

Eight new species of the genus *Nesamblyops* Jeannel (Anillini: Carabidae: Coleoptera) from New Zealand with notes about dispersal of the genus to the North Island

IGOR M. SOKOLOV

Systematic Entomology Laboratory, ARS, USDA, c/o Smithsonian P.O. Box 37012, National Museum of Natural History, Washington, DC 20013-7012, USA.  igor.sokolov@usda.gov;  https://orcid.org/0000-0001-7580-9208

Abstract

Species of flightless litter ground beetles of the tribe Anillini, genus *Nesamblyops*, from the North Island and from the north-eastern part of the South Island are revised. Eight new species are described and one previously known species, *Nesamblyops oreobius* (Broun), is re-described. *Nesamblyops oreobius*, the only hitherto recorded species from the North Island, is most similar to the group of two new species from the South Island, *N. confusus* n. sp. (type locality: New Zealand, Marlborough Sounds, Mount Stokes) and *N. lescheni* n. sp. (type locality: New Zealand, Marlborough Sounds, D'Urville Island), based on the structure of the male genitalia. The second species of the genus known from the North Island, *N. tararua* n. sp. (type locality: New Zealand, Wellington, Tararua Range) represents another lineage, based on the structure of the male genitalia, and is closely related to a group of three new species from the South Island, *N. brouni* n. sp. (type locality: New Zealand, Canterbury, Southern Alps, Lewis Pass), *N. distinctus* n. sp. (type locality: New Zealand, Marlborough, Richmond Range, Fabians Valley), and *N. townsendi* n. sp. (type locality: New Zealand, Marlborough Sounds, Tennyson Inlet). *Nesamblyops carltoni* n. sp. (type locality: New Zealand, Nelson, Richmond Range, Dun Mountain) and *N. parvulus* n. sp. (type locality: New Zealand, Marlborough Sounds, Mount Stokes), both from the South Island occupy an isolated position among the examined species. All species are illustrated with digital images of habitus, body parts, and drawings of genitalia. Distribution maps for all species are also provided. Geographical evidence of *Nesamblyops* dispersal to the North Island is discussed, based on distributional data.

Key words: Adephaga, distribution, dispersal, new species, North Island, South Island

Introduction

The genus *Nesamblyops* was established by R. Jeannel (1937) to accommodate two New Zealand anilline species, *N. subcaecus* (Sharp) and *N. oreobius* (Broun), originally described within the European genera *Cillenus* and *Tachys*, respectively. According to Jeannel (l.c.) the members of *Nesamblyops* are close to and share a lineage with species of *Zeanillus* Jeannel, another New Zealand genus of Anillini. They can be distinguished from *Zeanillus* by the structure of the elytral umbilical series of pores and the presence of pigmented eyes, a rare feature for the tribe, members of which are typically eyeless. Based on the structure of the umbilical series of pores Jeannel (1937) placed *Nesamblyops* in the newly erected tribe *Scotodipnina* (now a subtribe), where the genus sits currently. Since Jeannel's publication (l.c.), *Nesamblyops* has received little attention, no taxonomic or morphological analyses of members of the genus were done, and its species were cited in only a few publications, and without changes in their number and taxonomic positions (Jeannel 1963, Lorenz 2005). The treatment of New Zealand Anillini published by Moore (1980) did not change the species composition of the genus but added one more name to the list of synonyms of *N. oreobius*. Recently, two publications dealing with molecular data of taxa of the subfamily Trechinae confirmed the position of *Nesamblyops* within Anillini and treated the genus as a sister clade to all other representatives of the tribe (Andújar *et al.* 2016, Maddison *et al.* 2019). Currently only two species are recognized within the genus, namely, *N. oreobius* from the North Island, and, *N. subcaecus*, from the mid-western parts of the South Island. Both taxa were placed in the genus at time of its proposal by Jeannel (1937). Two more names are cited as synonyms, one presented by Jeannel (1937) and another one by Moore (1980).

I had an opportunity to investigate the material of Anillini from the private collection of J. Nunn (Dunedin, New Zealand) and the New Zealand Arthropod Collection (Landcare Research, Auckland, New Zealand), the latter collection provided many more *Nesamblyops* specimens available for this study. After preliminary sorting of the material, it turned out that examined specimens contained numerous, mostly undescribed species with various morphological, geographic, and faunistic patterns. Morphologically, some species with neighboring allopatric ranges are obviously related, while other species demonstrate no obvious relationships despite geographical proximity of their ranges or range overlap. Geographically, the majority of species are restricted in their distribution and are known from one or few adjacent localities, however, some species have large distributional ranges for such tiny creatures. In several cases species form regional faunistic assemblages with no species in common with assemblages of species from neighboring territories. These data indicate a long and complicated evolutionary history of the genus in New Zealand but allow taxonomic treatment of the fauna of *Nesamblyops* on a regional basis.

Microscopic investigation of fine morphology indicates that among representatives of *Nesamblyops*, taxonomic characters useful for species discrimination in many cases are limited to traits of male genitalia. However, in some cases external morphology of the specimens such as general body proportions, size, and shape of the pronotum provide additional tools for species diagnosis. Because of the presence of regional patterns in species distributions, locality records can also be very helpful.

This paper presents the results of a taxonomic study of the species of *Nesamblyops* inhabiting the North Island and the north-eastern part of the South Island (Fig. 1), in particular the Marlborough Sounds, Marlborough, and Nelson areas (Crosby *et al.*, 1998). The paper includes descriptions of eight new and a re-description of one of the two previously described species.

Material and methods

This study is based on examination of more than 670 specimens of *Nesamblyops* from the collection of the New Zealand Arthropod Museum (Auckland, New Zealand, further NZAC), and from the private collection of J. Nunn (Dunedin, New Zealand). Verbatim label data are given for type specimens of all newly described taxa, with label breaks indicated by a slash (“\”).

Measurements. All specimens were measured electronically using a Leica M420 microscope equipped with a Syncroscopy AutoMontage Photomicroscopy system (SYNCROSCOPY, Synoptics Ltd.). Measurements for various body parts are encoded as follows: LH = length of head, measured along midline from anterior margin of labrum to the virtual line, connecting posterior supraorbital setae; WH = width of head, at level of anterior supraorbital setae; WPm = maximal width across pronotum; WPa = width across anterior angles of pronotum; WPp = width across basilateral setae of pronotum; LP = length of pronotum from base to apex along midline; WE = width of elytra, at level of 4th umbilicate setae; LE = length of elytra and pygidium, from apex of scutellum to apex of pygidium; SBL = standartized body length, a sum of LH, LP and LE. SBL measurements are given in mm; others are presented as nine ratios: body proportions-WH/WPm, WPm/WE, LE/SBL, WE/SBL and LP/LE, and proportions of body parts-WPa/WPp, WPm/WPp, WPm/LP, WE/LE. All values are given as mean ± standard deviation.

Illustrations. Digital photographs of the dorsal habitus of new species were taken with the AutoMontage system using a Leica M420 microscope. Line drawings of selected body parts were made using a camera lucida on an Olympus BX 50 microscope.

Dissections. Method of dissections follows that of Sokolov (2013) and Sokolov and Kavanaugh (2014).

Type material. The author had no opportunity to examine type material of *Nesamblyops*. The concept of the genus used here is based on material identified by B. P. Moore during his work on New Zealand fauna of Anillini. Species concept of *N. oreobius* is based on the examination of modern material obtained from the typical localities of this species.

Terms. Terms used in the paper follow Sokolov *et al.* (2004) and Sokolov (2013).

Species ranking. Species recognition is in accordance with our previous approach (Sokolov *et al.* 2004).

Descriptions. The scheme of descriptions follows that of Ball and Shpeley (2009).



FIGURE 1. Map of New Zealand, showing parts of the North and South Islands highlighted with red color, where fauna of *Nesambylops* has been studied. Geometric symbols show the type localities for two hitherto described species of *Nesambylops*: *N. oreobius* (black circle) and *N. subcaecus* (black square).

Taxonomic Treatment

Order Coleoptera Linnaeus, 1758

Family Carabidae Latreille, 1802

Subfamily Trechinae Bonelli, 1810

Tribe Anillini Jeannel, 1937

***Nesamblyops brouni*, sp. nov.**

Figs. 2A, 4A, 5A–C, 7A, 9

Type material. **HOLOTYPE**, male, in NZAC, labeled: \ W. Lewis Pass, 2000'. 23.3.65 N.A.Walker \ DSIR\ No \ NZ PB\ . **PARATYPES** (47 specimens, in NZAC, dissected 10 exx.), 2 males and 5 females labeled same as holotype; 2 males and 2 females labeled: \ Lewis Pass 762m Canterbury \ 19 Mar 65 G.W. Ramsay J.I. Townsend \ moss 65/283 \ DSIR\ No \ NZ PB\ ; 1 male labeled: \ Lewis Pass Canterbury 23 Mar 65 Litter 65/108 \ Litter 65/108 \ DSIR\ No \ NZ PB\ ; 2 males and 1 female labeled: \ Leafmould \ Lewis Pass 18–24.11.61 G.Kuschel \ DSIR\ No \ NZ PB\ ; 1 male and 3 females labeled: \ Maruia Saddle 1900' 2-6-65 moss J.I.Townsend \ DSIR\ No \ NZ PB\ ; 1 female labeled: \ E.S.Brookes leaf mould Sept. 1948 \ Maruia Springs Lewis Pass Westland \ A.E.Brookes Collection \ Teneral \ NZ PB\ ; 1 male and 2 females labeled: \ Howard Val BR 7Oct68 S.Edridge \ moss 68/143 \ DSIR\ No \ NZ PB\ ; 2 females labeled: \ Col. T.Hall 27-3-1915 \ Howard Nelson South Is. \ T.Broun Collection \ A.E.Brookes Collection \ DSIR\ No \ NZ PB\ ; 3 females labeled: \ L.Rotoiti 2000' 27.7.65 Grey Duck Bay moss under Mt.beech \ DSIR\ No \ NZ PB\ ; 2 females labeled: \ L.Rotoiti Nelson leaf litter 21-3-65 N.A.Walker \ DSIR\ No \ NZ PB\ ; 1 female labeled: \ L.Rotoiti NN 23 Dec 64 J.I.Townsend \ Litter 64/49 \ DSIR\ No \ NZ PB\ ; 1 male and 1 female labeled: \ Mt. Hope Nelson 3.3.1915 \ *Tachys* N.Sp. \ T.Broun Collection \ A.E.Brookes Collection \ DSIR\ No \ NZ PB\ ; 1 male labeled: \ Hope 10.12.16 \ not. 2677 \ T.Broun Collection \ A.E.Brookes Collection \ DSIR\ No \ NZ PB\ ; 1 female labeled: \ var.2677 \ Hope 10.12.16 \ T.Broun Collection \ A.E.Brookes Collection \ DSIR\ No \ NZ PB\ ; 1 male labeled: \ Glenhope 10-12-14 \ not.2677 \ T.Broun Collection \ A.E.Brookes Collection \ DSIR\ No \ NZ PB\ ; 1 male and 1 female labeled: \ Glenhope 10-12-14 \ var.2677 \ T.Broun Collection \ A.E.Brookes Collection \ DSIR\ No \ NZ PB\ ; 1 female labeled: \ Coll. T.Hall 27.3.1915 \ Glenhope Nelson 10.12.1914 \ 2677 var. \ T.Broun Collection \ A.E.Brookes Collection \ NZ PB\ ; 1 male labeled: \ Lamb Val. 1400' Glenhope 19.7.65 moss under open silver and black beech J.I.Townsend \ DSIR\ No \ NZ PB\ ; 5 females labeled: \ Kaka—Glenhope Rd. 28.7.64 J.I.Townsend \ NZ PB\ ; 1 male labeled: \ nr.ft. Hope Saddle 1800' 19.7.65 mixed moss J.I.Townsend \ DSIR\ No \ NZ PB\ ; 1 female labeled: \ New Zealand BR Nelson Lakes NP Speargrass Tck Mt Robert \ On mossy log 30-Nov-05 \.

Etymology. The specific epithet is a Latinized eponym in the genitive case, and is based on the surname of Captain Thomas Broun, a New Zealand entomologist of the 19th century in recognition of his significant contributions to the study of New Zealand coleopterans, including publications of descriptions of New Zealand aniline beetles.

Type locality. New Zealand, South Island, Canterbury, Southern Alps, Lewis Pass.

Recognition. Adults of this species (Fig. 2A) are practically indistinguishable from the adults of many *Nesamblyops* species based on external characters (cf. with Figs. 2B–C) and are distinguished from them by the structure of the male genitalia.

Description. Large for genus (SBL range 1.76–2.02 mm, mean 1.89 ± 0.078 mm, n=17).

Habitus. Body form (Fig. 2A) markedly convex, elongate ovoid, general proportions wide (WE/SBL 0.41 ± 0.011), head narrow relative to pronotum (WH/WPm 0.68 ± 0.016), proportions of pronotum in comparison to elytra average for genus (WPm/WE 0.75 ± 0.017).

Color. Body color brunneorufous, appendages testaceous.

Prothorax. Pronotum (Fig. 4A) moderately long in comparison to elytra (LP/LE 0.42 ± 0.013) and moderately transverse (WPm/LP 1.23 ± 0.026), with lateral margins arcuately constricted posteriorly (WPm/WPp 1.30 ± 0.025). Anterior angles indistinct, posterior angles obtuse ($108\text{--}116^\circ$), rounded. Width between posterior angles greater than between anterior angles (WPa/WPp 0.87 ± 0.024). Basal margin almost rectilinear, slightly convex at middle.

Elytra. Ovoid, narrowly depressed along suture, comparatively long (LE/SBL 0.59 ± 0.008) and moderately wide (WE/LE 0.69 ± 0.020). Humeri completely rounded. Lateral margins slightly divergent at basal half, subparallel at middle and evenly rounded to apex in apical third.

Male genitalia. Median lobe of aedeagus (Fig. 5C) moderately arcuate and moderately twisted. Shaft subparallel basally, tapering in apical half. Apex moderately curved dorsally with narrowly rounded tip. Apical orifice long, occupies almost half of the shaft length. Ventral margin of median lobe straight. Walls of shaft without poriferous canals. Dorsal copulatory sclerites in form of characteristic “bird’s head” plate, surrounded by distinct scaled membranous field. Spines of internal sac absent. Left paramere (Fig. 5A) comparatively wide, with shortly attenuate apex, bearing three long setae. Right paramere (Fig. 5B) of moderate length, bearing three long setae, which are slightly longer the length of paramere. Ring sclerite as in Fig. 7A.

Female internal genitalia. Not examined.

Geographical distribution. This species is distributed from the Lewis Pass of North Canterbury along the Spenser Mountains northward up to the Hope Range in the Nelson area (Crosby *et al.* 1998) (Fig. 9, green circles). So, the range of this species includes both sides of the Buller River valley.

Habitat. Specimens were collected from leaf litter, leaf mould, moss in *Nothofagus* forests (labels mention silver *N. menziesii*, black *N. solandri* var. *solandri*, and mountain *N. solandri* var. *cliffortioides* beeches).

Relationships. The structure of the male genitalia of *N. brouni* suggests its relatedness to the other species having dorsal copulatory sclerite in a shape of “bird’s head”, such as *N. tararua*, *N. distinctus*, and *N. townsendi*. Based on the details of the sclerite configuration and the state of the scaled membranous field it is postulated that *N. brouni* is a sister taxon to *N. distinctus*.

Nesamblyops carltoni, sp. nov.

Figs. 2B, 4B, 5D–F, 7B, 10

Type material. **HOLOTYPE**, male, in NZAC, labeled: \ Wooded Pk. East Summit Dun Mountain Nelson \ 14 Sept 71 G.W. Ramsay \ Litter 71/116 \ DSIR\ No \ NZ PB\; **PARATYPES** (146 specimens, in NZAC, dissected 9 exx.), 81 males and females labeled same as holotype; 1 male and 3 females labeled: \ Wooded Pk. Dun Track Sdle Nelson 14 Sept. 71 \ G.Ramsay \ litter 71/109 \ DSIR\ No \ NZ PB\; 1 female labeled: \ Dun Mt. 2000' 28.11.43 E.S. Gourlay \ E.S. Gourlay Acc. 1970 Ent. Div. \ NZ PB\; 2 males and 2 females labeled: \ Dun Mt. 2500' 13.11.61 Nelson G.Kuschel \ 61/1 \ DSIR\ No \ NZ PB\; 1 female labeled: \ Leafmould \ Dun Mt. 2500' 13.11.61 G.Kuschel \ NZ PB\; 1 male and 2 females labeled: \ Dun Track Nelson 14 Sept 71 \ G.Ramsay \ Litter 71/112 \ NZ PB\; 1 male labeled: \ Just beyond 3rd. House Dun Mt. Nelson J.I. Townsend \ DSIR\ No \ NZ PB\; 1 female labeled: \ Pelorus Bridge 100' 15.10.65 L.P. Marchaut \ moss in bush 65/512 \ NZ PB\; 1 female labeled: \ Pelorus Val. 29-4-64 litter J.I. Townsend \ DSIR\ No \ NZ PB\; 4 males and 2 females labeled: \ Upper Maitai, 7-3-49 E.S. Gourlay \ E.S. Gourlay Acc. 1970 Ent. Div. \ NZ PB\; 1 female labeled: \ Upper Maitai,(c.) 19-5-41 E.S. Gourlay \ E.S. Gourlay Acc. 1970 Ent. Div. \ *Nesamblyops oreobius* Broun E.B.Britton det. 1960 \ NZ PB\; 1 female labeled: \ Upper Maitai, 13-2-57 E.S. Gourlay \ NZ PB\; 16 males and females labeled: \ Upper Maitai 3.5.50 E.S. Gourlay \ Carabidae \; 3 males and 3 females labeled: \ Maungatapu Sdle. 2400' \ Nel. 15.11.67 J.I.Townsend \ moss sample 67/83 \ DSIR\ No \ NZ PB\; 1 female labeled: \ Maungatapu 3000' 17.4.38 E.S. Gourlay \ E.S. Gourlay Acc. 1970 Ent. Div.\; 4 males and 2 females labeled: \ NEW ZEALAND NN Whangamoa Sdle 700m Slaters Rd 4 May 1997 J S Dugdale *N menziesii N truncata* kamahi litter \ NZ PB\; 5 males and 2 females labeled: \ Nelson, N.Z. Whangamoa Saddle 14.9.74 J.I.Townsend leafmould \ Coll. J.I. Townsend \; 2 females labeled: \ Titirangi Marlborough 2Oct 69 F.Alack \ Litter 69/174 \ NZ PB\; 1 male and 2 females labeled: \ Titirangi Marl. 22.x.69 F.A. Alack \ Litter 69/174 \ DSIR\ No \ NZ PB\.

Additional material: \ Wairoa Gorge Nelson 5-4-60 J.I. Townsend \ NZ PB\ (4 females).

Etymology. The specific epithet is a Latinized eponym in the genitive case and is based on the surname of Christopher E. Carlton, Professor and former Director of Louisiana State Arthropod Museum, Baton Rouge, Louisiana, United States, who triggered my interests in research of the members of the tribe Anillini in the USA as well as in New Zealand.

Type locality. New Zealand, South Island, Nelson, Richmond Range, Dun Mountain.

Recognition. Adults of this species (Fig. 2B) are virtually similar to the adults of many *Nesamblyops* species (cf. with Figs. 2A, 3B), however can be easily distinguished from them by the shape of posterior angle of pronotum, formed by tiny blunt denticle, and the structure of the male genitalia.

Description. Large for genus (SBL range 1.75–2.03 mm, mean 1.89 ± 0.078 mm, n=29).

Habitus. Body form (Fig. 2B) markedly convex, elongate ovoid, general proportions wide (WE/SBL 0.40 ± 0.010), head narrow relative to pronotum (WH/WPm 0.67 ± 0.016), proportions of pronotum in comparison to elytra average for genus (WPm/WE 0.76 ± 0.019).

Color. Body color brunneopiceous, appendages testaceous.

Prothorax. Pronotum (Fig. 4B) moderately long in comparison to elytra (LP/LE 0.43 ± 0.011) and moderately transverse (WPm/LP 1.23 ± 0.026), with lateral margins arcuately constricted posteriorly (WPm/WPp 1.26 ± 0.022). Anterior angles indistinct, posterior angles obtuse ($106\text{--}115^\circ$), in form of protruding blunt denticles with faint sinua-

tion anteriorly. Width between posterior angles greater than between anterior angles (WPa/WPp 0.85 ± 0.032). Basal margin almost rectilinear, slightly convex at middle.

Elytra. Ovoid, narrowly depressed along suture, comparatively long (LE/SBL 0.58 ± 0.007) and moderately wide (WE/LE 0.69 ± 0.020). Humeri completely rounded. Lateral margins slightly divergent at basal half, subparallel at middle and evenly rounded to apex in apical third.

Male genitalia. Median lobe of aedeagus (Fig. 5F) moderately arcuate and moderately twisted. Shaft subparallel, tapering in apical third. Apex slightly curved dorsally with narrowly rounded tip. Apical orifice of moderate length, reaches one third of the shaft length. Ventral margin of median lobe straight. Walls of shaft with numerous poriferous canals. Dorsal copulatory sclerites in form of characteristic “bird’s head” plate, with apically attenuated dorsal part. Scaled membranous fields lacking. Spines of internal sac absent. Left paramere (Fig. 5D) comparatively narrow, with shortly attenuate apex, bearing three long setae. Right paramere (Fig. 5E) elongated, bearing three long setae, which are slightly shorter the length of paramere. Ring sclerite as in Fig. 7B.

Female internal genitalia. Not examined.

Geographical distribution. The range of this species stretches along the eastern coast of Tasman Bay from the Wairoa George in the south to Titirangi Bay of the Marlborough Sound region (Crosby *et al.* 1998) to the north (Fig. 10, black circles).

Habitat. Specimens were collected from leaf litter, leaf mold, moss in bush and *Nothofagus* forests (labels mention kamahi shrub *Weinmannia racemosa*, silver *N. menziesii*, and hard *N. truncata* beeches).

Relationships. Based on the structure of the male genitalia *N. carltoni* occupies an isolated position among examined species of the genus.

Nesamblyops confusus, sp. nov.

Figs. 2C, 4C, 5G–I, 10

Type material. **HOLOTYPE**, male, in NZAC, dissected, labeled: \ Mt Stokes 1160m Marlborough 12 Oct 67 \ J.I.Townsend \ Litter 67/244 \ DSIR\ No \ NZ PB\ . **PARATYPES** (2 specimens, in NZAC, dissected 1 male), 1 female labeled same as holotype; 1 male labeled: \ Mt Stokes Marl. 11.x.67 J.I.Townsend \ moss 67/247 \ DSIR\ Ns \ NZ PB\ .

Etymology. The specific epithet is a Latin adjective, *confusus*, in the masculine form, meaning “having been mixed”, and refers to the similarity between the external appearance of the new species and its closest relatives.

Type locality. New Zealand, South Island, Marlborough Sounds, Mount Stokes.

Recognition. Adults of this species (Fig. 2C) are practically indistinguishable from the adults of many *Nesamblyops* species based on external characters (cf. with Figs. 2A–B, 2F) and are distinguished from them by the structure of the male genitalia.

Description. Average size for genus (SBL range 1.64–1.67 mm, mean 1.66 ± 0.017 mm, n=3).

Habitus. Body form (Fig. 2C) markedly convex, elongate ovoid, general proportions wide (WE/SBL 0.42 ± 0.012), head narrow relative to pronotum (WH/WPm 0.68 ± 0.038), in comparison with other species pronotum less bulky in comparison to elytra (WPm/WE 0.72 ± 0.027).

Color. Body color dark brunneous, appendages testaceous.

Prothorax. Pronotum (Fig. 4C) moderately long in comparison to elytra (LP/LE 0.42 ± 0.024) and moderately transverse (WPm/LP 1.24 ± 0.013), with lateral margins arcuately and strongly constricted posteriorly (WPm/WPp 1.35 ± 0.026). Anterior angles indistinct, posterior angles strongly obtuse ($123\text{--}127^\circ$), widely rounded. Width between posterior angles slightly greater than between anterior angles (WPa/WPp 0.93 ± 0.054). Basal margin slightly convex.

Elytra. Ovoid, narrowly depressed along suture, comparatively long (LE/SBL 0.59 ± 0.015) and moderately wide (WE/LE 0.71 ± 0.034). Humeri completely rounded. Lateral margins slightly divergent at basal third, subparallel at middle and evenly rounded to apex in apical third.

Male genitalia. Median lobe of aedeagus (Fig. 5I) moderately slightly arcuate and moderately twisted. Shaft arcuate, tapering in apical half. Apex slightly enlarged and straight with rounded tip. Apical orifice long, occupies almost half of the shaft length. Ventral margin of median lobe slightly concave in apical part. Walls of shaft with few poriferous canals apically. Dorsal copulatory sclerites with distinct V-shaped structure, directed with its sharp end

apically. Scaled membranous fields lacking. Spines of internal sac absent. Left paramere (Fig. 5G) comparatively wide, with shortly attenuate apex, bearing three long setae. Right paramere (Fig. 5H) short and wide, bearing three long setae, which are slightly longer the length of paramere.

Female internal genitalia. Not examined.

Geographical distribution. This species is known only from Mount Stokes in the Marlborough Sounds area (Crosby *et al.* 1998) (Fig. 10, green circle).

Habitat. According to label data specimens were collected from moss without more precise data about plant communities.

Relationships. The structure of the male genitalia suggests the relationship of *N. confusus* to other species having a similar V-shaped structure of dorsal copulatory sclerites in the internal sac of the median lobe, such as *N. oreobius* (Broun) and *N. lescheni*.

Nesamblyops distinctus, sp. nov.

Figs. 2D, 4D, 5J–L, 7C, 9

Type material. **HOLOTYPE**, male, in NZAC, dissected, labeled: \ Head of Fabians Valley 920m Marlborough 23 Oct 63 \ J.I. Townsend \ Litter 63/28 \ DSIR\ No \ NZ PB\ . **PARATYPES** (3 specimens, in NZAC, dissected 1 male), 1 male and 2 females labeled same as holotype.

Additional material: \ Mt. Riley 2400' Blenheim Dist. 24.vii.66 A.K. Walker \ litter from dry ridge under rata, beech and cedar trees 66/217 \ DSIR\ No \ (1 female).

Etymology. The specific epithet is a Latin adjective, *distinctus*, in the masculine form, meaning “distinguished”, and refers to the distinctive shape of the sclerites in the internal sac of male genitalia, allowing to distinguish this species from his closest relatives.

Type locality. New Zealand, South Island, Marlborough, Richmond Range, Fabians Valley.

Recognition. Adults of this species (Fig. 2D) can be distinguished from the adults of majority species of *Nesamblyops* by the distinctive shape of pronotum (Fig. 4D), however are practically indistinguishable from the adults of some *Nesamblyops* species (cf. with Figs. 3C) and are distinguished from all of them by the structure of the male genitalia.

Description. Large for genus (SBL range 1.93–2.26 mm, mean 2.06 ± 0.130 mm, n=5).

Habitus. Body form (Fig. 2D) markedly convex, elongate ovoid, general proportions wide (WE/SBL 0.42 ± 0.011), head narrow relative to pronotum (WH/WPm 0.66 ± 0.008 , proportions of pronotum in comparison to elytra average for genus (WPm/WE 0.76 ± 0.011).

Color. Body color brunneopiceous, appendages testaceous.

Prothorax. Pronotum (Fig. 4D) moderately long in comparison to elytra (LP/LE 0.43 ± 0.022) and moderately transverse (WPm/LP 1.28 ± 0.055), with lateral margins almost rectilinear and slightly constricted posteriorly (WPm/WPp 1.23 ± 0.016). Anterior angles indistinct, posterior angles obtuse ($105\text{--}115^\circ$), dented, and slightly protruding backwards. Width between posterior angles greater than between anterior angles (WPa/WPp 0.80 ± 0.030). Basal margin slightly concave.

Elytra. Ovoid, narrowly depressed along suture, comparatively long (LE/SBL 0.58 ± 0.008) and wide (WE/LE 0.72 ± 0.026). Humeri completely rounded. Lateral margins slightly divergent at basal half, shortly subparallel at middle and evenly rounded to apex in apical half.

Male genitalia. Median lobe of aedeagus (Fig. 5L) moderately arcuate and moderately twisted. Shaft subparallel basally, tapering in apical half. Apex moderately curved dorsally with narrowly rounded tip. Apical orifice long, occupies almost half of the shaft length. Ventral margin of median lobe straight. Walls of shaft without poriferous canals. Dorsal copulatory sclerites in form of characteristic “bird’s head” plate with apically attenuated dorsal part, and surrounded by distinct scaled membranous field. Spines of internal sac absent. Left paramere (Fig. 5J) comparatively wide, with shortly attenuate apex, bearing three long setae. Right paramere (Fig. 5K) of moderate length, bearing three long setae, which are slightly shorter the length of paramere. Ring sclerite as in Fig. 7C.

Female internal genitalia. Not examined.

Geographical distribution. This species is known from two localities on the Richmond Range in the Marlborough area (Crosby *et al.* 1998) (Fig. 9, red circles).



FIGURE 2. Digital images of habitus of New Zealand *Nesambyops* species, dorsal aspect. **A**—*N. brouni* (Lewis Pass, North Canterbury, SO), **B**—*N. carltoni* (Dun Mountain, Nelson, SO), **C**—*N. confusus* (Mount Stokes, Marlborough Sounds, SO), **D**—*N. distinctus* (Fabians Valley, Marlborough, SO), **E**—*N. lescheni* (D'Urville Island, Cook Strait, Marlborough Sounds, SO), **F**—*N. oreobius* (Mount Pirongia, Waikato, NO). Scale bar 1.0mm.

Habitat. Specimens were collected from litter “under rata, beech and cedar trees”.

Relationships. Based on the structure of the male genitalia *N. distinctus* forms a natural group with other species having a similar dorsal copulatory sclerite in the internal sac of the median lobe, such as *N. brouni*, *N. tararua*, and *N. townsendi*. Based on the details of the sclerite configuration and the state of the scaled membranous field, it is postulated that *N. distinctus* is a sister taxon to *N. brouni*.

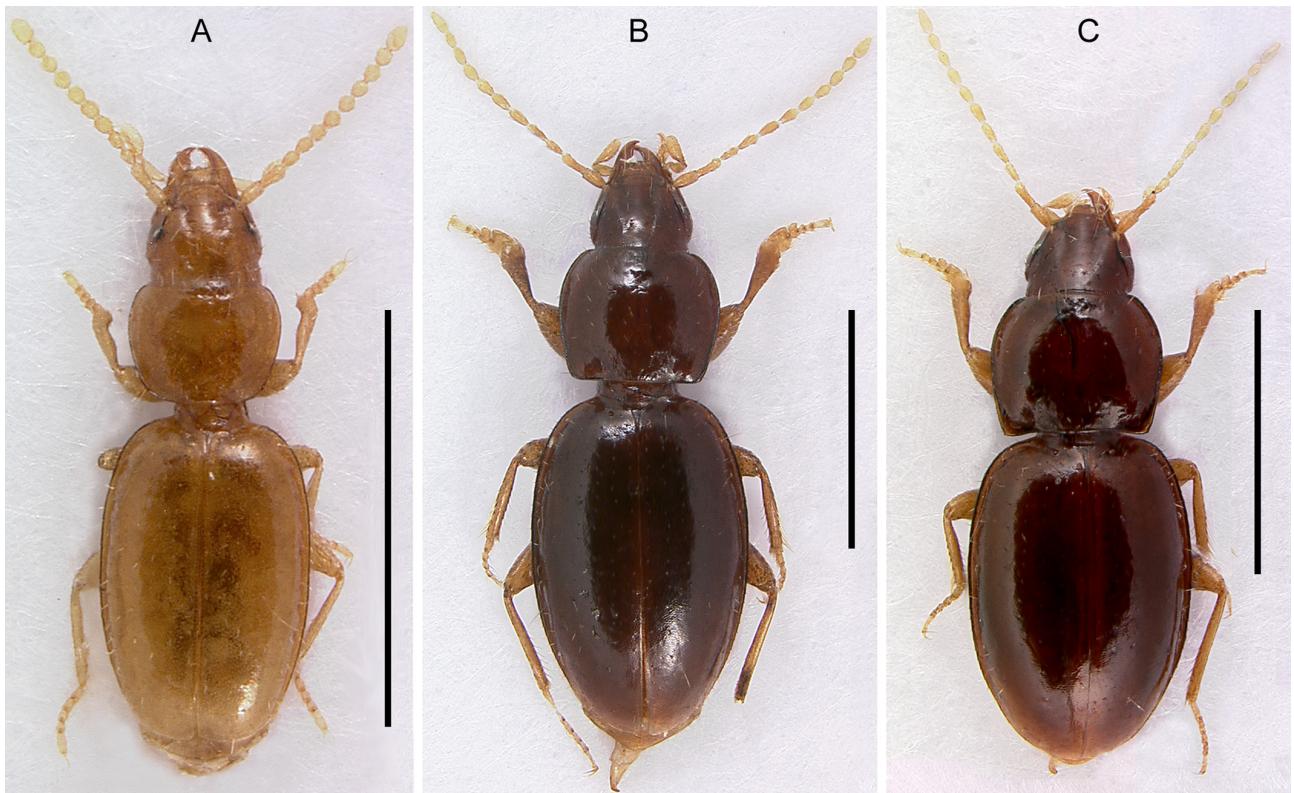


FIGURE 3. Digital images of habitus of New Zealand *Nesamblyops* species, dorsal aspect. **A**—*N. parvulus* (Mount Stokes, Marlborough Sounds, SO), **B**—*N. tararua* (Judd Ridge, Tararua Range, Wellington, NO), **C**—*N. townsendi* (Tennyson Inlet, Marlborough Sounds, SO). Scale bar 1.0mm.

Nesamblyops lescheni, sp. nov.

Figs. 2E, 4E, 5M–O, 7E, 8B, 10

Type material. HOLOTYPE, male, in NZAC, labeled: \ E. Attempt Hill, D'Urville Isd. 28-9-63 Litter J.I.Townsend \ J.I.Townsend Collection \ *Nesamblyops oreobius* (Broun) Det. I.Townsend. PARATYPES (13 specimens, in NZAC, dissected 1 male and 1 female), 1 male and 11 females labeled same as holotype; 1 female labeled: \ Coll. A.C.O'Connor, October, 1942 \ D'Urville Is. Cook Strait, N.Z. \ A.E.Brookes Collection \ DSIR\ No \ NZ PB\.

Etymology. The specific epithet is a Latinized eponym in the genitive case and is based on the surname of Richard A.B. Leschen, New Zealand coleopterist (New Zealand Arthropod Collection, Maanaki Whenua—Landcare Research, Auckland, New Zealand), who made material of New Zealand Anillini available for this study.

Type locality. New Zealand, South Island, Marlborough Sounds, D'Urville Island.

Recognition. Adults of this species (Fig. 2E) can be distinguished from adults of many *Nesamblyops* species (cf. with Figs. 2A–C, 3A–C) by their smaller size and characteristic body proportions, as well by the structure of the male genitalia.

Description. Of moderate size for genus (SBL range 1.43–1.68 mm, mean 1.54 ± 0.091 mm, n=12).

Habitus. Body form (Fig. 2E) markedly convex, elongate ovoid, general proportions wide (WE/SBL 0.42 ± 0.013), head narrow relative to pronotum (WH/WPm 0.69 ± 0.013), proportions of pronotum in comparison to elytra average for genus (WPm/WE 0.77 ± 0.034).

Color. Body color brunneorufous, appendages testaceous.

Prothorax. Pronotum (Fig. 4E) moderately long in comparison to elytra (LP/LE 0.43 ± 0.024) and moderately transverse (WPm/LP 1.28 ± 0.037), with lateral margins arcuately constricted posteriorly (WPm/WPp 1.29 ± 0.027). Anterior angles indistinct, posterior angles obtuse ($106\text{--}115^\circ$), but distinct. Width between posterior angles greater than between anterior angles (WPa/WPp 0.89 ± 0.015). Basal margin almost rectilinear, slightly convex at middle.

Elytra. Ovoid, narrowly depressed along suture, comparatively long (LE/SBL 0.58 ± 0.012) and wide (WE/LE 0.72 ± 0.021). Humeri completely rounded. Lateral margins slightly divergent at basal third, subparallel at middle and evenly rounded to apex in apical third.

Male genitalia. Median lobe of aedeagus (Fig. 5O) slightly arcuate and moderately twisted. Shaft subparallel, tapering in apical third. Apex short and semicircular. Apical orifice short, occupies about one third of the shaft length. Ventral margin of median lobe widely concave. Walls of shaft with numerous poriferous canals. Dorsal copulatory sclerites with distinct V-shaped structure, directed with its sharp end apically. Scaled membranous fields lacking. Spines of internal sac absent. Left paramere (Fig. 5M) comparatively wide, with shortly attenuate apex, bearing three long setae. Right paramere (Fig. 5N) short and wide, bearing three long setae, which are slightly longer the length of paramere. Ring sclerite as in Fig. 7E.

Female internal genitalia. Spermatheca (Fig. 8B) sclerotized, of bulb-like shape with wider rounded apical part and narrower rounded basal part. Length of spermatheca shorter than the lengths of either spermathecal gland or spermathecal duct. Spermathecal duct short without coils. Attachments of spermathecal duct and gland to spermatheca close together.

Geographical distribution. This species is known only from the D'Urville Island in the Marlborough Sounds area (Crosby *et al.* 1998) (Fig. 10, red circles). Possibly, *N. lescheni* is an endemic of this island.

Habitat. Labels do not include specific information about habitats.

Relationships. The structure of the male genitalia suggests relationship of *N. lescheni* to other species with similar V-shaped structure of dorsal copulatory sclerites in the internal sac of the median lobe, such as *N. confusus* and *N. oreobius*.

Nesamblyops oreobius (Broun) (dissected 16 specimens)

Figs. 2F, 4F, 5P–R, 7D, 8A, 11

= *Tachys oreobius* Broun, 1893: 1399.

= *Tachys coriaceus* Broun, 1908: 421. Synonymy established by Moore (1980: 400).

= *Anillus monticola* Broun, 1910: 10. Synonymy established by Jeannel (1937: 281).

Examined material (more than 280 specimens): **WO:** Mt.Karioi, nr base, nr summit, 11 Oct 1981, C.F.Butcher, litter 81/95 (5ex.); Tangarakau Gorge, 450m, 18-4-65, N.A.Walker, litter (1ex.); Mt.Pirongia, 962m, 16 Jan 1977, A.K.Walker, litter 77/2 (2ex.), Mt.Pirongia, 2500', 23-9-64, litter, G.Kushel (1ex.); TeKauri Scenic Reserve, nr Kawhia, 20 Sep 1981, C.F.Butcher, litter 81/89 (6ex.); Waitomo, Maori L., Tumutumu Rd., 24 May 1983, J.C.Watt, litter and soil 83/60 (5ex.); Waipuna Reserve near Waitomo, 28 Oct 1977, A.R. Ferguson, litter 77/134 (4ex.); Herangi Range, 500m, above Mangatoa Saddle, 9 Dec 1982, J.S.Dugdale, mixed swards and bryophytes 82/134 (8ex.); Mohoenui, Gribbons Road, 26 Jun 1977, N.H.Mancer or G.W.Ramsay, litter 77/78 (118ex.); Mt.Messenger, 610', Taranaki, 24.xi.68, J.S.Dugdale, litter 68/196 (1ex.); **TK:** Pouakai Range, 1006m, Ahuwakawa Track, 11 Jan 1978, J.C.Watt, litter 78/11 (30ex.), same but, 1067m, litter and moss 78/10 (5ex.), same but, 1220m, 9 Jan 1978, litter 78/13 (4ex.); Mt.Egmont, 3500', 2-4.1.82, G.Kushel, leafmould (9ex.); Mt.Egmont, 823m, Taranaki, 29 Nov 70, A.W.Don, litter (3ex.); Mt.Egmont, 4600', Stratford side, 25.x.68, J.S.Dugdale, mat plants 68/198 (2ex.); Mt.Egmont, 1000m, Stratford Rd., 22 Feb 1984, B.M.May, litter 84/52 (1ex.); Egmont NP, Ngatoro TK, 650m, 19.III.1998, Larochelle, Larivière, wet broadleaf forest along mud flats, in litter & rotten wood on & along big logs (1ex.); N Egmont, 23 Feb 1984, B.M.May, litter 84/51 (1ex.); 853m E Egmont, Nov 76, K.E.Fox, moss beside Kamahi Track (5ex.); Summit track, 4500', Mt.Egmont, 15.6.65, J.I.Townsend, moss sample from wet bank above Hooker Hut (1ex.); Stratford Plat., 4000', 15-6-65, moss, J.I.Townsend (5ex.); Stratford Plt. Rd., Mt.Egmont, 1800', 17-4-65, litter, N.A.Walker (2ex.), same but 2150' (3ex.), same but 2550' (1ex.), same but 2600' (1ex.), same but 3250' (1ex.), same but 3500' (2ex.); Mt Egmont NP, Stratford Mtn. House, 846m, 23 May 1986, C.L.Lyal, Leaf litter, CL 474 (2ex.); Wilkies Pools, track litter, Dawson Falls, 3200', 16-6-65, J.I.Townsend (2ex.); Dawson Falls, 975m, Mt.Egmont, Taranaki, 16 Jun 65, J.I. Townsend, litter 65/387 (1ex.); Pouakai Hump, 1220m, 3 Dec 1975, A.K.Walker, dry moss 75/213 (4ex.); W edge Hump, Plat. Pouakai Ra., 2 Dec 1975, J.S. Dugdale, litter 75/200 (1ex.); Pouakai Ra, 1372m, Summit Ridge, 10 Jan 1978, J.C.Watt, litter 78/9 (2ex.), same but 1400m, litter 78/8 (1ex.); Pouakai Trig, Pouaki Range, 3 Dec 1975, litter 75/206 (4ex.), same but moss 75/208 (12ex.), same but litter 75/209 (3ex.); Pouakai Saddle, 1220m, Pouakai Ra., 3 Dec 1975, J.S. Dugdale, litter 75/202 (2ex.), same but *Poa colensoi* swards 75/203 (10ex.), same but litter 75/204 (9ex.), same but litter 75/205 (6ex.); Pouakai Ra. Hut, 1280m, 2 Dec 1975, A.K. Walker, litter 75/210 (1ex.); Tangarakau Gorge, 31-12-78 (1 ex.).

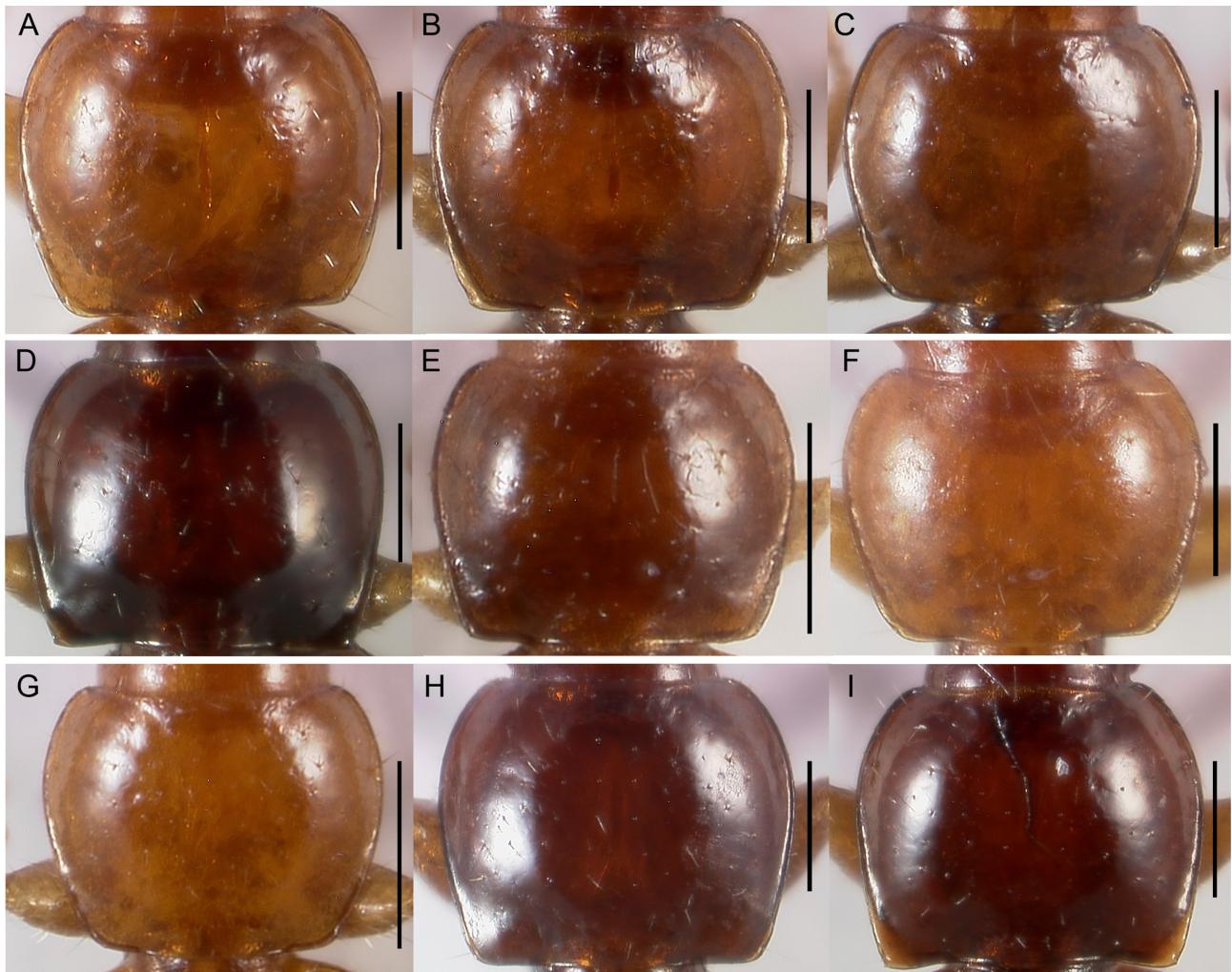


FIGURE 4. Digital images of pronota of New Zealand *Nesambylops* species, dorsal aspect. **A**—*N. brouni* (Lewis Pass, North Canterbury, SO), **B**—*N. carltoni* (Dun Mountain, Nelson, SO), **C**—*N. confusus* (Mount Stokes, Marlborough Sounds, SO), **D**—*N. distinctus* (Fabians Valley, Marlborough, SO), **E**—*N. lescheni* (D'Urville Island, Cook Strait, Marlborough Sounds, SO), **F**—*N. oreobius* (Mount Pirongia, Waikato, NO), **G**—*N. parvulus* (Mount Stokes, Marlborough Sounds, SO), **H**—*N. tararua* (Judd Ridge, Tararua Range, Wellington, NO), **I**—*N. townsendi* (Tennyson Inlet, Marlborough Sounds, SO). Scale bar 0.2mm.

The description of *N. oreobius* contains little diagnostic information that allows correct identification. Below, I redescribe the species to make comparison of *N. oreobius* with other species easier.

Type locality. New Zealand, North Island, Waikato, Mount Pirongia.

Recognition. Adults of this species (Fig. 2F) are practically indistinguishable from the adults of many *Nesambylops* species based on external characters (cf. with Figs. 2A–C) and are distinguished from them by the structure of the male genitalia.

Description. Medium sized for genus (SBL range 1.51–1.83 mm, mean 1.68 ± 0.100 mm, n=23).

Habitus. Body form (Fig. 2F) markedly convex, elongate ovoid, general proportions wide (WE/SBL 0.40 ± 0.008), head narrow relative to pronotum (WH/WPm 0.70 ± 0.014), proportions of pronotum in comparison to elytra average for genus (WPm/WE 0.76 ± 0.027).

Color. Body color brunneorufous, appendages testaceous.

Prothorax. Pronotum (Fig. 4F) moderately long in comparison to elytra (LP/LE 0.41 ± 0.016) and moderately transverse (WPm/LP 1.26 ± 0.021), with lateral margins arcuately and strongly constricted posteriorly (WPm/WPp 1.34 ± 0.032). Anterior angles indistinct, posterior angles obtuse ($111\text{--}124^\circ$), rounded. Width between posterior angles greater than between anterior angles (WPa/WPp 0.93 ± 0.029). Basal margin almost rectilinear, slightly convex at middle.

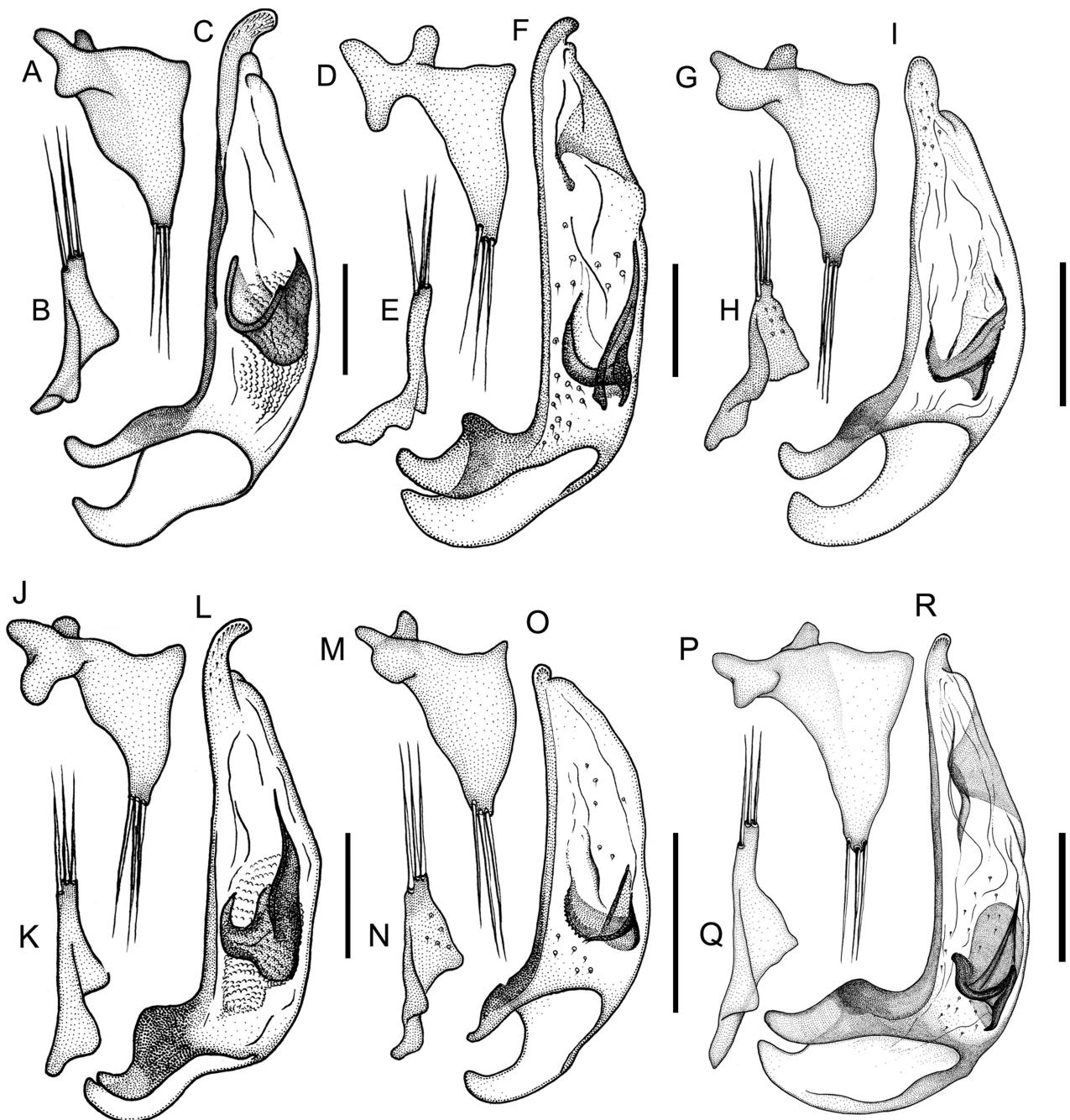


FIGURE 5. Line drawings of male genitalia of New Zealand *Nesamblyops* species. *N. brouni* (Lewis Pass, North Canterbury, SO): **A**—left paramere, left lateral aspect, **B**—right paramere, right lateral aspect, **C**—median lobe, right lateral aspect. *N. carltoni* (Dun Mountain, Nelson, SO): **D**—left paramere, left lateral aspect, **E**—right paramere, right lateral aspect, **F**—median lobe, right lateral aspect. *N. confusus* (Mount Stokes, Marlborough Sounds, SO): **G**—left paramere, left lateral aspect, **H**—right paramere, right lateral aspect, **I**—median lobe, right lateral aspect. *N. distinctus* (Fabians Valley, Marlborough, SO): **J**—left paramere, left lateral aspect, **K**—right paramere, right lateral aspect, **L**—median lobe, right lateral aspect. *N. lescheni* (D'Urville Island, Cook Strait, Marlborough Sounds, SO): **M**—left paramere, left lateral aspect, **N**—right paramere, right lateral aspect, **O**—median lobe, right lateral aspect. *N. oreobius* (Mount Pirongia, Waikato, NO): **P**—left paramere, left lateral aspect, **Q**—right paramere, right lateral aspect, **R**—median lobe, right lateral aspect. Scale bar 0.1mm.

Elytra. Ovoid, narrowly depressed along suture, comparatively long (LE/SBL 0.58 ± 0.008) and wide (WE/LE 0.72 ± 0.026). Humeri completely rounded. Lateral margins slightly divergent at basal half, shortly subparallel at middle and evenly rounded to apex in apical half.

Male genitalia. Median lobe of aedeagus (Fig. 5R) strongly arcuate and moderately twisted. Shaft subparallel in basal half, tapering in apical half. Apex slightly curved dorsally with narrowly rounded tip. Apical orifice occupies about one third of the shaft length. Ventral margin of median lobe straight. Walls of shaft with poriferous canals at basal half. Dorsal copulatory sclerites with V-shaped plate, directed with its sharp end apically. Scaled membranous fields lacking. Spines of internal sac absent. Left paramere (Fig. 5P) comparatively wide, with shortly attenuate apex, bearing three long setae. Right paramere (Fig. 5Q) moderately long and wide, bearing three long setae, which are shorter the length of paramere. Ring sclerite as in Fig. 7D.

Female internal genitalia. Spermatheca (Fig. 8A) sclerotized, of bulb-like shape with wide circular apical part and narrow basal part. Length of spermatheca shorter than the lengths of either spermathecal gland or spermathecal duct. Spermathecal duct short without coils. Attachments of spermathecal duct and gland to spermatheca close together.

Geographical distribution. This species is distributed only on the North Island, where it is known from the Taranaki and Waikato areas (Crosby *et al.* 1998) from Mount Taranaki (former Mount Egmont) in the south, north to Mount Pirongia (Fig. 11).

Habitat. According to label data, specimens were collected from leafmold, litter, and moss without more precise data about plant communities.

Relationships. The structure of the male genitalia of *N. oreobius*, especially the V-shaped sclerite of the internal sac suggests a possible relationship to the other species with similar configuration of copulatory sclerites, such as *N. confusus* and *N. lescheni*.

Nesamblyops parvulus, sp. nov.

Figs. 3A, 4G, 6A–C, 7F, 10

Type material. **HOLOTYPE**, male, in NZAC, labeled: \ Mt Stokes 1172m Kenepuru Snds Marl. 11.x.67 J.McBurney \ moss 67/243 \ DSIR\ Ns \ NZ PB\ . **PARATYPES** (24 specimens, in NZAC, dissected 4 exx.), 3 males and 6 females labeled same as holotype; 3 males and 8 females labeled: \ Mt Stokes 1160m Marlborough 12 Oct 67 \ J.I.Townsend \ Litter 67/244 \ DSIR\ Ns \ NZ PB\ ; 1 male: \ Mt Stokes Marl. 3850' 12.x.67 J.I.Townsend \ Litter 67/244 \ DSIR\ Ns \ NZ PB\ ; 1 male and 1 female labeled: \ Mt Stokes 3850'Marl. 13.x.67 J.I.Townsend \ Litter 67/245 \ DSIR\ Ns \ NZ PB\ ; 1 male labeled: \ Mt.Stokes 3850' 11.x.67 \ Kenepuru Sounds J.I.Townsend \ moss sample 67/243 \ .

Etymology. The specific epithet is a Latin adjective, *parvulus*, in the masculine form, diminutive of Latin *parvus* meaning “small”, and refers to the small size of the new species.

Type locality. New Zealand, South Island, Marlborough Sounds, Mount Stokes.

Recognition. Adults of this species (Fig. 3A) can be distinguished from adults of many *Nesamblyops* species (cf. with Figs. 2A–C, 3B–C) by the small size, elongated habitus, diagnostic shape of pronotum (Fig. 4G) as well by the structure of the male genitalia.

Description. Small for genus (SBL range 1.26–1.49 mm, mean 1.37 ± 0.081 mm, n=15).

Habitus. Body form (Fig. 3A) moderately convex, elongate ovoid, general proportions slightly wide (WE/SBL 0.39 ± 0.025), head wide relative to pronotum (WH/WPm 0.75 ± 0.023), proportions of pronotum in comparison to elytra average for genus (WPm/WE 0.74 ± 0.063).

Color. Body color rufostestaceous, appendages testaceous.

Prothorax. Pronotum (Fig. 4G) moderately long in comparison to elytra (LP/LE 0.40 ± 0.021) and moderately transverse (WPm/LP 1.23 ± 0.034), with lateral margins arcuately and strongly constricted posteriorly (WPm/WPp 1.37 ± 0.047). Anterior angles indistinct, posterior angles very obtuse ($126\text{--}141^\circ$), almost effaced. Width between anterior angles equals the width between posterior angles (WPa/WPp 1.00 ± 0.047). Basal margin slightly concave.

Elytra. Elongate-ovoid, moderately depressed along suture, comparatively long (LE/SBL 0.60 ± 0.013) and slightly narrow for genus (WE/LE 0.66 ± 0.032). Humeri completely rounded. Lateral margins slightly divergent at basal fourth, subparallel at middle and evenly rounded to apex in apical third.

Male genitalia. Median lobe of aedeagus (Fig. 6 C) slightly arcuate and slightly twisted. Shaft diverging basally, tapering in apical half. Apex enlarged with straight rounded tip. Apical orifice long, occupies almost half of the shaft length. Ventral margin of median lobe straight basally, moderately enlarged in apical third. Walls of shaft

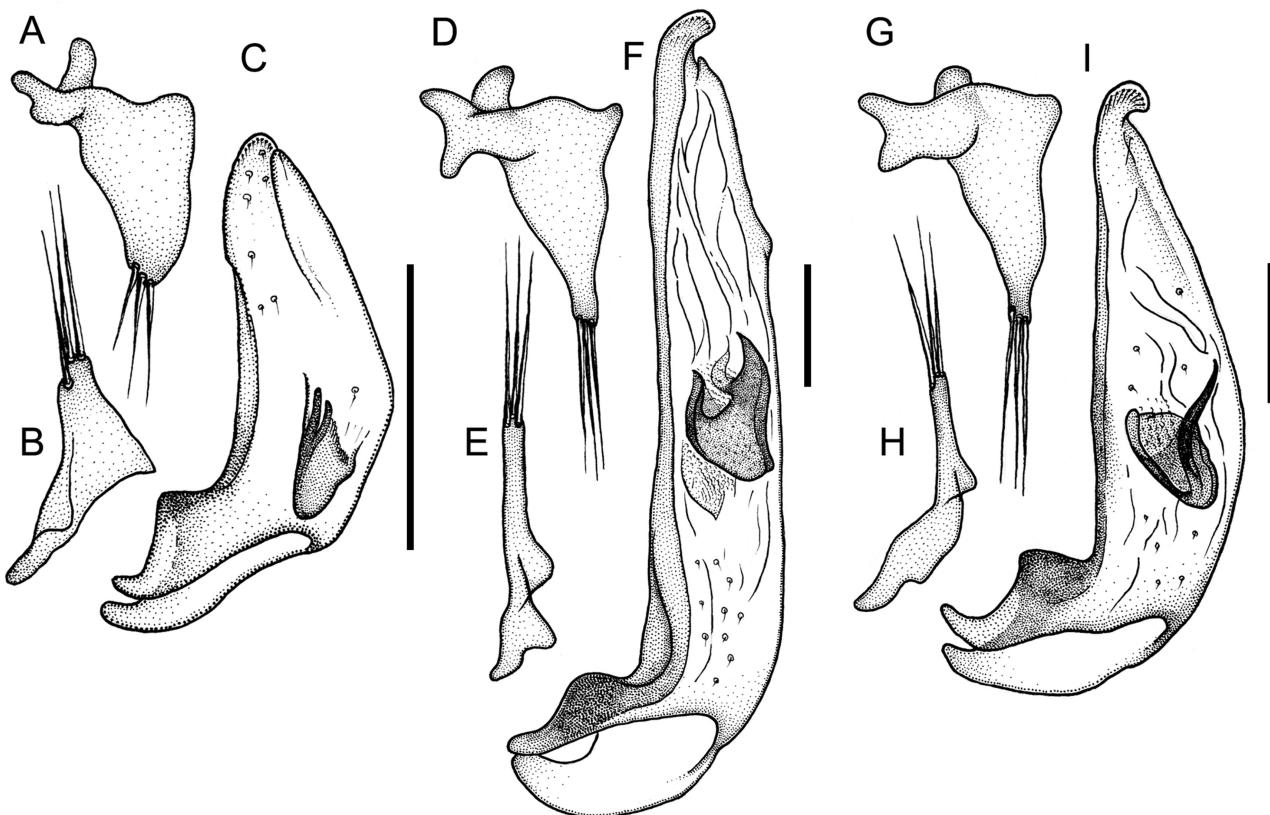


FIGURE 6. Line drawings of male genitalia of New Zealand *Nesamblyops* species. *N. parvulus* (Mount Stokes, Marlborough Sounds, SO): **A**—left paramere, left lateral aspect, **B**—right paramere, right lateral aspect, **C**—median lobe, right lateral aspect. *N. tararua* (Judd Ridge, Tararua Range, Wellington, NO): **D**—left paramere, left lateral aspect, **E**—right paramere, right lateral aspect, **F**—median lobe, right lateral aspect. *N. townsendi* (Tennyson Inlet, Marlborough Sounds, SO): **G**—left paramere, left lateral aspect, **H**—right paramere, right lateral aspect, **I**—median lobe, right lateral aspect. Scale bar 0.1mm.

with few poriferous canals apically. Dorsal copulatory sclerites in form of characteristic U-shaped plate, directed with its open end apically. Scaled membranous fields lacking. Spines of internal sac absent. Left paramere (Fig. 6A) wide, apex blunt, bearing three setae of moderate length. Right paramere (Fig. 6B) short and wide, bearing three long setae, which are slightly longer the length of paramere. Ring sclerite as in Fig. 7F.

Female internal genitalia. Not examined.

Geographical distribution. This species is known only from Mount Stokes in the Marlborough Sounds area (Crosby *et al.* 1998) (Fig. 10, yellow circle).

Habitat. According to label data specimens were collected from moss without more precise data about plant communities.

Relationships. Based on the structure of the male genitalia it is postulated that *N. parvulus* occupies an isolated position among the examined species of the genus. At Mount Stokes *N. parvulus* lives in sympatry and syntopically with *N. confusus*: according to the label data at least one sample included both species.

Nesamblyops tararua, sp. nov.

Figs. 3B, 4H, 6D–F, 7G, 9

Type material. HOLOTYPE, male, in NZAC, labeled: \ NEW ZEALAND WN Tararua Range Judd Ridge Otaki Forks 800m \ 5Nov 1980 C.F. Butcher litter 80/101 \ NZ PB\. **PARATYPES** (129 specimens glued on boards and triangles plus more than 20 specimens in plastic capsules, in NZAC, dissected 16 exx.), 9 males and 6 females labeled same as holotype; 5 males and 4 females labeled: \ NEW ZEALAND WN Tararua Ra Dundas Hut Ridge 950m 3 Dec 1984\ R.C. Craw Sifted litter 84/88\ Duplicate specimens in alcohol\NZ PB\; 1 female labeled: \ NEW ZEALAND WN Tararua Ra Dundas Hut Ridge 1350m, E side 6 Dec 1984 \ R.C. Craw Sifted litter 84/88\ Duplicate specimens in alcohol\ NZ PB\; 2

females labeled: \ NEW ZEALAND WN Tararua Ra Dundas Hut Ridge 990m 3 Dec 1984\ B.G.Bennet & T.K. Crosby Sifted litter 84/83 \ NZ PB; 1 female labeled: \ Tararua Ra Dundas Hut Ridge River Forks 900m 11 Feb 1985, G.W. Ramsay, litter 85/12 \ NZ PB; 2 females labeled: \ Tararua Ra., Dundas Hut Ridge, 800m, 13 Feb 1985, G.W. Ramsay, Sifted litter 85/16 \ NZ PB; 2 females labeled: \ Tararua Ra., Dundas Hut Ridge, 950m, 29 Nov 1984, R.C. Crow, in *Blechnum discolor* \ NZ PB; 1 female labeled: \ Tararua Ra., Dundas Hut Ridge, 990m, 13 Feb 1985\ C.F. Butcher Litter 85/19 \ NZ PB; 1 male and 1 female labeled: \ 10km S of Levin, Waikawa, 150m, 8 Mar 1978 S.B. & J. Peck \ litter \ S. & B. Peck Collection \ NZ PB; 1 male labeled: \ Nth. Manakau Rd 12.5.91 J.A. & J.I. Townsend\ J.I.Townsend Collection\; 1 male labeled: \ NEW ZEALAND WN Levin Kimberley Reserve 6 Nov 1980 C.F.Butcher\ litter 80/103 \ NZ PB; 2 females labeled: \ NEW ZEALAND WN Mt Holdsworth Start of Interior Track 30 Jan 1985 \ H.P. McColl Sifted litter 2/85 \ NZ PB; 4 males labeled: \ Mt. Holdsworth 2000' Tararuas 19.xi.68 S. Edridge\ moss 68/202 \ DSIR\ No \ NZ PB; 2 females labeled: \ NEW ZEALAND WN Tararua Range Judd Ridge Otaki Forks, 272m 5Nov 1980 \C.F. Butcher litter 80/102 \ NZ PB; 1 male and 1 female labeled: \ Tararua Ra. 17 Nov 68 S.Edridge \ N. D 3 \ 2000' litter 68/200 \ DSIR\ No \ NZ PB; 1 female labeled: \ NEW ZEALAND WN W. Peak Tararua Ra 1280m 14 Apr 1974 J.C. Watt \ Litter under *Olearia colensoi* & *Chionochloa* 74/31 \ NZ PB; 1 female labeled: \ Nr. Field Hut 3000' 6.9.65 J.I.Townsend moss in forest \; 1 male labeled: \ litter under grass track N. of Wharite 3000' 13.11.89 J.I.Townsend \ J.I.Townsend Collection \; 1 male labeled: \ Waiotauru Rd Akatarawa Range litter 16.11.91 J.Nunn \ J.I.Townsend Collection \; more than 10 specimens in plastic capsule labeled: \ Waiotauru Rd. 22-10-91 Akatarawa Range litter under silver beech J.I.Townsend \ J.I.Townsend Collection \; more than 10 specimens in plastic capsule labeled: \ Akatarawa Range Waiotauru Rd litter 16.11.91 J.I.Townsend \ *Nesamblyops oreobius* \ J.I.Townsend Collection \; 1 male labeled: \ leaf litter silver beech forest Waiotauru 830m 26.4.88 J. Cooksley Tararua Forest Park \ J.I.Townsend Collection \; 1 male labeled: \ NEW ZEALAND WN Tararua Forest Park Waiotauru Rd 20 Jul 1999 E.Spurr \ 7/S \ NZ PB; 1 male labeled: \ NEW ZEALAND WN Tararua Forest Park Waiotauru Rd 11 May 1999 E.Spurr \ 10/W \ NZ PB; 8 males and 4 females labeled: \ NEW ZEALAND WN Akatarawa Sdle 600m, 7 Mar 1978 S.B. Peck Litter \ S. & B. Peck Collection \ NZ PB; 3 males and 8 females labeled: \ NEW ZEALAND WN Akatarawa Sdle Tararua FP Tk 17 Jan 1984 H.P. McColl \ 8/84 litter \ Duplicate specimens in alcohol \ NZ PB; 1female labeled: \ Akatarawa Range S. of Saddle 1700' Leaf litter 8-9-85 A.J. Townsend \ Anillini *Nesamblyops oreobius* (Broun) \ J.I.Townsend Collection \; 1 male labeled: \ NEW ZEALAND WN Kaitoke Waterworks Swingbridge Tk 200m, 29 Jan 1985 \ C. Welch *Nothofagus truncata* litter \ NZ PB; 1 female labeled: \ NEW ZEALAND WN Kaitoke Waterworks Bush Walk, 200m 29 Jan 1985 \ C. Welch Mixed forest litter \ NZ PB; 1 male labeled: \ NEW ZEALAND WN Orongorongo V, W.N. 15 Jan 1995 \ Hard beech forest litter Tullgren #61 \ *Nesamblyops oreobius* Broun det. A. Larochelle 1995 \; 1 male and 1 female labeled: \ NEW ZEALAND WN Orongorongo V, W.N. 17 Dec 1993 \ Hard beech forest litter Tullgren #34 \ *Nesamblyops oreobius* Broun det. A. Larochelle 1995 \ NZ PB; 1 male labeled: \ NEW ZEALAND WN Orongorongo V, W.N. 17 Dec 1993 \ Hard beech forest litter Tullgren #35 \ *Nesamblyops oreobius* Broun det. A. Larochelle 1995 \ NZ PB; 3 females labeled: \ NEW ZEALAND WN Orongorongo V Stn Ridge 100m 27 Jan 1992 J.S. Dugdale \ Litter *Nothophagus solandri* emergence trap \ NZ PB; 1 female labeled: \ Orongorongo V. Well. 152m \ 23 Sep 69 J.S. Dugdale \ litter \ DSIR\ No \ NZ PB; 1 male labeled: \ Orongorongo Res. Stn. Well. \ 21 May 69 J.S. Dugdale \ litter \ DSIR\ No \ NZ PB; 1 male labeled: \ Orongorongo F.S. Wellington \ 18 Sep 69 J.C. Watt J.S. Dugdale \ litter \ DSIR\ No \; 1 female labeled: \ Orongorongo Res. Sta Wellington 21 May 69\ J.S. Dugdale \ litter \ DSIR\ No \ NZ PB; 1 female labeled: \ NEW ZEALAND WN Wainuiomata Whakanui Tr 10 Jan 1993 GR Grehan \ Moss, 700m beech/kamahi \ NZ PB; 1 male labeled: \ New Zealand WN Table Top Tararua FP 10.2.85 \ in leatherwood litter \ *Nesamblyops oreobius* det. J. Nunn \; 4 males and 1 female labeled: \ New Zealand WN 4km along Waiotauru Rd. 7-Nov-06 \ Washed soil sample. Taruarua Rng. \; 1 male labeled: \ New Zealand WN Waiotauru Rd. Tararua FP, 23.4.95 \ in leaf litter \.7 males labeled: \ Port Ligar 304m Marlborough 26 Oct 69 F. Alack \ Litter 69/175\ DSIR\ No \ NZ PB; 14 males and 8 females labeled: \ Port Ligar 1000' Marl. 26.x.69 F. A. Alack \ Litter 69/175\ DSIR\ No \ NZ PB; 1 male labeled: \ Canoe Bay Pelorus Snd. 2-9-62 J. I. Townsend \J. I. Townsend Collection \ *Nesamblyops oreobius* (Broun) Det. I. Townsend 1973 \.

Etymology. The specific epithet is a noun in apposition and refers to the name of the Mountain Range, where the type series was collected.

Type locality. New Zealand, North Island, Wellington, Tararua Range.

Recognition. Adults of this species (Fig. 3B) are practically indistinguishable from the adults of many *Nesamblyops* species based on external characters (cf. with Figs. 2A–B, 2D) and are distinguished from them by the structure of the male genitalia.

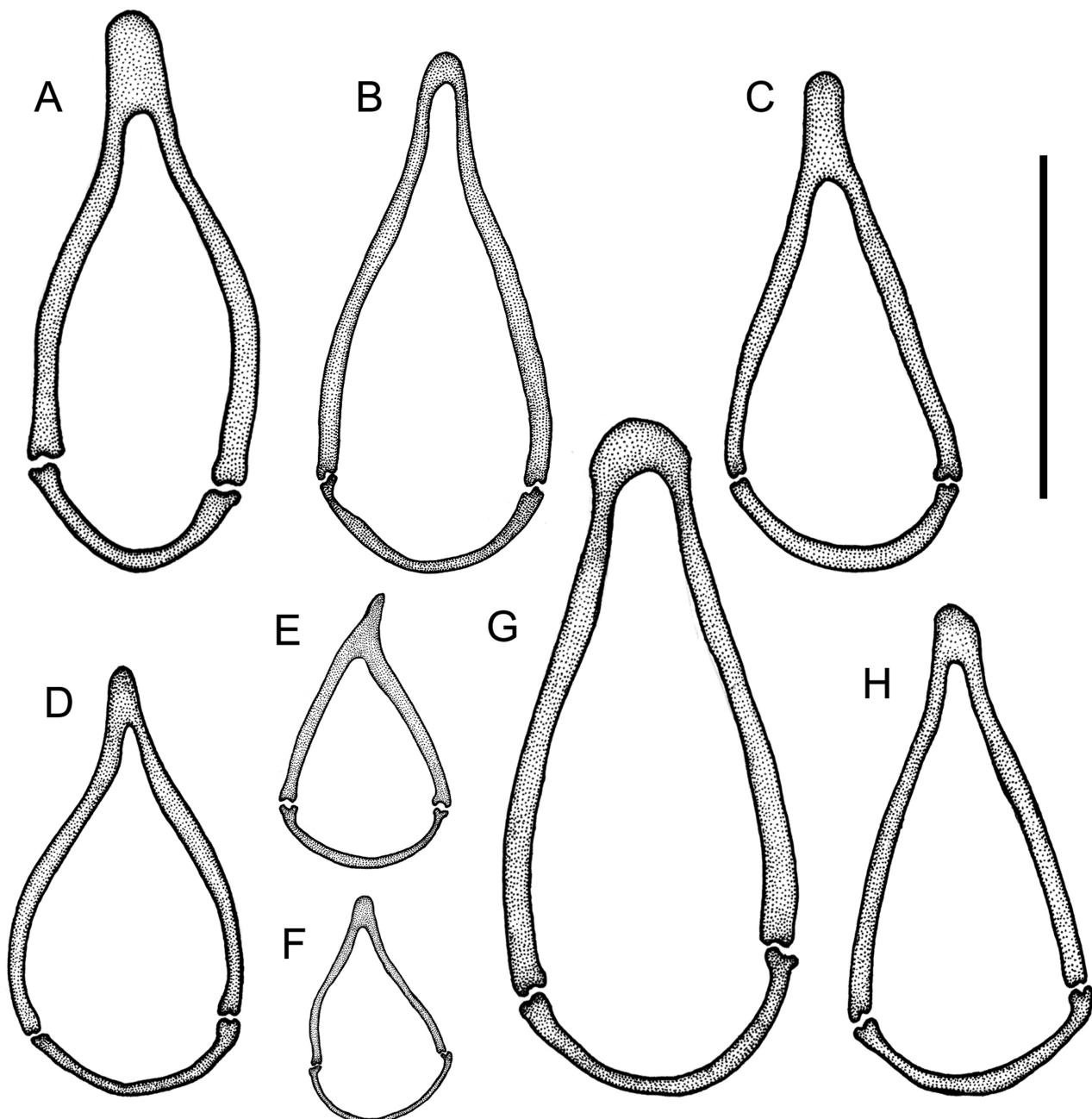


FIGURE 7. Line drawings of ring sclerite of New Zealand *Nesamblyops* species, male genitalia, dorsal aspect. **A**—*N. brouni* (Lewis Pass, North Canterbury, SO), **B**—*N. carltoni* (Dun Mountain, Nelson, SO), **C**—*N. distinctus* (Fabians Valley, Marlborough, SO), **D**—*N. oreobius* (Mount Pirongia, Waikato, NO), **E**—*N. lescheni* (D'Urville Island, Cook Strait, Marlborough Sounds, SO), **F**—*N. parvulus* (Mount Stokes, Marlborough Sounds, SO), **G**—*N. tararua* (Judd Ridge, Tararua Range, Wellington, NO), **H**—*N. townsendi* (Tennyson Inlet, Marlborough Sounds, SO). Scale = 0.4mm.

Description. Large for genus (SBL range 1.80–2.33 mm, mean 2.05 ± 0.162 mm, n=25).

Habitus. Body form (Fig. 3B) markedly convex, elongate ovoid, general proportions wide (WE/SBL 0.40 ± 0.010), head narrow relative to pronotum (WH/WPm 0.68 ± 0.017), proportions of pronotum in comparison to elytra average for genus (WPm/WE 0.75 ± 0.015).

Color. Body color brunneopiceous, appendages brunneorufous.

Prothorax. Pronotum (Fig. 4H) moderately long in comparison to elytra (LP/LE 0.41 ± 0.016) and moderately transverse (WPm/LP 1.21 ± 0.021), with lateral margins rectilinear constricted posteriorly (WPm/WPp 1.27 ± 0.038). Anterior angles indistinct, posterior angles slightly obtuse ($98\text{--}113^\circ$), rounded. Width between posterior angles greater than between anterior angles (WPa/WPp 0.86 ± 0.033). Basal margin almost straight.

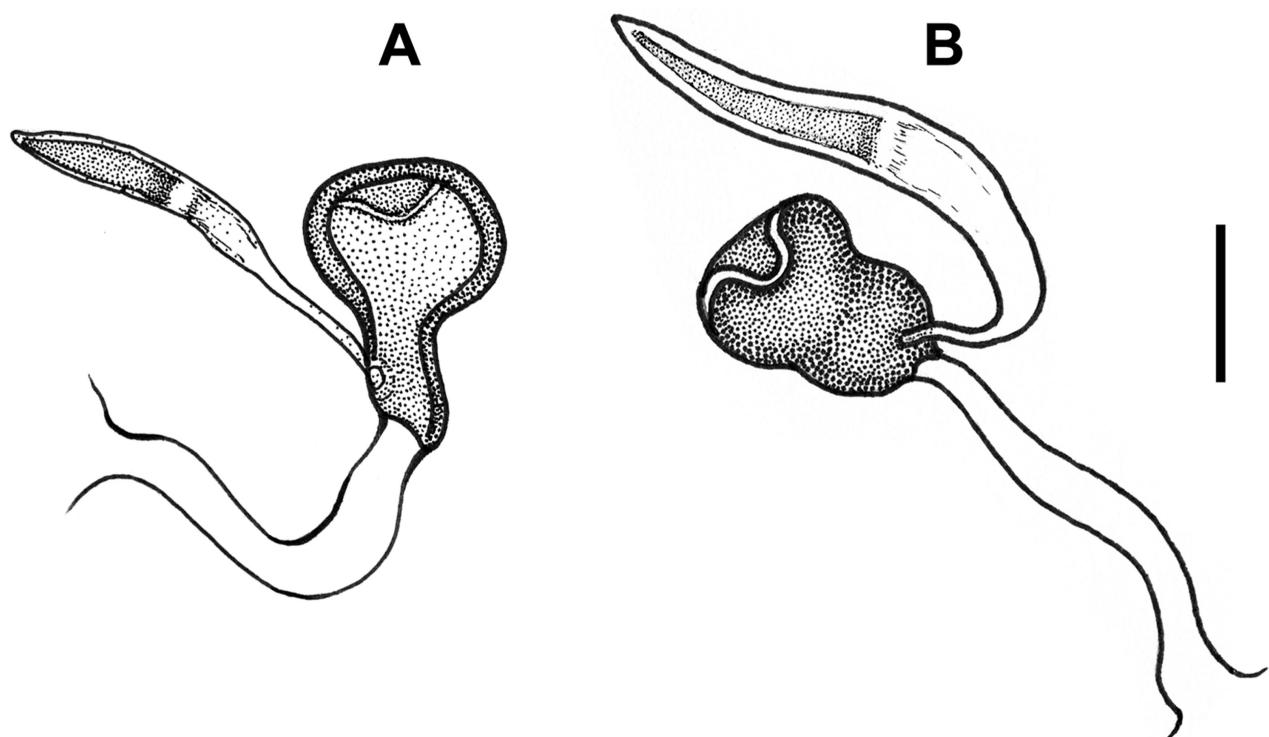


FIGURE 8. Line drawings of spermatheca of New Zealand *Nesamblyops* species. **A**—*N. oreobius* (Mount Pirongia, Waikato, NO), **B**—*N. lescheni* (D'Urville Island, Cook Strait, Marlborough Sounds, SO). Scale = 0.05mm.

Elytra. Ovoid, narrowly depressed along suture, comparatively long (LE/SBL 0.60 ± 0.012) and moderately wide (WE/LE 0.67 ± 0.024). Humeri completely rounded. Lateral margins slightly divergent at basal half, shortly subparallel at middle and evenly rounded to apex in apical half.

Male genitalia. Median lobe of aedeagus (Fig. 6F) strongly arcuate and moderately twisted. Shaft subparallel, tapering in apical third. Apex moderately curved dorsally with narrowly rounded tip. Apical orifice occupies almost third of the shaft length. Ventral margin of median lobe almost straight, slightly concave before apex. Walls of shaft with poriferous canals basally. Dorsal copulatory sclerites in form of characteristic “bird’s head” plate, surrounded by scaled membranous field. Spines of internal sac absent. Left paramere (Fig. 6D) of normal proportions, with moderately attenuate apex, bearing three long setae. Right paramere (Fig. 6E) long and narrow, bearing three long setae, slightly shorter the length of paramere. Ring sclerite as on Fig. 7G.

Female internal genitalia. Not examined.

Geographical distribution. The range of this species splits into two parts. The large northern area of the range occupies the southern parts of the North Island and stretches along the Rimutaka and Tararua Ranges north to Wharite Peak in the Ruahine Range at least, while the small southern part occupies the outer parts of Pelorus Sound to the north of Tennison Inlet in the Marlborough Sounds area (Crosby *et al.* 1998) of the South Island (Fig. 9, black circles). So, the range of this species includes adjacent territories of both the North and South Islands.

Habitat. Specimens were collected from litter and moss in forest, shrub, fern, and grass communities (labels mention silver *N. menziesii*, mountain *N. solandri*, and hard *N. truncata* beeches, leatherwood *Olearia colensoi*, and kamahi *Weinmannia racemosa* shrubs, fern *Lomaria* (= *Blechnum*) *discolor*, and tussock grass *Chionochloa*).

Relationships. The structure of the male genitalia of *N. tararua* suggests relationship to other species having dorsal copulatory sclerite in a shape of a “bird’s head,” such as *N. brouni*, *N. distinctus*, and *N. townsendi*. The details of the copulatory sclerite configuration suggest that *N. tararua* is close to *N. brouni*. The reduced scaled membranous field and the presence of an area with poriferous canals at the base of the shaft suggest that *N. tararua* may share common ancestry with *N. townsendi*. Significantly, males of *N. tararua* are the only members of the genus that possess unexpectedly great variation in the size and to a lesser extent in the shape of the median lobe (see Fig. 8). However, among different populations the dorsal sclerite is almost identical, and I was unable to find distinct and stable characters of the median lobe allowing consistent arrangement of this variability geographically. Within-group relationships of *N. tararua* are unclear.

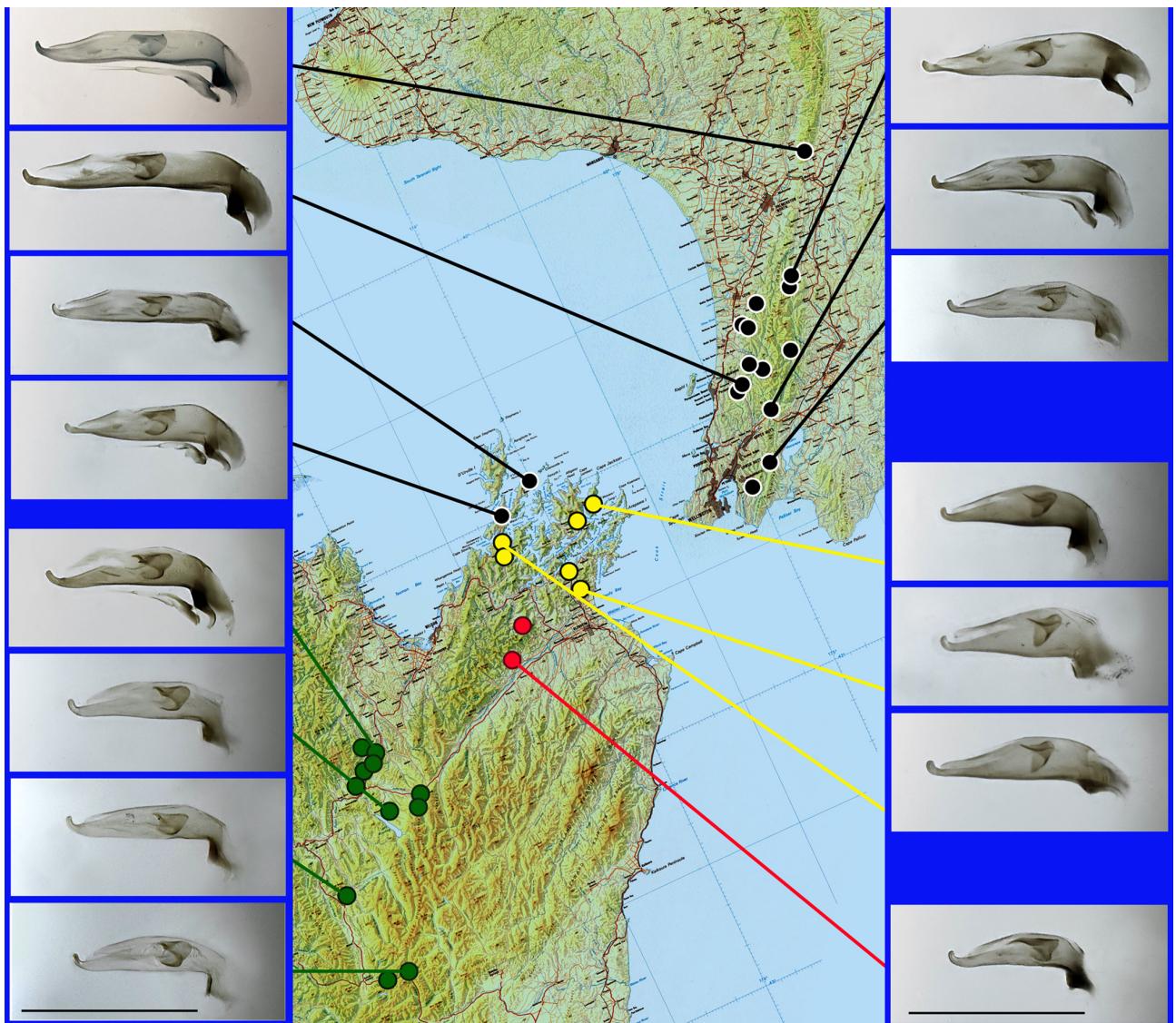


FIGURE 9. Distributional records for the *Nesambylops* species and images of male median lobe, obtained from specimens, collected in the line-connected with images localities. Black circles—*N. tararua*; yellow circles—*N. townsendi*; red circles—*N. distinctus*; green circles—*N. brouni*. Scale bar= 0.5mm.

Nesambylops townsendi, sp. nov.

Figs. 3C, 4I, 6G–I, 7H, 9

Type material. **HOLOTYPE**, male, in NZAC, labeled: Tennyson Inlet Marl. 22.5.64 J.I.Townsend \ Forest litter \ DSIR\ No \ NZ PB. **PARATYPES** (12 specimens, in NZAC, dissected 4 exx.), 1 female labeled same as holotype; 1 male labeled: \ Opouri Sdle. Tennyson Inlet Rd. 4.viii.67 \ F. Alack Litter 67/225 \ DSIR\ No \; 1 female labeled: \ Tennyson Inlet 22.5.64 litter J.I.Townsend \ NZ PB; 2 males and 2 females labeled: \ M Robinson Ridge Kenepuru Sd. 500m Marlborough \ 13 Mar 1970 J.I. Townsend \ litter 70/142 \ DSIR\ No \ NZ PB; 3 males labeled: \ Ship Cove 365m. SD 30 Nov. 72 J.S. Dugdale \ Litter 72/273 \ DSIR\ No \ NZ PB; 1 female labeled: \ Shakespeare Bay, Picton \ 11 Aug 69 J.McBurney \ DSIR\ No \; 1 female labeled: \ Marlborough Mt.Robertson 1,600 16-5-60 I. Mannering \ Leafmould \ NZ PB\.

Etymology. The specific epithet is a Latinized eponym in the genitive case, and is based on the surname of James Ian Townsend, a famous New Zealand carabidologist and the collector of the type series.

Type locality. New Zealand, South Island, Marlborough Sounds, Tennyson Inlet.

Recognition. Adults of this species (Fig. 3C) can be distinguished from the adults of majority species of *Nesambylops* by the distinctive shape of pronotum (Fig. 4I), however are practically indistinguishable from the adults of some *Nesambylops* species (cf. with Figs. 2D) and are distinguished from all of them by the structure of the male genitalia.

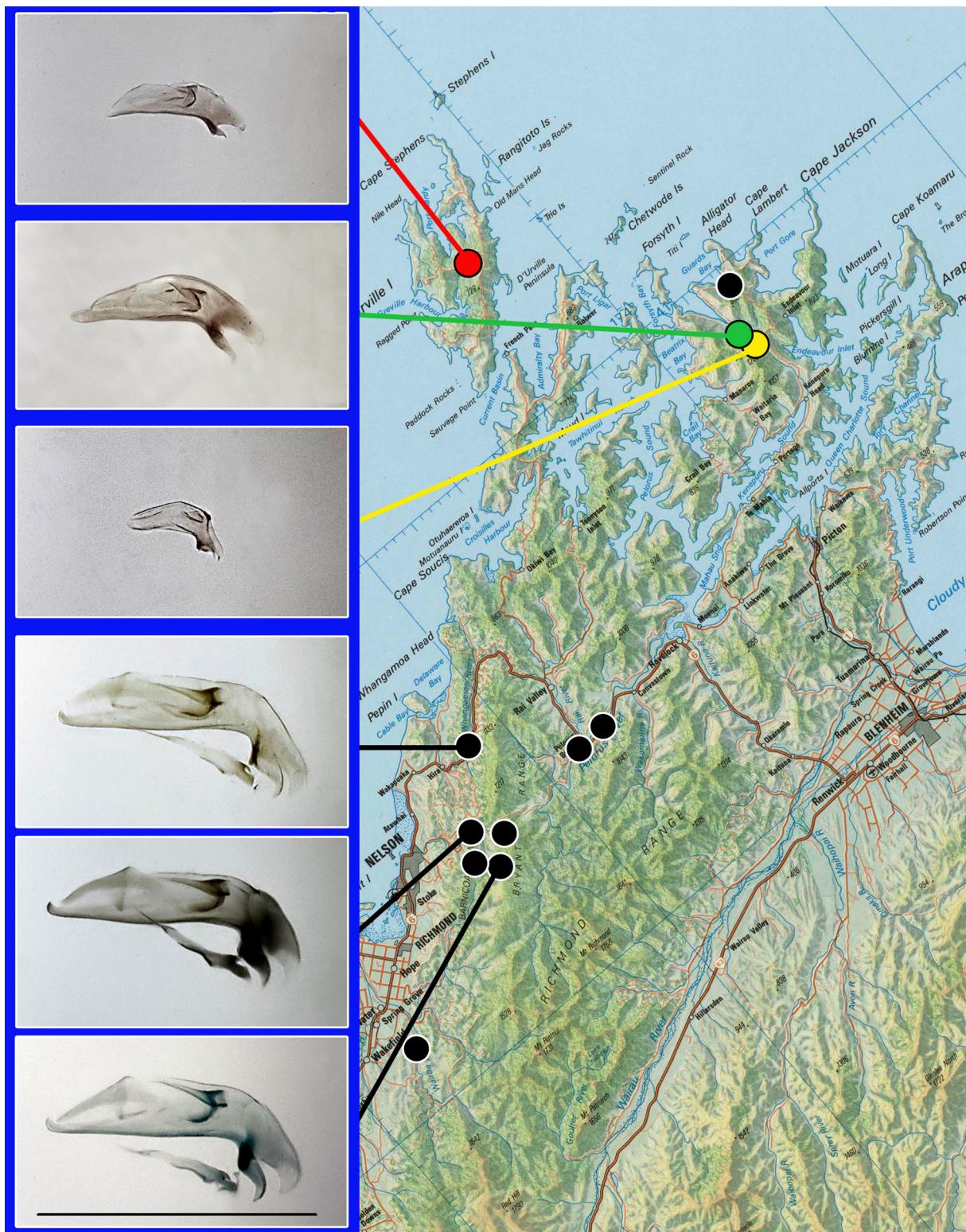


FIGURE 10. Distributional records for the *Nesamblyops* species and images of male median lobe, obtained from specimens, collected in the line-connected with images localities. Black circles—*N. carltoni*; yellow circles—*N. parvulus*; red circles—*N. lescheni*; green circles—*N. confusus*. Scale bar= 0.5mm.

Description. Large for genus (SBL range 1.85–2.05 mm, mean 1.95 ± 0.071 mm, n=6).

Habitus. Body form (Fig. 3C) markedly convex, elongate ovoid, general proportions wide (WE/SBL 0.41 ± 0.010), head narrow relative to pronotum (WH/WPm 0.66 ± 0.014), proportions of pronotum in comparison to elytra average for genus (WPm/WE 0.77 ± 0.013).

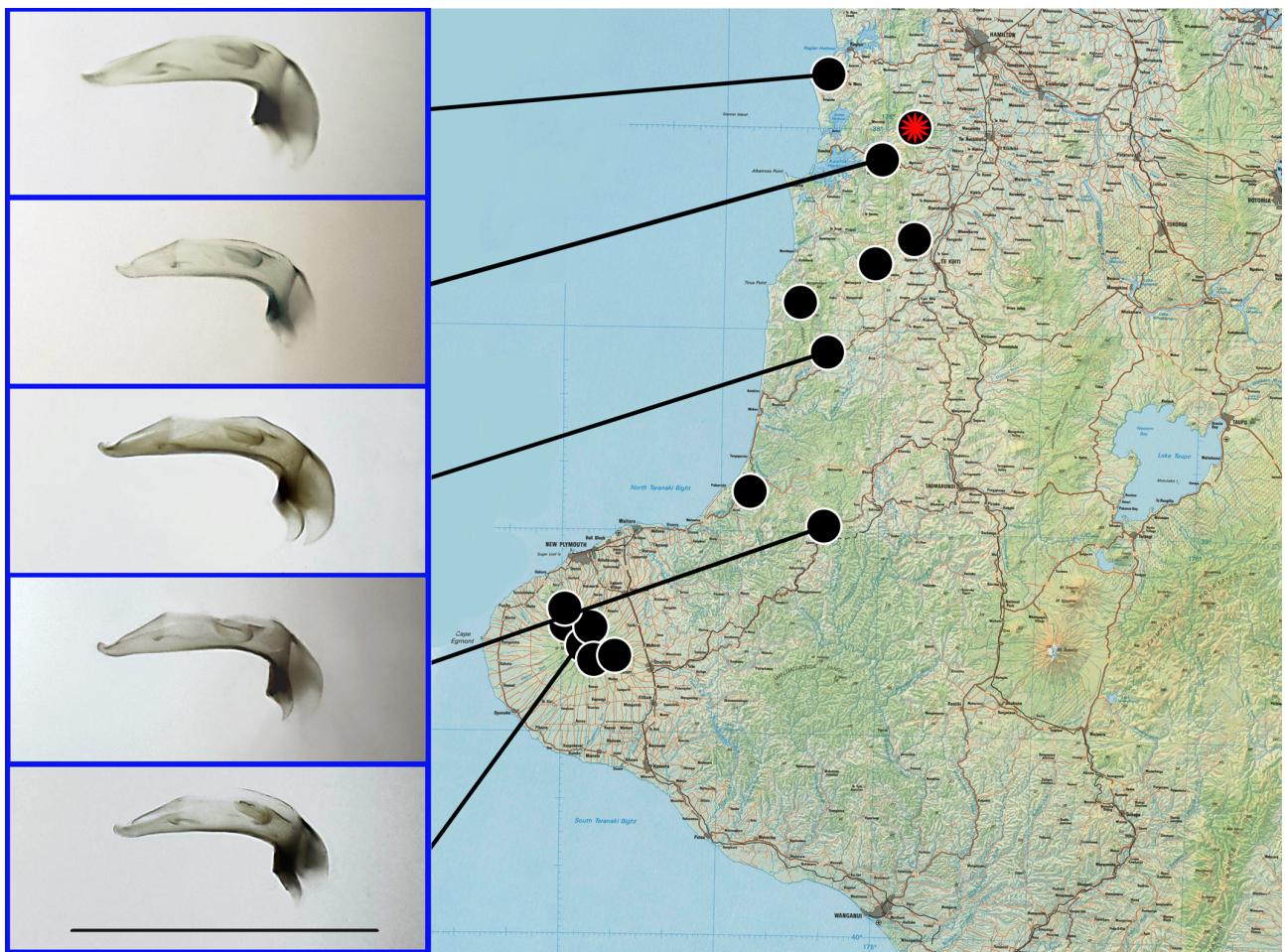


FIGURE 11. Distributional records for *Nesamblyops oreobius* (Broun) and images of male median lobe, obtained from specimens, collected in the line-connected with images localities. Red star—the type locality of *Tachys oreobius* Broun and *Anillus monticola* Broun. Scale bar= 0.5mm.

Color. Body color brunneopiceous, appendages brunneorufous.

Prothorax. Pronotum (Fig. 4I) moderately long in comparison to elytra ($LP/LE 0.44\pm 0.009$) and moderately transverse ($WPm/LP 1.22\pm 0.016$), with lateral margins rectilinear and slightly constricted posteriorly ($WPm/WPp 1.18\pm 0.019$). Anterior angles indistinct, posterior angles obtuse ($94\text{--}100^\circ$), dented, and slightly protruding backward. Width between posterior angles much greater than between anterior angles ($WPa/WPp 0.77\pm 0.009$). Basal margin concave.

Elytra. Ovoid, narrowly depressed along suture, comparatively long ($LE/SBL 0.59\pm 0.010$) and moderately wide ($WE/LE 0.69\pm 0.008$). Humeri completely rounded. Lateral margins slightly divergent at basal half, shortly subparallel at middle and evenly rounded to apex in apical half.

Male genitalia. Median lobe of aedeagus (Fig. 6I) strongly arcuate and moderately twisted. Shaft diverging basally, tapering in apical half. Apex moderately curved dorsally with narrowly rounded tip. Apical orifice long, occupies almost half of the shaft length. Ventral margin of median lobe straight. Walls of shaft with scattered poriferous canals. Dorsal copulatory sclerites in form of specific “bird’s head” plate, surrounded by small scaled membranous field. Spines of internal sac absent. Left paramere (Fig. 6G) of normal proportions, with moderately attenuate apex, bearing three long setae. Right paramere (Fig. 6H) long and narrow, bearing three long setae, slightly shorter the length of paramere. Ring sclerite as on Fig. 7H.

Female internal genitalia. Not examined.

Geographical distribution. This species is distributed within the Marlborough Sounds area (Crosby *et al.* 1998) (Fig. 9, yellow circles).

Habitat. According to label data specimens were collected from leafmold and litter without more precise data about plant communities.

Relationships. The structure of the male genitalia of *N. townsendi* suggests relationship to other species having

dorsal copulatory sclerite in a shape of “bird’s head,” such as *N. brouni*, *N. distinctus*, and *N. tararua*. The state of the scaled membranous field and the presence of the area with poriferous canals suggest that *N. townsendi* may share the common ancestry with *N. tararua*. Within-group relationships of *N. townsendi* remains to be examined.

Discussion

The nine species of *Nesamblyops* described or redescribed here represent only a minor part of the diversity of the genus. For that reason, detailed discussion with comprehensive analysis of the evolution of the group will be pending until all descriptions of the new species of the genus are completed. Below I review the distributional patterns of the examined species and present some considerations on the dispersal routes that shaped the modern distribution of *Nesamblyops* fauna on the North Island based on the morphological affinities of the species and their way of distribution.

The general range of all examined species occupies lands to the west of the Alpine Fault, following the well-known major biogeographical break between the Indo-Australian and the Pacific plates (Heads 2017). Two species are recorded from the North Island, while the other seven occur on the South Island. The ranges of these seven species on the South Island do not overlap with ranges of other described or undescribed species of *Nesamblyops* from the rest of the Island. Thus, it is highly likely that all examined species represent a piece of the New Zealand *Nesamblyops* fauna that underwent an autochthonous evolutionary history within the region. Since the female genitalia are largely not examined and external features of aniline beetles are of limited utility because of their well-known similarity to each other, the following considerations are based mostly on the characters of male genitalia. Based on those, all nine examined species can be arranged into three groups. The first group (*tararua*-species group) embraces species with a presumably apomorphic design of sclerites, characterized by the fusion of all structures in one sclerotized plate of distinctive shape with contours of a “bird head” (cf. Figs. 5C, 5L, 6F, 6I), and includes four species: *N. brouni*, *N. distinctus*, *N. townsendi*, and *N. tararua*. The ranges of these species are associated with mountainous landforms formed by orogenic processes and occupy the consecutive chain of ranges stretching in a north-eastern direction from the Southern Alps on the South Island up to Cook Strait and extending in a similar direction on the North Island from Cook Strait up to the northernmost parts of the Tararua Range. Along this continuous line allopatric ranges of species replace one another along latitude, except a small part of the range of *N. tararua*. The range of the latter includes a large territory on the North Island and a small area on the South Island; thus, it occupies both sides of Cook Strait. So, on the South Island *N. tararua* formally inhabits the same latitudinal zone as the more southern species *N. townsendi*. The second group comprises species with a presumably plesiomorphic design of sclerites, characterized by the conglomerate of sclerotized structures, with distant and ambiguous similarities in the shape and degree of sclerotization of sclerite structures (cf. Figs. 5I, 5O, 5R), and includes three species: *N. oreobius*, *N. lescheni*, and *N. confusus*. Copulatory sclerites in the basal part of the aedeagus of all of these species include a distinct V-shaped structure with linear sclerotizations apically and sclerotized fields of different shapes around sclerites. The ranges of these species are associated with either lowland or hilly parts, or mountains of volcanic origin on the North or South Islands and are distant and isolated from each other. The range of one member of this group, *N. oreobius*, represents the most northern part of the genus’ range. The third and the last group includes two species with uncertain morphological affinities, *N. carltoni* and *N. parvulus*. The ranges of both species are limited in their distribution to the South Island only. Their locality records suggest that in the Mount Stokes area (Marlborough Sounds), *N. carltoni* and *N. parvulus* presumably live in sympatry (Fig. 10, yellow and black circles). Locality records also show that in the same area *N. parvulus* lives syntopically with a species of the second group, *N. confusus* (Fig. 10, yellow and green circles). In addition, the Mount Stokes area is also a part of the range of *N. townsendi*, a species of the first group (Fig. 9, yellow circles). Altogether, the distributional data show that the Mount Stokes area is inhabited by representatives of all three groups of *Nesamblyops* known from the region and thus harbors representatives of both species’ groups known to occur on the North and South Islands. This fact indicates that, historically, the Marlborough Sounds area may have played an important role as an intersection of migration routes of the *Nesamblyops* species dispersing between the South and North Islands. In our case, the modern faunal connections between the Islands are carried out through the conspecific populations for the first group and through the presumably sister species for the second group; apparently this pattern has implications for the timing of past dispersal and vicariance events.

Since the fact that the center of the biodiversity of *Nesamblyops* is confined to the South Island, I assume that the

North Island, historically, was lacking the representatives of the genus. However, eventually the Island underwent at least two dispersal events of the *Nesambylops* species. Taking into account that the Alpine Fault passes through the Marlborough Sounds region, I suggest that at the very least the evolutionary history of the *tararua*-species group and its migration to the South Island were associated with the regional development of the landmasses of the Alpine Fault and the evolution of Cook Strait. Apparently, the members of the group reached the South Island before the formation of Cook Strait, which only appeared in the mid Pleistocene (Lewis *et al.* 1994). The formation of Cook Strait split the range of the most northern species of the group, *N. tararua*, between the Islands. Since that event, both populations of the species have presumably never been in contact, and, accordingly, the minimal time of the break in gene flow between the southern and northern populations of *N. tararua* can be estimated as c. 450ka BP. Close relationships among taxa on the southern parts of the North Island and the Marlborough Sounds area of the South Island are not unique for the representatives of the New Zealand fauna and have been recorded for other animal groups, for instance, for the species of the mite harvestmen of the genera *Aoraki* and *Rakaia* (Opiliones, Arachnida) (Boyer and Giribet 2009), and the chirping cicada *Amphipsalta strepitans* (Kirkaldy) (Cicadidae, Hemiptera) (Marshall *et al.* 2012).

Acknowledgements

I am grateful to the staff of the Louisiana State Arthropod Museum, LSU, Baton Rouge, USA, including Curator, Victoria M. Bayless and the former director, Christopher E. Carlton, for their diversified assistance and patience that made this paper possible, and, especially, for permission to use the Museum's equipment. I appreciate help with SEM imaging provided by the staff of the former Microscopy Center at Louisiana State University School of Veterinary Medicine (Baton Rouge, LA). I also would like to thank Richard A.B. Leschen (Landcare Research, Auckland, New Zealand) for the loan of specimens in his care.

The mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA; the USDA is an equal opportunity provider and employer.

References

- Andújar, C., Faille, A., Pérez-González, S., Zaballos, J.P., Vogler, A.P. & Ribera, I. (2016) Gondwanian relicts and oceanic dispersal in a cosmopolitan radiation of euedaphic ground beetles. *Molecular Phylogenetics and Evolution*, 99, 235–246.
<https://doi.org/10.1016/j.ympev.2016.03.013>
- Ball, G.E. & Shpeley, D. (2009) A taxonomic review of the genus *Apenes* LeConte (Coleoptera: Carabidae: Lebiini) in the West Indies, with descriptions of new species and notes about classification and biogeography. *Annals of the Carnegie Museum*, 78, 79–191.
<https://doi.org/10.2992/007.078.0201>
- Boyer, S.L. & Giribet, G. (2009) Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones, Cyphophthalmi). *Journal of Biogeography*, 36, 1084–1099.
- Broun, T. (1893) s.n. In: *Manual of the New Zealand Coleoptera. Part VII*. Government Printing Office, Wellington, pp. 1395–1504.
- Broun, T. (1908) Descriptions of new species of New Zealand Coleoptera. *Annals and Magazine of Natural History*, Series 8, 2, 405–422.
- Broun, T. (1910) Descriptions of new genera and species of Coleoptera. *New Zealand Institute bulletin*, 1, 3–78.
- Crosby, T.K., Dugdale, J.S. & Watt, J.C. (1998) Area codes for recording specimen localities in the New Zealand subregion. *New Zealand Journal of Zoology*, 25, 175–183.
<https://doi.org/10.1080/03014223.1998.9518148>
- Heads, M. (2017) *Biogeography and evolution in New Zealand*. CRC Press, Taylor & Francis Group, Boca Raton, 635 pp.
<https://doi.org/10.1201/9781315368177>
- Jeannel, R. (1937) Les Bembidiides endogés (Col. Carabidae). *Revue française d'Entomologie*, 3, 241–339.
- Jeannel, R. (1963) Monographie des “Anillini”, Bembidiides endogés [Coleoptera Trechidae]. *Mémoires du Muséum National d'Histoire Naturelle*, Série A, Zoologie, 28, 33–204.
- Lewis, K.B., Carter, L. & Davey, F.J. (1994) The opening of Cook Strait: Interglacial tidal scour and aligning basins at a subduction to transform plate edge. *Marine Geology*, 116, 3–4, 293–312.
[https://doi.org/10.1016/0025-3227\(94\)90047-7](https://doi.org/10.1016/0025-3227(94)90047-7)
- Lorenz, W. (2005) *Systematic list of extant ground beetles of the world (Insecta Coleoptera “Geadephaga”: Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae)*. Second edition. W. Lorenz, Tutzing, 530 pp.

- Maddison, D.R., Kanda, K., Boyd, O.F., Faille, A., Porch, N., Erwin, T.L. & Roig-Juñent, S. (2019) Phylogeny of the beetle supertribe Trechitae (Coleoptera: Carabidae): Unexpected clades, isolated lineages, and morphological convergence. *Molecular Phylogenetics and Evolution*, 132, 2019, 151–176.
<https://doi.org/10.1016/j.ympev.2018.11.006>
- Marshall, D.C., Hill, K.B., Marske, K.A., Chambers, C., Buckley, T.R. & Simon, C. (2012) Limited, episodic diversification and contrasting phylogeography in a New Zealand cicada radiation. *BMC Evolutionary Biology*, 12 (177), 1–18.
<https://doi.org/10.1186/1471-2148-12-177>
- Moore, B.P. (1980) A synopsis of the New Zealand Anillini (Coleoptera: Carabidae: Bembidiinae), with descriptions of new genera and species. *New Zealand Journal of Zoology*, 7, 399–406.
<https://doi.org/10.1080/03014223.1980.10423793>
- Sokolov, I.M. (2013) A new genus and eight new species of the subtribe Anillina (Carabidae, Trechinae, Bembidiini) from Mexico, with a cladistics analysis and some notes on the evolution of the genus. *ZooKeys*, 352, 51–92.
<https://doi.org/10.3897/zookeys.352.6052>
- Sokolov, I.M., Carlton, C.E. & Cornell, J.F. (2004) Review of *Anillinus* with descriptions of 17 new species and a key to soil and litter species (Coleoptera: Trechinae: Bembidiini). *Coleopterists Bulletin*, 58, 185–233.
<https://doi.org/10.1649/611>
- Sokolov, I.M. & Kavanaugh, D.H. (2014) The *integripennis* species group of *Geocharidius* Jeannel, 1963 (Carabidae, Bembidiini, Anillina) from Nuclear Central America: a taxonomic review with notes about biogeography and speciation. *ZooKeys*, 443, 61–118.
<https://doi.org/10.3897/zookeys.443.7880>