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Tracing the origins of Antarctic periwinkles: an integrative morphological–molecular perspective on *Laevilacunaria* evolution

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In biogeography, related lineages often share similar range sizes and species richness due to inherited traits and shared geographic history. This expectation is based on phylogenetic niche conservatism and shared dispersal constraints. However, within the subfamily Laevilitorinae, this pattern is not observed: *Laevilitorina* shows broader distributions and higher species richness than *Laevilacunaria* despite similar developmental mode and habitat preferences. Combining multilocus genetic data, radular morphology and model-based historical biogeography, we aim to understand the origins of these disparities in range extent. The paraphyly detected in both *Laevilitorina* and *Laevilacunaria* genus indicates a more complex history than a simple older–younger genus contrast, with age and diversification distributed across four clades. Our dated analyses place the time to the most recent common ancestor (TMRCA) of Laevilitorinae at 52.2 Mya, with diversification within clades from the Miocene to Pleistocene. The sister genera show process-level contrasts: in *Laevilitorina*, broad ranges in some lineages are consistent with intermittent, macroalgal raft-mediated connectivity, whereas *Laevilacunaria* exhibits restricted ranges consistent with rare, storm-facilitated rafting that enables colonization without sustained gene flow. Overall, our findings support how stochastic long-distance dispersal and establishment can shape biogeographic patterns in the Southern Ocean and underscore the need to update systematic classifications.

1. Introduction

The Southern Ocean is divided into distinct Antarctic and subantarctic biogeographic regions [1,2], with high endemism and complex faunal associations shaped by dispersal, life-history traits and historical barriers [2–4]. Despite this pronounced bioregionalization, faunal associations within and between provinces do not follow a single general rule and depend on the focal clade. For example, closely related lineages often share range size and richness due to inherited life-history traits [5,6], whereas contrasts arise from differences in dispersal, speciation–extinction dynamics, and geographic and ecological barriers [2–4]. Across Antarctic benthos, the prevalence of brooding over broadcast spawning documented in echinoderms, polychaetes (annelids) and molluscs has been linked to evolutionary success defined as lineage’s ability to persist, diversify and expand through time, typically proxied by species richness and geographic range [7]. Accordingly, shared developmental traits can align distribution and species richness among related lineages [5,6], whereas departures among sister taxa are better explained by lineage-specific evolutionary history [8].

Littorinid snails are characteristic of the shallow rocky shores of the Southern Ocean [4,9]. This group includes three intertidal and subtidal genera: *Laevilitorina* Pfeffer 1886, *Laevilacunaria* Powell 1951 [10] and *Pellilitorina* Pfeffer 1886. Both *Laevilacunaria* and *Laevilitorina* are the only representatives of the subfamily Laevilitorinae [4,10,11], while *Pellilitorina* belongs to the subfamily Lacuninae. Like many species of Littorinidae, the vast majority of *Laevilitorina* and *Laevilacunaria* species have been registered from intertidal and shallow subtidal environments [12]. In addition, species of *Laevilitorina* and *Laevilacunaria* are sympatric and even syntopic, living associated with different species of macroalgae in Antarctic and subantarctic environments [10,13–18]. Another significant trait these two genera share is their life cycle without a free-living pelagic larval stage. Instead, females deposit egg masses on rocks or macroalgal fronds, and juveniles hatch directly after 1 to 4 months [19,20]. It has been predicted that species with such protected benthic development modes should exhibit a low dispersal potential and present narrow geographical ranges [20,21].

It is interesting to highlight that although *Laevilacunaria* and *Laevilitorina* species share a similar development mode and habitat preferences, their distributions and diversity patterns are very different. *Laevilitorina* is one of the marine gastropod genera with the broadest distribution in high latitudes of the Southern Hemisphere, including the Southern Ocean [17]. Its current range includes the west and east coast of South America, south of 50°S, New Zealand, southern Australia, Tasmania, the Antarctic Peninsula, the Weddell Sea, East Antarctica and most of the subantarctic islands (Falkland/Malvinas Islands, South Georgia, Crozet, Kerguelen, Heard, Macquarie, Campbell, Auckland, Antipodes, Bounty). In contrast, the genus *Laevilacunaria* exhibits a restricted distribution across the Southern Ocean, mainly in maritime Antarctica (Antarctic Peninsula and the South Shetland Islands), West Antarctica, South Georgia, and geographically distant subantarctic islands like Crozet and the Kerguelen archipelago [22].

Another critical aspect that differentiates these two genera is the pattern of species richness. For example, the World Register of Marine Species database (WoRMS) (<http://www.marinespecies.org>) currently recognizes 25 species of *Laevilitorina* across its distribution, including four species recently described from the Magellanic region [11]. By contrast, *Laevilacunaria* includes only three species: *L. antarctica*, *L. bennetti* and *L. pumilio*. However, a recent phylogeographic study of *L. antarctica* revealed that populations from South Georgia and the Antarctic Peninsula could represent distinct evolutionary units [23]. Thus, a detailed revision of *Laevilacunaria* species is highly relevant to better understand the systematics, the actual diversity pattern and the evolution of this interesting group of littorinid snails. Considering the differences and similarities mentioned above, questions arise as to what have been the main evolutionary processes and mechanisms that influenced current patterns of distribution and species richness of these genera? Here, we use morphological and molecular tools to: (i) examine the taxonomic status of species within *Laevilacunaria*, (ii) infer the evolutionary origin and timing of *Laevilacunaria* diversification in the context of Laevilitorinae, and (iii) assess how these evolutionary histories relate to the richness and contrasting distribution patterns of *Laevilacunaria* and *Laevilitorina* across the Southern Ocean.

These two genera of littorinids represent interesting models to explore the underlying processes and evolutionary mechanisms that have shaped their contrasting biogeographic patterns despite sharing the same mode of development and similar habitats in the Southern Ocean.

2. Material and methods

(a) Specimen sample collection

We designed sampling to reflect the known distribution of Laevilitorinae across major Southern Ocean provinces and to capture species-level ranges. Across 19 localities (2017–2023), we sampled all described species of *Laevilacunaria* and covered its full geographic extent, including West Antarctica and subantarctic islands (South Georgia, Kerguelen, Crozet; figure 1, electronic supplementary material, table S1). For *Laevilitorina*, we obtained broad coverage in the Magellan province, Falkland/Malvinas, West Antarctica, South Georgia, Kerguelen, Crozet, Marion and Macquarie, thus sampling most recognized species from these provinces; however, New Zealand/Australian *Laevilitorina* were unavailable, a limitation given their importance within the subfamily’s range. As Lacuninae outgroups, we included *Pellilitorina* (West Antarctica, Kerguelen) and *Risellopsis* (South Island, New Zealand) (figure 1, electronic supplementary material, table S1). Across sites, individuals were collected intertidally or from shallow subtidal habitats and preserved in 95% ethanol following Rosenfeld *et al.* [17,18]; each specimen was photographed for morphological analysis.

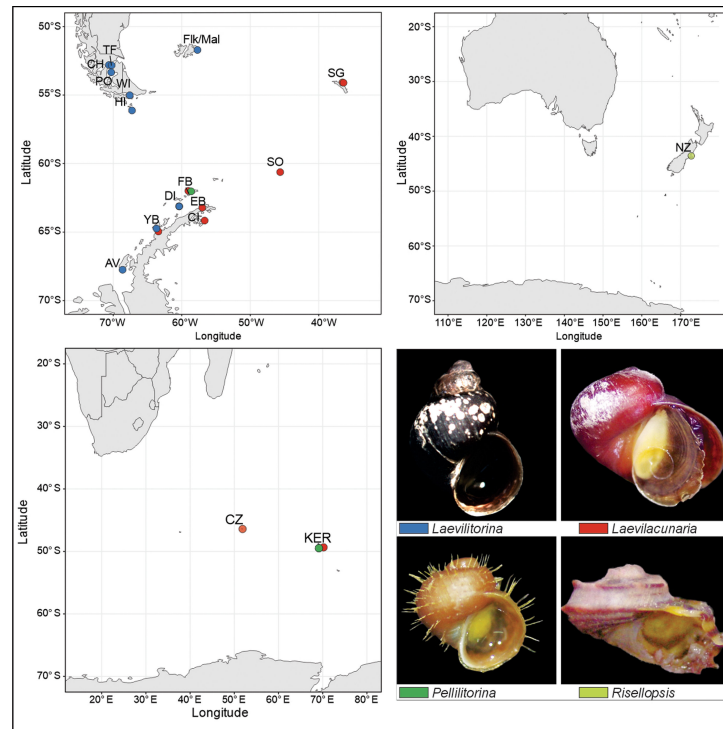


Figure 1. Map of the sampling sites of *Laevilacunaria* species, the sister genus *Laevilitorina* and the Lacuninae genera *Pellilitorina* and *Risellopsis* in the Southern Hemisphere included in this study. The colours below each panel indicate the sites of collection of each genus. CH: Chabunco Beach, PO: Porvenir, Flk/Mal: Falkland Is/Malvinas, TF: Tierra del Fuego, WI: Puerto Williams, HI: Horn Island, SG: South Georgia Island, SO: South Orkney, FB: Fildes Bay, EB: Esperanza Bay, CI: Cockburn Island, DI: Deception Island, YB: Yelcho Base, AV: Avian Island, CZ: Crozet Island, KER: Kerguelen Island, NZ: New Zealand.

(b) Morphological identification

Species were identified following Powell [24] Engl [25] and through their original descriptions [26–28]. In addition, to confirm each of the identifications, the radular morphology of the different species was revised. Radular morphology was examined by stereomicroscopy and checked with the revision of v. Martens & Pfeffer [27], Preston [28] and Powell [24].

(c) DNA extraction and sequencing

DNA extractions were performed using the DNeasy Blood & Tissue Kit (Qiagen) from portions of the animal's foot or from the whole animal in the case of very small individuals. A modified protocol was applied for small amounts of tissue [29]. Four molecular markers, previously utilized in littorinid phylogenies, were used for this study [30–32]. These genes include the mitochondrial cytochrome *c* oxidase subunit I (cox1; 620 bp), 12S ribosomal RNA (12S rRNA; 320 bp), 16S ribosomal RNA (16S rRNA; 480 bp) and the nuclear gene 28S ribosomal RNA (28S rRNA; 1300 bp). Detailed PCR protocols are available in the electronic supplementary material, table S2. Forward and reverse sequences were manually examined using Phred scores to ensure all sequenced bases matched and were of good quality. Contigs were assembled using Geneious 10.2.2 [33] and independently aligned using Muscle [34] with standard settings.

(d) Phylogenetic reconstruction

The phylogenetic reconstructions included 2–9 individuals of *Laevilacunaria* and *Laevilitorina* per species. To elucidate the phylogenetic relationships of *Laevilacunaria* species, 12S rRNA, 16S rRNA, cox1 and 28S rRNA sequences available from GenBank were aligned with our datasets (electronic supplementary material, table S3) using Multiple Alignment using Fast Fourier Transform (MAFFT 6) [35] with default parameters [34] and then manually checked. Optimal nucleotide substitution models and partitioning schemes were selected for each marker separately using the corrected Akaike information criteria (AIC) in PartitionFinder v. 2.1, allowing for cox1 codon partitioning [36] (electronic supplementary material, table S4). The datasets of the different loci were combined in sequencematrix v. 1.8 [37].

Phylogenetic analyses were conducted on individual loci and concatenated datasets using maximum likelihood (ML) in IQ-TREE (Efficient software for phylogenomic inference) [38] and Bayesian analyses (BA) in MrBayes v. 3.2.6 [39]. Individual gene trees were unable to resolve the relationship due to limited phylogenetic information in the Littorinidae (polytomies with poor bootstrap values; see electronic supplementary material, figures S1–S3) (see [31,32]). Therefore, concatenated sequences were used to infer the phylogenetic relationships within the group. Two data matrices were used for the analyses. The first used three concatenated loci (12S+ rRNA+cox1+28S rRNA), which were aligned against 152 marine littorinid species obtained from GenBank [31,32]. The GenBank accession number for 152 species of littorinid used in the dating analysis is given in

electronic supplementary material, table S2 in Reid *et al.* [31] and electronic supplementary material, table S2 in Saha *et al.* [32]. The tree was rooted with *Pomatias elegans* and *P. rivulare* and included the subfamily Littorininae and Lacuninae to test for the monophyly of the subfamily Laevilitorininae (*Laevilitorina* + *Laevilacunaria*). In the second matrix, we used four concatenated genes (12S+16S+cox1+28S) to resolve the phylogenetic relationships within Laevilitorininae more accurately. In this case, the phylogenetic trees were built using as sister taxa, *Pellilitorina*, *Bembicium*, *Melarhaphe* and rooted with the genus *Littorina*. For the two matrices, ML statistical support for the nodes was estimated by an ultra-fast bootstrap algorithm with 1000 pseudoreplicates [40]. Bayesian inference posterior probability support values (PP) were estimated using the Markov chain Monte Carlo algorithm (MCMC), running four chains for 10×10^7 generations, with trees sampled every 1000 generations, with the initial 10% of parameter values discarded as 'burn-in'. Convergence was assessed by checking that split frequencies had an average standard deviation below 0.01 and all parameters had effective sample sizes (ESS) >200 using tracer v. 1.6 [41]. Maximum clade credibility trees were generated using treeAnnotator v. 2.4.7 [42] and visualized with FigTree v. 1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree>).

(e) Species delimitation analysis and phylogenetic reconstruction

For species-delimitation analyses within Laevilitorininae, single-locus (cox1) and multilocus (12S rRNA+cox1 +16S rRNA+28S rRNA) analyses were performed. For single-locus, the automatic barcoding gap discovery (ABGD) [43] and the multirate Poisson Tree Processes (mPTP) [44] were used. Species-delimitation analyses using ABGD and mPTP were performed on their respective web servers (<http://www.abi.snv-jussieu.fr/public.abgd>) and (<https://species.h-its.org/>). For the multilocus analyses, Bayesian Phylogenetics and Phylogeography (BPP) was applied using BP&P 4.7.0 [45]. The four markers were used as inputs for BPP under the A11 model (A11: species delimitation = 1, species tree = 1). Specimens were *a priori* assigned to species based on the number of species from the results of the phylogenetic analysis. For the adjustment of the analysis variables, the BP&P instructions were followed [45]. Two independent MCMC analyses were run for 100 000 generations with the 'burn-in' = 10 000.

(f) Divergence time estimation

To estimate divergence times, we generated a Bayesian time-calibrated phylogeny based on the concatenated dataset using BEAST v. 2.7.3 software [46]. Given the absence of reliable fossil calibrations for *Laevilacunaria* and related taxa, we employed two secondary calibrations based on previously published biogeographic studies. The first calibration corresponds to the crown age of Laevilitorininae 56 million years ago (Mya) (66–46 Mya). Both calibrations were modelled using lognormal prior distributions. We partitioned the data by marker and unlinked substitution and clock models across loci to account for variation in substitution rates. A birth–death tree prior and the Optimised Relaxed Clock (ORC) model were used in the final analysis, following additional runs that evaluated model sensitivity [47]. To improve convergence and reduce computation time, we used the maximum likelihood (IQ-TREE) and Bayesian (MrBayes) topologies as a starting tree and applied a monophyletic constraint to the *Laevilitorina* clade 2 + *Laevilacunaria* clade 2 group, which was strongly supported in both ML and Bayesian inference (BI) trees and consistent with prior studies [48]. The final divergence time analysis was run for 500 million generations, sampling every 50 000 steps, with a 25% burn-in. Convergence and mixing were assessed in Tracer v. 1.7.2, ensuring ESS values >200 for all key parameters. Results were summarized using TreeAnnotator v. 2.5.1 [48], and the chronogram obtained under the birth–death + ORC model is presented in the main text.

To assess the impact of calibration priors on divergence time estimates, we conducted a sensitivity analysis under three alternative scenarios. Details of the analysis, including all scenarios, are provided in the electronic supplementary material (figures S4–S6).

(g) Ancestral-range distribution

For the estimation of the ancestral geographic range, we used the BioGeoBEARS package in R [49]. As species of the genus *Laevilacunaria* are distributed along the Antarctic Peninsula and on islands in the Southern Ocean with different geological ages, we assumed founder-event speciation played a significant role as a biogeographic process [29,49,50]. For the analysis, we compared six standard models: (i) Dispersal-Extinction-Cladogenesis (DEC), (ii) Dispersal-Vicariance Analysis (DIVALIKE), and (iii) BAYAREALIKE [51], with and without founder effect (+j), using the default parameters of each model; in the +j variants, j was left free. We set a maximum of four areas per node and defined the biogeographic regions based on the following classification: Antarctic West, Magellan, South Georgia (as a transitional zone) and Subantarctic Islands of the South Indian Ocean. Inference was by maximum likelihood, and model selection was based on log-likelihood (LnL), Akaike Information Criterion (AIC) and small-sample corrected Akaike Information Criterion (AICc). Finally, because New Zealand/Australian *Laevilitorina* species were not sampled, root and early Laevilitorininae nodes may be biased (e.g. underrepresentation of Australasian states and wider uncertainty in basal reconstructions). In contrast, our focal *Laevilacunaria* inferences rely on complete genus-level sampling across provinces and are therefore expected to be less sensitive to this limitation.

3. Results

(a) Taxonomic identification and radular morphology

Morphologically, we were able to identify the three species described in the genus *Laevilacunaria*: *L. antarctica*, *L. bennetti* and *L. pumilio* (figure 2). In addition, we recorded individuals of *L. bennetti* in South Georgia, where the species had not previously been reported. Our specimens from South Georgia match the diagnostic external morphological and radular characteristics of *L. bennetti* from West Antarctica but show slight differences in external morphology and are more consistent in radular morphology. Because these differences prevent a definitive assignment without specific integrative review, we use the conservative designation '*Laevilacunaria cf. bennetti*' to indicate the closest match, pending further study. In relation to radular morphology, we were able to confirm the identifications of the different species, and we also detected two major morphologies of the rachidian tooth: (a)(i) the broad chisel-shaped central cusps observed in *Laevilacunaria antarctica* and *L. pumilio*, (figure 2c,f,g), (b) (ii) broad central cusp with numerous small denticles observed in *L. bennetti* and *L. cf. bennetti* (figure 2i,o). In addition, radular morphology showed differences between individuals from South Georgia and West Antarctica, in both *L. antarctica* and *L. bennetti* (figure 2c,f,i,o). In the case of *L. antarctica* from South Georgia, the inner and outer marginal teeth showed two to three pointed cusps in the inner side (figure 2c). In the case of *L. bennetti* from the Antarctic Peninsula and *L. cf. bennetti* from South Georgia, the rachidian, lateral and inner marginal teeth present numerous small denticles (figure 2i,o). The main difference is that the external marginal tooth of *L. cf. bennetti* from South Georgia has a single cuspid without denticles (figure 2o), while *L. bennetti* has four denticles (figure 2i).

The radula of *L. pumilio* had not been previously described, and therefore, this is the first radular description of the species. It presents a rachidian tooth with a wide and rounded cuspid without denticles (the rachidian central tooth corresponds more to the type of morphology (a) described previously), an internal lateral with seven cusps, the largest is wide and rounded and is accompanied by two small outer cusps and four small inner cusps. The inner marginal presents nine cusps; the main cusp is rounded, accompanied by one very pointed outer cusp and seven pointed inner cusps of similar size. The outer marginal is 'fork-shaped' with seven pointed cusps (figure 2g,h,i).

(b) Sequence analysis

The first concatenated matrix included 169 littorinid specimens. Each sample comprised sequences from the 12S rRNA, *cox1* and 28S genes, totalling 2590 bp after alignment using MAFFT. Lengths of the *cox1*, 12S and 28S gene fragments consisted of 620 bp, 435 bp and 1535 bp, respectively. Of the 2590 sites, a total of 1031 (42.7% *cox1*; 22.2% 12S; 35.1% 28S) were phylogenetically informative.

In the second dataset, which included the species of the subfamily Laevilitorinae (*Laevilitorina*+*Laevilacunaria*), *Pellilitorina setosa*, *Bembicium auratum*, *Melarhaphé neritoides* and three species of *Littorina*, the matrix of nucleotide alignment consisted of a total of 2818 bp, of which the *cox1*, 12S, 16S and 28S consisted of 620 bp, 321 bp, 499 bp and 1373 bp, respectively, after alignment using MAFFT. Out of 2813 sites, a total of 1035 (26.7% *cox1*; 11.4% 12S; 24.9% 16S; 37% 28S) were phylogenetically informative. The GenBank accession numbers for newly generated sequences in this study are given in electronic supplementary material, table S1.

(c) Phylogenetic analysis and species delimitation

The phylogenetic analysis of the Littorinidae recovered the monophyly of the subfamily Laevilitorinae with maximum support in both reconstructions (100% ML and 1.0 PP) (figure 3). The sister group to the Laevilitorinae is not fully resolved in our analysis, but our results suggested that the sister group may belong to the Lacuninae (figure 3).

Within Laevilitorinae, neither *Laevilacunaria* nor *Laevilitorina* were recovered as monophyletic (figure 3). *Laevilacunaria* split into two distinct clades: LAC1, which included *Laevilacunaria antarctica* and *Laevilacunaria pumilio*, and LAC2, which comprised *Laevilacunaria bennetti* and *Laevilitorina wandelensis*. Notably, LAC2 was nested within a larger group together with two *Laevilitorina* clades, though with weak BI supports (<0.80 PP) (figure 3).

The second phylogenetic analysis, conducted on the concatenated dataset of four genes and using *Pellilitorina*, *Bembicium*, *Melarhaphé* and *Littorina* as outgroups, recovered the same overall topology but with stronger statistical support ($\geq 85\%$ ML; ≥ 0.90 PP) (figure 4). This analysis consistently resolved four major clades within Laevilitorinae: two *Laevilacunaria* clades (LAC1 and LAC2) and two *Laevilitorina* clades (LLC1 and LLC2) (figure 3). Clade LAC2 formed a strongly supported cluster with *Laevilitorina* clade 2 (LLC2), which included *Laevilitorina umbilicata*, *Laevilitorina venusta*, *Laevilitorina fueguina*, *Laevilitorina magellanica* and *Laevilitorina pepita* (figure 4). Sister to this grouping was *Laevilitorina* clade 1 (LLC1), composed of *Laevilitorina caliginosa*, *Laevilitorina latior* and *Laevilitorina hicana* (figure 4). Finally, LAC1 represented the most phylogenetically distinct clade within Laevilitorinae (figure 4).

The three species delimitation methods (ABGD, mPTP and BPP) consistently recovered the same evolutionary units in both *Laevilitorina* and *Laevilacunaria*, aligning with the lineages previously identified by González-Wevar, Segovia *et al.* [48] for *Laevilitorina* (figure 4). For *Laevilacunaria*, we identified distinct lineages within both major clades (figure 4). In LAC1, *L. pumilio* from Crozet formed a separate lineage (figure 2i,f), while *L. antarctica* was divided into two close lineages, one in West Antarctica (figure 2d,e) and the other in South Georgia (figure 2a,b). In LAC2, the analysis separated *L. bennetti* from West Antarctica (figure 2j,k) from *L. cf. bennetti* from South Georgia (figure 2m,n) (figure 4).

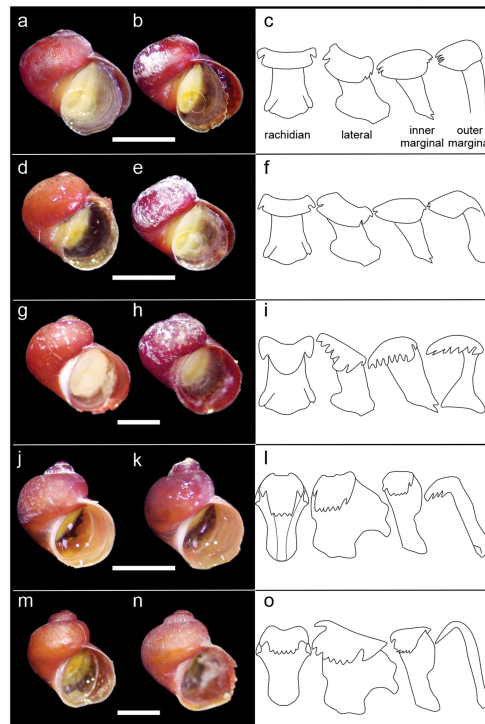


Figure 2. (a, b) *Laevilacunaria antarctica* from South Georgia, shell morphology and (c) radula. (d, e) *Laevilacunaria antarctica* from South Orkney and Cockburn Island, shell morphology, respectively and (f) radula. (g, h) *Laevilacunaria pumilio* from Kerguelen and Crozet Islands, shell morphology, respectively and (i) radula. (j, k) *Laevilacunaria bennetti* from Esperanza Bay and Fildes Bay Island, shell morphology, respectively and (l) radula. (m, n) *Laevilacunaria cf. bennetti* from South Georgia shell morphology and (o) radula. Scale bar = 1 mm.

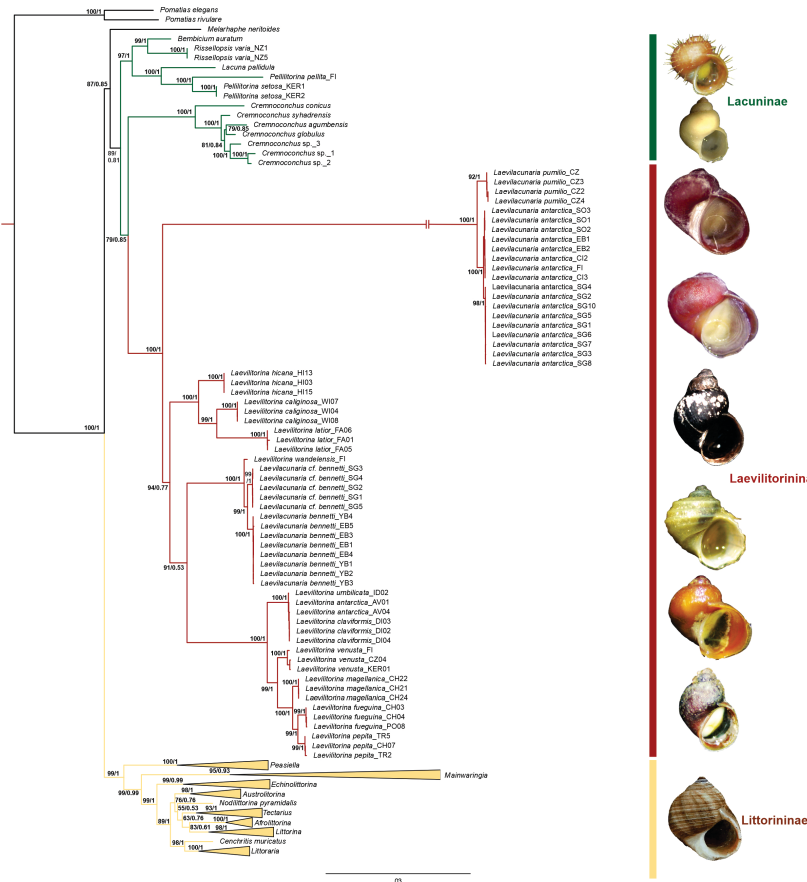


Figure 3. Phylogenetic reconstruction of the relationships among Littorinidae based on multilocus data (12S+cox1+28S) of 169 species of the family Littorinidae, using the genus *Pomatias* (family Pomatiidae) as the outgroup, showing the monophyly of the subfamily Laevilitorinae. The rectangles in yellow, red and green show the different subfamilies of Littorinidae. The full length of the stem leading to *Laevilacunaria antarctica* clade is not shown; this is twice as long. Bayesian posterior probability (PP) and maximum likelihood bootstrap (ML) values are shown above and under the nodes.

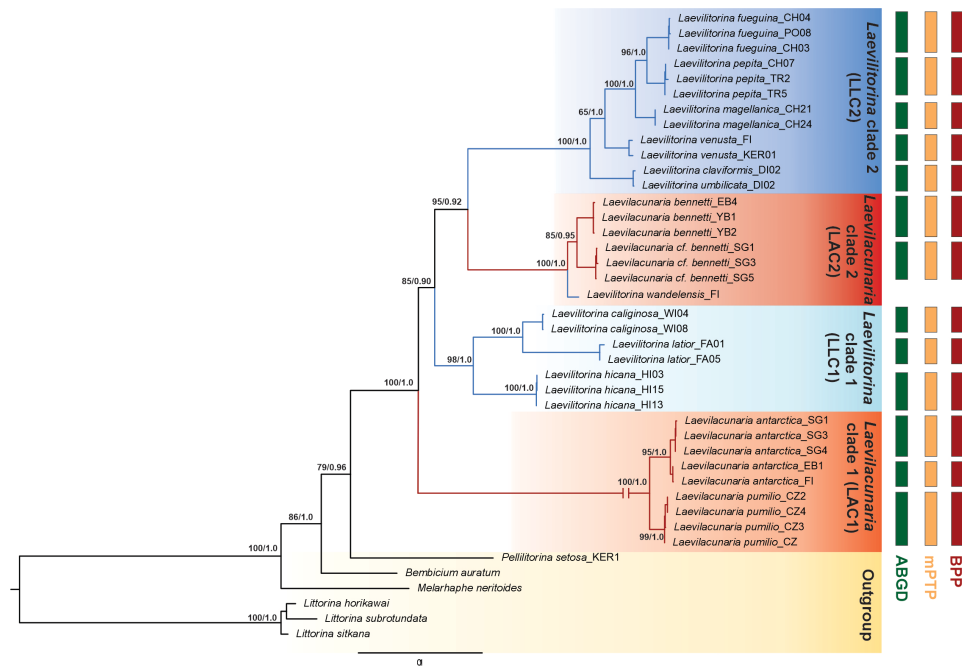


Figure 4. Phylogenetic reconstruction of the relationships among Laevilitorininae based on multilocus data (12S+cox1+16S+28S), using the genus *Pellilitorina*, *Bembicium*, *Melarthaphe* and *Littorina* as outgroups, showing the paraphyletic genus *Laevilacunaria* and *Laevilitorina*. The full length of the stem leading to LAC1 is not shown; this is twice as long. The red lines show the *Laevilacunaria* species, and the blue lines show the *Laevilitorina* species analysed. The rectangles in green, red and yellow show the different delimitations for species analysis. Bayesian posterior probability (PP) and maximum likelihood bootstrap (ML) values are shown above and under the nodes.

(d) Divergence time estimation and ancestral-range probabilities

The ancestral-range reconstruction and molecular dating analysis of the concatenated dataset provided estimates of the timing of diversification and spatial origin of *Laevilacunaria* in the Southern Ocean (figure 4). Ancestral range estimation favoured the DEC+J (LnL = -24.82; AICc = 55.64) model of species evolution (DEC, with a founder event component +J) (electronic supplementary material, table S5). The ancestral area reconstruction and divergence time analyses indicate that the TMRCA of the subfamily Laevilitorininae occurred approximately 52.72 Mya (highest posterior density (HPD) 63.40–43.12 Mya) and support an origin during the final stage of the break-up of Gondwana. At that time, the lineage split into two groups. The first group (LAC1) was distributed across the subantarctic islands where it diversified during the Early Miocene (approximately 7.93, HPD 11.7–4.6 Mya). This lineage later expanded into West Antarctica before finally dispersing to South Georgia during the mid-Pleistocene (approximately 1.4 Mya, HPD 2.3–0.7 Mya). The separation of the second group (LLC1 and LAC2-LLC2) between the Magellanic ancestor of LLC1 and LAC2-LLC2 took place during the Eocene (approximately 49, HPD 59.9–38.5 Mya) (figure 5). Subsequently, the West Antarctic ancestor of LAC2 and LLC2 split during the middle to late Eocene (approximately 43.2, HPD 53.6–33.7 Mya). The LAC2 had an ancestral range across the West Antarctic and diversified during the Miocene. First, the separation between *Laevilitorina wandelensis* and *L. bennetti*/L. cf. *bennetti* occurred at 10.85 Mya (HPD 15.9–6.49 Mya), before the split of *L. bennetti* and *L. cf. bennetti* at 7.8 Mya (HPD 13.3–3.8 Mya) with the dispersal from the West Antarctic ancestor to South Georgia (figure 4).

4. Discussion

(a) Evolutionary origin and diversification of Laevilitorininae and Laevilacunaria

We present the first integrated biogeographic analyses of *Laevilacunaria* and its sister genus *Laevilitorina* in the Southern Ocean, along with the first global phylogeny of Littorinidae encompassing all three described subfamilies. Based on the phylogeny of Littorininae by Reid, Dyal [32] and the work on *Cremnoconchus* by Saha, Chakraborty [33], our dataset provides the most complete molecular framework for the family to date. We include genera of Laevilitorininae and two genera of Lacuninae, and recover the monophyly of Littorinidae [33] and Laevilitorininae, along with additional unexpected systematic results (see electronic supplementary material, S2). Within Laevilitorininae, the two currently recognized genera (*Laevilacunaria*, *Laevilitorina*) are paraphyletic and are divided into four clades. Thus, the present phylogenetic reconstruction, the divergence dates estimated within the subfamily and the differences in radular morphology, suggest that the diversity should be recognized at the genus level (figures 3 and 4). For more details of the taxonomic arrangement within Laevilitorininae and *Laevilacunaria*, see electronic supplementary material, S2. However, we caution that our biogeographic scenarios remain provisional, as *Laevilitorina* from New Zealand/Australia was not available. This gap limits geographic coverage and may bias basal nodes in

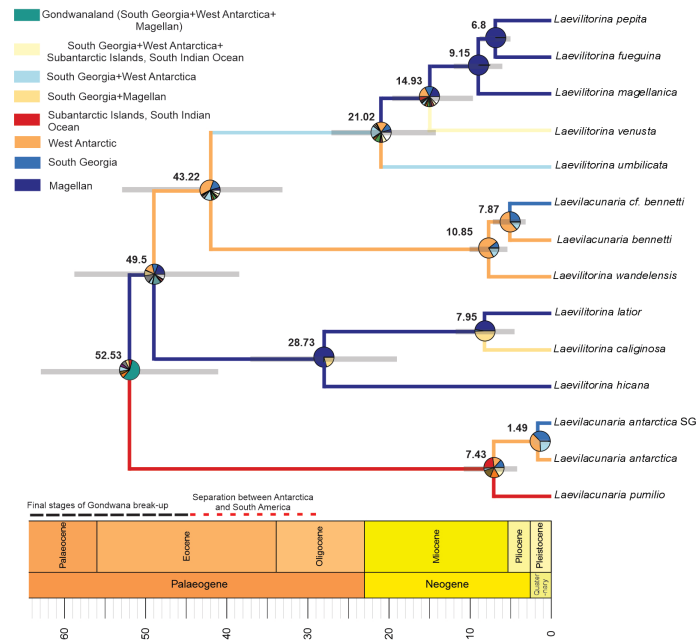


Figure 5. Historical biogeography and timing of divergence of *Laevilacunaria* in the Southern Ocean using the concatenated dataset. The maximum clade credibility tree shows the median divergence time estimates with 95% height posterior distribution. The coloured pie chart represents ancestral-range probabilities at each node as recovered by BioGeoBEARS. Different colours represent different regions and geographical ranges.

both phylogeny and ancestral range reconstruction. Consequently, we present our reconstruction as a biogeographic scenario that will need to be validated with expanded Australasian sampling.

Our analyses revealed that the ancestor of the subfamily Laevilitorininae originated during the late stages of Gondwana fragmentation (63.40–43.12 Mya). Our data suggest that the TMRCA of Laevilitorininae was close to the Early Eocene Climatic Optimum (*ca* 50 Mya) [52]. At this time, the southern continental landmasses were still closely connected, with a land bridge between South America and Antarctica [53,54] and seafloor spreading slowly between Australia and Antarctica [55]. This period followed the Cretaceous–Palaeogene mass extinction (66 Ma); during this climatic optimum [56], radiation of benthic marine taxa occurred [52]. Although the origin of Laevilitorininae has not been previously hypothesized due to the lack of fossils within this group [11], our analyses relate the group's ancient history to the break-up of the supercontinent Gondwana, followed by rapid diversification into four well-supported clades. Yet this biogeographic hypothesis is an incomplete phylogenetic reconstruction because we could not obtain the *Laevilitorina* species from New Zealand and Australia. Therefore, the estimation of the TMRCA of Laevilitorininae is provisional and may give us a more recent age than considering the full distribution of the genus. BioGeoBEARS involves simplifying assumptions about dispersal, vicariance, and extinction and uses a fixed tree and homogeneous parameters over time [50]. Our four-region coding and four-area maximum per node are also simplifying schemes. Still, the key patterns we propose—colonization by episodic long-distance dispersal and establishment (LDDE) (Kerguelen–West Antarctica; West Antarctica–South Georgia)—provide a basis for future studies with greater coverage and more integrative models.

The two clades of *Laevilacunaria* had ancestors with different distributions. For LAC1, the ancestor would have inhabited subantarctic environments, probably in the Kerguelen Islands. During the Miocene, LDDE events facilitated the colonization of West Antarctica, followed by subsequent dispersal to South Georgia during the Pleistocene (figure 5). The TMRCA of the clade LAC2-LLC2 would have originated in West Antarctica and diverged during the Eocene (HPD 53.6–33.7 Mya). As in LAC1, an LDDE event from West Antarctica to South Georgia Island would have occurred during more recent times. Subsequently, the TMRCA of LLC1 and LAC2-LLC2 was approximately 49 Mya (HPD 59.9–38.5 Mya) and the final split between LAC2 and LLC2 was approximately 43 Ma (HPD 53.6–33.7 Mya), close to the middle to late Eocene, a period of significant change in the Southern Ocean that involved the beginning of the isolation of Antarctica through the opening of the Drake Passage and the onset of the Antarctic Circumpolar Current (ACC) [52,57]. In this sense, the origin and diversification of these clades could be related to a vicariant process driven by the separation of South America and Antarctica and the initiation of the ACC. This same vicariant process has also been hypothesized for other molluscs, such as the incubating microbivalves of the genus *Kidderia* [53], as well as the two clades of *Laevilitorina* [54].

Subsequently, during the Miocene (23 and 6 Mya), these four clades diversified independently in South America, Antarctica and the subantarctic islands. Speciation likely reflected the Middle Miocene Climatic Transition, with a major expansion of East and West Antarctic ice sheets and intensification of the ACC [55]. The intensification of the ACC during the mid-Miocene not only isolated the continent thermally but also enabled the formation of a giant mixing ring [55,56]. These oceanographic changes were key drivers in the evolution of the Southern Ocean biota [58–60]. The establishment of a strong and deep ACC may have generated an effective oceanographic barrier, maintaining most of the *Laevilacunaria* (LAC1 and LAC2) lineages south of the ACC. More recently, both clades of *Laevilacunaria* diversified in West Antarctica, Subantarctic Islands, and South Georgia between the lower Miocene and the Pleistocene, 7.9–1.4 Mya. During this period, it has been suggested that several groups of marine invertebrates underwent diversification processes [61,62], especially shallow molluscs [3,54,63,64].

(b) Long-distance dispersal events in *Laevilacunaria* and the importance of rafting

Ancestral-range analyses suggest LDDE events from subantarctic islands to West Antarctica and from West Antarctica to South Georgia, implying that this process has played an essential role in establishing the current geographic distribution in *Laevilacunaria*. It is important to note that *Laevilacunaria* species are associated with various species of macroalgae [14,16,19,65]. In the case of *L. pumilio*, the only species north of the Antarctic Polar Front (APF), on the Kerguelen and Crozet Islands, colonization from these islands to West Antarctica occurred around approximately 7.9 Mya. This time coincides with the appearance of the floating ancestor of the genus *Durvillaea* (between 9.7 and 3.4 Mya) [66]. *D. antarctica* is a brown macroalga that forms dense kelp forests and has a buoyancy trait highly relevant to the dynamics of the Southern Ocean [67]. The fronds of this macroalga are thick and leathery and float through internal inflation. Around 70 million rafts have been reported drifting at any given time, with about 30% still bearing holdfasts, which support the greatest faunal diversity [68]. The holdfasts firmly adhere to rocky substrates, sometimes ripping out pieces of rock, and they also create microclimates that buffer cold and heat for the invertebrate communities travelling on them [69]. Thus, individuals of *Laevilacunaria* or their egg masses could well have dispersed via rafting using buoyant seaweeds as a vector during this period. New evidence shows that floating algae can cross the oceanographic barriers of the Southern Ocean to reach Antarctic coasts [70,71]. These macroalgal rafts may carry a variety of passengers, including marine invertebrates or their egg masses attached to the fronds [23,66].

In contrast to subantarctic environments, on Antarctic shores, the only buoyant macroalgae species is *Crystosphaera jacquinotti*, but its populations do not have the density or extent that *Macrocystis pyrifera* and *Durvillaea antarctica* exhibit on subantarctic shores [66]. However, long-distance colonization by rafting on non-buoyant macroalgae has been documented [67]. Indeed, Antarctic species that do not possess flotation structures, such as *Adenocystis utricularis*, *Himantothallus grandifolius* and *Desmarestia anceps*, have been seen floating in the Southern Ocean [68]. Therefore, these macroalgae could also be potential dispersal vectors for Antarctic species that lack a pelagic larval stage. Notably, both *L. antarctica* and *L. bennetti* have been reported to inhabit the fronds of these macroalgae [14,65,72].

However, despite the connectivity along the Southern Ocean through macroalgal rafts [70,71], our results show that these dispersal events in *Laevilacunaria* were rare. These low-frequency events likely triggered the founder effect, and the subsequent absence of gene flow between populations would have promoted speciation [73]. In this sense, these dispersal events, coupled with the lack of gene flow, would not only have generated genetic divergence between lineages but also a differentiation in radular morphology. For example, *L. pumilio* is the only species present in the subantarctic area and is the one with the most distinct radular morphology in the LAC1 clade (figure 2i). In the case of the lineages of *L. cf. bennetti* and *L. antarctica* found on South Georgia, they would have colonized the island independently from West Antarctica at 7.8 and 1.4 Mya, respectively (figure 4). In this sense, the analysed individuals of *L. antarctica* and *L. cf. bennetti* from South Georgia showed differences in radular morphology compared with individuals from West Antarctica.

(c) The relevance of stochastic events in the historical connectivity

Oceanographic processes in the Southern Ocean, characterized by high wind speeds and intense wave conditions linked to atmospheric storms, can both hinder and facilitate the passive, and very occasional, dispersal of organisms [70]. Consistent with this, recent oceanographic evidence shows that storms—through their extreme waves and winds—produce effects on raft-mediated LDDE that cannot be inferred from average conditions [74]. During these specific events, most kelp rafts cross the APF and other fronts. Furthermore, storms enhance the coastal detachment of macroalgae (boosting the supply of rafts) and speed up their transport, with displacements of up to approximately 50 km per day, nearly twice the average current velocity [74]. Altogether, this new evidence suggests that oceanographic barriers can sometimes be permeable under specific oceanographic and climatic conditions, enabling sporadic crossings of various rafting organisms through the APF, allowing long-distance connectivity among subantarctic islands. In light of this new evidence and our findings of discrete and rare dispersal events across the history of *Laevilacunaria*, we propose that colonization from Kerguelen to West Antarctica and from West Antarctica to South Georgia likely occurred during extreme and infrequent oceanographic storms, rather than ongoing gene flow, which ultimately led to population differentiation. Future population-genomic analyses will be essential to quantify contemporary connectivity (if any) and test the rarity and timing of these events.

In *Laevilacunaria*, the evidence aligns with the broader pattern that raft-mediated biogeographic outcomes can differ markedly among closely related groups and depend on multiple factors such as life-history traits, ecology, raft durability and storm frequency/intensity, among others [75]. In a comparative analysis with other Southern Ocean gastropods, *Siphonaria* maintains species-level connectivity through intermittent cohorts moving in *Durvillaea* from the Magellan province towards Kerguelen, whereas *Nacella* appears not to have maintained dispersal and establishment through time; consequently, multiple lineages with limited distributions are now observed. This contrast reflects both the stronger association of *Siphonaria* with *Durvillaea* holdfasts and its protected benthic development, which allows egg masses and subsequently juveniles to remain in rafts, versus indirect development in *Nacella* and the progressive loss of passengers on rafts [75]. *Margarella* similarly contrasts a single subantarctic species widely distributed north of the APF (*M. violacea*) with multiple species south of the APF, despite shared macroalgal associations, reinforcing that macroscale and microscale factors jointly determine rafting outcomes. Within *Laeviliatorininae*, most species exhibit restricted geographic ranges, with two notable exceptions, *L. caliginosa* and *L. venusta*. The key difference observed in these species could be associated with their natural history and closer association with macroalgae. Overall, the key question is why some lineages maintained restricted ranges after colonization while others

succeeded in preserving connectivity. In line with Spencer, Fraser [75], who emphasize multiple modulators of biogeographic outcomes, it will be interesting to test how host-associated microbiomes might influence colonization success and maintenance of connectivity. This emerging approach, based on microbiome filtering and phylogeographic structuring, has already been tested in *Nacella* [76]. To corroborate this, it will be crucial in the future to integrate data on habitat association, thermal physiology and microbiome profiling across populations in other Southern Ocean molluscs.

Finally, our results in Laevittorininae align with a broader pattern documented in the Southern Ocean biota: rare and stochastic LDDE events contribute importantly to the biogeographic structure in extreme environments of many organisms, far beyond marine invertebrates. For example, in marine mammals, such as the Kerguelen subspecies of Comerson's dolphin (*Cephalorhynchus commersonii kerguelensis*), signs of postglacial colonization from South America and current isolation from its source are consistent with a single ancient interbreeding followed by incipient divergence, rather than sustained gene flow [77]. In seabirds, genomic studies indicate that species such as *Pygoscelis papua* (gentoo), of coastal habitat, show structuring and expansion by stepping stones with attenuation of founder effects, evidencing episodic barrier permeability and dependence on life-history traits [78]. In notothenid fishes, research on *Harpagifer* suggests recent colonizations and disjunctions compatible with infrequent crossings of fronts and subsequent isolation [75,79]. Taken together, these lines of evidence, together with our results, reinforce the idea that stochastic LDDE associated with life-history traits is an important process that structures the biogeographic patterns of the Southern Ocean.

Ethics. All the specimens were captured under the Chilean legislation (Technical Memorandum PINV E-2021-159 SUBPESCA) and treated following the bioethics requirements of Instituto de Ecología y Biodiversidad (IEB) and Instituto Antártico Chileno (INACH).

Data accessibility. Individual loci data are available from the Dryad Digital Repository [80]. The data provided in the electronic supplementary material are available in the Zenodo repository [81]. Supplementary material is available online [82].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. S.R.S.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, validation, visualization, writing—original draft, writing—review and editing; C.M.: data curation, methodology, resources, validation, writing—review and editing; M.A.V.: data curation, formal analysis, methodology, software; H.S.: resources, supervision, validation, writing—review and editing; T.S.: resources, validation, writing—review and editing; P.B.: resources, validation, writing—review and editing; P.V.: methodology, writing—review and editing; G.S.: resources, software, writing—review and editing; Q.J.: resources, validation, writing—review and editing; E.P.: conceptualization, funding acquisition, resources, supervision, validation, writing—review and editing; C.G.-W.: conceptualization, funding acquisition, methodology, resources, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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