

Original Article

A revision of the higher latitude periwinkle species *Laevitorina caliginosa sensu lato*

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[Version of Record, published on 22 November 2023; <http://zoobank.org/urn:lsid:zoobank.org:pub:AEDB799C-B7FE-40B0-BFEF-30D3E0AE2A6F>]

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ABSTRACT

The marine gastropod genus *Laevitorina* is exclusive to the Southern Hemisphere, with 21 species from southern South America, Antarctica, Australia, New Zealand, and sub-Antarctic Islands. We present a comprehensive revision of *Laevitorina*, using molecular and morphological analyses, to address formally the interspecific divergences within the nominal taxon *Laevitorina caliginosa* s.l. We confirm the validity of *L. caliginosa* and *Laevitorina venusta*, and we demonstrate that specimens from the Strait of Magellan and Hornos Island constitute four new species here described: *Laevitorina magellanica* sp. nov., *Laevitorina pepita* sp. nov., *Laevitorina fueguina* sp. nov., and *Laevitorina hicana* sp. nov. All six species are clearly distinguishable genetically, morphologically, and through radular tooth shape and configurations. *Laevitorina venusta* is broadly distributed across the Antarctic Peninsula, South Georgia, and sub-Antarctic Islands (Marion, Crozet, Kerguelen, and Macquarie), whereas *L. caliginosa* s.s. appears geographically restricted to Cape Horn, the Falkland/Malvinas Islands, and South Georgia. The identification of populations from Macquarie Island as *L. caliginosa* is dubious; we suggest that these records are likely to pertain to *L. venusta*. This detailed revision of *Laevitorina*, whereby hidden diversity was detected, significantly enriches our knowledge of the evolutionary history of this group.

Keywords: Antarctica; speciation; molecular phylogeny; biogeography; South America; Bayesian analysis; Gastropoda; new species; morphological comparison; vicariance

INTRODUCTION

Periwinkles of the family Littorinidae include > 200 species of small marine gastropods highly abundant on littoral ecosystems across temperate and tropical regions (Williams *et al.* 2003). Littorinids represent one of the most ubiquitous molluscan

components of marine near-shore hard-substrate communities and are some of the most intensively studied organisms in ecology (Eschweiler *et al.* 2009), evolution (Johannesson 2003), speciation (Williams and Reid 2004, Galindo and Grahame 2014), physiology (McMahon 2001, Liao *et al.* 2017, Dwane *et al.*

al. 2021), behaviour (Ng *et al.* 2017), reproduction (Johanesson *et al.* 1995, Ng *et al.* 2019), and systematics (Reid 1989, 1996, Williams *et al.* 2003, Reid *et al.* 2012, González-Wevar *et al.* 2022). Moreover, periwinkles have been widely used as model organisms in microevolutionary studies of natural selection and genetic differentiation (Johanesson *et al.* 1995, McQuaid 1996, Wildings *et al.* 2001, Reid *et al.* 2006) and for macroevolutionary studies including adaptive radiation and historical biogeography (Reid *et al.* 1996, 2012, Williams *et al.* 2003, Reid and Williams 2004). Nevertheless, most of the evolutionary studies on this family have been conducted on temperate groups, and little is known about the origin, the evolutionary relationships, and the diversification of higher-latitude Antarctic and sub-Antarctic taxa (González-Wevar *et al.* 2022).

Laevilitorina Pfeffer, 1886 is the most species-rich genus of high-latitude littorinids, with 21 nominal species (<http://marinespecies.org>) occurring across the Southern Ocean and nearby waters (Rosenfeld *et al.* 2022). Species of this genus are gonochoric and exhibit benthic-protected development, in which small juveniles emerge directly from egg masses (Simpson and Harrington 1985). The predominance of this reproductive mode in Southern Ocean marine invertebrates, and particularly in higher-latitude littorinids, seems to represent a key evolutionary feature that has enhanced diversification and speciation potential (Reid 1989, Poulin and Feral 1996, Poulin *et al.* 2002, Pearse *et al.* 2009, Thatje 2012, Chenuil *et al.* 2018, Crame 2018, Halanych and Mahon 2018).

Four species [*Laevilitorina brunensis* (C. E. Beddome, 1883), *Laevilitorina johnstoni* (Cotton, 1945), *Laevilitorina kingensis* (May, 1924), and *Laevilitorina mariae* (Tenison Woods, 1876)] are currently found in southern Australia, whereas *Laevilitorina alta* (Powell, 1940) is endemic to the North Island of New Zealand. The remaining species are restricted to Antarctic and sub-Antarctic hard-bottom ecosystems, where they can be abundant on intertidal and subtidal macroalgae, on which they graze and reproduce (Iken 1999, Amsler *et al.* 2015, 2019, Rosenfeld *et al.* 2017). Three *Laevilitorina* species are restricted to the Antarctic Peninsula: *Laevilitorina antarctica* (E. A. Smith, 1902), *Laevilitorina claviformis* Preston, 1916, and *Laevilitorina wandelensis* (E. Lamy, 1906). Other Antarctic Peninsula species (*Laevilitorina umbilicata* Pfeffer, 1886 and *Laevilitorina pygmaea* Pfeffer, 1886) are also found on sub-Antarctic South Georgia, where they coexist with two apparently endemic taxa, *Laevilitorina granum* Pfeffer, 1886 and *Laevilitorina venusta* Pfeffer, 1886. Several species are restricted to geographically isolated sub-Antarctic islands: *Laevilitorina latior* Preston, 1912 from the Falkland/Malvinas Islands and *Laevilitorina heardensis* Dell, 1964 from Heard Island, while *Laevilitorina macphersonae* (Dell, 1964), and *Laevilitorina hamiltoni* (E. A. Smith, 1898) are endemic to Macquarie Island. Additionally, several species are restricted to sub-Antarctic islands of New Zealand, including *Laevilitorina bifasciata* Suter, 1913 and *Laevilitorina delli* (Powell, 1955) from the Antipodes Islands, *Laevilitorina aucklandica* (Powell, 1933) from the Auckland, Chatham, and Stewart Islands, and *Laevilitorina antipodum* (Filhol, 1880) from Campbell and Auckland Islands.

Despite the high levels of endemism and the restricted geographical distribution recorded in most of the members of the genus, a single taxon, *Laevilitorina caliginosa* A. Gould, 1849,

exhibits an apparently broad distribution. Populations occur all around the Southern Ocean, including southern South America, the Falkland/Malvinas Islands, the Antarctic Peninsula, South Georgia, Marion, Crozet, Kerguelen, and Macquarie Islands (Simpson and Harrington 1985, Reid 1989, Reid *et al.* 2012, Griffiths and Waller 2016). This species represents one of the few examples of a near-shore marine invertebrate distributed across the whole Southern Ocean and, accordingly, constitutes a very interesting biogeographical model for evolutionary studies.

Nevertheless, as Reid *et al.* (1996) argued, a revision of *Laevilitorina* is essential to understand the systematics, patterns of diversity, and distribution of this cold-adapted, morphologically confusing group of periwinkles. Subsequently, a recent study of *L. caliginosa* using multilocus phylogenetic reconstructions, species-delimitation analyses, and divergence-time estimations (González-Wevar *et al.* 2022) identified seven species-level clades within this nominal taxon. Moreover, geometric morphometric analyses identified significant statistical differences among the clades (González-Wevar *et al.* 2022). Accordingly, the diversification of *Laevilitorina* does not fit with a cryptic speciation scenario: cladogenesis was, in fact, accompanied by morphological differentiation. The single Antarctic ‘*caliginosa*’ clade was shown to have an expanded distribution including Marion, Crozet, Kerguelen, and Macquarie Islands. In particular, most diversity was found in southern South America, with the presence of six different species, with at least four of them undescribed (González-Wevar *et al.* 2022).

In this study, we present a taxonomic revision of the higher-latitude *Laevilitorina* species examined by González-Wevar *et al.* (2022), in which we describe four new South American taxa. Simultaneously, we revise the accepted distribution of some Antarctic and sub-Antarctic species of the genus, making key adjustments to previously published records. This study constitutes a first step in a comprehensive revision of this broadly distributed group of Antarctic and sub-Antarctic periwinkles. In making this revision, we provide new information concerning the evolution, patterns of diversity, and biogeography of an important element of the Southern Ocean near-shore marine benthic biota.

MATERIALS AND METHODS

Taxon sampling

Specimens of *L. caliginosa* *s.l.* were collected between 2015 and 2021 from different localities in the Southern Ocean across the species distribution from southern South America, including the Strait of Magellan (Chabunco, Port Famine, Leñadura, and Porvenir) and Cape Horn (Beagle Channel, Hornos Island), to the Falkland/Malvinas Islands, and from maritime Antarctica and several sub-Antarctic Islands (South Georgia, Marion, Crozet, Kerguelen, and Macquarie) (for georeference details, see Rosenfeld *et al.* 2022). We include in this revision individuals of four new *Laevilitorina* species (González-Wevar *et al.* 2022), described below. These new taxa exhibit morphological features that do not match those described for nominal species in the genus from the Southern Ocean, particularly those from southern South America. In addition to the material used by González-Wevar *et al.* (2022), we included in this revision 20 individuals from Macquarie Island. Lineages from the Falkland/Malvinas Islands were not considered in this revision, owing to

the lack of material. Specimens were fixed in ethanol (95%) for molecular analyses, and phylogenetic reconstructions included ≥ 10 individuals for each recognized *Laevitorina* lineage. Each individual was photographed for morphological analyses. Non-type material examined, and nucleic acids are available in the collection of the Laboratorio de Genómica y Ecología Molecular Antártica y sub-Antártica (LAGEMAS) at Universidad Austral de Chile, Valdivia, Chile. The respective voucher and accession numbers are listed by [González-Wevar et al. 2022](#).

Shell and radular morphology

The identification of species was done following [Arnaud and Bandelt \(1976\)](#), [Reid \(1989\)](#), and [Engl \(2012\)](#) and through the original descriptions ([A. Gould 1849](#), [von Martens and Pfeffer 1886](#), [E. A. Smith 1902](#), [Preston 1912, 1916](#)). Shell dimensions were measured using the Micrometrics® SE software in an OLYMPUS® CX31 stereomicroscope attached to a camera. Morphological measurements were taken following [Reid \(2007\)](#) and included the following: shell height (H), corresponding to the maximum dimension parallel to the axis of coiling; shell breadth (B), corresponding to the maximum dimension perpendicular to H; and the length of the aperture (LA), corresponding to the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip. Shell shapes of the analysed species were quantified as the ratios, H/B and H/LA [relative spire height (SH)]. Other characteristics, such as sculpture and shell coloration, were also examined.

In order to avoid ontogenetic variation in shell and radular morphology, we included in the analyses only adult specimens. Radulae of *Laevitorina* specimens were dissected and placed in sodium hydroxide solution (10%) for 6 h at 50°C before being rinsed with distilled water. Radular morphology was examined by scanning electron microscopy (SEM) at Universidad Austral de Chile Microscopy Center and compared with previous radular analyses of other *Laevitorininae* species. Other radulae were incubated in household bleach for 30 s, rinsed in distilled water, and photographed using a stereomicroscope.

Molecular phylogenetics

We sequenced fragments of the mitochondrial cytochrome *c* oxidase subunit I (COI) and the nuclear 28S rRNA. Primers and the PCR conditions and sequencing procedures followed [González-Wevar et al. \(2022\)](#). Sequences were assembled and edited independently using GENEIOUS v.5.1.7 ([Kearse et al. 2017](#)) and MEGA X ([Kumar et al. 2018](#)), whereas alignments and the base composition of nucleotide sequences used MUSCLE ([Edgar 2004](#)) in MEGA. *Laevitorina* sequences are available in GenBank under the following accession numbers: COI (MZ321820–MZ321864) and 28S rRNA (MZ381414–MZ381445). *Laevitorina* phylogenies were estimated using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BA) following [González-Wevar et al. \(2022\)](#). Before the analyses, we executed a saturation test for both genes in DAMBE v.5 ([Xia 2013](#)). These analyses recorded little evidence of saturation for either of the analysed fragments. Based on the phylogenetic relationships obtained by [González-Wevar et al. \(2022\)](#), we selected as outgroup the sister genus *Laevilacunaria*.

Phylogenetic analyses were carried out using MEGA (MP and ML) and MRBAYES v.1.3.1 (BA) ([Huelsenbeck and Ronquist](#)

[2001](#)). Nucleotide substitution models for ML and BA were determined for each marker independently and for the concatenated dataset in jMODELTEST 2 ([Darriba et al. 2012](#)), using the Akaike information criterion (AIC) and the Bayesian information criterion (BIC), respectively. Nodal support values in MP and ML reconstructions were estimated using non-parametric bootstrap with 1000 pseudoreplicates ([Felsenstein 1981](#)). Likewise, Bayesian posterior probabilities were estimated through the Metropolis coupled Markov chain Monte Carlo (MCMC) algorithm following [González-Wevar et al. \(2022\)](#). Posterior probability densities were plotted as a maximum clade credibility tree using TREEANNOTATOR v.1.6.1 (<http://beast.bio.ed.ac.uk/TreeAnnotator>) and visualized using FIGTREE v.1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>).

RESULTS

As previously demonstrated ([González-Wevar et al. 2022](#)), the mitochondrial (COI) and nuclear (28S rRNA) reconstructions divided the nominal species *L. caliginosa* into several different species-level clades, which fell into two main monophyletic groups. Main clade I comprised species from the Strait of Magellan (*Laevilacunaria magellanica* sp. nov., *Laevilacunaria fueguina* sp. nov., and *Laevilacunaria pepita* sp. nov.), in addition to *L. venusta* from the Antarctic Peninsula and sub-Antarctic Islands (South Georgia, Marion, Crozet, Kerguelen, and Macquarie), and a presumptive species-level clade including the nominal Antarctic species *L. antarctica*, *L. umbilicata*, and *L. claviformis* ([Fig. 1](#); light red rectangle). Main clade II contained *L. caliginosa* s.s., with populations from Cape Horn (Beagle Channel, Navarino Island, Ushuaia, and Hornos Island), the Falkland/Malvinas Islands, and South Georgia, and the species *Laevilacunaria hicana* sp. nov. from Hornos Island ([Fig. 1](#); light blue rectangle).

SYSTEMATICS

Class Gastropoda Cuvier, 1795

Subclass Caenogastropoda Cox, 1960

Order Littorinimorpha Golikov & Starobogatov, 1975

Superfamily Littorinoidea [Children, 1834](#)

Family Littorinidae [Children, 1834](#)

Subfamily Laevitorininae [Reid, 1989](#)

Genus *Laevitorina* [Pfeffer, 1886](#)

Laevitorina Pfeffer, 1886: 81.

Type species: Littorina caliginosa [A. Gould, 1849](#) [type by subsequent designation ([Suter 1913](#))].

Laevitorina magellanica [González-Wevar & Rosenfeld](#) sp. nov.

([Fig. 2](#))

Laevitorina caliginosa – [Ríos and Gerdes 1997](#): 51; [Mutschke et al. 1998](#): 13; [Ingólfsson 2005](#): 176; [Rosenfeld et al. 2018](#): 9.

Laevitorina caliginosa L1 – [González-Wevar et al. 2022](#): 1527.

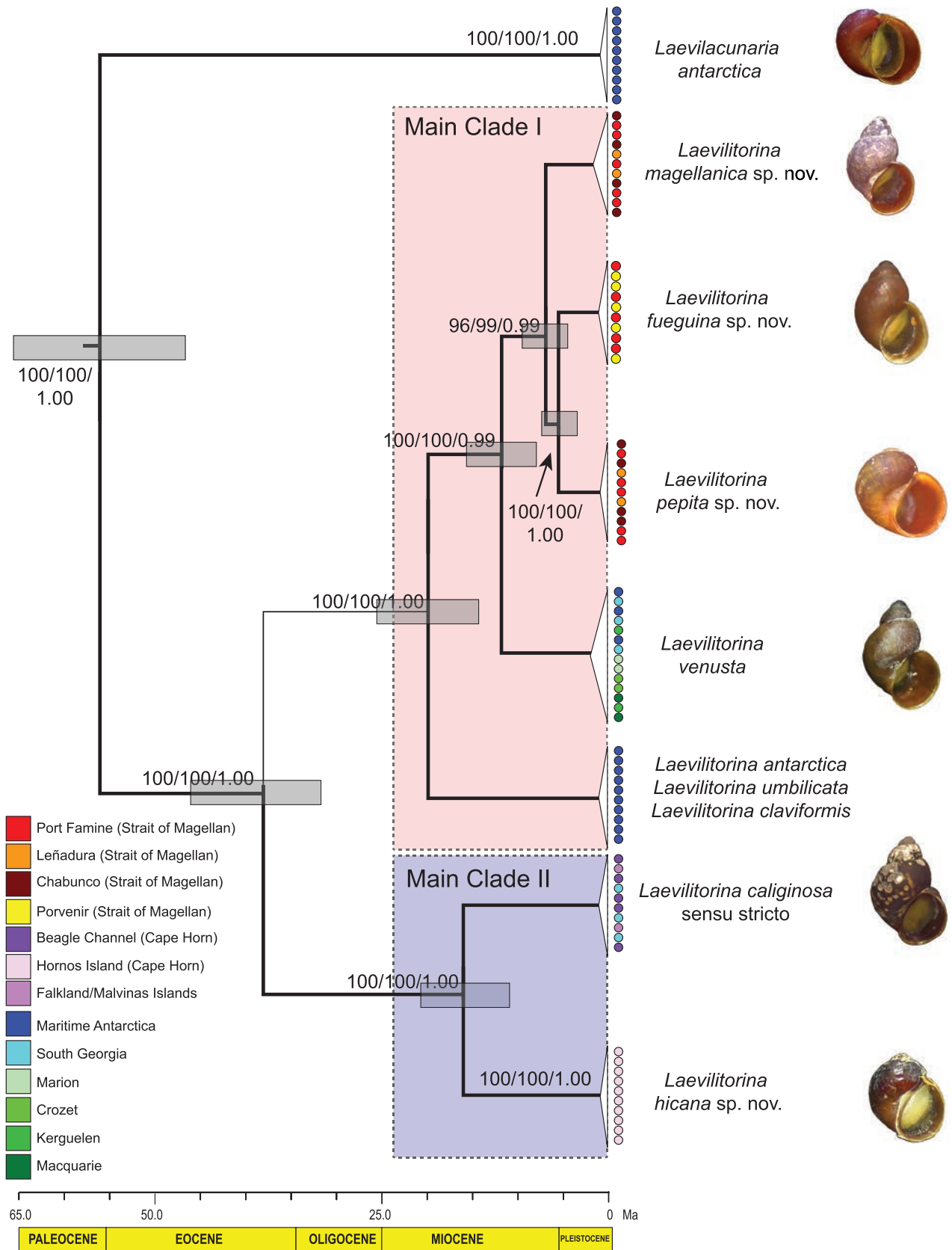


Figure 1. Bayesian maximum credibility tree of Laevilitorininae (*Laevilitorina* and *Laevilacunaria*) relationships based on mitochondrial DNA (*COI*) and nuclear DNA (28S rRNA) sequences. Bootstrap support values for maximum parsimony, maximum likelihood, and Bayesian posterior probabilities are shown above the nodes (in that order). Divergence time estimations were performed based on mitochondrial DNA sequences using a calibrated littorinid phylogeny following Reid et al. (2012).

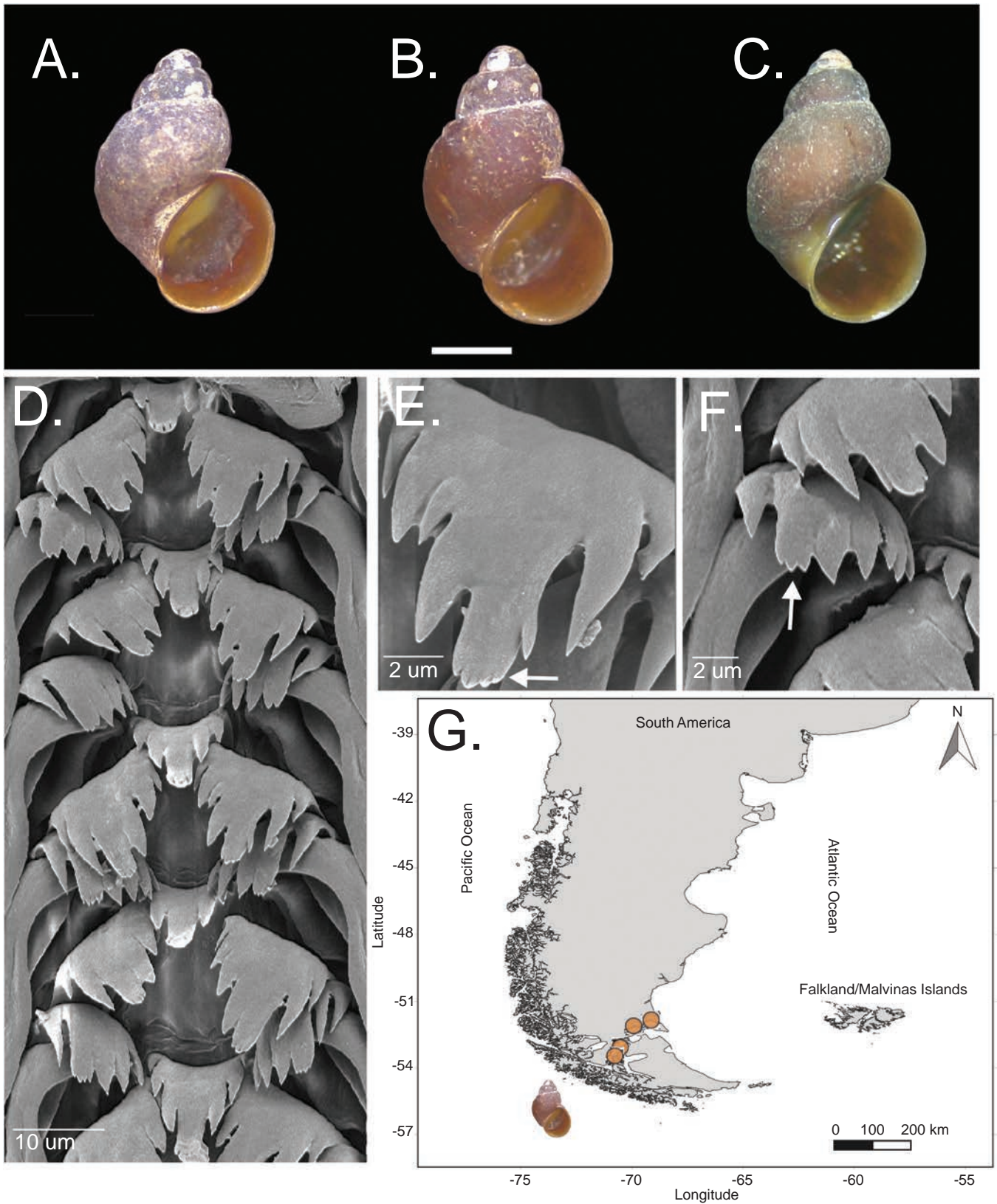


Figure 2. *Laevitorina magellanica*, Chabunco, Strait of Magellan, southern South America. Scale bars: 1 mm unless specified otherwise. A–C, shell morphology and coloration of *L. magellanica* in the Strait of Magellan. D–F, radular morphology (SEM), showing a general view (D), lateral view (E), and inner marginal showing denticles (white arrows; F). G, distribution of *L. magellanica* in the Strait of Magellan.

Zoobank registration: zoobank.org:act:BF37AA2E-2ADB-45F9-8EDA-6EAEA4B479A5.

Holotype: MNHNCL MOL-205424, ~25 km north of Punta Arenas (−52.987406°S, −70.812342°W), Strait of Magellan, Chile, 21 June 2015, collected by Claudio González-Wevar and Sebastián Rosenfeld.

Paratypes: MNHNCL MOL-205425; MNHNCL MOL-205426; MNHNCL MOL-205427; MNHNCL MOL-205428.

Description

Shell: Small (maximum height 4.03 mm), typical *Laevilitorina* morphology: fusiform with rounded to almost straight whorls, suture impressed, concave spire profile, apex blunt. Aperture rounded, slightly ovoid and $\leq 54\%$ of total H (Fig. 2A–C). Macroscopic spiral and axial sculpture absent. Multiple fine growth lines over whole shell. Columella smooth, inner lip barely reflected over narrow and shallow umbilicus; outer lip thin, simple; no evidence of thickening. Colour variable: reddish to dark or olive brown, often with small white spots, irregular in size and position. Operculum corneous. Mature H 3.01–4.06 mm (H/B = 1.25–1.53, SH = 1.77–2.01) (Supporting Information, Table S1).

External anatomy: Ventral area of foot orange, cephalic area black.

Radula: Rachidian: seven cusps, central cusp rounded, longest, in some cases with small denticles at end (Fig. 2D). First pair of flanking cusps pointed, about half size of central cusp; outer cusps smaller, also pointed. Lateral: six or seven cusps, main cusp more rounded with denticulate end, accompanied by two pointed outer cusps and three or four inner ones (Fig. 2E). Inner marginal: six or seven cusps, pointed and of similar size, except for broader main cusp, which terminates with denticulate end (Fig. 2F). Outer marginal: nine thin and pointed cusps.

Holotype dimensions: Length 3.19 mm, width 2.34 mm.

Depositories: Holotype MNHNCL MOL-205424. Museo Nacional de Historia Natural, Chile.

Type locality: Chabunco (52°59'14.66"S, 70°48'44.43"W), Strait of Magellan, Chile (Fig. 2G).

Habitat: Rocky intertidal shores of the central micro-basin of the Strait of Magellan. *Laevilitorina magellanica* is commonly found in rock crevices, underneath boulders and/or also on the beds of the mytilid *Perumytilus purpuratus* (Lamarck, 1819).

Material studied: Faro San Isidro, Strait of Magellan (−53.785572°S, −70.973522°W), $n = 30$; Port Famine, Strait of Magellan (−53.609464°S, −70.931500°W), $n = 80$; Punta Carrera, Strait of Magellan (−53.586367°S, −70.923372°W), $n = 50$; Leñadura, Strait of Magellan (−53.213428°S, −70.938350°W), $n = 50$; Chabunco (−52.987496°S, −70.812342°W), $n > 100$; Possession Bay (−52.232083°S, −69.297419°W), $n = 20$ (Fig. 2G).

Etymology: The type locality of this species is the Strait of Magellan.

Remarks: In general, owing to the significant morphological plasticity recorded in the nominal species *L. caliginosa* (Reid 1989; Engl 2012), this new species was previously reported from the Strait of Magellan as *L. caliginosa*. Nevertheless, in terms of morphology, this new *Laevilitorina* species is characterized by its small size. In contrast to *L. caliginosa* and *L. fueguina*, which exceed 5 mm in shell height, the maximum size of *L. magellanica* does not exceed 4.10 mm. Moreover, *L. magellanica* differs from *L. fueguina* by having a larger spire size and slightly more convex whorls and differs from *L. caliginosa* by having a larger aperture length. Moreover, *L. magellanica* differs from other Antarctic and sub-Antarctic *Laevilitorina* in having denticles on the main cusps of the lateral and inner marginal teeth (Fig. 2E, F).

***Laevilitorina fueguina* González-Wevar & Rosenfeld sp. nov.**

(Fig. 3)

Laevilitorina caliginosa L2 – González-Wevar et al. 2022: 1527.

Zoobank registration: zoobank.org:act:D3644473-71B7-4D0E-B8B7-65DFC0761650.

Holotype: MNHNCL MOL-205434, ~100 km south of Porvenir (−53.313637°S, −70.458217°W), Tierra del Fuego, Strait of Magellan, 22 May 2016, collected by Claudio González-Wevar and Sebastián Rosenfeld.

Paratypes: MNHNCL MOL-205435; MNHNCL MOL-205436; MNHNCL MOL-205437; MNHNCL MOL-205438.

Description

Shell: Small (maximum height 5.84 mm), typical *Laevilitorina* morphology: fusiform with rounded to almost convex whorls, suture impressed, concave spire profile, apex blunt. Macroscopic spiral and axial sculpture absent, but fine growth lines on whole shell. Aperture ovoid, expanded and $\leq 56\%$ of total H (Fig. 3A–C). Peristome continuous, columella smooth and oblique, inner lip barely reflected over narrow and shallow umbilicus; outer lip thin, simple, with no evidence of thickening. Teleoconch opaque but last whorl slightly translucent. Colour uniformly reddish brown to dark brown (Fig. 3A–C). Operculum corneous. Mature H 4.70–5.84 mm (H/B = 1.00–1.41, SH = 1.60–2.00) (Supporting Information, Table S2).

External anatomy: Ventral area of foot orange, cephalic area black.

Radula: Rachidian: shows seven cusps, central cusp longest (Fig. 3D), sometimes rounded with small denticles at end (Fig. 3E). First pair of flanking cusps pointed; outer cusps much smaller, pointed or rounded. Lateral: six or seven cusps (Fig. 3F), main cusp more rounded, accompanied by two or three pointed outer cusps and three continuously smaller inner cusps. Inner marginal: six or seven cusps, of similar size, main cusp rounded, accompanied by one or two pointed outer cusps and four rounded inner cusps. Outer marginal: seven to nine thin and pointed cusps.

Holotype dimensions: Length 5.49 mm, width 4.25 mm.

Depositories: Holotype MNHNCL MOL-205434. Museo Nacional de Historia Natural, Chile.

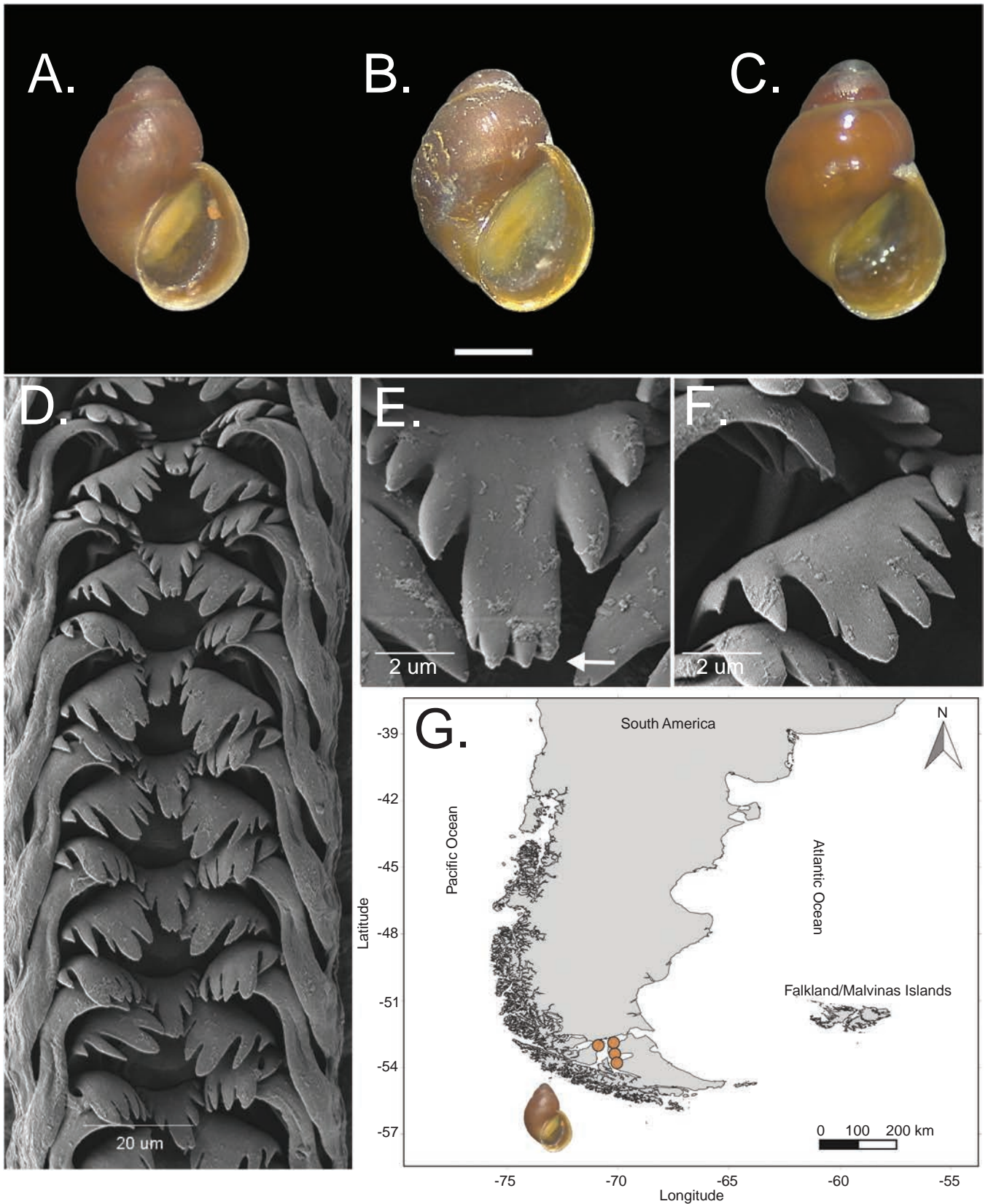


Figure 3. *Laevitorina fueguina*, Boquerón and Chabunco, Tierra del Fuego and Brunswick Peninsula, southern South America. Scale bars: 1 mm unless specified otherwise. A–C, shell morphology and coloration of *L. fueguina* from Boquerón, Tierra del Fuego (A, B) and from Chabunco, Strait of Magellan (C). D–F, radular morphology (SEM), showing a general view (D), rachidian showing denticles (white arrow; E), and lateral view (F). G, distribution of *L. fueguina* in the Strait of Magellan.

Type locality: Boquerón, Tierra del Fuego (−53.753758°S, −70.143961°W), Strait of Magellan, Chile (Fig. 3G).

Habitat: Rocky intertidal to subtidal shores on both sides of the Strait of Magellan, including Tierra del Fuego (Fig. 3G).

Material studied: Chabunco (−52.987406°S, −70.812342°W), *n* = 20; Santa María Bay, Tierra del Fuego (−53.392628°S, −70.373514°W), *n* = 30; Boquerón, Tierra del Fuego (−53.753758°S, −70.143961°W), *n* = 40.

Etymology: The type locality of this *Laevitorina* species is Tierra del Fuego Island in the Strait of Magellan.

Remarks: *Laevitorina fueguina* is characterized by its reddish-brown colour (Fig. 3A–C) and the presence of denticles on the main teeth of the rachidian, which may vary in number from two to four (Fig. 3D, E). The coloration of *L. fueguina* is similar to that of the Antarctic nominal species *L. claviformis* and *L. umbilicata*. Shell morphology of *L. fueguina* resembles that of *L. caliginosa* s.s. and *L. magellanica*, but levels of molecular divergence, species delimitation analyses, radular morphology, shell coloration, and geometric morphometrics differentiate it as a distinct evolutionary unit.

***Laevitorina pepita* González-Wevar & Rosenfeld sp. nov.**

(Fig. 4)

Laevitorina caliginosa L3 – González-Wevar et al. 2022: 1527.

Zoobank registration: zoobank.org:act:C823DE09-7B80-427F-A2E9-2CE096719C69.

Holotype: MNHNCL MOL-205429, ~25 km north of Punta Arenas (−52.987406°S, −70.812342°W), Strait of Magellan, 21 June 2015, collected by Claudio González-Wevar and Sebastián Rosenfeld.

Paratypes: MNHNCL MOL-205430; MNHNCL MOL-205431; MNHNCL MOL-205432; MNHNCL MOL-205433.

Description

Shell: Small (maximum length 3.8 mm), fusiform with rounded to convex whorls, suture impressed, concave spire profile, apex blunt. Aperture ovoid, between 66% and 73% of total H (Fig. 4A–C; Supporting Information, Table S3). Multiple fine growth lines, sometimes with soft spiral colour bands on the last whorl (Fig. 4A). Columella smooth, inner lip barely reflected over narrow umbilicus, outer lip thin, simple, and with no evidence of thickening. Teleoconch opaque, but last whorl slightly translucent. Colour very variable: creamy, pale brown, brown, and olive green. Some individuals have small white spots, irregular in size and position. Operculum corneous. Mature H 2.4–3.8 mm (H/B = 1.01–1.09, SH = 1.39–1.54) (Supporting Information, Table S3).

External anatomy: Ventral area of foot orange, cephalic area black.

Radula: Rachidian: seven cusps, central cusp long, rectangular and pointed (Fig. 4D, E). First pair of flanking cusps pointed; outer cusps much smaller, pointed or rounded. Lateral: five or

six cusps, main cusp rectangular and pointed, accompanied by one smaller pointed outer cusp and three continuously smaller inner cusps. Inner marginal: six cusps, main cusp pointed and rectangular (Fig. 4F), accompanied by one smaller pointed outer cusp and four pointed inner cusps of similar size. Outer marginal: seven or eight thin and pointed cusps.

Holotype dimensions: Length 3.73 mm, width 3.17 mm.

Depositories: Holotype MNHNCL MOL-205429. Museo Nacional de Historia Natural, Chile.

Type locality: Chabunco (−52.987406°S, −70.812342°W), Strait of Magellan, Chile (Fig. 4G).

Habitat: Rocky intertidal to subtidal shores at the northern side of the Strait of Magellan (Fig. 4G).

Material studied: Faro San Isidro, Strait of Magellan (−53.785572°S, −70.973522°W), *n* = 30; Port Famine, Strait of Magellan (−53.699404°S, −70.931500°W), *n* = 80; Punta Carrera, Strait of Magellan (−53.586367°S, −70.923372°W), *n* = 50; Leñadura, Strait of Magellan (−53.213428°S, −70.938350°W), *n* = 20; Chabunco, Strait of Magellan (−52.987406°S, −70.812342°W), *n* = 60; Possession Bay, Strait of Magellan (−52.232083°S, −69.297419°W), *n* = 20.

Etymology: The morphology of *L. pepita* resembles a small seed = ‘pepita’ in Spanish.

Remarks: Among the Strait of Magellan species, *L. pepita* exhibits the most distinct morphology and coloration (Fig. 4A–C). This taxon exhibits a great variability of shell coloration, with the presence of spiral colour bands. It has a very short spire, and the last whorl is more globose than in the other South American *Laevitorina* species. The radula of *L. pepita* is similar to that of *L. magellanica*, but the latter may exhibit denticles on the main cusps of the lateral and marginal teeth. This species, like *L. magellanica*, inhabits the intertidal zone and is also found in empty shells of the barnacle *Notochthalamus scabrosus* (Darwin, 1854).

***Laevitorina venusta* Pfeffer, 1886**

(Fig. 5)

Hydrobia caliginosa – Smith, 1879: 173, pl. 9, fig. 8; Watson 1886: 613.

Laevitorina venusta – von Martens and Pfeffer 1886: 85, pl. 1, fig. 9a, b; Castellanos 1989: 18; Zelaya 2005: 118; Rosenfeld et al. 2022: 66, fig. 1c.

Littorina (*Laevitorina*) *coriacea* – Melvill and Standen 1907: 130, pl. 1, fig. 2.

Laevitorina coriacea – Engl, 2012: 103.

Laevittorina caliginosa – E. Lamy, 1905: 478; E. Lamy, 1906: 112; E. Lamy, 1911: 8.

Laevitorina caliginosa var. *fulleri* – Gaillard, 1971.

Laevitorina caliginosa – Thiele, 1912: 235; Powell, 1957: 128; Arnaud and Bandel 1976: 215, pl. 1, fig. 1; Cantera and Arnaud 1985: 40; Arnaud et al. 1986: 13; Jazdzewski et al. 2001: 93; Waller et al. 2006: 662; Engl 2012: 102; Amsler et al. 2015: 1175; Aghmich et al. 2016: 193; Martín et al. 2016: 212; Schrödl

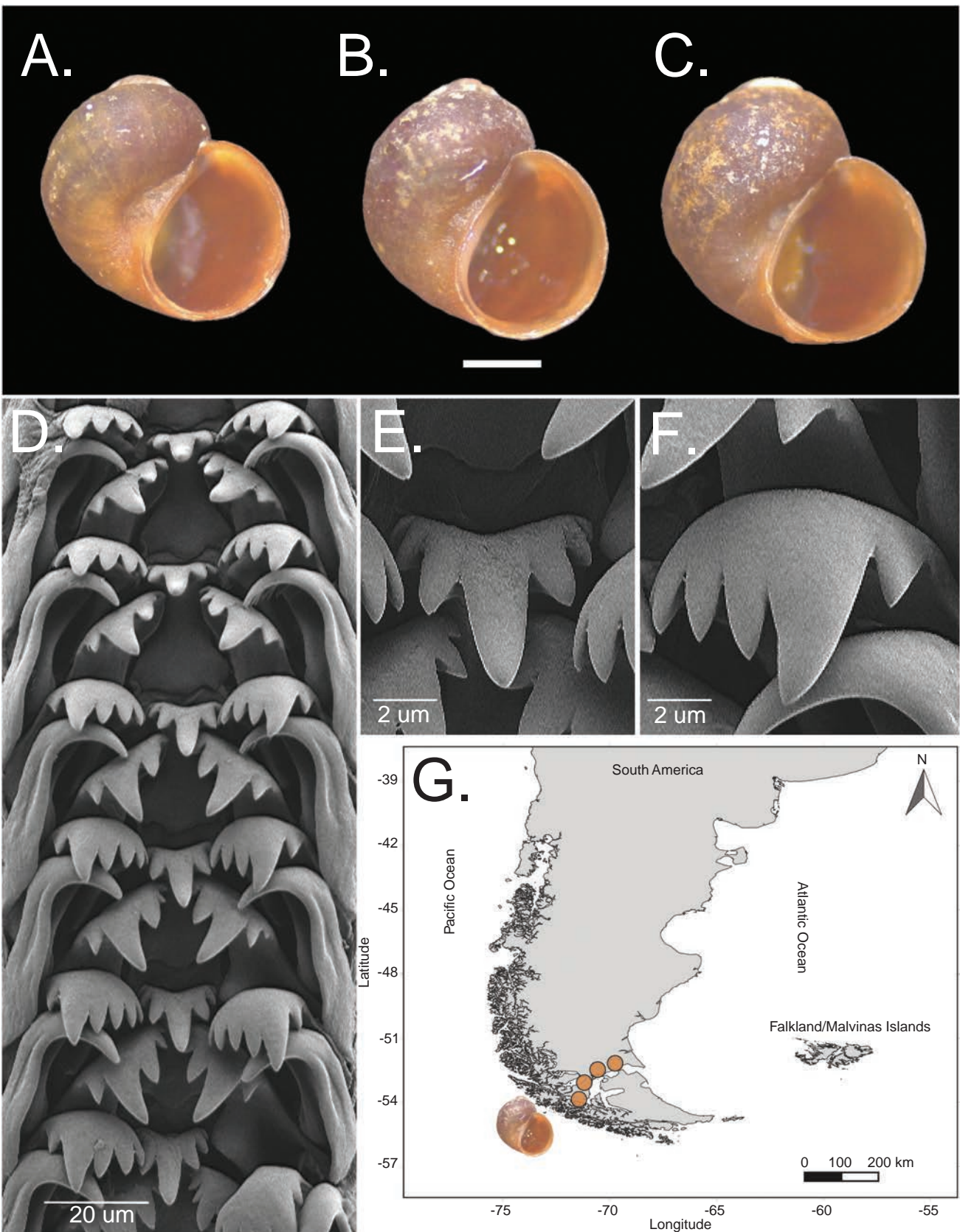


Figure 4. *Laevitorina pepita*, Chabunco, Strait of Magellan, southern South America. Scale bars: 1 mm unless specified otherwise. A–C, shell morphology and coloration of specimens collected at Chabunco, Strait of Magellan. D–F, radular morphology (SEM), showing a general view (D), rachidian (E), and inner marginal (F). G, the distribution of *L. pepita* in the Strait of Magellan.

et al. 2016: 40; Rosenfeld et al. 2017: 4; Valdivia et al. 2020: 5; Amsler et al. 2022: 248.

Laevilitorina caliginosa L4 – González-Wevar et al. 2022: 1527.

Description

Shell: Small (maximum height 8 mm), typical *Laevilitorina* morphology: fusiform, with rounded to almost convex whorls, suture impressed, concave spire profile, apex blunt (Fig. 5A–G). Aperture varies from rounded to ovoid, between 46% and 55% of total H (Supporting Information, Table S4). Macroscopic spiral and axial sculpture absent, but multiple fine growth lines cover shell. Columella smooth, inner lip barely reflected over narrow and shallow umbilicus, outer lip thin, simple and with no evidence of thickening. Teleoconch opaque, but the last whorl slightly translucent. Significant colour variability characterizes populations of *L. venusta*, ranging across dark red, grey, brown, dark brown, and black (Fig. 5A–G). Some individuals uniformly coloured, others with small white spots, irregular in size and position. Operculum corneous. Mature H 3.2–8 mm (H/B = 1.21–1.40, SH = 1.66–1.98) (Supporting Information, Table S4).

External anatomy: Ventral area of foot orange, cephalic area black.

Radula: Rachidian: five to seven cusps, the central cusp is long, rectangular and very rounded (Fig. 5H–J), sometimes with a few small denticles at the end (Fig. 5I); first pair of flanking cusps pointed; outer cusps may be present as low, pointed cusps. Lateral: six or seven cusps, main cusp largest, broadest and rounded, accompanied by two smaller, pointed outer cusps and three or four continuously smaller pointed inner cusps. Inner marginal: five or six cusps, main cusp pointed and rectangular, accompanied by one or two smaller, very pointed outer cusps and four pointed inner cusps of similar size. Outer marginal: eight or nine thin and pointed cusps.

Habitat: Rocky intertidal to subtidal shores of the Antarctic Peninsula, the South Shetland Islands, and Signy Island, in addition to sub-Antarctic Islands including South Georgia, Marion, Crozet, Kerguelen, and Macquarie (Fig. 5K).

Material studied: Penguin Island, South Shetland Islands (–62.103992°S, –57.939050°W); Arctowski Base, Admiralty Base, King George Island, South Shetland Islands (–62.158336°S, –58.467525°W); Fildes Bay, King George Island, South Shetland Islands (–62.207967°S, –58.956914°W), *n* = 100; Rizopatrón Base, Coppermine Cove, Robert Island, South Shetland Islands (–62.390567°S, –59.659075°W), *n* = 50; Hannah Point, Livingstone Island, South Shetland Islands (–62.651181°S, –60.594664°W), *n* = 50; Prat Base, Greenwich Island, South Shetland Islands (–62.479594°S, –59.669044°W), *n* = 100; Deception Island, South Shetland Islands (–62.930139°S, –60.606333°W), *n* = 40; Yelcho Station, Doumer Island, South Bay, Anvers Island, Antarctic Peninsula (–64.893792°S, –63.562572°W), *n* = 50; Carvajal Base, Adelaide Island, Antarctic Peninsula (–67.761989°S, –68.915303°W), *n* = 50; Avian Island, Marguerite Bay, Antarctic Peninsula (–67.772225°S, –68.897947°W), *n* = 100; O’Higgins Base, Covadonga Bay, Antarctic Peninsula (–63.320436°S, –57.898353°W), *n* = 80; Signy Research

Station, Signy Island, South Orkneys Islands (–60.722839°S, –45.587817°W), *n* = 30; Cumberland Bay, South Georgia (–54.283364°S, –36.486956°W), *n* = 100; Ships Cove, Marion Island (–46.854506°S, –37.845100°E), *n* = 10; Baie American, Crozet Islands (–46.426181°S, 51.861806°E), *n* = 50; Port-aux-Français, Kerguelen Islands (–49.352733°S, 70.218303°E), *n* = 100; Port Christmas, Kerguelen Islands (–48.677607°S, 69.023604°E), *n* = 30; Îles du Prince-de-Monaco, Kerguelen Islands (–49.606278°S, 69.235900°E), *n* = 30; Garden Cove, Macquarie Island (–54.501287°S, 158.936221°E), *n* = 20.

Remarks: Several specimens in the study by González-Wevar et al. (2022) collected from South Georgia that fell in the L4 clade of *L. caliginosa* s.l. were characterized by a short spire and 4.5 convex whorls, with the aperture height occupying little more than half of the total shell height; the columellar callus was sharp, white, and expanded towards the umbilicus (morphological characteristic highlighted by von Martens and Pfeffer 1886), all features consistent with the original description of *L. venusta* (Pfeffer, 1886). Moreover, the type locality of *L. venusta* is South Georgia. Thus, in this revision we conclude that the L4 ‘caliginosa’ lineage of González-Wevar et al. (2022) is, in fact, *L. venusta*. The genetic data show that this species also includes populations from maritime Antarctica (South Shetlands Islands and the Antarctic Peninsula), in addition to geographically distant sub-Antarctic Islands (South Georgia, Marion, Crozet, Kerguelen, and Macquarie). *Laevilitorina venusta* and *L. caliginosa* s.s. are the *Laevilitorina* species with broadest morphological variability and geographical distributions. We also include *L. coriacea* (Melvill and Standen 1907) from the South Orkney Islands as a synonym; previously (e.g. Engl 2012), this taxon was considered synonymous with *L. caliginosa*.

Laevilitorina caliginosa (A. Gould, 1849)

(Fig. 6)

Littorina caliginosa – A. Gould, 1849: 83; A. Gould 1852: 198; A. Gould 1856: pl. 14 [sic.], fig. 240.

Laevilitorina caliginosa – von Martens and Pfeffer 1886: 81, pl. 1, fig. 8a–d; Tryon 1887: 254, pl. 46, fig. 29; Melvill and Standen 1907: 130; Strebel 1908: 50; Melvill and Standen 1912: 348; Melvill and Standen 1914: 118; Powell 1951: 107, pl. 1, fig. 26; Guzmán and Ríos 1981: 262; Ríos and Guzmán 1982: 215; Adami and Gordillo 1999: 186; Zelaya 2005: 118, fig. 21; Ojeda et al. 2014: 499; González-Wevar et al. 2022: 7; Rosenfeld et al. 2022: 66, fig. 1a.

Littorina (*Laevilitorina*) *caliginosa* – Melvill and Standen 1907: 130; Melvill and Standen 1912: 348.

Paludestrina caliginosa – Rochebrune and Mabille 1889: 42.

Laevilittorina caliginosa – Pelseneer, 1903: 8.

Laevilitorina cf. *caliginosa* – Dell, 1971: 204.

Laevilitorina caliginosa L5 – González-Wevar et al. 2022: 1527.

Material studied: Puerto Williams, Beagle Channel (–54.932414°S, –67.603289°W), *n* = 50; Lapataia Bay, Beagle Channel (–54.849706°S, –68.478319°W), *n* = 25; Hornos Island, Cape Horn (–55.967394°S, –67.218736°W), *n* = 50; Hookers Point, Falkland/Malvinas Islands (–51.700953°S, –57.780369°W), *n* = 50; Cumberland Bay, South Georgia (–54.283364°S, –36.486956°W), *n* > 30.

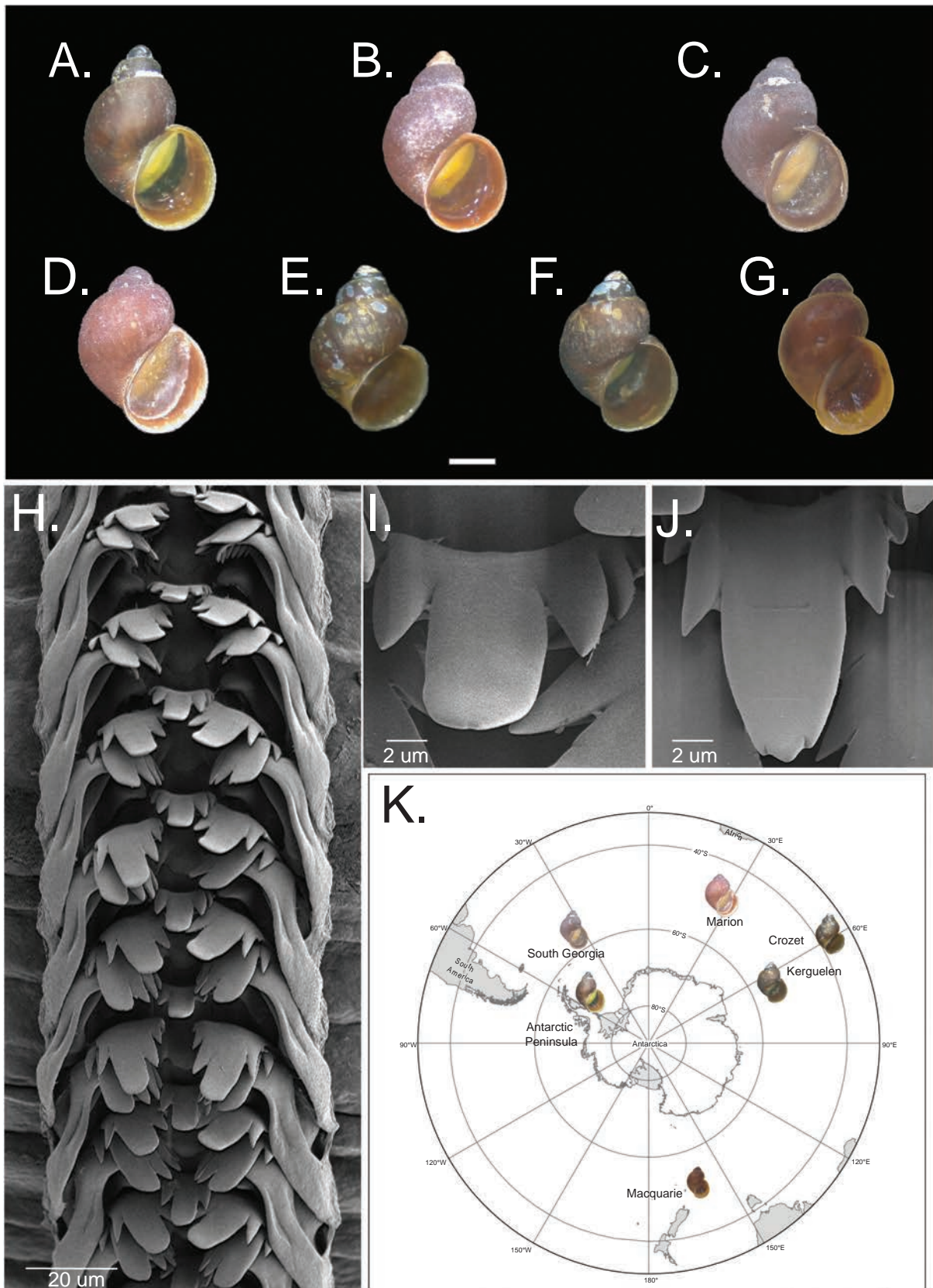


Figure 5. *Laevitorina venusta*, Southern Ocean. Scale bars: 1 mm unless specified otherwise. A–G, variation in shell morphology and coloration of the species across its distribution in different provinces of the Southern Ocean. The specimens of *L. venusta* are from: Greenwich Island, South Shetland Islands, Antarctic Peninsula (A); Covadonga Bay, the Antarctic Peninsula (B); South Georgia (C); Marion Island (D); Crozet Island (E); Kerguelen Island (F); and Macquarie Island (G). H–J, radular morphology (SEM), showing a general view (H), rachidian (I), and rachidian from an individual from Antarctica showing small denticles (J). K, distributional pattern of *L. venusta* across the Southern Ocean.

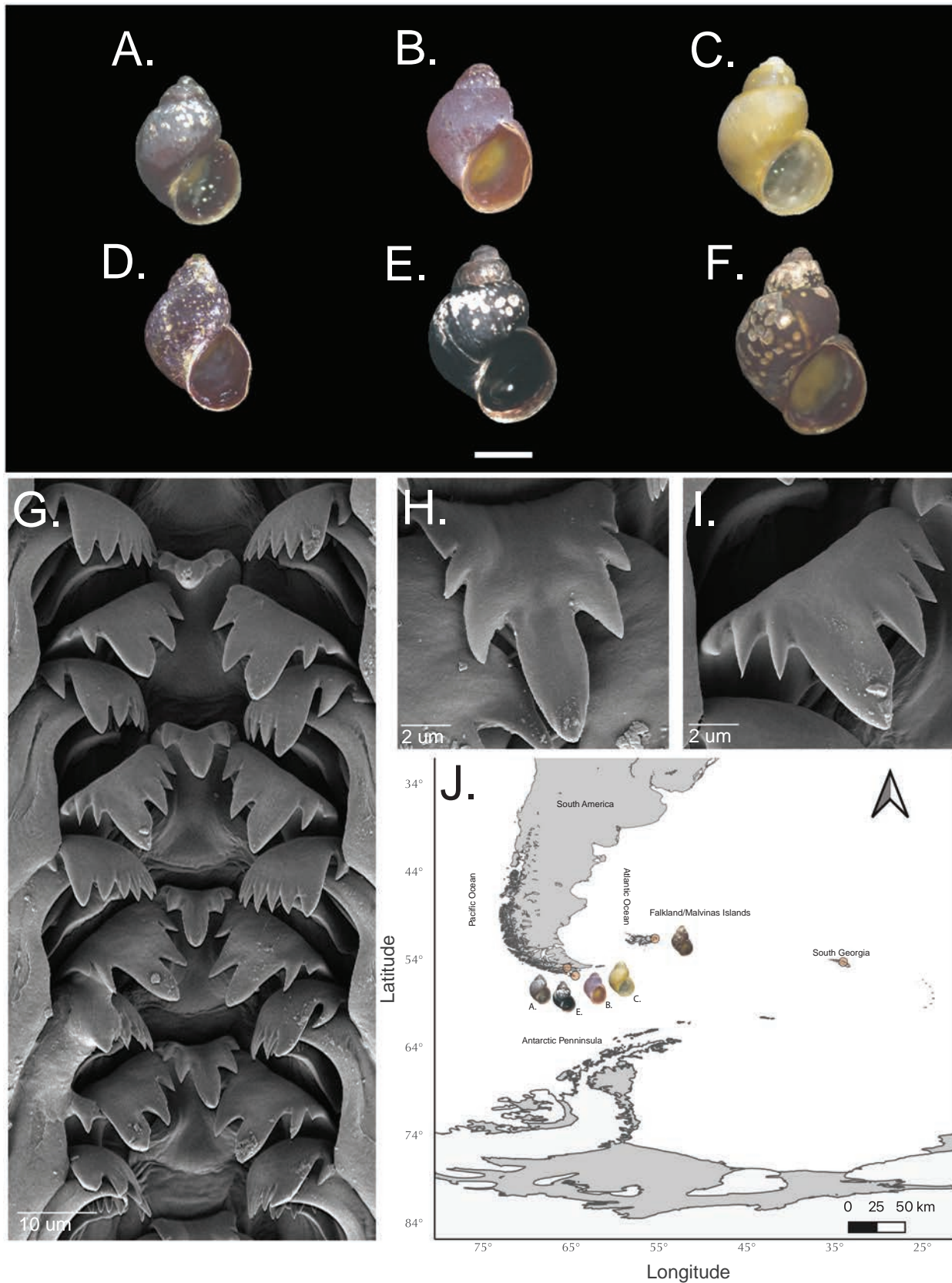


Figure 6. *Laeviltorina caliginosa*, Southern South America, South Georgia, and Falkland/Malvinas Islands. Scale bars: 1 mm unless specified otherwise. A–F, specimens of *L. caliginosa* from: Caleta Paula, Beagle Channel (A); Robalo Bay, Beagle Channel (B); Hornos Island (C); Puerto Williams, Beagle Channel (D); Ushuaia, Beagle Channel (E); and Falkland/Malvinas Islands (F). G–I, radular morphology (SEM), showing a general view (G), rachidian (H), and lateral view (I). J, distribution of *L. caliginosa* in the southern tip of South America, the Falkland/Malvinas Islands, and South Georgia.

Description

Shell: Small (maximum length 6.48 mm), typical *Laevilitorina* morphology: fusiform, with rounded to almost convex whorls, suture impressed, concave spire profile, apex blunt. Aperture varies from rounded to ovoid, between 47% and 51% of total H (Fig. 6A–F). Macroscopic spiral and axial sculpture absent, but multiple fine growth lines cover the surface of the shell. Columella smooth, inner lip barely reflected over narrow and shallow umbilicus, outer lip thin, simple, and no evidence of thickening. Teleoconch opaque, but last whorl slightly translucent. Significant colour variability among different sites: creamy-white (Fig. 6C), brown (Fig. 6B), dark brown, or black (Fig. 6A, D–F). Small and irregular white spots visible in all analysed specimens. Operculum corneous. Mature H 3.5–6.49 mm. (H/B = 1.25–1.65, SH = 1.92–2.14) (Supporting Information, Table S5).

Radula: Rachidian: five to seven cusps, central cusp long, rectangular, pointed; first pair of flanking cusps pointed; outer cusps may be present as low, pointed cusps (Fig. 6G, H). Lateral: five or six cusps, main cusp being the largest, broadest and rounded, accompanied by two smaller pointed outer cusps and two or three continuously smaller inner cusps (Fig. 6I). Inner marginal: seven cusps, main cusp pointed and rectangular, accompanied by one smaller pointed outer cusp and five pointed inner cusps of similar size. Outer marginal: 12–16 thin and short cusps.

Habitat: Rocky intertidal to subtidal shores across the southern tip of South America in the Cape Horn region, including the Beagle Channel, Hornos Islands, Falkland/Malvinas Islands, and South Georgia, also associated with kelps.

Remarks: Shell shape and coloration are variable among the specimens collected from different localities in southern South America, the Falkland/Malvinas Islands, and South Georgia. For instance, individuals from Hornos Island collected from crustose algae exhibited creamy-white and brownish green coloration with white spots, mimicking their habitat. In contrast, specimens collected from bare boulders at Puerto Williams and Ushuaia (Beagle Channel) were dark green, brown, grey, and black with white spots. In the original description of the species (A. Gould 1849; see also A. Gould 1852), the specimens presented a shell with a green-brown coloration and an aperture almost 50% of the total height of the shell (A. Gould 1856). This original description is consistent with specimens collected in the area of Cape Horn and the Beagle Channel, near the type locality of Terra del Fuego (A. Gould 1849, 1852; not Kerguelen Island, as reported by Suter 1913, Powell 1951, 1955a, b; 1979). Individuals from these localities were the only ones that exhibited an average LA/H of < 50% (0.49 ± 0.01) (Supporting Information, Table S5). Together, the morphological characteristics and the location of collection sites allow us to identify the molecular *Laevilitorina* L5 lineage as *L. caliginosa* s.s.

Interestingly, Powell (1951) provided one of the first descriptions of the radular morphology of *L. caliginosa*, using specimens from South Georgia, and the radula configuration coincides with our observations, especially in the shape of the central rachidian tooth, which is long, rectangular, but with a sharp termination (Fig. 6H). In contrast, the central tooth of *L. venusta* individuals from Kerguelen is rectangular but rounded (Arnaud and Bandel 1976; this study).

Laevilitorina hicana González-Wevar & Rosenfeld sp. nov.

(Fig. 7)

Laevilitorina caliginosa L6 – González-Wevar et al. 2022: 1527.

Zoobank registration: zoobank.org:act:3EF20FE5-7CEF-48A2-B85F-9E1FB7099152.

Material examined

Holotype: MNHNCL MOL-205439, Hornos Island (–55.965656°S, –67.251533°W), Cape Horn, 20 November 2016, collected by Sebastián Rosenfeld.

Paratypes: MNHNCL MOL-205440; MNHNCL MOL-205441.

Description

Shell: Small (maximum shell height 3.73 mm), fusiform, with rounded to almost convex whorls, suture impressed, concave spire profile, apex blunt. Aperture ovoid and $\leq 64\%$ of total H (Fig. 7A–C). Macroscopic spiral and axial sculpture absent, but multiple fine growth lines cover shell. Columella smooth, inner lip barely reflected over narrow and shallow umbilicus, outer lip thin, simple, and no evidence of thickening. Teleoconch opaque, but last whorl slightly translucent. Colour dark brown and black with small white spots, irregular in size and position. Operculum corneous. Mature H 3.73–1.20 mm (H/B = 1.05–1.36, SH = 1.48–1.75 mm) (Supporting Information, Table S6).

External anatomy: Ventral area of the foot orange, cephalic area black.

Radula: Rachidian: five cusps, central cusp long, rectangular, and pointed (Fig. 7D). First pair of flanking cusps pointed, outer cusps smaller and pointed. Lateral: five cusps, main cusp long, rectangular, and pointed, accompanied by two smaller pointed outer cusps and two continuously smaller inner cusps. Inner marginal: five cusps, main cusp pointed and rectangular, accompanied by one smaller, pointed outer cusp and three pointed inner cusps (Fig. 7E). Outer marginal: 10 or 11 thin and pointed cusps (Fig. 7F).

Holotype dimensions: Length 3.73 mm, width 2.74 mm.

Depositories: Holotype MNHNCL MOL-205439. Museo Nacional de Historia Natural, Chile.

Type locality: Hornos Island (–55.965656°S, –67.251533°W), Cape Horn, Chile.

Habitat: Rocky intertidal shores of Hornos Island, inside empty barnacle shells (Fig. 7G).

Material studied: Hornos Island (–55.965656°S, –67.251533°W), $n = 30$.

Etymology: The type locality of this new *Laevilitorina* species is part of the traditional territory of the Yagán (Yaghan) people. In the Yagán language, the word ‘hica’ means sea.

Remarks: In terms of morphology, this *Laevilitorina* differs from the other Cape Horn species (*L. caliginosa* s.s.) by exhibiting a

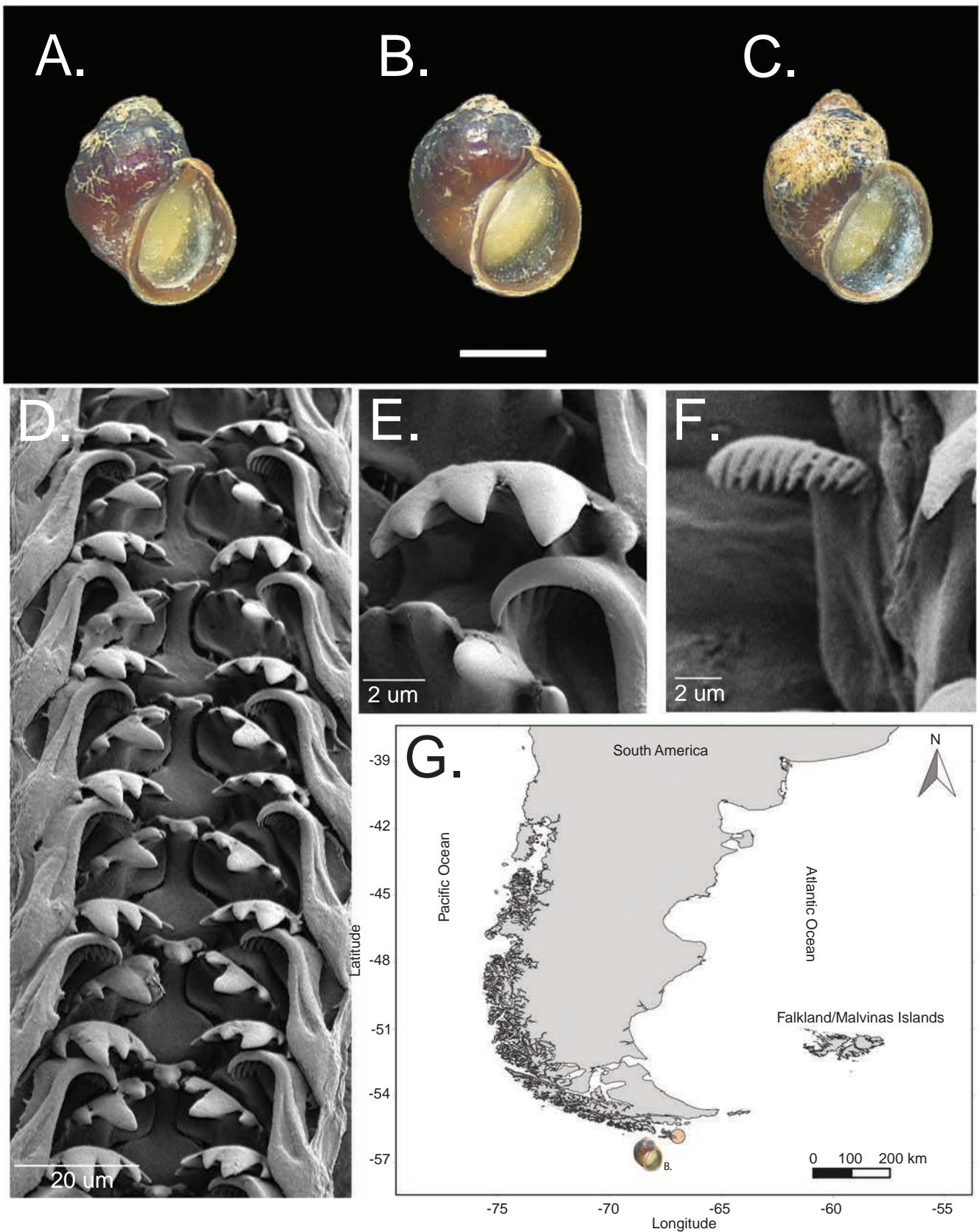


Figure 7. *Laeviltorina hicana*, Hornos Island, southern South America. Scale bars: 1 mm unless specified otherwise. A–C, shell morphology and coloration of specimens collected from Hornos Island. D–F, radular morphology (SEM), showing a general view (D), lateral view (E), and outer marginal (F). G, distribution of *L. hicana* at Hornos Island, Cape Horn, southern South America.

globose shell and by having an aperture that occupies on average $\leq 64\%$ of total shell height (Supporting Information, Table S6). *Laevilitorina hicana* is morphologically more similar to *L. pepita* from the Strait of Magellan, but the latter has an even more globose shell and an LA/H ratio of 0.68 ± 0.03 . Moreover, *L. pepita* sometimes has spiral colour bands on the last whorl. The current species is rare: of all the areas we have been able to sample around the Magellanic province, it was recorded only at Hornos island. *Laevilitorina hicana*, like *L. magellanica* and *L. pepita*, can be found inside empty barnacle shells.

DISCUSSION

In recent decades, molecular-based studies have revolutionized our understanding of the evolution of the benthic Southern Ocean biota (Strugnell *et al.* 2008; González-Wevar *et al.* 2011, 2013, 2017, 2018, 2019, 2021, 2022, Fraser *et al.* 2012, 2014, Poulin *et al.* 2014, Moon *et al.* 2017). Through integrative biogeographical analyses, it has been possible to infer evolutionary relationships, tempo, and modes of origin and diversification, in addition to genuine biogeographical and diversity patterns in this vast region (Wilson *et al.* 2009; Allcock and Strugnell 2012, Riesgo *et al.* 2015, González-Wevar *et al.* 2017, 2019, 2022, Chenuil *et al.* 2018, Crame 2018, Halanych and Mahon 2018).

Multilocus phylogenetic reconstructions and detailed morphological analyses in *Laevilitorina* highlighted the necessity for a revision in the group. On the one hand, new molecular and morphological analyses recognized at least seven species-level clades within *L. caliginosa* (González-Wevar *et al.* 2022). Moreover, the ostensible broad distribution of this taxon was erroneous, because most of the seven newly revealed species exhibited far narrower distributions. Nevertheless, as we have shown, one species, *L. venusta*, does indeed have an extraordinarily wide geographical range across Antarctic and sub-Antarctic provinces. On the other hand, phylogenetic reconstructions of the Antarctic species *L. antarctica*, *L. claviformis*, and *L. umbilicata* failed to discriminate them as different evolutionary units. Future studies of the group will require inclusion of populations of *L. umbilicata* and *L. antarctica* from their respective type localities (South Georgia and East Antarctica). Additionally, specimens from Antarctic (*L. wandelensis*) and South Georgian (*L. pygmaea* and *L. granum*) taxa, in addition to species from other biogeographical areas, such as Australia and New Zealand, should be included in further sampling.

The taxonomy of *Laevilitorina* has been reviewed by several authors (Powell 1951, Dell 1964, Arnaud and Bandel 1976, Castellanos 1989, Reid 1989, Zelaya 2005, Engl 2012). Most studies, however, were centred on and/or restricted to populations from South Georgia, Kerguelen, Macquarie, South Orkney Island, and the Antarctic Peninsula; none, other than the study by Castellanos (1989), who included South American *Laevilitorina* individuals in their analyses, examined South American or Falkland/Malvinas samples. Hence, there was a considerable knowledge gap concerning *Laevilitorina* morphological and radular diversity across these areas.

Powell (1951) recognized two major divisions in *Laevilitorina* based on radular morphologies: (i) species showing prominent and narrowly pointed cusps on both central and lateral teeth; and

(ii) species with broad, chisel-shaped central cusps and broad lateral teeth. Our results show that the species *L. hicana* and *L. caliginosa* (main clade II in Fig. 1) fit well with the description (i). In contrast, species belonging to the main clade I (*L. magellanica*, *L. pepita*, *L. fueguina*, and *L. venusta*) possess radulae with a central tooth showing a wide and rectangular central cusp and, and in some cases, with a chisel-shaped form, fitting with Powell's description (ii). Whether these radular differences simply reflect the deep evolutionary divergence between these two clades or, alternatively, are driven by ecological and substrate differences remains to be seen. Comparisons of juvenile and adult radulae might be informative about the latter possibility.

Interestingly, the radular configuration described by Bandel and Arnaud (1976) and Reid (1989) for what were identified as *L. caliginosa* from Kerguelen islands and Macquarie, respectively, corresponds to the central tooth morphology described for *L. coriacea* from South Orkney (Powell 1951) and *L. venusta* from South Georgia, Crozet, Kerguelen, Signy Island, and the Antarctic Peninsula (von Martens and Pfeffer 1886; this study). In fact, our new molecular analyses (mitochondrial DNA) of *L. caliginosa*-like specimens ($n = 20$) from Macquarie Island assigned these individuals to *L. venusta*. Consequently, we suggest that samples from this sub-Antarctic Island population identified as *L. caliginosa* are, in fact, *L. venusta*.

Likewise, a key characteristic recorded in species from the main clade I (*L. magellanica*, *L. fueguina*, *L. pepita*, and *L. venusta*) that differentiates them from those of the main clade II (*L. caliginosa* and *L. hicana*) is the presence of small denticles on the central tooth, which vary in frequency and number. *Laevilitorina fueguina* is the species that presented these denticles most frequently (Fig. 3E). In the case of *L. venusta*, only one Antarctic Peninsula population showed this feature. Additionally, it is important to mention that although the radula of *L. venusta* throughout its distribution was variable, particularly in the shape of the lateral and marginal teeth, the morphological pattern of the central tooth was constant across the species distribution in the Antarctic Peninsula and sub-Antarctic islands (Fig. 5I).

The systematic implications of this *Laevilitorina* revision are noteworthy because it gives new and valuable information concerning the diversity patterns, evolutionary relationships, and biogeographical affinities of this important Southern Ocean littorinid genus across different Antarctic and sub-Antarctic provinces. As noted by González-Wevar *et al.* (2022), *Laevilitorina* appeared as a poorly represented genus in southern South America with a single species, *L. caliginosa*, and a second, *L. latior*, restricted to the Falkland/Malvinas Islands. In fact, however, it has been demonstrated that the southern tip of South America possesses at least six different species of *Laevilitorina* that diversified during the last 20 Myr. *Laevilitorina magellanica*, *L. fueguina*, and *L. pepita* are restricted to the Strait of Magellan, where they evolved *in situ* for several million years. *Laevilitorina hicana* is apparently restricted to Hornos Island, and *L. caliginosa* s.s. extends its distribution east and northwards to the Falkland/Malvinas Islands and east and southwards to South Georgia. Finally, the species *L. venusta* has a wide distribution across the Antarctic Polar Front towards sub-Antarctic Islands, such as South Georgia, Marion, Crozet, Kerguelen and Macquarie. Such an extended, trans-Antarctic Polar Front distribution is

unexpected considering the benthic protected developmental mode of *Laevilitorina* and because it represents the first example of a near-shore marine invertebrate species occurring in both Antarctic and sub-Antarctic provinces. The broad distribution of *L. venusta* implies that this taxon is a better long-distance disperser than its congeners, which exhibit narrower distributions in southern South America. As hypothesized by González-Wevar *et al.* (2022), *L. venusta* might be more closely associated with long-distance dispersal vectors, such as buoyant macroalgae.

Our work leaves many questions unanswered. Additional sampling is needed to confirm the probable synonymies of *L. antarctica* and *L. claviformis* with *L. umbilicata*. Regarding the status of the remaining species (see Rosenfeld *et al.* 2022), especially those from Australia, New Zealand, and their respective sub-Antarctic islands, little can be said at this point. Access to molecular-grade samples is needed, which is likely to require careful fieldwork in numerous physically challenging locations.

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

ACKNOWLEDGEMENTS

We are grateful to the Government of South Georgia & South Sandwich Islands (GSGSSI), South Atlantic Environmental Research Institute (SAERI), Natural History Museum (NHM) London, and the Shallow Marine Surveys Group (SMSG) for organizing the research cruise (Operation *Himantothallus*, Darwin Plus Marine Biodiversity Research Cruise, *Pharos* SG-11-2021) and Tritonia Scientific Ltd for diving operations and dive safety. We also are grateful to the officers and crew of the *Pharos* SG for their professionalism and support. We also thank Jaime Ojeda, Andrés Mansilla, Ricardo Rozzi, and Roy Mackenzie and the staff of the lighthouse of Gonzalo Island for their invaluable support for the development of field research at the permanent ecological studies site implemented in Navarino Island, Diego Ramírez archipelago, and Hornos Island. We greatly appreciate the editorial work of the Associate Editor and the useful suggestions of two independent referees.

CONFLICT OF INTEREST

None declared.

FUNDING

This study was funded by different projects and institutions, including the Millennium Science Initiative Program (ICN2021_002 to S.R., C.S.M., E.P., and C.A.G.-W.), Initiation Fondecyt 11140087, Fondecyt Regular Project 1210787, and INACH RG_17-18 to C.A.G.-W. and E.P., ANID/BASAL FB210018 to S.R. and C.S.M., and INACH DG_10-22 to S.R. We also appreciate the support of the following projects: Fondecyt Postdoctoral 3210063 to C.S.M. and IPEV program PROTEKER (#1044). The research cruise was funded by GSGSSI and a Darwin Plus Grant (DPLUS122) to the NHM.

AUTHOR CONTRIBUTIONS

Morphological measurements and analyses were done by SR and CGW.

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