipt-

0001155; 2x SDEI, SDEI-Dipt-0001130 & SDEI-Dipt-0001153). 1♂ South Island, Clutha, Catlins Coastal Rain Forest Park, Catlins River Valley, silver beech forest, Malaise trap, 27.01–05.03.2002, leg. M. & C. Jaschhof (SDEI, SDEI-Dipt-0000799).

Description. *Male*. **Head** brown; eye bridge three facets wide, two at margin. Flagellomeres brown, concolourous with scape and pedicel; fourth flagellomere 2.3–2.9 times as long as wide; necks of flagellomeres differentiated; surface of flagellomeres rough with deep pits; sensilla of two different lengths present; setae sparsely scattered, approximately as long as flagellomere width, bases of setae slightly raised. Prefrons and clypeus moderately bulging. Maxillary palp three-segmented; first palpomere longest, third longer than second; first palpomere with three to four bristles and an inconspicuous patch of sensilla. **Thorax** brown, paler than head; laterally brighter. Posterior pronotum bare. Anterior pronotum with seven to eleven bristles. Episternum 1 with five to nine bristles. Mesonotum with five to six longer bristles among the lateral bristles; row of dorsocentral bristles well developed. Scutellum with two robust and some shorter bristles. Katepisternum bicoloured, basal part pale brown, apically brown; as long as high. **Wing.** Length 2.1–2.3 mm; width/length ratio 0.36–0.40. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, all without macrotrichia; apical fourth of R_5 with additional macrotrichia on ventral side; bM bare; r-m with one macrotrichium or without macrotrichia; R_1 short, 0.46–0.54 times as long as R; M-fork longer than M stem; c/w ratio 0.67–0.74; r-m/bM ratio 1.0–1.3. Haltere pale brown. **Legs** pale brown; coxal bristles dark. Fore tibia with one to four bristles among vestiture; tibial organ comprising half of tibial apex, consisting of a transverse patch of bristles surrounded by a robust circular border. Mid tibia with seven to nine robust bristles among vestiture, located anterio- and posterioventrally. Hind tibia with twelve to twenty robust bristles at anterioventral, posterior and posterioventral sides and a longitudinal row of robust bristles, which comprises three-fifths of tibial length. Basal tarsomere of all legs with conspicuous robust bristles. All tibial spurs equal in length. Claws with one robust tooth and several minor teeth. **Abdomen.** Pale brown, with dark bristles. **Hypopygium** (Fig. 49) brown. Gonocoxites wider than long, ventrally u-shaped and not fused, without a basal lobe of bristles. Gonostylus elongate, slightly curved inwards, 3.1–3.4 times longer than wide, inner base with a protruding angle (*ba* in Fig. 49); apically with dense setae and a group of approximately five to six spines; subapically with two or three medium-sized whip-lash hairs; dorsal side of apex of gonostylus slightly constricted. Tegmen wider than long, base very strongly sclerotized with short, robust parameral apodeme; lateral margin of tegmen with a sclerotized edge, scattered with several small teeth, apically not fused; dorsal structures on tegmen well developed, as long as two-thirds of tegmen length. Area of teeth with 17 to 28 conspicuous teeth. Ejaculatory apodeme short, broad, and very dark, with a broad, u-shaped base. Posterior portion of gonocoxal apodeme broad and brown. Anterior portion of gonocoxal apodeme small.

Body size: 2.1–2.3 mm.

Female. Unknown.

Genetic distances. The maximum p-distance between all five available COI sequences is 0.15%. Some COI sequences are identical with *Psl. gonotegmenta* and *Psl. subtilitegmenta*. Both available 28S sequence are identical and do not show any differences to those of *Psl. frederickedwardsi*, *Psl. gonotegmenta*, *Psl. huttoni*, *Psl. jaschhofi*, *Psl. macrotegmenta*, *Psl. robustotegmenta*, *Psl. subtilitegmenta*, *Psl. tonnoiri*, and *Psl. wernermohrigi*.

Etymology. The epithet of the new species is composed of the two Latin words *plica* (crease) and *tegmen* (cover; technical term for a part of the sciarid hypopygium).

Distribution. New Zealand.

Discussion. *Pseudolycoriella plicitegmenta* belongs to those species of the *Psl. macrotegmenta* complex that bear several teeth on the lateral tegmen margin. This sclerotized margin is apically interrupted. This combination can be also found in *Psl. macrotegmenta*, *Psl. robustotegmenta*, and *Psl. subtilitegmenta* and some specimens of *Psl. gonotegmenta*. *Pseudolycoriella plicitegmenta* can be distinguished from *Psl. macrotegmenta* by the different shape of the gonostylus and the presence of the dorsal structure on the tegmen. *Pseudolycoriella gonotegmenta* and *Psl. robustotegmenta* have a R_1/R ratio greater than 0.6 while the R_1/R ratio of *Psl. plicitegmenta* is less than 0.6. *Pseudolycoriella robustotegmenta* differs significantly because it has a massive tegmen margin, long dorsal structures on the tegmen, and a long ejaculatory apodeme.

***Pseudolycoriella subtilitegmenta* sp. n.**
(Fig. 53)
urn:lsid:zoobank.org:act:NomenclaturalActs/7E7F889A-66DB-46DB-8B60-FB995BB62FC9

Material studied. *Holotype male*. New Zealand: South Island, Clutha, Catlins, Purakaunui Scenic Reserve, mixed podocarp/broadleaf/*Nothofagus* forest, Malaise trap, 27.01–05.03.2002, leg. M. & C. Jaschhof (NZAC, SDEI-Dipt-0001151). *Paratypes*. 2♂♂ same locality and same date as holotype (NZAC, SDEI-Dipt-0001136; SDEI, SDEI-Dipt-0001133). 1♂ North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, mixed podocarp/broadleaf forest, Malaise trap, 26.11–28.12.2002, leg. M. & C. Jaschhof & U. Kallweit (SDEI).

Description. *Male*. **Head** brown; eye bridge three facets wide, two at margin. Flagellomeres brown, concolourous with scape and pedicel; fourth flagellomere 2.5–2.8 times as long as wide; necks of flagellomeres differentiated; surface of flagellomeres rough with deep pits; sensilla of two different lengths present; setae sparsely scattered, approximately as long as flagellomere width, bases of setae on small elevations. Prefrons and clypeus slightly bulging. Maxillary palp three-segmented; first palpomere longest, third longer than second; first palpomere with two to five bristles and an inconspicuous patch of sensilla; one of the bristles on first and second palpomere robust and elongated. **Thorax** brown, concolourous with head. Posterior pronotum bare. Anterior pronotum with six to nine long bristles. Episternum 1 with five to nine long bristles. Mesonotum with five to six longer bristles among the lateral bristles; row of dorsocentral bristles well developed. Scutellum with two robust and some shorter bristles. Katepisternum slightly longer than high. **Wing.** Length 2.3–2.4 mm; width/length ratio 0.36–0.38. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, all without macrotrichia; apical 25%–40% of R_5 with additional macrotrichia on ventral side; bM bare, r-m with one or two macrotrichia; R_1 short, 0.64–0.71 times as long as R; M-fork longer than M stem; c/w ratio 0.67–0.70; r-m/bM ratio 1.0–1.2. Haltere pale brown. **Legs** pale brown, trochanter slightly darker; coxal bristles dark. Fore tibia with one or two bristles among the vestiture; tibial organ comprising half of tibial apex, consisting of a transverse patch of bristles surrounded by a robust circular border. Mid tibia with seven to eight robust bristles among vestiture, located anterio- and posteriorventrally. Hind tibia with 16 to 22 robust bristles on anterioventral, posterior and posterioventral sides and a longitudinal row of robust bristles, which extends along two-thirds of the length of the tibia. Basal tarsomere of all legs with conspicuous robust bristles. All tibial spurs equal in length. Claws with one robust tooth and several minor teeth. **Abdomen.** Brown, with dark bristles. **Hypopygium** (Fig. 53) brown. Gonocoxites wider than long, ventrally v-shaped and not fused, without a basal lobe of bristles. Gonostylus elongated, apex slightly angled and slightly tapered; without an angle at the base of the gonostylus, 2.7–3.2 times longer than wide; apically with dense setae and a group of approximately five to seven spines; subapically with two to three medium-sized whip-lash hairs. Tegmen wider than long, base very strongly sclerotized with medium-sized, robust parameral apodeme; lateral margin of tegmen with a fine sclerotized edge, which is separated into four fragments: one lateral fragment with a few lateral teeth and one apicolateral fragment (the paratype from the North Island shows fused fragments of each tegmen side); dorsal structures on tegmen developed, as long as half of the length of the tegmen. Area of teeth absent. Ejaculatory apodeme short, broad, and dark, with a broad and extended v-shaped base. Posterior portion of gonocoxal apodeme broad and brown. Anterior portion of gonocoxal apodeme broad.

Body size: 2.2–2.6 mm.

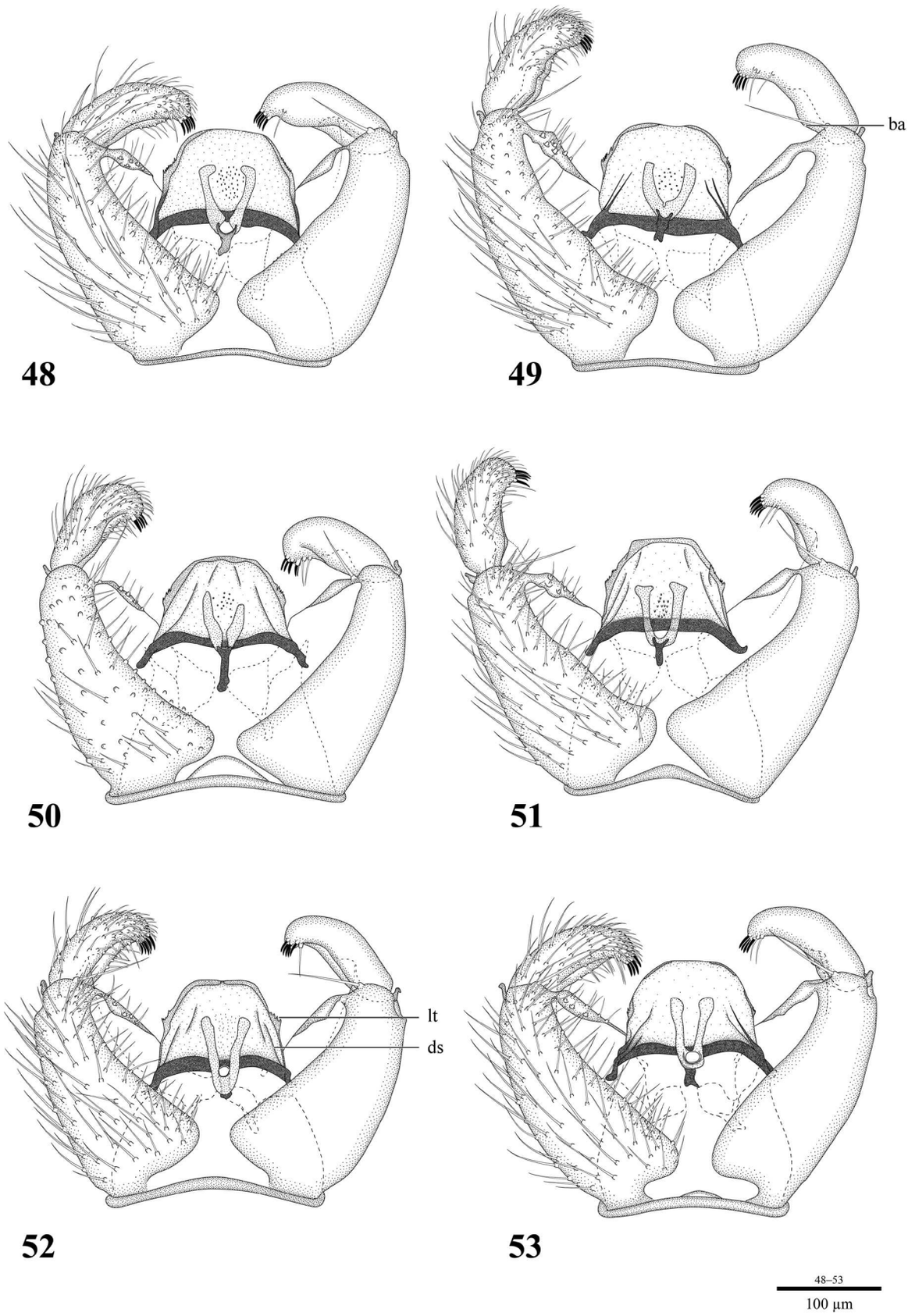
Female. Unknown.

Genetic distances. All three available COI sequences are identical and do not show any pairwise distance. These COI sequences are identical with that of *Psl. gonotegmenta*. One available 28S sequence is identical to those of *Psl. frederickedwardsi*, *Psl. gonotegmenta*, *Psl. huttoni*, *Psl. jaschhofi*, *Psl. macrotegmenta*, *Psl. plicitegmenta*, *Psl. robustotegmenta*, *Psl. tonnoiri*, and *Psl. wernermohrigi*.

Etymology. The epithet of the new species is composed of the two Latin words *subtilis* (fine, delicate) and *tegmen* (cover; technical term for a part of the sciarid hypopygium).

Distribution. New Zealand.

Discussion. *Pseudolycoriella subtilitegmenta* is the only species among the species of the *Psl. macrotegmenta* complex with lateral teeth and a very thin sclerotized margin on the tegmen. Furthermore, the area of teeth is absent, which is also only found in *Psl. tonnoiri* and *Psl. breviseta*. *Pseudolycoriella subtilitegmenta* is the only species in this group with a tapered gonostylus apex.



FIGURES 48–53. *Pseudolycoriella macrotegmenta* complex, hypopygia. **48.** *Pseudolycoriella macrotegmenta* Mohrig **49.** *Pseudolycoriella plicitegmenta* **sp. n. 50.** *Pseudolycoriella wernermohrigi* **sp. n. 51.** *Pseudolycoriella huttoni* **sp. n. 52.** *Pseudolycoriella gonotegmenta* **sp. n. 53.** *Pseudolycoriella subtilitegmenta* **sp. n.** Abbreviations: ba = basal angle; ds = dorsal structure on the tegmen; lt = teeth on lateral side of the tegmen.

***Pseudolycoriella gonotegmenta* sp. n.**
(Fig. 52)
urn:lsid:zoobank.org:act:9BD9CFA2-AA84-4340-BA03-C94C77EC9748

Material studied. *Holotype male*. New Zealand: South Island, Buller, Rahu Scenic Reserve, 12 km NW Springs Junction, altitude 550 m, mixed *Nothofagus*/podocarp forest, Malaise trap, 27.11–25.12.2001, leg. M. & C. Jaschhof (NZAC, SDEI-Dipt-0001495). *Paratypes*. 2♂♂ North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, mixed podocarp/broadleaf forest, Malaise trap, 26.11–28.12.2002, leg. M. & C. Jaschhof & U. Kallweit (all SDEI). 2♂♂ North Island, Masterton, Tararua Forest Park, Blue Range Hut Track 10 km SW Mt. Bruce, mixed *Nothofagus*/podocarp/broadleaf forest, sweep net, 02.02.2002, leg. M. Jaschhof (NZAC; SDEI). 1♂ South Island, Buller, Ahaura, Granville State Forest, altitude 170–250 m, *Nothofagus truncata* forest, Malaise trap, 01.12.1994, leg. J. Hutcheson (NZAC). 2♂♂ South Island, Buller, 5 km W Maruia Springs, mixed *Nothofagus* forest, Malaise trap, 26.11–25.12.2001, leg. M. & C. Jaschhof (NZAC, SDEI-Dipt-0000977 & SDEI, SDEI-Dipt-0000984). 1♂ South Island, Buller, Lake Daniells Track 7 km E Springs Junction, mixed red/silver beech forest, Malaise trap, 24.11–26.12.2001, leg. M. & C. Jaschhof (SDEI).

Description. *Male*. **Head** brown; eye bridge three facets wide, two at margin. Flagellomeres brown, concolourous with scape and pedicel; fourth flagellomere 2.6–2.9 times as long as wide; necks of flagellomeres differentiated; surface of flagellomeres rough with deep pits; sensilla of two different lengths present; setae sparse, approximately as long as flagellomere width, bases of setae with slightly raised coronas. Prefrons and clypeus moderately bulging. Maxillary palp three-segmented; first palpomere longest, third longer than second; first palpomere with two to six bristles and an inconspicuous patch of sensilla; usually one of the bristles on first and second palpomere elongated. **Thorax** brown, laterally extensively brightened. Posterior pronotum bare. Anterior pronotum with five to seven long bristles. Episternum 1 with six to eleven long bristles. Mesonotum with five to six longer bristles among the lateral bristles; row of dorsocentral bristles well developed. Scutellum with two to four robust and some shorter bristles. Katepisternum as long as high. **Wing.** Length 2.0–2.3 mm; width/length ratio 0.35–0.41. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, all without macrotrichia; apical 25%–40% of R_5 with additional macrotrichia on ventral side; bM and r-m bare; R_1 short, 0.64–0.77 times as long as R; M-fork longer than stem of M or—in one case—as long as stem of M; c/w ratio 0.66–0.71; r-m/bM ratio 0.7–1.2. Haltere pale brown. **Legs** pale brown; coxal bristles dark. Fore tibia with one to three bristles among vestiture; tibial organ comprising half of tibial apex, consisting of a transverse patch of bristles surrounded by a robust circular border. Mid tibia with four to six robust bristles among vestiture, located anterio- and posterioventrally. Hind tibia with seven to 17 robust bristles on anterioventral, posterior and posterioventral sides and a longitudinal row of robust bristles, which extends two-thirds to four-fifths of tibial length. Basal tarsomere of all legs with conspicuous robust bristles. All tibial spurs equal in length. Claws with one robust tooth and several minor teeth. **Abdomen.** Pale brown, with dark bristles. **Hypopygium** (Fig. 52) brown. Gonocoxites wider than long, ventrally u-shaped and not fused, without a basal lobe of bristles. Gonostylus elongate, apically curved inwards, apex slightly tapered, without an angle at the base of the gonostylus, 2.6–3.3 times longer than wide; apically with dense setae and a group of approximately five to six spines; subapically with one to three medium-sized whip-lash hairs. Tegmen wider than long, base very strongly sclerotized with short, robust parameral apodeme; lateral margin of tegmen with a sclerotized edge, scattered with several small teeth, apically mostly fused (two exceptions with membranous gaps at apex); dorsal structures on tegmen well developed, as long as half tegmen length. Area of teeth with seven to 40 conspicuous teeth. Ejaculatory apodeme short, broad, and dark. Posterior portion of gonocoxal apodeme broad and brown. Anterior portion of gonocoxal apodeme broad and short.

Body size: 1.7–2.4 mm.

Female. Unknown.

Genetic distances. The maximum p-distance between all three available COI sequences is 0.20%. Some of these COI sequences are identical with that of *Psl. plicitegmenta*. The one available 28S sequence is identical to those of *Psl. frederickedwardsi*, *Psl. huttoni*, *Psl. jaschhofi*, *Psl. macrotegmenta*, *Psl. plicitegmenta*, *Psl. robustotegmenta*, *Psl. subtilitegmenta*, *Psl. tonnoiri*, and *Psl. wernermohrigi*.

Etymology. The epithet of the new species is composed of the Greek word γωνοζ (*gonos*, edge) and the Latin word *tegmen* (cover; technical term for a part of the sciarid hypopygium).

Distribution. New Zealand.

Discussion. With the margin of the tegmen apically fused, *Psl. gonotegmenta* resembles *Psl. huttoni* and *Psl.*

wernermohrigi. *Pseudolycoriella huttoni* differs by having a u-shaped base of the ejaculatory apodeme, a lower R_1/R ratio (0.56 *vs*. 0.64–0.77), and a smaller anterior portion of gonocoxal apodeme. *Pseudolycoriella wernermohrigi* has a much longer ejaculatory apodeme, a longer parameral apodeme, and a longer anterior portion of gonocoxal apodeme. In specimens where fragmentation of the tegmen margin has occurred, as for example in two paratypes of *Psl*. *gonotegmenta*, the base of the ejaculatory apodeme has to be examined to enable separation from *Psl*. *plicitegmenta*. In *Psl*. *gonotegmenta* this base is long and broadly v-shaped while *Psl*. *plicitegmenta* has a short a u-shaped base. In addition *Psl*. *plicitegmenta* possess a basal angle on the gonostylus, which is lacking in *Psl*. *gonotegmenta*.

***Pseudolycoriella robustotegmenta* sp. n.**

(Figs 7 & 54)

urn:lsid:zoobank.org:act:NomenclaturalActs/3346FE28-2271-4E55-8DB1-4CA3ED714633

Material studied. *Holotype male*. New Zealand: North Island, Bay of Plenty, Katikati, Uretara mangrove area, Malaise trap, 04.09–22.10.2016, leg. P.A. Maddison (NZAC, SDEI-Dipt-0001358). *Paratype*. 1♂, North Island, Bay of Plenty, Katikati, Te Mania catchment, Malaise trap, 19.09–27.10.2016, leg. P.A. Maddison (SDEI, SDEI-Dipt-0001371).

Description. *Male*. **Head** (Fig. 7) brown; eye bridge two to three facets wide. Flagellomeres brown, concolourous with scape and pedicel; fourth flagellomere 2.7–2.9 times as long as wide; necks of flagellomeres differentiated; surface of flagellomeres rough with deep pits; sensilla of two different lengths present; setae sparse, approximately as long as flagellomere width, bases of setae with coronas. Prefrons and clypeus moderately bulging. Maxillary palp three-segmented; first palpomere longest, third longer than second; first palpomere with three to four bristles and an inconspicuous patch of sensilla; first and second palpomere each with one longer bristle. **Thorax** brown, laterally brighter. Posterior pronotum bare. Anterior pronotum with four to seven bristles. Episternum 1 with five to six bristles. Mesonotum with five longer lateral bristles; row of dorsocentral bristles present. Scutellum with two robust and some shorter bristles. Katepisternum brown, basally slightly brightened; as long as high. **Wing.** Length 2.0–2.2 mm; width/length ratio 0.37–0.38. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, all without macrotrichia; apical fourth of R_5 with five to six additional macrotrichia on ventral side; bM bare; r-m with one macrotrichium (exceptionally the left wing of the holotype shows two macrotrichia on r-m); R_1 short, 0.55–0.57 times as long as R; M-fork shorter than M stem; c/w ratio 0.68–0.70; r-m 0.8 times as long as bM. Haltere pale brown. **Legs** pale brown; coxal bristles dark; trochanter darkened. Fore tibia with one robust bristle among the vestiture; tibial organ comprising more than half of the tibial apex, consisting of a patch of bristles surrounded by a robust circular border. Mid tibia with two anterioventral and two posterioventral robust bristles among the vestiture. Hind tibia with several robust bristles on anterioventral, posterior and posterioventral sides and a longitudinal row of robust bristles, which extends along four fifths of the tibial length. Basal tarsomere of all legs with conspicuous robust bristles. All tibial spurs equal in length. Claws with one robust tooth and several minor teeth. **Abdomen.** Pale brown, with long dark bristles. **Hypopygium** (Fig. 54) brown. Gonocoxites wider than long, ventrally not fused, without a basal lobe of bristles. Gonostylus long and evenly curved, 2.8–3.1 times longer than wide; apically with dense setae and a group of approximately four to five spines; subapically with two to three medium-sized whip-lash hairs; inner base of gonostylus with an angle. Tegmen strongly sclerotized, wider than long, base very strongly sclerotized with long parameral apodeme; lateral margin of tegmen with a broad sclerotized edge; laterally scattered with several small teeth; sclerotized edge interrupted apically; dorsal structures well developed, reaching apex of the tegmen. Area of teeth with ten to twenty conspicuous teeth. Ejaculatory apodeme medium-sized, broad, and very dark, with a broad, u-shaped base. Posterior portion of gonocoxal apodeme broad and brown. Anterior portion of gonocoxal apodeme broad and short.

Body size: 2.2–2.3 mm.

Female. Unknown.

Genetic distances. Both available COI sequences are identical and do not show any p-distances. The nearest neighbour is *Psl*. *gonotegmenta*, diverging by a minimum of 0.61%. Both available 28S sequence are identical and do not show any differences to those of *Psl*. *frederickedwardsi*, *Psl*. *gonotegmenta*, *Psl*. *huttoni*, *Psl*. *jaschhofi*, *Psl*. *macrotegmenta*, *Psl*. *plicitegmenta*, *Psl*. *subtilitegmenta*, *Psl*. *tonnoiri*, and *Psl*. *wernermohrigi*.

Etymology. The name of the newly described species is composed of the two Latin words *robustus* (robust) and *tegmen* (cover; technical term for a part of the sciarid hypopygium).

Distribution. New Zealand.

Discussion. *Pseudolycoriella robustotegmenta* can be distinguished from the remaining species of this complex by the strongly developed margin of the tegmen, robust dorsal structures on the tegmen reaching the apex, and the base of vein M longer than the M-fork.

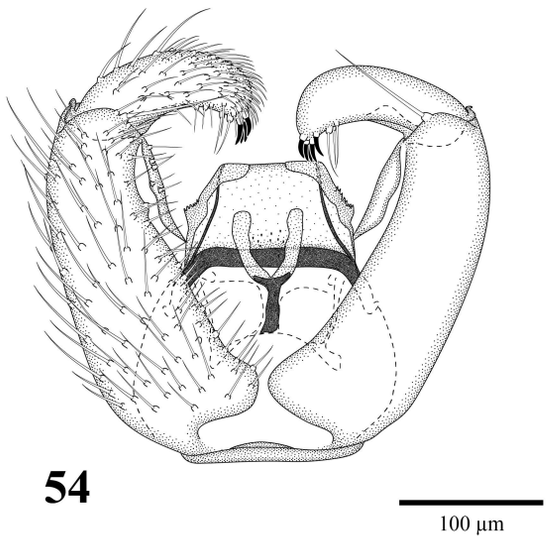


FIGURE 54. *Pseudolycoriella robustotegmenta* **sp. n.**, hypopygium.

Pseudolycoriella huttoni sp. n.

(Fig. 51)
urn:lsid:zoobank.org:act:6434BD19-1F69-47FD-A8FB-5A73560A1082

Material studied. *Holotype male*. New Zealand: North Island, Taupo, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, podocarp/broadleaf forest; Malaise trap, 26.11–28.12.2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC, SDEI-Dipt-0000621).

Description. *Male*. **Head** brown; eye bridge two to three facets wide. Flagellomeres brown, concolourous with scape and pedicel; fourth flagellomere 2.9 times as long as wide; necks of flagellomeres differentiated; surface of flagellomeres rough with deep pits; sensilla of two different lengths present; setae sparse, approximately as long as flagellomere width, bases of setae with slightly raised coronas. Prefrons and clypeus moderately bulging. Maxillary palp three-segmented; first and third palpomere equal in length, longer than second; first palpomere with five bristles and an inconspicuous patch of sensilla; first and second palpomere with one longer outward orientated bristle. **Thorax** brown, lateral slightly brightened. Posterior pronotum bare. Anterior pronotum with five bristles. Episternum 1 with nine bristles. Mesonotum with five longer lateral bristles; row of dorsocentral bristles present. Scutellum with two robust and some shorter bristles. Katepisternum nearly as long as high. **Wing.** Length 2.3 mm; width/length ratio 0.38. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, except weak stem of M, all without macrotrichia; apical third of R_5 with nine additional macrotrichia on ventral side; bM bare; left r-m bare, right r-m with one macrotrichium; R_1 short, 0.56 times as long as R; M-fork longer than M stem; c/w ratio 0.70; r-m 0.8 times as long as bM. Haltere paler brown than thorax. **Legs** pale brown; coxal bristles dark; trochanter slightly darker. Fore tibia with one robust bristle among vestiture; tibial organ comprising more than half of tibial apex, consisting of a patch of bristles surrounded by a robust circular border. Mid tibia with six robust bristles among the vestiture, located on anterioventral and posterioventral side. Hind tibia with several robust bristles at anterioventral, posterior and posterioventral sides and a longitudinal row of robust bristles, which comprises one half of tibial length. Basal tarsomere of all legs with conspicuous robust bristles. All tibial spurs equal in length. Claws with one robust tooth and several minor teeth. **Abdomen.** Pale brown, with long dark bristles.

Hypopygium (Fig. 51) brown. Gonocoxites wider than long, ventrally not fused, without a basal lobe of bristles. Gonostylus long and apically curved, giving it a hump-backed appearance, 2.8 times longer than wide; apically with dense setae and a group of approximately five spines; subapically with three medium-sized whip-lash hairs; inner base of gonostylus without a remarkable angle. Tegmen strongly sclerotized, slightly wider than long, base very strongly sclerotized with long parameral apodemes; lateral margin of tegmen with a sclerotized edge; laterally scattered with several small teeth; sclerotized edge surrounds apex of tegmen; dorsal structures well developed, as long as two-thirds of tegmen. Area of teeth present, comprising fifteen teeth. Ejaculatory apodeme short, broad, and very dark, with a long, u-shaped, pale brown base. Posterior portion of gonocoxal apodeme broad and brown. Anterior portion of gonocoxal apodeme very short.

Body size: 2.6 mm.

Female. Unknown.

Genetic distances. Only one COI sequence was available. The nearest neighbour is *Psl. tonnoiri*, diverging by a minimum of 2.74%. The one available 28S sequence is identical to those of *Psl. frederickedwardsi*, *Psl. jaschhofi*, *Psl. macrotegmenta*, *Psl. plicitegmenta*, *Psl. robustotegmenta*, *Psl. subtilitegmenta*, *Psl. tonnoiri*, and *Psl. wernermohrigi*.

Etymology. The epithet was selected to honour Frederick Wollaston Hutton (1836–1905), who described the first New Zealand sciarid fly in 1881.

Distribution. New Zealand.

Discussion. *Pseudolycoriella huttoni* is morphologically very similar to *Psl. wernermohrigi*, but shows a considerable difference in the genetic analysis (Fig. 61). As reliable distinguishing characters the length of the ejaculatory apodeme and the length of the anterior portion of gonocoxal apodeme can be used.

Pseudolycoriella wernermohrigi sp. n.

(Fig. 50)

urn:lsid:zoobank.org:act:NomenclaturalActs/F62E7CA7-79FB-44C4-AC2C-FD9403DDAD27

Literature. *Pseudolycoriella macrotegmenta* Mohrig, 1999: Mohrig & Jaschhof (1999): 41–43 [misidentification].

Material studied. *Holotype male*. New Zealand: North Island, Western Bay of Plenty, Katikati, Te Mania catchment, Malaise trap, 19.09–27.10.2016, leg. P.A. Maddison (NZAC, SDEI-Dipt-0001223). *Paratypes*. 10♂♂ same locality and same date as holotype (5x NZAC, SDEI-Dipt-0000670, SDEI-Dipt-0000674, SDEI-Dipt-0001227, SDEI-Dipt-0001238 & SDEI-Dipt-0001245; 5x SDEI, SDEI-Dipt-0000665, SDEI-Dipt-0001234, SDEI-Dipt-0001334, SDEI-Dipt-0001235 & SDEI-Dipt-0001373). 1♂ North Island, Auckland, Pukororo Miranda, Te Kama forest remnant, litter, 13.11.2014, leg. P.A. Maddison (NZAC, SDEI-Dipt-0001270). 2♂♂ North Island, Thames-Coromandel, Coromandel Range, 5 km east of Coromandel, dense *Podocarpus* secondary wood with tree ferns, sweep net, 28.12.1992, leg. M. Jaschhof (PWMP; SDEI [both specimens previously misidentified, published as paratypes of *Psl. macrotegmenta* in Mohrig & Jaschhof 1999]). 1♂♂ North Island, Wairoa, Urewera National Park, Huiarau Range 30 km southeast of Murupara, altitude 600–1,000 m, *Podocarpus-Nothofagus* wood, sweep net, 23.12.1992, leg. M. Jaschhof (PWMP [previously misidentified, published as paratype of *Psl. macrotegmenta* in Mohrig & Jaschhof 1999]). 1♂ North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, mixed podocarp/broadleaf forest, malaise trap, 26.11–28.12.2002, leg. M. & C. Jaschhof & U. Kallweit (SDEI). 7♂♂ North Island, Taupo, Pureora Forest Park, Waipapa Reserve, altitude 600 m, mixed podocarp/broadleaf forest, sweep net, 04–05.02.2002, leg. M. Jaschhof (3x NZAC, SDEI-Dipt-0000824; 4x SDEI, SDEI-Dipt-0000822 & SDEI-Dipt-0000825). *Additional material*. 2♂♂ same locality and same date as holotype (all SDEI, SDEI-Dipt-0000681 & SDEI-Dipt-0001232).

Description. *Male*. **Head** brown; eye bridge two to three facets wide. Flagellomeres brown, concolourous with scape and pedicel; fourth flagellomere 2.5–2.9 times as long as wide; necks of flagellomeres differentiated; surface of flagellomeres rough with deep pits; sensilla of two different length present; setae sparse, approximately as long as flagellomere width, bases of setae with slightly raised coronas. Prefrons and clypeus bulging. Maxillary palp three-segmented; first palpomere longest, third longer than second; first palpomere with two to six bristles and an inconspicuous patch of sensilla; first and second palpomeres each with one longer outward orientated bristle. **Thorax** brown, laterally brighter. Posterior pronotum bare. Anterior pronotum with four to seven bristles. Episternum 1 with

five to seven bristles. Mesonotum with five to seven longer lateral bristles; row of dorsocentral bristles present. Scutellum with two robust and some shorter bristles. Katepisternum brown; as long as high. **Wing.** Length 2.0–2.3 mm; width/length ratio 0.35–0.42. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, all without macrotrichia; apical quarter of R_5 with two to five additional macrotrichia on ventral side; bM and r-m bare (exceptionally one of the misidentified paratypes from the type series of *Psl. macrotegmenta* bears one macrotrichium on r-m on the right wing); R_1 short, 0.51–0.71 times as long as R; M-fork longer than M stem; c/w ratio 0.68–0.74; r-m 0.8–1.1 times as long as bM. Haltere brown. **Legs** pale brown; coxal bristles dark; trochanter darkened. Fore tibia mostly with one to two robust bristles among the vestiture, two exceptions with no bristles among vestiture; tibial organ comprising more than half of tibial apex, consisting of a patch of bristles surrounded by a robust circular border. Mid tibia with five to six robust bristles among vestiture, located on anterioventral and posterioventral side. Hind tibia with several robust bristles on anterioventral, posterior and posterioventral sides and a longitudinal row of robust bristles, which comprises three quarters of tibial length. Basal tarsomere of all legs with conspicuous robust bristles. All tibial spurs equal in length. Claws with one robust tooth and several minor teeth. **Abdomen.** Pale brown, with long dark bristles. **Hypopygium** (Fig. 50) brown. Gonocoxites wider than long, ventrally not fused, without a basal lobe of bristles. Gonostylus long and apically curved, giving it a hump-backed appearance, 2.6–3.2 times longer than wide; apically with dense setae and a group of approximately five to seven spines; subapically with two medium-sized whip-lash hairs; inner base of gonostylus without a noticeable angle. Tegmen strongly sclerotized, slightly wider than long, base very strongly sclerotized with long parameral apodemes; lateral margin of tegmen with a sclerotized edge; laterally scattered with several small teeth; sclerotized edge surrounds apex of tegmen, exceptionally with a small interruption apically; dorsal structures well developed, at least as long as two-thirds of tegmen or reaching apex of the tegmen. Area of teeth mostly impoverished, without teeth or with a few tiny teeth (maximally up to fifteen; one exception with twenty teeth). Ejaculatory apodeme long, broad, and very dark, with a long base. Posterior portion of gonocoxal apodeme broad and brown. Anterior portion of gonocoxal apodeme narrow and long.

Body size: 2.0–2.5 mm.

Female. Unknown.

Genetic distances. The maximum p-distance between all twelve available COI sequences is 1.82% (0.61%, if the specimens SDEI-Dipt-0000681 & SDEI-Dipt-0001232 are omitted). The nearest neighbour is *Psl. macrotegmenta*, diverging by a minimum of 1.84%. The maximum p-distance between all twelve available 28S sequences is 0.06%. Some of these sequences are identical to those of *Psl. frederickedwardsi*, *Psl. gonotegmenta*, *Psl. huttoni*, *Psl. jaschhofi*, *Psl. macrotegmenta*, *Psl. plicitegmenta*, *Psl. robustotegmenta*, *Psl. subtilitegmenta*, and *Psl. tonnoiri*.

Etymology. The newly described species is named after Prof. Dr Werner Mohrig (1937–2019), who had fruitfully worked on sciarid taxonomy for over five decades.

Distribution. New Zealand.

Discussion. Three of the paratypes of *Psl. macrotegmenta*, designated by Mohrig & Jaschhof (1999), actually represent *Psl. wernermohrigi*. Both cryptic species share the remarkable lateral teeth on the tegmen margin with five other species (*Psl. dentitegmenta*, *Psl. huttoni*, *Psl. plicitegmenta*, *Psl. gonotegmenta*, and *Psl. subtilitegmenta*). However, unlike *Psl. macrotegmenta*, the sclerotized margin of the tegmen of *Psl. wernermohrigi* is broad and surrounds the apex without any gap. This character can also be found in *Psl. huttoni*, but compared to this species and the other species with lateral teeth on the tegmen, *Psl. wernermohrigi* has the longest ejaculatory apodeme. Only *Psl. dentitegmenta* has an ejaculatory apodeme of a similar length, but has a tegmen with major differences.

Two specimens (SDEI-Dipt-0000681 & SDEI-Dipt-0001232) were identified as *Psl. wernermohrigi* based on morphology. However, their genetic data differ from other conspecific specimens, which were also barcoded. Their highest p-distance for the COI gene with regard to other *Psl. wernermohrigi* specimens is 1.82%, which is a high value in this species complex. Consequently, both specimens are in a sister-group relationship with respect to the remaining *Psl. wernermohrigi* specimens (Fig. 61). Thus, the existence of a further species cannot be completely ruled out. Both specimens were treated as additional material and not included in the type series.

***Pseudolycoriella dentitegmenta* sp. n.**
(Fig. 60)
urn:lsid:zoobank.org:act:4C5B54A5-1BA7-478F-9879-5C3DCCEF1815

Material studied. *Holotype male*. New Zealand: North Island, Taupo, Pureora Forest, Select Loop Road, Malaise trap, 15.07–23.08.2001, leg. M. & C. Jaschhof (NZAC, SDEI-Dipt-0000594).

Description. *Male*. **Head** brown; eye bridge one to three facets wide. Flagellomeres brown, paler than head, concolourous with scape and pedicel; fourth flagellomere 3.1 times as long as wide; necks of flagellomeres differentiated; surface of flagellomeres rough with deep pits; sensilla of two different lengths present; setae sparse, approximately as long as flagellomere width, bases of setae with slightly raised coronas. Prefrons and clypeus moderately bulging. Maxillary palp three-segmented; first palpomere longest, third slightly longer than second; first palpomere with three bristles and an inconspicuous patch of sensilla. **Thorax** brown, slightly paler than head. Posterior pronotum bare. Anterior pronotum with seven bristles. Episternum 1 with ten bristles. Mesonotum with five longer bristles among the lateral bristles; row of dorsocentral bristles well developed. Scutellum with two robust and some shorter bristles. Katepisternum bicoloured, basal part pale brown, apically brown; as long as high. **Wing.** Length 2.9 mm; width/length ratio 0.38. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct, all without macrotrichia; apical third of R_5 with additional macrotrichia on ventral side; bM bare; r-m with one macrotrichium; R_1 short, 0.71 times as long as R; M-fork longer than M stem; c/w ratio 0.71; r-m and bM equal in length. Haltere pale brown. **Legs** pale brown; coxal bristles dark. Fore tibia without bristles among vestiture; tibial organ comprising half of tibial apex, consisting of a transverse patch of bristles surrounded by a robust circular border. Mid tibia with two robust bristles; one anterioventrally and one posterioventrally among the vestiture. Hind tibia with several robust bristles on anterioventral, posterior and posterioventral sides and a longitudinal row of robust bristles, which extends two-thirds of tibial length. Basal tarsomere of all legs with conspicuous robust bristles. All tibial spurs equal in length. Claws with one robust tooth and several minor teeth. **Abdomen.** Pale brown, with dark bristles. **Hypopygium** (Fig. 60) brown. Gonocoxites wider than long, ventrally v-shaped and not fused, without a basal lobe of bristles. Gonostylus long and slender, curved slightly inwards, 3.9 times longer than wide; apically with dense setae and a group of approximately six spines; subapically with two medium-sized whip-lash hairs. Tegmen longer than wide, base very strongly sclerotized with medium-sized, robust parameral apodeme; lateral margin of tegmen with a sclerotized margin; several small teeth scattered on lateral and subapical margin; apex of tegmen membranous; dorsal structures on tegmen indicated. Area of teeth with 15 conspicuous teeth. Ejaculatory apodeme medium-sized, broad, and very dark, with a broad, horseshoe-shaped base. Posterior portion of gonocoxal apodeme broad and brown. Anterior portion of gonocoxal apodeme not present.

Body size: 2.8 mm.

Female. Unknown.

Genetic distances. No genetic data available.

Etymology. The epithet of the new species is composed of the two Latin words *dentis* (teeth) and *tegmen* (cover; technical term for a part of the sciarid hypopygium).

Distribution. New Zealand.

Discussion. Due to the presence of several small spines and two whip-lash hairs on the gonostylus *Psl*. *dentitegmenta* can easily be recognized as a species of the *Psl*. *macrotegmenta* group. However, it is unique because of the long tegmen with many scattered subapical teeth. Furthermore *Psl*. *dentitegmenta* has the longest body length, wing length, and length-width ratio of the gonostylus in this species complex.

***Pseudolycoriella breviseta* Mohrig, 1999**
(Fig. 59)

Literature. *Pseudolycoriella breviseta* Mohrig, 1999: Mohrig & Jaschhof (1999): 41, Fig. 21 a–f.—Macfarlane *et al*. (2010): 441.

Material studied. *Holotype male*. New Zealand: North Island, Northland, Waipoua Forest, 45 km northwest of Dargaville, sweep net, 31.12.1992, leg. M. Jaschhof (PWMP). *Paratypes*. 3♂♂ same location and same date as holotype (all PWMP). 2♂♂ North Island, Northland, Puketi Forest, Waipapa River Valley, sweep net, 01–02.01.1993, leg. M. Jaschhof (PWMP & SDEI).

Description. See Mohrig & Jaschhof (1999).

Genetic distances. No genetic data available.

Remarks. Due to the numerous short spines on the gonostylus and the short whip-lash hairs *Psl. breviseta* belongs to the *Psl. macrotegmenta* complex. The lateral projections on the tegmen are unique among the species of the genus *Pseudolycoriella*. Unfortunately, no new records could be obtained; consequently, no genetic information for this species is available. According to the New Zealand Arthropod Collection (2019) the sixth paratype of *Psl. breviseta* (NZAC02016075) that was not examined in the present study is labelled with a different sampling locality compared to Mohrig & Jaschhof (1999). Instead of Puketi Forest the sampling locality is given as East Egmont (North Island, Taranaki, Mount Egmont National Park), which would be the southernmost locality of this species.

Pseudolycoriella frederickedwardsi Köhler, 2016

(Fig. 57)

Literature. *Pseudolycoriella macrotegmenta* Mohrig, 1999: Mohrig & Jaschhof (1999): 41–43 [misidentification].—*Pseudolycoriella frederickedwardsi* Köhler, 2016: Köhler & Mohrig (2016): 101–103, Fig. 5 A-D.

Material studied. *Previously published material*: 1♂ New Zealand: North Island, Thames-Coromandel, Coromandel Range, 5 km east of Coromandel, *Podocarpus* wood, 28.12.1992, leg. M. Jaschhof (PWMP [misidentified, wrongly designated as paratype *Psl. macrotegmenta* in Mohrig & Jaschhof (1999)]). *New records*. 7♂♂ North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, mixed podocarp/broadleaf forest [type locality], sweep net, 03–04.02.2002, leg. M. Jaschhof (3x NZAC, SDEI-Dipt-0000945, SDEI-Dipt-0000947 & SDEI-Dipt-0001530; 4x SDEI, SDEI-Dipt-0000772, SDEI-Dipt-0001531 & SDEI-Dipt-0001535). 7♂♂ North Island, same locality as previous, Malaise trap, 26.11–28.12.2002, leg. M. & C. Jaschhof & U. Kallweit (3x NZAC, SDEI-Dipt-0001221, SDEI-Dipt-0001224 & SDEI-Dipt-0001537; 4x SDEI, SDEI-Dipt-0000756, SDEI-Dipt-0001237, SDEI-Dipt-0001241 & SDEI-Dipt-0001247). 5♂♂, North Island, Taupo, Pureora Forest, Select Loop Road, altitude 500 m, mixed mature podocarp forest, Malaise trap, 15.07–23.08.2001, leg. M. & C. Jaschhof (2x NZAC, SDEI-Dipt-0000568 & SDEI-Dipt-0001507; 3x SDEI, SDEI-Dipt-0001508, SDEI-Dipt-0001509 & SDEI-Dipt-0001510). 4♂♂ North Island, Taupo, Pureora Forest Park, Waipapa Reserve, altitude 600 m, mixed podocarp/broadleaf forest, sweep net, 04–05.02.2002, leg. M. Jaschhof (1x NZAC; 3x SDEI, SDEI-Dipt-0000823).

Description. See Köhler & Mohrig (2016).

Genetic distances. The maximum p-distance between all eleven available COI sequences is 0.46%. The nearest neighbour is *Psl. huttoni*, diverging by a minimum of 2.75%. The maximum p-distance between all twelve available 28S sequences is 0.17%. Some of these sequences are identical to those of *Psl. gonotegmenta*, *Psl. huttoni*, *Psl. jaschhofi*, *Psl. macrotegmenta*, *Psl. plicitegmenta*, *Psl. robustotegmenta*, *Psl. subtilitegmenta*, *Psl. tonnoiri*, and *Psl. wernermohrigi*.

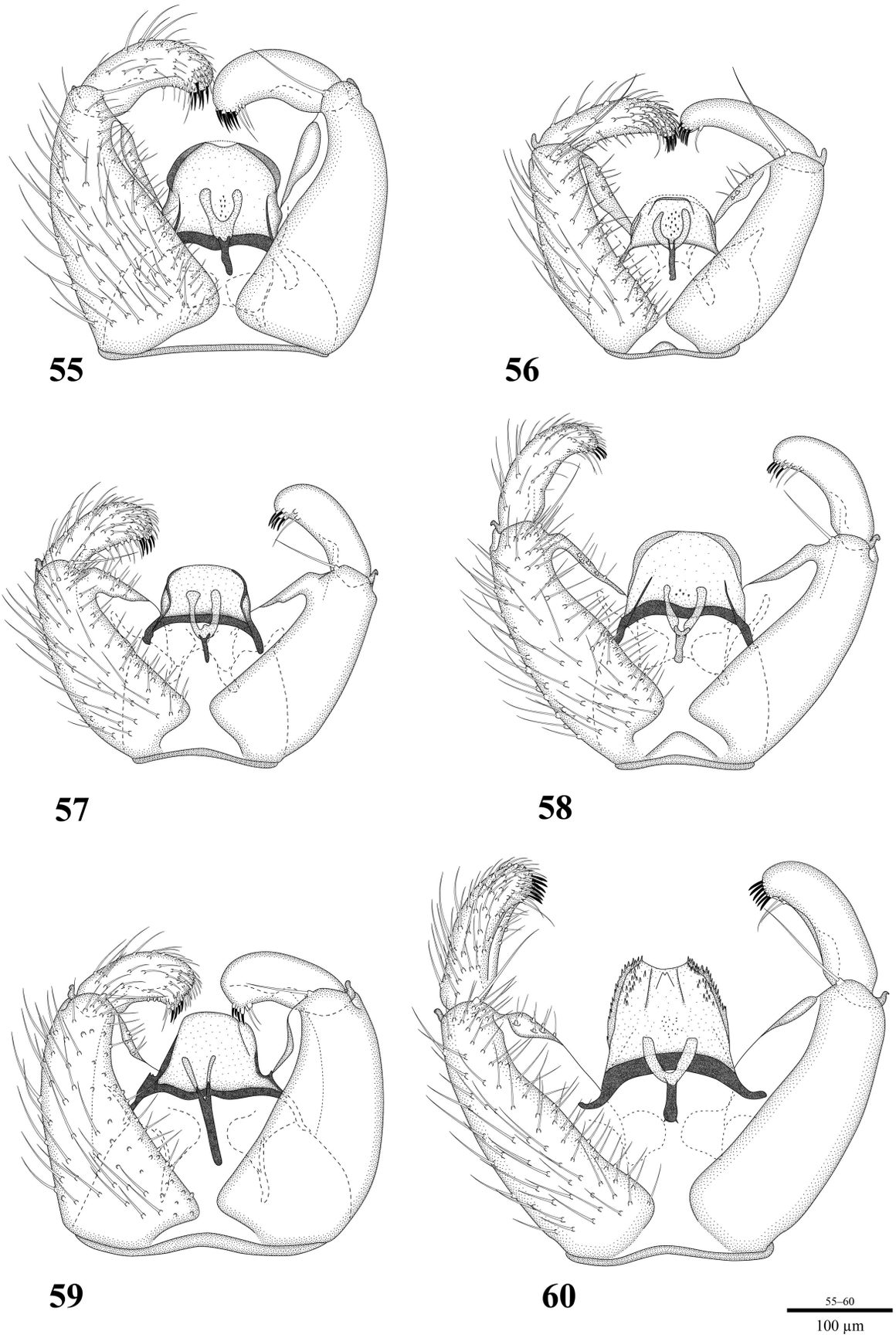
Remarks. Among the paratypes of *Psl. macrotegmenta*, designated by Mohrig & Jaschhof (1999), there was one specimen of *Psl. frederickedwardsi* (see *Psl. macrotegmenta*). Dorsal structures on the tegmen, which occur in several species of this complex, are absent.

Pseudolycoriella tonnoiri Köhler, 2016

(Fig. 58)

Literature. *Pseudolycoriella tonnoiri* Köhler, 2016: Köhler & Mohrig (2016): 104–106, Fig. 6 A–D.

Material studied. *New records*. 6♂♂ New Zealand: North Island, Ruapehu, Tongariro NP, Mangawhero River Valley 3 km NE Ohakune, altitude 690 m, mixed podocarp/broadleaf forest, sweep net, 03–04.02.2002, leg. M. Jaschhof (3x NZAC, SDEI-Dipt-0000813, SDEI-Dipt-0000856 & SDEI-Dipt-0001532; 3x SDEI, SDEI-Dipt-0001534). 3♂♂ same locality as previous, Malaise trap, 26.11–28.12.2002, leg. M. & C. Jaschhof & U. Kallweit (1x NZAC, SDEI-Dipt-0001536; 2x SDEI, SDEI-Dipt-0000597 & SDEI-Dipt-0000980). 2♂♂ South Island, Selwyn,



FIGURES 55–60. *Pseudolycoriella macrotegmenta* complex, hypopygia. **55.** *Pseudolycoriella fiordlandia* **sp. n. 56.** *Pseudolycoriella jaschhofi* **sp. n. 57.** *Pseudolycoriella frederickedwardsi* Köhler **58.** *Pseudolycoriella tonnoiri* Köhler **59.** *Pseudolycoriella breviseta* Mohrig **60.** *Pseudolycoriella dentitegmenta* **sp. n.**

Cass, Middle Bush, *Nothofagus solandri* forest, stream site, Malaise trap, 17.11.1998, leg. P.M. Johns (NZAC, SDEI-Dipt-0000719; SDEI, SDEI-Dipt-0000722). 3♂♂ South Island, Clutha, Catlins, Purakaunui Scenic Reserve, mixed podocarp/broadleaf/*Nothofagus* forest, Malaise trap, 27.01–05.03.2002, M. & C. Jaschhof (1x NZAC, SDEI-Dipt-0000531; 2x SDEI, SDEI-Dipt-0001140 & SDEI-Dipt-0001152).

Description. See Köhler & Mohrig (2016).

Genetic distances. The maximum p-distance between all eleven available COI sequences is 0.15%. The nearest neighbour is *Psl. gonotegmenta*, diverging by a minimum of 2.75%. All four available 28S sequences are identical and do not show any differences to those of *Psl. frederickedwardsi*, *Psl. gonotegmenta*, *Psl. huttoni*, *Psl. jaschhofi*, *Psl. macrotegmenta*, *Psl. plicitegmenta*, *Psl. robustotegmenta*, *Psl. subtilitegmenta*, and *Psl. wernermohrigi*.

Remarks. The presence of the dorsal structures on the tegmen has to be added to the description of Köhler & Mohrig (2016). These structures do not exceed half the length of the tegmen.

***Pseudolycoriella jaschhofi* sp. n.**

(Fig. 56)

urn:lsid:zoobank.org:act:6010CE99-5267-410E-8C40-D522E7D378B3

Material studied. *Holotype male*. New Zealand: South Island, Buller, Lewis Pass, altitude 850 m, tussock grassland at beech forest edge, Malaise trap, 26.11–25.12.2001, leg. M. & C. Jaschhof (NZAC, SDEI-Dipt-0001199). *Paratypes*. 12♂♂ same locality and same date as holotype (6x NZAC, SDEI-Dipt-0001036, SDEI-Dipt-0001207, SDEI-Dipt-0001209 & SDEI-Dipt-0001210; 6x SDEI, SDEI-Dipt-0001198, SDEI-Dipt-0001201, SDEI-Dipt-0001203 & SDEI-Dipt-0001217). 5♂♂ South Island, Southland, Fiordland, Fiordland NP, 4 km E Milford Sound, mixed broadleaf/*Nothofagus* forest, sweep net, 07.01.2002, leg. M. Jaschhof (3x NZAC, SDEI-Dipt-0001332, SDEI-Dipt-0001341 & SDEI-Dipt-0001342; 2x SDEI, SDEI-Dipt-0000892 & SDEI-Dipt-0000896). 8♂♂ South Island, Southland, Fiordland, Fiordland NP, Hollyford River Valley, Moraine Creek Track, mixed podocarp/*Nothofagus* forest, Malaise trap, 05–24.01.2002, M. & C. Jaschhof (4x NZAC, SDEI-Dipt-0001343, SDEI-Dipt-0001345, SDEI-Dipt-0001512, SDEI-Dipt-0001513; 4x SDEI, SDEI-Dipt-0001344, SDEI-Dipt-0001511, SDEI-Dipt-0001514 & SDEI-Dipt-0001515). 8♂♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, Deer Flat, *Nothofagus* forest, Malaise trap, 04–24.01.2002, leg. M. & C. Jaschhof (4x NZAC; 4x SDEI). 1♂ same locality as previous, Malaise trap, 01–20.12.2002, leg, M. & C. Jaschhof & U. Kallweit (SDEI, SDEI-Dipt-0000962). 6♂♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, opposite Earl Mountain Tracks, *Nothofagus* forest, Malaise trap, 05–24.01.2002, leg. M. & C. Jaschhof (3x NZAC, SDEI-Dipt-0000848, SDEI-Dipt-0000850 & SDEI-Dipt-0000851; 3x SDEI, SDEI-Dipt-0000852, SDEI-Dipt-0000868 & SDEI-Dipt-0000872). 4♂♂ South Island, Southland, Otago Lakes, Fiordland NP, Hollyford River Valley S Divide Creek, mixed *Nothofagus*/broadleaf forest, Malaise trap, 06–24.01.2002, leg. M. & C. Jaschhof (2x NZAC; 2x SDEI).

Description. *Male*. **Head** brown; eye bridge one to three facets wide. Flagellomeres concolourous with scape and pedicel; fourth flagellomere 2.6–3.1 times as long as wide; necks of flagellomeres differentiated; surface of flagellomeres rough with deep pits; sensilla of two different length; setae sparsely scattered, approximately as long as flagellomere width, bases of setae with slightly raised coronas. Prefrons and clypeus moderately bulging. Maxillary palp three-segmented; first palpomere longest, third slightly longer than second; first palpomere with up to five bristles and an inconspicuous small patch of sensilla. **Thorax** pale brown, paler than head. Posterior pronotum bare. Anterior pronotum with two to five bristles. Episternum 1 with four to ten bristles. Mesonotum with several longer bristles among the laterals and among the dorsocentral bristles. Scutellum with four robust and some shorter bristles. Katepisternum bicoloured, basal part pale brown, apical third brown; as long as high. **Wing.** Length 1.9–2.2 mm; width/length ratio 0.35–0.41. Membrane transparent and without macrotrichia, anal area present; all posterior veins distinct except faint stem of M, all without macrotrichia; apical quarter of R_5 with two to seven additional macrotrichia on ventral side; bM and r-m bare, r-m exceptionally with one to two macrotrichia; R_1 short, 0.67–0.80 times as long as R; M-fork longer than stem of M; c/w ratio 0.67–0.72; r-m and bM equal in length. Haltere pale brown. **Legs** pale brown; coxal bristles dark. Fore tibia with one to two bristles among vestiture on ventral side; tibial organ comprising more than half of tibial apex, consisting of a transverse patch of bristles surrounded by a robust circular border. Mid tibia with one or two anterioventral and two to four posterioventral robust bristles among vestiture. Hind tibia with several robust bristles on anterioventral, posterior and posterioventral sides and a longitudinal row of robust bristles, which extends along two-thirds of length of tibia. Basal tarsomere of all legs with conspicuous robust

bristles. All tibial spurs equal in length. Claws with teeth. **Abdomen.** Pale brown, with dark bristles. **Hypopygium** (Fig. 56) as pale brown as abdomen. Gonocoxites wider than long; ventrally v-shaped and not fused, without a basal lobe of bristles. Gonostylus slender, apical quarter curved inwards, 3.3–4.0 times longer than wide; apically with dense setae and a group of approximately eight small spines; subapically one short whip-lash hair, which is two times as long as the apical spines. Tegmen broad and membranous, only strongly sclerotized on lateral and basal margins; wider than long, with short parameral apodemes; apically membranous with a robust hood-like structure; dorsal structures absent. Area of teeth with six to 20 conspicuous teeth. Ejaculatory apodeme short and very dark with a large base. Posterior portion of gonocoxal apodeme long and brown. Anterior portion of gonocoxal apodeme apodeme long.

Body size: 1.8–2.5 mm.

Female. Unknown.

Genetic distances. The maximum p-distance between all 13 available COI sequences is 1.83%. The nearest neighbour is *Psl. teo*, diverging by a minimum of 4.92%. The maximum p-distance between all three available 28S sequences is 0.49% (this high p-distance results from some ambigious positions at the beginning of one sequence [SDEI-Dipt-0001511]). Some of these sequences are identical to those of *Psl. frederickedwardsi*, *Psl. gonotegmenta*, *Psl. huttoni*, *Psl. macrotegmenta*, *Psl. plicitegmenta*, *Psl. robustotegmenta*, *Psl. subtilitegmenta*, *Psl. tonnoiri*, and *Psl. wernermohrigi*.

Etymology. The new species is named after Dr Mathias Jaschhof, to honour his work on the Sciaroidea and to express the author's thanks for his manifold support.

Distribution. New Zealand.

Discussion. Among the species of the *Psl. macrotegmenta* complex this new species can easily be recognised by the hood-like structure on the tegmen, which otherwise only appears in *Psl. aotearoa* and *Psl. zealandica*. Furthermore, *Psl. jaschhofi* has a very elongated gonostylus, which it only shares with the otherwise unmistakable *Psl. dentitegmenta*. *Pseudolycoriella attrita* Mohrig from Papua New Guinea has very similarly shaped gonostyli and tegmen (Mohrig, 2013), but a much smaller body size and shorter flagellomeres (1.8 *vs*. 2.6–3.1). Additionally, the two gonostylar spines of *Psl. attrita* are well developed and clearly visible among the apical setae, while in *Psl. jaschhofi* the spines are more numerous and not so easy to distinguish from the apical setae.

***Pseudolycoriella fiordlandia* sp. n.**

(Fig. 55)

urn:lsid:zoobank.org:act:0CEEA4EF-C3F2-427F-86D4-B4A203964228

Material studied. *Holotype male*. New Zealand: South Island, Southland, Fiordland, Fiordland NP, 3 km E Milford Sound, mixed podocarp/broadleaf forest, Malaise trap, 01–21.12.2002, leg. M. & C. Jaschhof & U. Kallweit (NZAC). *Paratypes*. 5♂♂ South Island, Southland, Otago Lakes, Fiordland NP, Eglinton River Valley, Deer Flat, *Nothofagus* forest, Malaise trap, 01–20.12.2002, leg. M. & C. Jaschhof & U. Kallweit (2x NZAC; 3x SDEI).

Description. *Male*. **Head** brown; eye bridge two to three facets wide. Scape and pedicel concolourous with flagellomeres; fourth flagellomere 2.4–2.8 times as long as wide; necks of flagellomeres differentiated; surface of flagellomeres rough with deep pits; sensilla of two different lengths; setae sparsely scattered, approximately as long as flagellomere width, more curved towards the apex; some setae on the basal flagellomeres with conspicuous bases. Prefrons and clypeus moderately bulging. Maxillary palp three-segmented; first palpomere longest, third slightly longer than second; first palpomere with three to four bristles and an inconspicuous patch of sensilla. **Thorax** pale brown, slightly paler than head. Posterior pronotum bare. Anterior pronotum with five to eight bristles. Episternum 1 with six to eight bristles. Mesonotum with several longer bristles among the lateral bristles and among the dorsocentral bristles. Scutellum with four robust and some shorter bristles. Katepisternum bicoloured, basal part pale brown, apical third brown; as long as high. **Wing.** Length 1.8–2.0 mm; width/length ratio 0.39–0.42. Membrane transparent and without macrotrichia, anal area well developed; all posterior veins distinct except faint stem of M, all without macrotrichia; apical quarter of R_5 with macrotrichia on the ventral and dorsal side; bM and r-m bare, r-m exceptionally with one to two macrotrichia (in three of the paratypes, only developed on one wing each); R_1 short, 0.58–0.80 times as long as R; M-fork longer than stem of M; c/w ratio 0.60–0.75; r-m/bM 0.6–0.8 (not easy to measure due to faint stem of M). Haltere brown. **Legs** pale brown, except mid and hind coxae which are slightly darker; coxal bristles dark. Fore tibia with one to two spines among vestiture on ventral side; tibial organ comprising

more than half of tibial apex, consisting of a patch of bristles surrounded by a robust circular border. Mid tibia with three to four robust anterioventral and up to two posterioventral spines among the vestiture. Hind tibia with a dorsal, posterioventral and a ventral row of robust spines; the dorsal one three-quarters of the tibia length. Basal tarsomere of all legs with conspicuous robust spines. All tibial spurs equal in length. Claws with two teeth. **Abdomen.** Pale brown, with dark bristles. **Hypopygium** (Fig. 55) pale brown, like the abdomen. Gonocoxites longer than wide; ventrally v-shaped and not fused, without a basal lobe of bristles; apex of gonocoxites stretched. Gonostylus curved, bean shaped, 2.8–3.4 times longer than wide; in basal third with a robust insertion area for the adductor tendon; apically with dense setae and a group of approximately ten small spines, which are not easy to distinguish; subapically one to two long whip-lash hairs. Tegmen large and strongly sclerotized; as long as wide, with very robust parameral apodemes; margin of tegmen laterally sclerotized and with a prominent ledge on each side; sclerotized margin apically interrupted by a small membranous area; dorsal structures present. Area of teeth with approximately ten tiny teeth. Ejaculatory apodeme very dark with a large slightly paler base. Posterior portion of gonocoxal apodeme apodeme broad and brown. Anterior portion of gonocoxal apodeme apodeme medium-sized and dark.

Body size: 1.6–1.9 mm.

Female. Unknown.

Genetic distances. No genetic data available.

Etymology. The new species is named after the Fiordland National Park where the type locality and the second sampling site are located.

Distribution. New Zealand.

Discussion. *Pseudolycoriella fiordlandia* has a unique tegmen with conspicuous lateral ledges and very robust parameral apodemes. In addition, the gonostyli are more curved than in the other species of this complex.

Phylogenetic tree

According to the software Modelfinder (implemented in IQ-TREE), the best DNA substitution model for the three concatenated nuclear and mitochondrial genes is GTR+F+R4 (general time reversible model with unequal rates and unequal base frequencies (Tavaré 1986)). The phylogenetic tree based on this model is shown in Figure 61. The Log-likelihood of this tree is -18,016.987. The calulation strongly supports the monophyly of the Sciaridae but does not yield an adequately supported UFBootstrap value for the *Pseudolycoriella* cluster. The first internal branching results in two major subclades both with high UFBoot support. One major subclade contains an undescribed *Psl.* species from China and the New Zealand *Psl. macrotegmenta* complex, whose status as a monophyletic group is highly supported. The first internal branching of the *Psl. macrotegmenta* complex is *Psl. jaschhofi* and remaining species of this complex. The remaining species do not show high genetic distances. The clusters of specimens belonging to *Psl. wernermohrigi* and *Psl. frederickedwardsi* are supported by high UFBootstrap values (≥ 99%). Another highly supported cluster contains a mixture of four species—*Psl. gonotegmenta*, *Psl. plicitegmenta*, *Psl. subtilitegmenta* and *Psl. robustotegmenta*. None of these four species can be discriminated by the genetic markers used.

The second major subclade of *Pseudolycoriella* consists of *Psl. cavatica* + (an undescribed *Psl.* species from Korea + (the remaining New Zealand representative of *Pseudolycoriella* + (*Psl. horribilis* + another undescribed *Psl.* species from Korea))). The clade of the remaining representatives of *Pseudolycoriella* shows an unsolved trichotomy of the supported *Psl. jejuna* complex, a supported branch of the *Psl. zealandica* complex and an unsupported branch of *Psl. kaikoura* + *Psl. bispina* complex. The branch of the *Psl. jejuna* complex and nearly all its internal nodes with only two exceptions are highly supported. The two internal nodes of the *Psl. zealandica* complex are supported by the UFBootstrap approximation. Nearly all internal nodes of the *Psl. bispina* complex are also highly supported. Only the position of *Psl. teo* within the *Psl. bispina* complex remains uncertain.

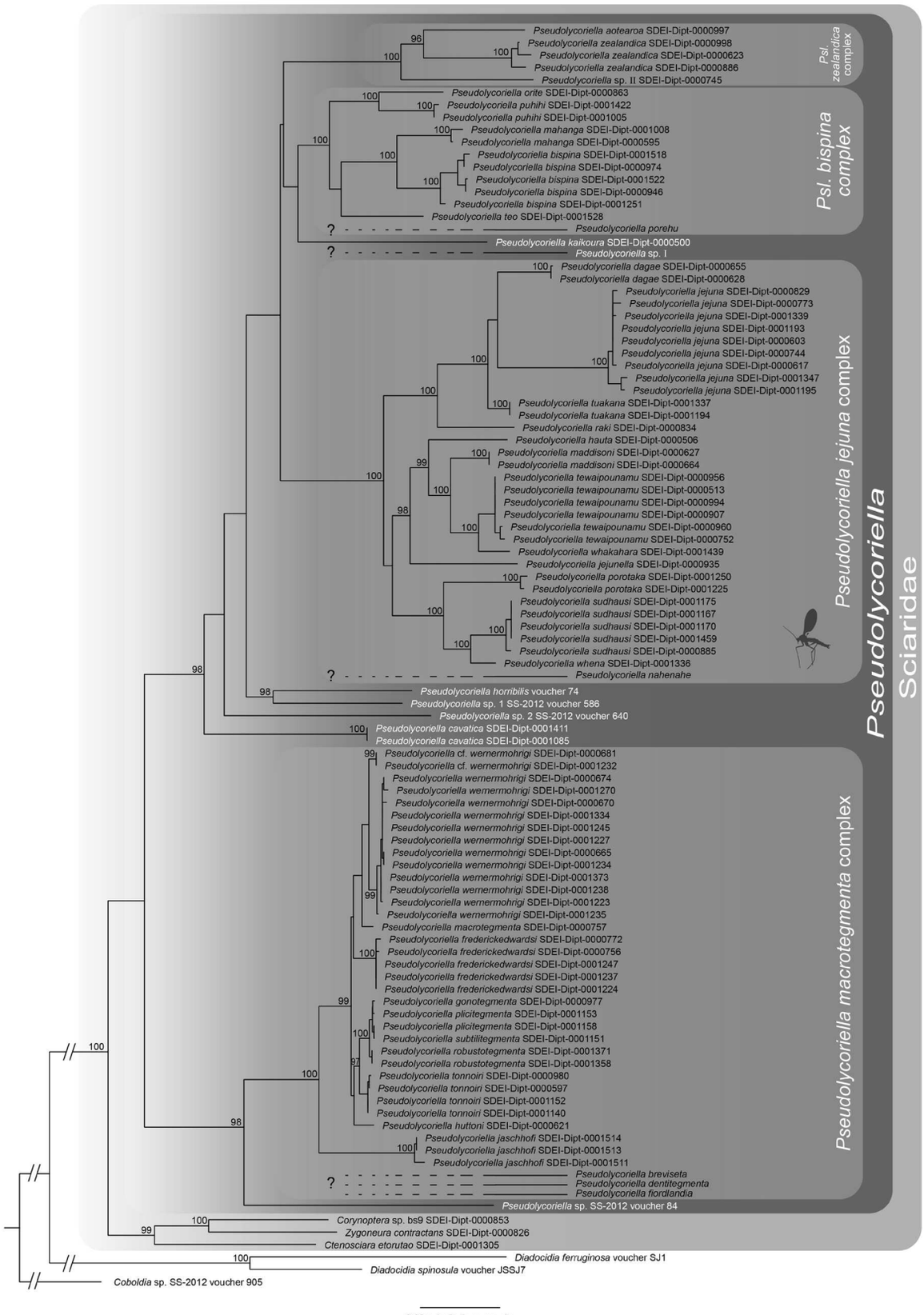


FIGURE 61. Phylogenetic tree of the New Zealand *Pseudolycoriella* species inferred from Maximum Likelihood analysis based on three concatenated genes (COI, 16S, and 28S; total length 3,053 bp) applying the model GTR+F+R4. Ultrafast bootstrap values (UFBoot; 1,000 replicates) are given if these values are greater than or equal to 95%. Intraspecific UFBoot values are not specified. *Pseudolycoriella* species without available genetic data are also inserted and assigned to a species complex according to the morphological results.

Discussion

The present study demonstrates a high diversity of New Zealand *Pseudolycoriella* species. The number of species has increased from seven to 36. Twenty-eight species were described as new for science and one species—the widely distributed *Psl. cavatica*—is newly recorded for New Zealand. Two further species are only represented by female specimens and have not yet been described. Hopefully future projects will record and recognise their male counterparts by barcode matching. These undescribed species and the circumstance that it was not possible to provide new records for *Psl. breviseta* indicates that even more, still unknown New Zealand *Pseudolycoriella* species are to be expected. The existence of such a large proportion of new species is not unusual in sciarids. For instance, Savage *et al*. (2019) stated that 129 described Canadian sciarid species exist, compared to 2,863 BINs. Even in the comparatively well studied Western Palaearctic the use of molecular techniques has revealed hitherto unknown cryptic species complexes (Heller *et al*. 2016). Subsequently, the small community of sciarid taxonomists still faces a mammoth task.

Interestingly, apart from two species—the probably introduced *Psl. cavatica* and the autochthonous *Psl. kaikoura*—nearly all New Zealand *Psl*. species are grouped in only four different species complexes. In the present study the term "species complex" is used instead of "species group". The reason is that in sciarid taxonomy "species groups" are used for a provisional clustering of similar species mostly for determination purposes and without detailed consideration of the underlying phylogenetic relationship. Another reason for avoiding the term "species group" is that three of the discovered species complexes could be incorporated into the *Psl. bruckii* group without any problems. Only the *Psl. macrotegmenta* complex can be considered as a separate group of species, which is not covered by the currently used species group concepts for *Pseudolycoriella*. Among these *Pseudolycoriella* taxa, the applicability of molecular markers, in particular the frequently used COI gene, differs greatly. Of the New Zealand members of the *Psl. bruckii* group (represented by *Psl. cavatica* and *Psl. kaikoura* and the species complexes grouped around *Psl. bispina*, *Psl. jejuna*, and *Psl. zealandica*) the genetic distances are sufficient enough to allow an allocation of a sequence to a known species. The lowest p-distance between two specimens of different species ranges from 3.51% (between *Psl. tewaipounamu* and *Psl. whakahara*) to 12.21% between (*Psl. aotearoa* and *Psl. zealandica*). Only the intraspezific p-distance of *Psl. puhihi* is in this range (4.44%). Otherwise this value lies between 0% and 3.07% in *Psl. bispina*. The median of the lowest interspecific p-distances is 7.14%. The median of the intraspecific p-distances is 0.76%. Contrary to the *Psl. bruckii* group, the COI p-distances between species of the *Psl. macrotegmenta* complex are lower and do not always allow a clear delimitation of the species. This issue is best illustrated by *Psl. gonotegmenta*, *Psl. plicitegmenta*, and *Psl. subtilitegmenta*, which partly show identical sequences. Among the remaining species the value of the lowest p-distance ranges between 0.61% (between *Psl. gonotegmenta* and *Psl. robustotegmenta*) to 4.92% between (*Psl. jaschhofi* and *Psl. teo*). The median is 1.84%. The intraspecific p-distances range from 0% to 1.83% (*Psl. jaschhofi*), with a median of 0.15%. Such inapplicability of COI barcoding has also been observed in other insect groups, e.g. in some sawflies (Prous *et al*. 2017) and in some hoverflies (Haarto & Ståhls 2014). It is to be assumed that the *Psl. macrotegmenta* complex has undergone a recent radiation and that this speciation process is not yet reflected by the nuclear 28S gene. In the mitchondrial COI gene the radiation is only partially mirrored, e.g. three species that are morphologically well separated show identical COI sequences, possibly due to incomplete lineage sorting. Introgression may also be a factor. In this context, it is noteworthy that two of these probably recently diverged species—*Psl. plicitegmenta* and *Psl. subtilitegmenta*—were caught at the same locality, i.e., occur sympatrically. This implies the existence of adequate reproductive barriers. Some other sibling species pairs were caught at the same localities, e.g. *Psl. jejuna*/*Psl. tuakana* and *Psl. aoteraoa*/*Psl. zealandica*. However, in these cases at least the COI sequences support the morphological species delimitation.

A temporary result of the present study is a predominance of the genus *Pseudolycoriella* with 36 species compared to a total of 82 New Zealand sciarid species. This highly unnatural situation will change with further taxonomic work in the other Sciarid genera of New Zealand. It is highly likely that the genera *Corynoptera* Winnertz and *Ctenosciara* Tuomikoski also contain several undescribed species and cryptic species complexes in New Zealand.

Acknowledgment

The author is indebted to the DGaaE (German Society of general and applied Entomology) for their generous funding and to Frank Menzel (Müncheberg, Germany) for the possibility to work with these puzzling and challenging gnats at the SDEI. The extensive collections of Catrin and Mathias Jaschhof (both Färjestaden, Sweden), and Peter A. Maddison (Katikati, New Zealand) were an elementary and indispensable resource for this study. Other collectors, who kindly caught sciarids in New Zealand, were Ian Hogg, John Hutcheson, Peter M. Johns, Uwe Kallweit, Roderick P. Macfarlane, and Andreas Stark. Werner Mohrig, who passed away on 26th April 2019, and Duncan Sivell (formerly London, UK) are thanked for loans of type material from collections curated by them. Pekka Vilkamaa (Helsinki, Finland) also kindly provided some specimens for this study. Valerie Levesque-Beaudin (Guelph, Canada) gave some helpful information about the specimens held in the Centre for Biodiversity Genomics. Katja Kramp (Müncheberg) introduced the author into molecular lab techniques and the methodology of genetic analyses. Furthermore, she and Marko Prous (Müncheberg) discussed and answered several questions about these issues. Without the assistance of Christian Kutscher (Müncheberg) no SEM investigation would have been possible. Andrew Liston (Müncheberg) proofread the manuscript and improved the language significantly. Finally, Adam Broadley (Melbourne, Australia) and Hans-Georg Rudzinski (Schwanewede, Germany) carried out the extremely helpful task of reviewing the manuscript. The author would like to express his sincere thanks to everyone.

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Article

Northern Richness, Southern Dead End—Origin and Dispersal Events of *Pseudolycoriella* (Sciaridae, Diptera) between New Zealand's Main Islands

Arne Köhler [1,2,*] and Thomas Schmitt [1,3]

[1] Senckenberg German Entomological Institute, 15374 Müncheberg, Germany; thomas.schmitt@senckenberg.de
[2] Developmental Biology, Institute of Biology, Martin Luther University of Halle-Wittenberg, 06120 Halle (Saale), Germany
[3] Entomology and Biogeography, Institute of Biochemistry and Biology, Faculty of Science, University of Potsdam, 14476 Potsdam, Germany
* Correspondence: arne.koehler@senckenberg.de

Simple Summary: The New Zealand species of a genus of black fungus gnats show clear phylogeographic patterns, at the species level and above. North Island harbours more species than South Island, and according to our phylogeographic analyses, was more often the starting point of dispersal events to South Island than vice versa. We therefore deduce that North Island is a radiation centre. Initial colonisations of New Zealand took place three times, most likely starting from Australia, with the earliest in the late Miocene.

Abstract: Sciaridae (Diptera) is a widespread insect family of which some species can reach high abundances in arboreal habitats. This trait, together with their (passive) mobility, enables them to quickly colonise suitable habitats. To reveal the biogeographic history of the New Zealand members of the sciarid genus *Pseudolycoriella*, we analysed three molecular markers of selected species and populations in a Bayesian approach. At the intra- and interspecific levels, we detected a pattern of northern richness vs. southern purity, which has probably developed as a result of Pleistocene glacial cycles. Since the late Miocene, we identified 13 dispersal events across the sea strait separating New Zealand's main islands. As nine of these dispersal events were south-directed, North Island can be considered the centre of radiation for this genus. An unequivocal re-colonisation of North Island was only observed once. Based on the inclusion of three undescribed species from Tasmania and on previously published data, three colonisations of New Zealand are likely, all of them assumed to be of Australian origin. One of these most probably took place during the late Miocene, and the other two during the late Pliocene or at the Pliocene–Pleistocene boundary.

Keywords: Australia; colonisation; intraspecific distribution; island biogeography; phylogeography

Citation: Köhler, A.; Schmitt, T. Northern Richness, Southern Dead End—Origin and Dispersal Events of *Pseudolycoriella* (Sciaridae, Diptera) between New Zealand's Main Islands. *Insects* **2023**, *14*, 548. https://doi.org/10.3390/insects14060548

Academic Editors: Pekka Vilkamaa and Jukka Salmela

Received: 27 April 2023
Revised: 2 June 2023
Accepted: 7 June 2023
Published: 12 June 2023

1. Introduction

New Zealand and its biogeography have been investigated by generations of natural scientists. In this context, the origin of its unique biota as well as their distributions have been a focus of interest, and several studies have already addressed the biogeography of New Zealand's insects (see [1–3]). The cause of this uniqueness is New Zealand's outstanding geological genesis, and in particular its long and ongoing isolation from neighbouring landmasses. At the end of the Mesozoic, Zealandia—a landmass that comprised what today is New Caledonia and New Zealand—separated from Australia and then was further fragmented [1,4]. These fragments then experienced even more drastic geological events. At the Oligocene–Miocene boundary, the future New Zealand was affected by major inundations and almost entirely disappeared in the ocean, although the archipelago was never completely submerged [5,6]. The re-emerging landmasses were strongly affected

by plate tectonics, as a new plate boundary had formed in the Eocene, with today's North Island and the western part of South Island located on the Australian plate, while the remaining part of today's South Island is located on the Pacific plate. The land masses that represent the two extant main islands were separated by sea most of the time [7,8]. In the Pleistocene, ca. 1 Ma ago [8], eustatic lowering of the sea level formed land connections between the islands for the first time. However, due to the glacial cycles with their associated sea level oscillations, land bridges were ephemeral. Another still persisting consequence of these Pleistocene cycles is the well-known "beech gap"—a region in central South Island where the iconic southern beeches (*Nothofagus* spp.) have not re-colonised glacially devastated areas [9].

In arboreal habitats, Sciaridae are rich in species and in abundance [10]. These globally distributed gnats are minute to medium-sized, and due to their uniform habitus, they are easy to recognize as a group, but determination to the species level usually proves to be challenging. Therefore, it is not surprising that, despite their prominence and commonness, only the small minority of pest species has attracted wider attention. This is regrettable, because due to their ecological role as decomposers [11,12], their ability to establish populations at high abundances [10], and their ability to fly or disperse passively, they seem to be well-suited as model organisms for the assessment of biogeographic events. For instance, airborne dispersal was recorded at altitudes up to 3350 m above the South Pacific [13], and they have been found in arthropod fallout on snow fields near the summit of Mt. Teide on Tenerife [14]. Even the drifting of different developmental stages with plant material, or pure surface-floating, is easily conceivable [15].

A sciarid taxon well-suited for unravelling the colonisation and biogeographic history of New Zealand might be the genus *Pseudolycoriella*. In the course of a recent revision by Köhler [16], the number of known species on these islands rose from seven to thirty-eight. Two of these still do not have valid names, because formal descriptions are lacking: males of these—a prerequisite for species descriptions in sciarids—are not available. Only one of these New Zealand species, *P. cavatica*, is also known from other countries. Its wide distribution (recorded from Australia, Hawaii, New Caledonia, Seychelles, South Africa, and Tristan da Cunha [16]), intraspecific molecular data [17], and lack of a closer phylogenetic relationship to any other *Pseudolycoriella* species occurring in New Zealand [16] support the hypothesis that *P. cavatica* is an introduced species. Accordingly, this species was omitted from the subsequent analyses. Of the 37 autochthonous and endemic New Zealand species (both described and undescribed), 25 are known from more than one sample site. These species can be roughly assigned to four broad distribution patterns (Table 1). Only three native species are distributed throughout New Zealand. Another four species are found on North Island and the northern part of South Island. Twelve species are restricted to North Island, and six to South Island. The relative distribution of endemics in *Pseudolycoriella* on the two main islands differs significantly from the ratio expected according to Trewick et al. [18], who reviewed the regional insect endemicity of five major regions, but also from the expectation in relation to the area ratio of the two islands (Chi-square goodness of fit test: $X^2 \approx 4.5$ resp. $X^2 \approx 4.1$, $\alpha = 0.05$, df = 1). Thus, compared to South Island, North Island has a higher number of species than expected. Even the number of species currently known from only one sample site tends to show this biased distribution across both islands (six species from North Island vs. six from South Island).

Consequently, we decided to attempt a phylogenetic study in order to make these inhomogeneous distribution patterns comprehensible. We address the question of whether there is evidence that these patterns are the result of Pleistocene glaciation, or even of older geological phenomena. We also intend to draw conclusions on New Zealand's black gnat colonisation history. These data are compared against the background of the already known biogeographic patterns of New Zealand insects.

Table 1. Distribution of 26 out of 38 *Pseudolycoriella* species found at more than one sample locality across New Zealand according to Köhler [16]. A probably introduced species is marked with an asterisk.

Widely Distributed on Both Islands	Distributed on North Island and Northern South Island	Endemic to North Island	Endemic to South Island
P. cavatica *	*P. dagae*	*P. aoteraoa*	*P. fiordlandia*
P. subtilitegmenta	*P. gonotegmenta*	*P. bispina*	*P. jaschhofi*
P. tonnoiri	*P. macrotegmenta*	*P. breviseta*	*P. jejunella*
P. zealandica	*P. whena*	*P. frederickedwardsi*	*P. mahanga*
		P. jejuna	*P. sudhausi*
		P. maddisoni	*P. tewaipounamu*
		P. orite	
		P. porotaka	
		P. puhihi	
		P. raki	
		P. robustotegmenta	
		P. wernermohrigi	

2. Materials and Methods

Specimens were either collected by Catrin and Mathias Jaschhof in 2001 and 2002 (collecting permit #9900/143/3/04 issued by the Department of Conservation, New Zealand) or by Peter A. Maddison from 2014 to 2016. Thus, our biogeographic analyses are based on the material previously used by Köhler [16] for a taxonomic revision and description of new species. In addition to the material from New Zealand, specimens from Tasmania collected with Malaise traps at the Warra Long-term Ecological Research Site [19] were incorporated in the analyses.

DNA extraction and sequencing were performed as in Köhler [16]. We analysed three genes: cytochrome c oxidase subunit I (COI; 658 bp), the domains IV and V of the mitochondrial large subunit rRNA gene (16S; 538 bp), and the nuclear 28S ribosomal gene (28S; 1857 bp). The gene selection was based on the first phylogenetic study of sciarids by Shin et al. [11]. This mixture of rapidly evolving mitochondrial genes and a more conservative nuclear gene seems to be appropriate for the time scale under investigation, as already applied by Köhler [16]. In some cases, residual DNA from the DNA extraction by Köhler [16] was re-sequenced to eliminate ambiguities in COI or 16S sequence of some specimens. For this purpose, the primer Psl_COI_for (5′–ATTATAATTTTTTTYATAGTDATACC–3′) was designed and successfully applied. All sequences are available from GenBank, with the corresponding GenBank accession numbers listed in the electronic supplement (Table S1).

To enable intraspecific spatial analyses, the software Popart 1.7 [20] was used to generate median-joining haplotype networks [21] based on COI and 16S sequences. For the interspecific relationships and especially for the divergence time estimates, a Bayesian analysis was performed using the multilocus sequence data package *BEAST from the program BEAST 2.6.0 [22]. As two different monophyletic *Pseudolycoriella* species clades exist in New Zealand [16], we conducted two independent *BEAST analyses. Input files were generated with Beauti [23] using the following parameter settings: the HKY model as a substitution model, estimated base frequencies, four gamma categories, a strict clock model, and a birth–death model for the speciation process. If specimens of a species had identical haplotypes in all three genes, only the haplotype combination of one specimen was included in the input files. The input files comprise sequences from 95 specimens of 35 species (35 specimens of 13 species belonging to the *P. macrotegmenta* clade, and 60 specimens of 22 species of the second monophyletic group).

The (current) lack of fossil sciarids from New Zealand (this taxon is not mentioned by Schmidt et al. [24]) and of *Pseudolycoriella* globally does not permit direct calibration. Thus, fixed substitution rates were used: 0.01345 for the mitochondrial markers and 0.0006 for the nuclear marker. These rates were derived by Papadopoulou et al. [25] for the

same genes used in the present study based on the biogeography of tenebrionoid beetles driven by the formation of the Mid-Aegean trench 9–12 Ma ago. The Markov Chain Monte Carlo (MCMC) was set to a length of 20,000,000 generations with a sampling interval of 7500 iterations. The obtained samples were checked for sufficient effective sample size (ESS) values using the software Tracer 1.7.1 [26]. The initial 10% of the sampled generations were discarded as burn-in. The coalescence tree was generated with TreeAnnotator [23].

To draw inferences about the ancestral origin of New Zealand *Pseudolycoriella* species, the RASP 4.2 software [27,28] was used, applying the statistical dispersal–extinction–cladogenesis model (S-DEC). For this purpose, all specimen records were assigned to four major regions, i.e., Tasmania, North Island, the northern part of South Island, and the southern part of South Island including Stewart Island. Thereby, South Island was divided along 43°S, roughly corresponding to the northern edge of the "beech gap" [9]. A contiguous distribution is assumed for *P. subtilitegementa*, which was recorded in southern North Island and southern South Island [16].

For easier comprehension, all nodes of the two resulting chronograms are numbered consecutively, and branches are named after their delimiting nodes (indicated in the text with braces).

3. Results

3.1. Intraspecific Biogeographic Patterns

Four species were well-suited for the analyses of intraspecific biogeographic patterns. Two of these are distributed across both main islands, i.e., *P. tonnoiri* and *P. zealandica*. For these, 26 COI and 20 16S sequences as well as 44 COI and 42 16S sequences, respectively, were available. The calculated haplotype networks revealed a subdivision into populations on both sides of Cook Strait (Figure 1). While *P. tonnoiri* possesses two haplotypes, which only differ in one single substitution in COI (Figure 1A), *P. zealandica* was found to have a tripartite population structure with clear spatial structure (Figure 1B). The genetic diversity of the latter declines from North Island to South Island: five different haplotypes of both COI and 16S were recorded for North Island from two geographically very close localities (the corresponding points overlap in Figure 1B), while only three COI haplotypes and one 16S haplotype were obtained for South Island.

The two species *P. tewaipounamu* and *P. sudhausi* solely inhabit South Island and exhibit remarkable haplotype patterns. *Pseudolycoriella tewaipounamu* (50 COI, 46 16S sequences) has three genetic lineages exhibiting a clear phylogeographic pattern: in the north-west (Buller District; yellow circles in Figure 2A), the south-west (Westland and Southland Districts; red circles), and the south-east (Clutha District; blue circles) of South Island. The genetic diversity of the populations within these lineages varies strongly. Specimens from the north-western lineage exhibit the greatest differences and diversity in COI; the south-eastern lineage is also genetically diverse and well differentiated from the north-western lineage, while the sequences of the south-western lineage are all identical and represent a haplotype shared with the north-western lineage (Figure 2A). The 16S haplotype network indicates a pattern consistent with that of COI, although the differences at the population level are less marked or absent. The only major difference is the occurrence of a second haplotype in the south-western linage, resulting from an additional transition.

For *P. sudhausi* (19 COI, 16 16S sequences), three clusters are distinguished: on Stewart Island (blue circles in Figure 3A), and in the south-western (south of Fiordland; red circles) and western parts of South Island (north of Fiordland and on the West Coast; yellow circles). The shortest known geographic distance between sampling localities belonging to different genetic clusters lies in Fiordland and is only about 23 km (Figure 3B). Specimens of a southern lineage population were sampled along the Eglinton River West Branch valley, while members of the northern lineage were caught in the Hollyford River valley.

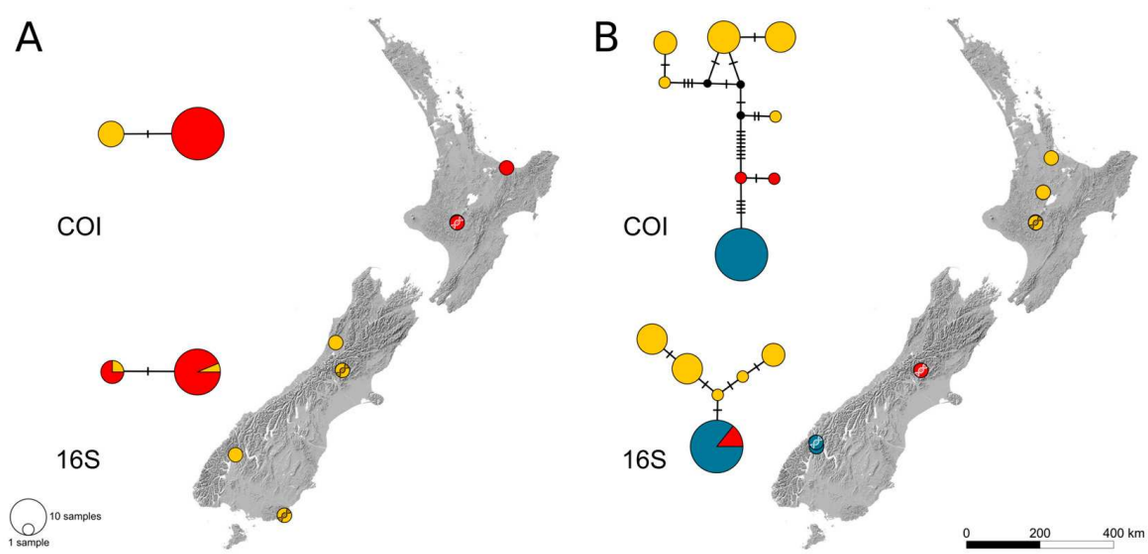

Figure 1. Haplotype networks (top COI, bottom 16S) and sample locations of (**A**) *Pseudolycoriella tonnoiri* and (**B**) *Pseudolycoriella zealandica*. Map sourced from the LINZ Data Service (CC BY 4.0 licence). Colours indicate different populations. Localities with successfully barcoded specimens are indicated by a DNA symbol.

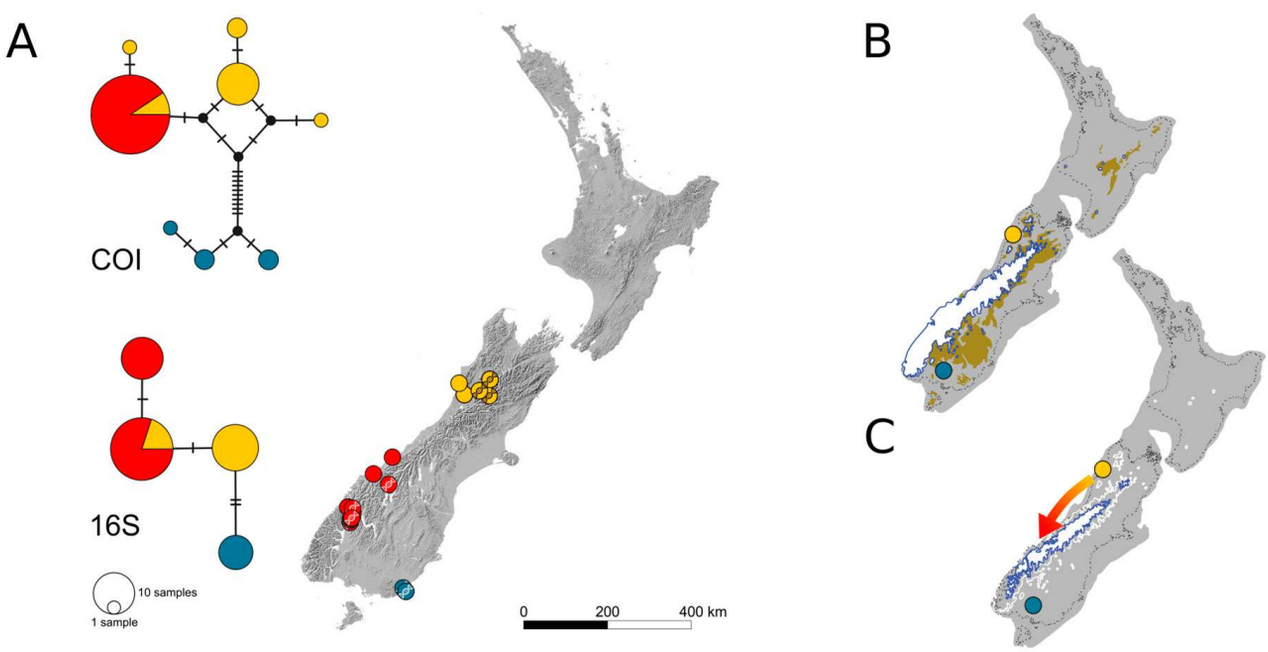

Figure 2. (**A**) Haplotype networks (top COI, bottom 16S) and sample locations of *Pseudolycoriella tewaipounamu*. Colours indicate different populations. Localities with successfully barcoded specimens are indicated by a DNA symbol. Map sourced from the LINZ Data Service (CC BY 4.0 licence). (**B**) Hypothetically separated populations during the Last Glacial Maximum (LGM) after McGlone et al. [29]. Glaciers coloured in white, tundra in light brown. (**C**) Hypothetical glacier retreat after the LGM and potential dispersal (indicated by an arrow). Glacier extent after the −4 °C model of Golledge et al. [30]. The ice shield extent during LGM is outlined in white.

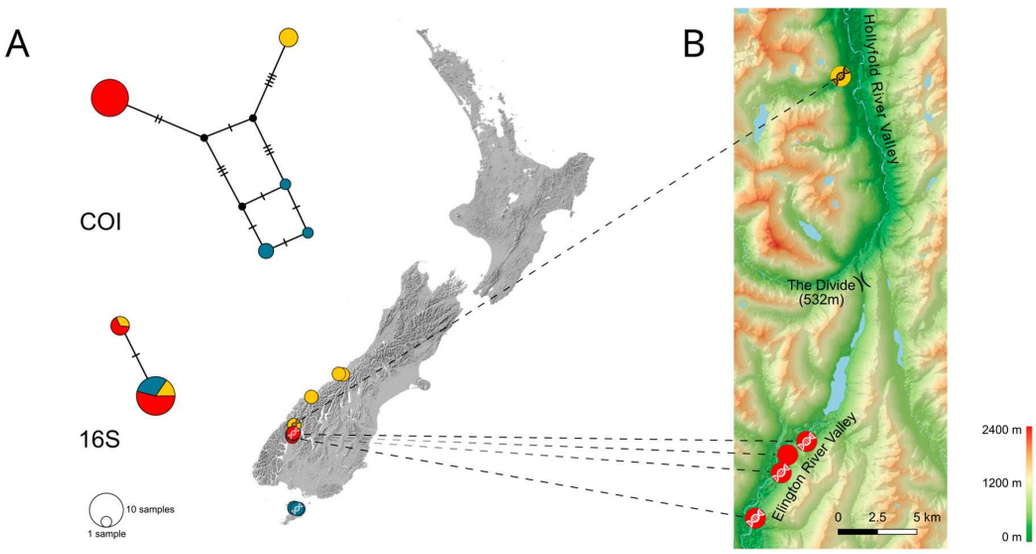

Figure 3. (**A**) Haplotype networks (top COI, bottom 16S) and sample locations of *Pseudolycoriella sudhausi*. Colours indicate different populations. Localities with successfully barcoded specimens are indicated by a DNA symbol. Map sourced from the LINZ Data Service (CC BY 4.0 licence). (**B**) Elevation map of the contact zone of two lineages of *P. sudhausi* in the south-east of South Island. Map based on ASTER GDEM data, provided by the Ministry of Economy Trade and Industry, Japan, and the National Aeronautics and Space Administration, USA.

3.2. Interspecific Differentiation and Phylogeny

The first monophylum of autochthonous New Zealand *Pseudolycoriella* species comprises the species closely related to *P. macrotegmenta* and is partitioned into three subclades (Figure 4). One includes the majority of nine species (*P. macrotegmenta* s. str. clade) and stands in a sister relationship with a subclade composed of three still—undescribed species from Tasmania. The most basal subclade is represented by a single New Zealand species (*P. jaschhofi*) and originated in a species split during the Pliocene or Pleistocene (node 1, 2.98 Ma; 95% HPD interval: 1.87–4.30 Ma). Of the subsequent eleven speciation events, three most likely took place in the early Pleistocene, while the others occurred not earlier than one million years ago. According to a RASP analysis, the most recent common ancestor (MRCA) of the *P. macrotegmenta* s. str. clade most likely inhabited North Island (node 5, 63.1%). The MRCA of the Tasmanian species and the *P. macrotegmenta* s. str. clade was probably distributed across Tasmania and North Island (node 2, 43.5%). The second most likely scenario—a solely Tasmanian distribution—has a probability value of 17.9%. For node 1, i.e., the most basal one, the probability values for the different distribution scenarios are close together and do not exceed 12.5%; thus, the distribution at this node remains unsolved.

The chronogram of the second monophyletic group of New Zealand *Pseudolycoriella* species (Figure 5) replicated the tripartite structure already shown in Köhler [16]. Accordingly, the naming of the three subclades after species whose names have been known for decades is retained (*P. zealandica*, *P. bispina*, and *P. jejuna* clade; indicated by different colours in Figure 5). Compared with the *P. macrotegmenta* clade, this monophyletic group has a longer speciation history. The first speciation occurred in the late Miocene (node 18, 9.95 Ma; 95% HPD interval: 7.45–12.38 Ma), and was followed by 20 species splits until the Pleistocene, evenly distributed across time. The phylogeographic analysis yielded a probability value of 51.8% that the MRCA of this group inhabited North Island (node 18). The *P. zealandica* clade is the youngest of these three taxa; the basal species split took place in the early Pliocene (node 19, 4.95 Ma; 95% HPD interval: 3.64–6.35 Ma). Its MRCA probably inhabited entire New Zealand (72.8%). The basal splits of the other species clades were assigned to the late Miocene: the speciation of the MRCA of the *P. bispina* clade was

estimated at 7.90 Ma (node 24; 95% HPD interval: 6.02–9.62 Ma) and that of the *P. jejuna* clade at 6.09 Ma (node 33; 95% HPD interval: 4.92–7.41 Ma). The most likely distribution of the MRCA of the *P. bispina* clade was North Island (87.3%). The probability values of the distribution of the *P. jejuna* clade are as follows: entire New Zealand 41.9%; North Island and the northern part of South Island 22.8%; and only North Island 29.0%. Based only on the highest probability values assigned to each MRCA of the 20 species splits that occurred in the three *Pseudolycoriella* clades, nine MRCAs were distributed in North Island, nine in both main islands, and two (nodes 38 and 41) in South Island.

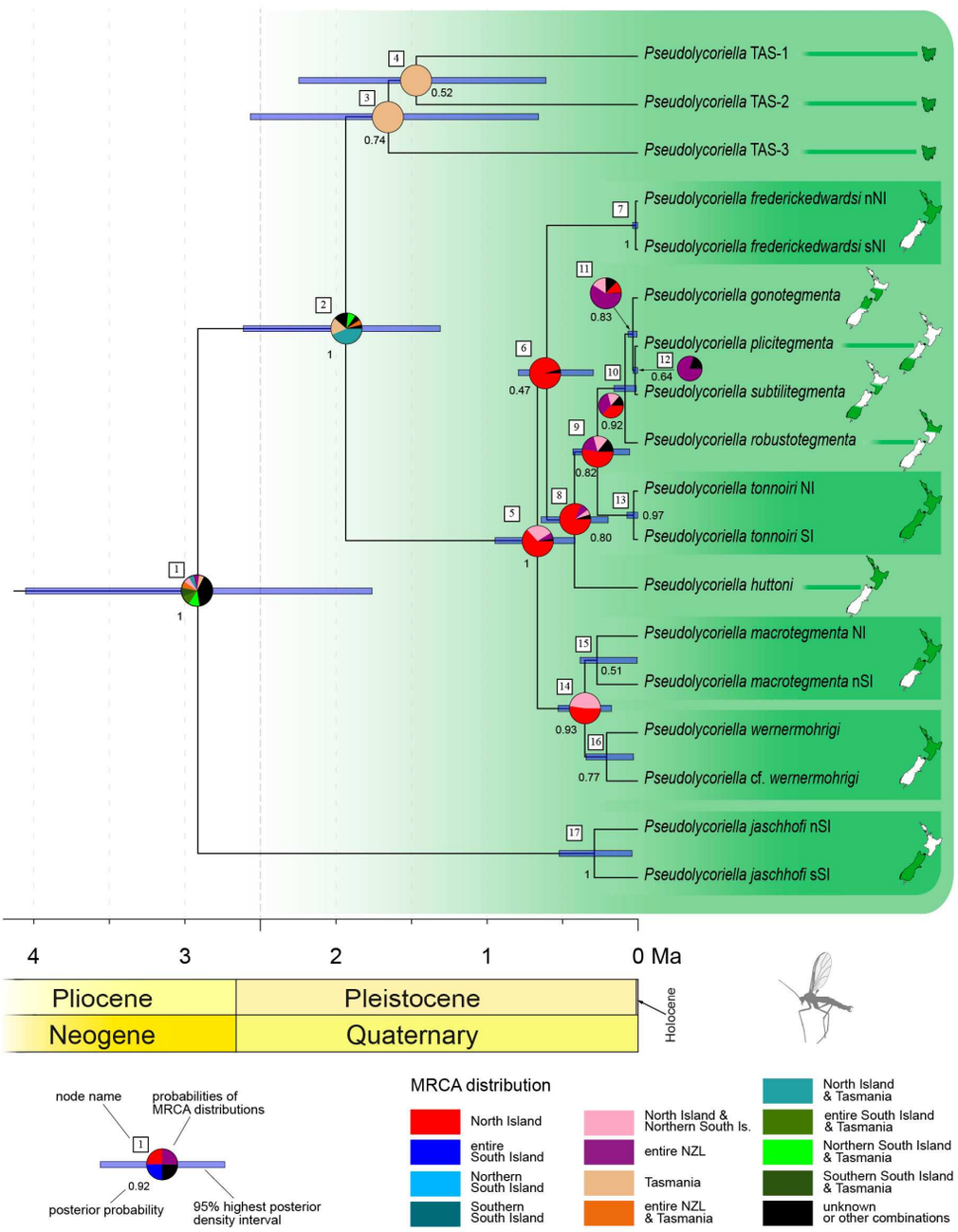

Figure 4. Chronogram of the *Pseudolycoriella macrotegmenta* species clade according to a *BEAST analysis (based on COI, 16S, and 28S). For each interspecific node, the probability of distributions of the respective taxon is depicted as a pie chart obtained from a RASP analysis (S-DEC). The distribution of each extant species is given by inserted maps (NI, North Island; nNI, northern North Island; nSI, northern South Island; SI, South Island; sNI, southern North Island; TAS, Tasmania).

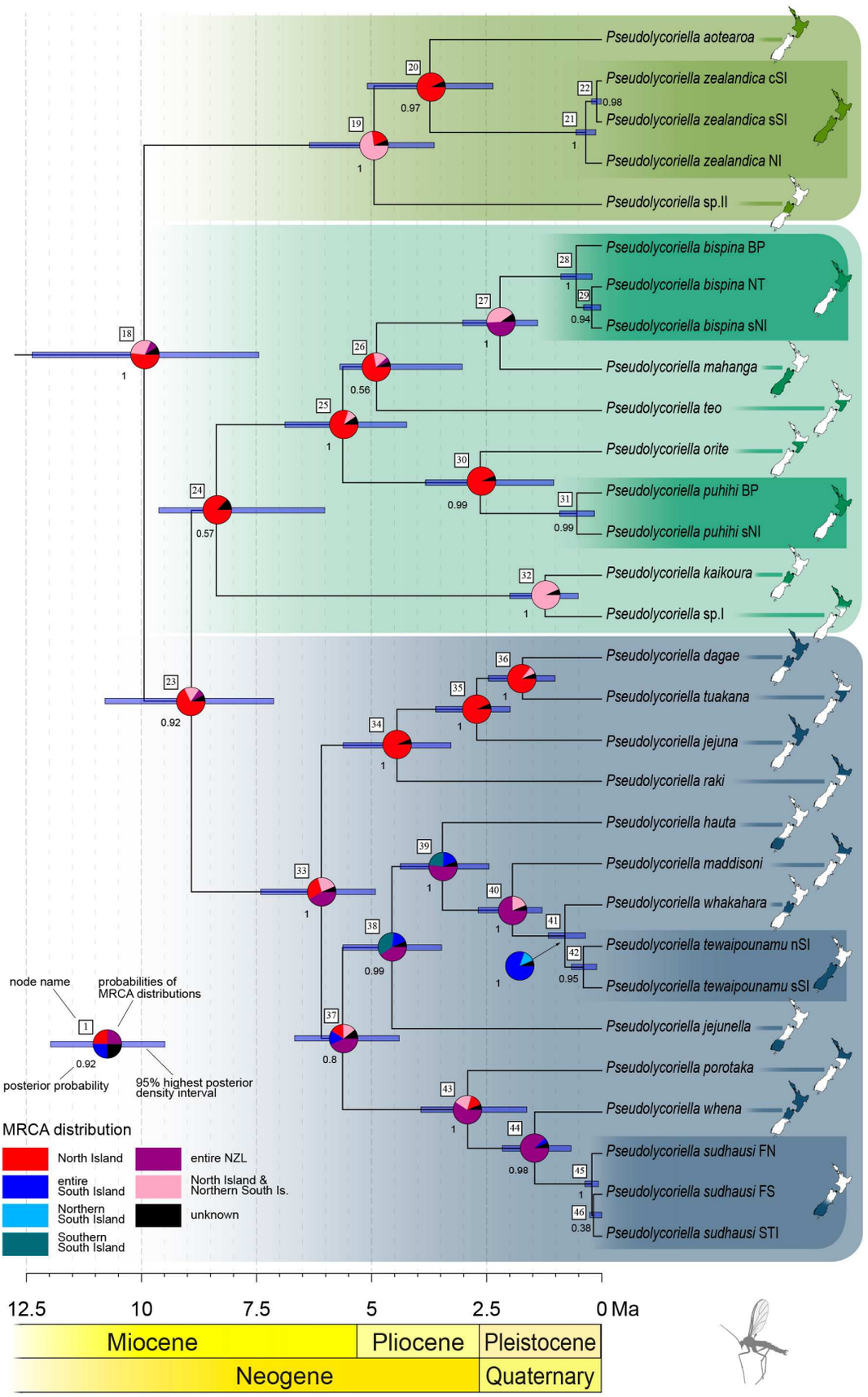

Figure 5. Chronogram consisting of the *Pseudolycoriella zealandica*, *P. bispina*, and *P. jejuna* clades according to a *BEAST analysis (based on COI; 16S, and 28S). For each interspecific node, the probability

of the stem species' distribution is depicted as a pie chart obtained from a RASP analysis (S-DEC). The distribution of each extant species is given by inserted maps (BP, Bay of Plenty; cSI, central South Island; FN, Fiordland North; FS, Fiordland South; NI, North Island; nSI, northern South Island; SI, South Island; NT, Taupo North; sNI, southern North Island; sSI, southern South Island; STI, Stewart Island).

Supplementary Tables S2 and S3 give the time estimates and probability values for each region of origin for all species distributions shown in Figures 4 and 5.

4. Discussion

4.1. Ice Ages and Their Influence on New Zealand's Scarids

The two analysed species, which are distributed across both large islands, i.e., *P. tonnoiri* and *P. zealandica*, both show spatial structuring of their haplotypes, with a clear split along Cook Strait. However, the level of diversity of haplotypes and their geographic distribution differs greatly between these species. In *P. tonnoiri*, the lineages differ in only a single base substitution. However, this species belongs to the *P. macrotegmenta* s. str. clade, whose species are generally not strongly genetically differentiated. This led Köhler [16] to the conclusion that their radiation is more recent than in other New Zealand *Pseudolycoriella* species groups. Consistent with this, the split between the two lineages of *P. tonnoiri* has an estimated median age of 28 ka, making it the most recent in our analysis (node 13 in Figure 4). As its ancestor (node 9 in Figures 4 and 6A–C) most likely inhabited only North Island, the most parsimonious explanation is that this region was the origin of *P. tonnoiri*. Interestingly, *P. tonnoiri* was recently reported from Auckland Island, more than 450 km south of New Zealand's main islands [31]. Thus, its occurrence on the remote Auckland Island might be a consequence of an ongoing southward dispersal.

In contrast, *P. zealandica* possesses several haplotypes, which are well-differentiated from each other by several mutational steps and exhibit a clear spatial structure. The genetic diversity of this species decreases from North Island to South Island, making an origin on North Island and a later dispersal to South Island the most probable scenario. *Pseudolycoriella zealandica* clearly manifests a pattern of northern richness and southern purity (also known as out-of-north pattern; cf. [18]). The tripartite spatial haplotype structure of *P. tewaipounamu* repeats this pattern, although the species is restricted to South Island. The phylogeographic structure within this species might be explained by the last ice age: two genetic lineages, estimated to be at least 112 ka old (node 42 in Figure 6), were forced to retreat into northern and south-eastern refugia on South Island as the ice shield of the Southern Alps reached its largest extent during the Last Glacial Maximum (LGM, Figure 2B). Shulmeister et al. [32] found evidence for a gradual warming during the early deglaciation instead of an abrupt warming. Thus, the retreat of the Southern Alps' ice sheet presumably started earlier on its northern margin. This might have allowed a leading-edge southwards expansion out of the north-western refugium, while the south-eastern lineage was still trapped (Figure 2C). It should be mentioned in this context that the Catlins (i.e., the most south-eastern part of South Island) have an extraordinary inventory of *Pseudolycoriella* species. Besides the aforementioned *P. tewaipounamu*, five other *Pseudolycoriella* species were collected there. Three of them (*P. hauta*, *P. plicitegmenta*, and *P. porehu*) were found exclusively in this region and seem to be endemic [16].

In the case of *P. sudhausi*, a recolonisation of the areas formerly covered by glaciers occurred not only from the North but also from the South. During postglacial range expansion, the lineages originating in the south-western and the western parts of South Island spread with the advancing forest habitats, finally meeting at the Divide (a pass of 532 m asl; Figure 3B) after approaching through two valley systems from opposite sides of the pass. However, a subsequent fusion of these lineages was probably prevented by high-density blocking [33]. The high density of specimens of a single lineage within the respective populations reduces the probability that immigrants from other populations will

find a suitable mate. Consequently, the possibility of them successfully reproducing with members of the local population is greatly reduced.

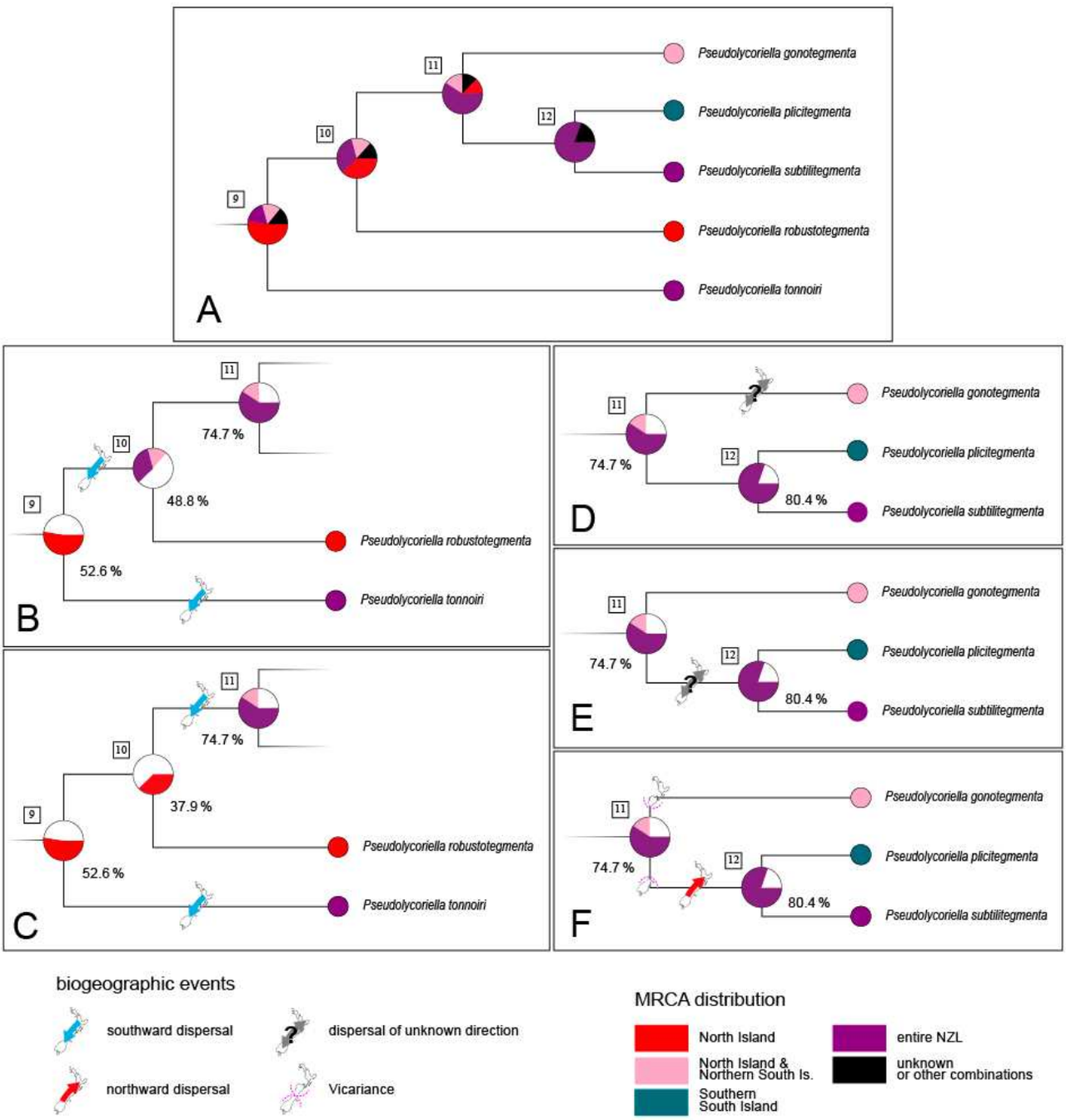

Figure 6. (**A**) Detail of Figure 4. (**B**,**C**) Possible scenarios for the current distribution patterns outgoing from node 9. (**D**–**F**) Possible scenarios for the current distribution patterns outgoing from node 11. Used colour codes for biogeographic events and (stem) species distributions are given below. At each node, the probability values for the considered MRCA distribution are given.

The intraspecific phylogeographic patterns of these *Pseudolycoriella* species resemble those known for other New Zealand taxa. Thus, a phylogeographic break along Cook Strait has been observed for several insect species, such as *Kikihia subalpina* (Cicadidae, Hemiptera) [34] and *Talitropsis sedilotti* (Rhaphidophoridae, Orthoptera) [35]. Examples of spatially structured subpopulations on South Island were found in *K. subalpina* [34], as well as the zopherid beetles *Epistranus lawsoni* and *Pristoderus bakewelli* (Zopheridae,

Coleoptera) [36]. Consequently, if a sufficient degree of taxonomic knowledge exists, Sciaridae is also a group that is well-suited for biogeographic analyses. This is particularly due to their high (albeit passive) mobility and their ability to quickly establish dense and large populations, which apparently do not intermix with other intraspecific lineages at secondary contact zones [37].

4.2. Island Hopping and Speciation

Speciation events can only occur on one of the main islands due to the (almost) persistent separation of these islands and the limited gene flow between the separate *Pseudolycoriella* lineages (see above). In the case of a species distributed throughout New Zealand, the speciation must therefore have been followed by a colonisation event. Hence, two principal basic types of colonisation have to be distinguished within New Zealand: from North Island to South Island, and vice versa. In most cases, the direction of these colonisation events can be deduced from the region of origin of the respective lineage as revealed by RASP analyses, similar to the interpretation approach applied above to *P. tonnoiri*, where an intraspecific differentiation on North Island was followed by a southward dispersal. Similar reasoning can also be applied to *P. macrotegmenta* at the intraspecific level, where a southward dispersal most likely took place before differentiation into the two island-specific lineages (branch {14,15} in Figure 4).

Besides these biogeographically clear cases, RASP analyses did not always reveal a conclusive indication of the regions of origin of consecutive species. Thus, the results for the closely related species *P. gonotegmenta*, *P. plicitegmenta*, *P. robustotegmenta*, and *P. subtilitegmenta* (outgoing from node 10 in Figures 4 and 6A) suggest a sequence of MRCAs with a distribution across entire New Zealand (node 11 and 12). The existence of descendants of a widespread species which also occur on both large islands would contradict our hypothesis of limited dispersal and thus a restricted gene flow between these islands. This scenario would require additional colonisation and extinction events and thus violate the principle of parsimony. However, the probability values for the origin of the root (node 10) of this four-species complex do not allow a clear distinction between the scenarios that the MRCA inhabited entire New Zealand (Figure 6B) or solely North Island (Figure 6C). Thus, a southward dispersal event might be assigned to branch {9,10} or branch {10,11}. The biogeographic events outgoing from node 11 also remain vague. Starting with the ancient species at node 11, which most likely existed across entire New Zealand, we have to account for at least one dispersal event (Figure 6D–E). This dispersal must have taken place either during the anagenesis of *P. gonotegmenta* (Figure 6D) or during the existence of its adelphotaxon prior to the differentiation at node 12 (Figure 6E). However, we could not deduce the direction, because it was not possible to assign the species split at node 11 to any region. A third possibility is a vicariance event which took place during the time of differentiation at node 11 (Figure 6F). In this case, the adelphotaxon of *P. gonotegmenta* (i.e., branch {11,12}) inhabited the southern part of South Island, from where it must have rapidly dispersed northwards. The dating estimate according to *Beast analysis supports such a scenario: an estimated mean age of 30.4 ka (95% HPD interval: 3.2–68.6 ka) is given for node 11. Thus, the species' split coincides with the time frame of the LGM (29–31 ka according to Williams et al. [38]), when New Zealand's islands were connected and the Southern Alps were largely covered by glaciers. A spatial separation of populations by these glaciers might be regarded as a plausible cause for the differentiation into two species initiated at node 11. Nevertheless, we consider this particular dispersal event to have an undetermined direction and that it occurred after the time frame of node 11. In total, the *P. macrotegmenta* s. str. clade—all species descend from node 5—has most likely undergone three North-to-South dispersal events and one of unknown direction.

Several dispersal events were also detectable for the second monophyletic group of autochthonous New Zealand *Pseudolycoriella* species. A dispersal event at the intraspecific level was already shown above for *P. zealandica*, assigned to branch {21,22}. A second intraspecific dispersal, with the same direction, was detected for *P. dagae*. Above the species

level, dispersal events were identified during the existence of branches {18,19}, {24,32}, {26,27}, and {39,40} (Figure 5). The dispersal event during the existence of branch {39,40} is particularly important, because it is the only one that was unequivocally in the direction of South Island to North Island.

At the root of the *P. jejuna* clade, a similar situation exists to that described above for the *P. gonotegmenta* species group. RASP analysis again reveals an entire-New-Zealand distribution of the MRCA and also for one of its descendants (node 33 and 37 in Figures 5 and 7). The MRCA was either distributed across entire New Zealand or solely on North Island. Thus, two scenarios are plausible: a southward dispersal before the split at node 33 (Figure 7A), or this dispersal event occurring in the time frame between split 33 and 37 (Figure 7B). Both scenarios require three dispersal events: in the first scenario, three south-directed events, and in the second scenario, one south-directed and two north-directed dispersal events. On average, the probability values of ancestral species ranges are higher in the first scenario. However, because of this ambiguity, we instead assign the first southward dispersal event on the composite branches {23,33,37} to a single branch. The subsequent events on branches {37,43,44} and {44,present} were regarded as events for which the direction of dispersal cannot be resolved.

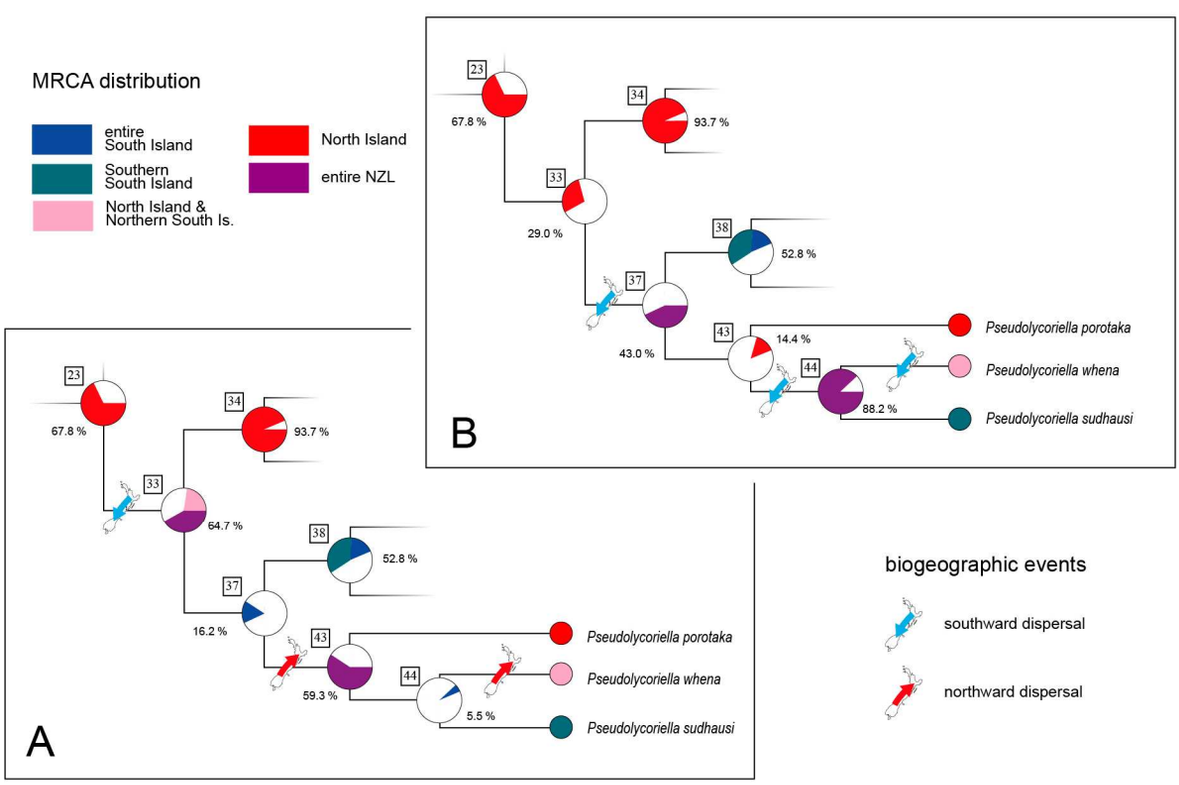

Figure 7. (**A**,**B**) Two possible scenarios for the current distribution patterns outgoing from node 23 in Figure 6. Used colour codes for biogeographic events and MRCA distributions are given. At each node, the probability values for the considered MRCA distribution are given.

Branches to which biogeographical events could be assigned were taken from both chronograms and are shown comparatively in Figure 8. A total of 13 colonisation events can be shown for both *Pseudolycoriella* species groups, with a clear directional disparity: nine events had a southern direction, one a northern direction, and three an unresolved direction. However, this picture is still incomplete, because genetic data are not available for all known species. Three of these genetically unsampled taxa inhabit North Island, and two South Island. Existing morphological data unfortunately do not allow their precise placement in the phylogenetic system (compare Figure 61 in Köhler [16]). Nevertheless, at least one further southward dispersal event has to be assumed for one species from South

Island (i.e., *P. porehu*), because morphology implies a closer relationship with the northern *P. orite* than the southern *P. mahanga* [16].

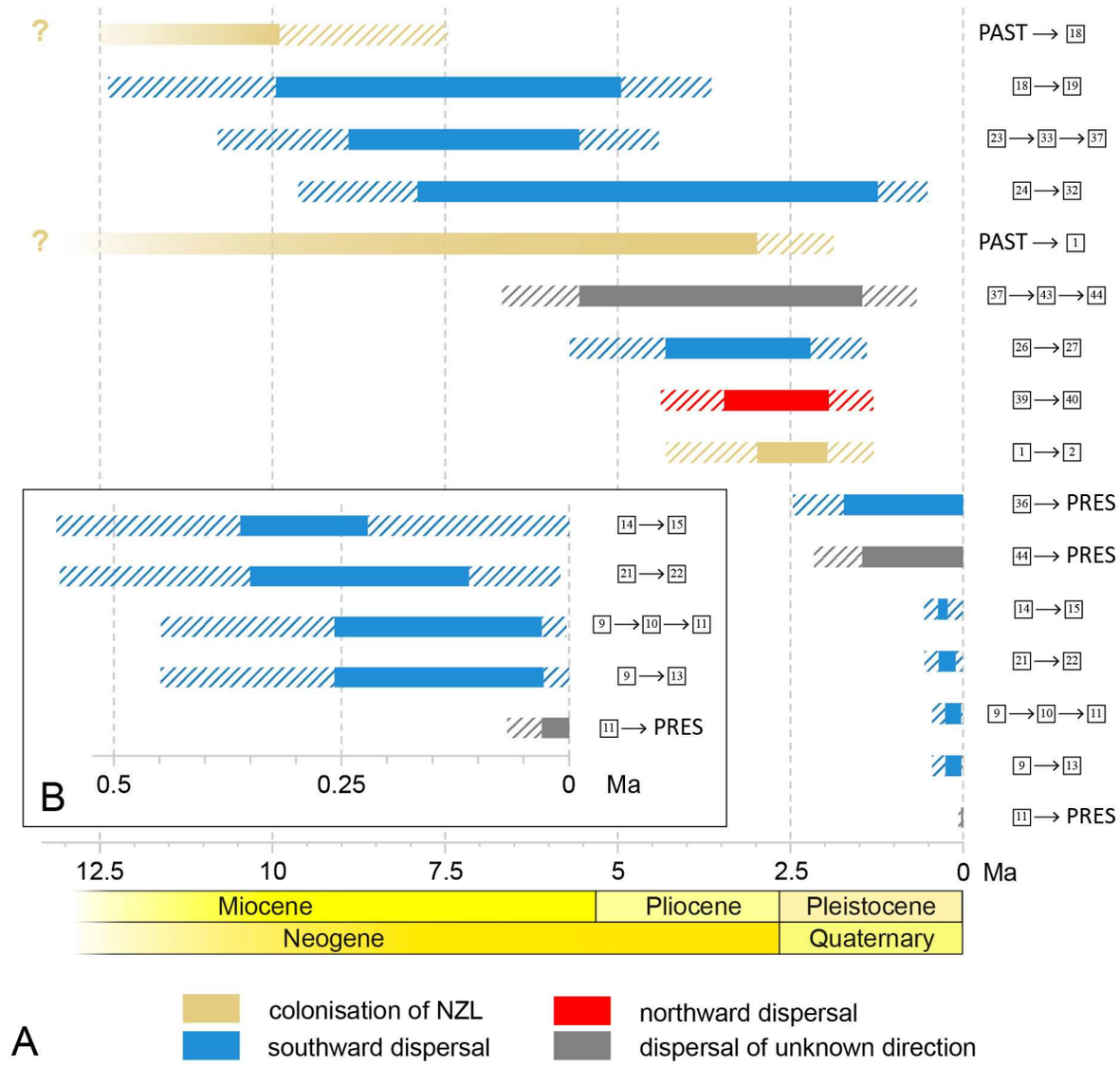

Figure 8. (**A**) Temporal comparison of all branches with dated biogeographic events from the chronograms in Figures 4 and 6. (**B**) Enlargement of the five most recent events. The branches are named after their bordering nodes given on the right. The outer 95% HPD interval of each branch bounding node is hatched. Used colour codes for biogeographic events are given below.

The dispersal events within New Zealand do not show any clear temporal pattern (Figure 8). Since the initial colonisation of New Zealand (see below), dispersal across the sea straits separating the main islands (Kuripapango Strait during the late Miocene–early Pliocene; Manawatu Strait during the late Pliocene; Cook Strait in recent years [8]), seems to be evenly distributed from the late Miocene to the present. Presumably, the number of events is too low and their resolution in time is not fine enough for the identification of possible periods with increased colonisation rates.

Due to imbalance in the migration direction, North Island has to be regarded as a radiation centre, while South Island is a receptor of immigrating taxa. Thus, taxa invading South Island from the North rarely speciated and even more rarely recolonised North Island. Consequently, the pattern of northern richness vs. southern purity, already demonstrated at the intraspecific level, is repeated at the species level.

In general, a poleward impoverishment of genetic diversity has commonly been observed, as shown by Hewitt [39] for Europe and North America, and is explained by the Pleistocene climatic cycles. The main reasons in the northern hemisphere are the extirpation of northern populations and the concentration of populations in southern refugia during glacial periods, and genetic bottlenecks during leading-edge expansions during interglacials. These general effects also apply to New Zealand, of course, with the compass directions reversed. However, forest communities persisted even in the southern parts of South Island during glacial maxima [4], speaking against a complete extinction of all southern populations of *Pseudolycoriella*. This assumption of constant survival of *Pseudolycoriella* even in the extreme South of New Zealand is clearly supported by our genetic data and also by the existence of species such as *P. hauta*, *P. plicitegmenta*, and *P. porehu*, which occur exclusively in this region.

Hence, an increased extinction rate cannot be considered to be the main cause of the lower biodiversity on South Island. As an alternative, a reduced speciation rate has to be taken into consideration, as observed by Buckley et al. [6] for zopherid beetles during the Miocene and Pliocene for New Zealand as a whole. At first glance, the presence of multiple forest refugia should lead to a greater number of geographically separated populations and thus to a higher probability of speciation events, but also to genetic bottlenecks. Furthermore, all southern populations presumably faced a time-lag in their postglacial dispersal opportunities, as we suggested for *P. tewaipounamu*. Therefore, southern populations could not colonise such large areas as their northern counterparts during interglacials. Consequently, they were not able to disperse to as many areas that became refugia during subsequent ice ages, which resulted in an on-average lower chance of becoming separated and erecting reproductive barriers within their ranges.

Although the existence of undiscovered *Pseudolycoriella* species is not unlikely, we consider our conclusions to be plausible. For one thing, we do not expect many undiscovered species, because although the focus of the fieldwork was on South Island, this was not reflected in a higher number of species compared to North Island. Furthermore, we consider it highly unlikely that our sample was so biased that the discovery of additional species would lead to significantly different patterns.

4.3. Colonisation of New Zealand

The most likely areas of origin for the colonisation of New Zealand are Australia and New Caledonia. Phylogenetic connections between Australia and New Zealand have been frequently observed, and were, for example, demonstrated for the well-known bioluminescent fungus gnat genus *Arachnocampa* (Keroplatidae, Diptera) [40]. However, links to New Caledonia are also possible, as for example known in New Zealand cicadas, for which two independent colonisations were identified: one from Australia and one from New Caledonia [41]. Although six publications from the last decade address the occurrence of *Pseudolycoriella* species in the countries neighbouring New Zealand, reporting 17 species for Australia and 14 for New Caledonia [42–47], the sciarid fauna of the Australasian and wider Pacific region is still poorly understood. Furthermore, all these studies are exclusively based on morphological analyses, which currently do not allow species-level hypotheses of relationships to be formulated, as would be possible with the use of appropriate molecular markers. Therefore, it was not possible to identify phylogenetic relationships outside New Zealand. The inclusion of three undescribed species from Tasmania in our study revealed that these represent a monophyletic group within the *P. macrotegmenta* lineage comprising New Zealand species. Thus, we must ask how often New Zealand was colonised by this genus.

In light of the fact that the genus *Pseudolycoriella* did not originate in New Zealand, as shown by the phylogenetic tree of Köhler [16], two mutually exclusive scenarios arise: two colonisation events by the MRCAs of the two monophyletic groups with a subsequent (re)colonisation of Tasmania starting from New Zealand, or three colonisation events. In the

latter case, the MRCA of the complete *P. macrotegmenta* lineage would also have originated in Tasmania/Eastern Australia.

To assess the likelihood of each possibility, we have to consider the ancient meteorological, oceanographic, and climatic conditions in the New Zealand region. An eastward aeolian or pleustonic transport of tiny dipterans from eastern Australia to New Zealand is easily conceivable because of (i) the steady westerly wind regime caused by the mid-latitude westerlies [48] as well as (ii) the eastward sea currents (eastern extension of the East Auckland Current between Australia and the northern tip of New Zealand [49] and the Subtropical Front reaching the southern parts of New Zealand [50]). Furthermore, these eastward-directed meteorological and oceanographic constellations are not of recent origin. Thus, the wind regime is assumed to already have existed in the Pliocene, as Li et al. [51] revealed that the westerlies experienced a poleward shift of 1.9 degrees 3.3 to 3.0 Ma ago. The sea currents reaching New Zealand are extensions of major global currents such as the South Pacific Gyre or the Antarctic Circumpolar Current, which also existed several million years ago [52].

Assuming that the probability of a single dispersal event is not homogeneously distributed over the associated branch of the chronogram, but rather that the colonisation events precede the splitting of the species only by a short time span, the first colonisation of New Zealand by an ancient *Pseudolycoriella* species might be hypothesised to have occurred approximately 10 Ma ago (on branch {past,18}). This is later than the mid-Miocene climatic optimum (~16.9–14.7 Ma [53]), after which the global climate started cooling down [54]. This cooling has also led to changes in New Zealand's vegetation structure [4,55,56], for example towards the dominance of southern beeches (*Nothofagus* spp.) in forest communities [55]. During this period, the rainforests in inland south-eastern Australia decreased, but the rainforest communities on the east coast persisted [57], which supports the hypothesis that the latter have been highly suitable for gnats and therefore might have served as a donor region for individuals drifting to New Zealand. For the other two potential colonisation events dated during the late Pliocene or to the Pliocene–Pleistocene boundary (on branches {past,1} and {1,2}), further cooling must be taken into consideration. Prebble et al. [56] dated the second major cooling episode of the last 30 Ma to this time frame. That the events in question are likely to have occurred during cooling periods, when species' ranges shift towards the equator [39], also points to an origin in temperate regions of Australia and not in tropical New Caledonia. However, the presumed steady patterns of air and water circulation cannot automatically be considered to have led to successful colonisation events, because these can be prevented by high-density blocking, as shown at a more regional and intraspecific level in the case of *P. sudhausi*. Consequently, in order to successfully colonise, arriving individuals would have to have a competitive advantage over the indigenous species in utilising the available resources. If climatic changes did not occur simultaneously in New Zealand and south-eastern Australia, the ancestors of today's New Zealand *Pseudolycoriella* species may already have been better adapted to cooler climates than New Zealand species using the same resources.

On the basis of all these considerations, we think that it is more likely that New Zealand was colonised three times by ancient *Pseudolycoriella* species originating from Australia. In this respect, our gnats are not special and join numerous examples of New Zealand insect taxa that originated in Australia [5]. Nevertheless, further faunistic and taxonomic work is needed on the sciarids of the Australian and the Oceanian realms, thus allowing increased use of Sciaridae to address biogeographic assessments.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/insects14060548/s1: Table S1. Sequenced specimens of *Pseudolycoriella* spp. (Sciaridae, Diptera) from New Zealand and Tasmania with GenBank accession numbers; Table S2. Time estimates and probability values for the MRCA distribution for each node of Figure 4; Table S3. Time estimates and probability values for the MRCA distribution for each node of Figure 5.

Author Contributions: Conceptualisation, A.K. and T.S.; analysis, A.K.; writing—original draft preparation, A.K. and T.S.; writing—review and editing, A.K. and T.S. All authors have read and agreed to the published version of the manuscript.

Funding: The first author was generously funded by the German Society for General and Applied Entomology (DGaaE; www.dgaae.de, accessed on 24 October 2016) and Senckenberg Leibniz Institution for Biodiversity and Earth System Research (SGN, accessed on 1 September 2019).

Data Availability Statement: The genetic data presented in this study are available on GenBank (accession numbers are given in Table S1) and at [58].

Acknowledgments: The seminal work of collecting New Zealand sciarids was kindly carried out by Catrin and Mathias Jaschhof (both Färjestaden, Sweden) and Peter A. Maddison (Katikati, New Zealand). Katja Kramp (Müncheberg, Germany) supported the first author in lab work. We want to thank our colleagues Stephan M. Blank, Frank Menzel, Martin Wiemers (all Müncheberg) and Martin Wendt (Paulinenaue, Germany) for fruitful discussions. Our colleague Andrew Liston (Müncheberg) significantly improved the English language of the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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6 Synopsis and outlook

6.1 Taxonomy and phylogenetics

As a result of this thesis, knowledge about the inventory of New Zealand's *Pseudolycoriella* fauna has increased significantly. The number of known species rose from five to 36, of which 30 were new to science. Additionally, two further species are likely to exist: some female specimens show unique sequences, but due to a lack of males, it was decided not to formally describe them. Traditionally, the taxonomy of Sciaridae is focused on the male genitalia and no universally applicable system for distinguishing females is yet available. Further, *P. setigera* (HARDY, 1960) was recognised as junior synonym of *P. cavatica*. The number of species in *Pseudolycoriella* in New Zealand has been increased sevenfold, and *Pseudolycoriella* thus becomes the most species-rich genus of New Zealand fungus gnats. However, this outcome is highly artificial, and only reflects the need for further investigation of other genera. Especially in the genus *Ctenosciara* TUOMIKOSKI, 1960, currently comprising eight species (one of them—*Ctenosciara etorutao* KÖHLER, 2016—was described in the course of this thesis), several unknown species are still awaiting description (personal observation).

It turned out that the morphological differences between several species are slight. *Pseudolycoriella jejuna* and *P. tuakana* KÖHLER, 2019 are good examples of two cryptic species that are morphologically very similar (fig. 25–36 in chapter 4), but whose genetic data show considerable differences. Accordingly, the nearest phylogenetic neighbour of *P. jejuna* is not *P. tuakana*, but *P. dagae* KÖHLER, 2019, whose COI sequence diverges by 5.9 %.

In total, four cryptic species complexes were recognized (fig. 61 in chapter 4), which are named after already known species among them (*P. bispina* complex, *P. jejuna* complex, *P. macrotegmenta* complex/species group and *P. zealandica* complex). To avoid confusion regarding the hierarchy if the term "species group" would be used for a minor part of a known species group, KÖHLER (2019) used the term "species complex" instead. The reason was that three of these taxa—the three lineages containing respectively *P. bispina*, *P. jejuna*, and *P. zealandica*—can be easily assigned to the *P. bruckii* group. The fourth species complex, i. e. species around *P. macrotegmenta*, does not fit into the *P. bruckii* group, and thus has to be added to the species group list of *Pseudolycoriella*.

The autochthonous New Zealand species derived from two radiations. The members of the *P. macrotegmenta* group comprise 13 species. Although this species group is not as genetically diverse as the descendants of the other radiation, its species can be distinguished morphologically. In contrast to the other *Pseudolycoriella* species, members of this species group have a higher number of gonostylar spines, which are reduced in size compared to the regular size in other species. Further, the typical apical whip-lash hair is reduced in size and doubled or tripled in some species. These features are considered to be autapomorphies of this species group.

The descendants of the second radiation could be assigned to the *P. bruckii* species group without any conflicts. Six species are grouped around *P. bispina*, of which one is still undescribed. The *P. jejuna*-lineage comprises thirteen species and the *P. zealandica*-lineage two described and one undescribed species. No autapomorphic character was found which supports their morphological circumscription as a monophylum, but the posterior probability in the Bayesian analysis does support their monophyly.

At a global scale, the number of species of *Pseudolycoriella* rises to 163, of which the autochthonous New Zealand species comprise nearly 23 %. This underlines the already clearly evident centre of biodiversity in the Australian region (fig. III).

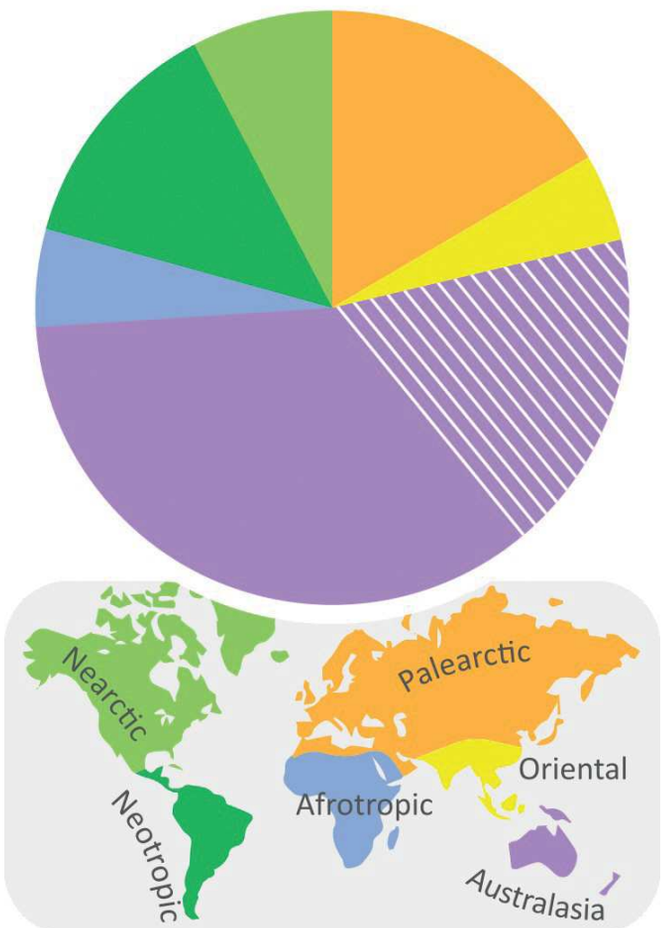

Figure III: Relative distribution of *Pseudolycoriella* species on the zoogeographic realms. Six species were recorded in more than one realm (see table I). The shaded area indicates species described during studies towards this thesis.

Previous investigations in Australia (SKUSE 1888, BROADLEY et al. 2016, MOHRIG et al. 2016, 2020); New Caledonia (VILKAMAA et al. 2012); Papua New Guinea (MOHRIG 2013); and Micronesia (STEFFAN 1969) yielded 59 species. Comparison with areas other than the Holarctic is surely premature, as the level of study is much lower. However, the faunas of the relatively well-studied realms of the Northern Hemisphere, i. e. Palaearctic and Nearctic [see MENZEL and MOHRIG (2000), MOHRIG et al. (2013)], contain respectively only 30 and seven species. Through this disparity, at least clearly apparent is that a majority of species occur in the southern hemisphere, as already surmised by MOHRIG et al. (2004).

Of course, such a rough statement is unsatisfactory, but without a reliable hypothesis on the phylogeny of this genus, no clearer conclusions can be reached. The systematics are still at the embryonic stage of defining more or less provisional species groups. The majority of species are either allocated to the *P. bruckii* group or are still unplaced, depending mainly on the type of data included in the original species description, or the existence of a recent revision. The remaining species groups are either small and of little phylogenetic significance apart from exhibiting simple sister relationships (*P. horribilis* group, *P. morenae* group, and *P. torva* group), or contain phenotypically similar species from the same geographic area (*P. aculeacera* group, *P. longicostalis* group, *P. quadrispinosa* group, *P. triacanthula* group, and the newly proposed *P. macrotegmenta* group). Of course, in some cases, species from outside the region of discovery could added to these species groups. In this way, *P. rubroalata* Mohrig, Kauschke & Broadley, 2018 from Australia was recognised as belonging to the *P. aculeacera* group, originally erected for species from the Dominican Republic. However, the characters used for grouping are a large gonostylus with a rounded apex, "more than one or two apical/subapical spines", and a tegmen without any additional structures (Mohrig et al. 2004). Probably this set of characters lacks a strong phylogenetic significance, and could also have evolved through convergence.

To draw far-reaching biogeographical conclusions, e. g. on the geographical origin and the subsequent global migration paths of *Pseudolycoriella*, a general revision of this genus including *Eugnoriste* and †*Protolycoriella* is urgently needed.

6.2 Biogeography of the New Zealand *Pseudolycoriella* species

One important finding of this thesis was the detection of spatial genetic differentiation within some *Pseudolycoriella* species. However, the extent of differences varies strongly. *Pseudolycoriella tonnoiri* Köhler, 2016 (fig. 1A in chapter 5) which belongs to the young *P. macrotegmen*ta group shows only a single substitution in COI, while the other three species viz. *P. sudhausi* Köhler, 2019 (fig. 3 in chapter 5), *P. tewaipounamu* Köhler, 2019 (fig. 2 in chapter 5), and *P. zealandica* (fig. 1B in chapter 5) demonstrated clear spatial structures, which can be explained by glacial refugia and postglacial expansion. All haplotypes of the southwestern population of *P. tewaipounamu* were identical with one haplotype of the population of the northern South Island. This might be explained by a leading-edge colonisation. According to this biogeographic concept, specimens from the leading edge periphery of the distribution area have a great reproductive advantage over individuals from the distribution core when colonising formerly vacant areas (Hewitt 1996). In the case of *P. sudhausi*, another biogeographic process might have operated. Between the sampling localities of different haplotypes, a spatial proximity of only 23 km (fig. 3B in chapter 5) was detected. Most likely, two lineages of *P. sudhausi* followed the retreating glaciers from north and south and finally met, without mixing, at a pass between the two valleys. This might be explained by high-density blocking, i. e. lineage mixing is prevented because later-arrived specimens are not able to establish in an already densely populated area (Waters et al. 2013).

The distribution pattern of *P. tewaipounamu* and *P. zealandica* represents a northern richness vs. southern purity pattern, which is well known within the New Zealand fauna. Trewick et al. (2011) listed several examples in their review of New Zealand's invertebrates. One of these is the forest-dwelling cicada *Kikihia subalpina* (Hudson, 1891), which has four different haplotypes on North Island and six on South Island, whereby the genetic diversity centre in the latter lies in the northern part of South Island and only two haplotypes have spread southwards (Marshall et al. 2009). As an explanation, these authors state the existence of forest refugia on North Island and northern South Island during the last glacial maximum and postglacial southward expansion.

After the discovery of spatial genetic structuring at the species level, the analysis was extended to all native New Zealand members of the genus *Pseudolycoriella* from which genetic data could be obtained, using a Bayesian approach and a subsequent reconstruction of the ancestral distributions. A great advantage of Bayesian or "molecular clock" approaches is that they provide estimated ages for nodes of the resulting cladogram, i. e. they produce a chronogram. However, the calibration of such a molecular clock is crucial, and it is best to calibrate the clock with fossils of known age and which can be assigned to a branch of a known cladogram (Sauquet 2013). Unfortunately, no fossils of *Pseudolycoriella* are known, neither for New Zealand nor worldwide. Menzel and Mohrig (2000) found some indications for a sister group relationship of *Pseudolycoriella* and the fossil genus †*Protolycoriella*, which is known from early Miocene Saxon amber (approximately 22 million years old), but this still needs verification in a general systematic revision. Even if this relationship should be proved, the fossil does not seem to be appropriate as a calibration point for the elucidation of the probably very recent species splits assumed in the *P. macrotegmenta* group. Accordingly, the substitution rates calculated by Papadopoulou et al. (2010) on the basis of the radiation of tenebrionoid beetles in the course of the formation of the Mid-Aegean trench 9–12 million years ago were used for the calibration. It is known that substitution rates varies across lineages and also across time scales (Ho & Lo 2013). Even so, at least the substitution rate for the COI gene proposed by Papadopoulou et al. (2010) is still widely used in studies for estimating coalescence dates of different insect taxa not closely related to beetles, e. g. springtails [Collembola; Lukić et al. (2020)], earwigs [Dermaptera; González-Miguéns et al. (2020)], and also in nematoceran Dipteran [Psychodidae, Diptera; Trájer et al. (2023)]. Nevertheless, due to the large evolutionary distance between beetles and gnats, the resulting time estimates must be treated with caution and might rather be regarded as approximations. For the intraspecific patterns of *Pseudolycoriella* species discussed above, median coalescence time estimates range from 28 ka (between the two haplotypes of *P. tonnoiri*) to 397 ka (between the northern and south-eastern linages of *P. tewaipounamu*) (see supplementary material of chapter 5). These estimates do not contradict the hypothesis that the intraspecific haplotype differences are the result of the Pleistocene glacial cycles. The origin of the *P. macrotegmenta* group accordingly lies in the Pliocene, around three million years ago [95 % highest posterior density interval

(HPD) 1.8–4.3 Ma]. The second New Zealand monophylum of *Pseudolycoriella* arose in the late Miocene, at approximately ten million years ago (95 % HPD interval 7.4–12.4 Ma).

Outgoing from the two chronograms and the derived distribution of the respective most recent common ancestor (figs 4–5 in chapter 5), 13 successful dispersal events across the sea straits separating New Zealand's main islands [the Kuripapango Strait during the late Miocene–early Pliocene, the Manawatu Strait during the late Pliocene, and the Cook Strait since 0.5 Ma (Trewick & Bland 2012)] were deduced. Nine of these events were directed North to South, while one event was in the opposite direction and three events had an unknown direction (fig. 8 in chapter 5). However, these numbers should be regarded as minimums, because genetic data could not be obtained for all species. A further southward dispersal event of the ancestor of *P. porehu* Köhler, 2019 is likely, based on the phylogenetic relationship (fig. 5 in chapter 5) and the morphologically justified sister relationship of *P. porehu* and *P. orite* Köhler, 2019. Due to the persistent separation of New Zealand's main islands for almost the entire time except during the glacials of the Pleistocene, individual speciation events can only have occurred on one of the islands. The ratio of north- to southwards directed dispersal events reveals that North Island acted as a centre of radiation from which dispersal to South Island took place. Less speciation apparently occurred on the latter, presumably because the southern populations are at a disadvantage in colonising formerly uncolonized areas from southern refugia during interglacial periods. The post-glacial dispersal of southern populations probably occurred after a time lag, whereas the northern populations were able to colonise larger, formerly deserted areas at earlier dates, as can be seen in the example of *P. tewaipounamu*. Therefore, on average, the southern populations had fewer opportunities to colonise areas that became refugia again during the subsequent ice ages, i. e. there were fewer opportunities for the formation of reproductive barriers.

Thus, the northern richness vs. southern purity pattern emerges again at the interspecific level. Astonishingly, a greater number of previously undetected species was found on the already investigated North Island than on South Island, which contradicts the initial hypothesis that the larger and less anthropogenically influenced South Island is inhabited by the greater number of undiscovered species. However, the genus *Pseudolycoriella* does not behave unusually with regard to the poleward impoverishment of genetic diversity that was observed in Europe and North America as a result of the Pleistocene glacial cycles (Hewitt 1996). In this context, the findings of Gardner et al. (2004) and Rawlence et al. (2021) on the phylogeography of tree species distributed in the south of South Island are of particular interest, as clearly parallel patterns are recognisable. The greatest genetic diversity of silver beech [*Nothofagus menziesii* (Hook. f., 1844); Nothofagaceae] is on northern South Island, with two haplotypes on North Island and only one on southern South Island (Rawlence et al. 2021). A similar picture emerges for the Rātā (*Metrosideros umbellata* Cavanilles, 1797; Myrtaceae)—a hotspot of genetic diversity in the upper north of South Island and one single haplotype each on North Island and the remaining South Island including Stewart Island (Gardner et al. 2004). It seems plausible that the sylvicolous genus *Pseudolycoriella* and many of these tree species co-inhabited glacial refugia on the densely wooded North Island (Newnham et al. 2013) and that the gnats followed the interglacial advances of the most cool-adapted tree species to the South during the warmer phases.

Few phylogeographic studies on New Zealand forest-inhabiting invertebrates exist above species level, as especially alpine and freshwater invertebrate taxa were so far the focus of such studies [see Buckley et al. (2015)]. A study by Marshall et al. (2008) on the radiation of the cicada genus *Kikihia* Dugdale, 1972, which mostly lives in lowland forests and scrub, is therefore of particular interest. The approximately 30 cicada taxa at species level and below also exhibit distinct distributions on North and South Island, with only a few species spanning the Cook Strait. Unfortunately, due to some polytomies, the given chronogram does not allow a clear conclusion on the distribution of their most recent common ancestor, but the two basal species are distributed exclusively on North Island, which appears to be a distribution pattern congruent with that of *Pseudolycoriella*. Also the chronogram by Marshall et al. (2012), which includes two other sylvicolous cicada species—*Amphipsalta cingulata* (Fabricius, 1775) and *A. zealandica* (Boisduval, 1835)—indicates a North Island distribution of their most recent common ancestor.

The inclusion of three as yet undescribed species from Tasmania (Australia) in the phylogenetic analysis allowed the fundamental question of the origin of *Pseudolycoriella* outside New Zealand to be addressed. Resulting from the analysis, three initial colonisations of New Zealand are postulated to have taken place, two of which were traced back to the *P. macrotegmenta* lineage. According to the phylogenetic analysis, one of these colonisation events most probably emanated from Australia. For the others, an Australian origin is quite conceivable because of the favourable ancient current and meteorological conditions. The estimated time frames lie in the late Miocene, the late Pliocene and the Pliocene–Pleistocene boundary, i. e. in periods in which major cooling took place in New Zealand—during the middle-late Miocene and during the late Pliocene to early Pleistocene (Prebble et al. 2017). Since the vegetation structure of New Zealand changed at the latest after the climatic optimum of the middle Miocene (Pole 2014), and if this change was delayed compared to Australia, individuals dispersing from there could have had an adaptive advantage over the native species, which would strengthen the assumption of an origin from temperate Australia instead of tropical New Caledonia. Interestingly, Arensburger et al. (2004) gave a similar time frame of ca. 10 Ma for the two colonisation events by ancestral cicadas, for which, in addition to Australia, New Caledonia could also be deduced as origin.

Even with the limited reliability of the time estimates for the arrival of ancestral *Pseudolycoriella* species, the hypothesis of Mohrig and Jaschhof (1999) that the *Pseudolycoriella* species of New Zealand belong to an old faunal layer, even a "Gondwana element", and that a faunal exchange via a land bridge between Melanesia and Indomalaya had existed, can be rejected.

Finally, the patterns of spatial genetic structuring revealed in the results, and the application of classical biogeographic concepts to explain them, proves that the genus *Pseudolycoriella* is suitable for biogeographical analyses. If the results should be found to be more widely applicable to the Sciaridae as a whole, then they contrast strongly with the impression of MENZEL and MOHRIG (2000), who stated that the Palaearctic Sciaridae are highly homogeneous due to the rare occurrence of endemics. Their argument that sciarids have a high degree of mobility, either through active migration in species capable of sustained flight or through passive drift via air currents, has shortcomings. It assumes an easy establishment in the new area, i. e. requires areas that are not habited by closely related or even conspecific lineages competing for the same resources, and thus neglects phenomena such as high-density blocking. Nevertheless, the high number of *Pseudolycoriella* species endemic to New Zealand is remarkable. A total of 37 endemic species (including two which are still undescribed) can be set against a single species, *Pseudolycoriella cavatica*, which is more widely distributed. The latter was probably introduced to New Zealand, as discussed in chapter 5. In contrast, for the Hawaiian Islands, only seven out of 22 species are considered to be endemic (MOHRIG et al. 2019). This is particularly astonishing, because the Hawaiian Islands are famous for the radiation of the dipteran family Drosophilidae. Starting from a single colonisation 25 million years ago, 689 species have evolved, of which 564 are endemic to this archipelago (RAMPASSO & O'GRADY 2022). How can these discrepancies be explained? Firstly, the review of the Hawaiian Sciaridae by MOHRIG et al. (2019) dealt with different genera, and only in the genera *Ctenosciara*; *Cratyna*; *Phytosciara* FREY, 1942; *Pseudolycoriella*; and *Scatopsciara* were Hawaiian endemics found, while for the species-rich genera *Bradysia* WINNERTZ, 1867; *Corynoptera*; and *Lycoriella* FREY, 1942 only species with wider distributions occurred. However, the existence of cryptic species has to be kept in mind. With the help of genetic markers, slight morphological differences, which were previously interpreted as variability, are becoming increasingly important for the delimitation of species, as the aforementioned species *P. jejuna* and *P. tuakana* have shown. Apart from such technical difficulties, however, the influence of different dispersal abilities of the various sciarid genera cannot be ruled out. It would therefore be appropriate to extend the molecular and morphological analysis to other New Zealand genera, to establish whether they show biogeographical patterns like *Pseudolycoriella* or not.

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Acknowledgements

I am deeply indebted to my parents, Ingrid and Dr Dieter KÖHLER, for making it possible for me to study biology, even though they knew that a degree in this discipline does not guarantee many job opportunities. During the long genesis of this work, I was lucky to have the constant support and motivation of my partner Ute KACZINSKI.

I am very grateful to the staff of the Senckenberg Deutsches Entomologisches Institut in Müncheberg for the friendly and inspiring working atmosphere (Accordingly, I am glad to have obtained a permanent position at this institution). Among all these nice colleagues, some have to be mentioned individually: Dr Frank MENZEL, the head of the section Diptera, gave me the opportunity to work with this fly family. Furthermore, he offered me the possibility to participate on several other projects on Sciaridae. Professor Dr Thomas SCHMITT, director of the institute, valuably convinced me to expand the scope of my thesis to include biogeographic aspects. Dr Katja KRAMP was kind enough to introduce me to the methods of molecular biology. Andrew LISTON proofread my English manuscripts without ever getting desperate. Christian KUTZSCHER helped me with creating SEM-images. Dr Martin WENDT helped with comments on the analysis software and the promotion procedure at the University of Halle.

Special thanks go to Lena HAVERMEIER, with whom I travelled to New Zealand for two months in 2009. Although this trip had a rather ornithological focus, it strongly influenced my thesis. When I joined the SDEI, Frank MENZEL offered me plenty of unrevised sciarid material from all over the world, but I chose the New Zealand fauna as my topic, because I had seen the habitats shortly before. For this valuable material and making it available at the SDEI I would like to thank Catrin and Mathias JASCHHOF (both Färjestaden, Sweden). Another part of the raw material was kindly provided by Peter A. MADDISON (Katikati, New Zealand).

Further, I would like to thank the Deutsche Gesellschaft für allgemeine und angewandte Entomologie (DGaaE, German Society for General and Applied Entomology) and the Senckenberg Gesellschaft für Naturforschung (SGN, Senckenberg Society for Nature Research) for their generous funding.

Curriculum vitae

Personal information

Name	Arne Köhler
Birth	16th November 1981 in Berlin, GDR
Family status	
Citizenship	German

Practical work

since Jan. 2020	Technical employee at the Hemimetabola Collection at the Senckenberg Deutsches Entomologisches Institut (SDEI, Senckenberg German Entomological Institute)
since Feb. 2012	Secretary of the Deutsche Gesellschaft für allgemeine und angewandte Entomologie (DGaaE, German Society for General and Applied Entomology)
Mar. 2013–Jul. 2019	Research associate at the SDEI · Collaboration in the projects "Sørgemygg i Norge (Sciaridae of Norway)" (2014–2016) and "Sørgemygg i norske skoger' (Sciaridae in Norwegian forests)" (2017–2019) of the Norwegian Taxonomy Initiative · Work on the project "The black fungus gnats of New Zealand" (from 1th April 2014)
Apr. 2011–Feb. 2013	Research assistant at the SDEI · Work as part of the research project "Vorkommen und Vektorkompetenz von Stechmücken" [Occurrence and vector competence of mosquitoes]
Mar. 2010–Mar. 2011	Freelance work at the SDEI · familiarisation with the group of Nematocera (Diptera)
Apr. 2009–Jul. 2012	Teaching assignments at the Free University of Berlin in the practical courses Zoological Identification Exercises and Zoological Basic Practical Course
Oct. 2006–Mar. 2009	Student assistant with teaching tasks (tutor) at the Free University of Berlin

Education

Jun. 2019	Matriculation at the Martin Luther University Halle-Wittenberg · Biology (Doctoral candidate)
Apr. 2003–Mar. 2009	Studies at the Free University of Berlin · Biology (Diploma)
Apr.–Dec. 2008	Diploma thesis (grade: very good) · Topic: „Phoretische und parasitische Beziehungen von Nematoden des Saftflusses zu Insekten" [Phoretic and parasitic relationships of sap flow nematodes to insects]
Apr. 2008	Diploma examinations in the subjects · Zoology (grade: very good) · Ecology (grade: very good) · Microbiology (grade: very good) · Palaeontology (grade: very good)
May 2009	Participation in a training course for bird ringers of the ringing office Hiddensee
Jul. 2001–Jun. 2002	Alternative civilian service at the Verein Jordsand zum Schutz der Seevögel und der Natur e. V.

Memberships

Entomology	· Deutsche Gesellschaft für allgemeine und angewandte Entomologie e. V. · Förderverein des Deutschen Entomologischen Instituts e. V.
Ornithology	· ·
Miscellaneous	·

Martin-Luther-Universität Halle-Wittenberg
Naturwissenschaftliche Fakultät I – Biowissenschaften
06099 Halle (Saale)

Statement of autorship

I hereby declare that I have not used any aids other than those indicated for the preparation of this dissertation, and that the results of other participants as well as passages and quotations taken verbatim and in terms of content from other works are identified as such.

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Eigenständigkeitserklärung

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Arne Köhler