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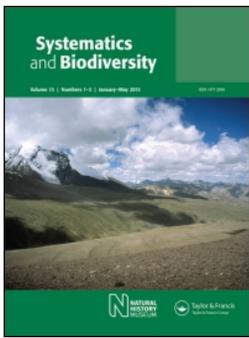
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## Research Article



# Systematics and biogeography of the subantarctic *Leptusa* (Coleoptera: Staphylinidae: Aleocharinae: Homalotini)

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*Leptusa atriceps* and *L. antarctica*, flightless representatives of the nearly global genus *Leptusa* in the remote and widely distributed subantarctic islands, are taxonomically revised. Identity and the widely disjunct distribution of *L. atriceps* on Falkland, South Georgia, Marion, Crozet and Kerguelen Islands are confirmed. *Leptusa antarctica* is found to be a complex of five species restricted to the subantarctic islands of New Zealand. Two of these species, *L. sparsepunctata* and *L. nesiotus* are here reinstated from synonymy and two others, *Leptusa insulae* sp. nov. and *Leptusa steeli* sp. nov., are described as new to science. The monophyly of subantarctic *Leptusa* species united in the subgenus *Halmaeusa* was determined by a phylogenetic study of five exemplar homalotine genera and 17 representatives of *Leptusa* from South America and the Holarctic based on 76 adult morphological characters. Phylogenetic placement of *Halmaeusa* was not firmly established. *Nanoglossa*, a temperate South American subgenus of *Leptusa* was found as a possible sister group to *Halmaeusa*. The distribution of *Halmaeusa* species with two to four species that occur sympatrically on Campbell and Auckland Islands, and other species distributed across several remote islands, provides a framework for future biogeographic study of the subantarctic *Leptusa*.

<http://www.zoobank.org/urn:lsid:zoobank.org:act:82509B9D-4BF6-47E1-B6F7-396ED193A0FA>; <http://www.zoobank.org/urn:lsid:zoobank.org:act:40A3D6FC-27FF-4070-88CA-1B519ABE760A>

**Key words:** biogeography; *Halmaeusa*; *Nanoglossa*; phylogeny; revision; rove beetles; Subantarctic region

## Introduction

Bounded in the north by the Sub-Tropical Convergence and in the south by the Antarctic Polar Front is the Subantarctic, a region of widely scattered islands and archipelagos with a distinctive and endemic biota on land and in sea. The islands themselves, from windswept barren rocks with little more than tussocks to fill the cracks to those having fully forested ecosystems, contain entire lineages whose ancestry and evolution remain controversial. Faunistic, cladistic, and descriptive studies have identified widespread and localized lineages in the Subantarctic region with trans-Antarctica links (Greve, Gremmen, Gaston, & Chown, 2005; Michaux & Leschen, 2005; Morrone, 1998; Stevens, Greenslade, Hogg, & Sunnucks, 2005) with many prone to long-distance dispersal events facilitated by westerly ocean

currents and retaining some level of regionalization (Moon, Perron, Martel, Holbrook, & Clair, 2017). Most uncertain is the origin and evolution of land-bound salt-water intolerant organisms with seemingly limited dispersal abilities. Are these lineages remnants of old Gondwanan clades, or are they derived from more northerly landmasses? Do the histories of widespread land-bound organisms of the subantarctics track ocean currents or do they exist as remnants on islands, ghosts of former land connections, or a combination of both? Except a few studies of widespread groups (e.g., McGaughan, Convey, Stevens, & Chown, 2010; Mortimer et al., 2011), the evolution of terrestrial, non-intertidal invertebrates of the Subantarctic region is particularly under-studied.

Beetles (Coleoptera) are relatively rich in diversity in the Subantarctic region, but surprisingly few genus-level lineages are widespread (Michaux & Leschen, 2005) and most groups are regionalized (e.g., Grobler, Bastos, Treasure, & Chown, 2011; Leschen, Butler, Buckley, &

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Ritchie, 2011). Here we provide a study of widespread subantarctic terrestrial rove beetles in the genus *Leptusa* Kraatz, 1856 (Aleocharinae: Homalotini: Bolitocharina). *Leptusa* is a megadiverse taxon comprised of 460 described species grouped in about 80 subgenera worldwide (Leschen & Newton, 2015), with most members (409 species) represented in the Palearctic region (Schülke & Smetana, 2015). They are presumably predatory, stenotopic, mostly flightless, often microphthalmous, and with species confined to the humid ground-based microhabitats. Like many litter inhabiting species, especially flightless forms, they are good models for understanding island biogeography because of their presumed limited abilities to naturally disperse across inhabitable land, not to mention many miles of sea. Whereas *Leptusa* from some of the New Zealand subantarctic islands may be strikingly abundant in leaf litter (Figs 2–5), we can attest to the absence of *Leptusa* from mainland New Zealand where *bona fide* members of the genus have not been collected despite intense country-wide litter sampling since the 1960s. The genus *Leptusa*

is also notably absent in Australia. It is possible that the presence of *Leptusa* on Australasian islands may be the result of dispersal, perhaps from southern South America where there is a number of species of the genus.

This paper aims to set the ground work for a rigorous biogeographic study of the Subantarctic *Leptusa*. We assess the taxonomic validity of all species present in the region, perform a morphology-based phylogenetic study necessarily involving broad outgroup sampling, and present biogeographic hypotheses to frame future research. In this study, we were limited by a lack of *Leptusa* samples suitable for molecular work and have instead carried out a careful morphology-based revision as the backbone for future research. Below we briefly provide geological background on islands having *Leptusa* species.

The subantarctic islands populated by *L. atriceps* (C. O. Waterhouse) have a wide range of formation dates (Chown, Lee, & Shaw, 2008). The Kerguelen Islands are part of the Northern Kerguelen Plateau (Bénard, Callot, Vially, & Loubrieu, 2010) which includes two large, active volcanic archipelagos: Kerguelen and Heard-McDonald

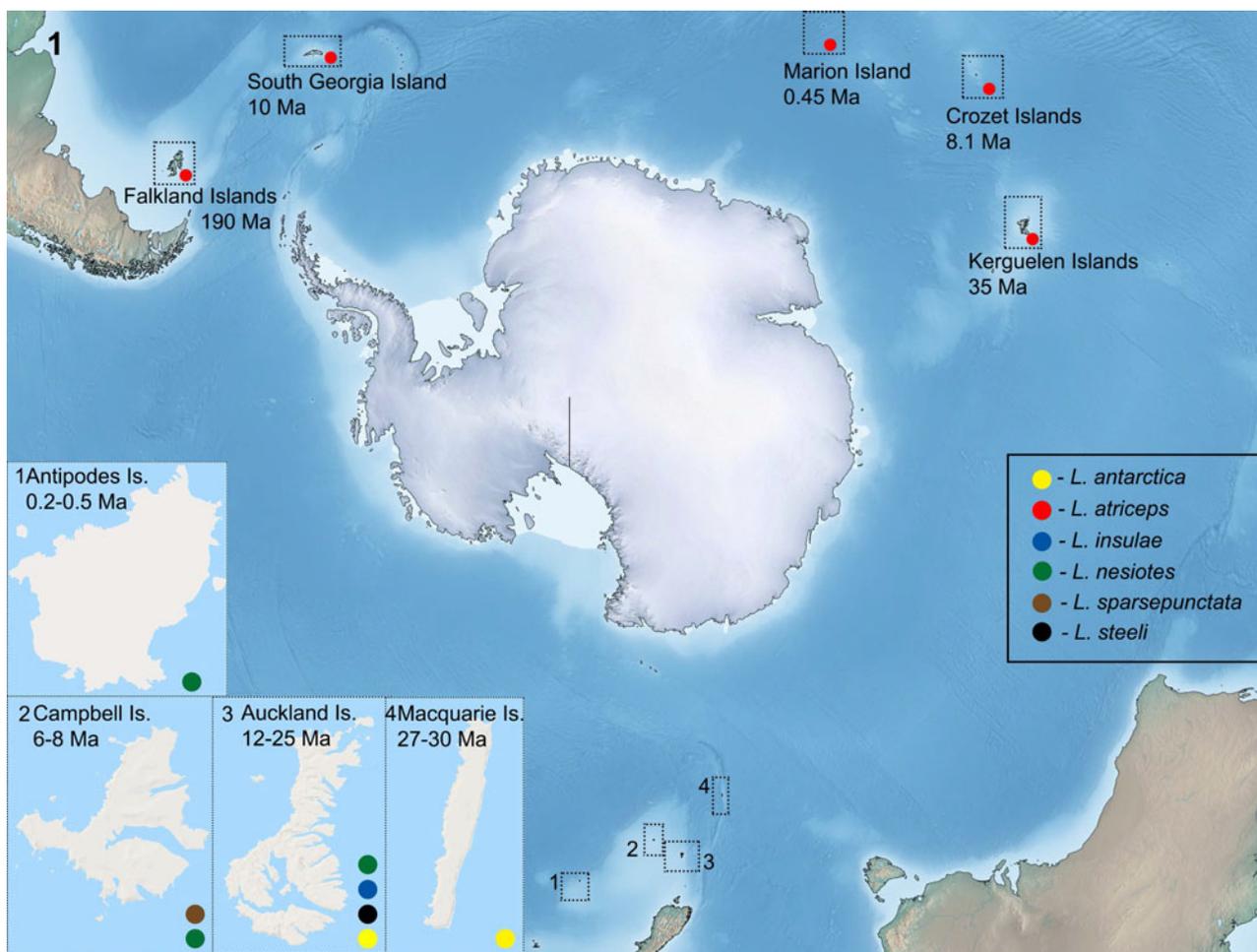


Fig. 1. Distribution of *Leptusa* (*Halmaeus*) in the Subantarctic Region.



**Figs. 2–5.** Subantarctic islands of New Zealand, landscapes and habitats of *Leptusa*. 2, Carnley Harbour looking north from Adams Island onto the Auckland Islands mainland showing tussock highlands and lowland forests of *Metrosideros umbellata* (photo credit: R. Leschen); 3, northern shore of Adams Island in the Auckland Island archipelago (photo credit: R. Leschen); 4, eastern view of the Western Arm of Carnley Harbour from Adams Island; 5, microhabitat sampling at Western Harbour on the Auckland Island mainland (photo credit: E. Edwards).

(Rotstein, Schlich, Munsch, & Coffin, 1992). The Kerguelen Islands appeared as a result of volcano eruption about 35 Mya. Possession Island in the Crozet Archipelago, of volcanic origin, has a minimum date of origin 8.1 Mya (Chevallier, Nougier, & Cantagrel, 1983). The volcanic Marion Island is one of two Prince Edward Islands in the southern Indian Ocean. Marion Island has never been connected to the continent and is still active (Hall, Meiklejohn, & Bumby, 2011) with eruptions that date back to 0.45 Mya (McDougall, Verwoerd, & Chevallier, 2001). South Georgia Island is a fragment of an isthmus of continental crust that once joined southern South America and the Antarctic Peninsula (Stone, 2014), part of a microcontinental block that was emergent at 10 Mya (Carter, Curtis, & Schwanethal, 2014). The Falkland Islands are a part of the Falkland Plateau, which is a remnant of the southern tip of Africa that remained attached to South America, now distant from Africa. The

Falkland Islands consist of two large islands (East Falkland and West Falkland) and ~700 smaller islands. This archipelago is about 500 kilometres east of the nearest part of the South American continent (Aldiss & Edwards, 1999) and dates back to 190 Mya (Mussett & Taylor, 1994).

*Leptusa* of the southern Pacific region occur on the Campbell Plateau and on the adjacent Macquarie Ridge with a single island, Macquarie Island. The Campbell Plateau is derived from West Gondwana that separated at 80 Mya (Leschen, Butler, Buckley, & Ritchie, 2011; Michaux & Leschen, 2005), and includes five subantarctic island groups that range in size from the small Bounty Island (1.35 square kilometres) to the large Auckland Island archipelago (611 square kilometres). All but Bounty and Snares Islands (which lack *Leptusa* species) are of volcanic origin and formation dates are 6–8 Mya for Campbell Island, 12–25 Mya for Auckland

Islands, 27–30 Mya for Macquarie Island, and 0.2–0.5 Mya for Antipodes Island (Adams, 1981).

## Materials and methods

### Examination of material and terminology

The examined material is kept in the following collections:

ANIC – Australian National Insect Collection, Canberra, Australia (C. Lemann); LUNZ – Lincoln University, Canterbury, New Zealand (J. Marris); NHM – The Natural History Museum, London, UK (M. Barclay); NHMD – Natural History Museum of Denmark (includes former ZMUC, Zoological Museum, University of Copenhagen), Copenhagen, Denmark (A. Solodovnikov); NHMW – Naturhistorisches Museum, Vienna, Austria (H. Schillhammer); NZAC – New Zealand Arthropod Collection, Landcare Research Manaaki Whenua, Auckland, New Zealand (R. Leschen, G. Hall); TMAG – Tasmanian Museum and Art Gallery, Hobart, Australia (S. Grove, K. Moore). Holotypes of the new species and most of the other material used in this study are deposited in NZAC, with duplicate paratypes and specimens deposited at NHMD. The material studied included card- or point-mounted specimens and some collected into 95% ethyl alcohol. Some males and females were disarticulated and examined on microslides following Hanley and Ashe (2003) and Leschen (2003). In total 55 microslides of fully dissected aleocharines were made for the study. For some others, the genitalia and apical abdominal sclerites were removed, cleared and mounted in Euparal on plastic cards pinned under their respective specimens. Habitus photos were taken using a Canon 7D camera mounted on a BK PLUS Lab System, Dun, Inc. Microslides were studied under Leica 205C and Zeiss Axioskop microscopes. Photos of the microslides were taken using Olympus DP50-CU camera mounted on a Zeiss Axioskop microscope. The SEM photos were taken with a JEOL JSM-6335F SEM. For SEM examination, samples were coated with platinum/palladium (80/20%) using a JEOL JFC-2300HR sputtercoater. All measurements are given in millimetres and taken with a microscope using an ocular micrometer. They were taken as follows: body length from the anterior margin of the labrum to the apex of the abdomen; body length without abdomen – from the anterior margin of the labrum to the posterior margin of the elytra; head length – from the anterior margin of the clypeus to the posterior margin of the head; head width – maximal, at temples right behind the eyes; pronotum length – from anterior to posterior margin along median line; pronotum width – maximal, at about anterior one-third of its length; elytral length – along the suture from the apex of scutellum to the

posterior margin of elytra. The following abbreviations were used for the measurements: L = length, W = width. Morphological terminology mainly follows Maruyama (2006) and Pace (1989) and updated with Lawrence, Beutel, Leschen, and Ślipiński (2010).

### Phylogeny

**Taxon sample.** We examine the phylogenetic relationships of the subantarctic *Leptusa* by including exemplar congeners from the Palearctic and South America rooted with other members of the tribe Homalotini. We are not certain if those southern species of *Leptusa* are congeneric with the Palearctic core of the genus where the type species *Leptusa pulchella* belongs because the entire genus remains very poorly known on a global scale. Rigorous phylogenetic attempts to either test *Leptusa* monophyly with respect to other genera of Homalotini or to search for natural lineages within the genus have not been carried out. As a result, a broad taxon sampling for our study is required (Table S1, see online supplemental material, which is available from the article's Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2018.1547329>). The ingroup includes all described species of *Leptusa* from the subantarctic islands of New Zealand that have been discovered as a result of the present revision (see the 'Taxonomy' section) and *L. atriceps* from other subantarctic islands. Together they form the subgenus *Halmaeusia*. Also, it includes *L. pulchella*, which is the type species of the genus *Leptusa*, and several other congeners from various subgenera. The outgroup includes 15 representatives of aleocharines from 10 tribes. Insufficient taxonomic knowledge of the aleocharine fauna of temperate South America, Australia and New Zealand prevented us from informed sampling of the 'non-*Leptusa*' lineages, which potentially could give rise to subantarctic species. These questions remain to be addressed in a much broader study. *Aleochara curtula* from the tribe Aleocharini that is presumably sister to nearly all other tribes of higher Aleocharinae (Osswald, Bachmann, & Gusarov, 2013) is used to root the phylogenetic trees.

**Characters.** We mostly scored the characters described by Ashe (2005), with some modifications. Some characters were added specifically for this taxon sample and analysis. A full character list is provided in Table S2 (see supplemental material online). A full character matrix can be downloaded as a nexus file from the [supplementary material](#) in this paper or from the Morphobank database at <https://morphobank.org/>.

## Phylogenetic data matrix and analysis

The character matrix was constructed in Mesquite ver. 3.31 (Maddison & Maddison, 2015). Unknown character states were coded with '?' and inapplicable states with '-'. Characters were treated as unordered and equally weighted. We analysed our data matrix using Bayesian inference (BI) in MrBayes v. 3.2.6 (Ronquist et al., 2012) on XSEDE via the CIPRES Science Gateway (Miller, Pfeiffer & Schwartz, 2010). We used the Mkv (Lewis, 2001) model and priors were set to default. Analyses consisted of four chains and two runs of 5 million generations and were repeated twice. They were conducted with gamma distribution for modelling of the among-site rate variation. Markov Chain Monte Carlo convergence was visualized in Tracer v. 1.6 (Rambaut, Suchard, Xie & Drummond, 2014) as well as by the examination of potential scale reduction factor (PSRF) values and average standard deviation of split frequencies in the MrBayes output. Posterior probabilities over 0.95, which are considered as statistically significant support, are reported on their respective nodes. The BI consensus tree was visualized using FigTree v. 1.4.2 (Rambaut, 2014). In addition to BI, we also carried out maximum parsimony (MP) analysis. Our data matrix was analysed in TNT (Goloboff & Catalano, 2016) using the 'traditional search' option under the following parameters: memory set to 99,999 trees, 1,000 replicates, 10 trees saved per replicate, trees collapsed after search. *Aleochara curtula* was set as the outgroup. Bremer support was calculated in TNT (Goloboff & Catalano, 2016) using suboptimal trees up to 20 steps longer. Character states were mapped onto the MP strict consensus tree using WinClada v. 1.00.08 (Nixon, 2002) under unambiguous optimization.

## Results

### Phylogenetic analysis

The BI analysis converged well before 5 million generations and the final average standard deviation of split frequencies stabilized well below 0.01. Most PSRF values were 1.000 (maximum value 1.003). The resulting BI tree is shown in Fig. 6.

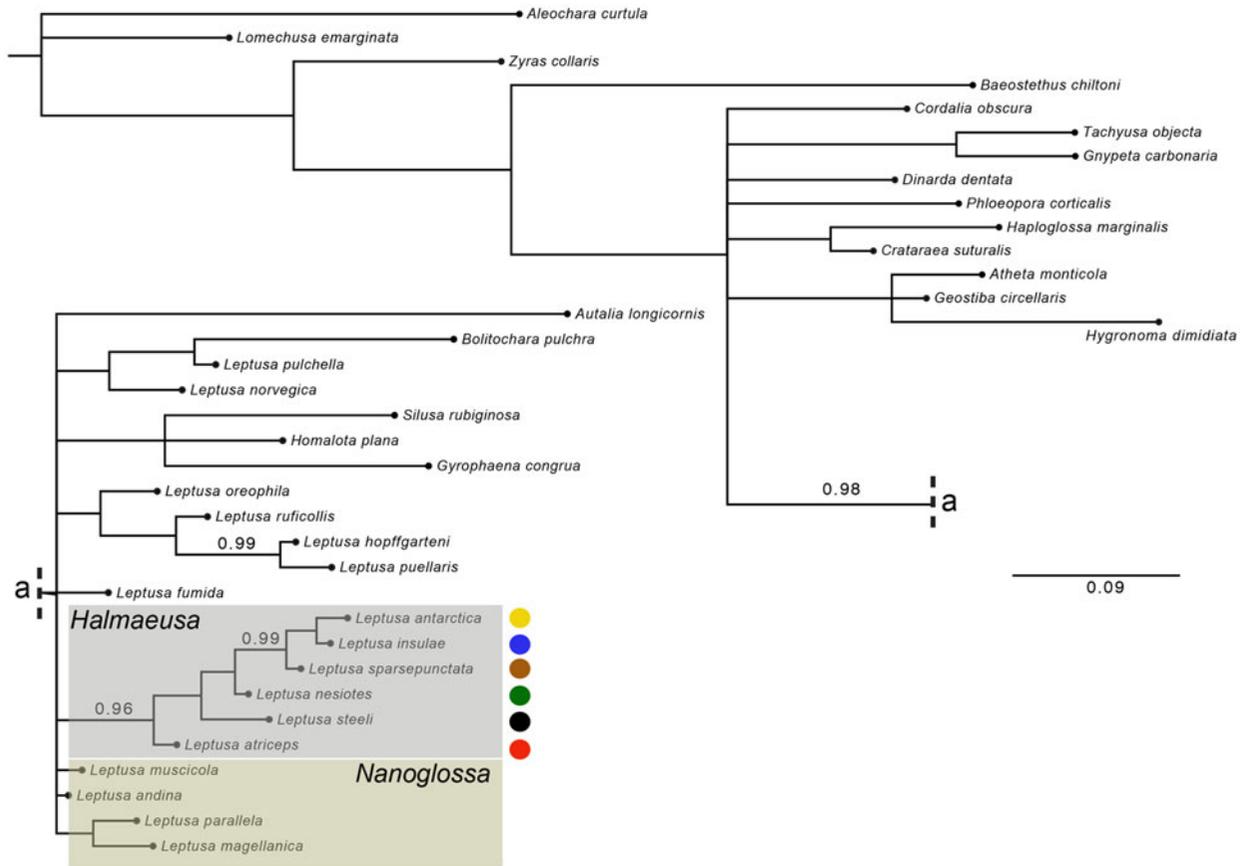
The MP analysis using traditional search resulted in 12 most parsimonious trees with 334 steps, consistency index (CI) = 32 and retention index (RI) = 56. The strict consensus tree with characters mapped is shown in Fig. 7.

BI and MP supported largely the same topology. The tribe Homalotini was supported by PP = 0.98 in the BI and includes a species from the tribe Autaliini (*Autalia longicornis*). The appearance of Autaliini within the Homalotini clade does not contradict the molecular

phylogeny of Osswald et al. (2013) where *Autalia longicornis* is a sister taxon to *Silusa opaca* (Homalotini: Silusina) with PP = 0.97. In the MP analysis Homalotini and *Autalia longicornis* form sister groups, the monophyly of the former having Bremer support = 2.

In the BI analysis the internal relationships of *Leptusa* are unresolved and the genus does not appear as a monophyletic group. The monophyly of *Leptusa* is also not supported in the MP analysis. In the BI the subgenus *Halmaeusa* (i.e., all subantarctic species) is resolved as a monophyletic group, with PP = 0.96, where *L. atriceps* is recovered as sister to all five other subantarctic species but without support. In MP the subgenus *Halmaeusa* is also recovered as a monophyletic group (Bremer support = 2) with *L. steeli* as a sister to remaining subantarctic species, though without statistical support. Noteworthy is the monophyly of the subgenus *Nanoglossa* (i.e., all sampled temperate South American species) and its sister relationships to *Halmaeusa* in the MP analysis, although not statistically supported and not recovered in the BI analysis. Lastly, our analysis confirms the conclusion of Leschen, Bullians, Michaux, & Ahn (2002) that *Baeostethus chiltoni* is not a member of *Leptusa* or even Homalotini, contrary to Pace (1989), who placed it in the *Leptusa* subgenus *Halmaeusa* together with *L. antarctica* and *L. atriceps* because of having the tarsal claws 'as long as last segment of tarsi'. This is a variable character that is well expressed only in *Baeostethus chiltoni* and to a lesser extent in *L. atriceps*. All other known species of *Halmaeusa* have the tarsal claws shorter than the last tarsal segment.

The MP analysis recovered one character that supported the sister relationship of *Nanoglossa* and *Halmaeusa*, the presence of an elongate ligula, a character that is variable in Homalotini, but was used to distinguish *Halmaeusa* from the remaining members of *Leptusa* by Steel (1964). The MP analysis recovered three characters as homoplasious synapomorphies of *Halmaeusa*: hind wings absent (55-1), lateral and mesal setae of mesonotum absent (49-1 and 54-0, respectively). Within *Halmaeusa* both BI and MP analyses recovered the same topology (*L. nesiotetes* (*L. sparsepunctata* (*L. antarctica* + *L. insulae*))) except with respect to which species is recovered as sister to the others. The BI analysis recovers *L. atriceps* as sister to the rest of *Halmaeusa*, while MP places *L. steeli* in this position instead and there is no statistical support for either placement. Various aspects of our analysis results are revisited below in the 'Discussion' section. For *Leptusa* as a whole, a global large-scale phylogenetic study is needed to assess its monophyly and its subgenera. Regarding *Halmaeusa*, our results suggest that this group of subantarctic species is



**Fig. 6.** A 50% consensus tree from Bayesian inference (BI) analysis. Posterior probabilities of 0.95 and over are shown at their respective nodes. Distributions of *Leptusa* (*Halmaeusa*) species colour coded as in Fig. 1.

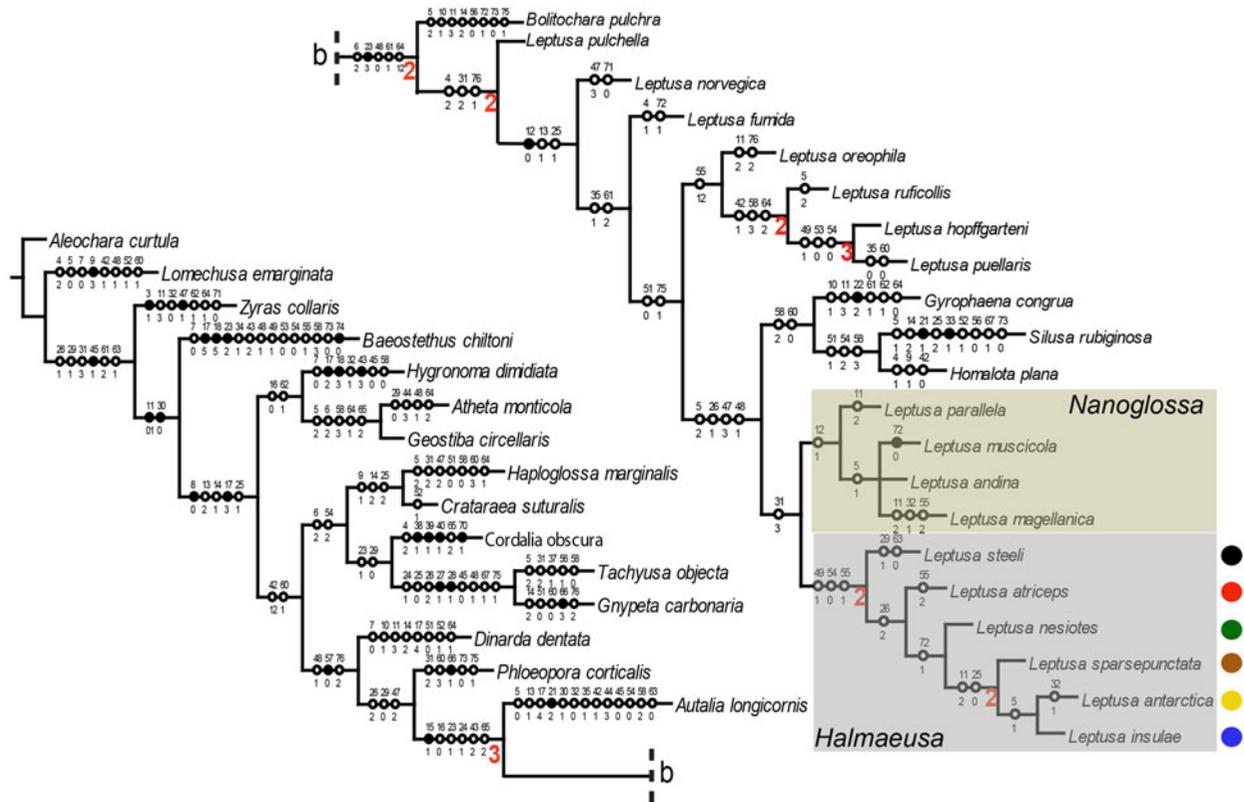
monophyletic. In the current circumstances there is no reason to change its present status as a subgenus of the genus *Leptusa*.

## Taxonomy

### Taxonomic history of subantarctic *Leptusa*.

Taxonomic knowledge of *Leptusa* is very fragmentary outside the Palaearctic, much of the Nearctic, and elsewhere. For example, there are no species described from Mexico, though there are several described from North America (Klimaszewski, Pelletier, & Majka, 2004; Pace, 1989). According to the current generic concept based on the monograph by Pace (1989), *Leptusa* is completely absent from mainland Australia, Madagascar, mainland New Zealand, the Pacific islands, as well as Antarctica, which is completely devoid of living Coleoptera. Likewise, the South American fauna of *Leptusa* is depauperate, with only 11 species known from Chile (two of them also occur in Argentina) (Newton, unpublished database, December 2015) and one unidentified species from Argentina (Pace, 2015).

The taxonomic history of the subantarctic species of the genus is very complex and reflects multiple layers of confusion. Among *Leptusa* of Subantarctic region *L. antarctica* was the first species discovered on Auckland Island (New Zealand) and was originally described in its own genus *Halmaeusa* (Kiesenwetter & Kirsch, 1877). *Leptusa atriceps* (C. O. Waterhouse, 1875) was described next from the Kerguelen Islands, in the genus *Phytosus* Curtis (Waterhouse, 1875). Soon after, *Phytosus darwini* F. H. Waterhouse, 1879 was described from the Falkland Islands (Waterhouse, 1879). Thirty years later Enderlein (1909), based on the material from Kerguelen and additional material from Crozet islands, erected a new genus for *P. atriceps*, *Antarctophytosus* Enderlein, 1909. He was either unaware of *P. darwini* or he did not suspect that the same taxon may also occur as far away as the Falkland Islands. Soon after, Cameron (1917) recorded *P. atriceps* on the Falkland Islands, confirmed its identity with the type specimen from Kerguelen Islands and moved this species to a new genus *Paraphytosus* Cameron, 1917 probably unaware of Enderlein's genus *Antarctophytosus*. Brèthes



**Fig. 7.** Strict consensus of 12 most parsimonious trees from the maximum parsimony (MP) analysis under equal weights. Circles along branches are unambiguously optimized synapomorphies from WinClada: black circles are unique synapomorphies; white circles are homoplasious synapomorphies. Numbers above the circles are characters and numbers below the circles are their states. Values of Bremer support above 1 are given at the respective nodes. Distributions of *Leptusa* (*Halmaeusia*) species colour coded as in Fig. 1.

(1925) described the genus *Austromalota* Brèthes, 1925 for a new species *A. rufimixta* Brèthes, 1925 from South Georgia Island. Womersley (1937) added the second species to the genus *Antarctophytosus*, *A. macquariensis* Womersley, 1937 from Macquarie Island. Jeannel (1940) synonymized *P. darwini* with *Antarctophytosus atriceps*, but recognized three subspecies from different islands, which he separated based on the shape of the pronotum and relative size of the head: *A. atriceps* s. str. from Kerguelen Islands, *A. atriceps bougainvillea*, described from Marion and Crozet Islands and *A. atriceps darwini* from the Falkland Islands. Probably Jeannel (1940) overlooked *Austromalota rufimixta*, because this species was not mentioned in that publication. The genera *Antarctophytosus*, *Paraphytosus* and *Austromalota* were synonymized with the genus *Halmaeusia* by Steel (1964) in his paper on the staphylinids of Campbell Island, where he mentioned *Halmaeusia atriceps* as a widely distributed subantarctic species. In the same paper, Steel also synonymized *A. rufimixta* with *Halmaeusia atriceps* and *A. macquariensis* with *H. antarctica*. Steel (1964) further developed

Kiesenwetter's view of *Halmaeusia* by adding two new species, *H. sparsepunctata* (Steel, 1964) and *H. nesiotes* (Steel, 1964), both also from the subantarctic islands of New Zealand. He noted that these taxa are close to the genus *Leptusa*, but differ by having elongate ligulae. In his paper on staphylinids of South Georgia, Steel (1970) synonymized the three subspecies of *H. atriceps* recognized by Jeannel (1940), because they were well within the morphological variation of a single wide-spread species.

Finally, Pace (1989) downgraded *Halmaeusia* to a subgenus of *Leptusa*, where he recognized only two valid species, *L. antarctica* and *L. atriceps* by placing *L. sparsepunctata* and *L. nesiotes* in synonymy with *L. antarctica* without any justification. He also included the New Zealand species *Baeostethus chiltoni* in this subgenus. Leschen, Bullians, Michaux, and Ahn (2002) subsequently reinstated *Baeostethus* as a monotypic genus and placed it in the tribe Liparocephalini. As a result, only two valid species of *Leptusa* have been known in the Subantarctic region prior to our revision: *L. antarctica* (Kiesenwetter & Kirsch, 1877) from the

subantarctic islands of New Zealand and *L. atriceps* (Waterhouse, 1875). The latter of these has an incredible distribution across several distant islands (Falkland, South Georgia, Marion, Crozet, and Kerguelen) and a notable list of synonyms due to intricate taxonomic history. More recently, Marris (2000) suspected new species of *Leptusa* on subantarctic Antipodes Islands, and Emberson (2002) recorded two species from the off-shore Chatham Islands. The specimens from Antipodes Islands were identified as *L. nesiotus* here, and the specimens from Chatham Islands are actually members of the Athetini with 4-5-5 tarsal formula, 3-segmented labial palps and short bifid ligula.

#### Genus *Leptusa* Kraatz, 1856

*Leptusa* Kraatz, 1856: 60; Pace, 1989: 25; Smetana, 1973: 3; Gusarov & Herman, 2003a: 115, 2003b: 191; Klimaszewski *et al.*, 2004: 3–42.

**Type species:** *Bolitochara pulchella* Mannerheim, 1830, designated by Gusarov and Herman (2003a).

#### Diagnosis

A detailed description can be found in Klimaszewski *et al.*, 2004: p. 6.

#### Subgenus *Halmaeusa* Kiesenwetter, 1877

**Type species:** *Leptusa (Halmaeusa) antarctica* Kiesenwetter, 1877; *Halmaeusa* (as genus) Kiesenwetter (original description), 1877: 161; *Antarctophytosus* Enderlein (original description), 1909: 377; Steel (synonymy), 1964: 366; *Paraphytosus* Cameron, 1917: 125; Steel (synonymy), 1964: 366; *Australomalota* Bréthes, 1925: 170; Steel (synonymy), 1964: 366; *Halmaeusa* (as subgenus of *Leptusa*) Pace, 1989: 244.

#### Diagnosis (after Steel (1964) with modifications)

Body almost parallel-sided. Microsculpture present but variable in strength.

Head prominent. Eyes small. Labrum transverse with anterior margin almost straight. Mandible short, the right with small median tooth. Ligula long, extends beyond fused labial palpomeres 1 and 2. Prosternum carinate, pronotal epipleura visible from side. Mesoventral process narrow. Scutellary shield short, completely hidden by pronotum. Elytra short with posterolateral margin strongly sinuate. Hind wings completely absent (New

Zealand species) or rudimentary (as short appendages of one-fourth length of elytra in *L. atriceps*).

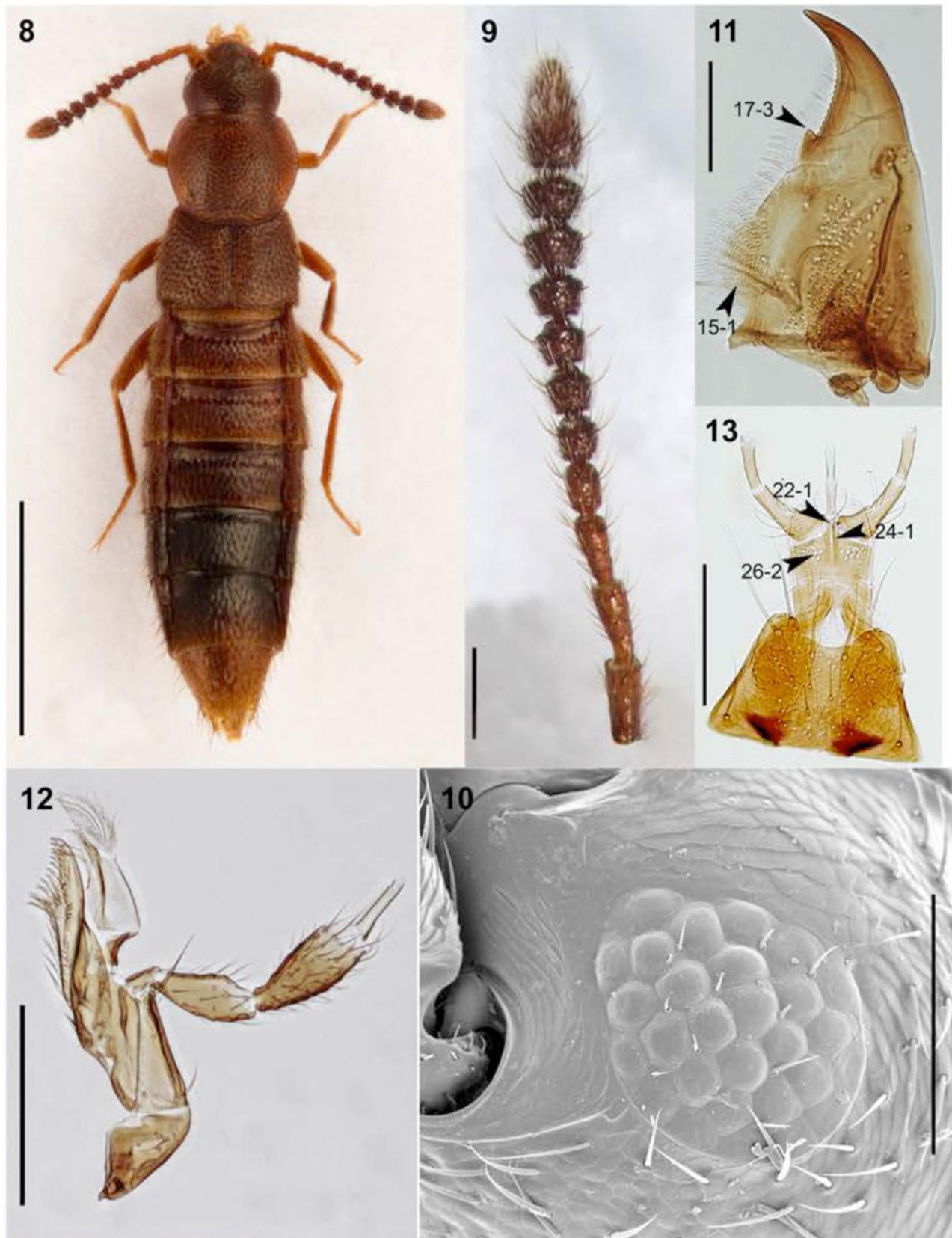
**Distribution:** Antipodes, Auckland, Campbell, Crozet, Falkland, Kerguelen, Macquarie, Marion, and South Georgia Islands.

#### Key to the *Leptusa (Halmaeusa)* species from the Subantarctic region

1. Body larger (body length 4–5 mm). Species from Crozet, Falkland, Kerguelen, Marion, and South Georgia Islands. .... *atriceps*
- Body smaller (body length 1.5–3.5 mm). Species from the subantarctic islands of New Zealand and Australia..2
2. Head, pronotum and elytra strongly and densely punctured; body larger (body length 2.5–3.5 mm).....3
- Head, pronotum and elytra weakly and less densely punctured; body smaller (body length 1.5–2.5 mm). .....4
3. Head distinctly narrower than base of pronotum (Fig. 8).....*antarctica* (Auckland and Macquarie Islands).
- Head distinctly wider than base of pronotum (Fig. 20).....*nesiotus* (Antipodes and Campbell Islands).
4. Macrosetae on apex and sides of abdomen longer than half of tergite VII length; body smaller (body length 1.5–1.8 mm)..... *steeli* sp. nov. (Auckland Island)
- Macrosetae on apex and sides of abdomen shorter than half of tergite VII length; body larger (body length 2.1–2.5 mm).....5
5. Last antennomere strongly elongated, at least twice as long as wide (Fig. 42). Apical teeth of maxilla sparsely placed (Fig. 44) ..... *insulae* sp. nov. (Auckland Island)
- Last antennomere less elongated, less than twice as long as wide (Fig. 26). Apical teeth of maxilla densely placed (Fig. 28) .....*sparsepunctata* (Campbell Island)

#### *Leptusa (Halmaeusa) antarctica* (Kiesenwetter & Kirsch, 1877) (Figs 8–19)

*Halmaeusa antarctica* Kiesenwetter, 1877: 161 (original description); *Antarctophytosus macquariensis* Womersley, 1937: 27 (original description); *Halmaeusa antarctica*: Steel, 1964: 367 (type revision, redescription, distribution, synonymy, description of larva); Pace, 1989: 246 (synonymy). In total 84 ♂♂ and 112 ♀♀ non-type specimens were examined from the Auckland



**Figs. 8–13.** *Leptusa (Halmaeus) antarctica* (Kiesenwetter, 1877). 8, habitus; 9, antenna; 10, eye; 11, right mandible; 12, maxilla; 13, labium. Scale bars: 8: 1 mm; 9, 10: 0.1 mm; 11: 0.05 mm; 12, 13: 0.2 mm.

Islands and Macquarie Island of New Zealand and Australia (see [supplemental material online](#)).

## Redescription

**Body** (Fig. 8) length: 2.5–3.7; without abdomen: 1.15–1.3. Colouration from reddish brown to dark brown. Antennae with first four antennomeres reddish and remaining dark brown. Legs reddish brown. Abdominal segments VI–VII and usually posterior half of V darker than rest of abdomen, apex of abdomen reddish–brown.

**Head** 1.1 times as wide as long with dense, coarse punctures (puncture width 0.02), and interspaces less than half their diameter. Microsculpture variable in strength. Temple subequal in length to eye or slightly longer. Gular plate wide at base and narrowed apicad. Antennae (Fig. 9) longer than head and pronotum combined. Eyes (Fig. 10), with no less than 28 ommatidia each. Right mandible as in Fig. 11. Maxilla (Fig. 12) with galea slightly shorter than lacinia. Labium (Fig. 13) with ligula subequal in length to first segment of labial palps. Prementum medial pseudopore field without pseudopores.

**Pronotum** 1.1–1.3 times as wide as long and about 1.4 times as wide as head.

**Elytra** about 0.8 times as long as pronotum. Elytral punctures dense, coarse, evenly distributed; their diameter (0.03) slightly larger than on pronotum and more expressed than on head; separated by less than half their diameter.

**Legs:** first segment of metatarsi very slightly longer than second (Fig. 14).

**Abdominal** tergites III–VII closely and rather strongly granulate, granules as large as elytral punctures.

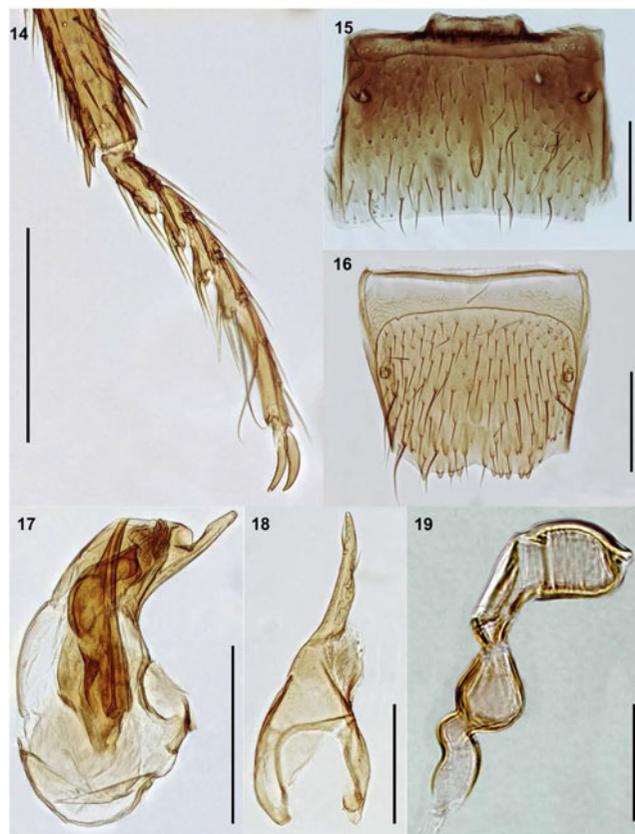
**Male:** Elytra raised on each side of suture and thus having distinct but not sharp longitudinal ridges along suture. Tergite VII (Fig. 15) rectangular, tuberculate with large tubercle in middle near posterior margin. Tergite VIII (Fig. 16) trapezoidal, with median tubercle; posterior margin medially emarginate, with distinct teeth-like tubercles. Median lobe of aedeagus as in Fig. 17. Paramere as in Fig. 18.

**Female:** Tergite VIII very slightly concave at anterior margin. Spermatheca as in Fig. 19.

**Larva** described in Steel (1964).

## Distribution

Based on Steel (1964) and material examined here, *L. antarctica* occurs on Auckland Islands (type locality) and Macquarie Island.



**Figs. 14–19.** *Leptusa (Halmaeus) antarctica* (Kiesenwetter, 1877). 14, metatarsi; 15, male tergite VII; 16, male tergite VIII; 17, median lobe of aedeagus; 18, paramere; 19, spermatheca. Scale bars: 14–18: 0.2 mm; 19: 0.05 mm.

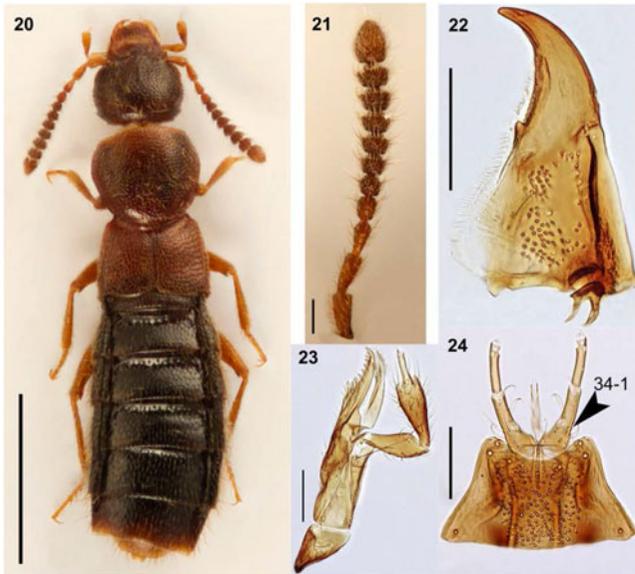
## Bionomics

*Leptusa antarctica* is commonly collected in leaf litter, rotten wood or in empty bird nests and burrows.

## Diagnostic remarks

The type material of *Leptusa antarctica* has been revised by Steel (1964). *Leptusa antarctica* can be easily separated from all subantarctic species of the subgenus except *L. nesiotes* by the dense punctation of the body. From *L. nesiotes*, it differs in having a more slender head. Additionally, males of *L. antarctica* can be distinguished from all other species by the large median tubercles on tergites VII and VIII and apical teeth on tergite VIII. The shape of the median lobe of the aedeagus of *L. antarctica* is nearly identical with *L. sparsepunctata*, but both species are easily distinguished externally by body punctation.

*Leptusa (Halmaeus) nesiotes* (Steel, 1964), status  
resurrected  
(Figs 20–24)



**Figs. 20–23.** *Leptusa (Halmaeus) nesioites* (Steel, 1964). 20, habitus; 21, antenna; 22, right mandible; 23, maxilla; 24, labium. Scale bars: 20: 1 mm; 21–24: 0.1 mm.

*Halmaeus nesioites* Steel, 1964: 369 (original description); *Leptusa nesioites*: Pace, 1989: 246 (as synonym of *L. antarctica*); Material examined: New Zealand: Campbell Islands: Campbell I.: Paratype: 1♀, Rocky Bay, 20.XII.1961, *Azorella*, leg. J. L. Gressitt (NZAC). In total 4 ♂♂ and 2 ♀♀ non-type specimens were examined from Antipodes Island of New Zealand (see [supplemental material online](#)).

### Redescription

**Body** (Fig. 20) length: 2.8–3.2; without abdomen: 1.3–1.5. Colouration from reddish-brown to dark-brown. Antennae with first four antennomeres reddish and remaining antennomeres dark brown. Legs reddish brown. Abdominal segments III–VII dark brown or almost black. Apex of abdomen reddish-brown.

**Head** 1.2 times as wide as long, with dense, coarse punctation (puncture width 0.02), interspaces more than half their diameter; microsculpture distinct. Temple almost equal in length to eyes or slightly longer. Gular plate parallel-sided. Antennae as in Fig. 21. Each eye with 32–34 ommatidia. Right mandible as in Fig. 22. Maxilla (Fig. 23) with galea distinctly shorter than lacinia; lacinia with teeth placed sparsely. Labium (Fig. 24) with ligula as long as first segment of labial palps. Prementum medial pseudopore field with few pseudopores.

**Pronotum** 1.3 times as wide as long and about 1.2 times as wide as head.

**Elytra** 0.8 times as long as pronotum. Elytral punctures dense, coarse, evenly distributed, less expressed than on pronotum, their diameter (0.02) subequal to those on pronotum, separated by interspaces less than half their diameter.

**Legs:** first segment of metatarsi slightly longer than second.

**Abdominal tergites III–VII** moderately densely granulate, granules slightly smaller than punctures on elytra; microsculpture absent or indistinct.

**Male:** Elytra more distinctly granulate in sutural area. Tergite VIII emarginate apically over its entire width. Median lobe of aedeagus almost the same as in *L. antarctica* except its apex forming slightly thicker process (Fig. 22 in Steel, 1964).

**Female** tergite VIII slightly concave medially; sternite VIII not modified. Spermatheca apparently not separable from that of *L. antarctica*.

**Larva** unknown.

### Distribution

Based on Steel (1964) and material examined here, *L. nesioites* occurs on the Campbell (type locality), Auckland, and Antipodes Islands.

### Bionomics

For the material of *L. nesioites* from Campbell Island Steel (1964) reported that it was collected under stones in a penguin rookery, under moss on rocks, amongst *Colobanthus* etc., and on low plants in a mollymawk colony. The material from Antipodes Island was collected mainly from under coastal mat plants.

### Diagnostic remarks

In the coarse punctation of the body and shape of the median lobe of aedeagus *Leptusa nesioites* is very similar to *L. antarctica*, but it can be separated from the latter by its darker body colouration, slightly finer and denser punctures, and by the absence of tubercles on the male abdominal tergites VII and VIII. From other subantarctic species *L. nesioites* differs in coarse body punctation, and in shape of the median lobe of the aedeagus. The species was described by Steel (1964) based on nine specimens, some of which were collected

on Campbell Island (holotype locality), and two specimens on the Auckland Islands, which we have not examined. Among the material we examined, only one female from Campbell Island matched the description of *L. nesiotus*, and none of the specimens from the Auckland Islands were of that species. Material of *L. nesiotus* reported by Steel from Auckland Island needs careful examination to confirm the species. Seven specimens from Antipodes Island match Steel's description of the species and a close study of the Antipodes material did not reveal any differences between that and the female paratype of *L. nesiotus* from Campbell Island that we examined. Pace (1989) placed *Leptusa nesiotus* in synonymy with *Leptusa antarctica* without justification. Based on the distinct difference between these species, we resurrect *L. nesiotus* from synonymy.

***Leptusa (Halmaeusa) sparsepunctata* (Steel, 1964),  
status resurrected  
(Figs 25–30)**

*Halmaeusa sparsepunctata* Steel, 1964: 371 (original description); *Leptusa sparsepunctata*: Pace, 1989: 246 (as synonym of *L. antarctica*).

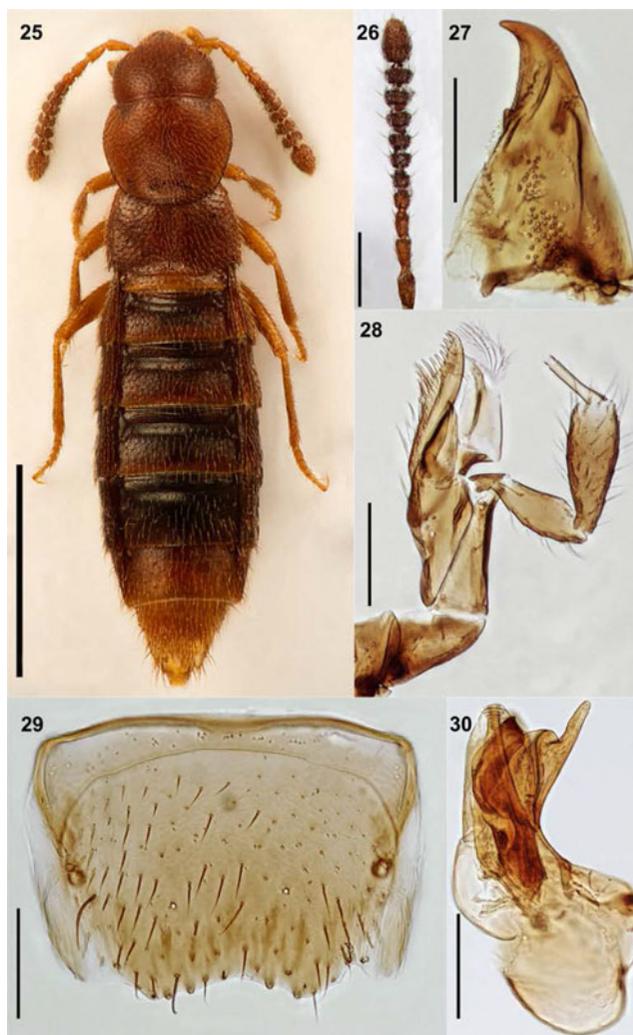
### Material examined:

New Zealand, Campbell Island:

Paratypes: 1♀, Tucker Cove, 1.XI.1961, moss, 10–200 m, leg. J. L. Gressit, (NHM); 1♂, 1♀, Perseverance Harbour, Lookout Bay, 3.II.1963, leaf mould under *Stilbocarpa* and leaf mould under tussock, leg. K. A. J. Wise (NZAC); 1♂, Courrejolles Pen., 14.XII.1961, mollymawk nest, 200 m., leg. J. L. Gressit, (NHM); 1♂, Smooth Water Bay, 16.II.1963, leaf mould under sedge, leg. K. A. J. Wise, (NHM); 1♂, Courrejolles Pen., 13.II.1963, mollymawk colony, 200 m., leg. K. A. J. Wise, (NHM); 1♂, Beeman Camp., 6–11.XII.1961, 2–50 m., leg. K. A. J. Wise (NHM); 1♀, Rocky Bay, 18.II.1962, Penguin colony, below Mt. Dumas, base of tussock, leg. K. A. J. Wise, (NHM); 1♀, Mt. Dummas summit, under stones, 6.II.1963, leg. K. Renneu (NHM); 1♀, Perseverance Harbour, Lookout Bay, 3.II.1963, leaf mould under *Stilbocarpa*, leg. K. A. J. Wise (NHM). In total 8 ♂♂ and 7 ♀♀ non-type specimens were examined from Campbell Island of New Zealand (see [supplemental material online](#)).

### Redescription

**Body** (Fig. 25) length: 2.1–2.7; without abdomen: 0.9–1.1. Body colouration from reddish brown to dark brown. Antennae with first four antennomeres yellowish



**Figs. 25–30.** *Leptusa (Halmaeusa) sparsepunctata* (Steel, 1964). 25, habitus; 26, antenna; 27, right mandible; 28, maxilla; 29, male tergite VIII; 30, median lobe of aedeagus. Scale bars: 25: 1 mm; 26: 0.2 mm; 27–30: 0.1 mm.

and remaining antennomeres brown. Legs reddish brown. Abdominal segments V–VII usually darker than rest of abdomen.

**Head** 1.2 times as wide as long, with strong microsculpture. Punctuation weak and sparse, poorly distinct punctures separated by interspaces less than half their diameter. Temple about 1.4 times as long as eye. Gular plate wide at base and narrowed apicad. Antennae as in Fig. 26. Eyes with no less than 19 ommatidia each. Right mandible as in Fig. 27. Maxilla (Fig. 28) with galea shorter than lacinia; lacinia with teeth placed densely. Labium with ligula subequal in length to first segment of labial palps. Medial field of prementum without pseudopores.

**Pronotum** 1.2–1.3 times as wide as long and about 1.2 times as wide as head.

**Elytra** 0.7 times as long as pronotum.

**Legs:** first four segments of metatarsi subequal in length.

**Abdomen** with microsculpture moderate with distinct but weak granules.

**Male:** Tergite VIII (Fig. 29) trapezoidal, narrowing apicad with posterior margin concave, with indistinct teeth-like tubercles. Median lobe of aedeagus as in Fig. 30.

**Female:** Tergite VIII very slightly concave at anterior margin.

**Larva** apparently not separable from that of *L. antarctica* (Steel, 1964).

### Distribution

Based on Steel (1964) and the material examined here, *L. sparsepunctata* is restricted to Campbell Island.

### Bionomics

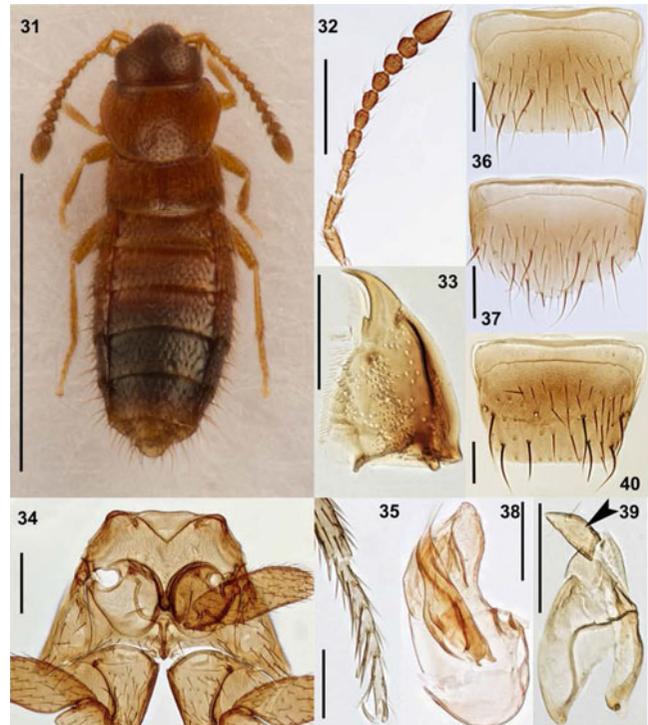
Based on Steel (1964) and the material examined here, *L. sparsepunctata* is found in leaf litter, in penguin and mollymawk colonies, and in albatross nests. One specimen was reported from seaweed on the shore.

### Diagnostic remarks

*Leptusa sparsepunctata* is similar to *L. antarctica* and *L. nesiotes*. From *L. antarctica* and from *L. nesiotes* (the only other species of *Leptusa* known from the Campbell Islands), it can be easily separated by very weak punctuation of the head and pronotum. Pace (1989) placed *L. sparsepunctata* in synonymy with *L. antarctica* without justification. Based on the morphological differences between these species, we resurrect *L. sparsepunctata* from synonymy.

***Leptusa (Halmaeusa) steeli* sp. nov.**  
(Figs 31–40)

Material examined: New Zealand, Auckland Islands: Auckland I.: Holotype: ♂, 'New Zealand, Auckland Island, Waterfall Inlet, litter along stream margins, S50 48.977, E166 12.042, 26.III.2006, leg. R. Leschen, E. Edwards' (NZAC); Paratypes: 31♂♂, 36♀♀, same data as in holotype (2♂♂, 2♀♀ at ZMUC, 29♂♂, 34♀♀ at NZAC); 1♀, Ranui Cove, 7-12.XI.1954, E. S. Gourlay



**Figs. 31–40.** *Leptusa (Halmaeusa) steeli* sp. nov. 31, habitus; 32, antenna; 33, right mandible; 34, mesoventral process; 35, metatarsi; 36, male tergite VIII; 37, male sternite VIII; 38, median lobe of aedeagus; 39, paramere (the arrow indicates the apical lobe); 40, female tergite VIII; Scale bars: 31: 1 mm; 32: 0.2 mm; 33–40: 0.1 mm.

(NZAC); 30♂♂, 39♀♀, Port Ross, Laurie Harbour, S50 33.444, E166 11.028, 27.III.2006, *Fuschia* leaf litter, leg. R. Leschen and E. Edwards (NZAC); 3♂♂, 2♀♀, Erebus & Terror Cove, 50°30'S, 166°19'E, 22.III.2000, leaf litter and under rotting wood, leg. M. Bullians, E. Edwards and R. Leschen (NZAC); 2♂♂, 2♀♀, Western Harbour, S50 49.196, E165 54.955, 25.III.2006, rotten wood and leaf litter, leg. E. Edwards and R. Leschen, (NZAC); 20♂♂, 26♀♀, Ranui Cove, 10.XI.1954, Ex. leafmould, The Lookout, leg. E. S. Gourlay (NZAC); 2♂♂, 1♀, Ranui Cove, 7-12.XI.1954, Ex. leafmould, The lookout, leg. E.S. Gourlay (NZAC); 1♂, 1♀, 19.IV.1944, leg. J. H. Sorensen (NZAC); Adams I.: 6♂♂, 3♀♀, Fairchild's Garden, S50 50.248, E165 55.342, 22.III.2006, megaherb leaf litter, leg. E. Edwards and R. Leschen (NZAC); 16♂♂, 19♀♀, McLaren Bay, area surrounding hut, S50 52.002 E166 01.553, 23.III.2006, leaf litter and rotten wood, leg. E. Edwards and R. Leschen (NZAC); 25♂♂, 35♀♀, Fairchild's Garden, S50 50.248 E165 55.342, 22.III.2006, *Dracophyllum*, *Metrosideros*, *Poa* and Megaherb leaf litter, leg. E. Edwards and R. Leschen (NZAC); 1♂, NE Ridge Mt Dick, 549 m.,

1.II.1966, moss, leg. G. Kuschel (NZAC); 1♂, Magnetic Cove stn., 28.I.1966, leaf litter, leg. G. Kuschel (NZAC).

### Description

**Body** (Fig. 31) length: 1.5–2; without abdomen: 0.6–0.8. Body colouration from reddish brown to dark brown; head darker. Antennae with first four antennomeres yellowish and remaining dark brown. Legs yellowish brown. Abdominal segments VI–VII and usually apical part of V darker than rest of abdomen, often almost black. Apex of abdomen reddish-brown.

**Head** 1.3–1.4 times as wide as long with strong micro-sculpture. Temple 0.8–0.9 times as long as eye. Gular plate wide at base and narrowed apicad. Antennae as in Fig. 32. Eyes with 17–19 ommatidia each. Right mandible as in Fig. 33. Maxilla with galea slightly shorter than lacinia; lacinia with densely placed teeth. Labium with ligula long, bilobed in apical one-fifth. Prementum medial pseudopore field with few pores.

**Pronotum** about 1.4–1.5 times as wide as long and about 1.4–1.5 times as wide as head.

**Elytra** 0.7 times as long as pronotum. Elytral punctuation coarse, evenly distributed, more expressed than on head.

**Legs:** first four segments of metatarsi (Fig. 35) subequal in length.

**Abdomen** with microsculpture on segments III–VII strong. Sides of abdominal segments III–VII with macrosetae up to 3 times as long as regular setae.

**Male:** Tergite VIII (Fig. 36) with apical margin straight. Sternite VIII (Fig. 37) triangular. Median lobe of aedeagus as in Fig. 38. Paramere as in Fig. 39.

**Female:** Tergite VIII as in Fig. 40.

**Larva** unknown.

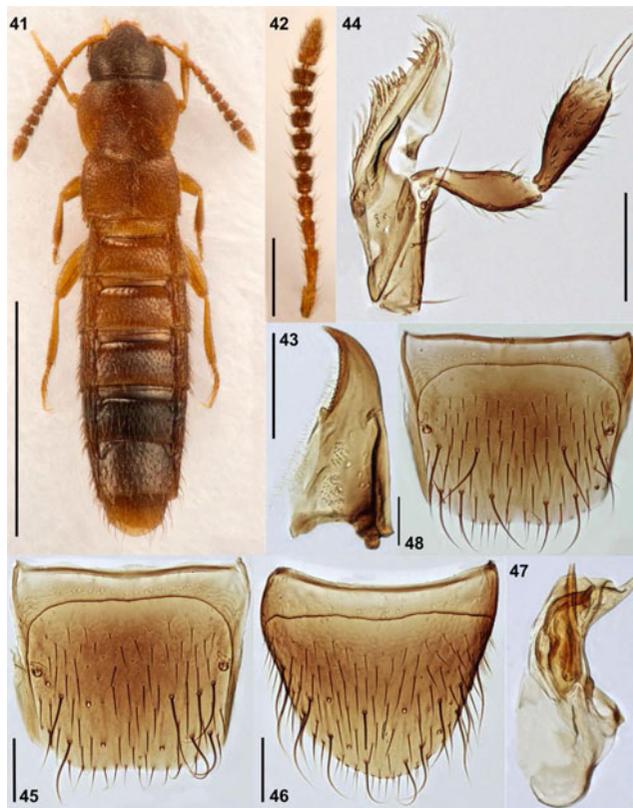
**Etymology.** This species is named in honour of William Owen Steel, who in particular worked on the subantarctic Staphylinidae in the middle of the 20th century.

### Distribution

The species is known only from the Auckland Islands.

### Bionomics

*Leptusa steeli* sp. nov. is commonly collected from leaf litter and rotten wood.



**Figs. 41–48.** *Leptusa (Halmaeus) insulae*, sp. nov. 41, habitus; 42, antenna; 43, right mandible; 44, maxilla; 45, male tegite VIII; 46, male sternite VII; 47, median lobe of aedeagus; 48, female tergite VIII. Scale bars: 41: 1 mm; 42: 0.2 mm; 43–48: 0.1 mm.

### Diagnostic remarks

*Leptusa steeli* sp. nov. is easily separated from other subantarctic species by the long macrosetae on the apex of abdomen and its relatively small body size. Additionally, males of *L. steeli* can be distinguished from other species by the shape of aedeagus, in particular the apex of aedeagus that does not form a long thin process and the apical lobe of paramere that is distinctly shorter than half of the length of the paramerite (Fig. 39, arrow).

*Leptusa (Halmaeus) insulae* sp. nov.  
(Figs 41–48)

Material examined: New Zealand: Auckland Islands: Auckland I.: Holotype: ♂, 'New Zealand AU, S50 48.977, E166 12.042, 26.III.2006, Waterfall Inlet, litter along stream margins, leg. E. Edwards and R. Leschen' (NZAC); Paratypes: 2♂♂, 4♀♀, same data as in holotype (1♂ 1♀ at ZMUC; 1♂ 3♀♀ at NZAC); Adams I.: 1♂, McLaren Bay, area surrounding hut, S50 52.002, E166

01.553, 23.III.2006, leaf litter and rotten wood, leg. E. Edwards & R. Leschen (NZAC); 1♀, NE Ridge Mn. Dick, 549 m, 1.II.1966, in moss, leg. G. Kuschel (NZAC).

### Description

**Body** (Fig. 41) length: 2.1–2.5, without abdomen: 0.9–1.1. Colouration from reddish brown to dark brown. Head and abdominal segments V–VII darker. Antennae with first three antennomeres yellowish and remaining dark brown. Legs reddish brown. Apex of abdomen yellow-brown.

**Head** 1.1 times as wide as long; with strong microsculpture and weak, poorly distinct punctures. Temple about 1.2 times as long as eye. Gular plate parallel-sided. Antennae as in Fig. 42. Eyes with no less than 21 ommatidia each. Right mandible as in Fig. 43. Maxilla (Fig. 44) with galea slightly shorter than lacinia; lacinia with teeth sparsely placed and forming distinct gap apicad. Prementum medial pseudopore field without pseudopores.

**Pronotum** 1.1–1.12 times as wide as long and 1.3 times as wide as head.

**Elytra** 0.8 times as long as pronotum; microsculpture strong; punctation weak.

**Legs** with first four segments of metatarsi almost equal in length.

**Abdomen** with microsculpture weak, tergites III–VII moderately granulate.

**Male:** Tergite VIII (Fig. 45) trapezoidal, with slight medio-apical emargination. Sternite VIII as in Fig. 46. Aedeagus as in Fig. 47.

**Female:** Tergite VIII (Fig. 48) with slightly concave anterior margin.

**Larva** unknown.

### Distribution

The species is known only from the Auckland Islands.

### Bionomics

Specimens of *Leptusa insulae* sp. nov. were collected in leaf litter along stream margins and rotten wood.

### Etymology

The name refers to the insular distribution of the species.



Fig. 49–54. *Leptusa (Halmaeus) atriceps* (Waterhouse, 1875). 49, habitus; 50, maxilla; 51, labium; 52, male tergite VIII; 53, medial lobe of aedeagus; 54, paramere. Scale bars: 49: 1 mm; 50, 51: 0.1 mm; 52–54: 0.2 mm.

### Diagnostic remarks

*Leptusa insulae* is very similar to *L. sparsepunctata* but differs in the parallel-sided shape of gular plate. From *L. nesiotae* it differs in the shape of the last antennomere. Additionally, males of *L. insulae* can be distinguished from all other species of *Halmaeus* by the median lobe of aedeagus which has no expansion of the apical process.

*Leptusa (Halmaeus) atriceps* (Waterhouse, 1875)  
(Figs 49–54)

*Phytosus atriceps*: C. O. Waterhouse, 1875: 54 (original description); *Phytosus darwini*: F. H. Waterhouse, 1879: 531 (original description); *Australomalota rufomixta*: Bréthes, 1925: 171 (original description); Steel, 1964: 366 (synonym of *Halmaeusia atriceps*); *Paraphytosus atriceps*: Cameron, 1917: 125; *Antarctophytosus atriceps atriceps*: Jeannel, 1940: 106 (redescription); *Antarctophytosus atriceps bougainvillei*: Jeannel, 1940: 111 (original description, description of larva); *Antarctophytosus atriceps darwini*: Jeannel, 1940: 106 (redescription, subspecies and synonymy status);

*Halmaeusia atriceps*: Steel 1970: 241 (redescription, synonymy, distribution);

*Leptusa (Halmaeusia) atriceps*: Pace 1989: 246; Slabber and Chown 2005: 195 (biology and physiology).

### Material examined:

France: Kerguelen Islands: Holotype: ♀, (card mounted with spermatheca in Euparal drop on plastic card mounted under specimen), “Holotype”/“Type H. T.”/“Type”/“Phytosus atriceps, (Type) C. Waterh.”/“Kerguelen”/“? gen. Sipalia Paraphytosus”/“Leptusa atriceps (Wat.) det. R. Pace 1985” (NHM); In total 9 ♂♂ and 8 ♀♀ non-type specimens were examined from the Kerguelen Islands, South Georgia Islands and Falkland Island (see [supplemental material online](#)).

### Redescription

**Body** (Fig. 49) length: 3.9–5.0, without abdomen: 1.7–2.0. Head and abdomen, except apex, dark brown. Pronotum, elytra and apex of abdomen light reddish brown. Antennae with first three antennomeres yellowish and remaining yellow-brown. Legs light reddish brown. Abdominal segments V and VI and darker than rest of abdomen. Apex of abdomen reddish-brown.

**Head** 0.9 times as wide as long with weak punctuation and strong microsculpture. Eyes with with no less than 36 ommatidia each. Temple about 1.3 times as long as eye. Gular plate parallel-sided. Maxilla (Fig. 50) with galea shorter than lacinia. Labium as in Fig. 51. Prementum medial pseudopore field with few pseudopores.

**Pronotum** 1.2 times as wide as long and about 1.2 times as wide as head; punctures and microsculpture as on head.

**Elytra** 0.9 times as long as pronotum; microsculpture as on head and pronotum.

**Legs**: first segment of metatarsi equal or very slightly longer than second segment.

**Abdomen** with microsculpture as on front parts and punctuation similar to those on elytra.

**Male**: Tergite VIII (Fig. 52) emarginate medio-apically. Median lobe of aedeagus as in Fig. 53; paramere as in Fig. 54.

### Distribution

The distribution of *Leptusa atriceps* on several subantarctic islands very remote from each other, Kerguelen Islands (type locality), Crozet, Marion, South Georgia, and Falkland Islands, is truly remarkable (Fig. 1).

### Bionomics

Based on Steel (1970) and the material examined here, *L. atriceps* is most common at the sea-shore. Also, it can be found away from the shore, in moss, grass tussocks, under rocks near freshwater streams, and in albatross nests and penguin rookeries.

### Diagnostic remarks

*Leptusa atriceps* is similar to *L. nesiotus* but differs in the larger body size and the fine and rather indistinct punctuation of the head and pronotum. Males of *L. atriceps* can be separated from other *Halmaeusia* species by the shape of the paramere.

### Remarks

Detailed descriptions of *L. atriceps* can be found in Jeannel (1940) and Steel (1970). Jeannel (1940) recognized three subspecies, *L. a. atriceps* from the Kerguelen Islands, *L. a. darwini* from the Falkland Islands and *L. a. bougainvillei* from Marion Island, which he separated based on differences in the relative size of the head and the shape of the pronotum. Our detailed morphological examination of the material from the Kerguelen, Falkland and South Georgia Islands and Jeannel's (1940) description of the material from Marion Island, revealed no consistent difference between samples from different islands. The intraspecific variability is continuous and confirms Steel's (1970) synonymy of Jeannel's subspecies.

### Biogeography of subantarctic *Leptusa*

Different geological ages and tectonic histories of the subantarctic islands indicate that the distribution of *Leptusa* species is either the result of vicariance that may stem from past mainland connections and inter-island connections that may have existed in the Campbell Plateau or cross-ocean dispersals. The latter, supported by remarkably

wide multi-island distributions of *L. atriceps* (Kerguelen, South Georgia, Falkland and Marion Islands), *L. nesiotus* (Campbell, Antipodes, Auckland Islands) and *L. antarctica* (Auckland and Macquarie Islands), was likely facilitated by the circumantarctic currents.

The subantarctic *Leptusa* form a monophylum corresponding to the subgenus *Halmaeusa*, but the limitations of our analysis make it difficult to recover its sister lineage. However, at least as suggested by the MP analysis, the *Halmaeusa* clade is sister to a clade formed by the temperate South American *Leptusa* (*Nanoglossa*) (Fig. 7). Such a sister group relationship, in turn, would suggest that *Leptusa* (*Halmaeusa*) of the subantarctic region may stem from an ancestor shared with the South American mainland *Leptusa* (*Nanoglossa*), implying that these two groups may have diverged from a widespread Gondwanan ancestor.

Alternatively, the entire *Halmaeusa* clade was centred in the southern Pacific and the presence of *L. atriceps* in the Southern Indian/Atlantic oceans represents an eastward dispersal facilitated by the Antarctic Circumpolar Current, a predominant process leading to geographic structuring in the subantarctic biota (e.g., González-Wevar et al., 2017; Moon et al., 2017). This process of dispersal over water has been evoked for many organisms, including spiders (Pugh, 2004), some of which may span temperate and tropical islands (Grehan, 2001). Ocean currents are generally slow (~0.7–2.7 km/h) and flow in predictable directions. The Antarctic Circumpolar Current (or West Wind Drift) flows clock-wise around Antarctica at ~2.75 km/h and is a means by which rafting organisms may travel between New Zealand and South America in less than 1 year (Gillespie et al., 2012). Organisms living in wood or with some other mechanism of protection from seawater can survive relatively well during transport (Thiel & Haye, 2006).

The islands populated by *L. atriceps* have a range of formation dates (see Introduction) and a genetic study is needed to determine exact origin, times of divergence and phylogenetic relationships among populations of *L. atriceps*. Island age and size may explain *Leptusa* species richness, with the Auckland Islands, the largest archipelago, containing four species, followed by the Campbell Islands with two species. The higher species diversity of *Leptusa* on the Auckland Islands is consistent with other groups of terrestrial animal species and with more extensive *Metrosideros* forest habitats there (Gressitt & Wise 1971; Michaux & Leschen, 2005). Moreover, sympatry of *Leptusa* congeners is high, similar to other staphylinid species (e.g., Carlton & Leschen, 2001). Based on recent collections from the Auckland Islands, there was one collection event that contained *L. insulae*, *L. antarctica*, and *L. steeli*, one event that contained *L. insulae* and *L. antarctica*, and three to five events that contained

the remaining pairings. There were no collections of all four species together.

Our study reveals a notable fauna of *Leptusa* of the subantarctic islands and outlines possible hypotheses regarding their subantarctic island biogeography. We call for a more rigorous quantitative exploration of these hypotheses once our target beetles are better known phylogenetically and DNA-grade material is available. Even though we have clarified the species composition of the subantarctic island fauna of *Leptusa*, current data suggest that with more material available, new species discoveries and distributional records for the known species are still likely.

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## Supplemental data

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