Facultad de Ciencias
Universidad de Chile

Diferencias en el éxito evolutivo de dos géneros de Littorinidae Antárticos: una aproximación desde la Biogeografía histórica.

Tesis entregada a la

Universidad de Chile

en cumplimiento parcial de los requisitos

para optar al Grado de Doctor(a) en Ciencias

con Mención en Ecología y Biología Evolutiva

Facultad de Ciencias

Por

Sebastián Alejandro Rosenfeld Sekulovic

Octubre, 2024

Director de Tesis: Dr. Elie Poulin

Co-Director de Tesis: Dr. Claudio González-Wevar

FACULTAD DE CIENCIAS
UNIVERSIDAD DE CHILE
INFORME DE APROBACION
TESIS DE DOCTORADO/MAGÍSTER

Se informa a la Escuela de Postgrado de la Facultad de Ciencias que la Tesis de Doctorado/ presentada por el/la candidato/a.

Sebastián Alejandro Rosenfeld Sekulovic

Ha sido aprobada por la comisión de Evaluación de la tesis como requisito para optar al grado de Doctorado en Ciencias con mención en Ecología y Biología Evolutiva, en el examen de Defensa Privada de Tesis rendido el día 4 de Septiembre del 2024

Director/a de Tesis:
Dr. Elie Poulin

Co-Director/a de Tesis:
Dr. Claudio González-Wevar

Comisión de Evaluación de la Tesis:

Dr. David Véliz
Dr. Felipe Hinojosa
Dr. Marco Méndez
Dr. Erasmo Macaya

Dedicado a mi querido padre que siempre me apoyo a seguir la carrera académica.

RESUMEN BIOGRÁFICO

Como Biólogo Marino nacido en la región de Magallanes siempre me intereso mi entorno natural y el maravilloso paisaje que me rodeaba desde niño. También, desde muy chico acompañaba a mi padre que era ingeniero forestal a los bosques de lenga donde él trabajaba. Por lo que, eso me marco mucho para elegir una carrera científica relacionada a las ciencias biológicas. El año 2005 ingrese a la carrera de Biología Marina en la Universidad de Magallanes, en donde curse mis estudios de pregrado. El año 2007 entre a trabajar al laboratorio del Dr. Andrés Mansilla, el cual siempre me ha entregado todo su apoyo hasta el día de hoy. Además, a través del Dr. Mansilla pude conocer al Dr. José Stuardo un reconocido taxónomo chileno de moluscos, el cual me recibió en su laboratorio el año 2008 y con el cual mantuve contacto por varios años. El poder conocer al Dr. Stuardo me inspiro a seguir el estudio de la taxonomía de moluscos marinos de la costa chilena y también de la Antártica. Durante mi magister tuve la oportunidad de empezar a colaborar con el Dr. Claudio González-Wevar y el Dr. Elie Poulin científicos que realizaban investigación hace varios años en invertebrados marinos Antárticos. Estos vínculos que genere con ellos me permitieron no solo expandir mis redes de trabajo sino también posicionarme como un especialista de moluscos marinos del Océano Austral. A lo largo de mi carrera académica he podido publicar muchos artículos científicos y libros de divulgación científica, lo que me ha posicionado como uno de los investigadores jóvenes más productivos en las ciencias marinas en la región de Magallanes.

Agradecimientos

El termino de este proceso académico es el resultado de un esfuerzo personal, pero también el incondicional apoyo de familia, profesores, colegas y amigos(as)

Quiero empezar agradeciendo a mi tutor el Dr. Elie Poulin por todo su apoyo durante todo el proceso de mi doctorado. Fueron años bastantes movidos desde que llegue a Santiago, pero siempre creíste en mí y valoraste mi trabajo y me diste mis espacios y libertad en los momentos difíciles que pase durante el doctorado. Valoro mucho tú conocimiento y experiencia y aprendí mucho de las reuniones de trabajo en donde analizabas mis resultados y cuestionabas mis escenarios (inflection point). Muchas gracias por todo y ahora que vamos a hacer colegas espero que sigamos trabajando a futuro.

El desarrollo de esta investigación se pudo realizar también por el invaluable apoyo de mi co-director de tesis el Dr. Claudio Gónzalez-Wevar. Hace más de 10 años que nos conocemos y trabajamos juntos y la verdad es que esa interacción a generado muchos frutos. He aprendido mucho de tú trabajo y rigurosidad y también valoro mucho tú peculiar sentido del humor y tú calidad humana. Tú fuiste una de las personas que más me insistió que hiciera doctorado y aunque me demoré en tomar la decisión finalmente lo pude concretar. Muchas gracias por todo tú apoyo incondicional durante todo este proceso y espero con ansias los proyectos de investigación que se vendrán a futuro.

Agradezco profundamente a mis profesores de la Universidad de Magallanes el Dr. Andrés Mansilla y el Dr. Ricardo Rozzi, los cuales siempre me han apoyado incondicionalmente y estuvieron pendientes del desarrollo de esta tesis durante mi estadía en Santiago. ¡¡¡¡Muchas gracias por todo!!!!

Toda investigación necesita financiamiento y por lo tanto quiero agradecer a varios proyectos que apoyaron esta tesis: primero quiero agradecer programa de la Iniciativa Científica Milenio ICN2021_002, por el financiamiento de los terrenos,

análisis de muestra, secuenciación y financiamiento de congresos nacionales e internacionales. También, al proyecto Fondecyt regular 1210787 por su apoyo en la obtención de muestras y análisis de laboratorio. Al Instituto Antártico Chileno, en especial al proyecto DG-10_22 del programa de Fondos de Apoyo a Tesis de Posgrado en Temas Antárticos por facilitar la entrega de recursos para la ejecución exitosa de los objetivos de esta investigación. Gracias a ANID y su beca Doctorado Nacional # 21200737 y en especial por la entrega de los beneficios complementarios que me permitieron realzar la calidad de esta tesis doctoral. Finamente, agradecer al Centro Internacional Cabo de Hornos ANID/BASAL FB210018 por su apoyo en los terrenos en la región de Magallanes.

Esta tesis no estuvo libre de complicaciones a la hora de los terrenos, el laboratorio y los análisis por lo que quiero agradecer a las personas con las que me vincule durante el doctorado y me permitieron avanzar en mi investigación. Agradezco a mi familia del laboratorio LEM por esas conversaciones de ciencias mientras compartíamos un café, también por la generación de ideas de investigación y también por su apoyo cuando no me amplificaban las PCR. En especial a Guillaume Schwob, Francisca Rodríguez, Valentina Bernal y Sandra Brito. Agradezco a Moisés Valladares por ayudarme en la fase final de mis análisis de datos y también a mi laboratorio en Punta Arenas LEMAS, por hacerme sentir en casa cada vez que viajaba a la región. En especial a Juan Pablo Rodríguez, Fabio Méndez, Zambra López y Francisco Bahamonde.

El termino de esta investigación no solamente requiere una apoyo académico y financiero sino también un apoyo emocional. Es por lo que quiero agradecer a mis dos mujeres más importantes en mi vida: Claudia y Violeta. Claudia tú constante apoyo en mi persona me permitió salir adelante en los momentos más difíciles de los últimos años. Nuestras conversaciones y reflexiones me ayudan a seguir transitando no solo la ciencia sino también la vida que estamos construyendo. Te admiro mucho como científica y como persona, muchas gracias por todo. Violeta, llegaste y ni te imaginas cuanto has cambiado mi vida y mi percepción de las cosas. Tú constante sonrisa y tú presencia me motivan a seguir siendo un mejor hombre y también un mejor científico.

Gracias por llegar a mi vida e iluminarla a través de tus ojos.

Quiero agradecer sinceramente y de corazón a mi familia nuclear mi madre Beatriz Sekulovic y a mis hermanos(as) Carolina y Gonzalo. Ya que me han brindado todo su apoyo y cariño a lo largo de toda mi trayectoria académica. Muchas gracias por creer en mí y por apoyarme los quiero mucho.

Quiero dedicar un espacio para agradecer a mi padre Mauricio Rosenfeld, que, aunque partiste ya hace muchos años, no hubiera podido llegar hasta esta instancia sin tú apoyo y motivación. Querido padre el término de este proceso va dedicado a tu memoria y con esto también cumplo la deuda que tenía pendiente contigo, muchas gracias por todo y espero que estes muy orgulloso.

Finalmente, quiero agradecer muy sinceramente a Fernando Basualdo por todo el apoyo incondicional que me has brindado desde siempre y especialmente cuando falleció mi padre tú seguiste impulsando mi carrera en la ciencia. Has sido como un segundo padre para mí y estoy muy agradecido por todo.

Índice

Abstract

Introduction

RESUMEN

Los litorínidos de altas latitudes incluyen tres géneros intermareales y submareales: *Laevilitorina* Pfeffer 1886, *Pellilitorina* Pfeffer 1886 y *Laevilacunaria* Powell 1951 (Reid 1989). El género *Laevilacunaria* se caracteriza por presentar una distribución restringida al Océano Austral (OA), principalmente algunas islas subantárticas (South Georgia, Crozet y Kerguelen) y Península Antártica. Contrariamente, *Laevilitorina* es uno de los géneros de gasterópodos marinos con mayor distribución en latitudes altas del hemisferio sur y el OA. Un rasgo importante que tienen ambos géneros es que presentan un ciclo de vida sin larva pelágica de vida libre. Por lo tanto, estos géneros representan un modelo biogeográfico muy interesante, ya que uno presenta una distribución más amplia y un mayor número de especies que el otro a pesar de que poseen modos de desarrollo y ecologías similares. Esta tesis busca establecer el origen y la diversificación de *Laevilitorina* y *Laevilacunaria* en el OA, además de abordar la taxonomía y sistemática de estos géneros. En primer lugar, ser realizó una actualización de las ocurrencias del género *Laevilitorina* a lo largo de su distribución, y además se realizó una revisión exhaustiva de su historia natural, para lograr una síntesis del estado actual de la sistemática y definir su distribución en altas latitudes. En segundo lugar, se abordó el estatus taxonómico de la especie *Laevilitorina caliginosa s.l* a lo largo de su distribución utilizando herramientas morfológicas y moleculares. En tercer lugar, se propuso una hipótesis sobre el origen y diversificación de las especies del género *Laevilitorina* y *Laevilacunaria* a partir de la reconstrucción filogenética y de rango geográfico ancestral con marcadores mitocondriales y nucleares a lo largo de sus distribuciones.

Los resultados muestran que al analizar morfológica y molecularmente distintas poblaciones de *L. caliginosa* a lo largo de su distribución, identificamos distintos linajes muy divergentes dentro de esta especie. Por lo que, se describieroncuatro nuevas especies para la región de Magallanes, en donde *L. pepita* sp. nov., *L. magellanica* sp. nov. y *L. fueguina* sp. nov. se encuentran en el Estrecho de Magallanes. La especie *L. hicana* sp. nov. se restringe a Isla Hornos en Cabo de Hornos. Asimismo, se pudo esclarecer que los registros de *L. caliginosa* para Antártica, South Georgia, Kerguelen, Crozet y Macquarie corresponden realmente a la especie *L. venusta*. De esta forma, *L. caliginosa* estaría restringida a la costa austral de Sudamérica, Malvinas y Georgias del Sur. Finalmente, al incluir las especies de *Laevilacunaria* al análisis filogenético se evidencio que los géneros *Laevilacunaria* y *Laevilitorina* son parafiléticos. En esta tesis se propone una reclasificación de *Laevilitorininae* en cuatro géneros distintos basados en diferencias moleculares y morfológicas. Además, nuestros resultados sugieren que el origen evolutivo y la diversificación de Laevilitorininae en el OA muestra que el ancestro de la subfamilia Laevilitorininae es Gondwánico, cuya primera diversificación coincide con la fase final de fragmentación del Gondwana. La diversificación temprana de este grupo habría estado influenciada por procesos de vicarianza en donde se formarían cuatro grandes clados. Finalmente, más recientemente los eventos de dispersión a la larga distancia con establecimiento jugaron un papel fundamental en la distribución geográfica actual de *Laevilacunaria* y *Laevilitorina*. Estos eventos, facilitados probablemente por *rafting* a través de macroalgas flotantes, permitieron que las especies de *Laevilacunaria* y *Laevilitorina* cruzaran barreras oceanográficas y colonizaran nuevas áreas.

ABSTRACT

The high-latitude littorinids include three intertidal and subtidal genera: *Laevilitorina* Pfeffer 1886, *Pellilitorina* Pfeffer 1886 and *Laevilacunaria* Powell 1951 (Reid 1989). The genus *Laevilacunaria* has a restricted distribution in the Southern Ocean (SO), mainly in some sub-Antarctic islands (South Georgia, Crozet and Kerguelen) and the Antarctic Peninsula. In contrast, *Laevilitorina* is one of the most widely distributed marine gastropod genera in high latitudes of the Southern Hemisphere and the SO. An important trait of both genera is that they have a life cycle without free-living pelagic larvae. Therefore, these genera represent a very interesting biogeographical model, since one presents a wider distribution and a greater number of species than the other despite having similar developmental modes and ecologies. This thesis aims to establish the origin and diversification of *Laevilitorina* and *Laevilacunaria* in the SO, in addition to addressing the taxonomy and systematics of these genera. First, an update of the occurrences of the genus *Laevilitorina* throughout its distribution was carried out, and a comprehensive review of its natural history was performed to achieve a synthesis of the current state of systematics and define its distribution in high latitudes. Second, the taxonomic status of the species *Laevilitorina caliginosa* s.l throughout its distribution was addressed using morphological and molecular tools. Third, a hypothesis on the origin and diversification of species of the genus *Laevilitorina* and *Laevilacunaria* was proposed based on phylogenetic and ancestral geographic range reconstruction with mitochondrial and nuclear markers throughout their distributions.

The results show that by morphologically and molecularly analyzing different populations of *L. caliginosa* throughout its distribution, we identified distinct and highly divergent lineages within this species. Therefore, four new species were described for the Magellanic region, where *L. pepita* sp. nov., *L. magellanica* sp. nov. and *L. fueguina* sp. nov. are found in the Strait of Magellan. The species L. hicana sp. nov. is restricted to Isla Hornos at Cape Horn. Likewise, it was possible to clarify that the records of *L. caliginosa* for Antarctica, South Georgia, Kerguelen, Crozet and Macquarie actually correspond to the species *L. venusta*. Thus, *L. caliginosa* would be restricted to the southern coast of South America, the Falklands and South Georgia. Finally, by including the species of *Laevilacunaria* in the phylogenetic analysis, it became evident that the genera *Laevilacunaria* and *Laevilitorina* are paraphyletic. In this thesis we propose a reclassification of Laevilitorininae into four distinct genera based on molecular and morphological differences. Furthermore, our results suggest that the evolutionary origin and diversification of Laevilitorininae in the OA shows that the ancestor of the Laevilitorininae subfamily is Gondwananic, whose first diversification coincides with the final phase of Gondwana fragmentation. The early diversification of this group would have been influenced by vicariance processes where four major clades would be formed. Finally, more recently long-distance dispersal events with establishment played a key role in the current geographic distribution of *Laevilacunaria* and *Laevilitorina*. These events, probably facilitated by rafting through floating macroalgae, allowed *Laevilacunaria* and *Laevilitorina* species to cross oceanographic barriers and colonize new areas.

ESTRUCTURA DE LA TESIS

Esta tesis consiste en una introducción general, tres capítulos, conclusiones generales y tres anexos. En la Introducción general, se presenta el contexto general de la biogeografía del Océano Austral y se revisa el estado actual del conocimiento sobre los litorínidos de altas latitudes*.* El Capítulo I consiste en el estudio de la distribución del género *Laevilitorina* en todo el hemisferio sur, a partir de datos publicados en literatura científica y registros de museos, completado por los diversos muestreos realizados durante el desarrollo de esta tesis. Este capítulo, concentró una revisión bibliográfica de los distintos registros de ocurrencia del género y su historia natural, con especial énfasis en las especies Antárticas y Subantárticas lo que permite tener un estado actualizado de su distribución y estatus taxonómico.

El Capítulo II retoma los comentarios y discusión del capítulo anterior en relación con el estatus taxonómico de la especie *Laevilitorina caliginosa*. El objetivo de este capítulo fue describir nuevas especies de *Laevilitorina* para la región de Magallanes y esclarecer el estatus taxonómico de la especie nominal *Laevilitorina caliginosa.* Este capítulo evalúa las relaciones filogenéticas de los distintos linajes dentro de *L. caliginosa*, utilizando una aproximación filogenética multi-locus (*cox*1 y 28S) y análisis morfológico de la concha y de la rádula.

Tras establecer la distribución (Capítulo I) y esclarecer el estatus taxonómico de las especies de *Laevilitorina* en la región de Magallanes (Capítulo II), realizamos una filogenia más completa incluyendo más especies de *Laevilitorina* de las Islas Malvinas y de Antártica junto con todas las especies de *Laevilacunaria* en el Capítulo III*.* El objetivo de este último capítulo fue esclarecer las relaciones filogenéticas dentro de la subfamilia Laevilitorininae (Laevilacunaria + Laevilitorina), además de presentar la filogenia más completa de la familia Littorinidae hasta la fecha. Este capítulo determina los tiempos y modos de diversificación de ambos géneros, con mayor énfasis en las especies de *Laevilacunaria*. Además, este capítulo evalúa si su distribución geográfica se debe a una diversificación antigua por vicarianza o a eventos de dispersión de larga distancia más recientes, utilizando una aproximación filogenética multi-locus (12S+16S+cox1+28S).

En la sección de Conclusiones generales, entregamos un resumen de los principales resultados y contribuciones de este estudio, proponiendo una nueva clasificación dentro de la subfamilia Laevilitorininae. Además, en esta sección planteamos algunas proyecciones, relacionadas principalmente con la necesidad de poder incorporar material de las especies de Nueva Zelanda y Australia y también resaltamos la importancia de la incorporación de herramientas morfológicas y moleculares para los estudios en sistemática y biogeografía.

INTRODUCCIÓN GENERAL

Biogeografía en el Océano Austral

Los análisis biogeográficos de los organismos marinos bentónicos del Océano Austral (OA) han identificado dos grandes regiones: Antártica y Subantártica (Koubi et al. 2014). Subantártica incluye i) la provincia Magallánica en la costa austral de Sudamérica, ii) las islas de Nueva Zelanda, iii) las islas subantárticas del Océano Índico y iv) la isla Macquarie (Fig. 1). Antártica representaría una única provincia que incluye el continente antártico y algunas islas situadas al sur del Frente Polar Antártico (FPA) como la Georgia del Sur, las islas Sandwich del Sur y la Isla Bouvet (Koubbi et al. 2014). A pesar de esta marcada bioregionalización, las asociaciones faunísticas dentro y entre estas provincias no pueden ser explicadas por una única hipótesis biogeográfica y dependen en gran medida del grupo de organismos analizado (Linse et al. 2006; Koubbi et al. 2014; González-Wevar et al. 2017, 2018, 2019, 2022). No obstante, se han propuesto algunas reglas biogeográficas generales entre las que se incluyen las altas tasas de endemismo de especies (> 70% en algunos grupos), la existencia de una única provincia Antártica, claramente separada de otras provincias subantárticas, y la marcada distinción entre las islas subantárticas asociadas a Sudamérica y las de Nueva Zelanda (Crame et al. 1999; Koubbi et al. 2014; Halanych & Mahon 2018).

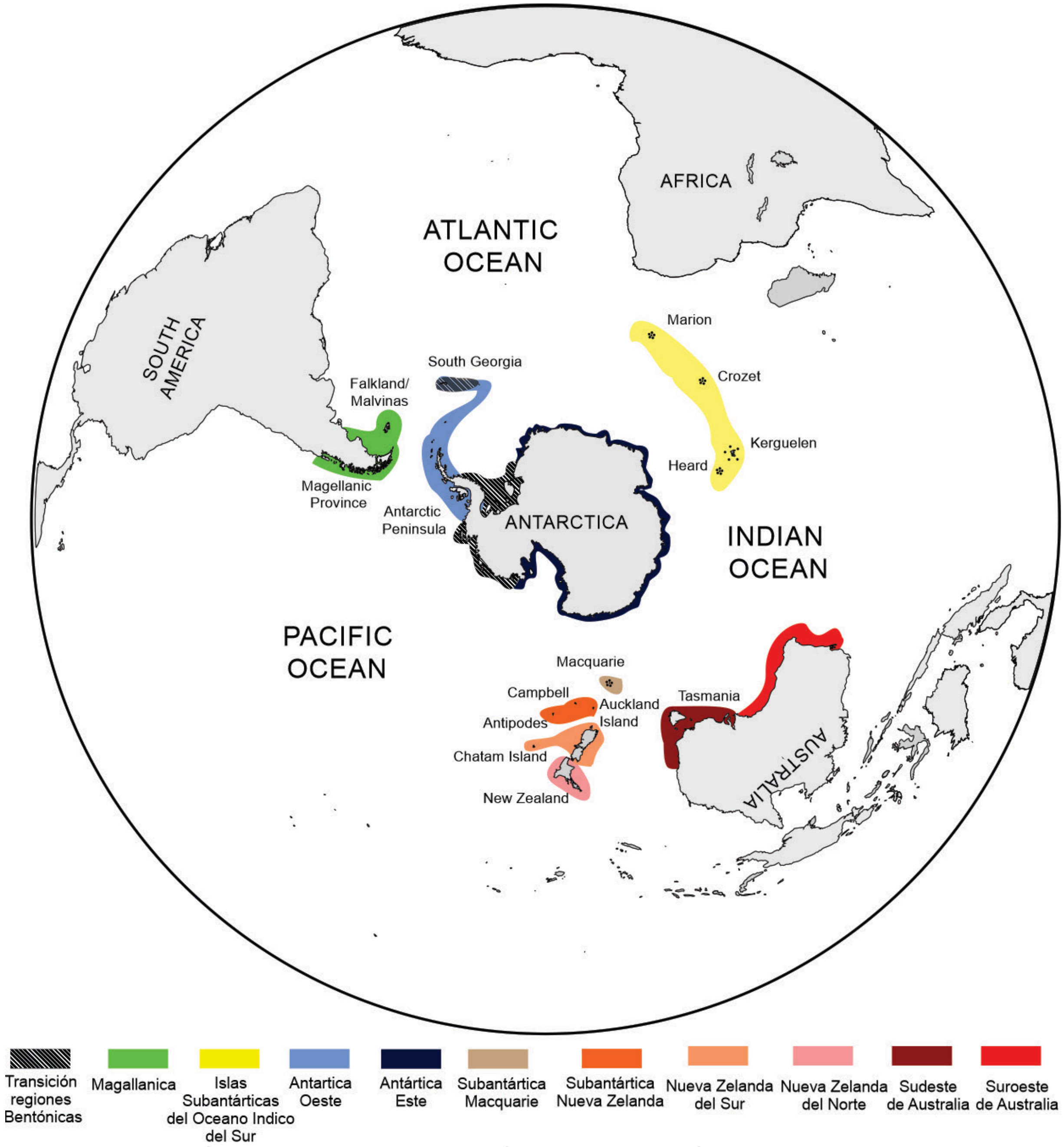


Figura 1) delimitación de las provincias biogeográficas marinas según Spalding et al. (2007) y Koubbi et al. (2014)

La presencia de especies de un mismo género en distintas provincias biogeográficas del OA puede explicarse a través de dos mecanismos diferentes: la vicarianza (e.g Paternello et al. 1996; Williams et al. 2003) y la dispersión a larga distancia con establecimiento (DLDE) (Sanmartin & Ronquist, 2004; Fraser et al. 2009; Crisp et al. 2011; González-Wevar et al. 2018). En primer lugar, la vicarianza por tectónica de placas ha sido descrita como un proceso biogeográfico clave que altera físicamente a las poblaciones, que generalmente ocurre producto de eventos geológicos importantes dando como resultado procesos de divergencia genética y especiación (Waters & Craw 2006). La DLDE como hipótesis alternativa a la vicarianza es un mecanismo a través del cual individuos adultos o propágulos (e.g. larvas planctónicas, masas de huevos), son dispersados de manera excepcional superando barreras impuestas por la distancia geográfica (e.g. Océanos) logrando establecerse en una nueva área (Crisp et al. 2011). Si no hay flujo genético (o es mínimo) entre el área ancestral y el área recientemente colonizada, las poblaciones separadas evolucionaran de manera independiente y, en última instancia, se producirá especiación (Crisp et al. 2011). Por lo tanto, entender los procesos que determinan los patrones biogeográficos de la biota marina en el OA, así como también conocer el origen de ciertos grupos endémicos son fundamentales para comprender su historia evolutiva y predecir sus posibles trayectorias en un escenario de cambio climático global (Barnes & Peck 2008). Durante las últimas dos décadas ha habido una discusión acerca del rol potencial de la vicarianza y de la DLDE en la biogeografía del OA, así como también al posible origen Antártico de algunos taxa. Los avances en las aproximaciones moleculares han contribuido a poner a prueba ambas hipótesis biogeográficas y actualmente existe un consenso sobre la relevancia combinada de ambos mecanismos en la evolución de la biota en el OA (e.g. Paternello et al. 1996;

Williams et al. 2003; González-Wevar et al. 2018; Fraser et al. 2019). La evolución de algunos grupos antárticos muestra niveles de divergencia genética asociados a los procesos de deriva continental (e.g. Paternello et al. 1996; Levicoy et al. 2021). Por ejemplo, el gasterópodo intermareal *Austrolitorina* distribuido en Sudamérica, Nueva Zelanda y Australia, evidenció tiempos de divergencia que se asocian a las últimas etapas de fragmentación de Gondwana (Williams et al. 2003). Por otra parte, existen evidencias recientes de que el origen y diversificación de varios taxa como invertebrados marinos (e.g. Poulin et al. 2014; González-Wevar et al. 2017, 2019, 2021), macroalgas (Billard et al. 2015; Ocaranza et al. 2018) e incluso pingüinos (Vianna et al. 2017; Frugone et al. 2018) se produjo no más allá de los 10 Mya, tiempo más reciente que la separación física de las masas continentales del OA o incluso del inicio de la CCA (González-Wevar et al. 2017, 2019, 2021; Poulin et al. 2014; Crame, 2018; Halanych & Mahon 2018).

Estudios filogenéticos actuales han puesto a prueba la hipótesis de si algunos géneros endémicos del OA se habrían originado y diversificado dentro de Antártica, y por lo tanto las especies que actualmente habitan las costas del OA corresponderían a taxones relictos, o si habrían colonizado posterior al aislamiento del continente Antártico (Göbbeler & Klussmann-Kolb 2010). Por ejemplo, la evidencia molecular en el orden de gasterópodos Pleurobranchomorpha sugieren que este grupo se habría originado en Antártica (Göbbeler & Klussmann-Kolb 2010). Sin embargo, en el caso *Bathyberthella* la edad de separación con el género hermano de aguas tropicales *Euselenops* habría ocurrido hace 20 Mya, produciéndose una recolonización de

Antártica mediada por un evento de DLDE en periodos más cálidos del Mioceno medio (Göbbeler & Klussmann-Kolb 2010).

Importancia del rafting como mecanismo de transporte en el OA

En general las asociaciones ecológicas son muy relevantes debido a que los organismos marinos que habitan en macroalgas pueden utilizarlas como alimento y refugió frente a la depredación, lo cual puede ser una ventaja frente a las especies que habitan exclusivamente sobre roca (Vermeij 1992). Además, los organismos que viven asociados a macroalgas podrían dispersar junto a ellas (Nikula et al. 2010, 2012; González-Wevar et al., 2021, 2022). En este sentido, para el caso de organismos con bajo potencial de dispersión, particularmente aquellas especies que carecen de estadios larvales de vida libre, la dispersión puede producirse a través de vectores bióticos como los “kelps” mediante rafting. El rafting es un mecanismo fundamental para la dispersión geográfica de los organismos asociados a macroalgas, ya que mantiene la conectividad entre las poblaciones locales y puede establecer nuevas poblaciones cuando se produce el asentamiento al llegar a nuevas zonas geográficas (Hinojosa et al. 2010, 2011; Fraser et al. 2011; Wichmann et al. 2012). A modo de ejemplo, estudios recientes en *Durvillaea antarctica* (cochayuyo) utilizando herramientas genómicas revelaron que individuos de esta especie logran viajar más de 20.000 km desde poblaciones de Islas subantárticas (Georgias del Sur e islas Kerguelen), pudiendo llegar hasta las costas de la Península Antártica. Durante este viaje pueden transportar varios organismos asociados que podrían revelarse como potenciales colonizadores (Fraser et al. 2018, 2022; Ávila et al. 2020). Por lo tanto, la alta dominancia de especies de macroalgas boyantes en Subantártica hace que el rafting sea un mecanismo de transporte importante que permite explicar procesos biogeográficos de DLDE en el OA (Waters 2008). Ejemplos de rafting sobre macroalgas ha sido documentado en isópodos (Nikula et al. 2010, 2012) crustáceos (Nikula et al. 2010) y moluscos (Cumming et al. 2014; González-Wevar et al. 2016, 2018, 2021).

En este sentido, es importante destacar que en moluscos costeros con bajo potencial de dispersión el rafting ha jugado un rol muy importante en los procesos evolutivos, en particular para distintos géneros de gasterópodos (González-Wevar et al. 2018, 2021). Por ejemplo, especies del género *Siphonaria* y *Margarella* se caracterizan por tener un modo de desarrollo bentónico protegido, sin estadios larvales de vida libre, y se distribuyen ampliamente a lo largo de la provincia Subantártica, desde Sudamérica hasta Kerguelen (González-Wevar et al. 2018, 2021). Este alto nivel de homogeneidad genética a través de miles de kilómetros se ha explicado principalmente por la conectividad de las poblaciones a través de DLDE mediada por el rafting (González-Wevar et al. 2018, 2021). Otro aspecto relevante, es lo que ocurre al norte y al Sur del FPA (González-Wevar et al. 2021). Por ejemplo, en el caso de *Margarella* se encuentra una sola especie al norte del FPA, distribuida a lo largo de la provincia Subantártica. En contraste, al sur del FPA, *Margarella* muestra un patrón biogeográfico totalmente distinto: i) existe un mayor número de especies a lo largo de la provincia Antártica y ii) las especies están restringidas principalmente a la provincia Antártica (González-Wevar et al. 2021). Este patrón tan contrastante se ha explicado principalmente porque al sur FPA, a lo largo de Península Antártica no existe la presencia de especies de “kelps” como *Durvillaea antarctica* y *Macrocystis pyrifera* y por lo tanto esto habría generado una menor conectividad entre poblaciones antárticas con las de Georgia del Sur favoreciendo así la diversificación del grupo (González-Wevar et al. 2021).

En resumen, las características ecológicas (e.g. hábitat, asociación a macroalgas) y del ciclo de vida de un grupo en particular pueden influir directamente en la historia biogeográfica y filogenética, afectando las tasas de evolución, diversificación, dispersión y extinción (Reid 1989; González-Wevar et al. 2021). Además, la existencia de eventos excepcionales de dispersión entre Subantártica y Antártica sugiere que la Antártica no estuvo y no está biológicamente aislada y que el rafting podría ser un fenómeno frecuente y contemporáneo a través del FPA (Fraser et al. 2020; Macaya et al. 2020; Fraser et al. 2022). En el OA, un grupo diverso y representativo de ambientes costeros que presentan algún grado de asociación con macroalgas son los distintos representantes de la familia Littorinidae (Reid 1989).

Litorínidos como modelos biogeográficos en latitudes altas del hemisferio sur

Una de las familias más representativa y diversa de moluscos someros antárticos y subantárticos son los Littorinidae (Powell, 1960). Los litorínidos de altas latitudes se dividen en tres géneros intermareales y submareales: *Laevilitorina* Pfeffer 1886, *Pellilitorina* Pfeffer 1886 y *Laevilacunaria* Powell 1951 (Reid 1989). El género *Laevilacunaria* se caracteriza por presentar una distribución restringida al OA, encontrándose en algunas islas subantárticas (South Georgia, Kerguelen y Crozet) y en la Península Antártica (Reid 1989; Schmider et al. 2023) (Fig. 2). Pellilitorina, presentan una distribución dentro del OA, encontrándose en Antártica Oeste, Antártica Este, Georgias del Sur y Kerguelen y Crozet. *Laevilitorina* es uno de los géneros de gasterópodos marinos con mayor distribución en latitudes altas del hemisferio sur y el OA (Reid 1989; Rosenfeld et al. 2022). Su distribución actual comprende Sudamérica, Nueva Zelanda, el Sur de Australia, Tasmania, Península Antártica, mar de Weddell, Antártica del Este, y varias islas subantárticas (Islas Falkland/Malvinas, Georgias del Sur, Crozet, Kerguelen, Heard, Macquarie, Campbell, Auckland, Antipodas) (Fig. 2).

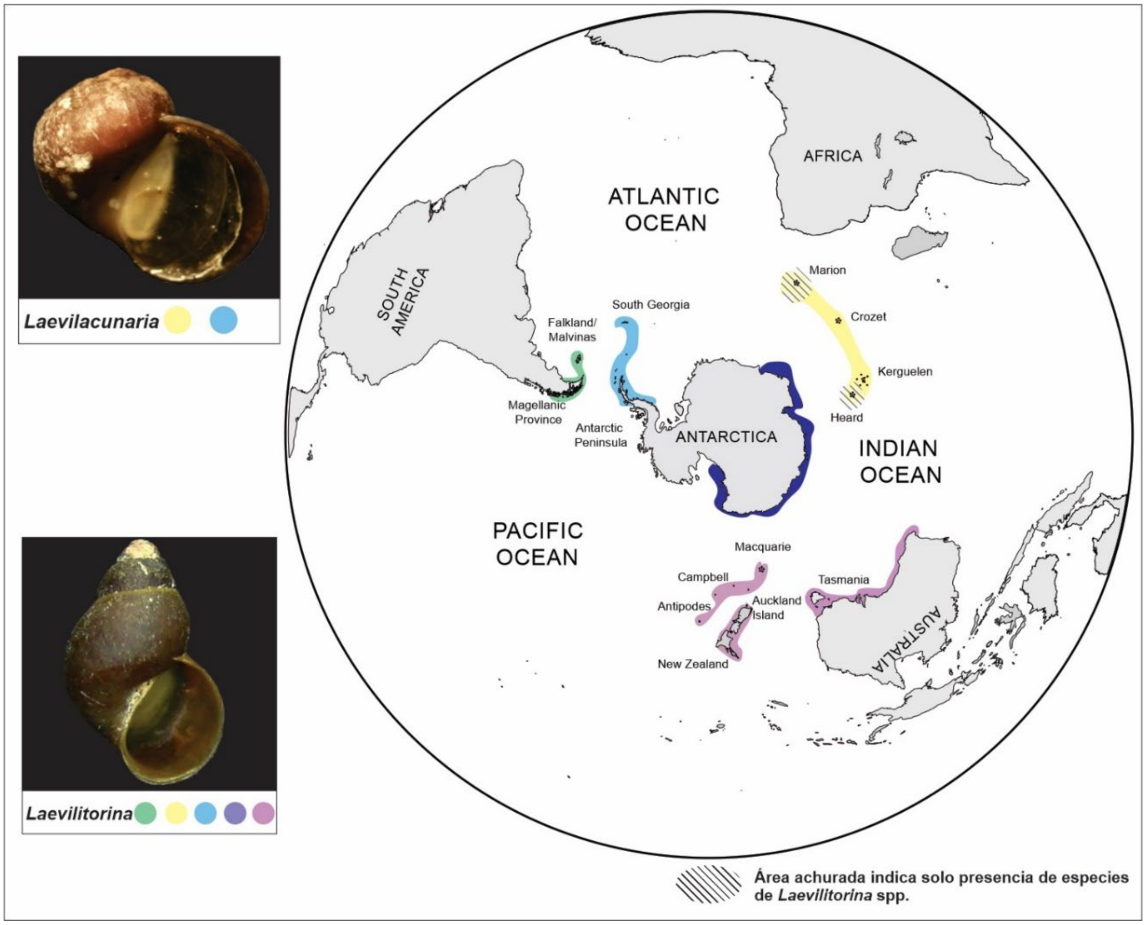


Figura 2. Mapa de la distribución de los géneros *Laevilitorina* y *Laevilacunaria* en el Océano Austral y areas adyacentes. Los colores debajo de cada panel indica la distribución geográfica de cada genero.

Al igual que muchas especies de Littorinidae la gran mayoría de las especies de estos tres géneros habitan costas rocosas someras donde pueden estar asociados a macroalgas (Simpson 1972; Reid 1989; Amsler et al. 2015; Rosenfeld et al. 2017). Sin embargo, a diferencia del patrón general de hábitat en los Littorinidae, *Laevilacunaria* puede ser comunes en ambientes submareales. Otro rasgo importante de los litorínidos antárticos y subantárticos, es que presentan un ciclo de vida sin larva pelágica de vida libre, en la cual, la hembra deposita masas de huevos en roca o frondas de macroalgas y posteriormente eclosiona un juvenil (Picken 1979; Simpson & Harrington 1985) (Fig. 3a). Una posible consecuencia de este modo de desarrollo bentónico protegido es que las especies presentarían un bajo potencial de dispersión, que daría como resultado un rango geográfico más estrecho (Simpson & Harrington 1985; Gonzalez-Wevar et al. 2022) (Fig. 3b). Efectivamente, una de las características del género *Laevilacunaria* es que presenta generalmente una distribución relativamente restringida al OA (Fig. 2). En contraste, *Laevilitorina* exhibe la distribución más amplia de los litorínidos Antárticos alcanzando zonas más templadas de Nueva Zelanda y Australia (Fig. 2).

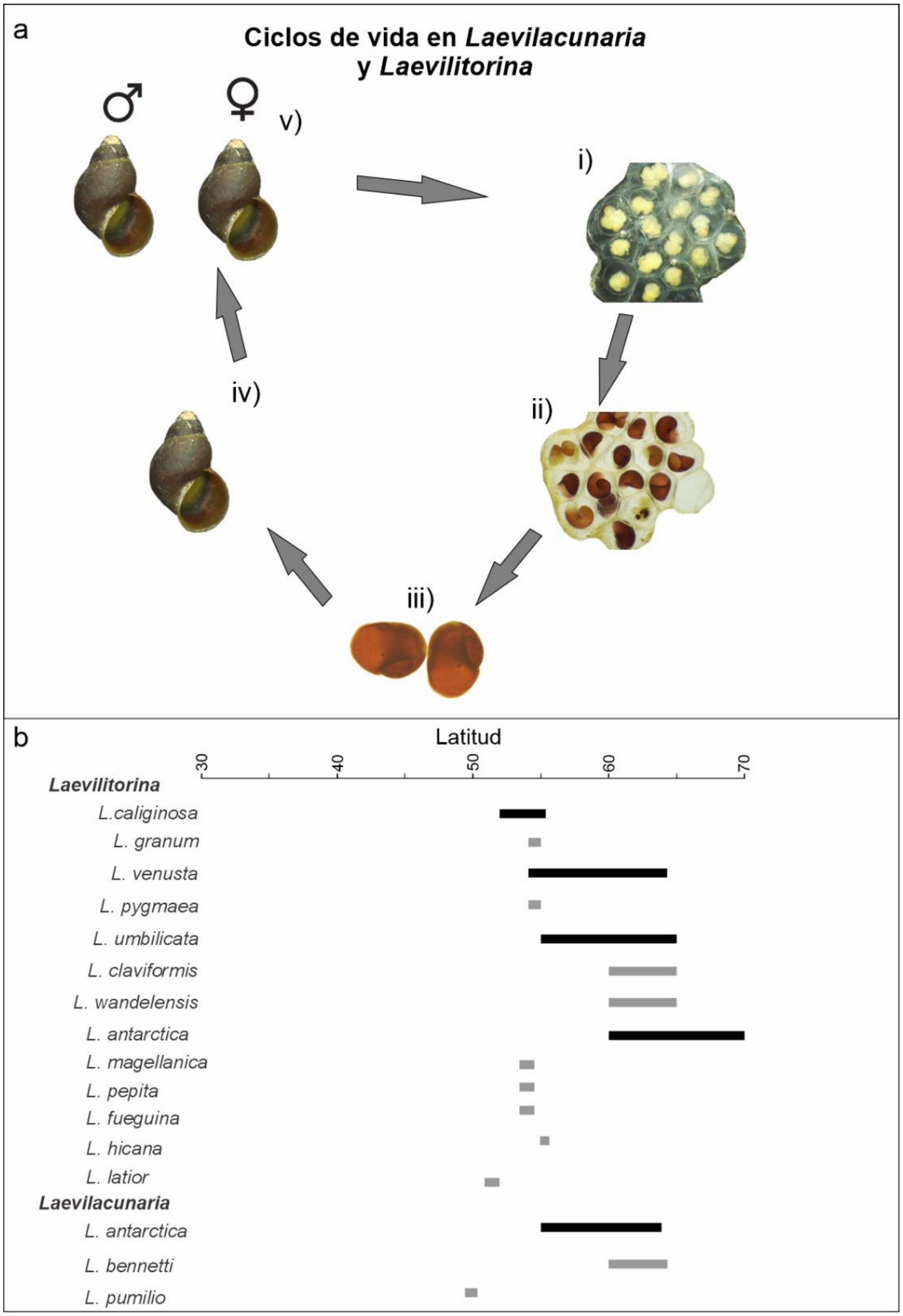


Figura 3. a) Ciclo de vida descrito para los géneros *Laevilacunaria* y *Laevilitorina* sin estadio larval planctótrifico, i) vista general de la masas de huevo con embriones en etapa temprana, ii) embriones en fase avanzada, iii) juveniles recién eclosionados, iv) adulto en desarrollo y v) Macho y hembra del género. B) Distribución latitudinal de las especies de *Laevilacunaria* y *Laevilitorina* en las provincias subantárticas y Antárticas, barras en gris indican la presencia en una sola área geográfica y barras en negros en dos o más. (Fotografías del ciclo, Rosenfeld et al. 2022)

Otro aspecto importante que diferencia a estos dos géneros es el patrón de riqueza de especies. Por ejemplo, en la actualidad la base de datos WoRMS (http://www.marinespecies.org) reconoce 25 especies de *Laevilitorina* en toda su distribución, con cuatro especies descritas recientemente de la región de Magallanes (Rosenfeld et al. 2023). La región de Antártica del Oeste es la más diversa en número de especies (S=7) (Fig. 4ab), seguida por la provincia Magallánica (Fig. 4ab) (S=6). Por el contrario, *Laevilacunaria* incluye sólo tres especies, siendo Antártica del Oeste el área con mayor número de especies de este género (S=2) (Fig. 4ab). Sin embargo, un reciente estudio filogeográfico de *L. antarctica* reveló que las poblaciones de Georgia del Sur y la Península Antártica podrían representar unidades evolutivas distintas (González-Wevar et al., 2024). Por tanto, una revisión detallada de las especies de *Laevilacunaria* será muy relevante para comprender mejor la sistemática, el patrón de diversidad actual y la evolución de este grupo de caracoles littorínidos. Teniendo en cuenta las diferencias y similitudes mencionadas, surgen preguntas como ¿cuáles han sido los principales procesos y mecanismos evolutivos que han influido en los patrones actuales de distribución y riqueza de especies de estos géneros?

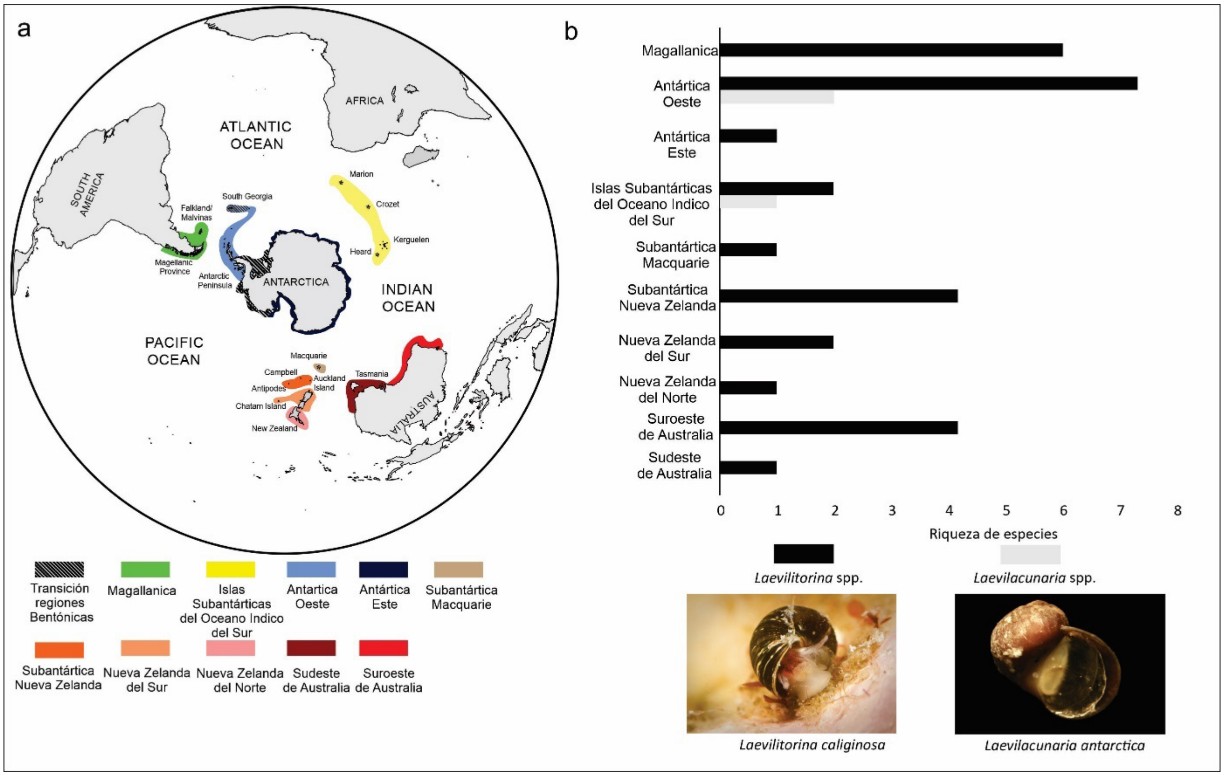


Figura 4 A) delimitación de las provincias biogeográficas marinas según Spalding et al. (2007) y Koubbi et al. (2014). B) riqueza de especies de *Laevilacunaria* y *Laevilitorina* en cada una de las provincias biogeográficas

Finalmente, estos dos géneros de littorínidos representan un modelo muy interesante para explorar los procesos subyacentes y el mecanismo evolutivo que han dado forma a sus patrones biogeográficos contrastados, a pesar de compartir el mismo modo de desarrollo y hábitats similares. Abordar el origen y la diversificación de *Laevilitorina* y *Laevilacunaria* a lo largo de su distribución y reconstruir la relación filogenética entre los litorínidos de latitudes más altas nos permitirá comprender mejor las trayectorias evolutivas de estos importantes gasterópodos del Océano Austral.

HIPÓTESIS Y OBJETIVOS

Hipótesis

H1: Considerando las similitudes ecológicas (hábitat) y del ciclo de vida (modo de desarrollo), y las marcadas diferencias en las distribuciones geográficas y la diversidad de especies entre los géneros *Laevilacunaria* y *Laevilitorina*: **la diversificación de *Laevilacunaria* habría ocurrido mediante eventos de dispersión a larga distancia con establecimiento (DLDE) desde islas Subantárticas hacía ambientes Antárticos, mientras que la diversificación en *Laevilitorina* se habría producido desde ambientes subantárticos o templados.**

En consecuencia, los análisis filogenéticos multi-locus y el análisis de reconstrucción del rango geográfico ancestral, debería mostrar que el género *Laevilacunaria* se originó en ambientes subantárticos y diversifico en Antártica, mientras que *Laevilitorina* habría tenido su centro de diversificación en áreas Subantárticas o templadas frías.

Objetivo General

Entender los mecanismos y procesos asociados al origen y diversificación del clado de litorínidos Antárticos *Laevilacunaria y Laevilitorina* a lo largo de su distribución y reconstruir los patrones biogeográficos históricos de los distintos linajes registrados.

CAPÍTULO I

ZooKeys 1127: 61–77 (2022)
doi: 10.3897/zookeys.1127.91310
https://zookeys.pensoft.net

DATA PAPER

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Complete distribution of the genus *Laevilitorina* (Littorinimorpha, Littorinidae) in the Southern Hemisphere: remarks and natural history

Sebastián Rosenfeld[1,2,3,4], Claudia S. Maturana[2,3,5], Hamish G. Spencer[6],
Peter Convey[2,3,7,8], Thomas Saucède[9], Paul Brickle[10,11], Francisco Bahamonde[1,3],
Quentin Jossart[9,12], Elie Poulin[2,5], Claudio Gonzalez-Wevar[2,13]

1 *Laboratorio de Ecosistemas Marinos Antárticos y Subantárticos, Universidad de Magallanes, Punta Arenas, Chile* **2** *Millennium Institute Biodiversity of Antarctic and Subantarctic Ecosystems (BASE), Las Palmeras 3425, Santiago, Chile* **3** *Cape Horn International Center (CHIC), Puerto Williams, Chile* **4** *Centro de Investigación Gaia-Antártica, Universidad de Magallanes, Avenida Bulnes 01855, Punta Arenas, Chile* **5** *Institute of Ecology and Biodiversity (IEB), Las Palmeras 3425, Santiago, Chile* **6** *Department of Zoology, University of Otago, Dunedin, New Zealand* **7** *British Antarctic Survey (BAS), Cambridge, UK* **8** *Department of Zoology, University of Johannesburg, Johannesburg, South Africa* **9** *Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté, 6, boulevard Gabriel, 21000, Dijon, France* **10** *South Atlantic Environmental Research Institute, Ross Road, Stanley, Falkland Islands, UK* **11** *School of Biological Sciences (Zoology), University of Aberdeen, Aberdeen, UK* **12** *Marine Biology, Université Libre de Bruxelles (ULB), Brussels, Belgium* **13** *Centro FONDAP IDEAL, Instituto de Ciencias Marinas y Limnológicas (ICML) Facultad de Ciencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile*

Corresponding author: Sebastián Rosenfeld (sebastian.rosenfeld@umag.c)

Academic editor: Frank Köhler | Received 5 August 2022 | Accepted 3 October 2022 | Published 2 November 2022

https://zoobank.org/44F6411B-41E1-4C99-86F0-62519C8CBA0F

Citation: Rosenfeld S, Maturana CS, Spencer HG, Convey P, Saucède T, Brickle P, Bahamonde F, Jossart Q, Poulin E, Gonzalez-Wevar C (2022) Complete distribution of the genus *Laevilitorina* (Littorinimorpha, Littorinidae) in the Southern Hemisphere: remarks and natural history. ZooKeys 1127: 61–77. https://doi.org/10.3897/zookeys.1127.91310

Abstract

Littorinid snails are present in most coastal areas globally, playing a significant role in the ecology of intertidal communities. *Laevilitorina* is a marine gastropod genus distributed exclusively in the Southern Hemisphere, with 21 species reported from South America, the sub-Antarctic islands, Antarctica, New Zealand, Australia and Tasmania. Here, an updated database of 21 species generated from a combination of sources is presented: 1) new field sampling data; 2) published records; 3) the Global Biodiversity Information Facility (GBIF) and The Atlas of Living Australia (ALA), to provide a comprehensive description of the known geographic distribution of the genus and detailed occurrences for each of the 21 species. The database includes 813 records (occurrences), 53 from field sampling, 174 from the literature, 128 from GBIF, and 458 from ALA. West Antarctica had the highest species richness (8 species), followed by sub-Antarctic islands of New Zealand (4 species) and the south-east shelf of Australia (4 species). The provinces of Magellan, New Zealand South Island, and sub-Antarctic Islands of the Indian Ocean include two species each. This study specifically highlights reports of *L. pygmaea* and *L. venusta*, species that have been almost unrecorded since their description. Recent advances in molecular studies of *L. caliginosa* showed that this species does not correspond to a widely distributed taxon, but to multiple divergent lineages distributed throughout the Southern Ocean. Ongoing molecular and taxonomic studies are necessary for a better understanding of the diversity and biogeography of this genus.

Keywords
Antarctic, endemism, Laevilitorininae, sub-Antarctic

Introduction

One of the most common challenges facing studies or the construction of inventories of biodiversity is the absence of detailed information on the distribution of taxa throughout the different geographical regions of the planet. Furthermore, species distribution data are usually scattered across different sources of information such as taxonomic reviews, species lists, reports and natural history collections (Beck et al. 2013). Therefore, it is important to merge these different sources into robust and freely accessible biodiversity databases. The Global Biodiversity Information Facility (GBIF) project has enabled the creation of a platform where museums, herbaria and researchers can publish their databases and make them freely available for use (Flemons et al. 2007). However, despite increasing the international effort devoted to the digitisation of specimen catalogues in museums and other repositories, even today only a small proportion of global records are estimated to have been made available online through the efforts of the GBIF and other platforms like the Ocean Biodiversity Information System (OBIS) (Ariño 2010; Maturana et al. 2019; OBIS 2022).

The family Littorinidae represents one of the most conspicuous and abundant components of intertidal communities that inhabit rocky shores across the world's coasts (Reid 1989). Being such a widespread and accessible group, they have been amongst the most intensively studied marine molluscs (Reid 2007; Reid and Williams 2012; González-Wevar et al. 2022). They play a significant role in the ecology of intertidal communities and have been widely used as models in microevolutionary studies of natural selection and genetic differentiation (Williams et al. 2003; Kess et al. 2018; Estevez et al. 2021; Bosso et al. 2022). In addition, with the advance of molecular tools, the systematics and taxonomy of the family have been updated (Reid and Williams 2004) to give a more accurate classification of species and description of their distributions. Members of the group are present in both hemispheres (Reid 1989; Williams et al. 2003). In the Southern Hemisphere, tropical and temperate species have received most research attention (e.g., Williams et al. 2003; Reid and Williams 2004). As a consequence, while some littorinids are known from southern South America and the Southern Ocean (SO), no recent taxonomic examinations are available and occurrence information remains scarce as and dispersed (Reid 1989).

Laevilitorina Pfeffer, 1886 is the most widely distributed genus of marine gastropods present at high latitudes in the Southern Hemisphere (Reid 1989). Its known distribution range includes South America, New Zealand, Australia, Tasmania, and Antarctic (West and East parts), and many peri-(sub)Antarctic islands (South Shetland Islands, South Orkney Islands, Falkland/Malvinas Islands, South Georgia, Crozet, Kerguelen, Heard, Macquarie, Campbell, Auckland, and Antipodes Island). The genus *Laevilitorina* Pfeffer, 1886 is characterised by a thick, generally smooth shell, a non-planktotrophic protoconch and a generally paucispiral operculum (Reid 1989; Warén and Hain 1996). At present, 21 species of *Laevilitorina* are taxonomically accepted (MolluscaBase 2022).

The present study documents the state of knowledge of the genus and provides an updated database, using a combination of recent sampling data, published records available in the literature, and available information from GBIF and other repositories. The objectives of the study are: i) to report new records of *Laevilitorina* species present in Antarctic and sub-Antarctic environments and ii) to evaluate the distribution and richness of *Laevilitorina* species throughout the Southern Hemisphere, using an updated database. The updated database will serve as a basis for future comprehensive systematic research on the genus, including the application of molecular phylogenetic approaches to help infer its regional evolutionary history.

Materials and methods

Construction of the database

Laevilitorina records across the Southern Hemisphere were compiled from four main sources: 1) field sampling data; 2) published literature; 3) data already present in GBIF and 4) the data present in the repository of the Atlas of Living Australia (ALA) (Belbin 2011). Duplicate records were removed to construct a unified database. In addition, the records available in GBIF and ALA were used to describe the distribution range of each species. To ensure the quality of the occurrence data, dubious records were excluded from the geospatial analysis. The criterion used to determine dubious records was records of species in geographic areas outside the distribution range described in the original descriptions and taxonomic revisions.

Twelve marine biogeographical provinces in the Southern Hemisphere were considered for the purpose of our geospatial analyses, including the Magellan province (southern South America and Falkland / Malvinas Islands), West Antarctic, East Antarctica, Indian Ocean sub-Antarctic islands (Prince Edward Islands, Crozet Island, Kerguelen and Heard Islands), Macquarie Island, New Zealand sub-Antarctic islands, Southern New Zealand, Northern New Zealand, South-east Australian Shelf, South-west Australian Shelf, West Central Australian Shelf and East Central Australian Shelf, as defined in Spalding et al. (2007) and Koubbi et al. (2014). All spatial analyses were carried out on the unified database.

Recent sampling data

New material was collected from multiple locations in southern South America between the Strait of Magellan (53°36'S, 70°55'W) and the Diego Ramirez archipelago (56°31.345'S, 68°43.622'W). In the Falkland/Malvinas Islands, specimens were collected from the intertidal zone of Hooker Point (51°42'S, 57°46'W). New Antarctic material was collected from the South Shetland Islands, Doumer Island, Palmer Land, and Avian Island under the framework of Antarctic Scientific Expeditions (**ECA**) 49, 53, 54 and 58 of the Chilean Antarctic Institute (**INACH**). Samples from the South Orkney Islands and South Georgia were obtained during British Antarctic Survey (**BAS**) and SAERI expeditions (2016–2017, 2017–2018 and 2021). Samples from Kerguelen and Crozet archipelagos were obtained through the PROTEKER project under the framework of the French Polar Institute Paul Emile Victor (**IPEV**) summer campaign 2017.

Sample collection

Samples were collected using two methods: 1) manual collection in the intertidal zone, with littorinids being sampled individually, and 2) SCUBA diving between 1 and 15 m depth, where substrates (e.g. sediments, macroalgae) were collected. Rock substrates were subsequently scraped to ensure that all species and specimens were collected. Each macroalga sample was placed in a plastic bag. After collection, specimens were kept alive and transported onboard or to the research station. Each sample was then gently agitated to detach the associated fauna. All *Laevilitorina* samples were immediately preserved in ethanol (95%) to be transported to the laboratory. Geographic coordinates were recorded using GPS for each sample location.

Taxonomic identification

Morphological observations were performed under an OLYMPUS stereomicroscope CX31. The following morphological measurements were taken, following Reid (2007): shell height (H), the maximum dimension parallel to the axis of coiling; shell breadth (B), the maximum dimension perpendicular to H; length of the aperture (LA), the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip. For determination to species level, each individual was identified following the taxonomic studies of Martens and Pfeffer (1886), Suter (1913), Powell (1951, 1955), Dell (1964), Arnaud and Bandel (1976), Waren and Hain (1996) and Zelaya (2005).

Published literature

To ensure maximum coverage of the generated dataset, information was gathered from all available scientific publications that have sampled or reviewed *Laevilitorina* species throughout the genus' distribution, from the description of the first species (Gould 1849) to the present. These records and their respective geographical positions were entered into a spreadsheet following the Darwin Core Standard structured procedure (Wieczorek et al. 2012). Taxonomy used in these publications was updated following the most recent systematic revision (Reid 1989; Waren and Hain 1996; Engl 2012; Bouchet et al. 2017; MolluscaBase 2022). We did not follow González-Wevar et al. (2022) for species names and databases, mainly because the lineages that would correspond to new species have not yet been formally described. However, the implications of these results for the taxonomy and biogeography of *Laevilitorina* are discussed (González-Wevar et al. 2022).

Digital database GBIF and ALA

All georeferenced records of the genus *Laevilitorina* were retrieved from the GBIF and ALA database on 12 September 2022 (Rosenfeld et al. 2022). The point-radius method was used for georeferencing records lacking precise geographic location (coordinates), by identifying locality description included in the relevant metadata of the reported collection. This method considers the precision, datum and specificity of the locality description to determine the coordinates (Wieczorek et al. 2004; Wieczorek and Wieczorek 2021). The species list was updated to exclude erroneous or suspect records, rule out possible synonymy and follow current taxonomy.

Results

Database summary

The complete database (https://www.gbif.org/dataset/cd023c5e-8729-41b2-b9df-1419289c0e40) includes 813 records. Most records (458) were obtained from the ALA repository, followed by literature (174) obtained from 63 reviewed articles, GBIF (128), and new sampling records (53).

Dubious records

Laevilitorina antarctica (Smith, 1902), originally described from Cape Adare in the Ross Sea, is also reported in GBIF from Macquarie Island (https://www.gbif.org/es/occurrence/search?taxon_key=9810991). However, this species has historically been reported primarily from the biogeographic provinces of East Antarctica and West Antarctica (Arnaud and Bandel 1976; Dell 1990). Therefore, the presence of *L. antarctica* on Macquarie Island requires confirmation and was not included in our database.

New record

This study includes the first record of the species *Laevilitorina delli* Powell, 1955, in GBIF database, previously described by Powell (1955) from the South Island of New Zealand and Antipodes Island.

Morphological identification

All newly collected *Laevilitorina* specimens identified in this study showed morphological characteristics corresponding to those described in the literature (Fig. 1a–f). The specimens of *L. pygmaea* Pfeffer, 1886 and *L. venusta* Pfeffer, 1886 identified from South Georgia are consistent with the morphological characteristics described by Martens and Pfeffer (1886) for these species (Fig. 1b, c). Individuals of *L. pygmaea* had a high spire, reddish-brown periostracum, with five convex whorls. The last whorl was 50% of the total height of the spire and the aperture was ~ 59% of the length of the last whorl (Fig. 1b). *L. venusta* individuals were between 3.7 and 5.6 mm in height, with a short spire, and 4.5 convex whorls. The aperture was wide, occupying a little more than half of the total height of the shell (54%); the columellar callus was sharp, white and expanded towards the umbilicus, all characteristics again consistent with Martens and Pfeffer (1886) (Fig. 1c).

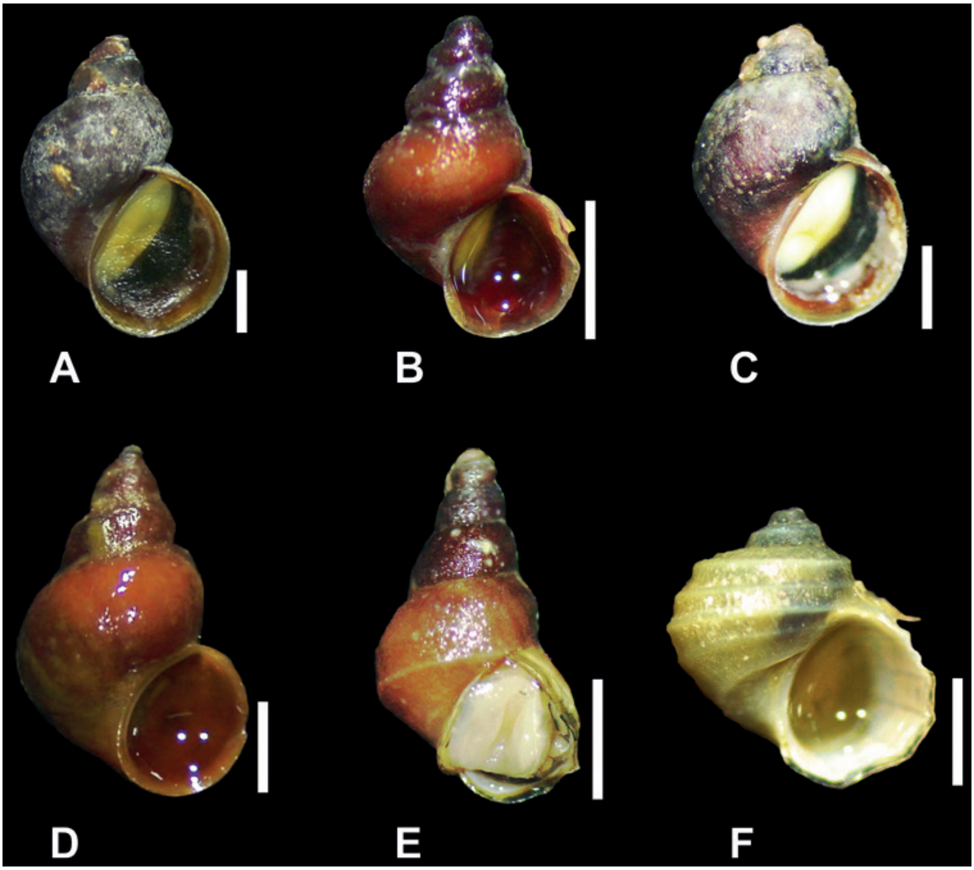


Figure 1. A *Laevilitorina caliginosa* (4.8 mm) **B** *Laevilitorina pygmaea* (2.5 mm) **C** *Laevilitorina venusta* (3.7 mm) **D** *Laevilitorina claviformis* (3.9 mm) **E** *Laevilitorina umbilicata* (2.8 mm) **F** *Laevilitorina wandelensis* (2.7 mm). Scale bars: 1 mm. Photographs by Sebastián Rosenfeld.

Species richness

A total of 21 species of *Laevilitorina* were recorded in the Southern Hemisphere; West Antarctica was the province with the highest species richness (S = 8, Fig. 2a, b), followed by the New Zealand sub-Antarctic islands, the south-east shelf of Australia (S = 4, Fig. 2a, b) and the south-west Australian Shelf (S = 3, Fig. 2a, b). The provinces of Magellan, south New Zealand, and Indian Ocean sub-Antarctic islands had two species each (Fig. 2 a, b) and the remaining provinces had only one species each (Fig. 2 a, b). However, based on the latest molecular study of González-Wevar et al. (2022), there are four new species-level lineages of *Laevilitorina* in the Magellan province where species richness would increase to six taxa (Fig. 2 a, b). The species with the highest number of records was *L. caliginosa* (Gould, 1849) (158). Most of these records came from the Magellan province (79), of which nine were from the Falkland/Malvinas Islands.

Within the West Antarctic province eight species were reported, of which *L. venusta* and *Laevilitorina granum* Pfeffer, 1886 were recorded exclusively from South Georgia (Fig. 3), while *L. wandelensis* (Lamy, 1906) and *L. antarctica* were recorded exclusively from Antarctic provinces, without no records from South Georgia (Fig. 3).

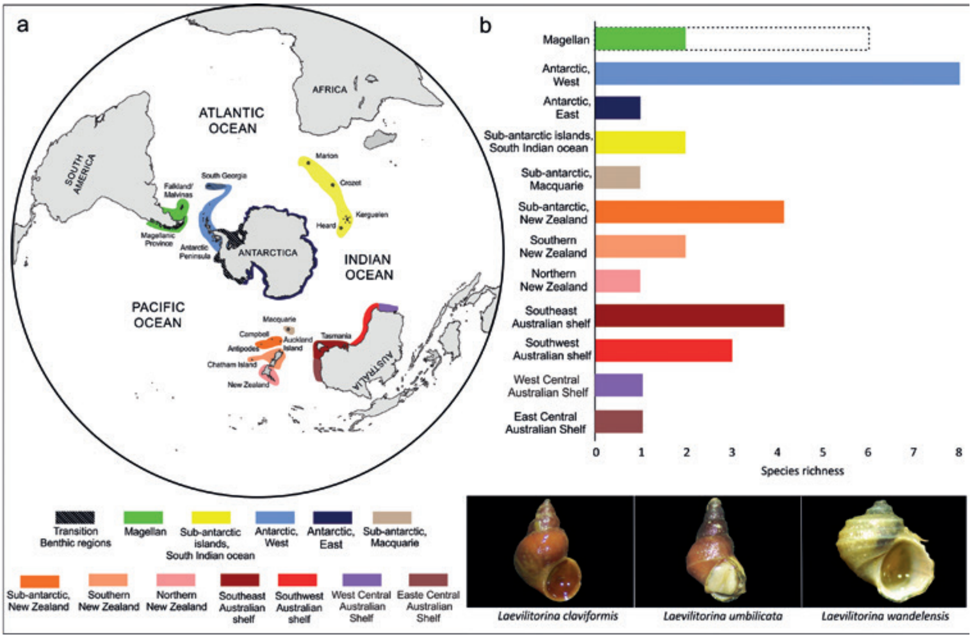


Figure 2. a Delimitation of Antarctic and Southern Ocean marine biogeographic provinces according to Spalding et al. (2007) and Koubbi et al. (2014) **b** Species richness of *Laevilitorina* in each of the biogeographical provinces. The dotted lines in the Magellan Province show the new richness value based on the revision of González-Wevar et al. (2022).

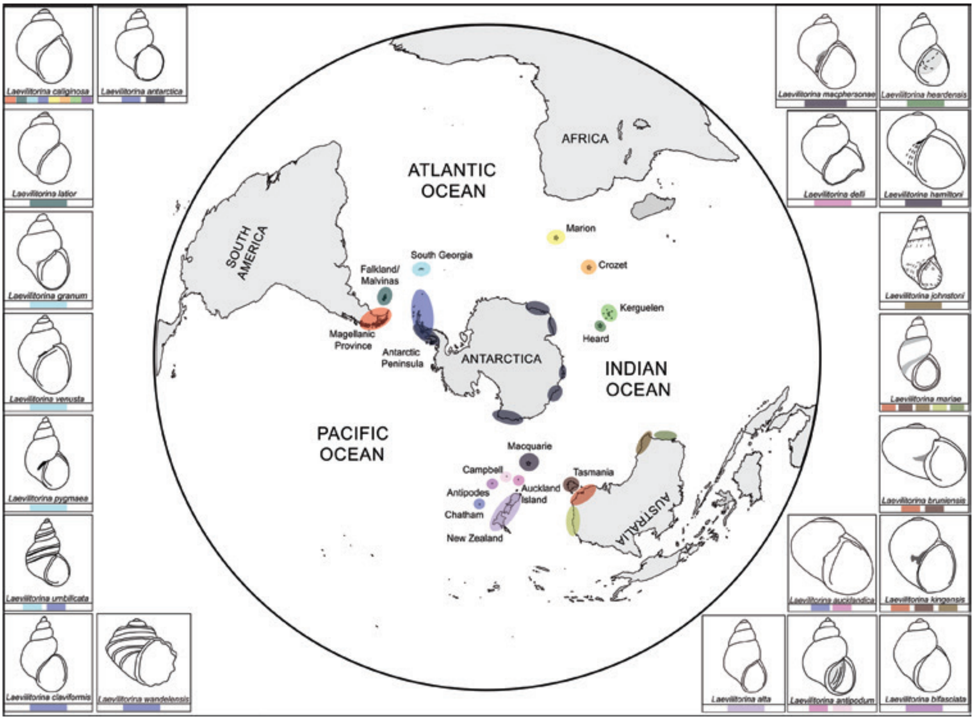


Figure 3. The distributions of the 21 different *Laevilitorina* species in the Southern Hemisphere. The colours below each panel indicate the geographic distribution of each species. Drawings of each species were made from holotypes or from illustrations made in published revisions (Gould 1849; Martens and Pfeffer 1886; Smith 1902; Lamy 1906; Suter 1913; Preston 1916; May 1924; Powell 1933; Powell 1940; Cotton 1945; Powell 1955; Dell 1964).

Only two species were recorded from the main New Zealand islands, *L. alta* (Powell, 1940) from North Island and *L. delli* from South Island. Three species were reported from Campbell, Antipodes and Auckland Islands, *L. aucklandica* (Powell, 1930), *L. bifasciata* Suter, 1913 and *L. antipodum* (Filhol 1880), none of which were shared with the North and South Islands of New Zealand (Fig. 3). In Australia, four species, *L. johnstoni* (Cotton, 1945), *L. mariae* (Tenison Woods, 1876), *L. bruniensis* (Beddome, 1883), and *L. kingensis* (May, 1924), were recorded from mainland Australia. *L. johnstoni* would be the only species restricted to mainland Australia, while *L. kingensis*, *L. mariae*, and *L. bruniensis* are also present in Tasmania (Fig. 3).

Based on our new sampling data only, we identified and reported seven *Laevilitorina* species in the Magellanic Province (*L. caliginosa*), Falkland/Malvinas Islands (*L. caliginosa*, *L. latior*), South Georgia (*L. caliginosa*, *L. pygmaea*, *L. venusta*; Fig. 1b, c), Kerguelen and Crozet Islands (*L. caliginosa*), South Orkney Islands (Signy Island) (*L. caliginosa*), and Antarctic Peninsula (*L. caliginosa*, *L. claviformis*, *L. umbilicata*, *L. wandelensis*; Fig. 1d–f), adding 43 new records to the previously available data. These new records are generally consistent with the existing literature and GBIF data, with the exceptions of (i) new records of *L. caliginosa* on Horn and Diego Ramirez Islands, (ii) *L. umbilicata* on Avian Island, and (iii) *L. caliginosa* on Lagotellerie Island, the latter two being the southernmost records of both species.

Discussion

The increasing application of integrated taxonomy coupled with new modelling approaches, requires data to be Findable, Accessible, Interoperable, and Reusable in the long term (Wilkinson et al. 2016). There is a need to revise the geographic distribution and taxonomic description of many taxa, as it can provide information about changes in the composition of communities in different environments, particularly in sensitive ecosystems (Maturana et al. 2019). A number of studies have already discussed the importance of making an updated revision of the taxonomic status of several *Laevilitorina* species throughout their distribution (Powell 1960; Reid 1989; Engl 2012).

The compilation and unification of records of *Laevilitorina* in the Southern Hemisphere presented here contributes to improve our knowledge of the diversity and biogeography of the members of the genus in twelve biogeographic provinces of the Southern Hemisphere. However, it is also important to note that, despite the unification and update of records of *Laevilitorina*, this study does not reflect the full systematic and biogeographic complexity of this genus. Distribution data are not currently available for many members of the genus, which have not been reported since their description. For example, among the five species of *Laevilitorina* described from South Georgia, three of them (*L. pygmaea*, *L. venusta*, and *L. granum*) have not been reported since their original description (Castellanos 1989), leaving doubts about the taxonomic validity of these species (Castellanos 1989; Reid 1989; Engl 2012).

In this study, the report of *L. pygmaea* is only the third record of the species, in addition to being the first record from shallow depths thereby extending our knowledge of its bathymetric range. Previously, *L. pygmaea* had been reported between 252 and 310 m depth (Castellanos 1989). Similarly, the record of *L. venusta* is the first report of this species since its description by Martens and Pfeffer (1886). In general, the morphology of new *L. pygmaea* and *L. venusta* specimens corresponded well with the original descriptions. However, in our individuals of *L. pygmaea* the aperture was slightly higher than that described by Martens and Pfeffer (1886). This difference could be due to morphological plasticity within *L. pygmaea*, as it has been reported for other species of the genus (Reid 1989; Engl 2012). In the case of *L. venusta*, our specimens presented characteristics and measurements similar to those described by Martens and Pfeffer (1886), where the length of the opening of our specimens represented ~ 54% of the total height of the shell, the same as the measurements of the holotype of Martens and Pfeffer (1886). The morphology of *L. venusta* is quite similar to that of the widely distributed *L. caliginosa*, a species characterised by wide morphological plasticity throughout its distribution (see Engl 2012; González-Wevar et al. 2022). However, measurements of specimens of *L. caliginosa* from the Falkland/Malvinas Islands and

South Georgia show a longer and more expanded aperture than *L. venusta*, occupying between 58 and 67% of the total height of the shell (Castellanos 1989; Zelaya 2005). In this sense, it would be interesting in the future to carry out molecular studies with the species of South Georgia to corroborate the validity of the species described in that site. The recent study by González-Wevar et al. (2022) was able to detect only two lineages of *Laevilitorina* there: i) one that would correspond to *L. caliginosa* and ii) a second lineage that is also distributed in the Antarctic Peninsula and expands its distribution towards sub-Antarctic islands of the Indian Ocean like Marion, Crozet, and Kerguelen. The latter does not resemble any known South Georgian species and probably represents a new species (González-Wevar et al. 2022).

Taxonomic uncertainties within the genus *Laevilitorina* are related both to the morphological plasticity that exists in at least some species (Reid 1989; Engl 2012) and also to practical logistical challenges in accessing species' type localities and the level of geographical accuracy relating to some records. For example, the type locality of *L. caliginosa* (Gould (1849) is described as "Terra del Fuego", which covers a large and diverse area and could generate many ambiguities for researchers attempting to collect correctly identified individuals from this locality. Tierra del Fuego is one of the largest islands in southern South America and extends south and east of the Strait of Magellan between the Atlantic and Pacific Oceans. Gould's description was made using material collected during the "United States Exploring Expedition" carried out between 1838 and 1842 (Gould 1849). Fortunately, in the narrative of this expedition (Wilkes 1845; chapter VI, "Terra del Fuego") it is specified that the ship was in Orange Bay located in Hoste Island (see Wilkes 1845: 123) when this material was collected. Consequently, the type locality of *L. caliginosa* can be defined as Orange Bay in Hoste Island, and not the coastal area of Tierra del Fuego.

Historically, because of the complexity of obtaining material due to the wide distribution of *Laevilitorina*, taxonomic revisions have been restricted to certain geographic areas (e.g., Powell 1951, 1957; Dell 1964; Arnaud and Bandel 1976; Zelaya 2005; Engl 2012). The most complete review published to date was by Reid (1989), where he analysed material from Antarctica (*L. antarctica*), sub-Antarctic Islands (*L. caliginosa* and *L. hamiltoni*), New Zealand (*L. alta*), and Australia (*L. bruniensis* and *L. mariae*). This represents a very low percentage of the diversity of the entire genus. In addition, some of the described species present morphological similarities, which makes identification more complex (Reid 1989) and therefore caution must be exercised with some historical records. Fortunately, several of the described species have material deposited in museums (e.g., ALA 2022), which would allow a more extensive revision of the group. Therefore, a systematic revision of *Laevilitorina* is currently very relevant to understand better the current status of this genus, its richness and distribution in the Southern Hemisphere.

Laevilitorina is one of the most widely distributed genera of marine gastropods at high latitudes in the Southern Hemisphere (Reid 1989; this study). The 21 species of *Laevilitorina* have different distribution patterns (Fig. 3). For example, seven of the 21 *Laevilitorina* species reported in this study have different distribution ranges (*L. caliginosa*, *L. latior*, *L. pygmaea*, *L. venusta*, *L. claviformis*, *L. umbilicata*, *L. wandelensis*) (Fig. 4b). *Laevilitorina latior* has been reported exclusively from the Falkland/Malvinas Islands (Preston 1912), *L. claviformis* and *L. wandelensis* exclusively from Antarctic Peninsula (Reid 1989; Engl 2012), and *L. venusta* only from South Georgia (Castellanos 1989; Zelaya 2005). *Laevilitorina umbilicata* and *L. pygmaea* have wider distribution ranges, including both South Georgia and the Antarctic Peninsula (Zelaya 2005; Engl 2012). *Laevilitorina caliginosa* has by far the widest distribution, being recorded in four Southern Ocean biogeographic provinces (i.e., Magellan, West Antarctica, Indian Ocean sub-Antarctic, and Macquarie Island). Nevertheless, as previously stated, the taxonomy within this taxon is much more complex than previously thought (González-Wevar et al. 2022).

The majority of *Laevilitorina* species inhabit shallow rocky coasts and may be associated with different species of macroalgae (Simpson 1972; Reid 1989; Amsler et al. 2015; Rosenfeld et al. 2017). Another important characteristic of this genus is the absence of pelagic larva: the female deposits egg masses on rocks or macroalgae from which the juvenile subsequently hatches (Picken 1979; Simpson and Harrington 1985) (Fig. 4a). In the literature, this type of benthic protected development is often assumed to be associated with restricted dispersal capability and hence narrow geographic range (Simpson and Harrington 1985; Barroso et al. 2022), a feature of the majority of *Laevilitorina* species (Fig. 4b). On the basis of reproductive strategy, the wide distribution of *L. caliginosa* is paradoxical and exceptional within the genus (Reid 1989; Griffiths and Waller 2016) (Fig. 4b). Some authors (Griffiths and Waller 2016; González-Wevar et al. 2022) have suggested that dispersal associated with dislodged rafts of the seaweed *Durvillaea antarctica* Hariot, 1882 may have facilitated the species' wider establishment, since both species co-occur across most of their distribution ranges. However, a recent phylogenetic study of *L. caliginosa* evidenced that this taxon does not correspond to a widely distributed species, but rather to multiple divergent lineages distributed along the SO (González-Wevar et al. 2022). In fact, phylogenetic reconstructions recognised the presence of at least seven *Laevilitorina* lineages within the nominal taxon *L. caliginosa*. Of these, six species are endemic to the Magellan Province and most of them are new to science (González-Wevar et al. 2022). Just one "caliginosa" lineage has a broad distribution that includes the Antarctic Peninsula, South Georgia and sub-Antarctic islands of the Indian Ocean (Marion, Crozet, and Kerguelen islands) (González-Wevar et al. 2022). Hence, the taxonomy of *Laevilitorina* is still unsettled and requires a detailed revision. Previously the Magellan province was considered as a species-poor area for *Laevilitorina*, in fact it represents an area where the genus diversified over the last 30 million years (González-Wevar et al. 2022).

This study shows a detailed review of the records, distribution and richness patterns of the genus *Laevilitorina* throughout its range. However, more research and sampling effort is still needed to "recover" and confirm many of the *Laevilitorina* species that are present throughout the sub-Antarctic Islands. In addition, based on the results of González-Wevar et al. (2022) and this work, we conclude that it is important to continue investigating this genus because: i) the recent discovery of new lineages in the Magellan province highlights the need for a thorough taxonomic

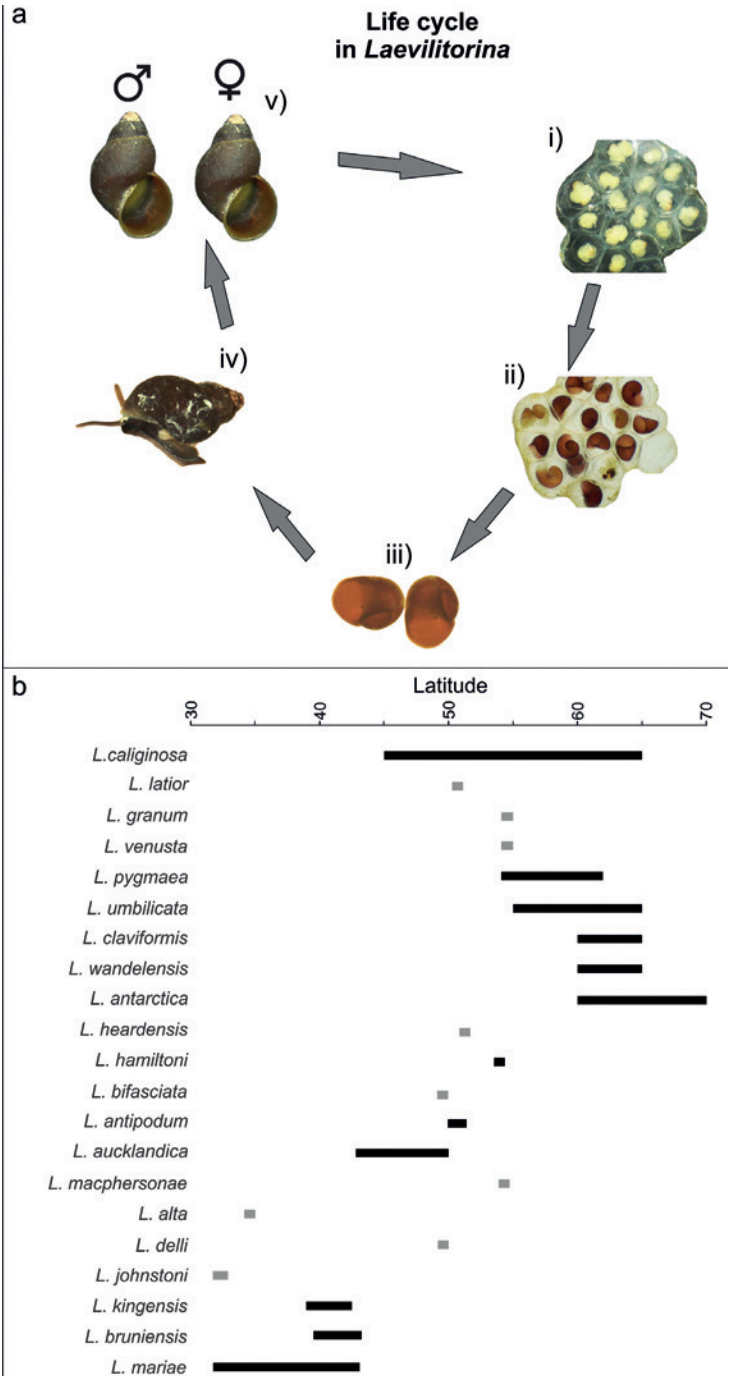


Figure 4. a Life cycle of members of the genus *Laevilitorina* without a planktotrophic larval stage, i) general view of the egg mass with early-stage embryos, ii) late-stage embryos, iii) recently hatched juveniles, iv) developing adult, and v) male and female of the genus (photographs S. Rosenfeld) **b** Latitudinal distribution of *Laevilitorina* species in the Southern Hemisphere, grey bars indicate presence in a single geographic area or island.

revision of *Laevilitorina* species and improved estimate of the genus diversity, and ii) the marked endemism of some species along with differences in species richness across the Southern Hemisphere marine provinces suggest contrasting biogeographical patterns of importance for conservation issues and evolutionary studies. Finally, these differences raise further questions about the underlying processes and mechanisms associated with the evolution of this genus in the Southern Hemisphere.

Acknowledgements

This work was funded by, ANID-Millennium Science Initiative Program ICN2021_002 to SR, CM, PC, EP, and CGW, Fondecyt Regular Project 1210787 to CGW and SR, and ANID/BASAL FB210018 to SR and CM. We also appreciate the support of the following projects: Fondecyt Postdoctoral 3210063 to CM, IPEV program PROTEKER (#1044). We are grateful to the Government of South Georgia & South Sandwich Islands (GSGSSI), South Atlantic Environmental Research Institute (SAERI), Natural History Museum (NHM) London, the Shallow Marine Surveys Group (SMSG) for organising 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. The research cruise was funded by GSGSSI and a Darwin Plus Grant (DPLUS122) to the NHM. We also are grateful to the officers and crew of the *Pharos SG* for their professionalism and support. S.R. gives particular thanks to the Chilean Navy, the Commander in Chief of the III Naval Zone, Rear Admiral Ivo Brito, the Chief of General Staff, Vice Admiral José Miguel Rivera, the National Oceanographic Committee, and the Naval Beagle Command, as well as the crew of the ship OPV 83 Marinero Fuentealba, and the helicopter and institutional logistics personnel. We also thank 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 the Diego Ramírez archipelago and Hornos Island. We especially thank Lafayette Eaton for English revision and editing and to the Subject editor Frank Köhler and two anonymous reviewers for their helpful comments.

References

Amsler MO, Huang I, Engl W, McClintock JB, Amsler CD (2015) Abundance and diversity of gastropods associated with dominant subtidal macroalgae from the western Antarctic Peninsula. Polar Biology 38(8): 1171–1181. https://doi.org/10.1007/s00300-015-1681-4

Ariño AH (2010) Approaches to estimating the universe of natural history collections data. Biodiversity Informatics 7(2): 81–92. https://doi.org/10.17161/bi.v7i2.3991

Arnaud P, Bandel K (1976) Comments on six species of marine Antarctic Littorinacea (Mollusca, Gastropoda). THETYS 8(3): 213–230.

ALA (2022) Atlas of Living Australia. https://bie.ala.org.au/search?q=Laevilitorina [Acceded 12 September 2022]

Barroso C, Lotufo T, Matos A, Carneiro P, Matthews-Cascon H (2022) The distribution of marine gastropods is more influenced by larval development than by adult characteristics. Marine Biology 169(6): e83. https://doi.org/10.1007/s00227-022-04069-0

Beck J, Ballesteros-Mejia L, Nagel P, Kitching I (2013) Online solutions and the 'Wallacean shortfall': What does GBIF contribute to our knowledge of species' ranges? Diversity & Distributions 19(8): 1043–1050. https://doi.org/10.1111/ddi.12083

Belbin L (2011) The Atlas of Livings Australia's Spatial Portal. In: Jones M, Gries C (Eds) Proceedings of the Environmental Information Management Conference, Santa Barbara, 39–43.

Bosso L, Smeraldo S, Russo D, Chiusano ML, Bertorelle G, Johannesson K, Butlin RK, Danovaro R, Raffini F (2022) The rise and fall of an alien: Why the successful colonizer Littorina saxatilis failed to invade the Mediterranean Sea. Biological Invasions 24(10): 3169–3187. https://doi.org/10.1007/s10530-022-02838-y

Bouchet P, Rocroi J, Hausdorf B, Kaim A, Kano Y, Nützel A, Parkhaev P, Schrödl M, Strong E (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61(1–2): 1–526. https://doi.org/10.4002/040.061.0201

Castellanos ZA (1989) Catálogo descriptivo de la malacofauna marina Magallánica 4. Mesogastropoda. Comisión de Investigaciones Científicas, Provincia de Buenos Aires, 44 pp.

Cotton BC (1945) Southern Australian Gastropoda. Part 1. Streptoneura. Transactions of the Royal Society of South Australia 69(1): 150–171.

Dell RK (1964) Marine Mollusca from Macquarie and Heard Islands. Record of the Dominion Museum Wellington 267–301.

Dell RK (1990) Antarctic Mollusca with special reference to the fauna of the Ross Sea. Bulletin - Royal Society of New Zealand 27: 1–311.

Engl W (2012) Shells of Antarctica. ConchBooks, Hackenheim, 402 pp.

Estevez D, Galindo J, Rolan-Alvarez E (2021) Negative frequency-dependent selection maintains shell banding polymorphisms in two marine snails (*Littorina fabalis* and *Littorina saxatilis*). Ecology and Evolution 11(11): 6381–6390. https://doi.org/10.1002/ece3.7489

Flemons P, Guralnick R, Krieger J, Ranipeta A, Neufeld D (2007) A web-based GIS tool for exploring the world's biodiversity: The Global Biodiversity Information Facility Mapping and Analysis Portal Application (GBIF-MAPA). Ecological Informatics 2(1): 49–60. https://doi.org/10.1016/j.ecoinf.2007.03.004

González-Wevar CA, Segovia NI, Rosenfeld S, Maturana CS, Jeldres V, Pinochet R, Saucède T, Morley SA, Brickle P, Wilson NG, Spencer HG, Poulin E (2022) Seven snail species hidden in one: Biogeographic diversity in an apparently widespread periwinkle in the Southern Ocean. Journal of Biogeography 49(8): 1521–1534. https://doi.org/10.1111/jbi.14453

Gould AA (1849) Descriptions of new species of shells, brought home by the U. S. Exploring Expedition. Proceedings of the Boston Society of Natural History 3: 83–85.

Griffiths HJ, Waller C (2016) The first comprehensive description of the biodiversity and biogeography of Antarctic and sub-Antarctic intertidal communities. Journal of Biogeography 43(6): 1143–1155. https://doi.org/10.1111/jbi.12708

Kess T, Galindo J, Boulding EG (2018) Genomic divergence between Spanish *Littorina saxatilis* ecotypes unravels limited admixture and extensive parallelism associated with population history. Ecology and Evolution 8(16): 8311–8327. https://doi.org/10.1002/ece3.4304

Koubbi P, De Broyer C, Griffiths HJ, Raymond B, d'Udekem d'Acoz C, Van de Putte AP, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Huettmann F, Post A, Ropert-Coudert Y, Stoddart M, Swadling KM, Wadley V (2014) Conclusions: present and future of Southern Ocean biogeography. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, Udekem d'Acoz C, Van de Putte AP, Danis B, David B, Grant S, Gutt J, Held C, Hosie G, Huettmann F, Post A, Ropert-Coudert Y (Eds) Biogeographic atlas of the Southern Ocean. Sicentific Committee on Antarctic Research, Cambridge, 470–475.

Lamy E (1906) Gastropodes Prosobranches et Pélécypodes. Expédition Antarctique Française (1903–05), Sciences Naturelles, Paris, 20 pp.

Martens E, Pfeffer G (1886) Die Mollusken von Süd–Georgien nach der Ausbeute der Deutschen Station 1882–83. Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 3: 65–135. https://doi.org/10.5962/bhl.title.12280

Maturana C, Rosenfeld S, Naretto J, Convey P, Poulin E (2019) Distribution of the genus *Boeckella* (Crustacea, Copepoda, Calanoida, Centropagidae) at high latitudes in South America and the main Antarctic biogeographic regions. ZooKeys 854: 1–15. https://doi.org/10.3897/zooke ys.854.29614

May WL (1924) Mollusca of King Island With description of five new species. Papers and Proceedings of the Royal Society of Tasmania 1923: 47–55.

MolluscaBase [Eds] (2022) MolluscaBase. *Laevilitorina* Pfeffer, 1886. World Register of Marine Species. https://www.marinespecies.org/aphia.php?p=taxdetails&id=196959 [on 2022-06-22]

OBIS (2022) Ocean Biogeographic Information System. Census of Marine Life. http://iobis.org/

Picken GB (1979) Non-pelagic reproduction of some Antarctic prosobranch gastropods from Signy Island, South Orkney Islands. Malacologia 19(1): 109–128.

Powell AWB (1933) New species of marine Mollusca from the subantarctic islands of New Zealand. Proceedings of the Malacological Society of London 20(5): 232–236. https://doi.org/10.1093/oxfordjournals.mollus.a064194

Powell AWB (1940) The marine Mollusca of the Auporian Province, New Zeland. Transactions of the Royal Society of New Zealand 70: 205–248.

Powell AWB (1951) Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. Discovery Reports 26: 47–196. https://doi.org/10.5962/bhl.part.16335

Powell AWB (1955) Mollusca of the southern islands of New Zealand. Department of Scientific and Industrial Research Cape Expedition Series Bulletin 15: 1–151. [5 pl]

Powell AWB (1957) Mollusca of Kerguelen and Macquarie Islands. B. A. N. Z. Antarctic Research Expedition, 1929–1931. Report B 6: 107–149.

Powell AWB (1960) Antarctic and Subantarctic Mollusca (catalogue). Records of the Auckland Institute and Museum 5(3–4): 117–193.

Preston HB (1912) Characters of six new pelecypods and two new gastropods from the Falkland Islands. Annals and Magazine of Natural History 9(8): 636–640 https://doi.org/10.1080/00222931208693180

Preston HB (1916) Descriptions of eight new species of marine Mollusca from the South Shetland Islands. Annals and Magazine of Natural History 18(8): 269–272. https://doi.org/10.1080/00222931608693847

Reid DG (1989) The comparative morphology, phylogeny, and evolution of the gastropod family Littorinidae. Littorinidae Philosophical Transactions of the Royal Society of London B 324: 1–110. https://doi.org/10.1098/rstb.1989.0040

Reid DG (2007) The genus *Echinolittorina* Habe, 1956 (Gastropoda: Littorinidae) in the Indo-West Pacific Ocean. Zootaxa 1420(1): 1–161. https://doi.org/10.11646/zootaxa.1420.1.1

Reid DG, Williams ST (2004) The subfamily Littorininae (Gastropoda: Littorinidae) in the temperate Southern Hemisphere: the genera *Nodilittorina*, *Austrolittorina* and *Afrolittorina*. Records of the Australian Museum 56(1): 75–122. https://doi.org/10.3853/j.0067-1975.56.2004.1393

Reid DG, Williams ST (2012) A global molecular phylogeny of 147 periwinkle species (Gastropoda, Littorininae). Zoologica Scripta 41(2): 125–136. https://doi.org/10.1111/j.1463-6409.2011.00505.x

Rosenfeld S, Aldea C, Ojeda J, Marambio J, Hüne M, Troncoso J, Mansilla A (2017) Molluscan assemblages associated with *Gigartina* beds in the Strait of Magellan and the South Shetland Islands (Antarctica): A comparison of composition and abundance. Polar Research 36(1): 1–10. https://doi.org/10.1080/17518369.2017.1297915

Rosenfeld S, Maturana C, González Wevar C, Poulin E, Gérard K, Naretto J, Ojeda J, Lopez Z, Brickle P, Saucède T, Kraft S, Aldea C (2022) Distribution and Occurrences of Laevilitorina across the Southern Hemisphere. Instituto de Biodiversidad de Ecosistemas Antárticos y Subantárticos (BASE). Occurrence dataset. https://doi.org/10.15468/dsacsj [accessed via GBIF.org on 2022-10-11]

Simpson R (1972) The ecology and biology of molluscs in the littoral and sublittoral zones at Macquarie Island, with special reference to Patinigera macquariensis (Finlay, 1927). Thesis presented for the Degree of Doctor of Philosophy. University of Adelaide.

Simpson RD, Harrington SA (1985) Egg masses of three gastropods, *Kerguelenella lateralis* (Siphonariidae), *Laevilitorina caliginosa* and *Macquariella hamiltoni* (Littorinidae), from Macquarie Island (sub- Antarctic). Journal of the Malacological Society of Australia 7(1–2): 17–28. https://doi.org/10.1080/00852988.1985.10673973

Smith EA (1902) Mollusca. In: Lankester ER, Bell J (Eds) Report on the collections of natural history made in Antarctic regions during the voyage of the Southern Cross. British Museum (Natural History), London, 201–213.

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, Mcmanus E, Molnar J, Recchia CA, Robertson J (2007) Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. Bioscience 57(7): 573–583. https://doi.org/10.1641/B570707

Suter H (1913) Manual of the New Zealand Mollusca with an atlas of quarto plates. Wellington, [xxiii +] 1120 pp. [(1913) and Atlas pls 1–72 (1915)] https://doi.org/10.5962/bhl.title.1716

Warén A, Hain S (1996) Description of Zerotulidae fam. Nov. (Littorinoidea), with comments on an Antarctic Littorinid Gastropod. The Veliger 39(4): 277–334.

Wieczorek J, Guo Q, Hijmans R (2004) The point-radius method for georeferencing locality descriptions and calculating associated uncertainty. International Journal of Geographical Information Science 18(8): 745–767. https://doi.org/10.1080/13658810412331280211

Wieczorek C, Wieczorek J (2021) Georeferencing Calculator. http://georeferencing.org/georef-calculator/gc.html [Accessed 10 March 2022]

Wieczorek J, Bloom D, Guralnick R, Blum S, Döring M, Giovanni R, Robertson T, Vieglais D (2012) Darwin Core: An evolving community-developed biodiversity data standard. PLoS ONE 7(1): e29715. https://doi.org/10.1371/journal.pone.0029715

Wilkes C (1845) Narrative of the United States Exploring Expedition. During the years 1838, 1839, 1840, 1841, 1842. Lea and Blanchard, Philadelphia, 1845. https://doi.org/10.5962/bhl.title.61621

Wilkinson M, Dumontier M, Aalbersberg IJ, Appleton G, Axton M, Baak A, Blomberg N, Boiten J, da Silva Santos LB, Bourne P, Bouwman J, Brookes A, Clark T, Crosas M, Dillo I, Dumon O, Edmunds S, Evelo C, Finkers R, Gonzalez-Beltran A, Gray AG, Groth P, Goble C, Grethe J, Heringa J, 't Hoen PC, Hooft R, Kuhn T, Kok R, Kok J, Lusher S, Martone M, Mons A, Packer A, Persson B, Rocca-Serra P, Roos M, van Schaik R, Sansone S, Schultes E, Sengstag T, Slater T, Strawn G, Swertz M, Thompson M, van der Lei J, van Mulligen E, Velterop J, Waagmeester A, Wittenburg P, Wolstencroft K, Zhao J, Mons B (2016) The FAIR Guiding Principles for scientific data management and stewardship. Scientific Data 3(1): e160018. https://doi.org/10.1038/sdata.2016.18

Williams ST, Reid DG, Littlewood DTJ (2003) A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism, and biogeography of the Southern Ocean. Molecular Phylogenetics and Evolution 28(1): 60–86. https://doi.org/10.1016/S1055-7903(03)00038-1

Zelaya DG (2005) Systematics and biogeography of marine gastropods molluscs from South Georgia. Spixiana 28(2): 109–139.

CAPÍTULO II

Zoological Journal of the Linnean Society, 2023, **XX**, 1–18
https://doi.org/10.1093/zoolinnean/zlad171
Advance access publication 22 November 2023
Original Article

Original Article

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

Sebastián Rosenfeld[1,2,3,4], Nicolás I. Segovia[5,6], Claudia S. Maturana[3,4], Cristián Aldea[1], Thomas Saucède[7], Paul Brickle[8,9], Hamish G. Spencer[10], Elie Poulin[3], Claudio A. González-Wevar[3,11,*]

[1]Centro de Investigación Gaia-Antártica, Universidad de Magallanes, Avenida Bulnes 01855, Punta Arenas, Chile
[2]Laboratorio de Ecosistemas Marinos Antárticos y Subantárticos, Universidad de Magallanes, Punta Arenas, Chile
[3]Instituto Milenio Biodiversidad de Ecosistemas Antárticos y Subantárticos (MI-BASE), Santiago, Chile
[4]Cape Horn International Center (CHIC), Universidad de Magallanes, Punta Arenas, Chile
[5]Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Chile
[6]Instituto Milenio en Socio-Ecología Costera (SECOS), Santiago, Chile
[7]Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté, 6, boulevard Gabriel, 21000, Dijon, France
[8]South Atlantic Environmental Research Institute, Ross Road, Stanley, Falkland Islands, UK
[9]School of Biological Sciences (Zoology), University of Aberdeen, Aberdeen, UK
[10]Department of Zoology, University of Otago, Dunedin, New Zealand
[11]Instituto de Ciencias Marinas y Limnológicas (ICML) – Centro de Investigación en Dinámicas de Ecosistemas de Altas Latitudes (Fondap IDEAL), Facultad de Ciencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile

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

[*]Corresponding author. Instituto de Ciencias Marinas y Limnológicas (ICML) - Centro de Investigación en Dinámicas de Ecosistemas de Altas Latitudes (Fondap IDEAL), Facultad de Ciencias, Universidad Austral de Chile, Casilla 567, 5090000, Valdivia, Chile. Instituto Milenio Biodiversidad de Ecosistemas Antárticos y Subantárticos (Mi-BASE), Las Palmeras 3425, 7800003, Ñuñoa, Santiago, Chile. E-mail: claudio.gonzalez@uach.cl

ABSTRACT

The marine gastropod genus *Laevilitorina* 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 *Laevilitorina*, using molecular and morphological analyses, to address formally the interspecific divergences within the nominal taxon *Laevilitorina caliginosa s.l.* We confirm the validity of *L. caliginosa* and *Laevilitorina venusta*, and we demonstrate that specimens from the Strait of Magellan and Hornos Island constitute four new species here described: *Laevilitorina magellanica* sp. nov., *Laevilitorina pepita* sp. nov., *Laevilitorina fueguina* sp. nov., and *Laevilitorina hicana* sp. nov. All six species are clearly distinguishable genetically, morphologically, and through radular tooth shape and configurations. *Laevilitorina 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 *Laevilitorina*, 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 (Johanesson 2003), speciation (Williams and Reid 2004, Galindo and Grahame 2014), physiology (McMahon 2001, Liao *et al.* 2017, Dwane *et*

Received 7 August 2023; revised 11 October 2023; accepted 17 October 2023

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 bruniensis* (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* (Powel, 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 *Laevilitorina* 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 *Laevilitorina* 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 Laevilitorininae 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. *Laevilitorina* sequences are available in GenBank under the following accession numbers: *COI* (MZ321820–MZ321864) and 28S rRNA (MZ381414–MZ381445). *Laevilitorina* 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 Laevilitorininae Reid, 1989

Genus *Laevilitorina* Pfeffer, 1886

Laevilitorina Pfeffer, 1886: 81.

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

Laevilitorina magellanica González-Wevar & Rosenfeld sp. nov.

(Fig. 2)

Laevilitorina caliginosa – Ríos and Gerdes 1997: 51; Mutschke *et al.* 1998: 13; Ingólfsson 2005: 176; Rosenfeld *et al.* 2018: 9.

Laevilitorina caliginosa L1 – González-Wevar *et al.* 2022: 1527.

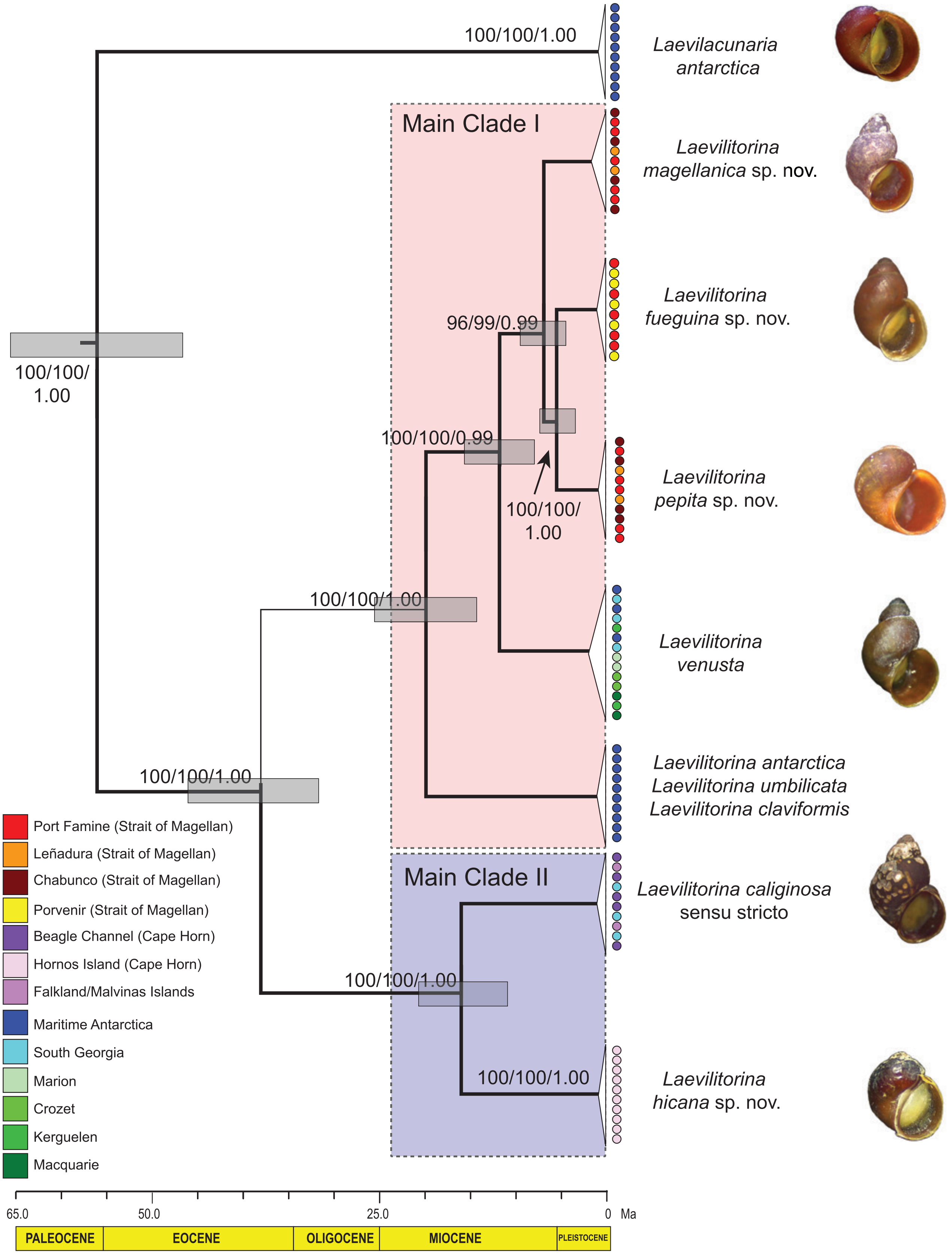


Figure 1. Bayesian maximum credibility tree of Laevilitorininae (*Laevilitorina* and *Laevilacunaria*) relationships based on mitochondrial DNA (*COI*) and nuclear DNA (28S rRNA) sequences. Bootstrap support values for maximum parsimony, maximum likelihood, and Bayesian posterior probabilities are shown 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).

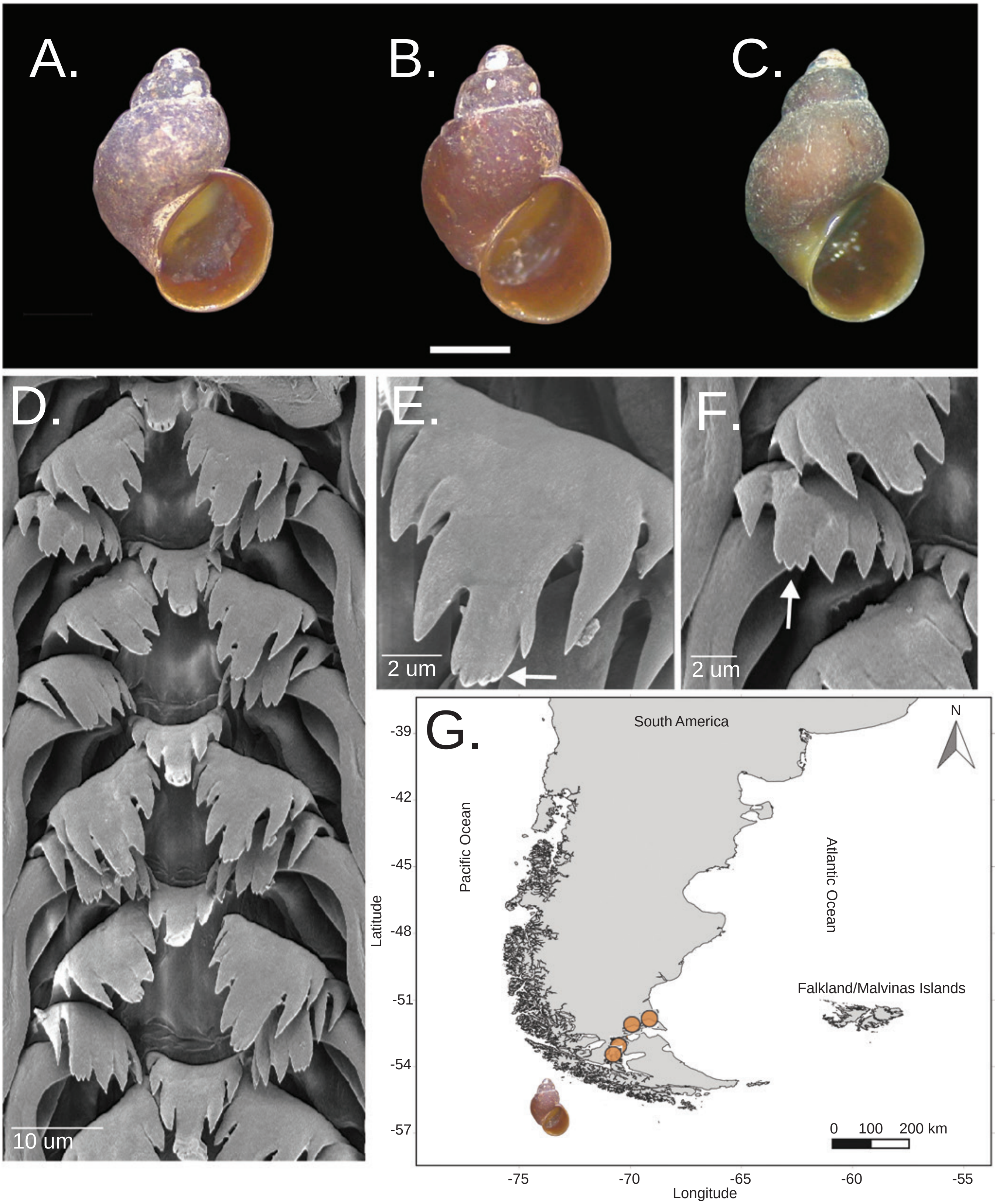


Figure 2. *Laevilitorina magellanica*, Chabunco, Strait of Magellan, southern South America. Scale bars: 1 mm unless specified otherwise. A–C, shell morphology and coloration of *L. magellanica* in the Strait of Magellan. D–F, radular morphology (SEM), showing a general view (D), lateral view (E), and 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 ≤ 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 ≤ 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 cuspids (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.

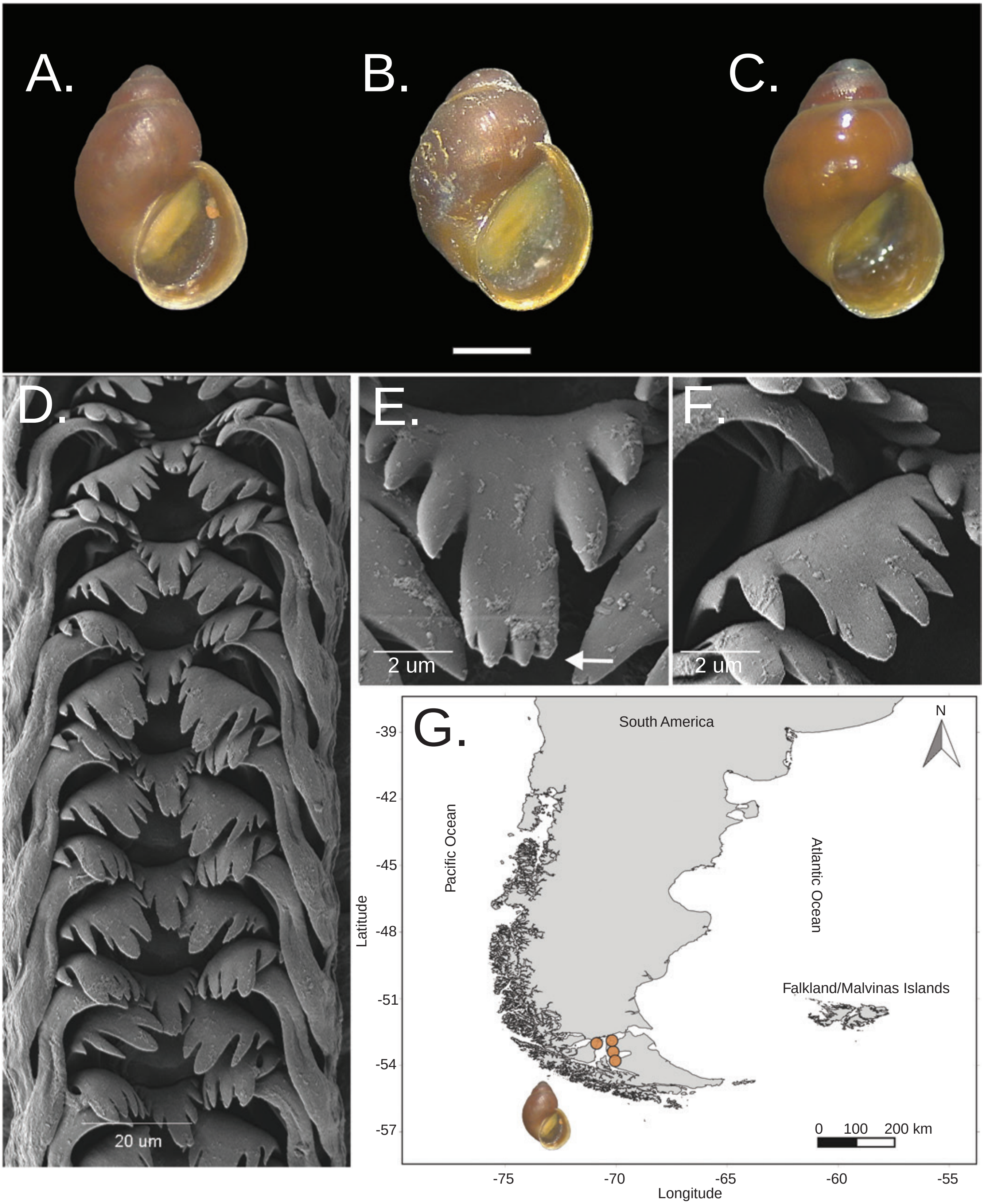


Figure 3. *Laevilitorina fueguina*, Boquerón and Chabunco, Tierra del Fuego and Brunswick Peninsula, southern South America. Scale bars: 1 mm unless specified otherwise. A–C, shell morphology and coloration of *L. fueguina* from Boquerón, Tierra del Fuego (A, B) and from Chabunco, Strait of Magellan (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 *Laevilitorina* species is Tierra del Fuego Island in the Strait of Magellan.

Remarks: Laevilitorina 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.

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

(Fig. 4)

Laevilitorina 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 *Laevilitorina* 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).

Laevilitorina venusta **Pfeffer, 1886**

(Fig. 5)

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

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

Laevilitorina coriacea – Engl, 2012: 103.

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

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

Laevilitorina 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

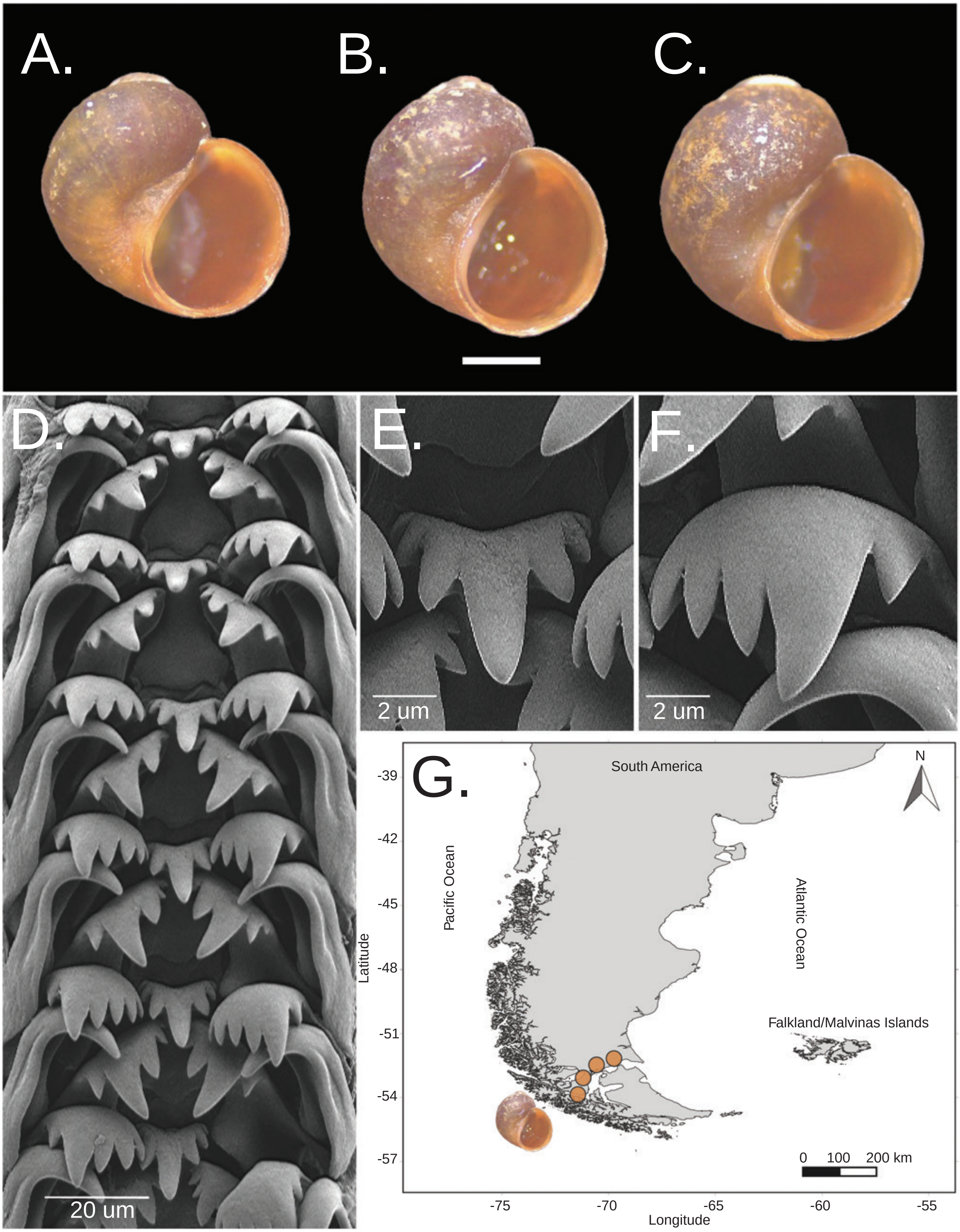


Figure 4. *Laevilitorina pepita*, Chabunco, Strait of Magellan, southern South America. Scale bars: 1 mm unless specified otherwise. A–C, shell morphology and coloration of specimens collected at Chabunco, Strait of Magellan. D–F, radular morphology (SEM), showing a general view (D), rachidian (E), and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

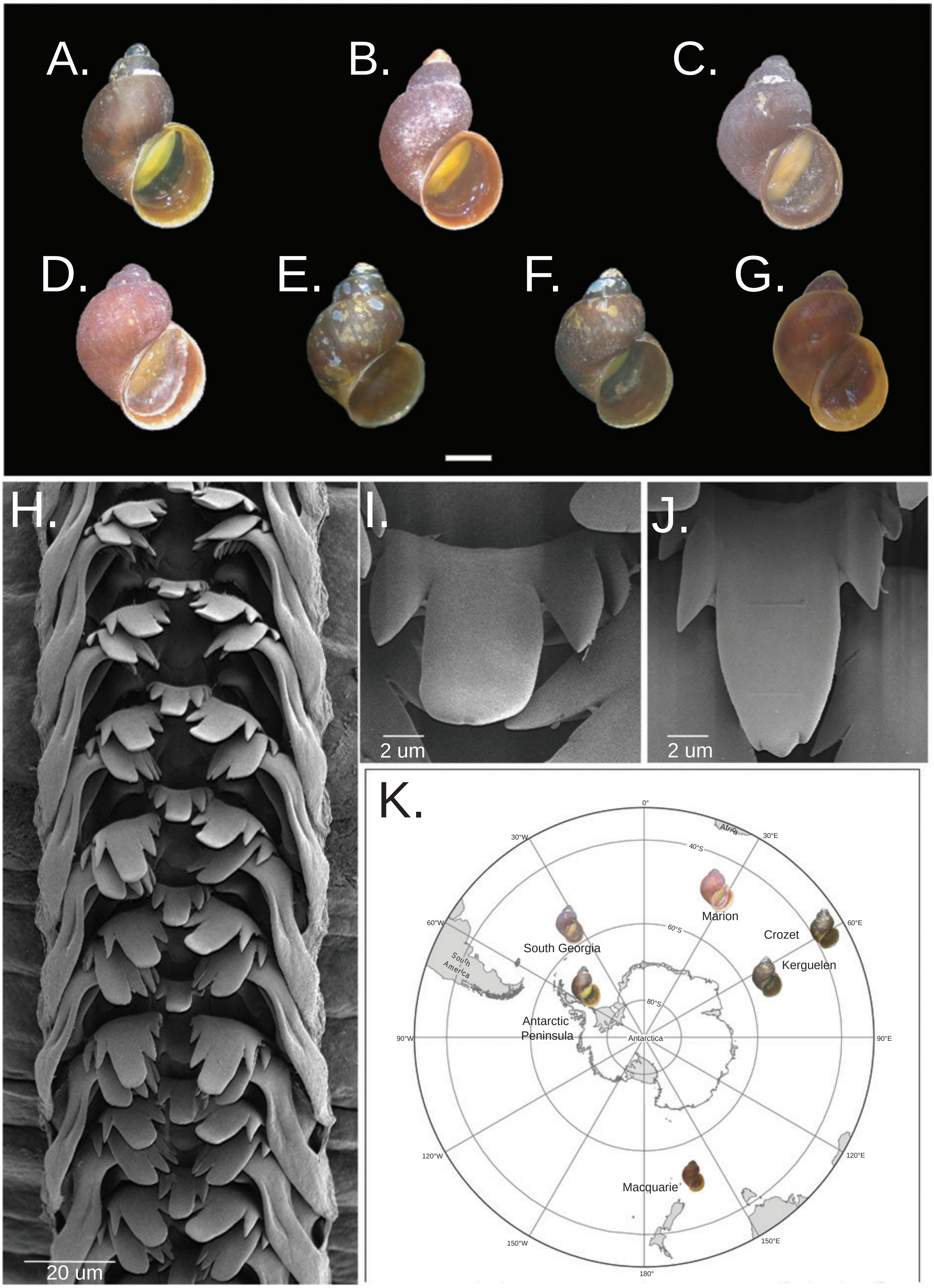


Figure 5. *Laevilitorina venusta*, Southern Ocean. Scale bars: 1 mm unless specified otherwise. A–G, variation in shell morphology and coloration of the species across its distribution in different provinces of the Southern Ocean. The specimens of *L. venusta* are from: Greenwich Island, South Shetland Islands, Antarctic Peninsula (A); Covandonga 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.

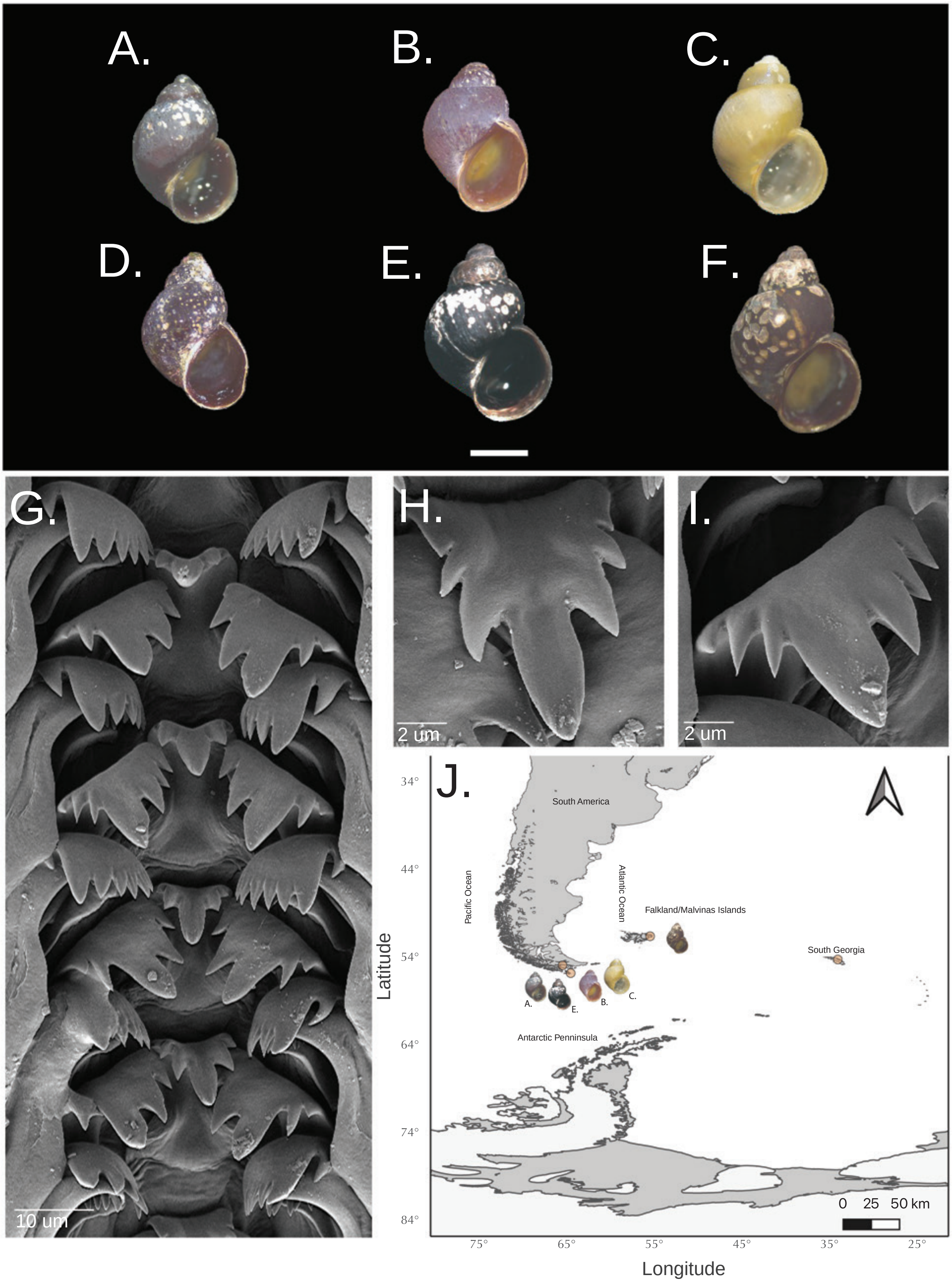


Figure 6. *Laevilitorina caliginosa*, Southern South America, South Georgia, and Falkland/Malvinas Islands. Scale bars: 1 mm unless specified otherwise. A–F, specimens of *L. caliginosa* from: Caleta Paula, Beagle Channel (A); Robalo Bay, Beagle Channel (B); Hornos Island (C); Puerto Williams, Beagle 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 ≤ 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

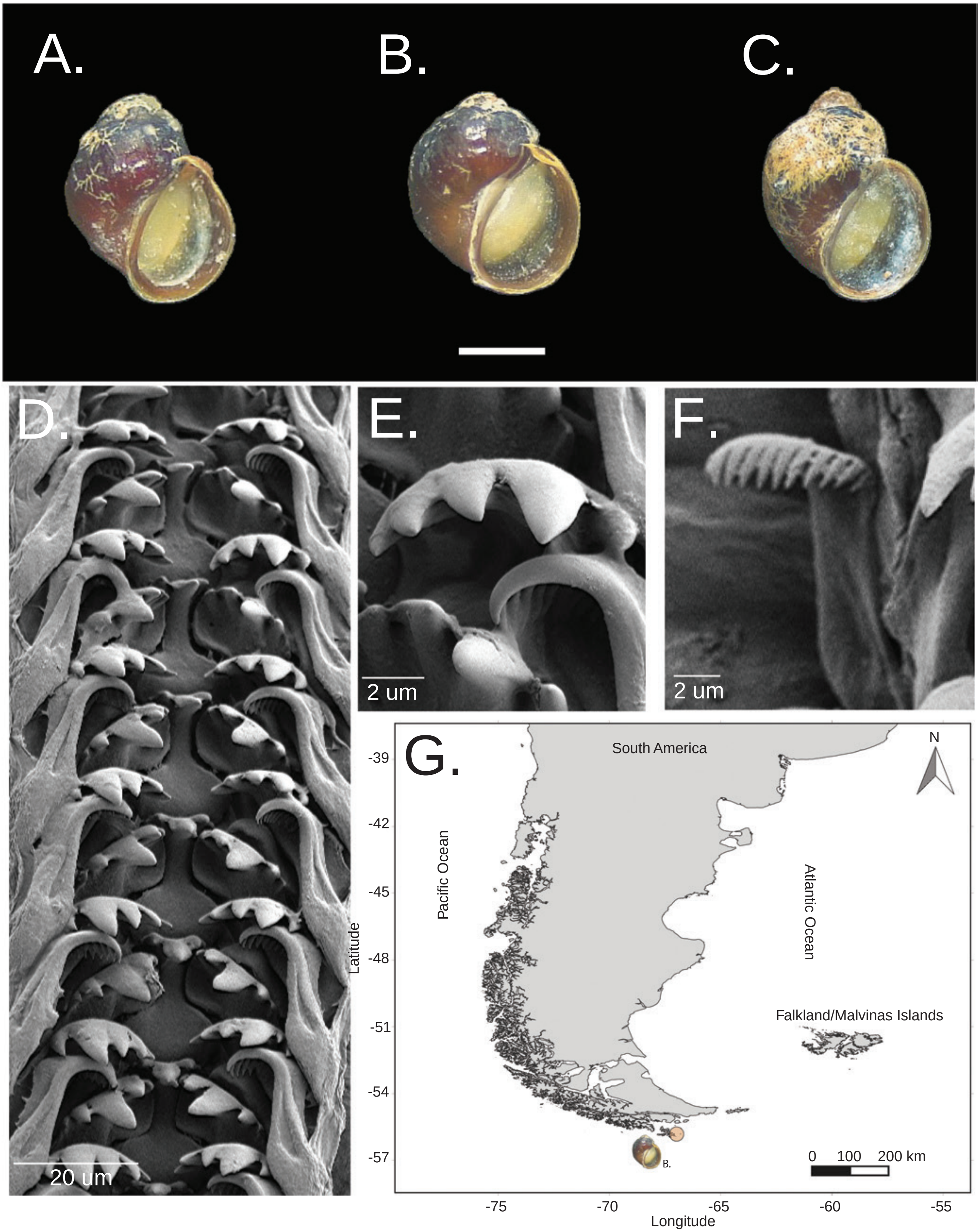


Figure 7. *Laevilitorina hicana*, Hornos Island, southern South America. Scale bars: 1 mm unless specified otherwise. A–C, shell morphology and coloration of specimens collected from Hornos Island. D–F, radular morphology (SEM), showing a general view (F), lateral view (E), and outer marginal (F). G,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

globose shell and by having an aperture that occupies on average ≤ 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. antartica* 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.

REFERENCES

Adami ML, Gordillo S. Structure and dynamics of the biota associated with *Macrocystis pyrifera* (Phaeophyta) from the Beagle Channel, Tierra del Fuego. *Scientia Marina* 1999;**63**:183–91. https://doi.org/10.3989/scimar.1999.63s1183

Aghmich A, Taboada S, Toll L *et al.* First assessment of the rocky intertidal communities of Fildes Bay, King George Island (South Shetland Islands, Antarctica). *Polar Biology* 2016;**39**:189–98. https://doi.org/10.1007/s00300-015-1814-9

Allcock AL, Strugnell JM. Southern Ocean diversity: new paradigms from molecular ecology. *Trends in Ecology & Evolution* 2012;**27**:520–8. https://doi.org/10.1016/j.tree.2012.05.009

Amsler CD, Amsler MO, Curtis MD *et al.* Impacts of gastropods on epiphytic microalgae on the brown macroalga Himantothallus grandifolius. *Antarctic Science* 2019;**31**:89–97. https://doi.org/10.1017/S0954102019000014

Amsler MO, Huang Y, Engl W *et al.* Abundance and diversity of gastropods associated with dominant subtidal macroalgae from the western Antarctic Peninsula. *Polar Biology* 2015;**38**:1171–81. https://doi.org/10.1007/s00300-015-1681-4

Amsler C, Miller L, Edwards E *et al.* Gastropod assemblages associated with *Himantothallus grandifolius*, *Sarcopeltis antarctica* and other subtidal macroalgae. *Antarctic Science* 2022;**34**:246–55. https://doi.org/10.1017/S0954102022000153

Arnaud P, Bandel K. Comments on six species of marine Antarctic Littorinacea (Mollusca, Gastropoda). *Tethys* 1976;**8**:213–30.

Arnaud P, Jazdzewski K, Presler P *et al.* Preliminary survey of benthic invertebrates collected by polish antarctic expeditions in Admiralty Bay (King George Island, South Shetland Islands, Antarctica). *Polish Polar Research* 1986;**1-2**:7–24.

Cantera JR, Arnaud PM. Les gastéropodes prosobranches des Îles Kerguelen et Crozet (sud de l'Océan Indien): comparaison écologique et particularités biologiques. *Comité National Français des Recherches Antarctiques* 1985;**56**:1–169.

Castellanos ZA. *Catálogo descriptivo de la malacofauna marina Magallánica 4. Mesogastropoda*. Comisión de Investigaciones Científicas, Provincia de Buenos Aires, 1989.

Chenuil A, Saucède T, Hemery LG *et al.* Understanding processes at the origin of species flocks with focus on the marine Antarctic fauna 2018. *Biological Reviews* 2018;**93**:481–504. https://doi.org/10.1111/brv.12354

Children JG. Mollusca. *Synopsis of the Contents of the British Museum* 1834;**28**:88–118.

Crame J. Key stages in the evolution of the Antarctic marine fauna. *Journal of Biogeography* 2018;**45**:986–94. https://doi.org/10.1111/jbi.13208

Darriba D, Taboada GL, Doallo R *et al.* jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 2012;**9**:772. https://doi.org/10.1038/nmeth.2109

Dell RK. Marine Mollusca from Macquarie and Heard Islands. *Record of the Dominion Museum Wellington* 1964;**4**:267–301.

Dell RK. The marine Mollusca of the Royal Society Expedition to Southern Chile, 1958–1959. *Records of the Dominion Museum* 1971;**7**:155–233.

Dwane C, Rundle SD, Tils O *et al.* Divergence in thermal physiology could contribute to vertical segregation in intertidal ecotypes of *Littorina saxatilis*. *Physiological and Biochemical Zoology* 2021;**94**:353–65. https://doi.org/10.1086/716176

Edgar RC. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics* 2004;**5**:113. https://doi.org/10.1186/1471-2105-5-113

Engl W. 2012. *Shells of Antarctica*. Hackenheim: ConchBooks.

Eschweiler N, Molis M, Buschbaum C. Habitat-specific size structure variations in periwinkle populations (*Littorina littorea*) caused by biotic factors. *Helgoland Marine Research* 2009;**63**:119–27. https://doi.org/10.1007/s10152-008-0131-x

Felsenstein J. Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution* 1981;**17**:368–76. https://doi.org/10.1007/BF01734359

Fraser CI, Nikula R, Ruzzante DE *et al.* Poleward bound: biological impacts of Southern Hemisphere glaciation. *Trends in Ecology & Evolution* 2012;**27**:462–71. https://doi.org/10.1016/j.tree.2012.04.011

Fraser CI, Terauds A, Smellie J *et al.* Geothermal activity helps life survive glacial cycles. *Proceedings of the National Academy of Sciences of the United States of America* 2014;**111**:5634–9. https://doi.org/10.1073/pnas.1321437111

Gaillard JM. Mollusca. In: van Zinderen Bakker EM, Winterbottom JM, Dyer RA (eds). *Marion and Prince Edward Islands*. Balkema AA: Cape Town, 1971; 291–300.

Galindo J, Grahame JW. Ecological speciation and the intertidal snail *Littorina saxatilis*. *Advances in Ecology* 2014;**2014**:1–9. https://doi.org/10.1155/2014/239251

González-Wevar CA, Nakano T, Cañete JI *et al.* Concerted genetic, morphological and ecological diversification in *Nacella* limpets in the Magellanic Province. *Molecular Ecology* 2011;**20**:1936–51. https://doi.org/10.1111/j.1365-294X.2011.05065.x

González-Wevar CA, Saucède T, Morley S *et al.* Extinction and recolonization of maritime Antarctica in the limpet *Nacella concinna* (Strebel, 1908) during the last glacial cycle: toward a model of Quaternary biogeography in shallow Antarctic invertebrates. *Molecular Ecology* 2013;**2013**:5221–36. https://doi.org/10.1111/mec.12465

González-Wevar CA, Hüne M, Segovia NI *et al.* Following the Antarctic Circumpolar Current: patterns and processes in the biogeography of the limpet *Nacella* (Mollusca: Patellogastropoda) across the Southern Ocean. *Journal of Biogeography* 2017;**44**:861–74. https://doi.org/10.1111/jbi.12908

González-Wevar CA, Segovia NI, Rosenfeld S *et al.* Unexpected absence of island endemics: long-distance dispersal in higher latitude sub-Antarctic *Siphonaria* (Gastropoda: Euthyneura) species. *Journal of Biogeography* 2018;**45**:874–84.https://doi.org/10.1111/jbi.13174

González-Wevar CA, Gérard K, Rosenfeld S *et al.* Cryptic speciation in Southern Ocean *Aequiyoldia eightsii* (Jay, 1839): Mio-Pliocene trans-Drake Passage separation and diversification. *Progress in Oceanography* 2019;**174**:44–54. https://doi.org/10.1016/j.pocean.2018.09.004

González-Wevar CA, Segovia NI, Rosenfeld S *et al.* Contrasting biogeographical patterns in *Margarella* (Gastropoda: Calliostomatidae: Margarellinae) across the Antarctic Polar Front. *Molecular Phylogenetics and Evolution* 2021;**156**:107039.https://doi.org/10.1016/j.ympev.2020.107039

González-Wevar CA, Segovia NI, Rosenfeld S *et al.* Seven snail species hidden in one: biogeographic diversity in an apparently widespread periwinkle in the Southern Ocean. *Journal of Biogeography* 2022;**49**:1521–34. https://doi.org/10.1111/jbi.14453

Gould AA. Descriptions of new species of shells, brought home by the U.S. exploring expedition. *Proceedings of the Boston Society of Natural History* 1849;**3**:83–5.

Gould AA. *Volume XII Mollusca and Shells United States exploring expedition during the years 1838, 1839, 1840, 1841, 1842*. Boston: Gould & Lincoln, 1852.

Gould AA. *Atlas. Mollusca and Shells. United States Exploring Expedition During the Years 1838, 1839, 1840, 1841, 1842.* Philadelphia: Sherman & Son, 1856.

Griffiths HJ, Waller CL. The first comprehensive description of the biodiversity and biogeography of Antarctic and Sub-Antarctic intertidal communities. *Journal of Biogeography* 2016;**43**:1143–55. https://doi.org/10.1111/jbi.12708

Guzmán L, Ríos C. Estructura del conjunto de macroorganismos de una playa de bloques y cantos rodados de Isla Wallonston, Archipielago del Cabo de Hornos. *Anales del Instituto de la Patagonia* 1981;**12**:258–70.

Halanych KM, Mahon AR. Challenging the dogma concerning biogeographic patterns of Antarctica and the Southern Ocean. *Annual Review of Ecology, Evolution, and Systematics* 2018;**49**:355–78. https://doi.org/10.1146/annurev-ecolsys-121415-032139

Huelsenbeck JP, Ronquist F. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 2001;**17**:754–5. https://doi.org/10.1093/bioinformatics/17.8.754

Iken K. Feeding ecology of the Antarctic herbivorous gastropod *Laevilacunaria antarctica* Martens. *Journal of Experimental Marine Biology and Ecology* 1999;**236**:133–48. https://doi.org/10.1016/s0022-0981(98)00199-3

Ingólfsson A. Community structure and zonation patterns of rocky shores at high latitudes: an interocean comparison. *Journal of Biogeography* 2005;**32**:169–82. https://doi.org/10.1111/j.1365-2699.2004.01150.x

Johannesson K. Evolution in *Littorina*: ecology matters. *Journal of Sea Research* 2003;**49**:107–17. https://doi.org/10.1016/s1385-1101(02)00218-6

Johannesson K, Johannesson B, Lundgren U. Strong natural selection causes microscale allozyme variation in a marine snail. *Proceedings of the National Academy of Sciences of the United States of America* 1995;**92**:2602–6. https://doi.org/10.1073/pnas.92.7.2602

Kearse M, Moir R, Wilson A *et al.* Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 2012;**28**:1647–9. https://doi.org/10.1093/bioinformatics/bts199

Kumar S, Stecher G, Li M *et al.* MEGA X: molecular evolutionary genetic analysis across computing platforms. *Molecular Biology and Evolution* 2018;**35**:1547–9. https://doi.org/10.1093/molbev/msy096

Liao M-L, Zhang S, Zhang G-Y *et al.* Heat-resistant cytosolic malate dehydrogenases (cMDHs) of thermophilic intertidal snails (genus *Echinolittorina*): protein underpinnings of tolerance to body temperatures reaching 55°C. *Journal of Experimental Biology* 2017;**220**:2066–75. https://doi.org/10.1242/jeb.156935

Martín A, Miloslavich P, Díaz Y *et al.* Intertidal benthic communities associated with the macroalgae Iridaea cordata and *Adenocystis utricularis* in King George Island, Antarctica. *Polar Biology* 2016:**39**:207–20. https://doi.org/10.1007/s00300-015-1773-1

McMahon RF. Acute thermal tolerance in intertidal gastropods relative to latitude, superfamily, zonation and habitat with special emphasis on the Littorinoidea. *Journal of Shellfish Research* 2001;**20**:459–67.

McQuaid CD. Biology of the gastropod family Littorinidae: role in the ecology of intertidal and shallow marine ecosystems. *Oceanography and Marine Biology: An Annual Review* 1996;**34**:263–302.

Melvill JC, Standen P. The Marine Mollusca of the Scottish National Antarctic Expedition, part I. *Transactions of the Royal Society of Edinburgh* 1907;**46**:119157.

Melvill JC, Standen P. The Marine Mollusca of the Scottish National Antarctic Expedition, part II. *Transactions of the Royal Society of Edinburgh* 1912;**48**:333–66.

Melvill JC, Standen P. Notes on Mollusca collected in the Northwest Falklands by Mr. Rupert Vallentin, F.L.S., with descriptions of some new species. *Annals & Magazine of Natural History* 1914;**13**:110–36.

Moon KL, Chown SL, Fraser CI. Reconsidering connectivity in the sub-Antarctic. *Biological Reviews of the Cambridge Philosophical Society* 2017;**92**:2164–81. https://doi.org/10.1111/brv.12327

Mutschke E, Ríos C, Montiel A. Situación actual de la macrofauna presente en el intermareal de bloques and cantos de Bahía Laredo, Estrecho de Magallanes. *Anales del Instituto de la Patagonia* 1998;**26**:5–29.

Ng TPT, Lau SLY, Seuront L *et al.* Linking behaviour and climate change in intertidal ectotherms: insights from littorinid snails. *Journal of Experimental Marine Biology and Ecology* 2017;**492**:121–31. https://doi.org/10.1016/j.jembe.2017.01.023

Ng TPT, Rolán-Alvarez E, Dahlén SS *et al.* The causal relationship between sexual selection and sexual size dimorphism in marine gastropods. *Animal Behaviour* 2019;**148**:53–62. https://doi.org/10.1016/j.anbehav.2018.12.005

Pearse JS, Mooi R, Lockhart SJ, Brandt A. Brooding and species diversity in the Southern Ocean: selection for brooders or speciation within brooding clades? In: Krupnik I, Lang MA, Miller SE (eds). *Smithsonian at the Poles: Contributions to International Polar Year Science*. New York: Smithsonian Institution Scholarly Press, 2009, 181–96.

Poulin E, Feral J-P. Why are there so many species of brooding Antarctic echinoids. *Evolution* 1996;**50**:820–30. https://doi.org/10.1111/j.1558-5646.1996.tb03891.x

Poulin E, Palma A, Féral J-P. Evolutionary versus ecological success in Antarctic benthic invertebrates. *Trends in Ecology &*

Evolution 2002;**17**:218–22. https://doi.org/10.1016/S0169-5347(02)02493-X

Poulin E, González-Wevar C, Díaz A *et al*. Divergence between Antarctic and South American marine invertebrates: what molecular biology tells us about Scotia Arc geodynamics and the intensification of the Antarctic Circumpolar Current. *Global and Planetary Change* 2014;**123**:392–9. https://doi.org/10.1016/j.gloplacha.2014.07.017

Powell AWB. Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. *Discovery Reports* 1951;**26**:47–196. https://doi.org/10.5962/bhl.part.16335

Powell AWB. Mollusca of the southern islands of New Zealand. *Department of Scientific and Industrial Research Cape Expedition Series Bulletin* 1955a;**15**:1–151.

Powell AWB. Mollusca of Kerguelen and Macquarie Islands, B.A.N.Z. *Antarctic Research Expedition, 1929–1931* 1955b;**Report B6**:107–49.

Powell AWB. Mollusca of Kerguelen and Macquarie Islands. B.A.N.Z. *Antarctic Research Expedition, 1929–1931* 1957; Report B6:107–49.

Powell AWB. New Zealand Mollusca: marine, land and freshwater shells. *Collins Auckland Editors*, 1979, 500 pp.

Preston HB. Characters of six new pelecypods and two new gastropods from the Falkland Islands. *Annals and Magazine of Natural History* 1912;**9**:636–40. https://doi.org/10.1080/00222931208693180

Preston HB. Descriptions of eight new species of marine Mollusca from the South Shetland Islands. *Annals and Magazine of Natural History* 1916;**18**:269–72. https://doi.org/10.1080/00222931608693847

Reid DG. The comparative morphology, phylogeny and evolution of the gastropod family Littorinidae. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 1989;**324**:1–110. https://doi.org/10.1098/rstb.1989.0040

Reid DG, Williams ST. The subfamily Littorininae (Gastropoda: Littorinidae) in the temperate Southern Hemisphere: the genera *Nodilittorina*, *Austrolittorina* and *Afrolittorina*. *Records of the Australian Museum* 2004;**56**:75–122. https://doi.org/10.3853/j.0067-1975.56.2004.1393

Reid DG, Rumback E, Thomas RH. DNA, morphology and fossils: phylogeny and evolutionary rates of the gastropod genus *Littorina*. *Philosophical Transactions of the Royal Society B: Biological Sciences* 1996;**351**:877–95. https://doi.org/10.1098/rstb.1996.0082

Reid DG, Lal K, Mackenzie-Dodds J *et al*. Comparative phylogeography and species boundaries in *Echinolittorina* snails in the central Indo-West Pacific. *Journal of Biogeography* 2006;**33**:990–1006. https://doi.org/10.1111/j.1365-2699.2006.01469.x

Reid DG, Dyal P, Williams ST. A global molecular phylogeny of 147 periwinkle species (Gastropoda, Littorininae). *Zoologica Scripta* 2012;**41**:125–36. https://doi.org/10.1111/j.1463-6409.2011.00505.x

Riesgo A, Taboada S, Avila C. Evolutionary patterns in Antarctic marine invertebrates: An update on molecular studies. *Marine Genomics* 2015;**23**:1–13. https://doi.org/10.1016/j.margen.2015.07.005

Rosenfeld S, Aldea C, Ojeda J *et al*. Molluscan assemblages associated with *Gigartina* beds in the Strait of Magellan and the South Shetland Islands (Antarctica): a comparison of composition and abundance. *Polar Research* 2017;**36**:1–10. https://polarresearch.net/index.php/polar/article/view/2640

Rosenfeld S, Maturana CS, Spencer HG *et al.* Complete distribution of the genus Laevilitorina (Littorinimorpha, Littorinidae) in the Southern Hemisphere: remarks and natural history. *Zookeys* 2022;**1127**:61–77. https://doi.org/10.3897/zookeys.1127.91310

Rosenfeld S, Marambio J, Ojeda J *et al*. Trophic ecology of two coexisting Sub- Antarctic limpets of the genus *Nacella*: spatio-temporal variation in food availability and diet composition of *Nacella magellanica* and *N. deaurata* in the Sub-Antarctic Ecoregion of Magellan. *ZooKeys* 2018;**738**:1–25. https://doi.org/10.3897/zookeys.738.21175

Schrödl M, Engl W, Aldea C *et al*. Gastropods, Gastropoda. In: Schories D, Kohlberg G (eds.), *Marine Wildlife King George Island Antarctica: Identification Guide*. Germany: privately published, 2016, 128–53.

Simpson RD, Harrington SA. Egg masses of three gastropods, *Kerguelenella lateralis* (Siphonariidae), *Laevilitorina caliginosa* and *Macquariella hamiltoni* (Littorinidae), from Macquarie Island (sub-Antarctic). *Journal of the Malacological Society of Australia* 1985;**7**:17–28. https://doi.org/10.1080/00852988.1985.10673973

Smith EA. Mollusca. In: Lankester ER, Bell J (eds.), *Report on the Collections of Natural History Made in Antarctic Regions During the Voyage of the Southern Cross*. London: British Museum (Natural History) Cromwell Road, 1902; 201–13.

Strugnell JM, Rogers AD, Prodöhl PA *et al*. The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics* 2008;**2008**:853–60.

Suter H. *Manual of the New Zealand Mollusca*. Wellington: Atlas of plates, 1913, [xxiii +] 1120. [(1913) and Atlas pls 1–72 (1915)].

Thatje S. Effects of capability for dispersal on the evolution of diversity in Antarctic benthos. *Integrative & Comparative Biology* 2012;**52**:470–82. https://doi.org/10.1093/icb/ics105

Thiele J. Die antarktischen Schnecken und Muscheln. In: von Drygalski E (ed.), *Deutsche Südpolar-Expedition (1901–1903)*, Vol. **13**, 1912, 183–286.

Tryon GW. *Manual of Conchology. Structural and Systematic with Illustrations of the Species*, Vol. **IX**. Philadelphia, 1887.

Valdivia N, Garrido I, Bruning P *et al*. Biodiversity of an Antarctic rocky subtidal community and its relationship with glacier meltdown processes. *Marine Environmental Research* 2020;**159**:104991. https://doi.org/10.1016/j.marenvres.2020.104991

von Martens E, Pfeffer G. Die Mollusken von Süd-Georgien nach der Ausbeute der Deutschen Station 1882–83. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* 1886;**3**:65–135.

Waller CL, Barnes DK, Convey P. Ecological contrasts across an Antarctic land–sea interface. *Austral Ecology* 2006;**31**:656–66. https://doi.org/10.1111/j.1442-9993.2006.01618.x

Watson RB. Report on the Scaphopoda and Gasteropoda collected by H.M.S. challenger during the years 1873–76. Report on the scientific results of the voyage of H.M.S. Challenger, 1873–1876. *Zoology* 1886;**15**:1–756.

Wilding CS, Grahame J, Mill PJ. Correlation of morphological diversity with molecular marker diversity in the rough periwinkle *Littorina saxatilis* (Olivi). *Journal of Shelfish Research* 2001;**20**:501–8.

Williams ST, Reid DG. Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*. *Evolution* 2004;**58**:2227–51. https://doi.org/10.1111/j.0014-3820.2004.tb01600.x

Williams ST, Reid DG, Littlewood DTJ. A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism, and biogeography of the Southern Ocean. *Molecular Phylogenetics and Evolution* 2003;**28**:60–86.

Wilson NG, Schrödl M, Halanych KM. Ocean barriers and glaciation: evidence for explosive radiation of mitochondrial lineages in the Antarctic sea slug *Doris kerguelenensis* (Mollusca, Nudibranchia). *Molecular Ecology* 2009;**18**:965–84. https://doi.org/10.1111/j.1365-294X.2008.04071.x

Xia X. DAMBE5: a comprehensive software package for data analysis in molecular biology and evolution. *Molecular Biology and Evolution* 2013;**30**:1720–8. https://doi.org/10.1093/molbev/mst064

Zelaya DG. Systematics and biogeography of marine gastropods molluscs from South Georgia. *Spixiana* 2005;**28**:109–39.

CAPÍTULO III

"Tracing the Origins of Antarctic Periwinkles: A Molecular Perspective on *Laevilacunaria* Evolution"

Sebastián Rosenfeld[1,2,3], Claudia S. Maturana[2,3], Moisés Valladares[4,5], Hamish G. Spencer[6], Thomas Saucède[7], Paul Brickle[8,9], Paula Vidal[2], Guillaume Schwob[2], Quentin Jossart[7,10], Elie Poulin[2], Claudio Gonzalez-Wevar[2,11]

[1] Laboratorio de Ecología Molecular (LEM), Facultad de Ciencias, Universidad de Chile.
[2] Instituto Milenio Biodiversidad de Ecosistemas Antárticos y Subantárticos (MI-BASE), Santiago, Chile
[3] Cape Horn International Center (CHIC), Puerto Williams, Chile
[4] Laboratorio de Biología Evolutiva, Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile
[5] Grupo de Biodiversidad y Cambio Global (GBCG), Departamento de Ciencias Básicas, Universidad del Bío-Bío, Chillán, Chile
[6] Department of Zoology, University of Otago, Dunedin, New Zealand
[7] Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté, 6, boulevard Gabriel, 21000, Dijon, France.
[8] South Atlantic Environmental Research Institute, Ross Road, Stanley, Falkland Islands, UK
[9] School of Biological Sciences (Zoology), University of Aberdeen, Aberdeen, UK
[10] Marine Biology, Université Libre de Bruxelles (ULB), Brussels, Belgium
[11] Instituto de Ciencias Marinas y Limnológicas (ICML), Centro Fondap IDEAL, Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile

Abstract

This study examines the phylogeny, systematics, and biogeography of the subfamily Laevilitorininae, focusing on the genus *Laevilacunaria*. Utilizing multi-locus genetic data and radular morphology, our findings indicate that both *Laevilacunaria* and *Laevilitorina* are paraphyletic, revealing a more intricate taxonomy and biogeography for the subfamily Laevilitorininae. The genus *Laevilacunaria*, previously underestimated in diversity, encompasses at least two distinct and highly differentiated clades. One *Laevilacunaria* clade includes Antarctic species and a species present north of the

Antarctic Polar Front (APF), while the other is confined to West Antarctica and South Georgia. Phylogenetic analyses suggest that the TMCRA of Laevilitorininae dates back to the final stage the breakup of Gondwana, with diversification events within each clade occurring from the Miocene to the Pleistocene. Our study proposes a new classification system for Laevilitorininae, recognizing four genera. Historical biogeography analyses underscore the roles of historical vicariance and more recent long-distance dispersal events, facilitated by macroalgal rafting, in shaping current distribution patterns. This research provides essential insights into the evolutionary history and systematics of Laevilitorininae, highlighting the importance of integrating molecular and morphological data. These findings contribute to understanding the complex biogeography and evolutionary history of Southern Ocean mollusks, highlighting the need for updated systematic classifications and offering insights into the patterns of endemism and species distribution within this unique marine ecosystem.

Introduction

Historically, two main biogeographic regions have been described within the Southern Ocean (Koubbi et al., 2014). First, the subantarctic region includes i) the Magellanic province on the southern coast of South America, ii) the New Zealand subantarctic Islands, iii) subantarctic islands of the Indian Ocean, and iv) Macquarie Island (sometimes included in ii). Second, the Antarctic region represents a single province that includes the Antarctic continent and some islands located south of the

Antarctic Polar Front (APF), such as South Georgia, the South Sandwich Islands, and Bouvet Island (Koubbi et al., 2014)). Despite this pronounced bioregionalization, faunal associations within and between these provinces cannot be explained by a single general biogeographical hypothesis and largely depend on the organism group analyzed (González-Wevar et al., 2023; González-Wevar et al., 2017; Linse et al., 2006). However, some general rules have been proposed, including high levels of endemism (> 70% in some groups), the existence of a single Antarctic province clearly separated from other subantarctic provinces, and a clear separation between subantarctic islands associated with South America and those from New Zealand (Crame, 1999; Halanych & Mahon, 2018; Koubbi et al., 2014). A main characteristic of some Antarctic benthos groups is the high number of brooding species compared to broadcast spawners. This developmental mode has been reported in several groups of marine invertebrates, such as echinoderms, arthropods, polychaetes and molluscs (Hain & Arnaud, 1992; Knox, 1977; Poulin et al., 2002), suggesting that it has had greater evolutionary success in Antarctic environments (Poulin et al., 2002).

Littorinid snails are characteristic of the shallow rocky shores of the Southern Ocean (González-Wevar et al., 2023; Powell, 1960). This group includes three intertidal and subtidal genera: *Laevilitorina* Pfeffer 1886, *Laevilacunaria* Powell 1951 (Reid, 1989) and *Pellilitorina* Pfeffer 1886. Both *Laevilacunaria* and *Laevilitorina* are the only representatives of the subfamily Laevilitorininae (González-Wevar et al., 2023; Reid, 1989; Rosenfeld et al., 2023a), 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 environments down to 64 m depth (Rosenberg, 2009). In addition, species of *Laevilitorina* and *Laevilacunaria* are sympatric and even syntopic living on different species of macroalgae in Antarctic and sub-Antarctic environments (Amsler et al., 2015; Martín et al., 2016; Reid, 1989; Rosenfeld et al., 2017; Rosenfeld et al., 2022; S. Rosenfeld et al., 2023b; Simpson, 1972). Another significant trait shared by these two genera is their life cycle without a free-living pelagic larval stage. Rather, females deposit egg masses on rocks or macroalgal fronds, and after 1 or 4 months juveniles hatch directly (Picken, 1979; Simpson & Harrington, 1985). It has been predicted that species with this protected benthic development mode, should exhibit a low dispersal potential and present narrow geographical ranges (Hoffman et al., 2011; Simpson & Harrington, 1985).

It is interesting to highlight that despite *Laevilacunaria* and *Laevilitorina* species sharing 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 widest distributions in high latitudes of the Southern Hemisphere including the Southern Ocean (Rosenfeld et al., 2022). Its current range includes the west and east coast of South America, south of 50ºS, 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 (Schmider-Martinez et al., 2023).

Another important aspect that differentiates these two genera is the pattern of species richness. For example, at present the WoRMS database (http://www.marinespecies.org) recognizes 25 species of *Laevilitorina* across its distribution, with four species recently described from the Magellanic region (Rosenfeld et al., 2023a). By contrast, *Laevilacunaria* includes only three species: *L. antarctica*, *L. bennetti*, and *L. pumilio*. A recent phylogeographic study of *L. antarctica*, however, revealed that populations from South Georgia and the Antarctic Peninsula could represent distinct evolutionary units (González-Wevar et al., 2024). 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?

These two genera of littorinids represent a very interesting models to explore the underlying processes and evolutionary mechanism that have shaped their contrasting biogeographic patterns, despite sharing the same mode of development and similar habitats. Addressing the origin and diversification of *Laevilacunaria* throughout its distribution and reconstructing the phylogenetic relationship among higher latitude litorinids will give us a better understanding of the evolutionary pathways of these important gastropods of the Southern Ocean.

Material and Methods

Specimen samples collection

Species of *Laevilacunaria* were collected between 2017 and 2023 in different localities across the Southern Ocean including maritime Antarctica and subantarctic Islands such as South Georgia, Crozet and Kerguelen (Figure 1, Table 1). In addition, specimens of different species of the sister genus *Laevilitorina* were collected in the Magellan province, Falkland/Malvinas Islands, West Antarctica and Subantarctic Islands (Figure 1, Table 1). Finally, genera of Lacuninae were also collected: *Pellilitorina* in West Antarctica and Kerguelen and *Risellopsis* in the South Island of New Zealand (Figure 1, Table 1). Individuals were collected following the sampling protocol of Rosenfeld et al., (2022) and Rosenfeld et al., (2023b). Specimens were fixed in ethanol (95%) for molecular analyses, and phylogenetic reconstructions included ≥ 4 individuals for each recognized *Laevilacunaria* lineage. Each individual was photographed for morphological analyses. The material examined, and nucleic acids are available in the collection of the Laboratorio de Ecología Molecular (LEM) at the Universidad de Chile and Laboratorio de Genomica y Ecologia Molecular Antartica y sub-Antartica (LAGEMAS) at Universidad Austral de Chile, Valdivia, Chile.

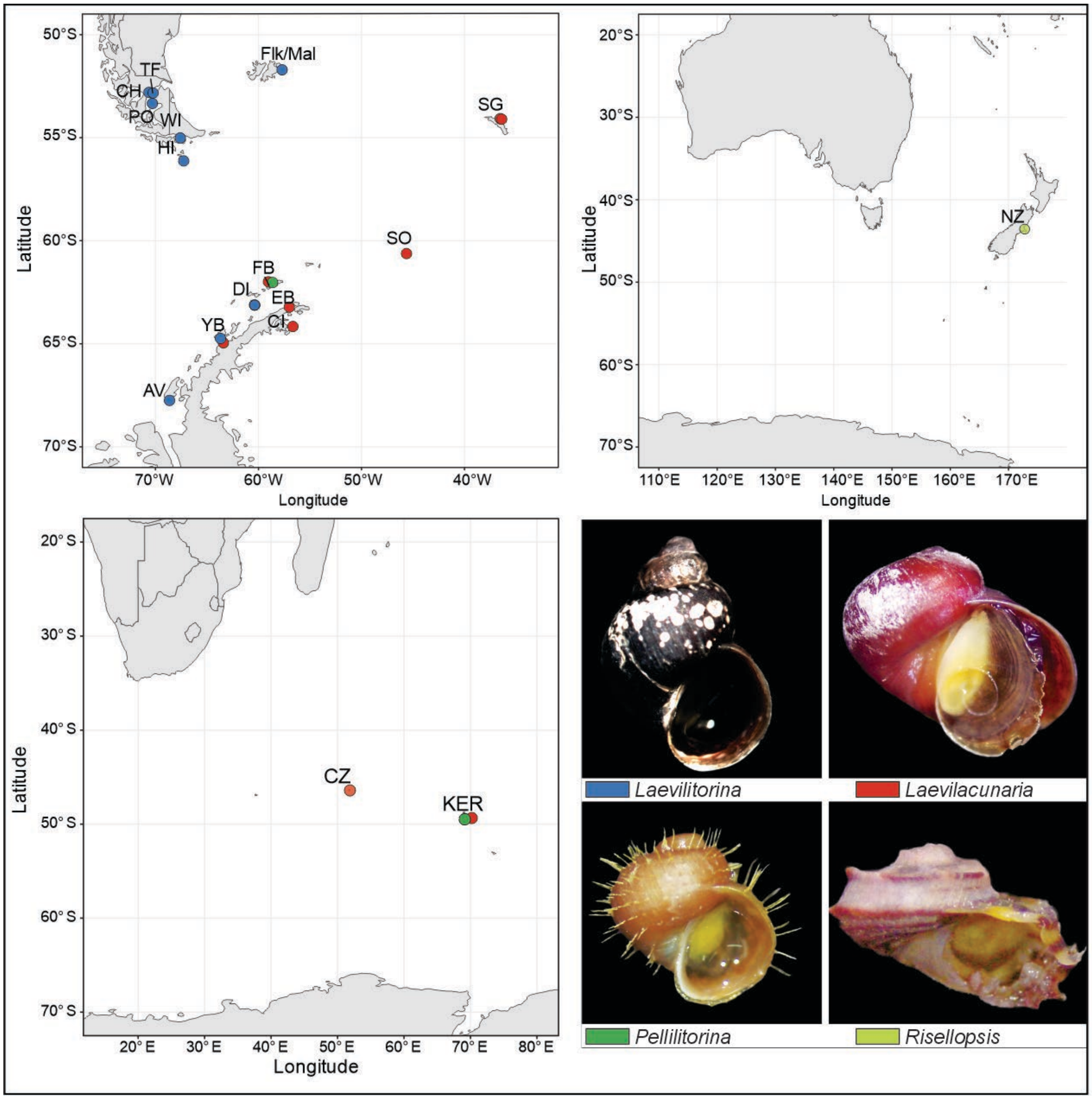


Figure 1. Map of the distribution of *Laevilacunaria* species, the sister genus *Laevilitorina* and the Lacuninae genera *Pellilitorina* and *Risellopsis* in the Southern Hemisphere included in this study. The colors below each panel indicate the sites of collection of each genus. CH: Chabunco Beach, 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.

Table 1. Sampling locations of Littorinidae reported in this study.

Subfamily to species	taxon	Localily	Coordinates	
Laevilitorininae			Latitude	Longitude
Laevilacunaria	*L. antarctica*	Esperanza Bay	-63.375819	-56.988351
		Fildes Bay	-62.214258	-58.915544
		Cockburn Island	-64.185902	-56.849553
		South Orkney	-60.65646	-45.57807
		South Georgia	-54.16385	-36.69373
	L. pumilio	Crozet island	-46.41364	51.86616
		Kerguelen Island	-49.35313	70.218303
	L. bennetti	Esperanza Bay	-63.375819	-56.988351
		Yelcho Station	-64.866203	-63.589664
	L. cf bennetti	South Georgia	-54.28345	-36.49690
Laevilitorina	*L. antarctica*	Avian Island	-67.766009	-68.878253
	L. claviformis	Deception Island	-62.970317	-60.498117
	L.umbilicata	Deception Island	-62.970317	-60.498117
	L. caliginosa	Puerto Williams	-54.936594	-67.688353
	L. fueguina	Chabunco beach	-52.989559	-70.812574
		Porvenir	-53.314868	-70.459373
	L. hicana	Horn Island	-55.967545	-67.219303
	L. latior	Port Stanley	-51.700536	-57.780469
	L. magellanica	Chabunco beach	-52.989559	-70.812574
	L. pepita	Chabunco beach	-52.989559	-70.812574
		Tierra del Fuego	-52.885401	-70.248368
	L. venusta	Crozet island	-46.41364	51.86616
		Fildes Bay	-62.214258	-58.915544
		Kerguelen Island	-49.35313	70.218303
	L. wandelensis	Fildes Bay	-62.214258	-58.915544
Lacuninae				
Pellilitorina	*P. setosa*	Kerguelen Island	-49.35313	70.218303
	P. pellita	Fildes Bay	-62.214258	-58.915544
Risellopsis	*R. varia*	New Zealand	-43.564626	172.758755

Morphological identification

The identification of species was done following Powell (1951), Reid (1989), and Engl (2012) and through the original descriptions (Preston, 1916; Smith, 1879; v Martens & Pfeffer, 1886). In addition, to confirm each of the identifications, the radular morphology of the different species was revised. Radulae of *Laevilacunaria* 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 stereomicroscopy and checked with the revision of v Martens and Pfeffer (1886), Preston (1916) and Powell (1951).

DNA extraction and sequencing

DNA extractions were performed from portions of the animal's foot, or from the whole animal in case of very small individuals, using the DNeasy Blood& Tissue Kit (Qiagen), with a modified protocol for small amounts of tissue (Maturana et al., 2021). Four molecular markers were used for this study: genes previously utilized in littorinid phylogenies (Reid et al., 2012; Saha et al., 2022; Williams et al., 2003). These genes include the mitochondrial cytochrome *c* oxidase subunit I (COI; 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). Amplification of the different markers were done following Williams et al., (2003). Primer details and annealing temperature (Tm) for corresponding genes are described in supplementary (Table S1). PCRs were performed in 25 µl reaction volume containing 2 µL template DNA (10–20 ng), 0.8 mM of each primer, 12,5 µL of Phusion Hot Start II High-Fidelity PCR MasterMix (Thermo Fisher Scientific, Vilnius, Lithuania) and sterilized Milli-Q water. The reaction conditions included an initial denaturation step of 3 min at 98◦C, followed by 34 cycles of 10 s at 98 ◦C, 30 s at a gene-specific annealing temperature (Table S1), 15s at 72 ◦C, and a final extension of 10 min at 72 ◦C. PCR amplicons were purified and sequenced in both directions at Macrogen (Korea). 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 (Kearse et al., 2012) and independently aligned using Muscle (Edgar, 2004) with standard settings. Conserved sites, variable sites and parsimony-informative sites for each region were estimated using MEGA 5 software.

Phylogenetic reconstruction

To elucidate the phylogenetic relationships of *Laevilacunaria* species, 12S rRNA, 16S rRNA, COI and 28S rRNA sequences available from GenBank were aligned with our datasets (see Table S2) using MAFFT 6 (Katoh et al., 2019) with default parameters (Edgar, 2004) and then manually checked. Optimal nucleotide substitution models and partitioning scheme were selected for each marker separately using the corrected Akaike information criteria (AIC) in partitionfinder v2.1, allowing for COI codon partitioning (Lanfear et al., 2017) (Table S3). The datasets of the different loci were combined in sequencematrixv1.8 (Vaidya et al., 2011).

Phylogenetic analyses were conducted on individual loci and concatenated datasets using maximum likelihood (ML) in IQ-TREE (Nguyen et al., 2015) and Bayesian analyses (BA) in MrBayes v3.2.6 (Ronquist & Huelsenbeck, 2003). Individual gene trees were unable to resolve the relationship due to limited phylogenetic information in the Littorinidae (polytomies with poor bootstrap values; see Fig S1, S2, S3) (see Reid et al., 2012; Saha et al., 2022). Therefore, concatenated sequences were used to construct the phylogenetic relationships in the group. Two data matrices were used for the analyses. The first used 3 concatenated loci (12S rRNA + COI + 28S rRNA), which were aligned against 152 marine littorinid species obtained from GenBank (Reid et al., 2012; Saha et al., 2022). The Genbank accession number for 152 species of littorinid used in the dating analysis is given in Table S1 in Reid et al., (2012) and Table S1 in Saha et al., (2022). 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 the 4 concatenated genes (12S+16S+COI+28S), to resolve more clearly the phylogenetic relationships within Laevilitorininae. 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 (Minh et al., 2013). 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 (Rambaut et al., 2014). Maximum clade credibility trees were generated using treeannotator2.4.7 (Drummond et al., 2012) and visualized with figtree 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree)

Species delimitation analysis Phylogenetic reconstruction

For species-delimitation analyses within the genus *Laevilacunaria*, single-locus (COI) and multi-locus (12S rRNA + COI + 16S rRNA + 28S rRNA) analyses were performed. For single-locus, the automatic barcoding gap discovery (ABGD) (Puillandre et al., 2012) and the multirate Poisson Tree Processes (mPTP) (Kapli et al., 2017) 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 multi-locus analyses BPP was applied using BP&P 4.7.0 (Yang & Rannala, 2014). The four markers were used as inputs for BPP under the A11 model (A11: species delimitation = 1, species tree = 1). For the “speciesmodelprior” we used the number 1 prior which assigns equal probabilities to the rooted species trees. 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 (Yang & Rannala, 2014). Two independent MCMC analyses were run for 100.000 generations with the “burn-in” = 10.000.

Divergence time estimation

To estimate divergence times, we generated a Bayesian time-calibrated phylogeny on the concatenated dataset using BEAST v2.7.3 software (Bouckaert et al., 2019). To mitigate potential instability in phylogenetic reconstruction and reduce computing time, we constrained the topology to our IB tree with a monophyletic constraint prior on the *Laevilitorina* clade 2 + *Laevilacunaria* clade 2 group. For calibration, we utilized two dates: first, the age of the most recent common ancestors of Laevilitorininae (TMCA) (56 Mya; 66-46 Mya) (González-Wevar et al., 2022), and second, the separation between the SSI/AP and SG clusters of *Laevilacunaria antarctica* (1.1 Mya; 2.0–0.55 Mya) according to the study by González-Wevar et al. (2024). We partitioned the sequences according to each marker and unlinked the site and clock models for all loci to account for varying substitution rates between them. We employed a strict clock and Yule model. Three independent runs of 100 million generations each were conducted, with samples collected every 10,000 iterations. Convergence of results was assessed using Tracer v1.7.2 (Rambaut et al., 2018), and the results were summarized in a single ultrametric tree using TreeAnnotator v2.5.1.

Ancestral range distribution

For the estimation of the ancestral geographic range we used the Biogeobears package in R (Matzke, 2014). This analysis calculates the ML of the ancestral geographical range and dispersal hypotheses along the time-calibrated phylogeny generated in beast using the complete concatenated dataset. As the 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 was likely to be a highly relevant biogeographic process (Cowie & Holland, 2006;

Maturana et al., 2021; Matzke, 2014). We therefore also explored the influence of founder event speciation by additionally analyzing the influence of the “+J” parameter in our analyses. We identified the model that exhibited the best fit based on both AIC and the likelihood ratio test. We established a maximum of four areas per node, and for the definition of the areas we followed the biogeographical classification of Koubbi et al., (2014) (Antarctic West, Magellan, South Georgia as a transitional zone and subantarctic Islands South Indian Ocean).

Results

Sequence analysis

The first concatenated matrix represented by 169 littorinid specimens. Each sample was composed of 12S rRNA, COI and 28S gene sequences, a total of 2590 bp, of which COI, 12S and 28S consisted of 620 bp, 435 bp and 1535 bp, respectively, after alignment using MAFFT. Of the 2590 sites, a total of 1031 (42.7% COI; 22.2% 12S; 35.1% 28S) were phylogenetically informative.

In the second data set which included the species of the subfamily Laevilitorininae (*Laevilitorina*+*Laevilacunaria*), *Pellilitorina setosa*, *Bembicium auratum*, *Melarhaphe neritoides*, and three species of *Littorina*, the matrix of nucleotide alignment consisted of a total of 2818 bp, of which the COI, 12S, 16S and 28S consisted of 620 bp, 321 bp, 499 bp and 1373 bp respectively post alignment using MAFFT. Out of 2813 sites, a total of 1035 (26.7 % COI; 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 Supplementary table 1.

Phylogenetic analysis and species delimitation

The phylogenetic analysis of the Littorinidae recovered the monophyly of the subfamily Laevilitorininae with maximum support in both reconstructions (100% ML and 1.0 PP) (Fig 2). The sister group to the Laevilitorinidae is not fully resolved in our analysis, but would appear to be the Lacuninae (89% ML and 0.81 PP), although the genus *Cremnoconchus* may be slightly closer (79% ML and 0.85 PP) (Fig. 2)

Within the Laevilitorininae neither *Laevilacunaria* and *Laevilitorina* were monophyletic (Fig. 2). We found 2 clades of *Laevilacunaria*: the first included the species *Laevilacunaria antarctica* and *Laevilacunaria pumilio* (LAC1) and the second comprised *Laevilacunaria bennetti* and *Laevilitorina wandelensis* (LAC2). In addition, LAC2 was placed within a larger group with the two *Laevilitorina* clades, but with some weak IB supports (<0.80 PP) (Fig. 2).

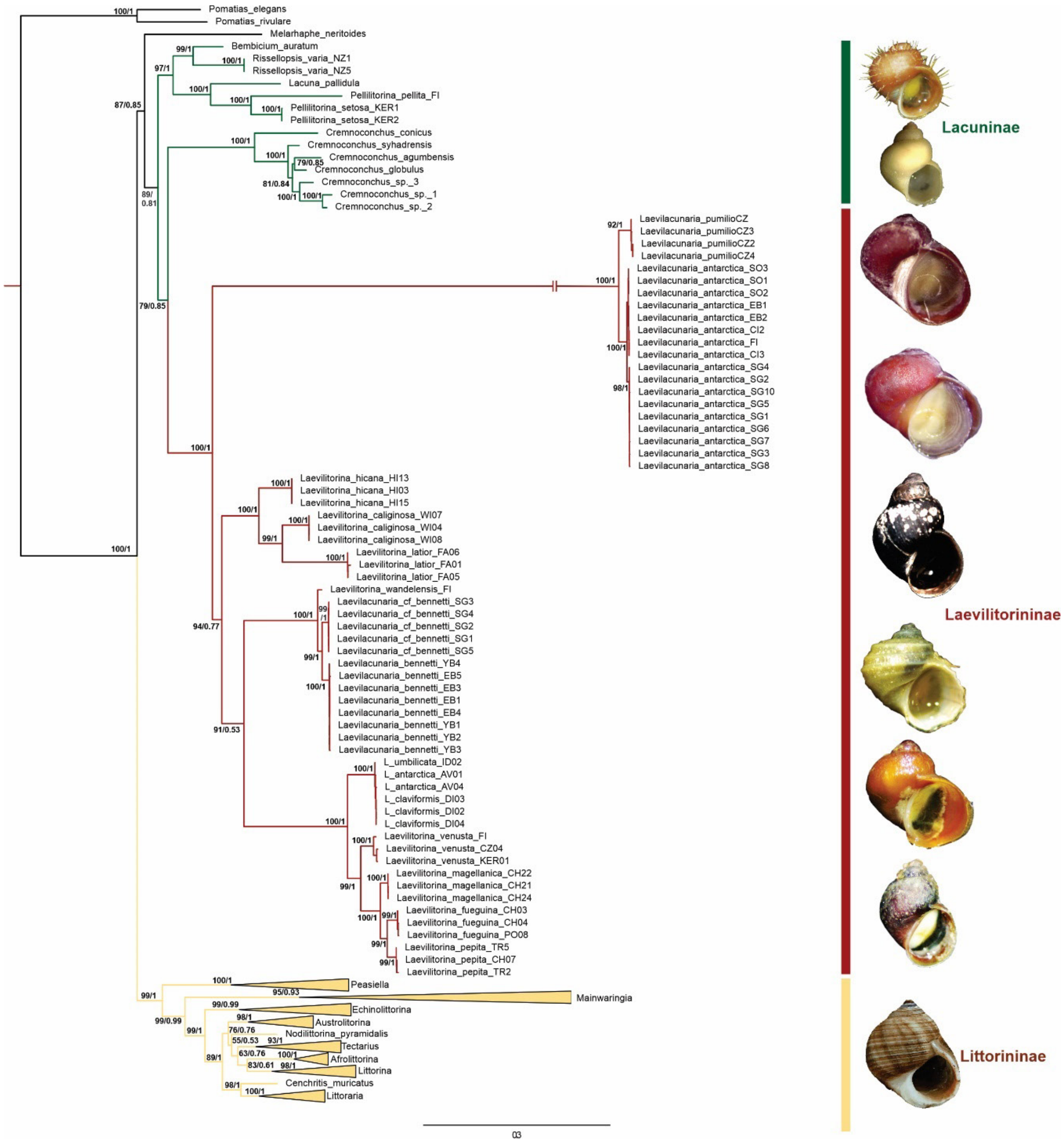


Figure 2. Phylogenetic reconstruction of the relationships among Littorinidae based on multilocus data (12S+COI+28S) of 169 species of the family Littorinidae, using the genus *Pomatias* (family Pomatiidae) as the outgroup, showing the monophyly of the Subfamily Laevilitorininae. The rectangles in yellow, 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.

The second phylogenetic analyses on concatenated dataset of the four genes with *Pellilitorina*, *Bembicium, Melarhaphe* and *Littorina* as outgroup recover the same topology but with stronger PP supports (≥85% ML; ≥0.90 PP) (Fig. 3). In this topology we recovered four major clades within Laevilitorininae (Fig. 3): two clades of *Laevilacunaria* and two clades of *Laevilitorina*. LAC2 clustered with *Laevilitorina* clade 2 (LLC2), which was composed of *Laevilitorina umbilicata*, *Laevilitorina venusta*, *Laevilitorina fueguina*, *Laevilitorina magellanica* and *Laevilitorina pepita* (Fig. 3). Sister to these two clades was *Laevilitorina* clade 1 (LLC1), which comprised *Laevilitorina caliginosa*, *Laevilitorina latior* and *Laevilitorina hicana* (Fig. 3). And finally, the most differentiated clade was the LAC1 clade.

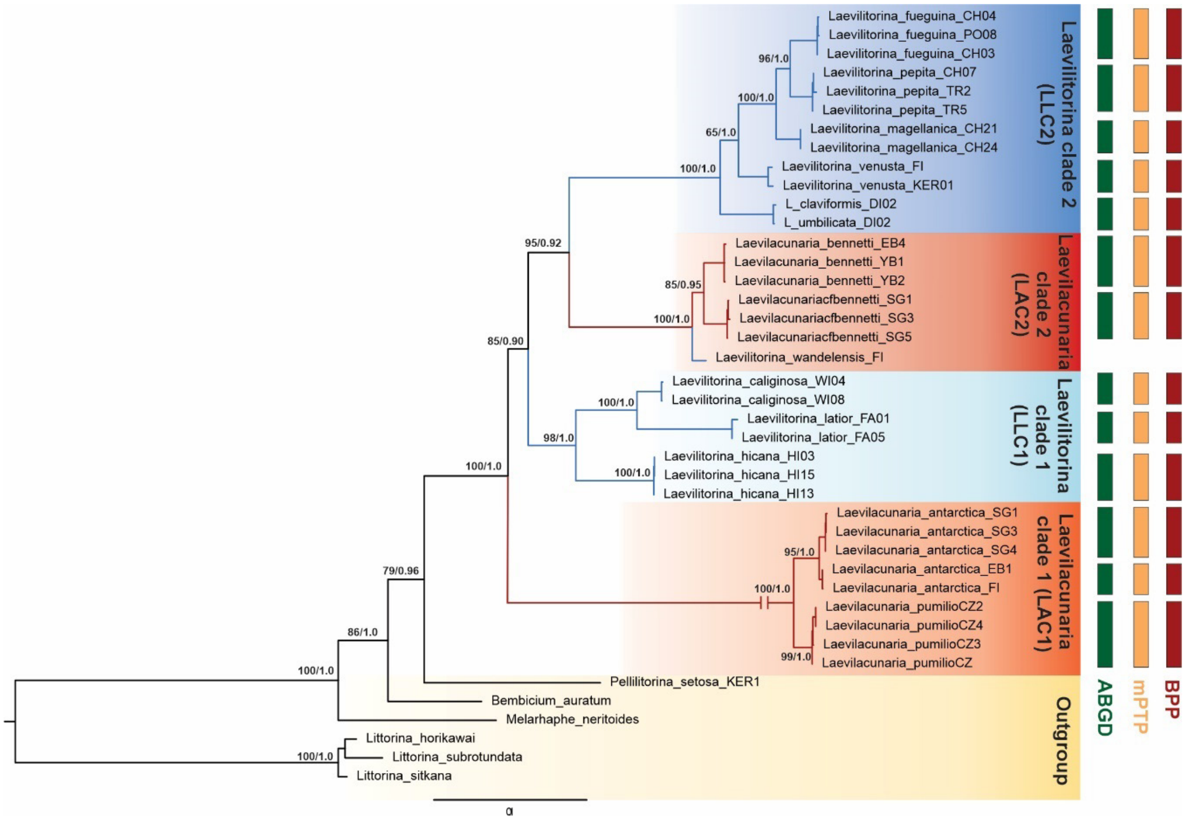


Figure 3. Phylogenetic reconstruction of the relationships among Laevilitorininae based on multilocus data (12S+16S+COI+28S), using the genus *Pellilitorina*, *Bembicium*, *Melarhaphe* and *Littorina* as outgroups, showing

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 analyzed. The rectangles in green, red, and yellow shows the different delimitations species analysis. Bayesian posterior probability (PP) and maximum likelihood bootstrap (ML) values are shown above and under the nodes.

The species delimitation analysis using ABGD, mPTP and BPP recovered the same lineages detected by González-Wevar et al., (2022) for the genus *Laevilitorina* (Fig. 3). For *Laevilacunaria* we identify distinct lineages in both *Laevilacunaria* clades (Fig. 3). In the case of LAC1 we have*: L. pumilio* from Crozet (Fig. 4i,f) and *L. antarctica* was divided into two divergent lineages, one in West Antarctica (Fig. 4d,e) and the other in South Georgia (Fig. 4a,b). For LAC2 the analysis separate *L. bennetti* from West Antarctica (Fig. 4j,k) from *L.* cf *bennetti* from South Georgia (Fig. 4m,n) (Fig. 3).

Radular Morphology

Radular morphology showed differences between the South Georgia Island lineages in both clades (1 and 2) of *Laevilacunaria* (Fig. 4 c,f,i,o). In the case of the South Georgia Island lineage of *L. antarctica*, the inner and outer marginal teeth showed 2 to 3 pointed cusps in the inner side. The radula of *L. pumilo* is the most distinct of this clade, presenting a rachidian tooth with a wide and rounded cuspid without denticles, an internal lateral with 7 cusps, the largest is wide and rounded and is accompanied by two small outer cusps, and four small inner cusps. The inner marginal present nine cusps, 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 (Fig. 4 g,h,i).

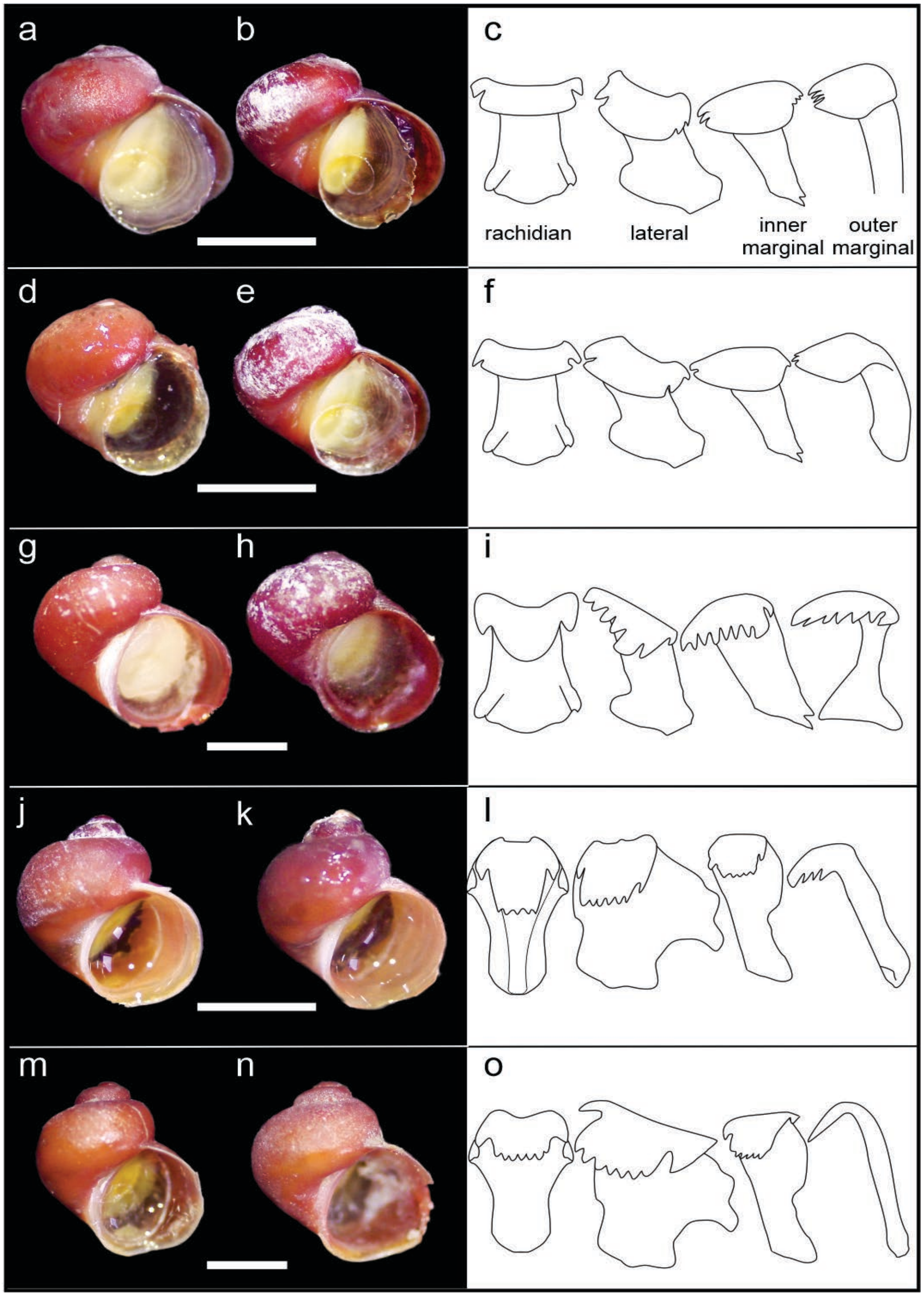


Figure 4. A-B *Laevilacunaria antarctica* from South Georgia, shell morphology and C, radula. D-E *Laevilacunaria antarctica* from South Orkney and Cockburn Island. shell morphology respectively and F, radula. G-H *Laevilacunaria pumilio* from Kerguelen and Crozet Islands, shell morphology respectively and I, radula. J-K *Laevilacunaria benetti* 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= 1mm.

For clade 2 of *Laevilacunaria*, the lineages of *L. bennetti* from Antarctic Peninsula and *L. cf bennetti* from South Georgia showed similar radular morphology, presenting numerous small denticles on the rachidian, lateral and inner marginal teeth and a single cusp on the outer marginal tooth. The main difference is that the external marginal tooth of *L. cf bennetti* has a single cuspid without denticles, while *L. bennetti* has 4 denticles.

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 (Fig. 4). Ancestral range estimation significantly favored the DEC+J (LnL = −24.88) model of species evolution (Dispersal-Extinction-Cladogenesis, with a founder event component +J), followed by the DEC model (LnL = −28.08) (p=0.033). The ancestral area reconstruction and divergence time of the TMRCA of the subfamily Laevilitorininae occurred ~50.72 Mya (HPD 59.85–40.37 Mya) suggested a Gondwanan origin. At that time, the genus split in two groups. The first group (LAC1) was distributed in the subantarctic Islands, diversified during the lower Miocene 6.44 (HPD 8.48–4.52 Mya) and colonized West Antarctica before finally dispersing to South Georgia during the mid-Pleistocene 1.3 Mya (HPD 1.65–0.97 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 36.51 (HPD 44.6–28.5 Mya) (Fig. 5). Subsequently, the West Antarctic ancestor of LAC2 and LLC2 split during the early Oligocene 32.68 (HPD 39.87–25.31 Mya). The LAC2 had an ancestral range across West Antarctic and diversified during the Miocene and Pliocene. First, the separation between *Laevilitorina wandelensis* and *L. bennettii*/*L. cf bennettii* occurred 7.73 Mya (HPD 10.7–5.41 Mya), before the split of *L. bennettii* and *L. cf bennettii* 5.11 Mya (HPD 7.3–2.99 Mya) with the dispersal from the West Antarctic ancestor to South Georgia (Fig. 4).

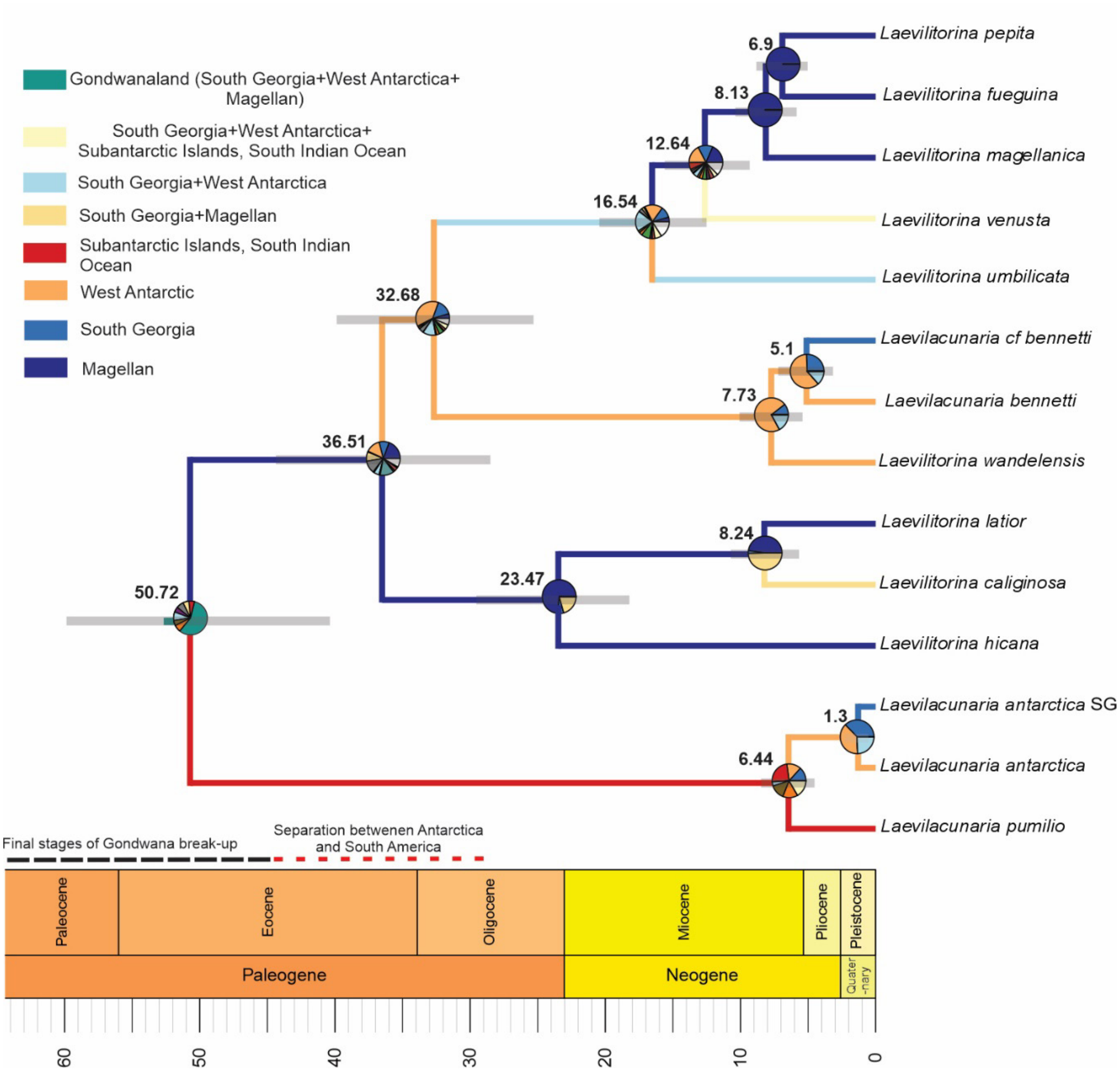


Fig. 5. Historical biogeography and timing of divergence of *Laevilacunaria* in the Southern Ocean using the concatenated data set. The maximum clade credibility tree shows the median divergence time estimates with 95% height posterior distribution. The coloured pie chart represents ancestral range probabilities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

Discussion

Evolutionary origin and diversification of Laevilitorininae and *Laevilacunaria*

We present the first integrated biogeographic analyses of the genus *Laevilacunaria* and its sister genus *Laevilitorina* in the Southern Ocean, as well as the first global phylogeny of Littorinidae including all 3 described subfamilies. Our analyses revealed that the ancestor of the subfamily Laevilitorininae originated in the late stages of Gondwana fragmentation (50.72 Mya; HPD 59.85-40. 37 Mya), with early separation into four well-supported clades currently found in (A) the subantarctic islands (Crozet and Kerguelen), Antarctica and South Georgia, (B) South America, Falkland/Malvinas Islands and South Georgia, (C) Antarctica and South Georgia Islands, and (D) South America, Antarctica, subantarctic Islands and South Georgia. Although the origin of Laevilitorininae has not been previously hypothesized due to the lack of fossils within this group (Reid, 1989), our analyses would suggest that the evolutionary history of this group in ancient times would be related to the breakup of the supercontinent Gondwana, including both vicariance and long-distance dispersal. However, it is important to mention that caution must be taken with this reconstruction, since, in this study we could not include the *Laevilitorina* species from New Zealand and Australia. Consequently, the age estimate of the TMRCA of Laevilitorininae is provisional and may be slightly older.

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 there were long-distance dispersal and establishment (LDDE) events to West Antarctica and, later, during the Pleistocene, to South Georgia (Fig. 5). The TMCRA of the clade LAC2-LLC2 would have originated in West Antarctica and would have diverged during the early Oligocene (32.68 Mya;HPD 39.87-25.31 Mya). As in LAC1, a LDDE event from West Antarctica to South Georgia Island would have occurred during more recent (Pliocene) times.

Our data suggest that the TMRCA of Laevilitorininae was close to the Early Eocene Climatic Optimum (*ca*. 50 Mya) (Crame, 2018). At this time, the southern continental landmasses were tightly clustered, including a land bridge between South America and Antarctica (Livermore et al., 2007; Livermore et al., 2005) and slow seafloor spreading between Australia and Antarctica (Blakey, 2008). This period is important in the history of the Antarctic fauna, since it followed the mass extinction that occurred at the Cretaceous-Paleogene boundary (66 Ma). During this climatic optimum (Reguero et al., 2002) important radiation of benthic marine taxa occurred (Crame, 2018). Subsequently, the TMRCA of LLC1 and LAC2-LLC2 1-2 was ~36 Ma (HPD 44.6–28.5 Mya) and the final split between LAC2 and LLC2 was ~32 Ma, close to the Eocene/Oligocene boundary, 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 ACC (Zachos et al., 2001) Scher et al., 2015). 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 mollusks, such as the incubating microbivalves of the genus *Kidderia* (Levicoy et al., 2021), as well as the two clades of *Laevilitorina* (González-Wevar et al., 2022).

Subsequently, during the Miocene (23 and 6 Mya), these four clades diversificated independently in South America, Antarctica, and subantarctic Islands. These speciation were likely associated with the Middle Miocene Climatic Transition, during which there was a major expansion of both the East and West Antarctic ice sheets and marked intensification of the ACC system (Crame, 2018). Significant oceanographic changes during this period were probably related to the complete formation of a deep ACC approximately 12 Mya (Dalziel et al., 2013). 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 (Crame, 2018). This change led to enhanced upwelling and nutrient pumping, processes that were progressively intensified as the East Antarctic Ice Sheet expanded and zonal winds increased (Crame, 2018). These oceanographic changes have been important drivers in the evolution of the Southern Ocean biota (Chenuil et al., 2018; Crame, 2018; González-Wevar et al., 2017; González-Wevar et al., 2022; Halanych & Mahon, 2018; Poulin et al., 2014). The establishment of a strong and deep ACC may have generated an effective oceanographic barrier maintaining mostly all the *Laevilacunaria* (clade 1 and 2) lineages South of the ACC. More recently, both clades of *Laevilacunaria* diversified in West Antarctica, Subantarctic Island and South Georgia between the lower Miocene and the Pleistocene, 7.7–1.3 Mya. During this period, it has been suggested that several groups of marine invertebrates underwent diversification processes (Strugnell, 2008; Dueñas et al., 2016), especially shallow mollusks (Gonzalez-Wevar et al. 2017, 2019, 2021, 2022). For a detailed discussion of the processes of diversification within the *Laevilitorina* clades see González-Wevar et al., (2022) and Sebastián Rosenfeld et al., (2023a).

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

Ancestral-range analyses suggest long-distance dispersal and establishment (LDDE) events from subantarctic islands to West Antarctica and from West Antarctic to South Georgia, implying that this process has played an important role in establishing the current geographic distribution in *Laevilacunaria.* Based on the geographic-range reconstruction, the current diversity observed in West Antarctica and, particularly, in South Georgia is likely to be the result of one or more colonization events, mediated by LDDE. It is important to note that *Laevilacunaria* species are associated with various species of macroalgae (Amsler et al., 2022; Amsler et al., 2015; Picken, 1979; Rosenfeld et al., 2017). In the case of *L. pumilio*, the only species north of the APF, on the Kerguelen and Crozet Islands, colonization from these islands to West Antarctica occurred around ~6 Mya. This time coincides with the appearance of the floating ancestor of the genus *Durvillaea* (between 9.7 and 3.4 Mya) (Fraser et al., 2020b). 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 (Fraser et al., 2022; Fraser et al., 2020a). These macroalgal rafts may carry a variety of passengers, including marine invertebrates or their egg masses attached to the fronds (Fraser, Velasquez, et al., 2020; González-Wevar et al., 2024). These new oceanographic models indicate that these algal rafts from the sub-Antarctic region can reach the Antarctic coasts monthly, thus increasing the probability of dispersal events from subantarctic species towards the Antarctic coasts (Fraser et al., 2020a).

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 5.1 and 1.3 Mya respectively (Fig. 4). 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 (Fraser et al., 2020b). Moreover, long-distance colonization by rafting on non-buoyant macroalgae has been documented (Fraser et al., 2013). Indeed, Antarctic species that do not possess flotation structures, such as *Adenocystis utriculais*, *Himantothallus grandifollium* and *Desmarestia anceps*, have been seen floating in the Southen Ocean (Macaya et al., 2020) Therefore, these macroalgae could also be potential dispersal vectors for Antarctic species that do not possess a pelagic larval stage. It is worth noting that both *L. antarctica* and *L. bennetti* have been reported to inhabit the fronds of these macroalgae (Amsler et al., 2022; Amsler et al., 2015) Martins et al. 2016)

Lastly, the oceanography processes of the Southern Ocean, characterized by high wind speeds and intense wave weather due to atmospheric storms, can either hinder or promote passive and occasional dispersal of organism (Fraser et al., 2020a). For instance, within the Scotia Sea, the ACC flows predominantly in a northeasterly direction (Damerau et al., 2014; Murphy et al., 2013), maintaining connectivity between Antarctic Peninsula and South Georgia Island (Damerau et al., 2014; Young et al., 2015). Therefore, the colonization of *Laevilacunaria* species from West Antarctica to South Georgia would have occurred by a LDDE event through rafting. This event would have been occasional, facilitating establishment on the island but without maintaining gene flow over time, resulting in the differentiation of the populations of these species.

Systematic implications for the Littorinidae and Laevilitorininae

This study, following the phylogeny of the subfamily Littorininae by Reid et al. (2012), and the work on *Cremnoconchus* by Saha et al. (2022), is the most complete molecular phylogeny of the family Littorinidae. We were able to include genera of the subfamily Laevilitorininae and two genera of Lacuninae. Previously, species from the subfamilies Laevilitorininae and Lacuninae had been used as outgroups to assess phylogenetic relationships within Littorininae (Reid et al., 2012; Williams et al., 2003). Within our analysis, we were able to recover the monophyly of the family Littorinidae (Saha et al., 2022) and the monophyly of the subfamily Laevilitorininae (Fig. 2). We should point out several unexpected and novel findings, however.

First, *Melarhaphe neritoides*, long presumed to belong to the Littorininae, did not cluster with other members of this subfamily and therefore its taxonomic position requires corroboration (see Reid et al., 2012).

Second, we found that *Cremnoconchus* sensu lato did not form a monophyletic group with the rest of the Lacuninae (Fig. 2). Indeed, it appeared (weakly) to be sister to the

Laevilitorininae (Fig. 2). If this position were confirmed, it would support the results and proposal of Saha et al., (2021), to separate *Cremnoconchus* at the subfamily level, an idea dating back to Preston (1915).

Within the other genera of Lacuninae we were able to corroborate to some extent what was found in the morphological phylogeny of Reid (1989), who found that the Lacuninae was composed of two large well-supported clades (Fig. 2). The first clade comprised the Australasian genera *Bembicium* and *Risellopsis* and the second consisted of the Northern Hemisphere genus *Lacuna* and the Circum-Antarctic genus *Pellilitorina* (Fig. 2). Nevertheless, although our study was able to incorporate the genera *Pellilitorina* and *Risellopsis*, the Lacuninae are still underrepresented compared to the other subfamilies (Reid et al., 2012; Saha et al., 2022; this study). Thus, integrative studies and the incorporation of more species are needed to elucidate the phylogenetic relationships and biogeographic history of the Lacuninae.

Within the Laevilitorininae our results show that the two genera currently recognized in this subfamily (*Laevilacunaria* and *Laevilitorinae*) are paraphyletic (Fig. 3). Previously, Reid (1989), using morphological data, had proposed that Laevilitorininae consisted solely of the genus *Laevilitorina*, albeit with five subgenera. The divergence dates we find within the family, however, suggest that the diversity should be recognized at the genus level. Our phylogeny (Fig. 2,3) suggests that four genera could be recognized. Unfortunately, because we have not sampled the type of one of Reid's subgenera, *Macquariella*, namely *Paludestrina hamiltoni* from Macquarie Island, we cannot be definitive about the correct names. Nevertheless, at this stage is would appear that LAC1 is *Laevilacunaria* s. str., whereas LAC2 corresponds to *Pellilacunella* Powell, 1951 (type species *Pelllitorina bennetti*). Within *Laevilitorina* LLC1 corresponds to *Laevilitorina* s. str., whereas LLC2 would require a new name. Nevertheless, sampling of species from New Zealand and Australia will be required to fully elucidate the systematics and taxonomy within the subfamily Laevilitorininae.

Although Reid (1989) and Engl (2012) considered *Laevilacunaria bransfieldensis* to be junior synonym of *Laevilacunaria antarctica*, our results would further support the views of Preston (1916) and Powell (1951) that they are specifically distinct. ABGD, mPTP and BPP analyses found that LAC1 comprised 3 species. Furthermore, our radula morphological data agree with those of Powell (1951): the inner and outer marginal teeth of individuals from West Antarctica have broad cusps with a small denticle on each side, whereas individuals from South Georgia Island have both marginals with a slightly smaller cusp and a greater number of denticles in the inner zone (Fig. 5). Thus, from molecular (González-Wevar et al., 2024; this study) and morphological (Powell, 1951; Preston, 1916; this study) evidence, *L. bransfiendensis* should no longer be considered a junior synonym of *L. antarctica. L. antarctica* is restricted to South Georgia and *L. bransfiendensis* to West Antarctica.

Similarly, LAC2, ABGD, mPTP and BPP analyses recovered two species within a nominal *L. bennetti*, 1 in South Georgia (undescribed) and another in West Antarctica (the type locality of *L. bennetti*). In addition, we were able to detect morphological differences at the radula level between both lineages, mainly in the marginal tooth (Fig. 5). *Laevilitorina wandelensis* could not be included in the delimitation analysis because we only have 1 individual, but the levels of morphological and molecular differentiation detected suggest that it is a third valid species within this clade (Waren & Hain, 1996; this study) and we note that it does not belong in *Laevilitorina*.

Concluding Remarks

This research provides significant insights into the phylogeny, systematics, and biogeography of the genus *Laevilacunaria s.l*. Our comprehensive analysis, which utilized multi-locus genetic data and radular morphology, revealed the paraphyly of *Laevilacunaria* and *Laevilitorina*. This finding requires a revision of the taxonomy and biogeography of the subfamily Laevilitorininae, indicating a more complex evolutionary history than previously understood. The study provides evidence for long-distance dispersal and establishment (LDDE) events as critical mechanisms shaping the current distribution patterns of *Laevilacunaria*. These events, facilitated by macroalgal rafting, underscore the combined roles of historical vicariance and recent dispersal in the biogeography of this group in the Southern Ocean. Moreover, our phylogenetic analyses suggest the reclassifying Laevilitorininae into four distinct genera based on molecular and morphological differences. This reclassification reflects the deep divergences and clear morphological distinctions observed within the clades. Additionally, we clarified the status of several species within *Laevilacunaria*, reinstating *Laevilacunaria bransfieldensis* as a valid species and identifying new species within LAC2.

Overall, this research enhances our understanding of the evolutionary history, systematics, and biogeographic patterns of Littorinidae in the Southern Ocean. It underscores the importance of integrating molecular and morphological data in taxonomic studies and highlights the need for further investigation into the *Laevilitorina* species from New Zealand and Australia to fully resolve the systematics within Laevilitorininae. This work also provides essential biogeographic information that could inform spatial conservation measures in the Southern Ocean.

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. The authors would like to thank the Chilean Antarctic Institute (INACH) and the Chilean Navy from the Aquiles and Oscar Viel ships for ECA53, ECA54 and ECA55 and the crew from the Betanzos ship during the ECA58 and ECA59. We also would like to thank Commandant Charcot and our Scientist leader Geoffroy Dekersauson from Ponant expedition LEGCC120323. We also thank Andres 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 Ramirez archipelago, and Hornos Island. We greatly appreciate the editorial work of the Associate Editor and the useful suggestions of two independent referees.

FUNDING

This study was funded by different projects and institutions, including the INACH project DG_10-22 to S.R, 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. 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.

References

Amsler, C. D., Miller, L. R., Edwards, R. A., Amsler, M. O., Engl, W., Mcclintock, J. B., & Baker, B. J. (2022). Gastropod assemblages associated with Himantothallus grandifolius, Sarcopeltis antarctica and other subtidal macroalgae. *Antarctic Science*, *34*(3), 246-255.

Amsler, M. O., Huang, Y. M., Engl, W., McClintock, J. B., & Amsler, C. D. (2015). Abundance and diversity of gastropods associated with dominant subtidal macroalgae from the western Antarctic Peninsula. *Polar Biology*, *38*, 1171-1181.

Blakey, R. C. (2008). Gondwana paleogeography from assembly to breakup—A 500 my odyssey. *Geological Society of America Special Papers*, *441*, 1-28.

Bouckaert, R., Vaughan, T. G., Barido-Sottani, J., Duchene, S., Fourment, M., Gavryushkina, A., . . . Drummond, A. J. (2019). BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Comput Biol*, *15*(4), e1006650. https://doi.org/10.1371/journal.pcbi.1006650

Chenuil, A., Saucède, T., Hemery, L. G., Eléaume, M., Féral, J. P., Améziane, N., . . . Havermans, C. (2018). Understanding processes at the origin of species flocks with a focus on the marine A ntarctic fauna. *Biological Reviews*, *93*(1), 481-504.

Cowie, R. H., & Holland, B. S. (2006). Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *Journal of Biogeography*, *33*(2), 193-198. https://doi.org/10.1111/j.1365-2699.2005.01383.x

Crame, J. A. (1999). An evolutionary perspective on marine faunal connections between southernmost South America and Antarctica. *Scientia Marina*, *63*(S1).

Crame, J. A. (2018). Key stages in the evolution of the Antarctic marine fauna. *Journal of Biogeography*, *45*(5), 986-994. https://doi.org/10.1111/jbi.13208

Dalziel, I., Lawver, L., Pearce, J. A., Barker, P., Hastie, A., Barfod, D., . . . Davis, M. (2013). A potential barrier to deep Antarctic circumpolar flow until the late Miocene? *Geology*, *41*(9), 947-950.

Damerau, M., Matschiner, M., Salzburger, W., & Hanel, R. (2014). Population divergences despite long pelagic larval stages: lessons from crocodile icefishes (Channichthyidae). *Molecular Ecology*, *23*(2), 284-299. https://doi.org/10.1111/mec.12612

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian Phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*(8), 1969-1973. https://doi.org/10.1093/molbev/mss075

Edgar, R. C. (2004). MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics*, *5*, 1-19. https://doi.org/10.1186/1471-2105-5-113

Engl, W. (2012). *Shells of Antarctica*. ConchBooks.

Fraser, C. I., Dutoit, L., Morrison, A. K., Pardo, L. M., Smith, S. D. A., Pearman, W. S., . . . Macaya, E. C. (2022). Southern Hemisphere coasts are biologically connected by frequent, long-distance rafting events. *Current Biology*, *32*(14), 3154-3160 e3153. https://doi.org/10.1016/j.cub.2022.05.035

Fraser, C. I., Morrison, A., & Olmedo Rojas, P. (2020a). Biogeographic processes influencing Antarctic and sub-Antarctic seaweeds. In *Antarctic Seaweeds* (pp. 43-57). https://doi.org/10.1007/978-3-030-39448-6_3

Fraser, C. I., Velasquez, M., Nelson, W. A., Macaya, E. C., & Hay, C. H. (2020b). The Biogeographic importance of buoyancy in Macroalgae: A case study of the southern bull-kelp genus *Durvillaea* (Phaeophyceae), including descriptions of two new species. *Journal of Phycology*, *56*(1), 23-36. https://doi.org/10.1111/jpy.12939

Fraser, C. I., Zuccarello, G. C., Spencer, H. G., Salvatore, L. C., Garcia, G. R., & Waters, J. M. (2013). Genetic affinities between trans-oceanic populations of non-buoyant macroalgae in the high latitudes of the Southern Hemisphere. *PLoS ONE*, *8*(7), e69138.

González-Wevar, C. A., de Aranzamendi, M. C., Segovia, N. I., Rosenfeld, S., Maturana, C. S., Molina, C. R., . . . Poulin, E. (2023). Genetic footprints of Quaternary glacial cycles over the patterns of population diversity and structure in three Nacella (Patellogastropoda: Nacellidae) species across the Magellan province in southern South America. *Frontiers in Marine Science*, *10*. https://doi.org/10.3389/fmars.2023.1154755

González-Wevar, C. A., Hüne, M., Segovia, N. I., Nakano, T., Spencer, H. G., Chown, S. L., . . . Poulin, E. (2017). Following the Antarctic Circumpolar Current: patterns and processes in the biogeography of the limpet Nacella (Mollusca: Patellogastropoda) across the Southern Ocean. *Journal of Biogeography*, *44*(4), 861-874. https://doi.org/10.1111/jbi.12908

González-Wevar, C. A., Poveda, Y., Segovia, N. I., Rosenfeld, S., Maturana, C. S., Jeldres, V., . . . Poulin, E. (2024). Both high and low dispersal? Apparently contradictory genetic patterns in the Antarctic littorinid gastropod Laevilacunaria antarctica. *Frontiers in Ecology and Evolution*, *11*. https://doi.org/10.3389/fevo.2023.1320649

González-Wevar, C. A., Segovia, N. I., Rosenfeld, S., Maturana, C. S., Jeldres, V., Pinochet, R., . . . Poulin, E. (2022). Seven snail species hidden in one: Biogeographic diversity in an apparently widespread periwinkle in the Southern Ocean. *Journal of Biogeography*, *49*(8), 1521-1534. https://doi.org/10.1111/jbi.14453

Hain, S., & Arnaud, P. M. (1992). Notes on the reproduction of high-Antarctic molluscs from the Weddell Sea. *Polar Biology*, *12*, 303-312.

Halanych, K. M., & Mahon, A. R. (2018). Challenging dogma concerning biogeographic patterns of Antarctica and the Southern Ocean. *Annual Review of Ecology, Evolution and Systematics*, *49*, 355-378. https://doi.org/10.1146/annurev-ecolsys-

Hoffman, J. I., Peck, L. S., Linse, K., & Clarke, A. (2011). Strong population genetic structure in a broadcast-spawning Antarctic marine invertebrate. *Journal of Heredity*, *102*(1), 55-66. https://doi.org/10.1093/jhered/esq094

Kapli, P., Lutteropp, S., Zhang, J., Kobert, K., Pavlidis, P., Stamatakis, A., & Flouri, T. (2017). Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. *Bioinformatics*, *33*(11), 1630-1638.

Katoh, K., Rozewicki, J., & Yamada, K. D. (2019). MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Brief Bioinform*, *20*(4), 1160-1166. https://doi.org/10.1093/bib/bbx108

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., . . . Drummond, A. (2012). Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, *28*(12), 1647-1649.

Knox, G. (1977). The Antarctic polychaete fauna: its characteristics, distribution patterns, and evolution. *Adaptation within Antarctic Ecosystems*, 1111-1127.

Koubbi, P., De Broyer, C., Griffiths, H. J., Raymond, B., d'Udekem d'Acoz, C., Van de Putte, A. P., . . . Wadley, V. (2014). Chapter 12: Conclusions: Present and future of Southern Ocean Biogeography. In Koubbi P., De Broyer C., Griffiths H.J., Raymond B., d'Udekem d'Acoz C., Van de Putte A.P., D. B. Danis B., G. J. Grant S., Held C., Hosie G., Huettmann F., Post A., Ropert- Coudert Y., Stoddart M., Swadling K.M., & W. V. (Eds.), *Biogeographic atlas of the Southern Ocean*. Scientific Committee on Antarctic Research.

Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., & Calcott, B. (2017). PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. *Molecular Biology and Evolution*, *34*(3), 772-773. https://doi.org/10.1093/molbev/msw260

Levicoy, D., Rosenfeld, S., & Cardenas, L. (2021). Divergence time and species delimitation of microbivalves in the Southern Ocean: the case of Kidderia species. *Polar Biology*, *44*(7), 1365-1377. https://doi.org/10.1007/s00300-021-02885-6

Linse, K., Griffiths, H. J., Barnes, D. K. A., & Clarke, A. (2006). Biodiversity and biogeography of Antarctic and sub-Antarctic mollusca. *Deep Sea Research Part II: Topical Studies in Oceanography*, *53*(8), 985-1008.

Livermore, R., Hillenbrand, C.-D., Meredith, M., & Eagles, G. (2007). Drake Passage and Cenozoic climate: An open and shut case? *Geochemistry, Geophysics, Geosystems*, *8*(1), n/a-n/a. https://doi.org/10.1029/2005gc001224

Livermore, R., Nankivell, A., Eagles, G., & Morris, P. (2005). Paleogene opening of Drake Passage. *Earth and Planetary Science Letters*, *236*(1-2), 459-470. https://doi.org/10.1016/j.epsl.2005.03.027

Macaya, E. C., Tala, F., Hinojosa, I. A., & Rothäusler, E. (2020). Detached seaweeds as important dispersal agents across the Southern Ocean. In *Antarctic Seaweeds* (pp. 59-81). https://doi.org/10.1007/978-3-030-39448-6_4

Martín, A., Miloslavich, P., Díaz, Y., Ortega, I., Klein, E., Troncoso, J., . . . Carbonini, A. K. (2016). Intertidal benthic communities associated with the macroalgae Iridaea cordata and Adenocystis utricularis in King George Island, Antarctica. *Polar Biology*, *39*, 207-220.

Maturana, C. S., Rosenfeld, S., Biersma, E. M., Segovia, N. I., González-Wevar, C. A., Díaz, A., . . . Jackson, J. A. (2021). Historical biogeography of the Gondwanan freshwater genus *Boeckella* (Crustacea): Timing and modes of speciation in the Southern Hemisphere. *Diversity and Distributions*, *27*(12), 2330-2343. https://doi.org/10.1111/ddi.13405

Matzke, N. J. (2014). Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology*, *63*(6), 951-970. https://doi.org/10.1093/sysbio/syu056

Minh, B. Q., Nguyen, M. A. T., & Von Haeseler, A. (2013). Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, *30*(5), 1188-1195.

Murphy, E. J., Hofmann, E. E., Watkins, J. L., Johnston, N. M., Piñones, A., Ballerini, T., . . . Fretwell, P. (2013). Comparison of the structure and function of Southern Ocean regional ecosystems: The Antarctic Peninsula and South Georgia. *Journal of Marine Systems*, *109-110*, 22-42. https://doi.org/10.1016/j.jmarsys.2012.03.011

Nguyen, L.-T., Schmidt, H. A., Von Haeseler, A., & Minh, B. Q. (2015). IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, *32*(1), 268-274.

Picken, G. B. (1979). Non-pelagic reproduction of some Antarctic Prosobranch gastropods from Signy Island, South Orkney Island. *Malacologia*, *19*(1), 109-128.

Poulin, E., González-Wevar, C., Díaz, A., Gérard, K., & Hüne, M. (2014). Divergence between Antarctic and South American marine invertebrates: What molecular biology tells us about Scotia Arc geodynamics and the intensification of the Antarctic Circumpolar Current. *Global and Planetary Change*, *123*, 392-399. https://doi.org/10.1016/j.gloplacha.2014.07.017

Poulin, E., Palma, A. T., & Féral, J.-P. (2002). Evolutionary versus ecological success in Antarctic benthic invertebrates. *Trends in Ecology & Evolution*, *17*(5), 218-222. http://www.cell.com/trends/ecology-evolution/abstract/S0169-5347(02)02493-X?_returnURL=http%3A%2F%2Flinkinghub.elsevier.com%2Fretrieve%2Fpii%2FS016953470202493X%3Fshowall%3Dtrue

Powell, A. W. B. (1951). Antarctic and subantarctic mollusca. Pelecypoda and Gastropoda. *Discovery reports.*, *26*, 47-196.

Powell, A. W. B. (1960). Antarctic and subantarctic Mollusca. *Records of the Auckland Institute and Museum*, *5*(3/4), 117-193.

Preston, H. B. (1915). *The fauna of British India including Ceylon and Burma: mollusca (freshwater Gastropoda and pelecypoda)*. Taylor & Francis, London 224p.

Preston, H. B. (1916). XXIX.—Description of eight new species of Marine Mollusca from the South Shetland Islands. *Journal of Natural History*, *18*(105), 269-272.

Puillandre, N., Lambert, A., Brouillet, S., & Achaz, G. (2012). ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology*, *21*(8), 1864-1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Rambaut, A., Suchard, M. A., Xie, D., & Drummond, A. J. (2014). *Tracer v1.6, Available from http://beast.bio.ed.ac.uk/Tracer.* In http://beast.bio.ed.ac.uk/Tracer

Reguero, M. A., Marenssi, S. A., & Santillana, S. N. (2002). Antarctic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments: biogeographic relationships. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *179*, 182-210.

Reid, D. (1989). The comparative morphology, phylogeny and evolution of the gastropod family Littorinidae. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *324*(1220), 1-110.

Reid, D. G., Dyal, P., & Williams, S. T. (2012). A global molecular phylogeny of 147 periwinkle species (Gastropoda, Littorininae). *Zoologica Scripta*, *41*(2), 125-136. https://doi.org/10.1111/j.1463-6409.2011.00505.x

Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, *19*(12), 1572-1574. https://doi.org/10.1093/bioinformatics/btg180

Rosenberg, G. (2009). Malacolog Version 4.1. 1. A database of Western Atlantic marine Mollusca. *Academy of Natural Sciences, Philadelphia, PA. Accessed at http://www. malacolog. org*.

Rosenfeld, S., Aldea, C., Ojeda, J., Marambio, J., Hüne, M., Troncoso, J. S., & Mansilla, A. (2017). Molluscan assemblages associated with Gigartina beds in the Strait of Magellan and the South Shetland Islands (Antarctica): a comparison of composition and abundance. *Polar Research*, *36*(1). https://doi.org/10.1080/17518369.2017.1297915

Rosenfeld, S., Maturana, C., Spencer, H. G., Convey, P., Saucède, T., Brickle, P., . . . Gonzalez-Wevar, C. (2022). Complete distribution of the genus Laevilitorina (Littorinimorpha, Littorinidae) in the Southern Hemisphere: remarks and natural history. *Zookeys*. https://doi.org/10.3897/zookeys.@@.91310

Rosenfeld, S., Segovia, N. I., Maturana, C. S., Aldea, C., Saucède, T., Brickle, P., . . . González-Wevar, C. A. (2023a). A revision of the higher latitude periwinkle species Laevilitorina caliginosa sensu lato. *Zoological Journal of the Linnean Society*. https://doi.org/10.1093/zoolinnean/zlad171

Rosenfeld, S., Maturana, C. S., Ganan, M., Rendoll Carcamo, J., Diaz, A., Contador, T., . . . Poulin, E. (2023b). Revealing the hidden biodiversity of Antarctic and the Magellanic Sub-Antarctic Ecoregion: A comprehensive study of aquatic invertebrates from the BASE Project. *Biodivers Data J*, *11*, e108566. https://doi.org/10.3897/BDJ.11.e108566

Saha, A., Chakraborty, S., Ravikanth, G., Praveen Karanth, K., & Aravind, N. A. (2022). Endemicity and radiation in waterfalls of the Western Ghats: The genus Cremnoconchus (Gastropoda: Littorinidae). *Mol Phylogenet Evol*, *174*, 107547. https://doi.org/10.1016/j.ympev.2022.107547

Schmider-Martinez, A., Maturana, C. S., Poveda, Y., Rosenfeld, S., Lopez-Farran, Z., Saucede, T., . . . Gonzalez-Wevar, C. (2023). Laevilacunaria (Mollusca, Gastropoda) in the Southern Ocean: A comprehensive occurrence dataset. *Biodivers Data J*, *11*, e111982. https://doi.org/10.3897/BDJ.11.e111982

Simpson, R., & Harrington, S. A. (1985). Egg masses of three gastropods, Kerguelenella lateralis (Siphonariidae), Laevilitorina caliginosa and Macquariella hamiltoni (Littorinidae), from Macquarie Island (sub-Antarctic). *Journal of the Malacological Society of Australia*, *7*(1-2), 17-28.

Simpson, R. D. (1972). *The ecology and biology of molluscs in the littoral and sublittoral zones at Macquarie Island, with speical reference to Patinigera macquariensis (Finlay 1927)* Adelaide].

Smith, E. A. (1879). Mollusca. *Philosophical Transactions of the Royal Society of London*, *168*, 167-192. http://www.jstor.org/stable/109229

v Martens, E., & Pfeffer, G. (1886). *Die Mollusken von Süd-Georgien nach der Ausbeute der Deutschen Station 1882-83: Von Prof. Dr. Eduard v. Martens und Dr. Georg Pfeffer. Mit 4 Tafeln Abbildungen*. Th. G. Meissner.

Vaidya, G., Lohman, D. J., & Meier, R. (2011). SequenceMatrix: concatenation software for the fast assembly of multi-gene dataset with character set and codon information. *Cladistics*, *27*, 171-180.

Waren, A., & Hain, S. (1996). Description of Zerotulidae fam. nov. (Littorinoidea), with comments on an Antarctic Littorinid gastropod. *The Veliger*, *39*(4), 277-334.

Williams, S. T., Reid, D. G., & Littlewood, D. T. (2003). A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism, and biogeography of the Southern Ocean. *Mol Phylogenet Evol*, *28*(1), 60-86. https://doi.org/10.1016/s1055-7903(03)00038-1

Yang, Z., & Rannala, B. (2014). Unguided species delimitation using DNA sequence data from multiple loci. *Molecular Biology and Evolution*, *31*(12), 3125-3135.

Young, E. F., Belchier, M., Hauser, L., Horsburgh, G. J., Meredith, M. P., Murphy, E. J., . . . Carvalho, G. R. (2015). Oceanography and life history predict contrasting genetic population structure in two Antarctic fish species. *Evolutionary Applications*, *8*(5), 486-509.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, *292*(5517), 686-693. https://doi.org/10.1126/science.1059412

Appendix ST1

Table S1. Forward (F) and reverse (R) primers used for the amplification of four genes and gene-specific annealing temperatures (Tm) used in Polymerase Chain Reaction.

Gene	Sequence 5'–3'	Reference	Tm (°C)
COI			
LCO1490 (F)	GGT CAA CAA ATC ATA AAG ATA TTG G	Folmer et al. (1994)	50.5
HCO2198 (R)	TTA ACT TCA GGG TGA CCA AAA AAT CA	Williams et al. (2003)	
12S			
12SALint (F)	ACT AGG ATT AGA TAC CCT ACT ATT C	Williams et al. (2003)	54.2
12SAHint (R)	CGA GRG TGA CGG GCG ATG TGT GCA	Williams et al. (2003)	
16S			
16Sar (F)	CGCCTGTTTATCAAAAACAT	Simon et al. (1991)	48
16Sbr (R)	CCGGTCTGAACTCAGATCACGT	Simon et al. (1991)	
28S			
LSU5 (F)	TAG GTC GAC CCG CTG AAY TTA AGC A	Littlewood et al. (2000)	52.5
LSU1600 (R)	AGC GCC ATC CAT TTT CAG G	Williams et al. (2003)	

Appendix ST2

Table S2. GenBank accession numbers for four markers for Littorinidae species used in the present study

Subfamily to species	Genus	taxon	COI	12S	28S	16S
Laevilitorininae						
	Laevilacunaria	*L. antarctica*_EB1	PP986835	PP988552	PP985559	PP987851
		*L. antarctica*_EB2	PP986836	PP988550	PP985560	
		*L. antarctica*_FI	PP986837	PP988555	PP985561	PP987850
		*L. antarctica*_CI2	PP986838	PP988556	PP985562	
		*L. antarctica*_CI3	PP986839	PP988557	PP985563	
		*L. antarctica*_SO1	PP986842	PP988553	PP985564	
		*L. antarctica*_SO2	PP986840	PP988554	PP985565	
		*L. antarctica*_SO3	PP986841	PP988551	PP985566	
		*L. antarctica*_SG1	PP986829	PP988543	PP985573	PP987852
		*L. antarctica*_SG2	PP986828	PP988544	PP985574	
		*L. antarctica*_SG3	PP986830	PP988546	PP985572	PP987848
		*L. antarctica*_SG4	PP986831	PP988547	PP985575	PP987849
		*L. antarctica*_SG5	PP986826	PP988548	PP985571	

	*L. antarctica*_SG6	PP986827	PP988549	PP985570	
	*L. antarctica*_SG7	PP986834	PP988541	PP985569	
	*L. antarctica*_SG8	PP986833	PP988542	PP985567	
	*L. antarctica*_SG10	PP986832	PP988545	PP985568	
	*L. pumilio*_CZ	PP986843	PP988558	PP985576	PP987853
	*L. pumilio*_CZ2	PP986845	PP988559	PP985577	PP987855
	*L. pumilio*_CZ3	PP986844	PP988560	PP985578	PP987856
	*L. pumilio*_CZ4	PP986846	PP988561	PP985579	PP987854
	*L. bennetti*_EB1	PP986874	PP988534	PP985526	
	*L. bennetti*_EB3	PP986875	PP988533	PP985529	
	*L. bennetti*_EB4	PP986876	PP988532	PP985528	PP987841
	*L. bennetti*_EB5	PP986881	PP988531	PP985527	
	*L. bennetti*_YB1	PP986877	PP988530	PP985524	PP987843
	*L. bennetti*_YB2	PP986879	PP988529	PP985525	PP987842
	*L. bennetti*_YB3	PP986878	PP988527	PP985530	
	*L. bennetti*_YB4	PP986880	PP988528	PP985531	
	*L. cf bennetti*_SG1	PP986884	PP988535	PP985532	PP987845
	*L. cf bennetti*_SG2	PP986882	PP988536	PP985533	
	*L. cf bennetti*_SG3	PP986885	PP988537	PP985536	PP987846
	*L. cf bennetti*_SG4	PP986886	PP988538	PP985535	
	*L. cf bennetti*_SG5	PP986883	PP988539	PP985534	PP987847
Laevilitorina	*L. antarctica*_AV1	PP986847	PP988500	PP985543	
	*L.antarctica*_AV4	PP986852	PP988501	PP985542	
	*L. claviformis*_DI2	PP986851	PP988502	PP985541	PP987832
	*L.claviformis*_DI3	PP986849	PP988503	PP985540	
	*L. claviformis*_DI4	PP986850	PP988504	PP985538	
	*L.umbilicata*_DI2	PP986848	PP988505	PP985539	PP987833
	*L. caliginosa*_WI04	PP986867	PP988518	PP985516	PP987834
	*L. caliginosa*_WI07	PP986865	PP988520	PP985517	
	*L. caliginosa*_WI08	PP986866	PP988519	PP985518	PP987835
	*L. fueguina*_CH03	PP986853	PP988508	PP985552	PP987822
	*L. fueguina*_CH04	PP986854	PP988506	PP985550	PP987823
	*L. fueguina*_PO08	PP986855	PP988507	PP985551	PP987824
	*L. hicana*_HI03	PP986871	PP988526	PP985519	PP987838
	*L. hicana*_HI13	PP986872	PP988524	PP985520	PP987840
	*L. hicana*_HI15	PP986873	PP988525	PP985521	PP987839
	*L. latior*_FA01	PP986870	PP988523	PP985556	PP987836
	*L. latior*_FA05	PP986868	PP988521	PP985557	PP987837
	*L. latior*_FA06	PP986869	PP988522	PP985558	
	*L. magellanica*_CH21	PP986856	PP988508	PP985544	PP987825
	*L. magellanica*_CH22	PP986857	PP988506	PP985545	
	*L. magellanica*_CH24	PP986858	PP988507	PP985546	PP987826
	*L. pepita*_CH07	PP986859	PP988512	PP985547	PP987827

		*L. pepita*_TR2	PP986861	PP988513	PP985548	PP987828
		*L. pepita*_TR5	PP986860	PP988514	PP985549	PP987829
		*L. venusta*_CZ4	PP986862	PP988517	PP985553	
		*L. venusta*_FI	PP986864	PP988515	PP985555	PP987830
		*L. venusta*_KE1	PP986863	PP988516	PP985554	PP987831
		*L. wandelensis*_FI		PP988540	PP985537	PP987844
Lacuninae						
	Pellilitorina	*P. setosa*_KER1	PP986823	PP988499	PP985515	PP987857
		*P. setosa*_KER2	PP986824		PP985514	
		*P. pellita*_FI	PP986825		PP985513	
	Risellopsis	*R. varia*_NZ1	PP986821		PP985522	
		*R. varia*_NZ5	PP986822		PP985523	

Appendix ST3

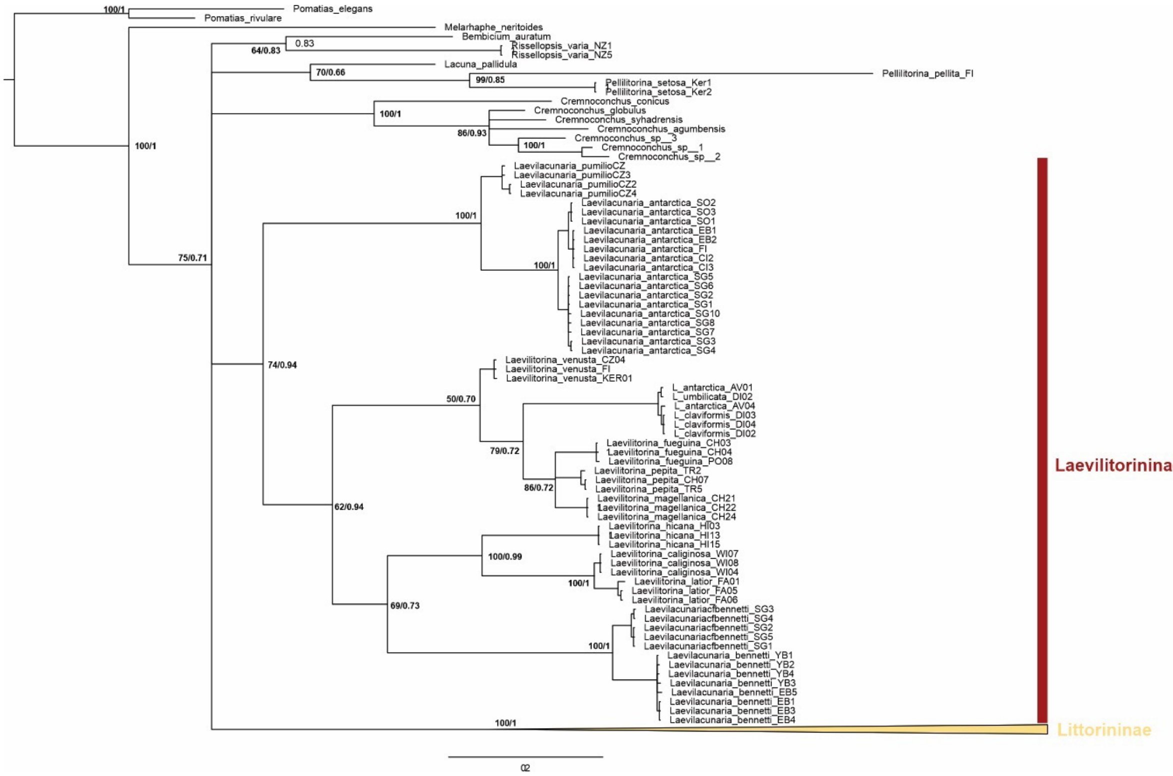
Table S3. List of gene-specific Nucleotide Substitution Models chosen by PartitionFinder

Gene	Best Model
COI	
codon position 1	GTR+I+G
codon position 2	GTR+G
codon position 3	GTR+I+G
12S	GTR+I+G
16S	GTR+I+G
28S	GTR+I+G

Appendix SF1

SI Figure 1: Phylogenetic reconstruction of the relationships among Littorinidae based on 12S gene. Bayesian posterior probability (PP) and maximum likelihood bootstrap (ML) values are shown above and under the nodes.

Appendix SF2



SI Figure 2: Phylogenetic reconstruction of the relationships among Littorinidae based on COI gene. Bayesian posterior probability (PP) and maximum likelihood bootstrap (ML) values are shown above and under the nodes.

Appendix SF3

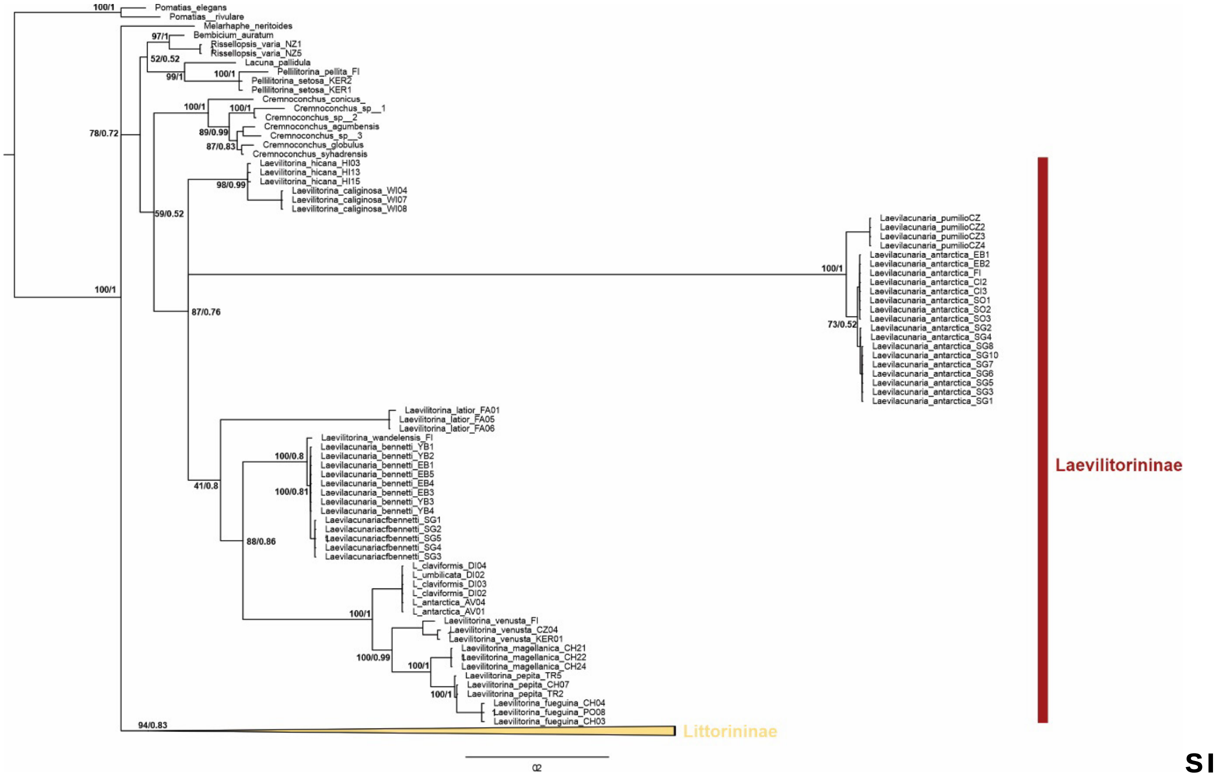


Figure 3: Phylogenetic reconstruction of the relationships among Littorinidae based on 28S gene. Bayesian posterior probability (PP) and maximum likelihood bootstrap (ML) values are shown above and under the nodes.

CONCLUSIONES GENERALES Y PROYECCIONES

Esta tesis representa un estudio detallado de la distribución, taxonomía, sistemática y biogeografía de los dos géneros que componen la subfamilia Laevilitorininae que habitan el Océano Austral. En este sentido, el primer capítulo abordó la distribución completa del género *Laevilitorina*, el cual está ampliamente distribuido a lo largo del hemisferio sur. Este estudio amplió significativamente el conocimiento sobre la distribución de *Laevilitorina*, reportando nuevos registros de especies como *L. pygmaea* y *L. venusta*, extendiendo su rango batimétrico y geográfico. Estos nuevos registros son esenciales para futuras investigaciones biogeográficas y ecológicas, proporcionando una base de datos más completa sobre la distribución de estas especies. Sin embargo, la falta de datos de distribución para muchas especies de *Laevilitorina* aún representa una limitación importante, destacando la necesidad de un mayor esfuerzo de muestreo y recopilación de datos en áreas menos estudiadas principalmente las Islas Subantárticas. Asimismo, nos dimos cuenta de la gran plasticidad morfológica observada en especies de *Laevilitorina*, lo cual genera una mayor complejidad a la identificación y clasificación taxonómica de este género. Las diferencias morfológicas dentro de una misma especie pueden dificultar su identificación precisa, lo que enfatiza la necesidad de análisis moleculares complementarios.

Una vez abordado la distribución del género *Laevilitorina* y el contexto taxonómico de este, proseguimos a realizar una revisión exhaustiva del grupo en la región de Magallanes utilizando herramientas morfológicas y moleculares. Las implicaciones sistemáticas de esta revisión de *Laevilitorina* son muy relevantes ya que proporcionan nueva y valiosa información sobre los patrones de diversidad, relaciones evolutivas y afinidades biogeográficas de este importante género del Océano Austral. *Laevilitorina*, anteriormente considerada pobremente representada en el sur de Sudamérica, ha demostrado poseer al menos seis especies diferentes que se diversificaron durante los últimos 20 millones de años. Especies como *L. magellanica*, *L. fueguina* y *L. pepita* están restringidas al Estrecho de Magallanes, donde evolucionaron in situ durante varios millones de años. *L. hicana* aparentemente se restringe a la Isla Hornos, y *L. caliginosa* extiende su distribución hacia las Islas Malvinas y Georgia del Sur. Finalmente, *L. venusta* tiene una amplia distribución a través del Frente Polar Antártico, hacia islas subantárticas como Georgia del Sur, Marion, Crozet, Kerguelen y Macquarie, siendo un ejemplo importante de dispersión a larga distancia en invertebrados marinos someros.

Las diferencias en la riqueza de especies y patrones biogeográficos de *Laevilitorina* en las provincias marinas del hemisferio sur tienen implicancias importantes para la conservación y estudios biogeográficos. El marcada endemismo de algunas especies y las variaciones en la distribución geográfica resaltan la importancia de comprender los procesos y mecanismos subyacentes que han influenciado los procesos evolutivos dentro del género. Investigar estos patrones biogeográficos y su relación con factores ambientales y ecológicos son cruciales para desarrollar estrategias de conservación y mejorar nuestro entendimiento de la biodiversidad marina en regiones Antárticas y Subantárticas.

Una vez revisada la taxonomía y sistemática en *Laevilitorina*, en el tercer capítulo incluimos todas las especies del género hermano *Laevilacunaria*, dentro de una filogenia global de la familia Littorinidae. Para ellos se utilizaron de 3 a 4 marcadores moleculares y el análisis morfológico de la rádula. En este capítulo se generaron varios resultados desde aspectos sistemáticos hasta biogeográficos. En primer lugar, las implicancias filogenéticas y sistemáticas de este estudio son muy relevantes. Se confirmó la monofilia de la subfamilia Laevilitorininae, pero se evidencio que los géneros *Laevilacunaria* y *Laevilitorina* son parafiléticos, lo que sugiere una clasificación taxonómica más compleja. Nuestros análisis sugieren la reclasificación de *Laevilitorininae* en cuatro géneros distintos basados en diferencias moleculares y morfológicas, reflejando profundas divergencias y distinciones morfológicas dentro de los clados. Además, se restableció a *Laevilacunaria bransfieldensis* como una especie válida, diferenciada de *Laevilacunaria antarctica*, y se identificó una nueva especie dentro del clado de *Laevilacunaria bennetti* Estos hallazgos enfatizan la necesidad de revisiones taxonómicas adicionales y la integración de datos moleculares y morfológicos para una comprensión completa de la historia evolutiva y las relaciones filogenéticas dentro de Laevilitorininae. Adicionalmente, esta tesis presenta la primera filogenia global de la familia Littorinidae en donde se incluyen a varios géneros de las subfamilias Laevilitorininae, Lacuninae y Littorininae. Este análisis más completo nos permitió observar no solo resultados dentro de Laevilitorininae sino también, evidenciar un contexto más global de las relaciones filogenéticas dentro de la familia Littorinidae. Por ejemplo, la posición del género *Cremnoconchus* plantea interrogantes sobre su clasificación taxonómica dentro de la subfamilia Lacuninae. Estos hallazgos resaltan la importancia de continuar explorando la sistemática de los littorínidos mediante enfoques integrativos que combinen datos moleculares y morfológicos para una comprensión más completa de sus relaciones evolutivas.

Desde la biogeografía histórica, este estudio sobre el origen evolutivo y la diversificación de Laevilitorininae y *Laevilacunaria* en el Océano Austral muestra que el ancestro de la subfamilia Laevilitorininae es Gondwánico, cuya primera diversificación coincide con la fase final de fragmentación del Gondwana hace aproximadamente 50.72 millones de años. La evolución temprana de este grupo estuvo influenciada por procesos de vicarianza en donde se formarían cuatro grandes clados y más recientemente por eventos de dispersión a larga distancia. Estos hallazgos sugieren que la historia evolutiva de Laevilitorininae estuvo relacionada con la separación final de Gondwana y los cambios climáticos y oceanográficos que ocurrieron durante el Paleógeno.

Mas recientemente los eventos de dispersión a larga distancia y establecimiento (LDDE) jugaron un papel fundamental en la distribución geográfica actual de *Laevilacunaria* y *Laevilitorina*. Estos eventos, facilitados rafting a través de macroalgas flotantes, permitieron que las especies de *Laevilacunaria* cruzaran barreras oceanográficas y colonizaran nuevas áreas. La evidencia sugiere que individuos de *L. pumilio* utilizaron algas flotantes como *Durvillaea* para dispersarse desde las islas subantárticas hacia Antártica Oeste. Este mecanismo de dispersión es respaldado por los nuevos modelos oceanográficos que muestran que las algas flotantes pueden llegar a las costas antárticas regularmente, llevando consigo una variedad de invertebrados marinos o sus masas de huevos. Esto destaca la importancia de los procesos de dispersión a larga distancia en la biogeografía de *Laevilacunaria* y su influencia en la diversificación de las especies en el Océano Austral. Estos hallazgos resaltan la complejidad de los patrones de dispersión y colonización en estos ambientes marinos extremos.

Finalmente, dentro de las proyecciones de este estudio es importante mencionar que es necesario realizar investigaciones futuras para incluir especies de *Laevilitorina* de Nueva Zelanda y Australia y así resolver la sistemática dentro de la familia Laevilitorininae. La ausencia de estas especies en el análisis actual limita la precisión de las estimaciones de la edad del ancestro común más reciente (TMRCA) de Laevilitorininae. Además, para avanzar en nuestra comprensión de la evolución y diversificación en el Océano Austral, es fundamental continuar integrando datos moleculares y morfológicos en estudios filogenéticos y biogeográficos. Futuras investigaciones podrían enfocarse en explorar en más detalle los mecanismos específicos de dispersión, como el rafting en macroalgas, y cómo estos han influenciado en la colonización y diferenciación genética de los moluscos marinos en el OA. Además, la inclusión de más especies y regiones geográficas ayudará a construir un marco más completo de la evolución de la biodiversidad en el Océano Austral, considerando tanto los cambios climáticos actuales como los históricos.

REFERENCIAS

Ávila C, C Angulo-Preckler, RP Martín-Martín et al. 2020. Invasive marine species discovered on non–native kelp rafts in the warmest Antarctic island. Sci Rep 10, 1639 https://doi.org/10.1038/s41598-020-58561-y

Barnes D & Peck L. 2008. Vulnerability of Antarctic shelf biodiversity to predicted regional warming Climate Research 37, 149–163.

Billard E, Reyes J, Mansilla A, et al. 2015. Deep genetic divergence between austral populations of the red alga Gigartina skottsbergii reveals a cryptic species endemic to the Antarctic continent Polar Biology 38, 2021–2034.

Cárdenas L, JC Leclerc JC, P Bruning *et al.* 2020. First mussel settlement observed in Antarctica reveals the potential for future invasions. *Sci Rep* 10, 5552. https://doi.org/10.1038/s41598-020-62340-0

Crame JA. 1999. An evolutionary perspective on marine faunal connections between southernmost South America and Antarctica. In: Arntz WE & C RÍOS. 1999. Magellan - Antarctic. Ecosystems that drifted apart: 1-14. Scientia Marina 63(1)

Crisp MD, SA Trewick & LG Cook. 2011. Hypothesis testing in biogeography. Trends in Ecology and Evolution 26(2)

Cumming RA, R Nikula, HG Spencer et al. 2014. Transoceanic genetic similarities of kelp-associated sea slug populations: long-distance dispersal via rafting? Journal of Biogeography 41, 2357–2370.

Fraser CI, L Dutoit, AK Morrison, LM Pardo, SD Smith, W Pearman, E Parvizi, JM Waters, EC Macaya**.** 2022. Southern Hemisphere coasts are biologically connected by frequent, long-distance rafting events. Current Biology, https://doi.org/10.1016/j.cub.2022.05.035

Fraser CI, M Velasquez, W Nelson, E Macaya, C Hay. 2020. The biogeographic importance of buoyancy in macroalgae: a case study of the southern bull-kelp genus *Durvillaea* (phaeophyceae), including descriptions of two new species. Journal of Phycology 56, 23–36

Fraser CI, R Nikula & JM Waters. 2011. Oceanic rafting of a coastal community. Proceedings of the Royal Society of London B 278, 649-655. doi: 10.1098/rspb.2010.1117.

Fraser CI, R Nikula, HG Spencer & JM Waters. 2009. Kelp genes reveal effects of subantarctic sea ice during the Last Glacial Maximum. PNAS doi_10.1073_pnas.0810635106.

Frugone MJ, A Lowther, D Noll et al. 2018. Contrasting phylogeographic pattern among Eudyptes penguins around the Southern Ocean. Scientific Reports 8, 17481

Göbbeler K, A Klussmann-Kolb. 2010. Out of Antarctica? – New insights into the phylogeny and biogeography of the Pleurobranchomorpha (Mollusca, Gastropoda). Molecular Phylogenetics and Evolution 55, 996–1007

González-Wevar C, N Segogia, S Rosenfeld, D Doll, CS Maturana, J Naretto et al. 2021. Contrasting biogeographical patterns in Margarella (Gastropoda: Calliostomatidae: Margarellinae) across the Antarctic Polar Front. Molecular Phylogenetics and Evolution 156, 107039

González-Wevar CA, Gérard K, Rosenfeld S, Saucède T, Naretto J, Díaz A, Morley SA, Brickle P, Poulin E. 2019. Cryptic speciation in Southern Ocean *Aequiyoldia eightsii* (Jay, 1839): MioPliocene trans-Drake Passage separation and diversification. Progress in Oceanography: https://doi.org/ 10.1016/j.pocean.2018.09.004.

González-Wevar CA, M Hüne, NI Segovia, T Nakano, HG Spencer, S Chown, T Saucède, G Johnstone, A Mansilla, E Poulin. 2017. Following the Antarctic Circumpolar Current: patterns and processes in the biogeography of the limpet *Nacella* (Mollusca: Patellogastropoda) across the Southern Ocean. Journal of Biogeography 44, 861–874.

González-Wevar CA, NI Segovia, S Rosenfeld, CS Maturana, V Jeldres, R Pinochet , T Saucède, SA Morley, P Brickle, NG Wilson, HG Spencer, E Poulin. 2022. Seven snail species hidden in one: Biogeographic diversity in an apparently widespread periwinkle in the Southern Ocean. Journal of Biogeography 49(8): 1521–1534. https://doi.org/10.1111/jbi.14453

González-Wevar CA, NI Segovia, S Rosenfeld, J Ojeda, M Hüne, J Naretto, T Saucède, P Brickle, S Morley, JP Féral, HG Spencer & E Poulin. 2018. Unexpected absence of island endemics: Long-distance dispersal in higher latitude sub-Antarctic *Siphonaria* (Gastropoda: Euthyneura) species. Journal of Biogeography, DOI 10.1111/jbi.13174

González-Wevar CA, S Rosenfeld, NI Segovia, M Hüne, K Gerard, J Ojeda & E Poulin. 2016. Genetics, gene flow, and Glaciation: The case of the South American Limpet Nacella mytilina. PLoS ONE 11, e0161963 https://doi.org/10.1371/journal.pone.0161963

González-Wevar CA, Y Poveda, N Segovia, S Rosenfeld, CS Maturana, V Jeldres, . . . E Poulin. 2024. Both high and low dispersal? Apparently contradictory genetic patterns in the Antarctic littorinid gastropod *Laevilacunaria antarctica*. *Frontiers in Ecology and Evolution*, *11*. https://doi.org/10.3389/fevo.2023.1320649

Halanych K & A Mahon. 2018. Challenging Dogma Concerning Biogeographic Patterns of Antarctica and the Southern Ocean. Annual Review of Ecology, Evolution and Systematics 49, 355–378.

Hinojosa IA, M Pizarro, M Ramos & M Thiel. 2010. Spatial and temporal distribution of floating kelp rafts in the channels and fjords of southern Chile. *Estuarine*, *Coastal* and *Shelf Science* 87, 367–377.

Hinojosa IA, M Rivadeneira & M Thiel. 2011. Temporal and spatial distribution of floating objects in coastal waters of central southern Chile and Patagonian fjords. *Continental Shelf* Research 3l, 172–186.

Koubbi P, C De Broyer, HJ Griffiths et al. 2014. Conclusions: present and future of Southern Ocean biogeography.in *Biogeographic Atlas of the Southern Ocean* (eds. C. De Broyer, P. Koubbi, HJ Griffiths, et al.) 470–475. Scientific Committee on Antarctic Research, Cambridge.

Levicoy D, Rosenfeld S & Cárdenas L. 2021. Divergence time and species delimitation of microbivalves in the Southern Ocean: the case of *Kidderia* species. 2021. Polar Biology 44, 1365–1377 https://doi.org/10.1007/s00300-021-02885-6

Linse K, HJ Griffiths, D Barnes et al. 2006. Biodiversity and biogeography of Antarctic and sub-Antarctic mollusca. Deep Sea Research Part II: Topical Studies in Oceanography 53, 985-100

Macaya, E. C., Tala, F., Hinojosa, I. A., & Rothäusler, E. 2020. Detached seaweeds as important dispersal agents across the Southern Ocean. In *Antarctic Seaweeds* (pp. 59-81). https://doi.org/10.1007/978-3-030-39448-6_4

Nikula R, CI Fraser, HG Spencer & JM Waters. 2010. Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. Marine Ecology Progress Series 405, 221–230 doi.org/103354/meps08523

Nikula R, HG Spencer & JM Waters. 2012. Passive rafting is a powerful driver of transoceanic gene flow. Biology Letters 9, 1–4.

Ocaranza-Barrera P, González-Wevar CA, Guillemin M-L, et al. 2019. Journal of Applied Phycology 31, 939 – 949.

Patarnello T, L Bargelloni, V Varotto & B Battaglia. 1996. Krill evolution and the Antarctic Ocean currents: Evidence of vicariant speciation as inferred by molecular data. Marine Biology 126, 603-608.

Picken GB 1979. Non-pelagic reproduction of some Antarctic Prosobranch gastropods from Signy Island, South Orkney Island. *Malacologia*, *19*(1), 109-128.

Poulin E, CA González-Wevar, A Díaz, K Gérard, M Hüne. 2014. Divergence between Antarctic and South American marine invertebrates: What molecular biology tells us about Scotia Arc geodynamics and the intensification of the Antarctic Circumpolar Current. Global and Planetary Change 123, 392–399.

Reid DG 1989. The comparative morphology, phylogeny, and evolution of the gastropod family Littorinidae Philosophical Transactions of the Royal Society of London B 324, 1–110.

Reid DG, P Dyal & S Williams 2012. A global molecular phylogeny of 147 periwinkle species (Gastropoda, Littorininae) *Zoologica Scripta*, 41, 125–136.

Rosenfeld S, C Aldea, J Ojeda, J Marambio, M Hüne, JS Troncoso & A Mansilla. 2017. Molluscan assemblages associated with Gigartina beds in the Strait of Magellan and the South Shetland Islands (Antarctica): a comparison of composition and abundance. *Polar Research*, *36*(1). https://doi.org/10.1080/17518369.2017.1297915

Rosenfeld S, C Maturana, HG Spencer, P Convey, T Saucède, P Brickle., . . . C Gonzalez-Wevar. 2022. Complete distribution of the genus Laevilitorina (Littorinimorpha, Littorinidae) in the Southern Hemisphere: remarks and natural history. *Zookeys*. https://doi.org/10.3897/zookeys.@@.91310

Rosenfeld S, NI Segovia, CS Maturana, C Aldea, T Saucède, P Brickle, . . . González-Wevar, CA. 2023. A revision of the higher latitude periwinkle species Laevilitorina caliginosa sensu lato. *Zoological Journal of the Linnean Society*. https://doi.org/10.1093/zoolinnean/zlad171

SanMartin I & F Ronquist. 2004. Southern Hemisphere Biogeography Inferred by Event-Based Models: Plant versus Animal Patterns. SYSTEMATIC BIOLOGY 53(2), 216-243

Schmider-Martinez A, CS Maturana, Y Poveda, S Rosenfeld, Z Lopez-Farran, T Saucede, . . . C Gonzalez-Wevar. 2023. Laevilacunaria (Mollusca, Gastropoda) in the Southern Ocean: A comprehensive occurrence dataset. *Biodivers Data J*, *11*, e111982. https://doi.org/10.3897/BDJ.11.e111982

Simpson RD. 1972. *The ecology and biology of molluscs in the littoral and sublittoral zones at Macquarie Island, with speical reference to Patinigera macquariensis (Finlay 1927)* Adelaide].

Simpson R & SA Harrington. 1985. Egg masses of three gastropods, Kerguelenella lateralis (Siphonariidae), Laevilitorina caliginosa and Macquariella hamiltoni

(Littorinidae), from Macquarie Island (sub-Antarctic). *Journal of the Malacological Society of Australia*, *7*(1-2), 17-28.

Vianna J, D Noll, GPM Dantas et al. 2017. Marked phylogeographic structure of Gentoo penguin reveals an ongoing diversification process along the Southern Ocean. Molecular Phylogenetics and Evolution 107, 486–498.

Waters JM & D Craw. 2006. Goodbye Gondwana? New Zealand Biogeography, Geology, and the Problem of Circularity. SYSTEMATIC BIOLOGY 55(2), 351-356.

Waters JM. 2008. Driven by the west wind drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. Journal of Biogeography, 35, 417–427. https://doi.org/10.1111/j.1365-2699.2007.01724.x

Williams ST, DG Reid & DTJ Littlewood. 2003. A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism, and biogeography of the Southern Ocean. Molecular Phylogenetics and Evolution 28, 60–86

ANEXO

Durante la ejecución de esta tesis además de los artículos publicados en los dos primeros capítulos de la tesis, se produjeron los siguientes manuscritos relacionados a los litorinidos Antárticos y Subantárticos en donde sus resultados fueron importantes para la ejecución de la esta tesis final.

- Claudio A. González-Wevar, Nicolás I. Segovia, **Sebastián Rosenfeld**, Claudia S. Maturana,Vanessa Jeldres, Ramona Pinochet,T homas Saucède,Simon A. Morley, Paul Brickle, Nerida G. Wilson, Hamish G. Spencer, Elie Poulin. 2022. Seven snail species hidden in one: Biogeographic diversity in an apparently widespread periwinkle in the Southern Ocean. Journal of Biogeography https://doi.org/10.1111/jbi.14453

- **Rosenfeld, S.**, Maturana, C., Gañan, M., Cárcamo, J. R., Díaz, A., Contador, T., & Poulin, E. (2023). Revealing the hidden biodiversity of Antarctic and the Magellanic Sub-Antarctic Ecoregion: A comprehensive study of aquatic invertebrates from the BASE Project. *Biodiversity Data Journal*, *11*, e108566.
    - IPT asociado en GBIF. Occurrences of aquatic invertebrates in the Antarctic and Subantarctic regions Published: Instituto Milenio BASE doi.org/ 10.15468/kn5xcg

- Schmider-Martínez, A., Maturana, C., Poveda, Y., **Rosenfeld, S.**, López-Farrán, Z., Saucède, T., Poulin E & González-Wevar, C. (2023). *Laevilacunaria* (Mollusca, Gastropoda) in the Southern Ocean: A comprehensive occurrence dataset. Biodiversity Data Journal, 11, e111982.

- González-Wevar CA, Y Poveda, N Segovia, **S Rosenfeld**, CS Maturana, V Jeldres, . . . E Poulin. 2024. Both high and low dispersal? Apparently contradictory genetic patterns in the Antarctic littorinid gastropod *Laevilacunaria antarctica*. *Frontiers in Ecology and Evolution*, *11*. https://doi.org/10.3389/fevo.2023.1320649

Received: 26 August 2021 | Revised: 6 April 2022 | Accepted: 7 May 2022

DOI: 10.1111/jbi.14453

Journal of Biogeography WILEY

RESEARCH ARTICLE

Seven snail species hidden in one: Biogeographic diversity in an apparently widespread periwinkle in the Southern Ocean

Claudio A. González-Wevar[1,2,3,4] | **Nicolás I. Segovia**[4,5] | **Sebastián Rosenfeld**[2,4,6] | **Claudia S. Maturana**[2,4] | **Vanessa Jeldres**[1,2,3] | **Ramona Pinochet**[1] | **Thomas Saucède**[7] | **Simon A. Morley**[8] | **Paul Brickle**[9,10] | **Nerida G. Wilson**[11,12] | **Hamish G. Spencer**[13] | **Elie Poulin**[2,4]

[1]Facultad de Ciencias, Instituto de Ciencias Marinas y Limnológicas (ICML), Universidad Austral de Chile, Valdivia, Chile

[2]Instituto Milenio Biodiversidad de Ecosistemas Antárticos y Subantárticos (BASE), Santiago, Chile

[3]Centro Fondap de Investigación en Dinámica de Ecosistemas Marinos de Altas Latitudes (IDEAL), Universidad Austral de Chile, Valdivia, Chile

[4]Departamento de Ciencias Ecológicas, Instituto de Ecología y Biodiversidad (IEB), Universidad de Chile, Santiago, Chile

[5]Facultad de Ciencias del Mar, Departamento de Biología Marina, Universidad Católica del Norte, Coquimbo, Chile

[6]Laboratorio de Ecosistemas Marinos Antárticos y Subantárticos, Universidad de Magallanes, Punta Arenas, Chile

[7]Biogéoscience, UMR CNRS 6282, Université de Bourgougne 6, Dijon, France

[8]British Antarctic Survey (BAS), Natural Environment Research Council, Cambridge, United Kingdom

[9]South Atlantic Environmental Research Institute, Falkland Islands, UK

[10]School of Biological Sciences (Zoology), University of Aberdeen, Aberdeen, UK

[11]Western Australian Museum, Perth, Western Australia, Australia

[12]University of Western Australia, Crawley, Western Australia, Australia

[13]Department of Zoology, University of Otago, Dunedin, New Zealand

Correspondence

Claudio A. González-Wevar, Instituto de Ciencias Marinas y Limnológicas (ICML), Facultad de Ciencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.

Email: claudio.gonzalez@uach.cl

Funding information

Agencia Nacional de Investigación y Desarrollo (ANID) Projects, Grant/Award Number: 1210787, 115336 and 3210063; Centro Fondap IDEAL, Grant/Award Number: 15150003; Instituto Antártico Chileno (INACH) Project, Grant/Award Number: RG_18-17; Projects Genomic Antarctic Biodiversity, Grant/Award Number: PIA CONICYT ACT172065 and PIA CONICYT AFB170008; BEA Team; UKRI-NERC; British Antarctic Survey; French Polar Institute; Western Australian Museum; Ferring Pharmaceuticals; ACE Foundation; Universidad de Magallanes

Handling Editor: Giacomo Bernardi

Abstract

Aim: The Antarctic Circumpolar Current imparts significant structure to the Southern Ocean biota. The Antarctic Polar Front is a major barrier to dispersal, with separate species (or sometimes intraspecific clades) normally occurring either side of this feature. We examined the biogeographic structure of an apparent exception to this rule in a widespread genus of the Southern Ocean, the periwinkle snail, *Laevilitorina*.

Location: Southern Ocean.

Taxon: Littorinidae, Laevilitorininae, *Laevilitorina*.

Methods: Using 750 specimens from 16 Southern Ocean *Laevilitorina* populations across >8000 km, we analysed mitochondrial COI and nuclear 28S sequences to uncover the evolutionary history of these marine near-shore snails. We utilized multilocus phylogenetic reconstructions, species-delimitation analyses, divergence-time estimations and geometric morphometrics.

Results: Molecular data revealed that the widespread nominal species *L. caliginosa* comprises seven species-level clades, all supported by morphological data, whereas the Antarctic nominal species *L. antarctica*, *L. claviformis* and *L. umbilicata* are conspecific. Six "*caliginosa*" clades are restricted to southern South America, but one lineage extends from Antarctica to distant sub-Antarctic islands on both sides of the APF.

Geometric morphometrics also identified significant differences among these clades, but uncoupled from genetic differentiation.

Main conclusions: The apparent trans-APF distribution of the poorly dispersing *Laevilitorina caliginosa* is largely illusory: this taxon consists of at least seven discrete species, only one of which has a trans-APF distribution. Similar to most *Laevilitorina* species, the remaining six "*caliginosa*" clades are narrow endemics. Biogeographical patterns in *Laevilitorina* reflect the role of vicariance associated with geological processes together with recent long-distance dispersal events. *Laevilitorina* originated near the Eocene/Oligocene boundary and diversified during the Miocene and the Pliocene. *Laevilitorina* is not a cryptic-species complex: speciation was accompanied by hitherto unrecognized morphological differentiation. This study represents the most detailed molecular work on Southern-Ocean littorinids and reveals unforeseen diversity across this globally important region.

KEYWORDS

Antarctic, cryptic species, dispersal, Littorinidae, species-delimitation analyses, sub-Antarctic, vicariance

1 | INTRODUCTION

The Southern Ocean occupies ~35 $\times 10^6$ km^2 around the Antarctic continent and is a major driver of global oceanic circulation (Rintoul, 2011). The composition, abundance and distribution of the biota in this vast region has been shaped by geologic, oceanographic and climatic processes since the fragmentation of the Gondwanan continental landmasses (Aronson et al., 2007; Halanych & Mahon, 2018; Koubbi et al., 2014). The Antarctic Circumpolar Current (ACC) flows clockwise from west to east and is delimited by two main fronts: the sub-Antarctic Front (SAF) and the southern ACC Front (sACCF) (Rintoul, 2011) (Figure 1). In between these fronts is the Antarctic Polar Front (APF), which constitutes an area where cold northward-flowing Antarctic waters meet relatively warmer sub-Antarctic currents (Gille, 2014). The position of the APF has major biogeographic consequences for the marine benthic life in the Southern Ocean (Crame, 2018; Halanych & Mahon, 2018; Koubbi et al., 2014; Poulin et al., 2014) because of the strong thermal boundaries and the deep-reaching flow of the ACC, which create barriers to poleward heat transport (Dufour et al., 2015). Hence, the APF impedes the dispersal of sub-Antarctic organisms into the Antarctic, and vice versa (Aronson et al., 2007; Clarke et al., 2005; Fraser et al., 2018). Accordingly, marine benthic communities in the Southern Ocean are highly endemic, strongly bio-regionalized (Figure 1) and exhibit major adaptations to cold, which makes them particularly vulnerable to global warming (Griffiths et al., 2017; Morley et al., 2020).

Comparative molecular analyses of co-distributed Antarctic and sub-Antarctic species of marine invertebrates (González-Wevar et al., 2017, 2019; Poulin et al., 2014; Thornhill et al., 2008), macroalgae (Billard et al., 2015) and even penguins (Frugone et al., 2019; Pertierra et al., 2020) have demonstrated the presence of different species-level clades on both sides of the APF. Moreover, evidence from a growing number of studies indicates that the origin and diversification of several near-shore marine organisms occurred no more than 10 Ma, long after the separation of continental landmasses and the initiation of the ACC (González-Wevar et al., 2017, 2018, 2019, 2021; Near et al., 2012; Poulin et al., 2014). Thus, although occasional dispersal must have occurred over long (evolutionary) timescales, there is little ongoing gene flow across the APF (Moon et al., 2017). So far, molecular data suggest that there is almost no evidence of successful biological dispersal into the Antarctic from lower latitudes since the last glacial period (Chenuil et al., 2018; Fraser et al., 2018; González-Wevar et al., 2012; Halanych & Mahon, 2018; Poulin et al., 2014).

Nevertheless, in spite of the dynamic oceanographic and tectonic settings that operated in the region during the last 50 Ma and its marked bio-regionalization, there are numerous examples of seemingly broadly distributed near-shore marine taxa. Molecular studies of most of them, however, have demonstrated that they consist of different evolutionary units in the Antarctic and sub-Antarctic (Billard et al., 2015; González-Wevar et al., 2019; Poulin et al., 2014; Thornhill et al., 2008), which in several cases include cryptic species complexes, common in Southern-Ocean marine invertebrates (Allcock et al., 2011; Baird et al., 2011; Chenuil et al., 2018; Janosik & Halanych, 2010; Wilson et al., 2009), or undescribed species reflecting overly conservative taxonomy (Arango et al., 2011). Although some studies have confirmed the presence of broadly distributed taxa, these cases are restricted to either the Antarctic continent (Díaz et al., 2018; Raupach et al., 2010) or around the sub-Antarctic (Fraser et al., 2009; González-Wevar et al., 2018, 2021; Güller et al., 2020). In summary, the ACC plays a major role connecting populations around the Antarctic continent and, separately, the sub-Antarctic, while the APF isolates antarctic and subantarctic biotas (Crame, 2018; Halanych & Mahon, 2018; Poulin et al., 2014).

Littorinid snails of the genus *Laevilitorina* comprise 21 nominal shallow-benthic periwinkle species (http://marinespecies.org), which live around the Southern Ocean including southern South America, the Antarctic Peninsula, and sub-Antarctic islands. *Laevilitorina*

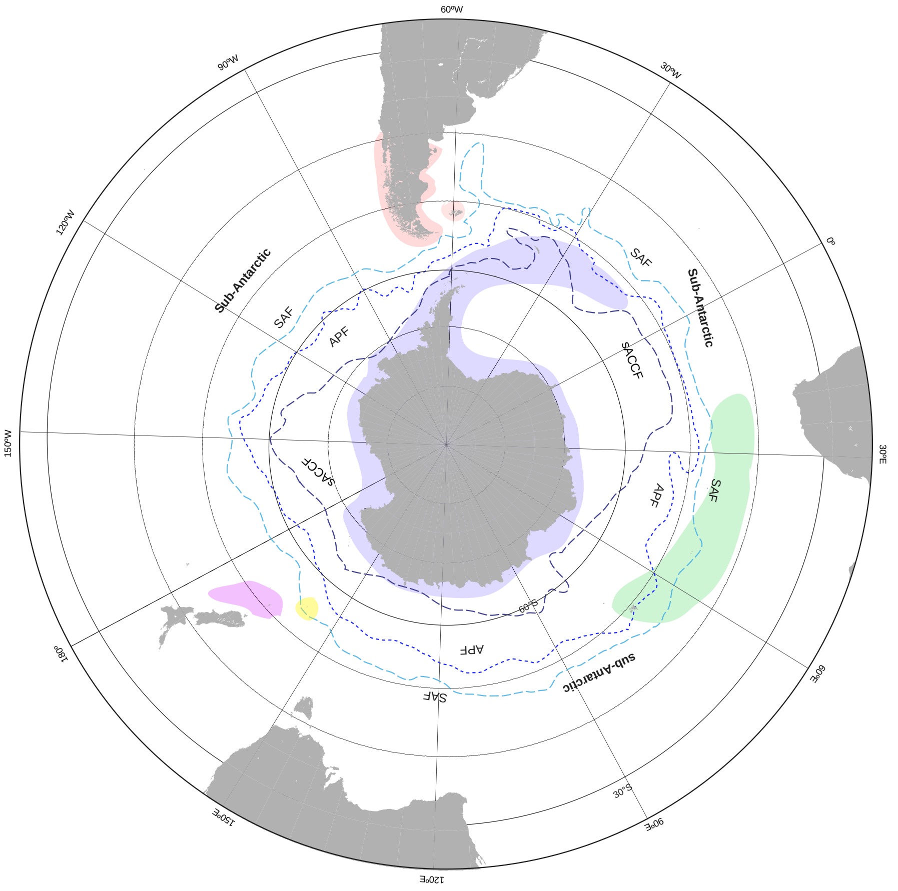


FIGURE 1 Schematic representation of the Southern Ocean (light blue) and the general benthic biogeographic provinces described for the region (modified from Koubbi et al., 2014). The Antarctic Circumpolar Current (ACC) is delimited by two main fronts: the sub-Antarctic Front (SAF) and southern ACC Front (sACCF). The Antarctic Polar Front (APF) lies between these main fronts. Recognized sub-Antarctic areas include Magellan province in southern South America (red), sub-Antarctic Islands of the Indian Ocean (green), Macquarie Island (yellow) and sub-Antarctic New Zealand islands (pink). A single Antarctic province (dark) includes the Antarctic continent and some islands located south of the APF (e.g. South Georgia, Bouvet).

species lack a free-swimming dispersive stage and exhibit protected benthic development with crawling juveniles emerging directly from egg masses (Simpson & Harrington, 1985). Accordingly, *Laevilitorina* species exhibit low autonomous vagility capacity and are poor dispersers, properties reflected by the fact that most of the species are narrow endemics. The single exception, *Laevilitorina caliginosa* (Gould, 1849), apparently shows a broad distribution with populations in southern South America, the Antarctic Peninsula and sub-Antarctic islands such as the Falkland/Malvinas, South Georgia, Marion, Crozet, Kerguelen and Macquarie (Figure 2a,b) (Griffiths & Waller, 2016; Reid, 1989; Simpson & Harrington, 1985).

The ostensible existence of a broadly distributed species with low dispersal potential is paradoxical and three hypotheses may be offered to explain it: (a) anthropogenic activities, (b) passive long-distance dispersal (LDD) mediated by floating objects (i.e. rafting), or (c) the presence of hidden diversity in the form of an unrecognized cryptic-species complexes. There is no evidence supporting the role of anthropogenic activities in the dispersal of marine organisms at the scale of the whole Southern Ocean. *Laevilitorina caliginosa* lives closely associated with buoyant macroalgae and LDD mediated by rafting could constitutes a reasonable explanation for its broad distribution (Griffiths & Waller, 2016). Additionally, as recorded in several Southern Ocean marine near-shore invertebrates (Baird et al., 2011; González-Wevar et al., 2017, 2019; Wilson et al., 2009), *L. caliginosa* could harbour genetically close, morphologically indistinguishable (i.e., cryptic) species.

In order to understand the evolutionary history of *Laevilitorina* in the Southern Ocean, we performed multi-locus molecular-phylogenetic reconstructions, mitochondrial and nuclear species-delimitation analyses, mitochondrial divergence-time estimations and geometric morphometric analyses to compare populations of *L. caliginosa* from different regions (South America, the Antarctic Peninsula and sub-Antarctic islands), as well as the Antarctic endemics, *L. antarctica*, *L. claviformis* and *L. umbilicata*. We aimed to reveal the phylogeographic structure within *Laevilitorina* and hence evaluate the potential role of vicariance and long-distance dispersal in the biogeography of the genus. We also used our data to shed light on the origin and diversification of *Laevilitorina* around the Southern Ocean. Moreover, geometric morphometric analyses allowed us to evaluate the relevance of cryptic speciation in the diversification of the group. Through addressing these issues, we provide new insights on evolutionary relationships, biogeographical and actual diversity patterns of a widespread element of the Southern Ocean, an area of the planet that has been relatively neglected in spite of its global importance.

2 | MATERIALS AND METHODS

2.1 | Sample collection, DNA preparation and sequence editing

Individuals of *Laevilitorina* were sampled from inter- and sub-tidal ecosystems across the Southern Ocean including *L. caliginosa* populations from southern South America, the Antarctic Peninsula and sub-Antarctic islands (Falkland/Malvinas, South Georgia, Marion,

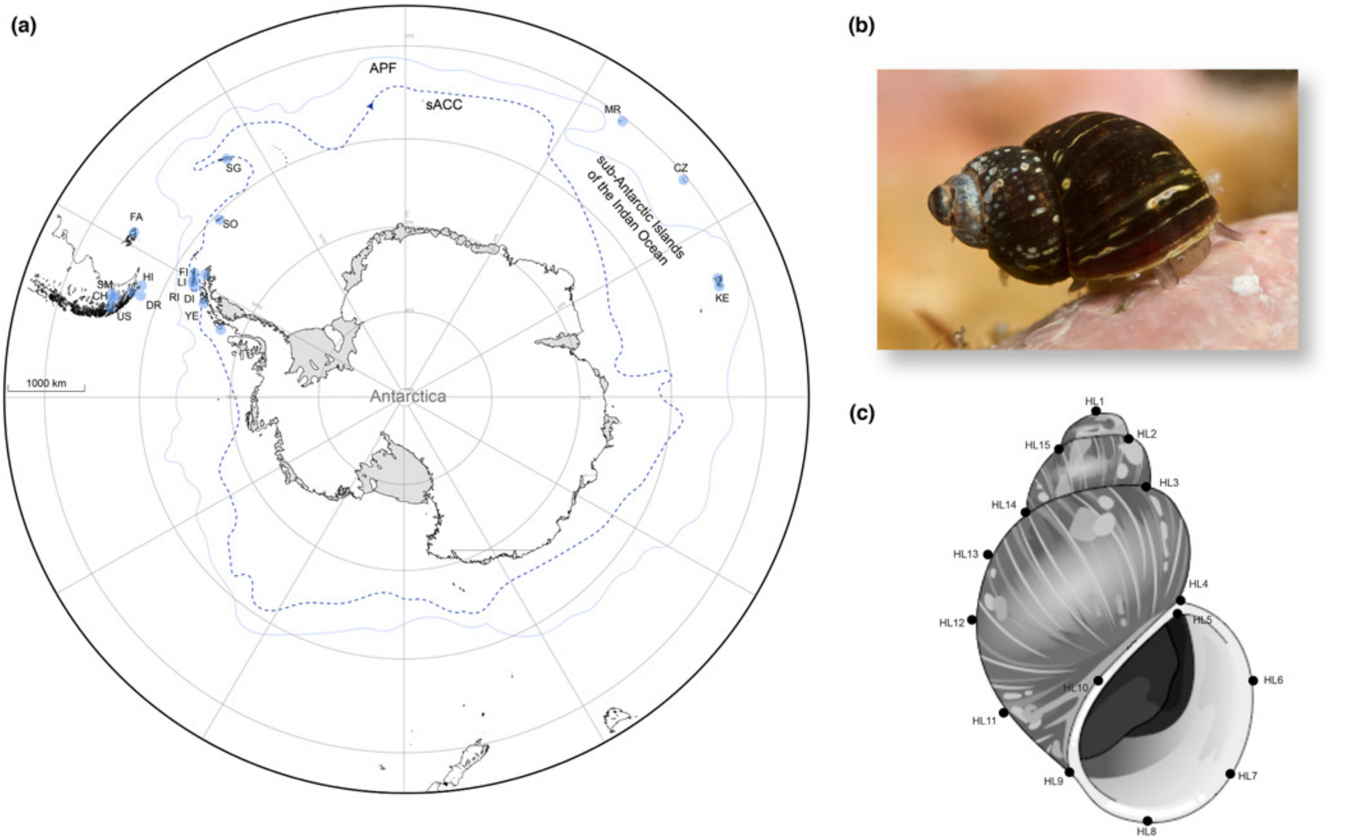


FIGURE 2 (a) Sampling of *Laevilitorina caliginosa* populations across its distribution in the Southern Ocean including populations from southern South America (SA), Antarctic Peninsula (AP) and sub-Antarctic islands of the Indian Ocean (sAIO). AV, Avian Island; CH, Cape Horn; CZ, Crozet Island; DI, Deception Island; DR, Diego Ramírez Island; FA, Falkland/Malvinas Islands; FI, Fildes Bay; HI, Hornos Island; KE, Kerguelen Islands; LI, Livingston Island; MR, Marion Island; RI, Robert Island; SG, South Georgia; SM, Strait of Magellan; SO, South Orkney Islands; YE, Doumer Island. APF and sACCF indicate the relative positions of the Antarctic Polar Front and the southern ACC Front, respectively. (b) Adult individual of *L. caliginosa* in its natural habitat in the Beagle Channel (photograph courtesy of Gonzalo Arriagada). (c) Ventral view of a shell of *L. caliginosa* showing the position of the 15 analysed landmarks (HL1 to HL15). The number of mtDNA/nucDNA *L. caliginosa*'s sequences per main area are SA ($n = 332/110$); AP ($n = 180/60$); SG ($n = 90/40$); MR ($n = 10/10$); CZ ($n = 50/20$); and KI ($n = 90/40$).

Crozet and Kerguelen) (Figure 2a; Table S1 and S2), as well as three endemic Antarctic-Peninsula nominal species (*L. antarctica*, *L. claviformis*, and *L. umbilicata*). Specimens were fixed in ethanol (95%) and taxonomic identification was based on the original descriptions and subsequent revisions (Engl, 2012; Gould, 1849; Preston, 1912, 1916; Reid, 1989; Smith, 1902; von Martens & von Pfeffer, 1886). Nucleic acids were prepared using a standard salting-out method (Aljanabi & Martinez, 1997) and the QIAGEN Dneasy Blood & Tissue Kit (QIAGEN Inc.). Universal primers were used to amplify a partial fragment of the mitochondrial cytochrome c oxidase subunit I (Folmer et al., 1994), and the nuclear rRNA 28S (Littlewood et al., 2000) genes. The nuclear fragment here analysed expands between the end of the ITS2 and D1 region and is suitable to infer phylogenetic relationships in littorinids (Reid et al., 2012). Forward and reverse sequences were assembled and edited independently using GENEIOUS 5.1.7 (Kearse et al., 2012). Alignments and base composition of nucleotide sequences were analysed separately in MUSCLE (Edgar, 2004) and MEGA X (Kumar et al., 2018), respectively. Mitochondrial codon usage was estimated using the effective number of codon value (ENC) (Wright, 1990) in DnaSP v.5 (Librado & Rozas, 2009). New *Laevilitorina* sequences have been deposited in GenBank under the following Accession Numbers: COI (MZ321820–MZ321864) and 28S rRNA (MZ322329–MZ322390 and MZ381414–MZ381445). Molecular information concerning the analysed specimens and museum material from the Western Australian Museum (WAM) is available in Table S1.

2.2 | Phylogenetic reconstructions

Mitochondrial (COI) and nuclear (28S rRNA) phylogenetic reconstructions included 5–10 individuals of *Laevilitorina caliginosa* per locality across the species distribution (Figure 2a), as well as at least 5 specimens of the Antarctic species. For comparative purposes, we also used 10 individuals of the Antarctic littorinid *Laevilacunaria antarctica*, a member of the sister genus. In addition, we included sequences of littorinid genera such as *Echinolittorina*, *Austrolittorina*, *Afrolittorina* and outgroups (*Lacuna pallidula* and *Bembicium auratum*) following Williams et al. (2003) and Reid et al. (2012). Phylogenetic relationships were estimated using maximum parsimony (MP), maximum likelihood (ML) and Bayesian analyses (BA). MP and ML analyses were performed in MEGA X, while BA were done using MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001). Nucleotide substitution models for ML and BA were estimated for each marker independently and for the concatenated dataset using, respectively, the Akaike information criterion (AIC) and the Bayesian information criterion (BIC) in JmodelTest v.2.1.10 (Darriba et al., 2012). The models TN93+I+ G|HKY+I+ G (COI), HKY+I+ G|T92+I+ G (28S rRNA) and GTR+I+ G (COI+28S rRNA) were selected as optimal for ML|BA analyses. Nodal supports for MP and ML analyses were inferred using non-parametric bootstrap (BS) with 1000 pseudo-replicates (Felsenstein, 1981). Bayesian-inference posterior probabilities (BPP) were estimated using the Metropolis coupled Markov-chain-Monte-Carlo algorithm (MCMC) running four chains for 100×10^6 generations and trees were sampled every 1000 generations. Stationarity of the analyses was inferred when the average standard deviation of split frequencies was less than 0.01 (Huelsenbeck & Ronquist, 2001). The initial 10% of the parameter values were discarded and posterior probabilities were estimated as the fraction of trees showing a particular node. Posterior-probability densities were summarized 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).

2.3 | Species-delimitation analyses and divergence-time estimations

Mitochondrial (COI) and nuclear (28S rRNA) species delimitation analyses in *Laevilitorina* were carried out independently using three different methods: the automatic barcoding gap discovery (ABGD) (Puillandre et al., 2012), the generalized mixed yule Coalescent (GMYC) (Pons et al., 2006) and the multi-rate Poisson Tree Processes (mPTP) (Zhang et al., 2013). Species-delimitation analyses using ABGD and mPTP were performed on their respective on the web-servers (http://www.abi.snv-jussieu.fr/public.abgd) and (https://species.h-its.org), respectively. The GMYC method (Ihaka & Gentleman, 1996) was performed in the R environment (R, version 2.4.1) using the package "splits" (Pons et al., 2006).

To estimate divergence times, a relaxed molecular-clock analysis was implemented for mtDNA sequences using an uncorrelated-lognormal (ucln) model of molecular evolutionary rate heterogeneity and the GTR+I+ G substitution model implemented in BEAST v.1.7.5 (Drummond et al., 2012; Drummond & Rambaut, 2007). A birth-death speciation prior was used to estimate branching rates in the phylogeny. Four chains were run twice for 200×10^6 generations and trees were sampled every 1000 generations. We used several calibration points previously estimated for the time of the most recent common ancestors (TMRCA) of the littorinid genera *Echinolittorina*, *Littorina*, *Littoraria*, *Austrolittorina*, *Afrolittorina* and *Tectarius* (Reid et al., 2012). The convergence of model parameters was estimated by plotting the marginal posterior probabilities versus the generations in Tracer (Rambaut et al., 2018). Effective sample-size values were estimated for each parameter to ensure the adequate mixing of the MCMC (ESSs >500).

2.4 | Geometric morphometric analyses

A total of 105 adult shells of *L. caliginosa* were photographed with a Leica EZ4W stereoscopic microscope. Shells were placed on a grid of 1 cm squares and stabilized using foam to standardize planar orientation. Shells were carefully oriented in ventral position with the aperture parallel to the grid facing the camera. Two lights were pointed at 45° angle above the shells and colour images were captured, measured and digitalized using the software Leica LAZ ES (Leica Microsystems). For comparative geometric morphometric analyses, specimens were grouped using a priori information based on molecular data and species-delimitation analyses.

Images were transformed into thin-plate splines (TPS) using tpsUtil (Rohlf, 2009) and landmarks were used to capture two-dimension Cartesian coordinates (*x*, *y*) in tpsDig 2.12 (Rohlf, 2009). Scaling was performed using tpsDig to correct for the size of the individual and to describe the shape of the object in terms of the spatial relationship between its parts rather than its dimensions. A total of 15 homologous landmark points (HL) (Figure 2c) were captured for each individual, which allowed us to decompose shell morphology under the criteria of homology, repeatability, coplanarity and shell-shape coverage following Bookstein (1991). Among the selected landmarks HL1–HL5, HL9 and HL12 – HL15 are Type I landmarks, representing direct juxtapositions of tissue types or probable homologies (Bookstein, 1991). Homologous landmark 1 (HL1) is the apex of the shell, whereas HL2–HL5 are upper and lower sutures of succeeding whorls. HL12, HL13 and HL15 are duplications of HL5, HL4 and HL2, respectively, on the left profile. The other landmarks were selected based on overall form of aperture and the last major whorl. Landmark coordinates for all specimens were analysed using MorphoJ v.1.06b (Klingenberg, 2011).

Landmarks were superimposed using Procrustes Fit, which maps the landmark configuration of each specimen in a dataset onto each other so that corresponding points are as close as possible. This process allows us to scale specimens to comparable sizes based on centroid size and minimizes the sum of squared distances between corresponding points (Rohlf, 1999). A principal component analysis (PCA) of shape was performed to determine the linear combination of variables that accounts for most of the variation in the data. The scores on the first two principal components were used in a canonical variate analysis (CVA) to discriminate among the analysed a priori groups. Finally, we estimated the percentage of correctly reassigned specimens through a discriminant function analysis (DFA) in MorphoJ.

Finally, to assess the relationship between molecular (uncorrected p-distances) and morphological (Procrustes distances) data in *Laevilitorina*, we performed a test of congruence among distance matrices (CADM) (Legendre & Lapointe, 2004). To do so, we used molecular and morphological distances with the CADM global function through the Kendall coefficient matrix concordance (W) implemented in the APE package (Paradis & Schliep, 2019). High and significant Kendall coefficients suggest a high concordance and therefore correlation between genetic and morphological matrices.

3 | RESULTS

3.1 | DNA polymorphism

The cytochrome c oxidase subunit I data set consisted of 250 individuals and 620 nucleotide positions coding for 206 amino acids. No insertions/deletions (indels) or stop codons were detected among the analysed individuals. A total of 253 variable positions (40.8%) were found in the COI data set and 239 of them were parsimoniously informative (94.4%). Mitochondrial sequences were A–T rich (62%). The final alignment of the nuclear gene 28S rRNA included 150 individuals and a fragment of 721 nucleotide positions. A total of 162 positions (22.4%) were variable in the 28S rRNA data set and 149 of them (91.9%) were parsimoniously informative. Nuclear sequences were G–C rich (54.5%). Mitochondrial and nuclear sequences were not saturated and we found no evidence for mtDNA codon bias (ENC = 39.28).

3.2 | Phylogenetic reconstructions

Multi-locus phylogenetic reconstructions using different methods clearly discriminated major taxonomic littorinid groupings, notably a monophyletic *Laevilitorina*, with high bootstrap and posterior probabilities (Figure 3). Within *Laevilitorina*, no topological inconsistencies were found between mtDNA and nucDNA reconstructions (Figure S1 and S2). Nevertheless, phylogenetic relationships within the genus were unexpected as none of the nominal species were monophyletic. On the one hand, all the methods and molecular markers distinguished seven species-level clades (=lineages) within the nominal *L. caliginosa* (Figure 3), with levels of mtDNA genetic divergence (uncorrected p-distances) between 21.4% and 3.0% (Table S3). On the other hand, phylogenetic reconstructions failed to distinguish the Antarctic nominal species *L. antarctica*, *L. umbilicata* and *L. claviformis* (Figure 3), and they shared haplotypes and alleles. Moreover, this Antarctic clade (*L. antarctica*/*L. claviformis*/*L. umbilicata*) falls within the "*caliginosa*" lineages, rendering the latter paraphyletic (Figure 3). Accordingly, the diversity in *L. caliginosa* fell into two non-sister clades with high levels of divergence (average > 15%) between them (Figure 3). The first group included (Figure 3 red clade) four lineages, three sympatric and, indeed, syntopic, from the Strait of Magellan, southern South America (L1–L3), and one from the Antarctic Peninsula and geographically distant sub-Antarctic islands of South Georgia, Marion, Crozet and Kerguelen (L4). The second group (Figure 3 blue clade) comprised three lineages (L5–L7) found across the southern tip of South America, the Falkland/Malvinas Islands and South Georgia. Lineage 5 (L5) was collected from the Beagle Channel, Cape Horn, the Falkland/Malvinas Islands and in South Georgia. Lineage 6 (L6) was limited to Hornos Island, Cape Horn and lineage 7 (L7) was restricted to the Falkland/Malvinas Islands.

3.3 | Species-delimitation analyses and divergence-time estimations

Mitochondrial (COI) and nuclear (28S rRNA) species delimitation analyses using ABGD, mPTP and GMYC corroborated phylogenetic reconstructions, and all recovered a total of eight *Laevilitorina* species. Seven of them were found within a nominal *L. caliginosa*; the eighth included the three Antarctic nominal species *L. antarctica*, *L. umbilicata*, and *L. claviformis* (Figure 3).

Mitochondrial divergence-time estimates are in basic agreement with previous studies of littorinids (Figure S3) (Reid et al., 2012; Williams et al., 2003). Estimates within *Laevilitorina* suggest that the TMRCA of the subfamily Laevilitorininae, (*Laevilitorina* + *Laevilacunaria*) occurred ~56 Ma, whereas the origin of the analysed lineages of *Laevilitorina* was ~38 Ma (HPD 45–34 Ma) (Figure 4). Subsequently, the separation between the ancestor of *L. antarctica*/*L.claviformis*/*L. umbilicata* and lineages L1–L4 took place during the Miocene ~20 Ma (27–16 Ma) (Figure 4). The separation between Strait of Magellan (L1–L3) and Antarctic Peninsula + sub-Antarctic islands (L4) lineages occurred ~12 Ma (16–8 Ma). *Laevilitorina* diversified in Cape Horn (L5/L7 from L6) and in the Strait of Magellan (L1 from L2/L3) during the Miocene between 16 Ma (21–12 Ma) and 7 Ma (10–5 Ma), respectively (Figure 4). Finally, *Laevilitorina* diversified in the Strait of Magellan (separation of L2 and L3) and Cape Horn (separation of L5 and L7) during the Pliocene ~3 Ma (5–2 Ma) (Figure 4).

3.4 | Geometric morphometrics

Principal components 1–3 (PC1–PC3) combined explained 70.4% of the total morphological variation of shells. The PCA showed some degree of separation amongst the seven analysed groups. HL3, HL6 and HL7 were the most distinct landmarks but there were significant overlaps amongst others (HL1, HL2, HL4 and HL5). PC1 was associated with variability in landmarks located on the apex and the sutures between major whorls on right and left profiles (HL1–HL4, HL14, HL15). PC2 was associated with variability in landmarks located at the junction between the end of suture and the aperture lip and the most external point on right profile of the last whorl (HL5, HL6, HL8, HL12 and HL13). PC3 was associated with landmark variability on the right profile of the last whorl and the aperture (HL6–HL9). Negative and positive values in PC1–PC2 (x-axis) were associated with rounded and elongated specimens, while negative and positive values in PC3 (x-axis) described narrower and broader individuals, respectively.

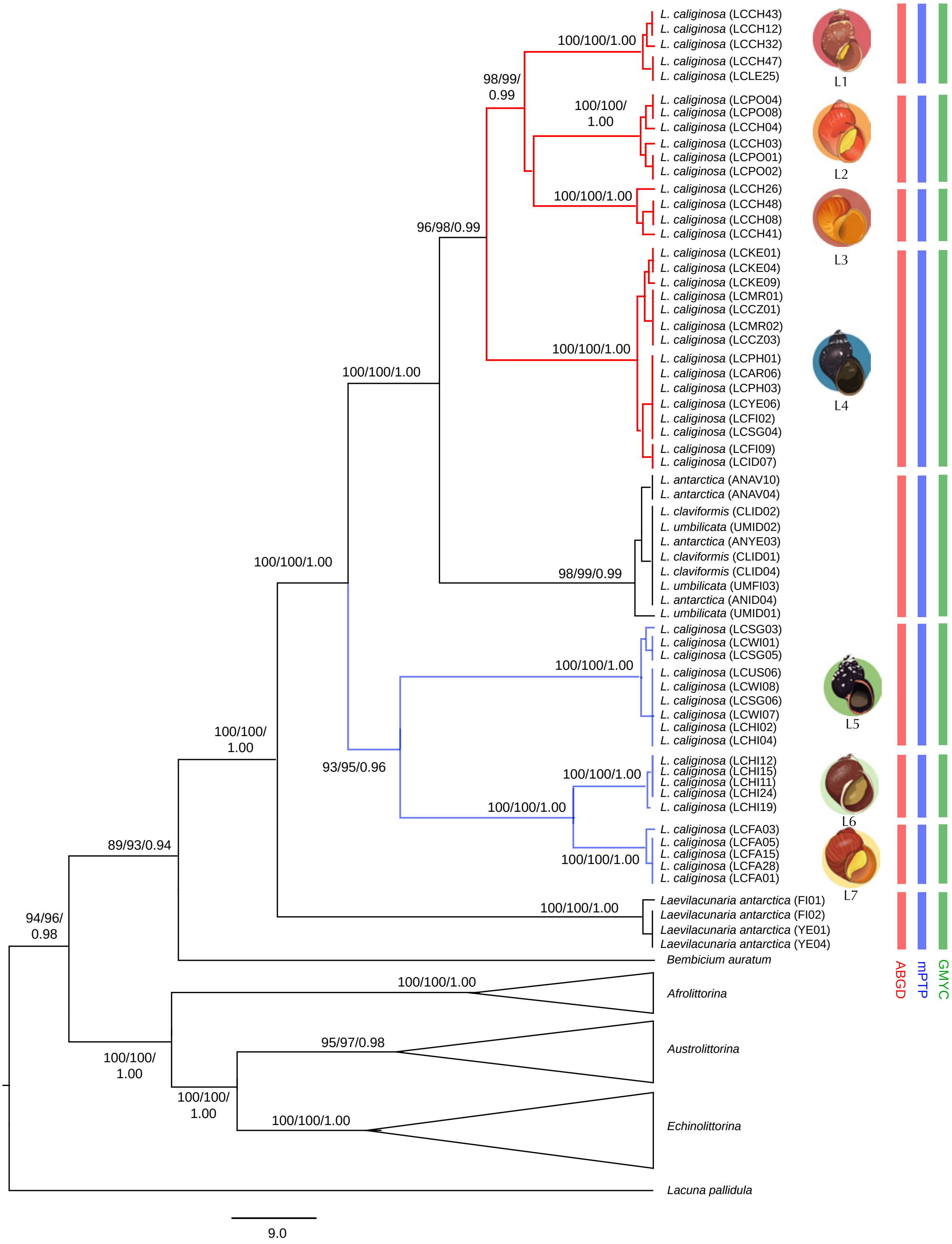


FIGURE 3 Bayesian maximum clade credibility tree of Littorinidae relationships based on multi-locus data with special emphasis on Laevilitorininae (*Laevilitorina* & *Laevilacunaria*) populations collected from around the Southern Ocean. The lineages (L1–L7) recorded within the nominal species *L. caliginosa* are showed. Red and blue rectangles indicate the paraphyletic groups of *Laevilitorina* lineages found within *L. caliginosa*. Bootstrap support (BS) values (MP and ML) and Bayesian posterior probabilities (BPP) are shown above the nodes (in that order).

The CVA based on the first two PCs accounted for 80.9% of the total variance and separated the groups in a similar way to the molecular results, showing marked morphological differences in four of the analysed lineages: L2, L3, L6 and L7 (Figure 5). In contrast, L1, L4 and L5 exhibited some degree of morphological similarity (Figure 5). Nevertheless, permutation tests based on Procrustes distances revealed that all the analysed lineages exhibited significant differences based on their morphological characteristics (Table S4). The DFA based on Procrustes distances established that most of the groups showed high percentage of correct allocation (>89%). Finally, Kendall coefficients of concordance (W) between genetic and morphological distance matrices showed a low and non-significant value ($W = 0.48$; $\chi^2 = 19.11$; $p = 0.52$) suggesting incongruence between genetic and morphological variation among the seven "*caliginosa*" lineages.

4 | DISCUSSION

In this study, we provide robust, yet unexpected, evidence about the biogeography of the marine snail genus *Laevilitorina* around the Southern Ocean. Through genetic and morphological data, we show that the species-level diversity in the genus has been both underestimated in southern South America and overestimated in the Antarctic Peninsula. As previously demonstrated in different groups of near-shore marine organisms including invertebrates, vertebrates and macroalgae, *Laevilitorina* includes different lineages that have been separated by the APF, probably since the separation of the continental landmasses where they are currently distributed. However, one "*caliginosa*" lineage showed a broad trans-APF distribution with populations across the Antarctic Peninsula and geographically distant sub-Antarctic islands. Biogeographical patterns in *Laevilitorina* require new evolutionary explanations, involving the combined role of historical vicariance and recent dispersal, illustrating some wider principles concerning Southern-Ocean biogeography.

The nominal taxon *L. caliginosa* has previously been considered one of the few poorly dispersing species exhibiting a wide circumpolar distribution across the APF. We show that, in fact, it comprises a suite of at least seven lineages, whose levels of genetic divergence clearly indicate species-level status, which is congruent with morphological differentiation in the group. However, CADM analysis showed no relationship between molecular and morphological distances suggesting that morphologic differentiation was uncoupled from species diversification in *Laevilitorina*.

Six of these heretofore unrecognized species have much narrower distributions in and around southern South America, three (L1–L3) in the Strait of Magellan, the remainder (L5–L7) in southern areas of Cape Horn, the Falkland/Malvinas Islands and South Georgia. The broadest distribution is exhibited by the seventh species (L4), which includes populations across the Antarctic Peninsula, South Georgia and geographically distant sub-Antarctic islands of the Indian Ocean (Marion, Crozet and Kerguelen) (Figure 6). Significantly, this range crosses the APF; thus, this *Laevilitorina* lineage (L4) represents the first confirmed example of a near-shore marine benthic invertebrate species found in both Antarctic and geographically distant sub-Antarctic ecosystems.

In contrast to the diversity recorded in southern South America, we show that the nominal species occurring on the Antarctic Peninsula, *L. antarctica*, *L. claviformis* and *L. umbilicata* are genetically indistinguishable, and should probably be considered as a single species. Moreover, phylogenetic reconstructions indicated that this species is nested within the "*caliginosa*" complex.

Geometric morphometric analyses showed that the genetically delineated *Laevilitorina* species exhibit significant morphological differences. Thus, unlike many radiations in the Southern Ocean including nudibranchs (Wilson et al., 2009), bivalves (González-Wevar et al., 2019), octopuses (Allcock et al., 2011), nemerteans (Thornhill et al., 2008), amphipods (Baird et al., 2011), pycnogonids (Arango et al., 2011), and echinoderms (Janosik & Halanych, 2010), *Laevilitorina* is not strictly a cryptic-species complex as speciation

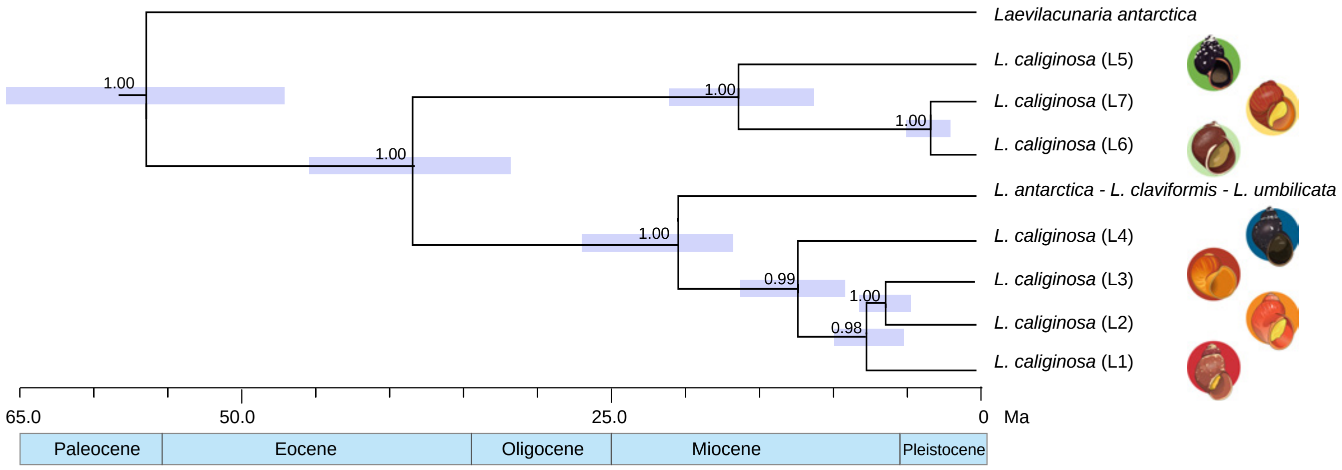


FIGURE 4 Divergence time estimations of Laevilitorininae (*Laevilitorina* + *Laevilacunaria*) based on mtDNA sequences using estimated calibrations by Reid et al. (2012). BPP values are indicated at nodes and shaded bars indicate 95% highest posterior density (HPD) intervals.

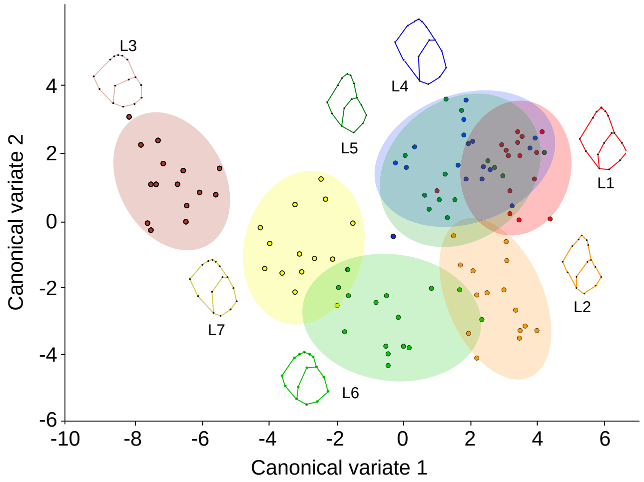


FIGURE 5 Canonical variate analyses based on the principal components (PC1 and PC2) of the morphological variation recorded among the lineages (L1–L7) within *L. caliginosa*. 90% mean confidence ellipses are illustrated for each group in matching coloration with the wireframe representations of the average ventral shape variation of each lineage.

has proceeded through molecular differentiation occurring in conjunction with morphological changes.

4.1 | Biogeographic implications

The findings of this study adumbrated above are noteworthy because it gives new and valuable information about actual diversity patterns, evolutionary relationships and the biogeography of nearshore marine benthic invertebrates across its distribution in the Southern Ocean. For instance, before this study, *Laevilitorina* appeared to be a poorly represented genus in South America, with the presence of a single mainland species, *L. caliginosa*, and a second, *L. latior*, restricted to the Falkland/Malvinas Islands. However, through this integrative study we demonstrate that South America represents a species-rich province where this genus diversified over the last 20 Ma (Figure 6). Most of the new diversity in *Laevilitorina* was found in the Strait of Magellan and in Cape Horn, as well as the Antarctic Peninsula, areas that have experienced geological events critical to the understanding of Southern-Ocean biogeography, such as the opening of the Drake Passage and the establishment of the ACC. In addition, during the last 50 years, southern South America and the Antarctic Peninsula have undergone one of the fastest responses anywhere to climate change (Meredith & King, 2005). Several authors (Cavanagh et al., 2021; Morley et al., 2020) have noted the relevance to understand and predict the consequences of global warming in this region, most notably local extinctions, and biological invasions.

During the last decade, several sub-Antarctic marine species have been reported in the Antarctic nearshore, demonstrating the existence of dispersal across the APF (Aronson et al., 2014; Avila et al., 2020; Cárdenas et al., 2020; Fraser et al., 2018). In short ecological timescales, several natural dispersal processes including airborne, oceanic eddy, rafting and hitchhiking on floating objects may allow the passage to and from Antarctica (Barnes et al., 2006). However, to date, exotic species recorded in Antarctica have failed to establish as permanent populations, probably due to physiological constraints (Fraser et al., 2018; López-Farrán et al., 2021).

The distribution of lineage 4 (L4) is then remarkable, both for its wide geographical extent and because it crosses the APF. These two aspects imply that this lineage is a good long-distance disperser, although why it should be so when its congeners are apparently poor at dispersing is unclear. It is possible that this species is more closely associated with LDD rafting vehicles such as *Durvillaea antarctica*. Future studies of the ecology of the various *Laevilitorina* lineages will be necessary to shed light on this puzzle. Despite these interesting results, the level of resolution of the analysed markers do not allow an accurate estimate of the occurrence, date, and directionality of dispersal events. Future genomic-based analyses including Antarctic lineage 4 (L4) and sub-Antarctic populations will help us understand these major biogeographical issues.

South Georgia is biogeographically interesting for *Laevilitorina* because of the presence of both Antarctic (L4) and sub-Antarctic (L5) lineages. This overlap is surprising, since the coastal gastropods of South Georgia generally have a greater affinity with those from the Weddell Sea sector rather than with South American ones (Zelaya, 2005). In fact, South Georgia represents the northernmost limit of many Antarctic molluscs (e.g., *Nacella concinna*) and, in some exceptional cases, the southernmost limit for several sub-Antarctic ones (e.g., *Siphonaria lateralis*). Nevertheless, we are not aware of any examples, confirmed through molecular analysis, of congeneric near-shore sub-Antarctic and Antarctic molluscan species that co-occur in South Georgia. Thus, *Laevilitorina* may represent the first case of an intertidal gastropod genus in South Georgia, with sympatric—indeed syntopic—South American and Antarctic lineages.

4.2 | Evolutionary diversification of *Laevilitorina* in the Southern Ocean

Our results suggest that the TMRCA of *Laevilitorina* was ~38 Ma (HPD interval 45–34 Ma), close to the Eocene/Oligocene boundary, a period of major change in the Southern Ocean involving the commencement of Antarctic isolation through the opening of major gateways (e.g., the Drake Passage) and the onset of the ACC (Scher et al., 2015; Zachos et al., 2001). Accordingly, the origin of the analysed lineages seems to be deeply connected to ancient vicariant processes driven by continental drift and the initiation of the ACC, as recently suggested for the microbivalve genus *Kidderia* (Levicoy et al., 2021). Subsequently, during the early Miocene, between 20 and 12 Ma, *Laevilitorina* diverged independently in Antarctica and South America, resulting in the ancestors of the eight lineages here found. These radiations were probably associated with the middle Miocene Climatic Transition, a period of drastic climatic shifts marked by the intensification of the ACC and the reestablishment of permanent continental Ice Sheets in East (10 Ma) and West

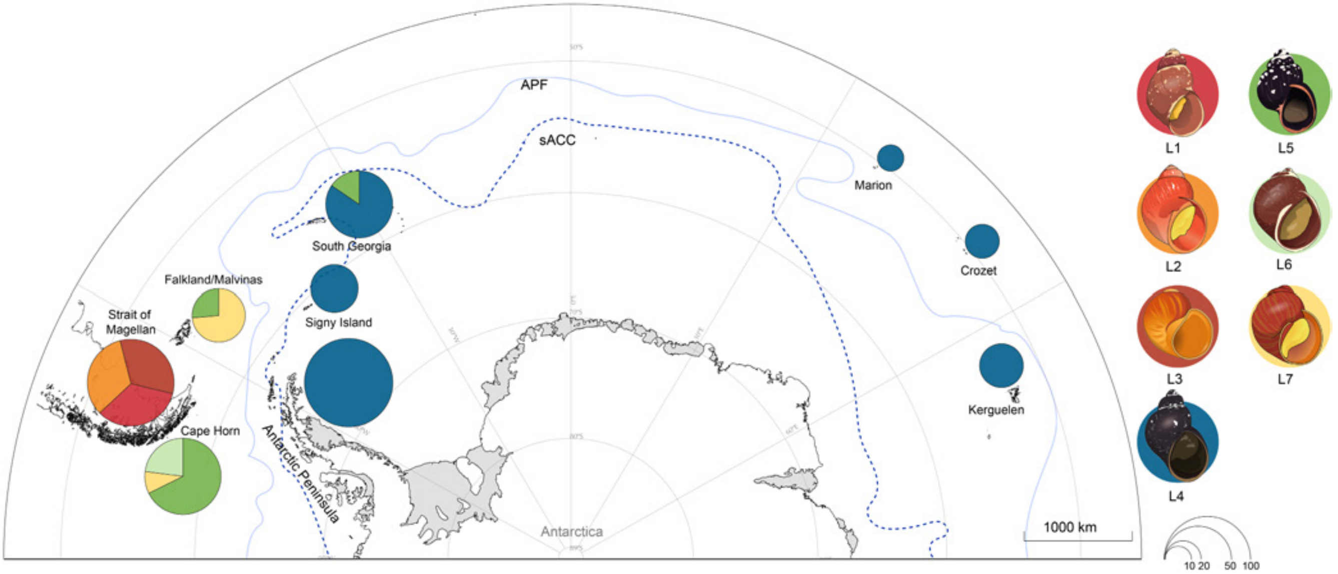


FIGURE 6 Distribution of the recorded lineages (L1–L7) within *L. caliginosa* around the Southern Ocean. Coloured circles show the frequencies and sample sizes. The approximate position of the APF and the sACC are marked with a solid blue and a dashed light blue line, respectively.

(5 Ma) Antarctica (Lewis et al., 2009; Verducci et al., 2009; Zachos et al., 2001). Major oceanographic changes during this period were likely related to the full achievement of a deep ACC ~12 Ma (Dalziel et al., 2013). Fluctuations in the latitudinal position and the strengthening of the ACC seem to be important drivers in the evolution of the Southern Ocean biota (Chenuil et al., 2018; Crame, 2018; González-Wevar et al., 2017, 2019; Halanych & Mahon, 2018; Poulin et al., 2014). The establishment of a strong and deep ACC may have generated an effective oceanographic barrier maintaining the separation of *Laevilitorina* lineages from Antarctica and South America.

More recently, *Laevilitorina* diversified in South America between the middle Miocene and the Pliocene, 16–3 Ma. Similar radiations have been identified in several groups of marine invertebrates during this period across the Southern Ocean including octopods (Strugnell et al., 2008), octocorals (Dueñas et al., 2016), bivalves (González-Wevar et al., 2019), patellogastropods (González-Wevar et al., 2017), trochoid gastropods (González-Wevar et al., 2021) and fishes (Near et al., 2012). Finally, the latest diversification of *Laevilitorina* in South America was probably driven by glacial processes of the Quaternary. Recurrent ice advances and retreats may have enhanced geographical isolation and speciation as inferred for several other South American marine organisms (Fraser et al., 2012; González-Wevar et al., 2011, 2017, 2019; Schächinger et al., 2022). A plausible scenario of this Quaternary diversification in *Laevilitorina* involves small refugial populations of these poorly dispersing snails undergoing substantial genetic drift. Such drift-dominated process is less likely to lead to adaptive morphological differentiation, which would explain our belated recognition of the separate species of *Laevilitorina*. Such pseudocryptic speciation has recently been inferred for the nudibranch genus *Tritoniella*, another poor disperser from the Antarctic and sub-Antarctic, which also separates species either side of the APF (Schächinger et al., 2022).

4.3 | Systematics of *Laevilitorina*

The detailed systematic consequences of our work will be dealt with elsewhere. Nevertheless, it is useful to give here some brief pointers and sound a note of caution. The original description of *L. caliginosa* used specimens collected from Orange Bay, Tierra del Fuego, and included only external morphological characteristics: a dark/brown/green shell coloration, an eroded first whorl and an aperture diameter occupying less than 50% of the total shell length (Gould, 1849). Morphological and coloration patterns found in L5 correspond to this description and specimens were collected from Navarino Island, Puerto Williams and Ushuaia Bay close to the type locality. Accordingly, L5 seems to represent the true *L. caliginosa* and, consequently, it seems that this species is restricted to the southern tip of South America, the Falkland/Malvinas Islands and South Georgia. We note that much of the biological and ecological information on what is purported to be *L. caliginosa* is based on Macquarie Island records (e.g., Reid, 1989; Simpson & Harrington, 1985), but the presence of L5 at Macquarie Island would require confirmation.

The morphological characteristics of *L. latior* (Preston, 1912) correspond well to those of found in L7. Moreover, L7 specimens were collected from very near the type locality of *L. latior*, Port Stanley, in the Falkland/Malvinas Islands (Preston, 1912). This evidence suggest that L7 is in fact *L. latior* and endemic to the Falkland/Malvinas Islands where it coexists with L5 (*L. caliginosa*).

Although the nominal Antarctic species *L. antarctica*, *L. claviformis* and *L. umbilicata* are similar in size and shape (Engl, 2012; personal observations), shells of *L. umbilicata* uniquely exhibit a profound suture and there is significant variation in colour. Thus, before formally synonymizing these taxa it will be necessary to collect and analyse more populations of *L. umbilicata* and *L. antarctica*, especially those from their respectively type localities of South Georgia and East Antarctica.

ACKNOWLEDGEMENTS

This study was funded ANID – Millennium Science Initiative Program – ICN2021_002, FONDAP IDEAL (15150003), GAB PIA CONICYT ACT172065, INACH Project RG_18-17, Program PR-06-CRN-18, ANID/BASAL FB210018, PIA CONICYT AFB170008 (IEB), Fondecyt Postdoctoral 3210063 and Fondecyt Regular Project 1210787. Many thanks to Angie Díaz, Karin Gérard, Andreas Schmider, Yarleth Poveda, for field assistance and samplings in southern South America and the Antarctic Peninsula. Many thanks to the Antarctic Circumnavigation Expedition (carried out by the Swiss Polar Institute, supported by the ACE Foundation and Ferring Pharmaceuticals). Alex Hickling, Javier Naretto and Rebecca Cumming are thanked for their field assistance while Lisa Kirkendale and Corey Whisson are thanked for their assistance with loans from the Western Australian Museum (WAM).

South American specimens were captured under the Chilean legislation (Technical Memorandum P.INV N° 258/ 2021 SUBPESCA). Field access facilities to Crozet and Kerguelen Islands were supported by the French Polar Institute-IPEV (program n°1044-Proteker) and the LTSER Zone Atelier Antarctique et Subantarctique (ZATA), France. We are grateful to the support of the South Atlantic Environmental Research Institute and the Shallow Marine Surveys Group of the collection of Laevilitorina samples in the Falkland Islands. Field access facilities to South Georgia was supported by the British Antarctic Survey (BAS) and the collected specimens were authorized under the permit number 2017/058 to C.S.M. BAS is supported by core funds from UKRI-NERC to the BEA Team.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

New COI and 28S rRNA sequences in *Laevilitorina* have been deposited in GenBank under the following accession numbers: MZ321820–MZ321864 (COI), MZ322329–MZ322390 and MZ381414–MZ381445 (28S rRNA).

ORCID

Claudio A. González-Wevar https://orcid.org/0000-0003-0807-8032
Nicolás I. Segovia https://orcid.org/0000-0003-3212-7527
Sebastián Rosenfeld https://orcid.org/0000-0002-4363-8018
Claudia S. Maturana https://orcid.org/0000-0002-4427-8093
Ramona Pinochet https://orcid.org/0000-0002-2991-2834
Thomas Saucède https://orcid.org/0000-0001-6056-4447
Simon A. Morley https://orcid.org/0000-0002-7761-660X
Paul Brickle https://orcid.org/0000-0002-9870-3518
Nerida G. Wilson https://orcid.org/0000-0002-0784-0200
Hamish G. Spencer https://orcid.org/0000-0001-7531-597X
Elie Poulin https://orcid.org/0000-0001-7736-0969

REFERENCES

Aljanabi, S. M., & Martinez, I. (1997). Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Research*, *25*(22), 4692–4693. https://doi.org/10.1093/nar/25.22.4692

Allcock, A. L., Barratt, I., Eléaume, M., Linse, K., Norman, M. D., Smith, P. J., Steinke, D., Stevens, D. W., & Strugnell, J. M. (2011). Cryptic speciation and the circumpolarity debate: A case study on endemic Southern Ocean octopuses using the COI barcode of life. *Deep-Sea Research Part II*, *58*(1–2), 242–249. https://doi.org/10.1016/j.dsr2.2010.05.016

Arango, C. P., Soler-Membrives, A., & Miller, K. J. (2011). Genetic differentiation in the circum-Antarctic sea spider *Nymphon australe* (Pycnogonida; Nymphonidae). *Deep-Sea Research Part II*, *58*(1–2), 212–219.

Aronson, R. B., Frederich, M., Price, R., & Thatje, S. (2014). Prospects for the return of shell-crushing crabs to Antarctica. *Journal of Biogeography*, *42*, 1–7. https://doi.org/10.1111/jbi.12414

Aronson, R. B., Thatje, S., Clarke, A., Peck, L. S., Blake, D. B., Wilga, C. D., & Seibel, B. A. (2007). Climate change and invasibility of the Antarctic benthos. *Annual Review of Ecology, Evolution, and Systematics*, *38*, 129–154. https://doi.org/10.1146/annurev.ecolsys.38.091206.095525

Avila, C., Angulo-Preckler, C., Martín-Martín, R. P., Figuerola, B., Griffiths, H. J., & Waller, C. L. (2020). Invasive marine species discovered on non-native kelp rafts in the warmest Antarctic Island. *Scientific Reports*, *10*, 1639. https://doi.org/10.1038/s41598-020-58561-y

Baird, H. P., Miller, K., & Stark, J. S. (2011). Evidence of hidden biodiversity, ongoing speciation and diverse patterns of genetic structure in giant Antarctic amphipods. *Molecular Ecology*, *20*(16), 3439–3454. https://doi.org/10.1111/j.1365-294X.2011.05173.x

Barnes, D. K. A., Hodgson, D. A., Convey, P., Allen, C. S., & Clarke, A. (2006). Incursion and excursion of Antarctic biota: Past, present and future. *Global Ecology and Biogeography*, *15*(2), 121–142. https://doi.org/10.1111/j.1466-822X.2006.00216.x

Billard, E., Reyes, J., Mansilla, A., Faugeron, S., & Guillemin, M.-L. (2015). Deep genetic divergence between austral populations of the red alga *Gigartina skottsbergii* reveals a cryptic species endemic to the Antarctic continent. *Polar Biology*, *38*, 2021–2034. https://doi.org/10.1007/s00300-015-1762-4

Bookstein, F. L. (1991). *Morphometric tools for landmark data: Geometry and biology*. Cambridge University Press.

Cárdenas, L., Leclerc, J.-C., Bruning, P., Garrido, I., Détrée, C., Figueroa, A., Astorga, M., Navarro, J. M., Johnson, L. E., Carlton, J. T., & Pardo, L. (2020). First mussel settlement observed in Antarctica reveals the potential for future invasions. *Scientific Reports*, *10*, 5552. https://doi.org/10.1038/s41598-020-62340-0

Cavanagh, R. D., Melbourne-Thomas, J., Grant, S. M., Barnes, D. K. A., Hughes, K. A., Halfer, S., Meredith, M. P., Murphy, E. J., Trebilco, R., & Hill, S. L. (2021). Future risk for Southern Ocean ecosystem services under climate change. *Frontiers in Marina Science*, *7*, 615214. https://doi.org/10.3389/fmars.2020.615214

Chenuil, A., Saucède, T., Hemery, L. G., Eléaume, M., Féral, J.-P., Améziane, N., David, B., Lecointre, G., & Havermans, C. (2018). Understanding processes at the origin of species flocks with a focus on the marine Antarctic fauna. *Biological Reviews*, *93*(1), 481–504. https://doi.org/10.1111/brv.12354

Clarke, A., Barnes, D. K. A., & Hodgson, D. A. (2005). How isolated is Antarctica? *Trends in Ecology & Evolution*, *20*(1), 1–3. https://doi.org/10.1016/j.tree.2004.10.004

Crame, J. (2018). Key stages in the evolution of the Antarctic marine fauna. *Journal of Biogeography*, *45*(5), 986–994. https://doi.org/10.1111/jbi.13208

Dalziel, I. W. D., Lawver, L. A., Pearce, J. A., Barker, P.F., Hastie, A. R., Barfod, D. N., Schenke, H–W., & Davis, M. B. (2013). A potential barrier to deep Antarctic circumpolar flow until the late Miocene? *Geology*, *41*(9), 947–950. https://doi.org/10.1130/G34352.1

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods*, *9*, 772. https://doi.org/10.1038/nmeth.2109

Díaz, A., Gérard, K., González-Wevar, C., Maturana, C., Féral, J.-P., David, B., Saucéde, T., & Poulin, E. (2018). Genetic structure and demographic inference of the regular sea urchin *Sterechinus neumayeri* (Meissner, 1900) in the Southern Ocean: The role of the last glaciation. *PLoS One*, *13*, e0197611. https://doi.org/10.1371/journal.pone.0197611

Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian Evolutionary Analysis by Sampling Trees. *BMC Evolutionary Biology*, *7*, 214. https://doi.org/10.1186/1471-2148-7-214

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian Phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*(8), 1969–1973. https://doi.org/10.1093/molbev/mss075

Dueñas, L. F., Tracey, D. M., Crawford, A. J., Wilke, T., Alderslade, P., & Sánchez, J. A. (2016). The Antarctic Circumpolar Current as a diversification trigger for deep-sea octocorals. *BMC Evolutionary Biology*, *16*, 2. https://doi.org/10.1186/s12862-015-0574-z

Dufour, C. O., Griffies, S. M., de Souza, G. F., Frenger, I., Morrison, A. K., Palter, J. B., Sarmiento, J. L., Galbraith, E. D., Dunne, J. P., Anderson, W. G., & Slater, R. D. (2015). Role of mesoscale eddies in cross-frontal transport of heat and biogeochemical tracers in the Southern Ocean. *Journal of Physical Oceanography*, *45*(12), 3057–3081. https://doi.org/10.1175/JPO-D-14-0240.1

Edgar, R. C. (2004). MUSCLE: A multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics*, *5*, 113. https://doi.org/10.1186/1471-2105-5-113

Engl, W. (2012). *Shells of Antarctica*. ConchBooks publishing.

Felsenstein, J. (1981). Evolutionary trees from DNA sequences: A maximum likelihood approach. *Journal of Molecular Evolution*, *17*, 368–376. https://doi.org/10.1007/BF01734359

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, *3*(5), 294–299.

Fraser, C. I., Morrison, A. K., Hogg, A., Macaya, E. C., van Sebille, E., Ryan, P. G., Padovan, A., Jack, C., Valdivia, N., & Waters, J. M. (2018). Antarctica's ecological isolation will be broken by storm-driven dispersal and warming. *Nature Climate Change*, *8*, 704–708. https://doi.org/10.1038/s41558-018-0209-7

Fraser, C. I., Nikula, R., Ruzzante, D. E., & Waters, J. M. (2012). Poleward bound: Biological impacts of Southern Hemisphere glaciation. *Trends in Ecology & Evolution*, *27*(8), 462–471. https://doi.org/10.1016/j.tree.2012.04.011

Fraser, C. I., Nikula, R., Spencer, H. G., & Waters, J. M. (2009). Kelp genes reveal effects of subantarctic sea during the Last Glacial Maximum. *Proceedings of the National Academy of Science, USA*, *106*(9), 3249–3253. https://doi.org/10.1073/pnas.0810635106

Frugone, M. J., López, M. E., Segovia, N. I., Cole, T. L., Lowther, A., Pistorius, P., Dantas, G. P. M., Petry, M. V., Bonadona, F., Steinfurth, A., Polanowski, A., Raya Rey, A., Lois, N. A., Pütz, K., Trathan, P., Wiencke, B., Poulin, E., & Vianna, J. A. (2019). More than the eye can see: Genomic insights into the drivers of genetic differentiation in Royal/Macaroni penguins across the Southern Ocean. *Molecular Phylogenetics and Evolution*, *139*, 106563. https://doi.org/10.1016/j.ympev.2019.106563

Gille, S. T. (2014). Meridional displacement of the Antarctic Circumpolar Current. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *372*(2019), 20130273–20130212. https://doi.org/10.1098/rsta.2013.0273

González-Wevar, C. A., Gérard, K., Rosenfeld, S., Saucède, T., Naretto, J., Díaz, A., Morley, S. A., Brickle, P., & Poulin, E. (2019). Cryptic speciation in Southern Ocean *Aequiyoldia eightsii* (Jay, 1839)_ Mio-Pliocene trans-Drake Passage separation and diversification. *Progress in Oceanography*, *174*, 44–54. https://doi.org/10.1016/j.pocean.2018.09.004

González-Wevar, C. A., Hüne, M., Segovia, N. I., Nakano, T., Spencer, H. G., Chown, S. L., Saucède, T., Johnstone, G., Mansilla, A., & Poulin, E. (2017). Following the Antarctic Circumpolar Current: Patterns and processes in the biogeography of the limpet *Nacella* (Mollusca: Patellogastropoda) across the Southern Ocean. *Journal of Biogeography*, *44*(4), 861–874. https://doi.org/10.1111/jbi.12908

González-Wevar, C. A., Nakano, T., Cañete, J. I., & Poulin, E. (2011). Concerted genetic, morphological and ecological diversification in *Nacella* limpets in the Magellanic Province. *Molecular Ecology*, *20*(9), 1936–1951. https://doi.org/10.1111/j.1365-294X.2011.05065.x

González-Wevar, C. A., Segovia, N. I., Rosenfeld, S., Noll, D., Maturana, C. S., Hüne, M., Naretto, J., Gérard, K., Díaz, A., Spencer, H. G., Saucède, T., Féral, J.-P., Morley, S. A., Brickle, P., Wilson, N. G., & Poulin, E. (2021). Contrasting biogeographical patterns in *Margarella* (Gastropoda: Calliostomatidae: Margarellinae) across the Antarctic Polar Front. *Molecular Phylogenetics and Evolution*, *156*, 107039. https://doi.org/10.1016/j.ympev.2020.107039

González-Wevar, C. A., Díaz, A., Gerard, K., Cañete, J. I., & Poulin, E. (2012). Divergence time estimations and contrasting patterns of genetic diversity between Antarctic and southern South America benthic invertebrates. *Revista Chilena de Historia Natural*, *85*, 445–456.

González-Wevar, C. A., Segovia, N. I., Rosenfeld, S., Ojeda, J., Hüne, M., Naretto, J., Saucède, T., Brickle, P., Morley, S., & Poulin, E. (2018). Unexpected absence of Island endemics: Long-distance dispersal in higher latitude sub-Antarctic *Siphonaria* (Gastropoda: Euthyneura) species. *Journal of Biogeography*, *45*(4), 874–884. https://doi.org/10.1111/jbi.1317

Gould, A. A. (1849). Descriptions of new species of shells, brought home by the U.S. Exploring Expedition. In *Proceedings of the Boston Society of Natural History* (pp. 3, 118–121). Cambridge.

Griffiths, H. J., Meijers, A. J. S., & Bracegirdle, T. J. (2017). More losers than winners in a century of future Southern Ocean seafloor warming. *Nature Climate Change*, *7*, 749–754. https://doi.org/10.1038/nclimate3377

Griffiths, H. J., & Waller, C. L. (2016). The first comprehensive description of the biodiversity and biogeography of Antarctic and Sub-Antarctic intertidal communities. *Journal of Biogeography*, *43*(6), 1143–1155. https://doi.org/10.1111/jbi.12708

Güller, M., Puccinelli, E., & Zelaya, D. G. (2020). The Antarctic Circumpolar Current as a dispersive agent in the Southern Ocean: Evidence from bivalves. *Marine Biology*, *167*, 143. https://doi.org/10.1007/s00227-020-03746-2

Halanych, K. M., & Mahon, A. R. (2018). Challenging dogma concerning biogeographic patterns of Antarctica and the Southern Ocean. *Annual Review of Ecology, Evolution, and Systematics*, *49*, 355–378. https://doi.org/10.1146/annurev-ecolsys-121415-032139

Huelsenbeck, J. P., & Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, *17*(8), 754–755. https://doi.org/10.1093/bioinformatics/17.8.754

Ihaka, R., & Gentleman, R. R. (1996). A language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, *5*(3), 299–314. https://doi.org/10.2307/1390807

Janosik, A. M., & Halanych, K. M. (2010). Unrecognized Antarctic biodiversity: A case study of the genus *Odontaster* (Odontasteridae; Asteroidea). *Integrative and Comparative Biology*, *50*(6), 981–992. https://doi.org/10.1093/icb/icq119

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., & Drummond, A. (2012). Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, *28*(12), 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Klingenberg, C. P. (2011). MorphoJ: An integrated software package for geometric morphometrics. *Molecular Ecology Resources*, *11*(2), 353–357. https://doi.org/10.1111/j.1755-0998.2010.02924.x

Koubbi, P., De Broyer, C., Griffiths, H. J., Raymond, B., d'Udekem d'Acoz, C., Van de Putte, A. P., Danis, B., David, B., Grant, S., Gutt, J., Held, C., Hosie, G., Huettmann, F., Post, A., Ropert-Coudert, Y., Stoddart, M., Swadling, K. M., & Wadley, V. (2014). Conclusions: Present and future of Southern Ocean biogeography. In C. De Broyer, P. Koubbi, H. J. Griffiths, B. Raymond, C. Udekem d'Acoz, A. P. Van de Putte, B. Danis, B. David, S. Grant, J. Gutt, C. Held, G. Hosie, F. Huettmann, A. Post, & Y. Ropert-Coudert (Eds.), *Biogeographic Atlas of the Southern Ocean* (pp. 470–475). Scientific Committee on Antarctic Research.

Kumar, S., Stecher, G., Li, M., Knyaz, C., & Tamura, K. (2018). MEGA X: Molecular Evolutionary Genetic Analysis across computing platforms. *Molecular Biology and Evolution*, *35*(6), 1547–1549. https://doi.org/10.1093/molbev/msy096

Legendre, P., & Lapointe, F.-J. (2004). Assessing congruence among distance matrices: Single-malt scotch whiskies revisited. *Australian & New Zealand Journal of Statistics*, *46*, 615–629.

Levicoy, D., Rosenfeld, S., & Cárdenas, L. (2021). Divergence time and species delimitation of microbivalves in the Southern Ocean: The case study of Kidderia species. *Polar Biology*, *44*, 1365–1377. https://doi.org/10.1007/s00300-021-02885-6

Lewis, A. R., Marchant, D. R., Ashworth, A. C., Hedenäs, L., Hemming, S. R., Johnson, J. V., Leng, M. J., Machlus, M. L., Newton, A. E., Raine, J. I., Willenbring, J. K., Williams, M., & Wolfe, A. P. (2009). Mid-Miocene cooling and the extinction of tundra in continental Antarctica. *Prodeedings of the National Academy of Science, USA*, *105*, 10676–10680. https://doi.org/10.1073/pnas.0802501105

Librado, P., & Rozas, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, *25*(11), 1451–1452. https://doi.org/10.1093/bioinformatics/btp187

Littlewood, D. T. J., Curini-Galletti, M., & Herniou, E. A. (2000). The interrelationships of Proseriata (Platyhelminthes: Seriata) tested with molecules and morphology. *Molecular Phylogenetics and Evolution*, *16*(3), 449–466. https://doi.org/10.1006/mpev.2000.0802

López-Farrán, Z., Guillaumot, C., Vargas-Chacoff, L., Paschke, K., Dulière, V., Danis, B., Poulin, E., Saucède, T., Waters, J., & Gérard, K. (2021). Is the southern crab *Halicarcinus planatus* (Fabricius, 1775) the next invader of Antarctica? *Global Change Biology*, *27*, 3487–3504. https://doi.org/10.1111/gcb.15674

Meredith, M. P., & King, J. C. (2005). Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophysical Research Letters*, *32*, L19604.

Moon, K. L., Chown, S. L., & Fraser, C. I. (2017). Reconsidering connectivity in the sub-Antarctic. *Biological Reviews*, *92*(4), 2164–2181. https://doi.org/10.1111/brv.12327

Morley, S. A., Abele, D., Barnes, D. K. A., Cárdenas, C. A., Cotté, C., Gutt, J., Henley, S. F., Höfer, J., Hughes, K. A., Martin, S. M., Moffat, C., Raphael, M., Stammerjohn, S. E., Suckling, C. C., Tulloch, V. J. D., Waller, C. L., & Constable, A. J. (2020). Global drivers on Southern Ocean ecosystems: Changing physical environments and anthropogenic pressures in an Earth System. *Frontiers in Marine Science*, *7*, 547188. https://doi.org/10.3389/fmars.2020.547188

Near, T. J., Dornburg, A., Kuhn, K. L., Eastman, J. T., Pennington, J. N., Patarnello, T., Zane, L., Fernández, D. A., & Jones, C. D. (2012). Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *Proceedings of the National Academy of Sciences USA*, *109*, 3434–3439. https://doi.org/10.1073/pnas.1115169109

Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528.

Pertierra, L. R., Segovia, N. I., Noll, D., Martinez, P. A., Pliscoff, P., Barbosa, A., Aragón, P., Raya Rey, A., Pistorius, P., Trathan, P., Polanowski, A., Bonadonna, F., Le Bohec, C., Bi, K., Wang-Claypool, C. Y., González-Acuña, D., Dantas, G. P. M., Bowie, R. C. K., Poulin, E., & Vianna, J. A. (2020). Cryptic speciation in gentoo penguins is driven by geographic isolation and regional marine conditions: Unforeseen vulnerabilities to global change. *Diversity and Distributions*, *26*(8), 958–975. https://doi.org/10.1111/ddi.13072

Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., Kamoun, S., Sumlin, W. D., & Vogler, A. P. (2006). Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology*, *55*(4), 595–609. https://doi.org/10.1080/10635150600852011

Poulin, E., González-Wevar, C., Díaz, A., Gérard, K., & Hüne, M. (2014). Divergence between Antarctic and South American marine invertebrates: What molecular biology tells us about Scotia Arc geodynamics and the intensification of the Antarctic Circumpolar Current. *Global and Planetary Change*, *123(Part*, B), 392–399. https://doi.org/10.1016/j.gloplacha.2014.07.017

Preston, H. B. (1912). Characters of six new Pelecypods and two new gastropods from The Falkland Islands. *Annals and Magazine of Natural History, Series*, *9*, 636–640. https://doi.org/10.1080/00222931208693180

Preston, H. B. (1916). Description of eight new species of marine mollusca from the South Shetland Islands. *Annals and Magazine of Natural History, Series*, *18*, 269–272. https://doi.org/10.1080/00222931608693847

Puillandre, N., Lambert, A., Brouillet, S., & Achaz, G. (2012). ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology*, *21*(8), 1864–1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Rambaut, A., Drummond, A. J., Xie, D., Baele, G., Suchard, M. A., & Suchard, M. A. (2018). Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, *67*(5), 901–904. https://doi.org/10.1093/sysbio/syy032

Raupach, M. J., Thatje, S., Dambach, J., Rehm, P., Misof, B., & Leese, F. (2010). Genetic homogeneity and circum-Antarctic distribution of two benthic shrimp species of the Southern Ocean, *Chorismus antarcticus* and *Nematocarcinus lanceopes*. *Marine Biology*, *157*, 1783–1797. https://doi.org/10.1007/s00227-010-1451-3

Reid, D. G. (1989). The comparative morphology, phylogeny and evolution of the gastropod family Littorinidae. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, *324*(1220), 1–110. https://doi.org/10.1098/rstb.1989.0040

Reid, D. G., Dyal, P., & Williams, S. T. (2012). A global molecular phylogeny of 147 periwinkle species (Gastropoda, Littorininae). *Zoologica Scripta*, *41*(2), 125–136. https://doi.org/10.1111/j.1463-6409.2011.00505.x

Rintoul, S. R. (2011). The Southern Ocean in the earth system. In P. Berkman, M. Lang, D. Walton, & O. Young (Eds.), *Science diplomacy: Antarctica, science and the governance of international spaces* (pp. 1–13). Smithsonian Institution Scholarly Press.

Rohlf, F. J. (1999). Shape statistics: Procrustres supeimpositions and tangent spaces. *Journal of Classification*, *16*, 197–223. https://doi.org/10.1007/s003579900054

Rohlf, F. J. (2009). tpsDig. Version 2.14. Department of Ecology and Evolution, State University of New York. Available at http://life.bio.sunysb.edu.morph/ 2009.

Schächinger, P. M., Schrödl, M., Wilson, N. G., & Moles, J. (2022). Crossing the polar front-Antarctic species discovery in the nudibranch genus *Tritoniella* (Gastropoda). *Organisms Diversity & Evolution*. https://doi.org/10.1007/s13127-022-00541-3

Scher, H. D., Whittaker, J. M., Williams, S. E., Latimer, J. C., Kordesch, W. E. C., & Delaney, M. L. (2015). Onset of Antarctic Circumpolar Current 30 million years ago as Tasmanian Gateway aligned with westerlies. *Nature*, *523*, 580–585. https://doi.org/10.1038/nature14598

Simpson, R. D., & Harrington, S. A. (1985). Egg masses of three gastropods, *Kerguelenella lateralis* (Siphonariidae), *Laevilitorina caliginosa* and *Macquariella hamiltoni* (Littorinidae), from Macquarie Island (sub-Antarctic). *Journal of the Malacological Society of Australia*, *7*(1–2), 17–28. https://doi.org/10.1080/00852988.1985.10673973

Smith, E. A. (1902). VII. Mollusca. Report on the collections of natural history made in the Antarctic regions during the voyage of the "Southern Cross". Reports on the Collection of Natural History. (pp. 201–213).

Strugnell, J. M., Rogers, A. D., Prodöhl, P. A., Collins, M. A., & Allcock, A. L. (2008). The thermohaline expressway: The Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics*, *24*(6), 853–860. https://doi.org/10.1111/j.1096-0031.2008.00234.x

Thornhill, D. J., Mahon, A. R., Norenburg, J. L., & Halanych, K. M. (2008). Open-ocean barriers to dispersal: A test case with the Antarctic Polar Front and the ribbon worm *Parborlasia corrugatus* (Nemertea: Lineidae). *Molecular Ecology*, *17*(23), 5104–5117. https://doi.org/10.1111/j.1365-294X.2008.03970.x

Verducci, M., Foresi, L. M., Scott, G. H., Sprovieri, M., Lirer, F., & Pelosi, N. (2009). The Middle Miocene climatic transition in the Southern Ocean: Evidence of paleoclimatic and hydrographic changes at Kerguelen plateau from planktonic foraminifers and stable isotopes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *280*(3–4), 371–386. https://doi.org/10.1016/j.palaeo.2009.06.024

von Martens, E., & von Pfeffer, G. (1886). Die Mollusken von Süd-Georgien nach der Ausbeute der Deutschen Station 1882–83. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten.*, *3*, 63–135.

Williams, S. T., Reid, D. G., & Littlewood, D. T. J. (2003). A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): Unequal evolutionary rates, morphological parallelism, and biogeography of the Southern Ocean. *Molecular Phylogenetics and Evolution*, *28*(1), 60–86. https://doi.org/10.1016/S1055-7903(03)00038-1

Wilson, N. G., Schrödl, M., & Halanych, K. M. (2009). Ocean barriers and glaciation: Evidence for explosive radiation of mitochondrial lineages in the Antarctic sea slug *Doris kerguelenensis* (Mollusca, Nudibranchia). *Molecular Ecology*, *18*(5), 965–984. https://doi.org/10.1111/j.1365-294X.2008.04071.x

Wright, F. (1990). The effective number of codons' used in a gene. *Gene*, *87*(1), 23–29. https://doi.org/10.1016/0378-1119(90)90491-9

Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, *292*, 686–693. https://doi.org/10.1126/science.1059412

Zelaya, D. (2005). Systematics and biogeography of marine gastropod molluscs from South Georgia. *Spixiana*, *28*, 109–139.

Zhang, J., Kapli, P., Pavidis, P., & Stamatakis, A. (2013). A general species delimitation method with applications to phylogenetic placements. *Bioinformatics*, *29*(22), 2869–2876. https://doi.org/10.1093/bioinformatics/btt499

BIOSKETCH

Author contributions: CAG-W, EP, HGS, NIS and SR conceived the idea of the study and designed the analyses. CAG-W, EP, SR, CSM, SM, TS, SAM, PB and NGW collected specimens from different localities across *L. caliginosa*'s distribution. CAG-W, VJ and NIS performed molecular experiments. CAG-W, VJ and NIS performed analyses of the recorded data. VJ, CAG-W and RP performed geometric morphometric analyses. C.A.G-W, EP, HGS, NIS and SR contributed intellectually to the interpretation and discussion of results. CAG-W, HGS, EP and SR wrote the paper. All authors read and approved the final version of the manuscript.

AUTHOR BIOGRAPHY

Claudio González-Wevar is an evolutionary biologist and a marine biogeography at Instituto de Ciencias Marinas y Limnológicas (ICML) at Universidad Austral de Chile, Valdivia–Chile. His research interest is focused on the understanding of biogegraphical patterns and processes in the Southern-Ocean near-shore marine benthic fauna. He is working in several groups of Southern-Ocean marine benthic molluscs using molecular analyses at different geographical and temporal scales.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: González-Wevar, C. A., Segovia, N. I., Rosenfeld, S., Maturana, C. S., Jeldres, V., Pinochet, R., Saucède, T., Morley, S. A., Brickle, P., Wilson, N. G., Spencer, H. G., & Poulin, E. (2022). Seven snail species hidden in one: Biogeographic diversity in an apparently widespread periwinkle in the Southern Ocean. *Journal of Biogeography*, *49*, 1521–1534. https://doi.org/10.1111/jbi.14453

Biodiversity Data Journal 11: e108566
doi: 10.3897/BDJ.11.e108566

Data Paper

Revealing the hidden biodiversity of Antarctic and the Magellanic Sub-Antarctic Ecoregion: A comprehensive study of aquatic invertebrates from the BASE Project

Sebastian Rosenfeld[‡,§,|], Claudia S. Maturana[‡,§], Melisa Gañan[‡,§,¶,#,¤,«], Javier Rendoll Cárcamo[‡,§,¶], Angie Díaz[‡,»], Tamara Contador[‡,§,¶,#], Cristian Aldea[|], Claudio Gonzalez-Wevar[‡,˄], Julieta Orlando[‡,˅], Elie Poulin[‡]

‡ Millennium Institute Biodiversity of Antarctic and Subantarctic Ecosystems (BASE), Santiago, Chile
§ Cape Horn International Center (CHIC), Puerto Williams, Chile
| Centro de Investigación Gaia-Antártica, Universidad de Magallanes, Punta Arenas, Chile
¶ Laboratorio de Estudios Dulceacuícolas Wankara, Programa de Conservación Biocultural Subantártica, Universidad de Magallanes, Puerto Williams, Chile
# Millennium Nucleus of Austral Invasive Salmonids - INVASAL, Concepción, Chile
¤ FEHM-Lab (Freshwater Ecology, Hydrology and Management), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona (UB), Diagonal 643, 08028, Barcelona, Spain
« Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Diagonal 643, 08028, Barcelona, Spain
» Departamento de Zoología, Universidad de Concepción, Concepción, Chile
˄ Facultad de Ciencias, Centro FONDAP IDEAL, Instituto de Ciencias Marinas y Limnológicas (ICML), Universidad Austral de Chile, Valdivia, Chile
˅ Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile

Corresponding author: Claudia S. Maturana (cmaturana.ciencias@gmail.com)

Academic editor: Huw Griffiths

Received: 23 Jun 2023 | Accepted: 11 Aug 2023 | Published: 17 Aug 2023

Citation: Rosenfeld S, Maturana CS, Gañan M, Rendoll Cárcamo J, Díaz A, Contador T, Aldea C, Gonzalez-Wevar C, Orlando J, Poulin E (2023) Revealing the hidden biodiversity of Antarctic and the Magellanic Sub-Antarctic Ecoregion: A comprehensive study of aquatic invertebrates from the BASE Project. Biodiversity Data Journal 11: e108566. https://doi.org/10.3897/BDJ.11.e108566

Abstract

Background

Antarctica, its outlying archipelagoes and the Magellanic Subantarctic (MSA) ecoregion are amongst the last true wilderness areas remaining on the planet. Therefore, the publication, citation and peer review of their biodiversity data are essential. The new Millennium Institute Biodiversity of Antarctic and Subantarctic Ecosystems (BASE), a Chilean scientific initiative funded by the National Agency of Research and Innovation, contributes 770 new records of aquatic invertebrates as a point of reference for present-day biodiversity research at these latitudes.

New information

The occurrence dataset presented here has never been released before and is the result of the systematic recording of occurrences of several taxa across the Antarctic, Subantarctic and Magellanic Subantarctic ecoregions. We collected data from marine and freshwater invertebrates across numerous samplings from 2008 to 2023. From the 770 occurrences, we identified 160 taxa, 125 at species level and 35 at the genus level. The database has been registered in the Global Biodiversity Information Facility (GBIF). The publication of this data paper was funded by the Belgian Science Policy Office (BELSPO, contract n°FR/36/AN1/AntaBIS) in the Framework of EU-Lifewatch as a contribution to the SCAR Antarctic biodiversity portal (biodiversity.aq)

Keywords

Cape Horn Biosphere Reserve, freshwater ecosystems, GBIF, macroinvertebrates, Southern Ocean

Introduction

The study and characterisation of biodiversity in the different ecosystems of the planet is a challenge and a task of grand proportions since it is estimated that the Earth is inhabited by about 10 million species, which requires a significant investment of funds and work to generate, collect and analyse biodiversity data (Troudet et al. 2017). In addition, due to the environmental crisis that ecosystems have experienced in recent decades and its diverse effects on biota, a global need for biodiversity data has been generated (Barnosky et al. 2011, Pecl et al. 2017). For this reason, data exchange practices and tools have been developed, such as the Global Biodiversity Information Facility (GBIF) and the Ocean Biodiversity Information System (OBIS), which follow the FAIR foundational principles (Wilkinson et al. 2016) that facilitate access and research process for species occurrence records. However, despite these international efforts devoted to the generation of data on biodiversity, even today, only a small proportion of global records are estimated to have been made available online (Ariño 2010, Maturana et al. 2019, Rosenfeld et al. 2022), with some critical knowledge biases detected in some taxonomic groups (Troudet et al. 2017, Rocha-Ortega et al. 2021, Llorente-Culebras et al. 2023).

The Southern Ocean (SO) surrounds Antarctica and is one of the main drivers of global ocean circulation (Rintoul and Garabato 2013). Regarding biodiversity, the distribution of organisms in the SO seabed ecosystems largely reflects the complex interplay of geological, oceanographic and biological elements through space and time (Griffiths et al. 2009) Interpretation of these distributions can help to understand better the role of the SO in the ecological processes of the Southern Hemisphere and project into the future the changes in the distributions of biota due to the effect of global change (Griffiths et al. 2009, Lopez-Farran et al. 2021). From another perspective, Antarctica and the SO have been under the Antarctic Treaty System since 1961, in which signatory nations agree to prioritise current and future management and protection of the continent's biodiversity and ecosystem values. Comprehensive protection of the Antarctica environment cannot be addressed without a complete, unbiased and systematic publication of biodiversity data ensuring the accomplishment of such a crucial endeavour (Wauchope et al. 2019, Hawes et al. 2023).

It is essential to highlight that, despite the research efforts in Antarctica and the SO in the last decades in generating knowledge in biodiversity, there are still many poorly-sampled and -studied areas and habitats. In this regard, the intertidal and shallow subtidal environments of Antarctica and Subantarctic environments are considerably less well-sampled than either the surrounding deep sea (Brandt et al. 2014, Ojeda et al. 2014, Griffiths and Waller 2016, Rosenfeld et al. 2017, Aldea et al. 2020, Jossart et al. 2023). Likewise, in continental environments, recent studies have identified important sampling gaps in Antarctica and Subantarctic ecoregions (Chown and Convey 2016, Maturana et al. 2019, Ganan et al. 2021, Hawes et al. 2023). The Subantarctic environments represent a large and remote geographic area and, due to its extreme conditions (climatic and oceanographic) (Griffiths and Waller 2016), it denotes a challenge when undertaking biodiversity inventories. For example, in the Magellanic Subantarctic ecoregion, it has been described that the diversity of representative and moderately known groups, such as molluscs, would be underestimated (Aldea et al. 2020, Rosenfeld et al. 2020). In addition, with the progress of molecular tools to date, new lineages continue to be detected in both invertebrates and vertebrates (Gonzalez-Wevar et al. 2018, Maturana et al. 2021, Rozzi et al. 2022). Therefore, in terms of biodiversity, the Subantarctic area in both terrestrial and marine environments still represents a knowledge gap compared even to Antarctica (Rozzi et al. 2012, Aldea et al. 2020, Contador et al. 2020). In summary, it is critical to fill gaps to generate and digitise open and accessible biodiversity databases across the different ecosystems and taxa.

The Chilean Institute of Biodiversity of Antarctic and Subantarctic Ecosystems (BASE) decided to contribute with the digitisation of the historical sampling fieldwork conducted by the authors across Antarctic, Subantarctic and Magellanic Subantarctic ecoregions. This effort will increase the biodiversity data available for these latitudes and improve our understanding of the magnitude of the potential effects of biodiversity loss.

General description

Purpose: These data aim to comprehensively describe the geographic distribution of aquatic macroinvertebrates in southern South America, Subantarctica and Antarctica ecoregions. Although this database only included four phyla - and therefore is not completely representative of the extant biodiversity in those regions - we aim to expand the work to include more phyla, species and geographic coverage. The development and continuously updated database will improve our knowledge of Antarctic and Subantarctic biodiversity and initiate long-term biodiversity monitoring across marine and terrestrial ecosystems to detect significant modifications due to global change.

Project description

Title: State of Antarctic and Subantarctic biodiversity

Personnel: Julieta Orlando, Claudia Maturana, Sebastián Rosenfeld, Melisa Gañán, Javier Rendoll

Study area description: Antarctic and Subantarctic ecoregions, including the Cape Horn Biosphere Reserve (CHBR)

Funding: ICM-ANID Program ICN2021_002

Sampling methods

Sampling description: Since the sampling was carried out by various groups of researchers from different ecosystems and habitats, the sampling methodology presents variations related to the field team and the particular conditions of each collection site. Additionally, each group of taxa requires different sampling techniques; however, here we present the two principal methodologies for collection of aquatic invertebrates.

Marine

The specimens were collected following a previous methodology (Rosenfeld et al. 2022). In particular, the different taxa were collected using three methods: 1) manual collection in the intertidal zone, with molluscs being sampled individually; 2) SCUBA diving between 1 and 15 m depth, where the sea urchins were manually collected; and 3) SCUBA diving between 1 and 20 m depth, where the substrates (e.g. sediments, macroalgae) were collected. Rock substrates were subsequently scraped to ensure that all species and specimens were collected. Each macroalga sample was placed in a plastic bag. After collection, specimens were kept alive and transported on-board or to the research station. Each sample was then gently agitated to detach the associated fauna.

For intertidal insect sampling, the intertidal area was surveyed during low tide and adult individuals were collected using an entomological aspirator (insect's pooter).

Freshwater

Individuals were collected from lakes, ponds and other freshwater bodies using a Surber net of 0.09 m^2 area and 243 µm mesh. A Malaise trap was also placed at each site to obtain adult representatives of the organisms needed to identify them to the lowest possible taxonomic level. Traps were placed in the late afternoon and left overnight at each site.

Quality control: All captures were identified up to species level following available taxonomic keys for the different groups. GPS positions were recorded for each sample location. Specimens were immediately preserved in ethanol (95%) to be transported to the laboratory. The specimens belonging to other phyla not included in this study were kept in ethanol 95%, classified by phylum waiting to be described and digitised.

Geographic coverage

Description: The geographic extent of the digitised dataset is placed in the following biogeographic areas (Fig. 1: 1) the southern part of the Magellan Province, including the Cape Horn Biosphere Reserve (CHBR); 2) the Subantarctic island of South Georgia; 3) the South Orkney Islands; 4) the South Shetland Islands; 5) the West and East Antarctic Peninsula and 6) Kerguelen Island.

Coordinates: 68 and 39 Latitude; 74 and 72 Longitude.

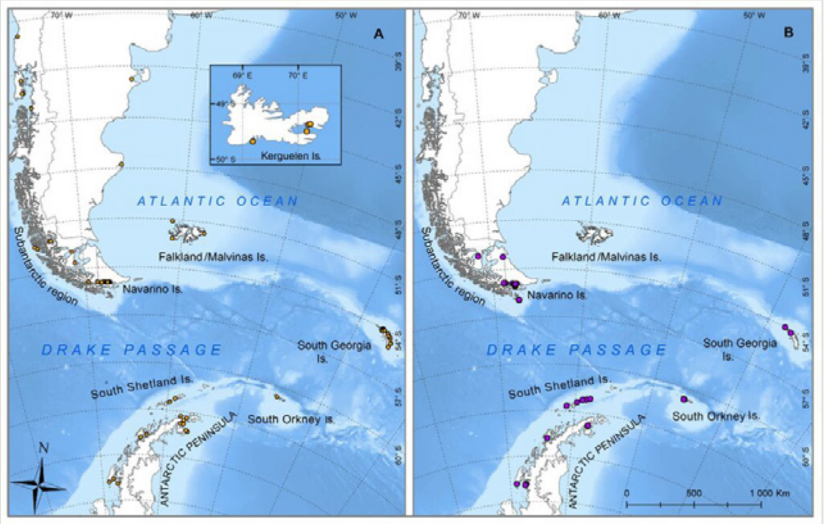


Figure 1. doi

Occurrence of marine (yellow circles) and freshwater (purple circles) invertebrates throughout all sampling sites.

Taxonomic coverage

Description: Morphological observations were performed under an OLYMPUS stereomicroscope CX31. Taxonomic identification of the molluscs was based on a complete study of the current literature (e.g. Troncoso et al. (2001), Aldea and Troncoso (2008), Engl (2012), Ibáñez et al. (2019)), as well as on classic works (Smith 1879, v Martens and Pfeffer 1886, Strebel 1908, Powell 1954) and systematics studies about specific taxa (Zelaya 2004, Pastorino 2005, Zelaya 2005, Pastorino 2016, Zelaya et al. 2020). The identification of echinoidea was based on Larrain (1975).

For specific taxonomic identifications in the Arthropoda database, we followed the available taxonomic keys (Ephemeroptera: Domínguez and Fernández (2009); Coleoptera: Libonatti et al. (2011); Plecoptera: Nieto 2004, McLellan and Zwick (2007); Branchiopoda: Rogers et al. (2008); Odonata: von Ellenrieder (2003)). For general freshwater macroinvertebrates identification, we used available taxonomic guides (Merritt and Cummins 1996, Domínguez and Fernández 2009).

The taxonomic coverage of the dataset consists of all captures of aquatic invertebrates from marine (sub- and intertidal) and freshwater (rivers, lakes and lagoons) habitats. This database comprises 770 occurrences across four invertebrate Phyla: Arthropoda, Annelida, Mollusca and Echinodermata. Of the total occurrences, 50.1% corresponded to Arthropoda, 47% to Mollusca, 2.3% to Echinodermata (1 species) and 0.5% to Annelida (1 taxon at genus level) (Fig. 2). The databases will be described below based on the type of environment (marine or freshwater) and discussed, based on the most representative taxa in terms of occurrences.

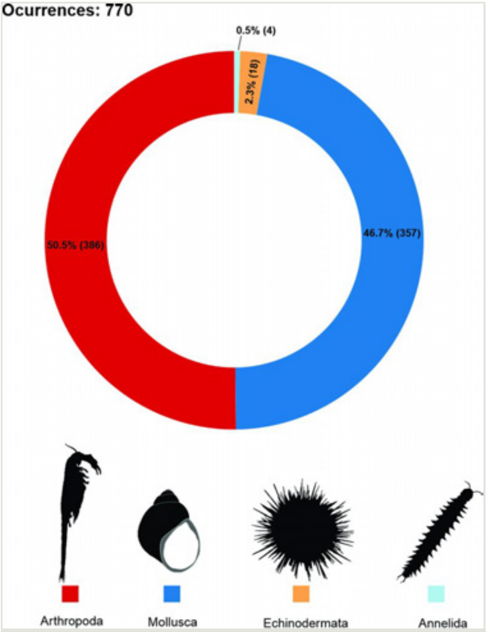


Figure 2. doi

Representation of total occurrences from four phyla. Data were collected from different expeditions to the Antarctic and Subantarctic regions. The absolute values of occurrences are represented in parentheses.

Marine

Considering all the revised specimens, the mollusc database includes 357 records, representing 104 taxa belonging to the classes Polyplacophora, Gastropoda and Bivalvia. Of the total number of taxa, 93 were identified at the species level, six at the genus level and five were left as "cf" (i.e. conferred) because there was no concrete background to identify it with certainty. Of the total occurrences, 277 are gastropods, corresponding to 76 recorded taxa; 40 are chitons, belonging to 10 species and 36 are bivalves, belonging to 17 species. The main families in terms of occurrence and number of species were Littorinidae, Eatoniellidae, Nacellidae, Muricidae and Calliostomatidae, accumulating together ~ 51% of the total occurrences and ~ 42% of the total species (Fig. 3).

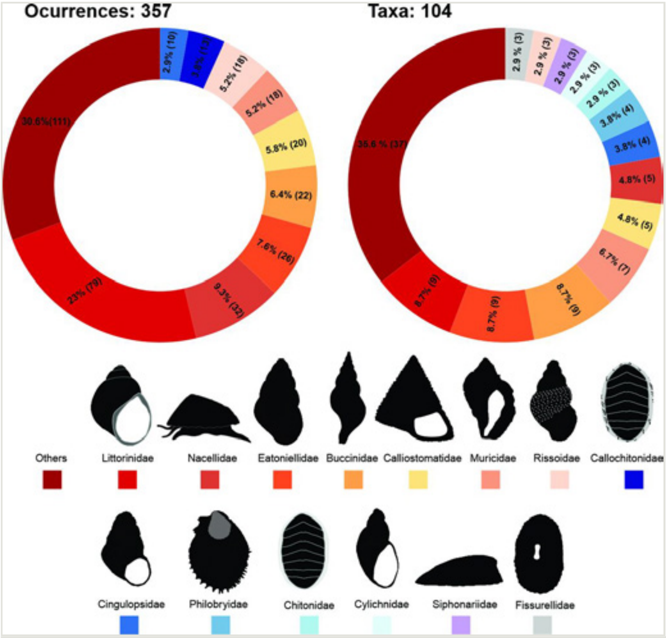


Figure 3. doi

Occurrences and total taxa by families from Mollusca database. Data were collected from different expeditions to the Antarctic and Subantarctic regions. The absolute values of occurrences and species are represented in parentheses.

Freshwater

The freshwater ecosystems included three phyla: Annelida, Mollusca and Arthropoda, the latter being the most complete in terms of taxonomic coverage, occurrences and geographic extent. Considering all the Arthropoda database, we included 374 records, from which Insecta was the most representative class (305 records), followed by Branchiopoda (38), Malacostraca (27) and Maxillopoda (4). Within the total records, we detected 48 taxa, from which 25 were identified at the species level and 23 at the genus level. We have detailed the most diverse orders regarding occurrences and taxonomic diversity (Fig. 4).

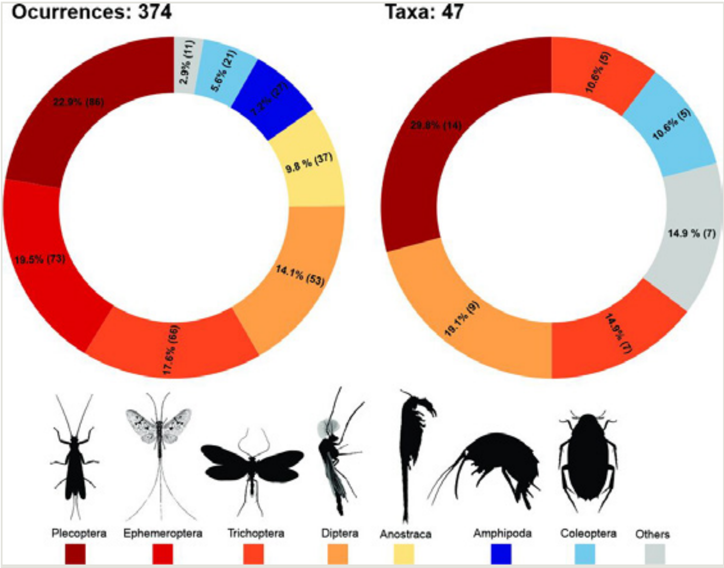


Figure 4. doi

Occurrences and total taxa by orders from the Arthropoda database. Data were collected from different expeditions to the Antarctic and Subantarctic regions. The absolute values of occurrences and species are represented in parentheses. Credits for images Maxime Dahirel (coleoptera) and Didier Descouens vectorised by T. Michael Keesey (trichoptera).

Taxa included:

Rank	Scientific Name
species	*Tonicina zschaui* (Pfeffer, 1886)
species	*Leptochiton kerguelensis* Haddon, 1886
species	*Callochiton steinenii* (Pfeffer, 1886)
species	*Callochiton puniceus* (Gould, 1846)
species	*Tonicia chilensis* (Frembly, 1827)
species	*Tonicia lebruni* Rochebrune, 1884
species	*Chiton magnificus* Deshayes, 1827
species	*Plaxiphora aurata* (Spalowsky, 1795)
species	*Nuttallochiton martiali* (Rochebrune, 1889)
species	*Ischnochiton stramineus* (G. B. Sowerby I, 1832)
species	*Hemiarthrum setulosum* Carpenter [in Dall], 1876
species	*Fissurellidea patagonica* (Strebel, 1907)
species	*Fissurella oriens* G. B. Sowerby I, 1834

species	*Puncturella conica* (d'Orbigny, 1841)
species	*Scurria ceciliana* (d'Orbigny, 1841)
species	*Nacella concinna* (Strebel, 1908)
species	*Nacella deaurata* (Gmelin, 1791)
species	*Nacella flammea* (Gmelin, 1791)
species	*Nacella mytilina* (Helbling, 1779)
species	*Nacella magellanica* (Gmelin, 1791)
species	*Margarella violacea* (P. P. King, 1832)
species	*Margarella antarctica* (Lamy, 1906)
species	*Margarella achilles* (Strebel, 1908)
species	*Margarella steineni* (Strebel, 1905)
species	*Margarella tropidophoroides* (Strebel, 1908)
species	*Munditia meridionalis* (Melvill & Standen, 1912)
species	*Onoba grisea* (Martens, 1885)
species	*Onoba kergueleni* (E. A. Smith, 1875)
species	*Subonoba turqueti* (Lamy, 1906)
species	*Rissoella powelli* Ponder, 1983
species	*Pickenia signyensis* Ponder, 1983
species	*Crepipatella dilatata* (Lamarck, 1822)
species	*Laevilacunaria antarctica* (Martens, 1885)
species	*Laevilacunaria bennetti* (Preston, 1916)
species	*Laevilitorina antarctica* (E. A. Smith, 1902)
species	*Laevilitorina claviformis* Preston, 1916
species	*Laevilitorina umbilicata* Pfeffer, 1886
species	*Laevilitorina caliginosa* (Gould, 1849)
species	*Laevilitorina pygmaea* Pfeffer, 1886
species	*Laevilitorina venusta* Pfeffer, 1886
species	*Pellilitorina pellita* (Martens, 1885)
species	*Pellilitorina setosa* (E. A. Smith, 1875)
species	*Eatoniella denticula* Ponder & Worsfold, 1994
species	*Eatoniella nigra* (d'Orbigny, 1840)

species	*Eatoniella kerguelenensis* (E. A. Smith, 1875)
species	*Eatoniella caliginosa* (E. A. Smith, 1875)
species	*Eatoniella contusa* Strebel, 1908
species	*Eatoniella subgoniostoma* Strebel, 1908
species	*Eatoniella strebeli* Ponder & Worsfold, 1994
species	*Eatoniella glacialis* (E.A. Smith, 1907)
species	*Eatoniella cana* Ponder, 1983
genus	*Marseniopsis* sp.
species	*Skenella umbilicata* Ponder, 1983
species	*Skenella georgiana* Pfeffer, 1886
species	*Skenella* cf. *wareni* Ponder & Worsfold, 1994
species	*Liotella crassicostata* (Strebel, 1908)
species	*Sinuber sculptum* (E. von Martens 1878)
species	*Eumetula pulla* (Philippi, 1845)
species	*Omalogyra antarctica* Egorova, 1991
species	*Microdiscula subcanaliculata* (E.A. Smith, 1875)
species	*Acanthina monodon* (Pallas, 1774)
species	*Trophon plicatus* (Lightfoot, 1786)
species	*Trophon geversianus* Pallas, 1774
species	*Trophon nucelliformis* P. G. Oliver & Picken, 1984
species	*Trophon brevispira* E von. Martens, 1885
species	*Fuegotrophon pallidus* (Broderip, 1833)
species	*Xymenopsis muriciformis* (P. P. King, 1832)
genus	*Prosipho* sp.
species	*Prosipho* cf. *chordatus* (Strebel, 1908)
species	*Prosipho* cf. *gracilis* Thiele, 1912
species	*Prosipho hedleyi* Powell, 1958
species	*Falsimohnia minor* (Strebel, 1908)
species	*Chlanidota densesculpta* (Martens, 1885)
species	*Pareuthria fuscata* (Bruguière, 1789)
species	*Microdeuthria michaelseni* (Strebel, 1905)

species	*Meteuthria martensi* (Strebel, 1905)
species	*Mathilda magellanica* P. Fischer, 1873
genus	*Flabellina* sp.
species	*Toledonia palmeri* Dell, 1990
species	*Toledonia* cf. *palmeri* Dell, 1990
species	*Toledonia parelata* Dell, 1990
species	*Scissurella petermannensis* Lamy, 1910
species	*Scissurella clathrata* Strebel, 1908
species	*Siphonaria lateralis* Gould, 1846
species	*Siphonaria fuegiensis* Güller, Zelaya & Ituarte, 2016
species	*Siphonaria lessonii* Blainville, 1827
species	*Onchidella marginata* (Couthouy in Gould, 1852)
species	*Turbonilla strebeli* Corgan, 1969
species	*Neobuccinum eatoni* (E. A. Smith, 1875)
species	*Kidderia subquadrata* (Pelseneer, 1903)
species	*Kidderia minuta* Dall, 1876
species	*Lissarca miliaris* (Philippi, 1845)
genus	*Lissarca* sp.
species	*Gaimardia trapesina* (Lamarck, 1819)
genus	*Philobrya* sp.
species	*Philobrya quadrata* (Pfeffer in Martens & Pfeffer, 1886)
genus	*Neolepton* sp.
species	*Laternula elliptica* (P. P. King, 1832)
species	*Limea pygmaea* (Philippi, 1845)
species	*Aequiyoldia* cf. *eightsii* (Jay, 1839)
species	*Altenaeum charcoti* (Lamy, 1906)
genus	*Hiatella* sp.
genus	*Lasaea* sp.
species	*Aulacomya atra* (Molina, 1782)
species	*Perumytilus purpuratus* (Lamarck, 1819)
species	*Arbacia dufresnii* (Blainville, 1825)

species	*Telmatogeton magellanicus* (Jacobs, 1900)
species	*Rhionaeschna variegata* (Fabricius, 1775)
genus	*Helobdella* sp.
species	*Lancetes angusticollis* (Curtis, 1839)
genus	*Lancetes* sp.
genus	*Liodessus* sp.
genus	*Luchoelmis* sp.
genus	*Haliplus* sp.
species	*Metamonius anceps* (Eaton, 1883)
species	*Massartelopsis irarrazavali* (Demoulin, 1955)
species	*Meridialaris chiloeensis* (Demoulin, 1955)
species	*Andesiops torrens* (Lugo-Ortiz & McCafferty, 1999)
species	*Aubertoperla kuscheli* Illies, 1963
genus	*Aubertoperla* sp.
genus	*Antarctoperla* sp.
genus	*Notoperla* sp.
species	*Rhithroperla rossi* (Froehlich, 1960)
species	*Udamocercia antarctica* (Enderlein, 1905)
genus	*Udamocercia* sp.
species	*Austrocosmoecus hirsutus* Schmid, 1955
species	*Monocosmoecus hyadesii* (Mabille, 1888)
genus	*Verger* sp.
species	*Mastigoptila brevicornuta* (Schmid, 1958)
species	*Rheochorema magellanicum* Flint, 1974
genus	*Rheochorema* sp
genus	*Sigara* sp.
species	*Parochlus steinenii* (Gercke, 1889)
species	*Gigantodax rufescens* (Edwards, 1931)
genus	*Gigantodax* sp.
genus	*Hexatoma* sp.
genus	*Hemerodromia* sp.

species	*Edwardsina dispar* Edwards, 1929
species	*Gigantodax igniculus* Coscaron & Wygodzinsky, 1962
genus	*Limonia* sp.
genus	*Aphroteniella* sp.
species	*Andesiops torrens* (Lugo-Ortiz & McCafferty, 1999)
genus	*Klapopteryx* sp
species	*Notoperla fuegiana* (Enderlein, 1905)
genus	*Pelurgoperla* sp.
genus	*Teutoperla* sp.
genus	*Aubertoperla* sp.
genus	*Metacosmoecus* sp.
species	*Pisidium magellanicum* (Dall, 1908)
species	Pectinidens diaphanum (P.P.King, 1832)
species	*Hyalella simplex* (Schellemberg, 1943)
genus	*Hyalella* sp.
genus	*Daphnia* sp.
genus	*Boeckella* sp.
species	*Andesiops peruvianus* (Ulmer, 1920)
species	*Metamonius anceps* (Eaton, 1883)
species	*Senzilloides panguipulli* (Navás, 1928)
species	*Limnoperla jaffueli* (Navás, 1928)
species	*Antarctoperla michaelseni* (Klapálek, 1904)
species	*Branchinecta gaini* Daday, 1910

Temporal coverage

Notes: All available records between 2008 and 2023.

Collection data

Collection name: BA

Specimen preservation method: ethanol 95%

Curatorial unit: plastic

Usage licence

Data resources

Data package title: Occurrences of aquatic invertebrates in the Antarctic and Subantarctic regions

Resource link: https://www.gbif.org/dataset/1eb4dc17-46f3-465e-9846-94e70d15ff78

Alternative identifiers: http://gbif-chile.mma.gob.cl/ipt/resource?r=aquatic_invertebrates

Number of data sets: 1

Data set name: Occurrences of aquatic invertebrates in the Antarctic and Subantartic regions

Data format: Darwin Core

Description: The dataset contains occurrence data from marine and freshwater invertebrates across numerous samplings from 2008 to 2023 (Gañán et al. 2023). From the 770 occurrences, we identified 160 taxa, 125 at species level and 35 at the genus level. A description of column headers used as given below.

Column label	Column description
occurrenceID	Unique identifier for each occurrence per taxa.
institutionCode	Unique identifier for the institution having custody of the object(s) or information referred to in the record.
collectionCode	The coden identifying the collection from which the record was derived.
catalogNumber	A unique identifier for the record within the dataset.
ocurrenceStatus	The statement about the presence of the Taxon at the given Location.
collectionID	The identifier for the collection or dataset from which the record was derived.
language	The language of the resource.
licence	The legal document giving official permission to share and adapt with appropiate credits.
bibliographicCitation	The bibliographic reference for the resource as a statement indicating how this record should be cited and attributed when used.
taxonRank	The taxonomic rank of the most specific name in the scientificName.
kingdom	The full scientific name of the kingdom in which the taxon is classified.
phylum	The full scientific name of the phylum in which the taxon is classified.

class	The full scientific name of the class in which the taxon is classified.
order	The full scientific name of the order in which the taxon is classified.
family	The full scientific name of the family in which the taxon is classified.
genus	The full scientific name of the genus in which the taxon is classified.
scientificName	The full scientific name in the lowest level taxonomic rank that was determined.
specificEpithet	The name of species epithet of the scientificName.
scientificNameAuthorship	The authorship information for the scientificName formatted according to the conventions of the applicable nomenclaturalCode.
acceptedNameUsageID	An identifier for the documented meaning of the name according to a source of the currently valid (zoological) or accepted (botanical) taxon. We included GBIF and World Register of Marine Species (WoRMS) website codes.
individualCount	The number of individuals present at the time of the Occurrence, if it were countable.
country	The name of the country or major administrative unit in which the Location occurs.
countryCode	The standard code for the country in which the Location occurs following the best practice using an ISO 3166-1-alpha-2 country code.
locality	The specific description of the place in which the collection was made.
island	The name of the island in which the Location occurs.
waterBody	The name of the water body in which the Location occurs. We include best practice to use a controlled vocabulary.
decimalLongitude	The geographic longitude in decimal degrees of the geographic centre of a Location. Positive values are east of the Greenwich Meridian, negative values are west of it. Legal values lie between -180 and 180, inclusive.
decimalLatitude	The geographic latitude in decimal degrees of the geographic centre of a Location. Positive values are north of the Equator, negative values are south of it. Legal values lie between -90 and 90, inclusive.
coordinateUncertaintyInMetres	The horizontal distance in metres from the given decimalLatitude and decimalLongitude describing the smallest circle containing the whole of the Location. We used the reasonable lower limit on or after 01-05-2020 of a GPS.
geodeticDatum	The geodetic datum upon which the geographic coordinates given in decimalLatitude and decimalLongitude are based.
georeferencedBy	A person or a list concatenated and separated of names of people who determined the georeference for the Location.
eventDate	The date-time when the event was recorded. We used best practice using the ISO 8601:1:2019.

year	The four-digit year in which the Occurrence was recorded, according to the Common Era Calendar.
month	The integer month in which the Occurrence was recorded.
minimumDepthInMetres	The lesser depth below the local surface in metres.
maximumDepthInMetres	The greater depth below the local surface in metres.
basisOfRecord	The specific nature of the data record. We used the recommended best practice of one of the Darwin Core classes.
type	The nature of the resource. We used the recommended best practice of one of the Darwin Core classes.
preparations	A list concatenated and separated of preparations and preservation methods for the specimen.
recordedBy	A person or a list of names of people responsible for recording the original Occurrence.
identifiedBy	A person or a list of names of people who assigned the Taxon to the subject.
habitat	A category or description of the habitat in which the Occurrence was recorded.
datasetID	The identifier for the set of data related to the metadata published in GBIF.
datasetName	The name identifying the dataset from which the record was derived. This column is related to the metadata published in GBIF.
occurrenceRemarks	Comments related to the framework of the published records.
associatedReferences	A list concatenated and separated of bibliographic reference of literature associated with the Occurrence.

Additional information

As with all datasets, there are two main topics that we want to call attention to and discuss.

Geographic regions and diversity gaps

Within Magellan Province, important differences exist amongst the regions included in this study. For example, CHBR had the highest number of records (440) of freshwater biodiversity overall across all the geographic regions, but in Brunswick/Strait of Magellan and Tierra del Fuego, there is a notorious gap in terms of biodiversity assessment, digitisation of inventories and sampling efforts (Fig. 5). Conversely, South Georgia and Antarctica are very similar in global marine biodiversity, with 166 and 145 occurrences, respectively. However, there are significant differences between marine and freshwater data (Fig. 5) within these regions, the former being the most extensive marine database in these latitudes. In particular, the Littorinidae represented more than 24% in the Antarctic

Peninsula and South Georgia; while in the Magellan Province, the families Nacellidae and Muricidae were the most representative, with 13.7% and 12.9%, respectively (Fig. 6).

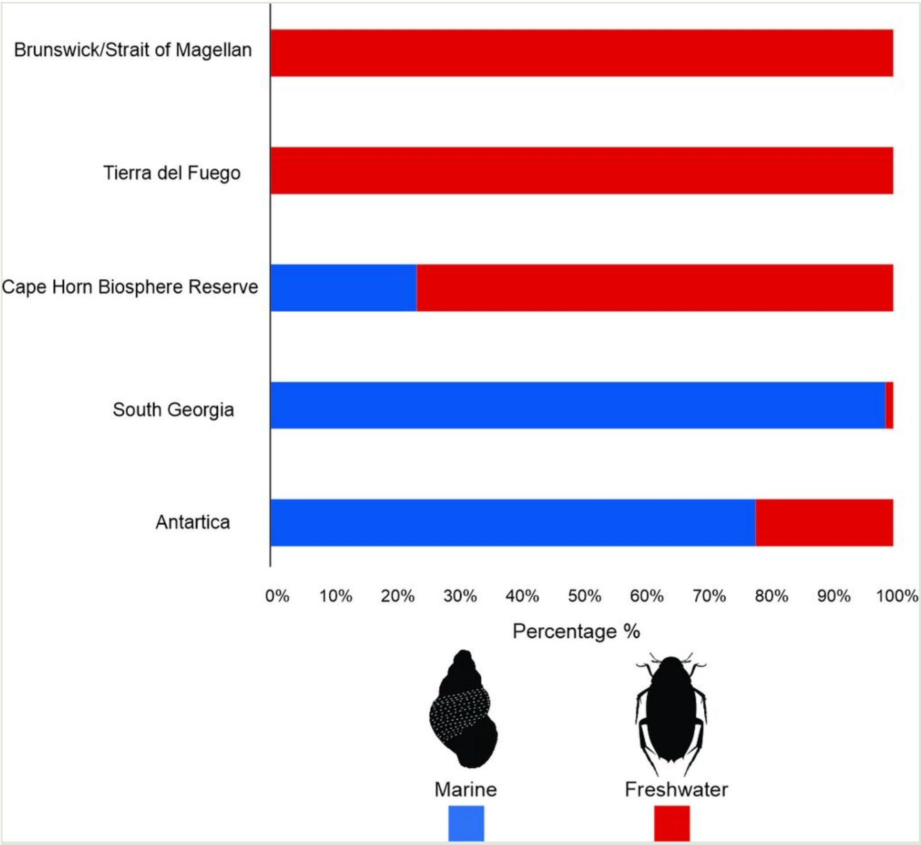


Figure 5. doi

Biodiversity of aquatic invertebrates from the different regions included in this study.

These results deserve to be highlighted as they point out where sampling and geographic exploration efforts should be aimed and to survey and digitise the under-represented taxa in the territory. In this regard, the highest number of records obtained in the CHBR (Fig. 5) could represent the result of the long-term monitoring of freshwater invertebrates in the area currently conducted by the new Cape Horn International Centre funded by the Chilean Agency of Research and Innovation.

New records and distribution extensions

Pickenia signyensis Ponder, 1983 (Fig. 7a) is a micro-gastropod that was described from Borge Bay on Signy Island and, until that time, only recorded for that geographic area (Ponder 1983). This genus is characterszed by the morphological characteristics of its radula, with absence of the central teeth (Ponder 1983, Fig. 7b). This species inhabits areas mainly associated with algae on rocky bottoms and, despite being locally common in Signy, no work on molluscan assemblages associated with macroalgae in the western Antarctic Peninsula has reported this species (Amsler et al. 2015, Martín et al. 2016, Rosenfeld et al. 2017, Amsler et al. 2022). Therefore, this study is the first report of *P. signyensis* outside of South Orkney, specifically in the southern part of the Antarctic Peninsula.

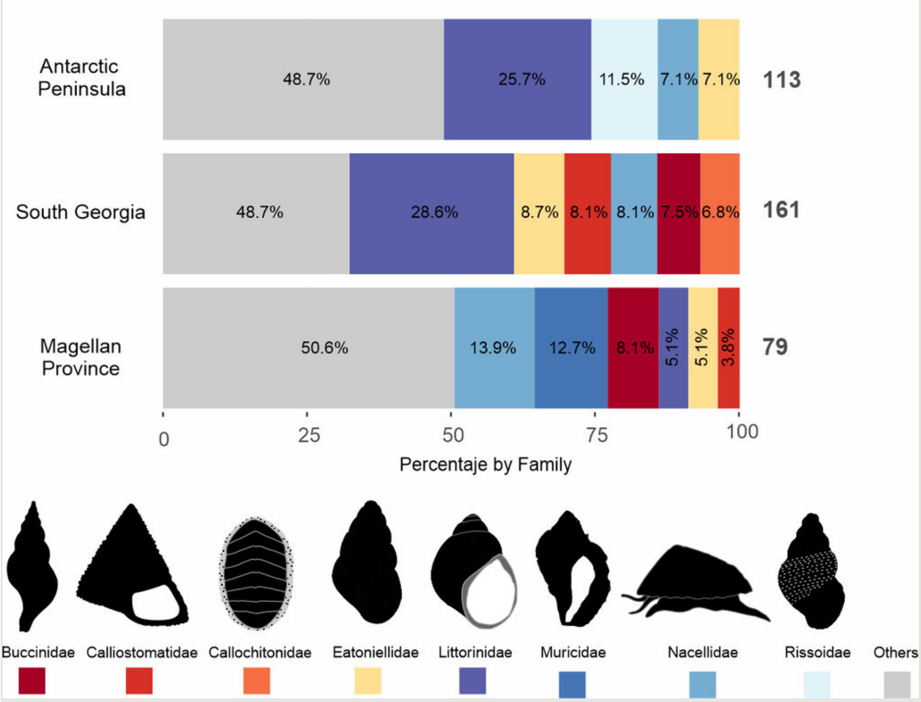


Figure 6. doi

Total occurrences and percentages per dominant molluscs' family. Data were collated from different expeditions to the Antarctic and Subantarctic regions. The absolute values of occurrences per area are represented in bold at the end of each bar.

Liotella crassicostata (Strebel, 1908) (Fig. 7c) does not present so many records since its description. It is distributed mainly in the southern part of the Magellan Province, mainly in Tierra del Fuego, Isla de los Estados and Burwood Bank (Strebel 1908, Di Luca and Zelaya 2019). It is characterised by presenting a teleoconch of up to 1.75 whorls, markedly convex in outline, with the last whorl comprising about 90% of the total shell height and a white surface, sculptured with 16 to 19 strong axial ribs per whorl (Di Luca and Zelaya 2019). Our analysed specimens measured approximately 0.7 mm in height and presented 16 axial ribs. This record would represent the first report in the South Georgia Islands.

Laevilacunaria antarctica (Martens, 1885) (Fig. 7d) is a species with a restricted distribution in the SO, mainly present in South Georgia Island, South Orkney and the western part of the Antarctic Peninsula (Reid 1989, Engl 2012, Amsler et al. 2015). This work represents the first record of a population of *L. antarctica* in the Weddell Sea, specifically on Cockburn Island, located in front of Seymour Island.

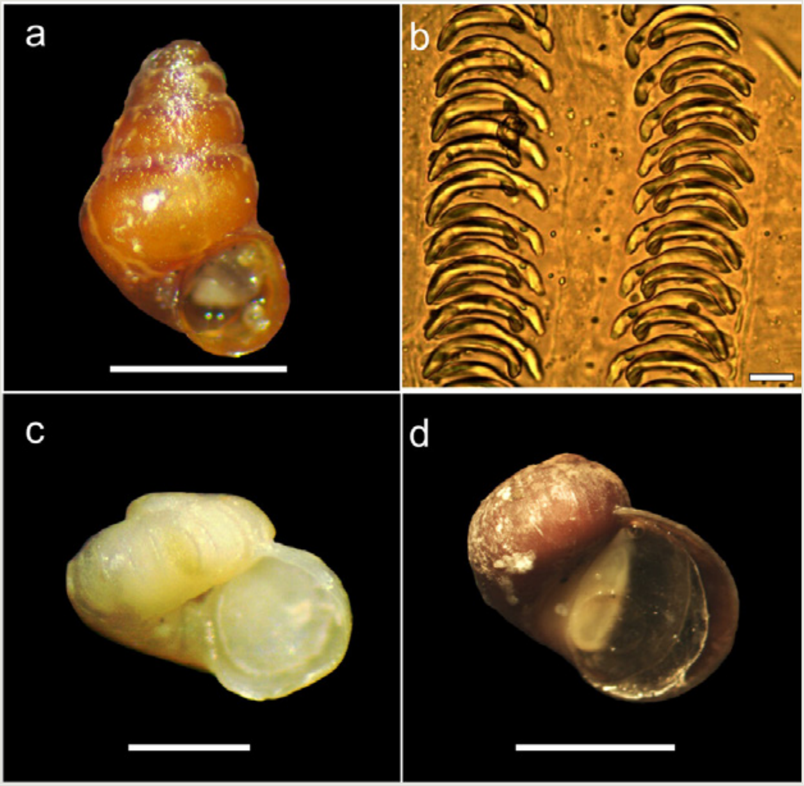


Figure 7. doi

Photographs of new records and distribution extension of marine invertebrates; **a** *Pickenia signyensis* (bar scale 1 mm); **b** Radula of *P. signyensis* where the absence of the central tooth is shown (bar scale 0.01 mm); **c** *Liotella crassicostata* (bar scale 0.4 mm); **d** *Laevilacunaria antarctica* Photographs by Sebastián Rosenfeld.

The Antarctic fairy shrimp *Branchinecta gaini* Daday, 1910 is an Anostraca species with a distribution from southern South America, Falkland/Malvinas Islands and South Georgia. Within maritime Antarctica, this shrimp occurs from the South Orkney Islands to the southern Antarctic Peninsula, including South Shetland Islands (Hawes 2009). This database contributes new records in the East Antarctic Peninsula (James Ross Island), the southern part of South Georgia and Brunswick Peninsula and Tierra del Fuego from the Magellan Region (see georeferencing information details in GBIF).

Regarding the general freshwater records, all the species found from the Diptera, Rhynchobdellida, Coleoptera, Ephemeroptera, Plecoptera, Trichoptera, Veneroida, Hygrophila, Amphipoda, Cladocera, Calanoida and Basommatophora orders correspond to the southernmost records of their known distribution. In addition, new records of *Parochlus steinenii* (Gercke, 1889) and *Boeckella* were obtained during the last expedition to South

Georgia and the Weddell Sea, but these occurrences will be updated into the existing GBIF databases (Maturana et al. 2018, Gañan et al. 2020).

With all this, these new records represent a significant contribution in occurrence data, which undoubtedly contributes to the knowledge of the biodiversity of aquatic invertebrates in the Sub-Antarctic ecoregion of Magallanes, the maritime Antarctic and the Antarctic Peninsula. Additionally, this database allows for contributions to further studies on species distribution, biogeography and ecological niche modelling, amongst others.

Acknowledgements

This work was possible thanks to the collaboration of researchers from the core team dedicated to studying marine and freshwater invertebrates. This initiative is funded by ANID-Millennium Science Initiative Program ICN2021_002 and ANID/BASAL FB210018. The Antarctic and Subantarctic expeditions, developed from 2008 to date, were financed by various research funds, mainly from the National Research Agency (FONDECYT 3210063, 1210787, PIA ACT 122065) and the Chilean Antarctic Program (DT_04-16, FP_01-21, DG_10-22). The authors would like to thank the Chilean Antarctic Institute (INACH) and the Chilean Navy from the Aquiles and Oscar Viel ships for ECA53, ECA54 and ECA55 and the crew from the Betanzos ship during the ECA58 and ECA59. We also would like to thank Commandant Charcot and our Scientist leader Geoffroy Dekersauson from Ponant expedition LEGCC120302023.

Author contributions

SR conceived the idea, SR, CSM, AD and MG built up and checked the dataset. MG made the map, constructed the metadata and published the occurrences dataset in GBIF IPT – Chile. JR, TC, CSM and SR made the taxonomic revision of the specimens. AD, TC, JR, SR, CSM, MG, CGW, JO and EP contributed with funds, expeditions logistics and sampling. SR and CSM developed the paper and CSM uploaded all the files to the Arphahub platform. All authors read and edited the submitted version and agreed on its present version.

References

- Aldea C, Troncoso JS (2008) Systematics and distribution of shelled molluscs (Gastropoda, Bivalvia and Scaphopoda) from the South Shetland Islands to the Bellingshausen Sea, West Antarctica. Sociedad Española de Malacología 26 (2): 43-117.
- Aldea C, Novoa L, Alcaino S, Rosenfeld S (2020) Diversity of benthic marine mollusks of the Strait of Magellan, Chile (Polyplacophora, Gastropoda, Bivalvia): a historical review of natural history. ZooKeys 963: 1-36. https://doi.org/10.3897/zookeys.963.52234

- Amsler CD, Miller LR, Edwards RA, Amsler MO, Engl W, Mcclintock JB, Baker BJ (2022) Gastropod assemblages associated with *Himantothallus grandifolius*, *Sarcopeltis antarctica* and other subtidal macroalgae. Antarctic Science 34 (3): 246-255.
- Amsler MO, Huang YM, Engl W, McClintock JB, Amsler CD (2015) Abundance and diversity of gastropods associated with dominant subtidal macroalgae from the western Antarctic Peninsula. Polar Biology 38: 1171-1181.
- Ariño AH (2010) Approaches to estimating the universe of natural history collections data. Biodiversity Informatics 7.
- Barnosky AD, Matzke N, Tomiya S, Wogan GO, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC, Mersey B, Ferrer EA (2011) Has the Earth's sixth mass extinction already arrived? Nature 471 (7336): 51-7. https://doi.org/10.1038/nature09678
- Brandt A, Griffiths H, Gutt J, Linse K, Schiaparelli S, Ballerini T, Danis B, Pfannkuche O (2014) Challenges of deep-sea biodiversity assessments in the Southern Ocean. Advances in Polar Science 25 (3): 204-212.
- Chown SL, Convey P (2016) Antarctic entomology. Annual Review of Entomology 61: 119-37. https://doi.org/10.1146/annurev-ento-010715-023537
- Contador T, Rendoll J, Mackenzie R, Rosenfeld S, Barroso O, Rozzi R, Goffinet B, Kennedy J, Convey P (2020) Comunidades de invertebrados terrestres del archipiélago Diego Ramírez (56°31’S), el sitio de estudios ecológicos de largo plazo más austral de américa: diversidad y afinidades con las islas subantárticas del océano austral. Anales del Instituto Patagonia 48 (2): 83-98.
- Di Luca J, Zelaya DG (2019) Gastropods from the Burdwood Bank (southwestern Atlantic): an overview of species diversity. Zootaxa 4544 (1): 78-41.
- Domínguez E, Fernández HR (2009) Macroinvertebrados bentónicos sudamericanos. In: Domínguez E, Fernández HR (Eds) Sistemática y biología. Miguel Lillo, Tucumán, Argentina.
- Engl W (2012) Shells of Antarctica. ConchBooks [ISBN 3939767441]
- Ganan M, Contador T, Rendoll J, Simoes F, Carolina P, Graham G, Castillo S, Kennedy J, Convey P (2021) Records of *Parochlus steinenii* in the Maritime Antarctic and sub-Antarctic regions. ZooKeys 1011: 63-71. https://doi.org/10.3897/zookeys.1011.56833
- Gañan M, Contador T, Rendoll J, Simoes F, Pérez C, Graham G, Castillo S, Kennedy J, Convey P (2020) Records of *Parochlus steinenii* in the Maritime Antarctic and sub-Antarctic regions. Universidad de Magallanes. https://doi.org/10.15468/2cfwd7
- Gañán M, Rosenfeld S, Maturana C, Contador T, Rendoll-Cárcamo J, Simoes F, Díaz A, Gerard K, Lopez Z, Brickle P, Saucède T, Aldea C, Cabrol L, Biersma EM, Convey P, Poulin E (2023) Occurrences of aquatic invertebrates in the Antarctic and Subantarctic regions. Occurrence dataset. Version 1.2. Instituto de Biodiversidad de Ecosistemas Antárticos y Subantárticos (BASE). URL: https://doi.org/10.15468/kn5xcg
- Gonzalez-Wevar C, Hune M, Rosenfeld S, Nakano T, Saucède T, Spencer HG, Poulin E (2018) Systematic revision of *Nacella* (Patellogastropoda: Nacellidae) based on a complete phylogeny of the genus, with the description of a new species from the southern tip of South America. Zoological Journal of the Linnean Society XX: 1-34. https://doi.org/10.1093/zoolinnean/zly067/5245194
- Griffiths H, Barnes DA, Linse K (2009) Towards a generalized biogeography of the Southern Ocean benthos. Journal of Biogeography 36 (1): 162-177.

- Griffiths HJ, Waller CL (2016) The first comprehensive description of the biodiversity and biogeography of Antarctic and Sub-Antarctic intertidal communities. Journal of Biogeography 43 (6): 1143-1155. https://doi.org/10.1111/jbi.12708
- Hawes I, Howard-Williams C, Gilbert N, Hughes K, Convey P, Quesada A (2023) The need for increased protection of Antarctica's inland waters. Antarctic Science1-25. https://doi.org/10.1017/s0954102022000463
- Hawes TC (2009) Origins and dispersal of the Antarctic fairy shrimp. Antarctic Science 21 (05): 477-482. https://doi.org/10.1017/s095410200900203x
- Ibáñez CM, Eernisse DJ, Méndez MA, Valladares M, Sellanes J, Sirenko BI, Pardo-Gandarillas MC (2019) Phylogeny, divergence times and species delimitation of *Tonicia* (Polyplacophora: Chitonidae) from the eastern Pacific Ocean. Zoological Journal of the Linnean Society 186 (4): 915-933.
- Jossart Q, Bauman D, Moreau CV, Saucede T, Christiansen H, Brasier MJ, Convey P, Downey R, Figuerola B, Martin P, Norenburg J, Rosenfeld S, Verheye M, Danis B (2023) A pioneer morphological and genetic study of the intertidal fauna of the Gerlache Strait (Antarctic Peninsula). Environmental Monitoring and Assessment 195 (4). https://doi.org/10.1007/s10661-023-11066-3
- Larrain AP (1975) Los equinoideos regulares fosiles y recientes de Chile. Gayana. Zoologia 35: 1-189.
- Libonatti ML, Michat MC, Torres PL (2011) Key to the subfamilies, tribes and genera of adult Dytiscidae of Argentina (Coleoptera: Adephaga). Revista Sociedad Entomologica Argentina 70 (3-4): 317-336.
- Llorente-Culebras S, Ladle R, Santos AC (2023) Publication trends in global biodiversity research on protected areas. Biological Conservation 281 https://doi.org/10.1016/j.biocon.2023.109988
- Lopez-Farran Z, Guillaumot C, Vargas-Chacoff L, Paschke K, Duliere V, Danis B, Poulin E, Saucede T, Waters J, Gerard K (2021) Is the southern crab *Halicarcinus planatus* (Fabricius, 1775) the next invader of Antarctica? Global Change Biology 27 (15): 3487-3504. https://doi.org/10.1111/gcb.15674
- Martín A, Miloslavich P, Díaz Y, Ortega I, Klein E, Troncoso J, Aldea C, Carbonini AK (2016) Intertidal benthic communities associated with the macroalgae *Iridaea cordata* and *Adenocystis utricularis* in King George Island, Antarctica. Polar Biology 39: 207-220.
- Maturana CS, Rosenfeld S, Naretto J, Convey P, Poulin E, Lopez Z, Gerard K, Jackson JA (2018) Occurrences of *Boeckella* at high latitudes in the Southern Hemisphere. Version 1.1. Universidad de Magallanes. https://doi.org/10.15468/zc6y59
- Maturana CS, Rosenfeld S, Naretto J, Convey P, Poulin E (2019) Distribution of the genus *Boeckella* (Crustacea, Copepoda, Calanoida, Centropagidae) at high latitudes in South America and the main Antarctic biogeographic regions. ZooKeys 854: 1-15. https://doi.org/10.3897/zookeys.854.29614
- Maturana CS, Rosenfeld S, Biersma EM, Segovia NI, González-Wevar CA, Díaz A, Naretto J, Duggan IC, Hogg ID, Poulin E, Convey P, Jackson J (2021) Historical biogeography of the Gondwanan freshwater genus *Boeckella* (Crustacea): Timing and modes of speciation in the Southern Hemisphere. Diversity and Distributions 27 (12): 2330-2343. https://doi.org/10.1111/ddi.13405
- McLellan ID, Zwick P (2007) New species of and keys to South American Gripopterygidae (Plecoptera). Illiesia 3 (4): 20-42.

- Merritt RW, Cummins KW (1996) An introduction to the aquatic insects of North America. Kendall Hunt [ISBN 0787232416]
- Nieto C (2004) South American Baetidae (Ephemeroptera): a new generic synonymy. Studies on Neotropical Fauna and Environment 39 (2): 95-101. https://doi.org/10.1080/01650520412331333747
- Ojeda J, Rosenfeld S, Marambio J, Rozzi R, Mansilla A (2014) Patrones estacionales y espaciales de la diversidad de moluscos intermareales de bahía Róbalo, canal Beagle, Reserva de la Biosfera Cabo de Hornos, Chile. Revista de Biologia Marina y Oceanografia 49 (3): 493-509.
- Pastorino G (2005) Recent Naticidae (Mollusca: Gastropoda) from the Patagonian Coast. The Veliger 47 (4): 225-258.
- Pastorino G (2016) Revision of the genera *Pareuthria* Strebel, 1905, *Glypteuthria* Strebel, 1905 and *Meteuthria* Thiele, 1912 (Gastropoda: Buccinulidae) with the description of three new genera and two new species from Southwestern Atlantic waters. Zootaxa 4179 (3): 301-344. https://doi.org/10.11646/zootaxa.4179.3.1
- Pecl GT, Araujo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, Clark TD, Colwell RK, Danielsen F, Evengard B, Falconi L, Ferrier S, Frusher S, Garcia RA, Griffis RB, Hobday AJ, Janion-Scheepers C, Jarzyna MA, Jennings S, Lenoir J, Linnetved HI, Martin VY, McCormack PC, McDonald J, Mitchell NJ, Mustonen T, Pandolfi JM, Pettorelli N, Popova E, Robinson SA, Scheffers BR, Shaw JD, Sorte CJ, Strugnell JM, Sunday JM, Tuanmu MN, Verges A, Villanueva C, Wernberg T, Wapstra E, Williams SE (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355 (6332). https://doi.org/10.1126/science.aai9214
- Ponder WF (1983) Rissoaform gastropods from the Antarctic and sub-Antarctic: The Eatoniellidae, Rissoidae, Barleeidae, Cingulopsidae, Orbitestellidae, and Rissoellidae (Mollusca, Gastropoda) of Signy Island, South Orkney Islands, with a review of the Antarctic and sub-Antarctic (excluding southern South America and the New Zealand sub-Antarctic Islands) species. Vol. 108. British Antarctic Survey [ISBN 0856651001]
- Powell AWB (1954) Antarctic and subantarctic Mollusca. Records of the Auckland Institute and Museum 5 (3/4): 117-193.
- Reid D (1989) The comparative morphology, phylogeny and evolution of the gastropod family Littorinidae. Philosophical Transactions of the Royal Society of London. B, Biological Sciences 324 (1220): 1-110.
- Rintoul SR, Garabato ACN (2013) Chapter 18 - Dynamics of the Southern Ocean circulation. In: Siedler G, Griffies S, Gould J, Church J (Eds) International Geophysics. Vol. 103. Elsevier, 21 pp. [ISBN 0074-6142].
- Rocha-Ortega M, Rodriguez P, Córdoba-Aguilar A (2021) Geographical, temporal and taxonomic biases in insect GBIF data on biodiversity and extinction. Ecological Entomology 46 (4): 718-728. https://doi.org/10.1111/een.13027
- Rogers DC, Zúñiga O, De los Ríos P (2008) Fairy shrimp (Branchiopoda: Anostraca) of Chile. Journal of Crustacean Biology 28 (3): 543-550. https://doi.org/10.1651/07-2953.1
- Rosenfeld S, Aldea C, Ojeda J, Marambio J, Hüne M, Troncoso J, Mansilla A (2017) Molluscan assemblages associated with Gigartina beds in the Strait of Magellan and the South Shetland Islands (Antarctica): a comparison of composition and abundance. Polar Research 36 (1). https://doi.org/10.1080/17518369.2017.1297915
- Rosenfeld S, Marambio J, Aldea C, Rodriguez J, Mendez F, Gonzalez-Wevar C, Gerard K, Contador T, Mackenzie R, Rozzi R, Mansilla A (2020) Actualización del catastro de

ensamble de moluscos costero-marinos del archipiélago Diego Ramírez (56°31’S), Chile: un refugio para la economía sustentable y conservación subantártica. Anales del Instituto Patagonia 48 (3): 113-125.

- Rosenfeld S, Maturana C, Spencer HG, Convey P, Saucède T, Brickle P, Bahamonde F, Jossart Q, Poulin E, Gonzalez-Wevar C (2022) Complete distribution of the genus *Laevilitorina* (Littorinimorpha, Littorinidae) in the Southern Hemisphere: remarks and natural history. ZooKeys https://doi.org/10.3897/zookeys.1127.91310
- Rozzi R, Armesto J, Gutiérrez J, Massardo F, Likens G, Anderson C, Poole A, Moses K, Hargrove E, Mansilla A, Kennedy J, Willson M, Jax K, Jones C, Callicott JB, Arroyo MK (2012) Integrating ecology and environmental ethics: Earth stewardship in the southern end of the Americas. Bioscience 62 (3): 226-236. https://doi.org/10.1525/bio.2012.62.3.4
- Rozzi R, Quilodrán C, Botero-Delgadillo E, Crego R, Napolitano C, Barroso O, Torres-Mura JC, Vásquez R (2022) El Rayadito subantártico: disponibilidad del binomio *Aphrastura subantarctica* (Passeriformes, Furnariidae). Boletín Museo Nacional de Historia Natural 71 (2): 9-15. https://doi.org/10.54830/bmnhn.v71.n2.2022.222
- Smith E (1879) Mollusca. Philosophical Transactions of the Royal Society of London 168: 167-192. URL: http://www.jstor.org/stable/109229
- Strebel H (1908) Die Gastropoden. Wissenschaftliche Ergebnisse der Schwedischen Sudpolar-expedition 1901-1903. Stockholm 6.
- Troncoso N, Vangoethem JL, Troncoso JS (2001) Contribution to the marine molluscan fauna of Kerguelen Islands, South Indian Ocean. Sociedad Española de Malacología 19 (1): 83-114.
- Troudet J, Grandcolas P, Blin A, Vignes-Lebbe R, Legendre F (2017) Taxonomic bias in biodiversity data and societal preferences. Scientific Reports 7 (1). https://doi.org/10.1038/s41598-017-09084-6
- v Martens E, Pfeffer G (1886) Die Mollusken von Süd-Georgien nach der Ausbeute der Deutschen Station 1882-83: Von Prof. Dr. Eduard v. Martens und Dr. Georg Pfeffer. Mit 4 Tafeln Abbildungen. Th. G. Meissner
- von Ellenrieder N (2003) A synopsis of the Neotropical species of '*Aeshna*' Fabricius: the genus *Rhionaeschna* Förster (Odonata: Aeshnidae). Tijdschrift voor Entomologie 146: 67-207.
- Wauchope HS, Shaw JD, Terauds A (2019) A snapshot of biodiversity protection in Antarctica. Nature Communication 10 (1). https://doi.org/10.1038/s41467-019-08915-6
- Wilkinson MD, Dumontier M, Aalbersberg IJ, Appleton G, Axton M, Baak A, Blomberg N, Boiten JW, da Silva Santos LB, Bourne PE, Bouwman J, Brookes AJ, Clark T, Crosas M, Dillo I, Dumon O, Edmunds S, Evelo CT, Finkers R, Gonzalez-Beltran A, Gray AJ, Groth P, Goble C, Grethe JS, Heringa J, t Hoen PA, Hooft R, Kuhn T, Kok R, Kok J, Lusher SJ, Martone ME, Mons A, Packer AL, Persson B, Rocca-Serra P, Roos M, van Schaik R, Sansone SA, Schultes E, Sengstag T, Slater T, Strawn G, Swertz MA, Thompson M, van der Lei J, van Mulligen E, Velterop J, Waagmeester A, Wittenburg P, Wolstencroft K, Zhao J, Mons B (2016) The FAIR Guiding Principles for scientific data management and stewardship. Scientific Data 3 https://doi.org/10.1038/sdata.2016.18

- Zelaya DG (2004) The genus *Margarella* Thiele, 1893 (Gastropoda: Trochidae) in the southwestern Atlantic Ocean. The Nautilus 118 (3): 112-120.
- Zelaya DG (2005) Systematic and biogeography of marine gastropod molluscs from South Georgia. Spixiana 28 (2): 109-139.
- Zelaya DG, Güller M, Ituarte C (2020) Filling a blank in bivalve taxonomy: an integrative analysis of Cyamioidea (Mollusca: Bivalvia). Zoological Journal of the Linnean Society 190: 558-591.

Biodiversity Data Journal 11: e111982
doi: 10.3897/BDJ.11.e111982

Data Paper

Laevilacunaria (Mollusca, Gastropoda) in the Southern Ocean: A comprehensive occurrence dataset

Andreas Schmider-Martínez[‡,§], Claudia S. Maturana[|,¶], Yarleth Poveda[#], Sebastián Rosenfeld[|,¤], Zambra López-Farrán[«], Thomas Saucède[»], Elie Poulin[|], Claudio González-Wevar[|,«]

‡ Instituto de Ciencias Marinas y Limnológicas (ICML), Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile
§ Centro i-mar, Universidad de Los Lagos, Puerto Montt, Chile
| Instituto de Biodiversidad de Ecosistemas Antárticos y Subantárticos (BASE), Santiago, Chile
¶ Cape Horn International Center (CHIC), Puerto Williams, Chile
# Universidad Austral de Chile, Valdivia, Chile
¤ Centro de Investigación Gaia-Antártica, Universidad de Magallanes, Punta Arenas, Chile
« Centro Fondap de Investigación en Dinámica de Ecosistemas Marinos de Altas Latitudes (IDEAL), Universidad Austral de Chile, Valdivia, Chile
» Biogéoscience, UMR CNRS 6282, Université de Bourgougne 6, Dijon, France

Corresponding author: Claudia S. Maturana (claudiamaturana@ug.uchile.cl)

Academic editor: Huw Griffiths

Received: 31 Aug 2023 | Accepted: 03 Oct 2023 | Published: 09 Oct 2023

Citation: Schmider-Martínez A, Maturana CS, Poveda Y, Rosenfeld S, López-Farrán Z, Saucède T, Poulin E, González-Wevar C (2023) Laevilacunaria (Mollusca, Gastropoda) in the Southern Ocean: A comprehensive occurrence dataset. Biodiversity Data Journal 11: e111982. https://doi.org/10.3897/BDJ.11.e111982

Abstract

Background

The present dataset is a compilation of georeferenced occurrences of the littorinid genus *Laevilacunaria* Powell, 1951 (Mollusca, Gastropoda) in the Southern Ocean. Occurrence data were obtained from field expeditions (Antarctic and sub-Antarctic sampling) between 2015 and 2022, together with a review of published literature including records from 1887 to 2022. Three *Laevilacunaria* species have been recorded from the Southern Ocean: *Laevilacunaria bennetti*, *L. antarctica* and *L. pumilio*.

New information

The present dataset includes 75 occurrences, representing the most exhaustive database of this Antarctic and sub-Antarctic littorinid genus. The publication of this data paper was funded by the Belgian Science Policy Office (BELSPO, contract n°FR/36/AN1/AntaBIS) in the Framework of EU-Lifewatch as a contribution to the SCAR Antarctic biodiversity portal (biodiversity.aq).

Keywords

Littorinids, *Laevilacunaria*, Laevilitorininae, Antarctic, sub-Antarctic, Southern Ocean

Introduction

Species-distribution knowledge is a key parameter to understand the composition and behaviour of communities in different environments. Many studies, based on species distributions, allow us to understand the evolutionary pathways and biogeographical patterns, as well as the processes and mechanisms associated with their origins and diversification (Pearse et al. 2009, Allcock and Strugnell 2012, Fraser et al. 2012, González-Wevar et al. 2013, Fraser et al. 2014, González-Wevar et al. 2016, González-Wevar et al. 2021, Rosenfeld et al. 2022). A number of initiatives are currently facing the challenge to record species and their distributions, including the Census of Marine Life (http://www.coml.org/about-census/), whose results were compiled in the Biogeographic Atlas of the Southern Ocean (De Broyer et al. 2014). This is undoubtedly a difficult scientific task, but several initiatives are trying to face it through freely available platforms, such as the Ocean Biodiversity Information System (OBIS) and Global Biodiversity Information Facility (GBIF), where different kinds of collectors including museums, herbaria and researchers can offer their respective datasets. The laboratory of *Genómica y Ecología Molecular Antártica y sub-Antártica* (LAGEMAS), located at the Universidad Austral de Chile, is also making an effort to nurture and update this open and free-access dataset of occurrence information on higher latitude littorinids for future studies in distribution, biogeography and modelling.

A baseline survey of Antarctic biodiversity indicated that molluscs are one of the most abundant and widely distributed groups and have been recorded in 85% of intertidal localities, more than arthropods (55%) or macroalgae (44%) (Griffiths & Waller 2016). The most ubiquitous mollusc species were the patellogastropod *Nacella concinna* (Antarctic limpet) and the littorinid *Laevilitorina caliginosa*, present in 56 and 45 of the 98 areas studied by Griffiths and Waller (2016), respectively.

The family of the intertidal gastropods Littorinidae Children, 1834, commonly known as periwinkles, includes more than 200 species in three subfamilies; Lacuninae, Laevilitorininae and Littorininae (Bouchet et al. 2005). These small gastropod snails are very abundant in shallow intertidal rocky ecosystems worldwide and particularly in temperate and tropical areas. Littorinids are some of the most extensively used model organisms in ecology (Eschweiler et al. 2009), evolution (Johannesson 2003, Reid et al. 2012), speciation (Williams et al. 2003), physiology (McMahon 2001) and reproduction (Johannesson et al. 1995). They have also been used for micro-evolutionary studies including natural selection and genetic differentiation (Reid et al. 2006) and macro-evolutionary studies, such as adaptive radiation and historical biogeography (Reid 1996, Williams et al. 2003, González-Wevar et al. 2022). Most of the studies in littorinids have been done in temperate groups and little is known about the origin and evolutionary relationships of higher latitude Antarctic and sub-Antarctic genera.

The Southern Ocean includes three littorinid genera: *Pellilitorina* Pfeffer, 1886, *Laevilacunaria* Powell, 1951 and *Laevilitorina* Pfeffer, 1886. The genus *Pellilitorina* belongs to the subfamily Lacuninae Gray, 1857, while *Laevilitorina* and *Laevilacunaria* are the extant members of the subfamily Laevilitorininae.

The genus *Laevilacunaria* includes three species: *L. bennetti* (Preston, 1916), *L. antarctica* (Martens, 1885) and *L. pumilio* (E. A. Smith, 1877). *Laevilacunaria antarctica* was originally described under the name *Lacuna antarctica* from South Georgia (Martens 1885). Similarly, *L. bennetti* was described as *Pellilitorina bennetti* from the South Shetland Islands, Antarctic Peninsula (Preston 1916) and *L. pumilio* was described as *Hydrobia pumilio* from the Kerguelen Islands (E. A. Smith 1877). Subsequently, based on morphological characteristics of the shell and radula, Powell (1951) described the genus *Laevilacunaria* and placed these three species in the genus. The distribution of *L. antarctica* includes hard rocky-bottom ice-free sublittoral ecosystems across maritime Antarctic, including the Antarctic Peninsula, South Shetland Islands, South Orkney Islands, Signy Island and South Georgia (Picken 1979, Iken 1999, Engl 2012, Amsler et al. 2015, Aghmich et al. 2016, Martin et al. 2016) The distribution of *L. bennetti* also includes rocky ice-free sublittoral ecosystems across the Antarctic Peninsula, South Shetland Islands and the Palmer Archipelago (Picken 1980, Amsler et al. 2015). Finally, *L. pumilio* was described in the sub-Antarctic Kerguelen Archipelago, but it has also been reported at the Bellinghausen Sea in the Antarctic Peninsula (Rosewater 1970, Ivanova and Grebelnyi 2017).

The Antarctic *Laevilacunaria* species (*L. antarctica* and *L. bennetti*) exhibit narrow bathymetric distributions, compared to other Antarctic marine invertebrates, that range from the upper intertidal to 90 m depth, with maximum abundance recorded at 12 m depth (Reid et al. 2012). Both species are highly abundant and have ecological importance in almost all marine ecosystems across the Antarctic Peninsula. As recorded in most Antarctic marine invertebrates, *Laevilacunaria* species exhibit marked seasonal, spatial and growth variability throughout their distributions. According to Picken (1979) and Amsler et al. (2015), the highest abundances of *L. antarctica* are found associated with macroalgae like *Desmarestia anceps*, *Desmarestia menziesii*, *Pseudophycodrys* sp. and over the fronds of *Plocamium*, *Leptosarca*, *Sarcopeltis*, *Ascoseira*, *Himantothallus*, *Pantoneura* sp. and *Phyllophora* sp., where they graze and reproduce. However, ecological studies suggest that *L. antarctica* does not feed on *Ascoseira mirabilis*, *Phaeurus antarticus* or *Himantothallus grandifolius* (Iken 1999). According to Iken (1999), *L. antarctica* feeds two thirds on epiphytic diatoms and a third on macroalgae. This is reflected in the taenioglosa-type radula of the species, a very plastic tool that allows it to feed on a wide spectrum of algae (Reid 1989, Iken 1999). Information concerning the species *L. bennetti* and *L. pumilio* is scarce; most of the records and references are associated with *L. antarctica*.

The present review documents the state of knowledge of the genus *Laevilacunaria* and provides an updated database for the Southern Ocean.

General description

Purpose: This dataset was created within the framework of the undergraduate thesis of the first author and part of the main research of the principal investigator. The main objective of the dataset is to build a baseline of the geographic distribution as a complement to the research on the biogeography of littorinids that is currently being carried out in the Laboratorio de Genomica y Ecología Molecular Antártica y Subantártica.

Project description

Title: Antarctic and sub-Antarctic littorinid database

Personnel: Andreas Schmider-Martínez, Claudia Maturana, Sebastián Rosenfeld, Claudio González-Wevar

Study area description: This study is centred on Antarctic and sub-Antarctic areas between latitudes 45°S and 69ºS, including different provinces of the Southern Ocean. It extends around 24,000 km from east to west and 8,000 km from north to south and covers an area of around 192 million km^2. The objective of this study is to integrate the most complete database of species occurrences for the Antarctic and sub-Antarctic genus *Laevilacunaria* across this area.

Design description: The present study provides a specific level dataset of *Laevilacunaria* including 75 records, using a combination of data collected during recent Antarctic campaigns and literature. This review is the most updated and exhaustive database on this important Antarctic littorinid genus and will be a base for future biogeographic and/or phylogeographic analyses.

Funding: Regular FONDECYT 1210787 Project, Initiation FONDECYT 11140087 project, Millennium Institute Biodiversity of Antarctic and Subantarctic Ecosystems (Mi-BASE) - Instituto Milenio ICN2021_002, Project Genomic Antarctic Biodiversity (GAB) - PIA CONICYT ACT172065, Research Center Dynamics of High Latitude Marine Ecosystems - Fondap-IDEAL 15150003, Postdoc FONDECYT 3210063, INACH DG_10-22 and Regular INACH RG_18-17 project.

Sampling methods

Description: The compilation of records for the database of the genus *Laevilacunaria* in the Southern Ocean was obtained by two different types of sources: 1) field sampling data obtained during the Chilean Antarctic Scientific Expedition (ECA) between the years 2015 (ECA51) and 2022 (ECA59), together with records from Crozet and Kerguelen Islands through the PROTEKER project (an Underwater Observatory at Kerguelen) supported by the French Polar Institute; and 2) literature review, museums and cruise reports. The search for public literature included scientific manuscripts and books concerning *Laevilacunaria* and species that were once included in the genera *Laevilitorina, Pellilitorina, Hydrobia* and *Lacuna*, which now belong to *Laevilacunaria*.

Sampling description: Occurrence data were compiled from Antarctic campaigns at different localities across the Southern Ocean (Fig. 1 and Table 1) including the South Shetland Islands (Penguin, Greenwich, King George, Livingstone, Robert, Deception), the west Antarctic Peninsula (Marguerite Bay, Isabel Riquelme Island, Doumer Island) (Fig. 2), the sub-Antarctic South Georgia Island during 2015-2022 and Crozet and Kerguelen Archipelagos (Fig. 3). The sampling was the result of an international and national collaboration network.

Table 1.

Field campaigns during 2015–2022 identifying which littorinids of the dataset were collected at each locality.

Locality	**Island**	**Species**	**Nº specimens**	**Date / ECA**	**ver.Coordinates**
Fildes Bay	King George Island	*L. antarctica* *L. bennetti*	13 20	2022/ECA59 2022/ECA59	62°12' S | 58°57' W
Admiralty Bay	King George Island	*L. antarctica*	10	2019/ECA56	62°12' S | 58°57' W
Pingüino Island	King George Island	*L. antarctica*	16	2020/ECA57	62°06' S | 77°52' W
Hannah Point	Livingston Island	*L. antarctica*	10	2017/54	62°39' S | 60°38' W
Coppermine Peninsula	Robert Island	*L. antarctica*	29	2017/ECA54	62°22' S | 59°42' W
Deception Island	Deception Island	*L. antarctica*	26	2017/ECA54	62°57' S | 60°40' W
Discovery Base	Greenwich Island	*L. antarctica* *L. bennetti*	48 13	2021/ECA58 2020/ECA58	62°28' S | 59°37' W

Locality	**Island**	**Species**	**Nº specimens**	**Date / ECA**	**ver.Coordinates**
South Bay	Doumer Island	*L. antarctica* *L. bennetti*	22 8	2017/ECA54 2021/ECA58	64°52' S | 63°35' W
Isabel Riquelme Island	Ant. Peninsula	*L. antarctica*	7	2019/ECA56	63°19' S | 57°53' W
Trinity Island	Trinity Island	*L. antarctica*	5	2020/ECA58	63°47' S | 60°44' W
South Georgia	South Georgia	*L. antarctica*	2	2021/ECA59	54°26' S | 36°33' W
Avian Island	Marguerite Bay	*L. antarctica* *L. bennetti*	21 5	2017/ECA54 2019/ECA56	67°46' S | 68°52' W
Kerguelen Islands	Kerguelen Archilepagos	*L. pumilio*	1	2021/ PROTEKER	46°24’ S| 51°52’ E
Crozet Islands	Crozet Island	*L. pumilio*	5	2021/ PROTEKER	49°21’ S| 70°13’ E

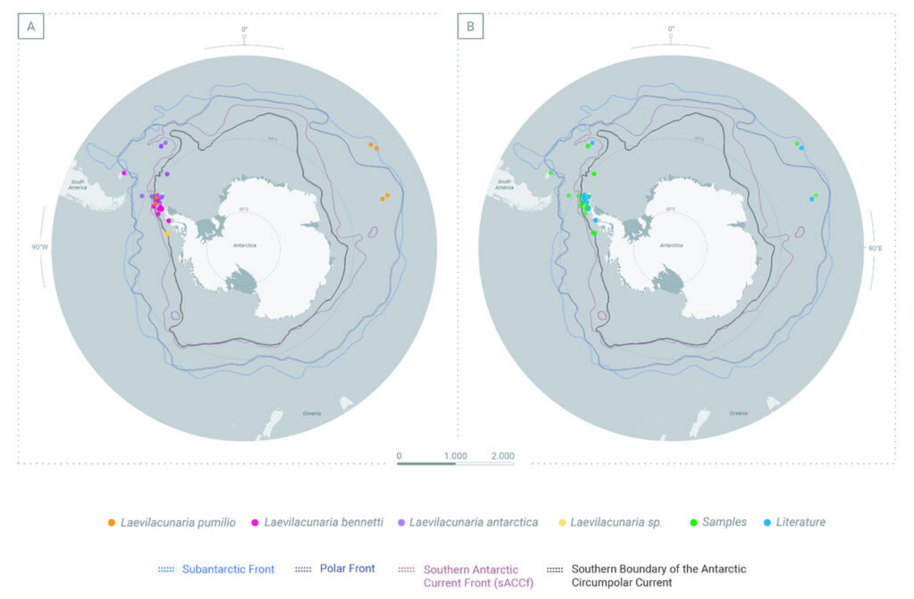


Figure 1. doi

Distribution of all records of the genus *Laevilacunaria* in the Southern Ocean (SO). **A** Distribution of the three different species of *Laevilacunaria* in the SO; **B** Distribution of the specimen of the genus *Laevilacunaria* reported in the Southern Ocean showing the origin of the sources; literature and sampling.

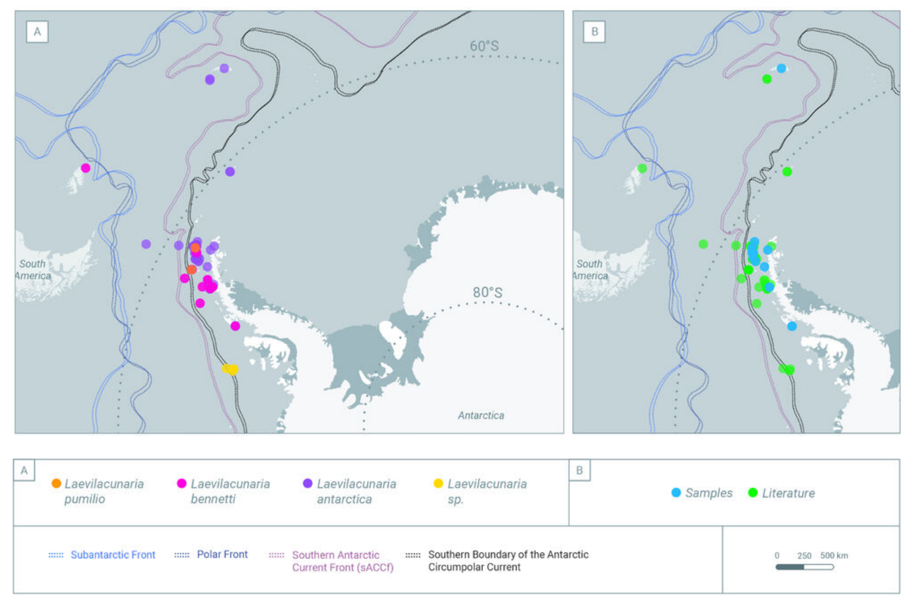


Figure 2. doi

The distribution of *Laevilacunaria* across the Antarctic Peninsula, showing: **A** Distribution of the three different species of *Laevilacunaria*; **B** Distribution of the individuals of the genus *Laevilacunaria* reported in the Southern Ocean showing the origin of the sources; literature and sampling.

An extensive revision of the genus *Laevilacunaria* was done in the ISI web of Knowledge searching for the current scientific name of the group: *Laevilacunaria* and species of *Laevilitorina*, *Pellilacunella*, *Pellilitorina*, *Lacuna* and *Hydrobia*, which now are included in *Laevilacunaria*, as well as other names like *Laevilacunaria/Pellilitorina brandsfieldensis* and *Laevilacunaria bennetti* which were also included in the examination. In order to obtain the distribution of the species, we collected information from manuscripts and books where *Laevilacunaria* was mentioned and included localities, dates, coordinates, expeditions, depths and years (Rosewater 1970, Arnaud and Bandel 1976, Picken 1979, Picken 1980, Iken 1999, Amsler et al. 2015, Simone 2018). All papers that mention the presence of *Laevilacunaria* using a quote were noted, but not necessarily included in the database, since they did not include geographical coordinates, locality description or were duplications of other references.

Quality control: Duplicate data were combined into a single record to construct a unified database. To evaluate the quality of the filtered dataset, all records were checked for mismatches between reported geographic location and the associated metadata. All taxonomic records were included for the geographic distribution.

Step description: Occurrences are presence-only data for two different sampling methodologies: 1) individual collection of *Laevilacunaria* by hand in intertidal pools during low tide periods and 2) SCUBA diving from 0 - 15 m depth where we collected: a) individuals directly by hand and/or b) substrate (sediment, macroalgae) and the associated fauna (Rosenfeld et al. 2022). All individuals were immediately preserved in ethanol (95%) for further molecular and morphological analyses at the LAGEMAS laboratory, Universidad Austral de Chile, Valdivia. Geographical coordinates were recorded using GPS for each sampling site.

Figure 3. doi

The distribution of *Laevilacunaria* in the Crozet Islands and Kerguelen Islands, showing: **A** Distribution of the three different species of *Laevilacunaria*; **B** Distribution of the individuals of the genus *Laevilacunaria* reported in the Southern Ocean showing the origin of the sources; literature and sampling.

Geographic coverage

Description: The genus *Laevilacunaria* is represented across the whole Southern Ocean and the adjacent Islands (Fig. 1): South Shetland Islands, Signy Island, Anvers Island, Elephant Island, archipelagos like the Archipelagos of Palmer, Archipelagos of Melchior and along the Antarctic Peninsula (Fig. 2), the sub-Antarctic Islands of Crozet, Kerguelen (Fig. 3) and South Georgia.

Laevilacunaria antarctica:

Individuals of *L. antarctica* were found on intertidal rocky ecosystems across the Antarctic Peninsula and the South Shetland Islands (Fig. 4a).

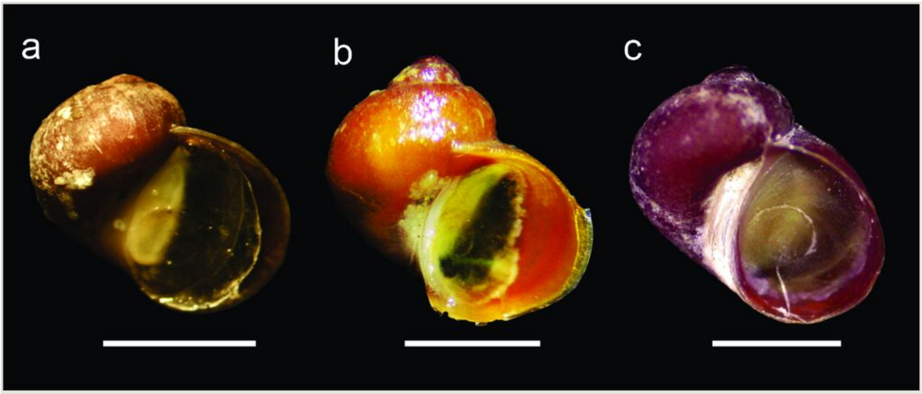


Figure 4. doi

Laevilacunaria spp. **a** *Laevilacunaria antarctica* (scale bar 2.5 mm); **b** *Laevilacunaria bennetti* (scale bar 2 mm); **c** *Laevilacunaria pumilio* (scale bar 1 mm). Photograph (a) from Rosenfeld et al. (2022), (b) and (c) by Sebastián Rosenfeld.

Laevilacunaria bennetti:

Laevilacunaria bennetti (Fig. 4b) was less abundant than *L. antarctica* and was found only at Fildes Bay (King George Island), Discovery Bay (Greenwich Island), South Bay (Doumer Island) and Avian Island (Marguerite Bay). The described distribution for this species includes Anvers Island, along the Archipelago of Palmer and the South Shetland Islands, the Bransfield Strait and the Schollaert Channel.

Laevilacunaria pumilio:

The elusive species *L. pumilio* (Fig. 4c) has been recorded in literature at the type locality, the Kerguelen Archipelago, Crozet Islands, with dubious records at Fildes Bay (King George Island, South Shetland Islands) and the Bellinghausen Sea. During the recent Proteker expedition, our French collaboration team recorded five *L. pumilio* from Crozet Islands and one from the Kerguelen Islands.

Coordinates: -70 and -46 Latitude; -78 and 70 Longitude.

Taxonomic coverage

Description: The complete record of the database in *Laevilacunaria* contains 75 occurrences, including the three species of the genus across their distributions in the Southern Ocean. The literature review includes 64 records of species of *Laevilacunaria*, of which 57 were used for the geographic distribution studies and seven were not included because they were quotes of other mentions. Of the 57 records, 41 were *L. antarctica*; 10 *L. bennetti*; three *L. pumilio* and three *Laevilacunaria* as a genus. The sampling records contain a total of 261 individuals, of which 209 were *L. antarctica*, 46 *L. bennetti* and six

L. pumilio. The time coverage of the dataset starts in 1877 (E. A. Smith 1877) and ends in 2022 with samples collected during ECA 58.

The present dataset is the most exhaustive and updated list of available occurrences and material of *Laevilacunaria* (Littorinidae) in the Southern Ocean. This collection provides information about the occurrence of three *Laevilacunaria* species: *Laevilacunaria antarctica* (Fig. 4a), *L. bennetti* (Fig. 4b) and *L. pumilio* (Fig. 4c). Occurrence distribution is shown in Fig. 1.

Taxa included:

Rank	Scientific Name
genus	*Laevilacunaria*
species	*Laevilacunaria antarctica*
species	*Laevilacunaria bennetti*
species	*Laevilacunaria pumilio*

Traits coverage

Taxonomic identification

All newly-collected *Laevilacunaria* specimens identified in this study (Fig. 4) showed morphological characteristics corresponding to those described in literature (Reid 1989, Engl 2012). Most of the studies in *Laevilacunaria* have been focused on *L. antarctica*, while *L. bennetti* and *L. pumilio* have not been considered. In fact, neither of these species has a particular study and *L. pumilio* has only been cited in its original description.

Temporal coverage

Notes: 1887-03-01 through 2022-02-08

Collection data

Collection name: Coleccion de Invertebrados del Laboratorio de Genómica y Ecologia Molecular de la Universidad Austral de Chile

Collection identifier: urn:UACh:LAGEMAS:Inv:Mol

Parent collection identifier: LAGEMAS

Specimen preservation method: alcohol 95%

Usage licence

Usage licence: Creative Commons Public Domain Waiver (CC-Zero)

IP rights notes: This work is licensed under a Creative Commons Attribution (CC-BY 4.0) License.

Data resources

Data package title: *Laevilacunaria* (Mollusca, Gastropoda) in the Southern Ocean: A comprehensive occurrence dataset.

Resource link: https://doi.org/10.15468/eequqq

Alternative identifiers: https://www.gbif.org/dataset/c70094e2-7607-42da-8fb2-76669ac5c1ac; http://gbif-chile.mma.gob.cl/ipt/resource?r=genus_laevi_base

Number of data sets: 1

Data set name: *Laevilacunaria* (Mollusca, Gastropoda) in the Southern Ocean: A comprehensive cccurrence dataset.

Data format: Darwin Core

Description: All data collected for analysis reported here, including the study samples and literature, have been deposited and incorporated in the available information on the Global Biodiversity Information Facility (Schmider-Martínez et al. 2023).

Column label	Column description
occurrenceID	Unique identifier for each occurrence per taxa.
occurrenceStatus	The statement about the presence of the Taxon at the given Location.
materialSampleID	The unique identifier for the MaterialSample.
collectionID	The identifier for the collection or dataset from which the record was derived.
taxonRank	The taxonomic rank of the most specific name in the scientificName.
kingdom	The full scientific name of the kingdom in which the taxon is classified.
phylum	The full scientific name of the phylum in which the taxon is classified.
class	The full scientific name of the class in which the taxon is classified.
order	The full scientific name of the order in which the taxon is classified.
family	The full scientific name of the family in which the taxon is classified.
genus	The full scientific name of the genus in which the taxon is classified.
scientificName	The full scientific name in the lowest level taxonomic rank that was determined.

specificEpithet	The name of species epithet of the scientificName.
scientificNameAuthorship	The authorship information for the scientificName formatted according to the conventions of the applicable nomenclaturalCode.
scientificNameID	The identifier for the nomenclatural details of a scientific name.
country	The name of the country or major administrative unit in which the Location occurs.
countryCode	The standard code for the country in which the Location occurs following the best practice using an ISO 3166-1-alpha-2 country code.
locality	The specific description of the place in which the collection was made.
island	The name of the island on which the Location occurs.
decimalLongitude	The geographic longitude in decimal degrees of the geographic centre of a Location. Positive values are east of the Greenwich Meridian, negative values are west of it.
decimalLatitude	The geographic latitude in decimal degrees of the geographic centre of a Location. Positive values are north of the Equator, negative values are south of it.
verbatimCoordinates	The verbatim original spatial coordinates of the Location.
coordinateUncertaintyInMetres	The horizontal distance in metres from the given decimalLatitude and decimalLongitude describing the smallest circle containing the whole of the Location. We used the reasonable lower limit on or after 01-05-2020- of a GPS.
eventDate	The date-time when the event was recorded. We used best practice using the ISO 8601:1:2019.
year	The four-digit year in which the Occurrence was recorded, according to the Common Era Calendar.
month	The integer month in which the Occurrence was recorded.
minimumDepthInMetres	The lesser depth below the local surface in metres.
maximumDepthInMetres	The greater depth below the local surface in metres.
individualCount	The number of individuals present at the time of the Occurrence if it was countable.
basisOfRecord	The specific nature of the data record. We used the recommended best practice of one of the Darwin Core classes.
type	The nature of the resource. We used the recommended best practice of one of the Darwin Core classes.
preparations	A list concatenated and separated of preparations and preservation methods for the specimen.
recordedBy	A person or a list of names of people responsible for recording the original Occurrence.
identifiedBy	A person or a list of names of people responsible for recording the original Occurrence.

samplingProtocol	Descriptions of the methods used during the sampling Event.
associatedReferences	A list concatenated and separated of bibliographic reference of literature associated with the Occurrence.
habitat	A category or description of the habitat in which the Event occurred.
associatedMedia	A list concatenated and separated of publications associated with the Occurrence.
rightsHolder	The laboratory owning and managing rights over the resource.
organismRemarks	Comments about the nomenclatural history of the specie.

Additional information

Discussion

The compilation of species distributions has increased in the last few years with different projects like the SCAR projects, National Antarctic Science projects, the Census of Marine Life (http://www.coml.org/about-census/), the Millennium Institute of Antarctic and sub-Antarctic Biodiversity (Mi-BASE) and the Biogeographic Atlas of the Southern Ocean (De Broyer et al. 2014), amongst others. Understanding species distribution patterns is pivotal for other scientific areas including evolution, biogeography, ecology and modelling studies; to have better knowledge of these topics would permit us to interpret the origins and the evolutionary routes and, thus, allow us to predict better future scenarios under current climate change. This study represents a contribution to improve our knowledge of biodiversity by increasing the open access database for future biogeographic and species modelling for Southern Ocean littorinids and particularly for *Laevilacunaria*.

Literature remarks

This study unifies the knowledge of biodiversity and geographical distribution records for *Laevilacunaria* using two different types of species reports (literature and sampling). The other two recognised species of the genus have only been mentioned in a couple of studies (including their original descriptions), which are not directly studies of marine invertebrates. Since then, *L. pumilio* only has been mentioned in three other studies: 1) Rosewater (1970), a summary of the family of the Littorinidae in the Indian Ocean; 2) Cantera and Arnaud (1984), a gastropod study and mention of *L. pumilio* by Crozet; 3) Ivanova and Grebelnyi (2017), studying the stomach content of anemones where *L. pumilio* was identified with a photograph. However, as previously stated, the actual presence of the Kerguelenian species *L. pumilio* in Antarctica requires further confirmation. *Laevilacunaria pumilio* is the only species of *Laevilacunaria* for which no description of radula morphology has been made. *Laevilacunaria bennetti* has been mentioned on five occasions since the first description of Preston (1916): 1) Powell (1951) showed several locations of the distribution of *L. bennetti* across the Antarctic; 2) Rosewater (1970), a summary of the family of the Littorinidae in the Indian Ocean; 3) Picken (1980), explaining the reproductive patterns of *L. bennetti*, the first study delivering information concerning the species; 4) Taylor and Reid (1990) and 5) Amsler et al. (2015), mentioned the presence of the species. By contrast, *L. antarctica* has been mentioned in more than 36 studies since the description of E. van Martens (1885) and has been included in at least 10 direct studies (Pfeffer 1886). The species is mentioned in almost all intertidal studies of the Antarctic Peninsula and the adjacent islands. There have been several studies about feeding strategy (Picken 1979, Reid 1989, Iken 1999, Amsler et al. 2015), the reproductive cycle (Picken 1979, Picken 1980), morphology (Engl 2012), radula morphology (Powell 1951, Arnaud and Bandel 1976, Simone 2018) and population genetics (González-Wevar et al. 2022), amongst others. *L. antarctica* is commonly cited in published literature and studies due to its abundance in the majority of Antarctic intertidal areas, while *L. bennetti* is mentioned less frequently. A plausible explanation for this bias is the morphological similarity of the two species (Powell 1951) and also the fact that *L. bennetti* mainly inhabits subtidal environments, while *L. antarctica* is commonly found from intertidal. Several studies mention that *L. antarctica* has been found in samples from 0-30 m depth, while *L. bennetti* is described as a more subtidal species with distribution between 6 and 16 m; field observation confirm this suggestion.

Another important mention is the transition of the species of the genus *Laevilacunaria. Laevilacunaria antarctica* underwent a taxonomic revision, transitioning from various genera. One reason for this is the synonymisation of the species *L. brandsfieldensis* with *L. antarctica*. *Laevilacunaria antarctica* was originally classified under the genus *Lacuna*, but was reclassified under *Laevilacunaria*, while *L. brandsfieldensis*, initially described as *Pellilitorina*, was later synonymised under *Laevilacunaria*. *Laevilacunaria pumilio* underwent a reclassification, moving from the genus *Hydrobia* to *Laevilitorina* and subsequently to *Laevilacunaria*. *Laevilacunaria bennetti* was transferred from *Pellilitorina* to *Laevilitorina* and ultimately to *Laevilacunaria*.

Distribution patterns

This study compiled the knowledge of the different types of species records (published literature and sampling) to establish the distribution patterns of the genus *Laevilacunaria*. The limits seem to be the adjacent sub-Antarctic islands; South Georgia Islands, Signy Island, Trinity Island, Kerguelen Island and Crozet Island. The majority of occurrence records appear to be the West Antarctic Peninsula part of the Antarctic Peninsula with its nearby Islands (Elephant Island, South Shetland Islands, Deception Island, Anvers Island amongst others) and archipelagos (Palmer Archipelago); only a few studies indicate its presence in East Antarctica. The reason could be the contrast in the ease of access to the intertidal between the western and eastern parts of the Antarctic continent.

To summarise, the compilation cannot encompass the whole distribution of the genus *Laevilacunaria*, but brings an important update to previously-published occurrences in a thorough single database. Future studies in the three recognised species of the *Laevilacunaria* are required to resolve the systematic and biographics at macro- and micro-evolutionary scales. This study gives a basis for diverse molecular studies to reconstruct the evolutionary roads of dispersion and speciation of the genus across the Southern Ocean.

Acknowledgements

The research was supported by projects FONDECYT Regular 1210787, FONDECYT Initiation 11140087, Institutos Milenio BASE ICN2021_002, PIA CONICYT ACT172065, Fondap-IDEAL 15150003, ANID/BASAL FB210018, INACH RG_18-17 to CGW and INACH DG_10-22 to SR. Postdoc FONDECYT 3210063 for CSM. The authors are thankful to Karin Gérard for helping in collecting individuals of littorinids for the study (SCUBA diving and intertidal work). A great thank you to the project PROTEKER for the sampling on Crozet and Kerguelen Islands. In addition, many thanks to Valentina Aliaga Vargas for the map designs and Dr. Lafayette Eaton for the English revision. Thanks to the Instituto Antártico Chileno (INACH) and the Universidad Austral de Chile for providing technical support to this project.

Author contributions

A.S-M author of this paper, creator of metadata, specimens collector, participated directly in the study design and running, data acquisition and analysis, manuscript writing. C.S.M manuscript and metadata writing, revision, uploaded all the files to the Arphahub platform. Y. P. analysed samples. S.R. reviewing and editing of the manuscript, specimens identification and collection. Z.L. reviewing and editing of the manuscript and metadata, specimens collector. T.S.: Specimens collector, E.P. manuscript revision. C.G-W.: research leader, participated directly in the study design and running, review and editing the manuscript, specimens collector, samples analyser, funding acquisition.

References

- Aghmich A, Taboada S, Toll L, Ballesteros M (2016) First assessment of the rocky intertidial communities of Fildes Bay, King George Island (South Shetland Islands, Antarctica. Polar Biology 39 (1): 189-198. https://doi.org/10.1007/s00300-015-1814-9
- Allcock AL, Strugnell JM (2012) Southern Ocean diversity: new paradigms from molecular ecology. Trends in Ecology & Evolution 27 (9): 520-528. https://doi.org/10.1016/j.tree.2012.05.009
- Amsler MO, Huang YM, Engl W, McClintock JB, Amsler CD (2015) Abundance and diversity of gastropods associated with dominant subtidal macroalgae from the western Antarctic Peninsula. Polar Biology 38: 1171-1181. https://doi.org/10.1007/s00300-015-1681-4
- Arnaud MP, Bandel K (1976) Comments on six species of marine Antarctic Littorinacea (Mollusca, Gastropoda). Thetys 8 (3): 213-230.
- Bouchet P, Frída J, Hausdorf J, Valdés A, Ponder B, Warén A (2005) Classification and nomenclator of gastropod families. Malacologia, International Journal of Malacology 85-397.
- Cantera JR, Arnaud PM (1984) Les gastéropodes prosobranches des iles Kerguelen et Crozet (Sud de l'Océan Indien) comparaison écologique et particularités biologiques. Comité national français des recherches antarctiques 56.

- De Broyer C, Koubbi C, Griffiths HJ, Raymond B, Udekem d, et al. (2014) Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research
- Engl W (2012) Shells of Antarctica. ConchBooks
- Eschweiler N, Molis M, Buschbaum C (2009) Habitat-specific size structure variations in periwinkle populations (*Littorina littorea*) caused by biotic factors. Helgoland Marine Research 63: 119-127. https://doi.org/10.1007/s10152-008-0131-x
- Fraser C, Terauds A, Smellie J, Convey P (2014) Geothermal activity helps life survive glacial cycles. Proceedings of the National Academy of Sciences 111 (15): 5634-5639. https://doi.org/10.1073/pnas.1321437111
- Fraser CI, Nikula R, Ruzzante DE, Waters JM (2012) Poleward bound: biological impacts of Southern Hemisphere glaciation. Trends in Ecology & Evolution 27 (8): 462-471. https://doi.org/10.1016/j.tree.2012.04.011
- González-Wevar C, Saucède T, Morley S, Chown S, Poulin E (2013) Extinction and recolonization of maritime Antarctica in the limpet *Nacella concinna* (Strebel, 1908) during the last glacial cycle: toward a model of Quaternary biogeography in shallow Antarctic invertebrates. Molecular Ecology 22 (20): 5221-5236. https://doi.org/10.1111/mec.12465
- González-Wevar C, Segovia N, Rosenfeld S, Maturana C, Jeldres V, Pinochet R, Saucède T, Morley S, Brickle P, Wilson N, Spencer H, Poulin E (2022) Seven snail species hidden in one: Biogeographic diversity in an apparently widespread periwinkle in the Southern Ocean. Journal of Biogeography 49 (8): 1521-1534. https://doi.org/10.1111/jbi.14453
- González-Wevar CA, Chown S, Morley S, Coria N, Saucède T, Poulin E (2016) Out of Antarctica: quaternary colonization of sub-Antarctic Marion Island by the limpet genus *Nacella* (Patellogastropoda: Nacellidae). Polar Biology 39 (1): 77-89. https://doi.org/10.1007/s00300-014-1620-9
- González-Wevar CA, Segovia N, Rosenfeld S, Noll D, Maturana SC, Hüne M, Naretto J, et al. (2021) Contrasting biogeographical patterns in *Margarella* (Gastropoda: Calliostomatidae: Margarellinae) across the Antarctic Polar Front. Molecular Phylogenetics and Evolution 156: 107039. https://doi.org/10.1016/j.ympev.2020.107039
- Griffiths HJ, Waller CL (2016) The first comprehensive description of the biodiversity and biogeography of Antarctic and Subantarctic intertidal communities. Journal of Biogeography 43 (6): 1143-1155. https://doi.org/10.1111/jbi.12708
- Iken K (1999) Feeding ecology of the Antarctic herbivorous gastropod *Laevilacunaria antarctica* Martens. Journal of Experimental Marine Biology and Ecology 236 (1): 133-148. https://doi.org/10.1016/S0022-0981(98)00199-3
- Ivanova NY, Grebelnyi SD (2017) On the food of the Antarctic sea anemone *Urticinopsis antarctica* Carlgren, 1927 (Actiniidae, Actiniaria, Anthozoa). Journal of the Marine Biological Association of the United Kingdom 97 (1): 29-34. https://doi.org/10.1017/S0025315415002131
- Johannesson K, Rolán-Alvarez E, Ekendahl A (1995) Incipient reproductive isolation between two sympatric morphs of the intertidal snail *Littorina saxatilis*. Evolution 49 (6): 1180-1190. https://doi.org/10.1111/j.1558-5646.1995.tb04445.x
- Johannesson K (2003) Evolution in *Littorina*: ecology matters. Journal of Sea Research 49 (2): 107-117. https://doi.org/10.1016/S1385-1101(02)00218-6
- Martin A, Miloslavich P, Díaz Y, Ortega I, Klein E, Troncoso J, Aldea C, Carbonini AK (2016) Intertidal benthic communities associated with the macroalgae *Iridaea cordata*

and *Adenocystis utricularis* in King George Island, Antarctica. Polar Biology 39 (2): 207-220. https://doi.org/10.1007/s00300-015-1773-1

- McMahon RF (2001) Acute thermal tolerance in intertidal gastropods relative to latitude, superfamily, zonation and habitat with special emphasis on the *Littorinoidea*. Journal of Shellfish Research 20 (1): 459-467.
- Pearse J, Mooi R, Lockhart S, Brandt A (2009) Brooding and species diversity in the Southern Ocean: selection for brooders or speciation within brooding clades? In: Krupnik I, Lang M, Miller S (Eds) Smithsonian at the Poles: Contributions to International Polar Year Science. Smithsonian Institution Scholarly Press https://doi.org/10.5479/si.097884601X.13
- Pfeffer G (1886) Übersicht der im Jahre 1881 vom Grafen Waldburg-Zeil im Karischen Meere gesammeltten Mollusken. Abhandlungen aus dem Gebiete der Naturwissenschaften von dem naturwissenschaftlichen Verein in Hamburg 9 (3): 1-14. URL: https://archive.org/details/abhandlungenaus01hambgoog/page/n54/mode/2up
- Picken GB (1979) Growth, production, and biomass of the Antarctic gastropod *Laevilacunaria antarctica* Martens 1885. Journal of Experimental Marine Biology and Ecology 40 (1): 71-79. https://doi.org/10.1016/0022-0981(79)90035-2
- Picken GB (1980) Reproductive adaptations of Antarctic benthic invertebrates. Biological Journal of the Linnean Society 14 (1): 67-75. https://doi.org/10.1111/j.1095-8312.1980.tb00098.x
- Powell AW (1951) Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. Discovery Reports 26: 47-196. https://doi.org/10.5962/bhl.part.16335
- Preston HB (1916) Description of eight new species of marine mollusca from the South Shetland Islands. Annals and Magazine of Natural History, Series 18: 269-272. https://doi.org/10.1080/00222
- Reid D (1996) Systematics and evolution of *Littorina*. 164. Ray Society Publishing, California, 463 pp. [ISBN 0903874261, 9780903874267]
- Reid DG (1989) The comparative morphology, phylogeny and evolution of the gastropod family Littorinidae. Philosophical Transactions of the Royal Society of London. B, Biological Sciences 324: 1-110. https://doi.org/10.1098/rstb.1989.0040
- Reid DG, Lal K, J. M, Kaligis F, Littlewood DT, Williams ST (2006) Comparative phylogeography and species boundaries in Echinolittorina snails in the central Indo-West Pacific. Journal of Biogeography 33 (6): 990-1006. https://doi.org/10.1111/j.1365-2699.2006.01469.x
- Reid DG, Dyal P, Williams ST (2012) A global molecular phylogeny of 147 periwinkle species (Gastropoda, Littorininae). Zoologica Scripta 41 (2): 125-136. https://doi.org/10.1111/j.1463-6409.2011.00505.x
- Rosenfeld S, Maturana CS, Spencer HG, Convey P, Saucède T, Brickle P, Bahamonde F, Jossart Q, Poulin E, González-Wevar CA (2022) Complete distribution of the genus *Laevilitorina* (Littorinimorpha: Littorinidae) in the Southern Hemisphere: remarks and natural history. ZooKeys 1127: 61-77. https://doi.org/10.3897/zookeys.1127.91310
- Rosewater K (1970) The Family Littorinidae in the Indo-Pacific, Part I. The Subfamily Littorininae. Indo-Pacific-Mollusca 2 (11).
- Schmider-Martínez A, Maturana C, Poveda Y, Rosenfeld S, et al. (2023) Review of the genus *Laevilacunaria* across its distribution in the Southern Ocean. 1.1. Instituto de Biodiversidad de Ecosistemas Antárticos y Subantártico. Release date: 2023-6-06. URL: http://gbif-chile.mma.gob.cl/ipt/resource?r=genus_laevi_base&v=1.1

- Simone LR (2018) Convergence with naticids: phenotypic phylogenetic study on some Antarctic littorinoideans, with description of the zerotulid new genus *Pseudonatica*, and its presence in Brazil (Mollusca, Caenogastropoda). Journal of the Marine Biological Association of the United Kingdom 98 (6): 1365-1381. https://doi.org/10.1017/S002531541700025X
- Taylor J, Reid D (1990) Shell microstructure and mineralogy of the Littorinidae: ecological and evolutionary significance. Hydrobiologia 193: 199-215. https://doi.org/10.1007/BF00028077
- Williams ST, Reid DG, Littlewood DT (2003) A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism, and biogeography of the Southern Ocean. Molecular phylogenetics and evolution 28 (1): 60-86. https://doi.org/10.1016/S1055-7903(03)00038-1

frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 06 February 2024
DOI 10.3389/fevo.2023.1320649

Check for updates

OPEN ACCESS

EDITED BY
Jasmine Lee,
British Antarctic Survey (BAS), United Kingdom

REVIEWED BY
Sally Lau,
James Cook University, Australia
Kara Layton,
University of Aberdeen, United Kingdom

*CORRESPONDENCE
Claudio A. González-Wevar
claudio.gonzalez@uach.cl

RECEIVED 12 October 2023
ACCEPTED 28 December 2023
PUBLISHED 06 February 2024

CITATION
González-Wevar CA, Poveda Y, Segovia NI, Rosenfeld S, Maturana CS, Jeldres V, Schmider-Martínez A, Gérard K, Spencer HG and Poulin E (2024) Both high and low dispersal? Apparently contradictory genetic patterns in the Antarctic littorinid gastropod *Laevilacunaria antarctica*. *Front. Ecol. Evol.* 11:1320649. doi: 10.3389/fevo.2023.1320649

Both high and low dispersal? Apparently contradictory genetic patterns in the Antarctic littorinid gastropod *Laevilacunaria antarctica*

Claudio A. González-Wevar[1,2,3]*, Yarleth Poveda[1,2,3], Nicolás I. Segovia[4,5], Sebastián Rosenfeld[2,6,7], Claudia S. Maturana[2,6], Vanessa Jeldres[1,2,3], Andreas Schmider-Martínez[1,2,3,8], Karin Gérard[2,9], Hamish G. Spencer[10] and Elie Poulin[2,11]

[1]Instituto de Ciencias Marinas y Limnológicas (ICML), Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile, [2]Instituto Milenio Biodiversidad de Ecosistemas Antárticos y Subantárticos (Mi-BASE), Las Palmeras, Ñuñoa, Santiago, Chile, [3]Centro Fondap de Investigación en Dinámica de Ecosistemas Marinos de Altas Latitudes (IDEAL), Universidad Austral de Chile, Valdivia, Chile, [4]Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Chile, [5]Instituto Milenio en Socio-ecología Costera (SECOS), Coquimbo, Chile, [6]Cape Horn International Center (CHIC), Puerto Williams, Chile, [7]Centro de Investigación Gaia-Antártica, Universidad de Magallanes, Punta Arenas, Chile, [8]Centro i-mar, Universidad de los Lagos, Puerto Montt, Chile, [9]Laboratorio de Ecosistemas Antárticos y Subantárticos (LEMAS), Universidad de Magallanes, Punta Arenas, Chile, [10]Department of Zoology, University of Otago, Dunedin, New Zealand, [11]Laboratorio de Ecología Molecular (LEM), Departamento de Ciencias Ecológicas, Universidad de Chile, Las Palmeras, Ñuñoa, Santiago, Chile

How the near-shore marine benthic communities survived Quaternary glaciations in Antarctica is a major question for Southern Ocean biogeographers. Several hypotheses that consider life-history traits, such as bathymetric ranges and developmental modes, have been proposed. Near-shore species with high dispersive potential are expected to show star-like genealogies, with broadly distributed haplotypes surrounded by closely related variants at low frequencies, a consequence of rapid population post-glacial expansion mediated by larvae. By contrast, shallow-water taxa with low dispersal potential are expected to evidence marked genetic structure or even consist of separate cryptic species, due to their survival in small refugial populations subject to repeated bottlenecks. In this study we performed phylogeographic analyses on the high-latitude littorinid *Laevilacunaria antarctica* across its distribution from maritime Antarctica to South Georgia. This species is a highly abundant near-shore gastropod, commonly found on macroalgae, with low autonomous vagility and exhibits benthic protected development with no free-living dispersive stages. Such characteristics make this species a suitable model to test the above hypotheses. Contrary to low dispersal potential predictions, *L. antarctica* comprises a single unstructured unit across its distribution in maritime Antarctica, exhibiting a typical high-dispersal star-like, short-branched genealogy centered on a dominant broadly distributed haplotype. The South Georgia population, however, consists of a separate genetic unit, strongly differentiated from those of the maritime Antarctic. We estimate that these two genetic groups separated ~1.2 My, long before the Last

Glacial Maximum and evolved independently in these areas. Our results thus provide partial support for the expected pattern for a near-shore marine benthic species with low innate dispersive potential. On a wider geographic scale (maritime Antarctica vs South Georgia), our results in *L. antarctica* provide support for the expected pattern for a near-shore marine benthic species with low innate dispersive potential. However, on a narrower scale (maritime Antarctica) life-history characters including the close association of the species with macroalgae, would allow dispersal and a species with low dispersal potential exhibits paradoxically an absence of genetic structure across hundreds of kilometers probably mediated by rafting.

KEYWORDS

maritime Antarctica, sub-Antarctic, South Georgia, *Laevilacunaria antarctica*, quaternary glaciations, postglacial recolonization, rafting, dispersal potential

Introduction

How the shallow benthic marine biota endured Quaternary glaciations, particularly the Last Glacial Maximum (LGM), is a major question in Antarctic biogeography (Barnes et al., 2006; Thatje et al., 2008; Allcock and Strugnell, 2012; Fraser et al., 2014; Riesgo et al., 2015; Chenuil et al., 2018; Crame, 2018; Lau et al., 2020; Baird et al., 2021). Ice advances across the Antarctic continental platform generated major landscape shifts and a drastic reduction of available habitats (Zachos et al., 2001; Pollard and DeConto, 2009; Fraser et al., 2012; González-Wevar et al., 2012; González-Wevar et al., 2013; McCay et al., 2016; Halanych and Mahon, 2018);. Accordingly, near-shore marine benthic communities would have been especially vulnerable as continental ice sheets extended over most of the narrow Antarctic shelf to about 500 m in depth (Ingólfson, 2004; Thatje et al., 2005; Barker et al., 2007; Dambach et al., 2012).

Quaternary glaciations severely impacted the abundance, demographic dynamics, structure, and spatial distribution of Antarctic (Convey et al., 2009; McGaughran et al., 2011; Fraser et al., 2012; González-Wevar et al., 2013; Riesgo et al., 2015; Chenuil et al., 2018; Guillemin et al., 2018; Halanych and Mahon, 2018; Maturana et al., 2020; Cakil et al., 2021; Levicoy et al., 2021) and sub-Antarctic (Waters, 2008; Fraser et al., 2009; Nikula et al., 2010; González-Wevar et al., 2011; González-Wevar et al., 2012; Cumming et al., 2014; Moon et al., 2017; González-Wevar et al., 2018; González-Wevar et al., 2021) near-shore marine organisms. Moreover, ice advances during glacial maxima would have enhanced speciation, particularly in species with nonpelagic developmental modes (direct developers), as populations became fragmented into small and isolated refugia across the Antarctic continental shelf (Brey et al., 1996; Pearse et al., 2009; Chenuil et al., 2018). Following this, interglacial periods generated the expansion of newly available habitats where populations and species would have expanded their distributions (Provan and Bennett, 2008; Marko et al., 2010; González-Wevar et al., 2013). Under a basic expansion-contraction model of Pleistocene biogeography (Provan and Bennett, 2008), refugial populations are expected to harbor higher levels of intraspecific genetic diversity compared to those that were heavily impacted by ice and/or recently recolonized ones (Marko, 2004; Maggs et al., 2008; Marko et al., 2010). Moreover, in some cases glaciations have been associated with the radiation and speciation of different marine near-shore invertebrates (Thornhill et al., 2008; Wilson et al., 2009; Allcock et al., 2011; Baird et al., 2011; Baird et al., 2021), a process also known as 'the Antarctic diversity pump' (Clarke and Crame, 1989; Clarke and Crame, 1992; Chenuil et al., 2018).

In a review of genetic signatures induced by Quaternary events in Antarctic taxa, Allcock and Strugnell (2012) proposed that two life-history traits, bathymetric ranges and developmental modes, played a key role. Shallow species with dispersive potential would exhibit star-like haplotype networks, with broadly distributed common haplotypes and closely related variants occurring at low frequencies. Such a pattern is associated with rapid population expansion, probably mediated by larvae dispersion, and has been recorded in the sea urchin *Sterechinus neumayeri* (Díaz et al., 2011), the nemertean *Parborlasia corrugatus* (Thornhill et al., 2008), the Antarctic limpet (González-Wevar et al., 2013) and the shrimp *Chorismus antarcticus* (Raupach et al., 2010). By contrast, the genetic signature predicted for shallow species with low dispersal potential includes disjunct haplotypes networks comprising multiple smaller genetic units, indicative of small populations isolated in glacial refugia that underwent bottlenecks. Due to the absence of free dispersive stages, recolonization is slow, allowing time for genetic drift and possible adaptive differentiation before secondary contact of isolated populations. Examples of taxa displaying this pattern include the amphipods *Eusirus* (Baird et al., 2011), the pycnogonid *Colossendeis megalonyx* (Krabbe et al., 2010), cephalopods (Allcock et al., 2011), and the nudibranch *Doris kerguelensis* (Wilson et al., 2009).

The high-latitude littorinid species *Laevilacunaria antarctica* (Martens van and Pfeffer, 1886) is one of the most abundant inter- and subtidal gastropods on macro-algae and rocky shores across ice-free areas of the Antarctic Peninsula and sub-Antarctic island of South Georgia (Cantera and Arnaud, 1984; Iken, 1999; Amsler et al., 2015; Martin et al., 2016; Amsler et al., 2019; Amsler et al., 2022; Schmider-Martínez et al., 2023). As with other Laevilitorininae genera such as *Laevilitorina* (Simpson and Harrington, 1985), *L. antarctica* exhibits low autonomous vagility, benthic protected development with the absence of free-living dispersive stages, a mode or reproduction where crawling juveniles emerge directly from egg masses. Generally, high-latitude littorinids are considered to be poor dispersers, with most species having narrow distributions restricted to particular areas of the Southern Ocean (González-Wevar et al., 2022; Rosenfeld et al., 2023). Based on its broad distribution and abundance across the maritime Antarctica, its narrow bathymetric range, and its reproductive mode, *L. antarctica* represents a suitable model to test the hypotheses proposed for Antarctic Quaternary biogeography of shallow marine benthic organisms.

In this study, we performed population-based molecular analyses of *Laevilacunaria antarctica* across its known distribution. We included more than 320 specimens collected from across the Antarctic Peninsula (AP) and the nearby South Shetland Islands (SSI), as well as from sub-Antarctic South Georgia (SG). Comparative mitochondrial (COI) and nuclear (28S rRNA) genetic analyses allowed us to unravel the legacy of Quaternary glaciations in the patterns of genetic diversity and structure of this species. Considering the lack of larval dispersive stages in the species and its narrow bathymetric range, we predicted that *L. antarctica* would display several disjunct haplotype networks separated into smaller genetic units, as recorded in other Antarctic species with similar life history traits. Through this research we aimed to understand how key elements of the near-shore Antarctic marine benthic communities endured Quaternary climate shifts associated with glacial and interglacial periods.

Materials and methods

Sample collection, DNA extraction and amplifications

Specimens of *L. antarctica* were collected by hand and by scuba divers from intertidal and subtidal rocky-shore ecosystems between 2015 and 2021 during the Chilean Scientific Antarctic Expeditions (ECAs) across the species distribution in the maritime Antarctica (AP and SSI) and SG (Figure 1; Table 1). The identification of specimens was done following the original descriptions and revisions (Martens van and Pfeffer, 1886; Smith, 1879; Preston, 1916; Powell, 1951) as well as recent literature (Arnaud and Bandel, 1979; Cantera and Arnaud, 1984; Engl, 2012). Individuals were fixed *in situ* using 95% ethanol and transported for further molecular analyses. All the specimens were photographed and measured for future comparative morphological studies. Preparation of DNA from the whole animal used the standard salting-out methodology (Aljanabi and Martinez, 1997) and the QIAGEN DNEasy Blood & Tissue kit (QIAGEN Inc.). We amplified a partial fragment of the mitochondrial cytochrome c subunit I gene (COI) using universal primers LCO1490 and HCO2198 (Folmer et al., 1994). Similarly, we used the universal primers 900F and 1600R (Littlewood et al., 2000) to amplify a fragment of the nuclear 28S rRNA gene. PCR amplicons were purified and sequenced in both directions at Macrogen Inc (Seoul, South Korea). Forward and reverse sequences were assembled and edited for each marker independently using GENEIOUS (http://www.geneious.com). Alignments and base composition of nucleotide sequences analyses were done for each marker in MUSCLE (Edgar, 2004) in MEGA 11 (Tamura et al., 2021), respectively. Wright's

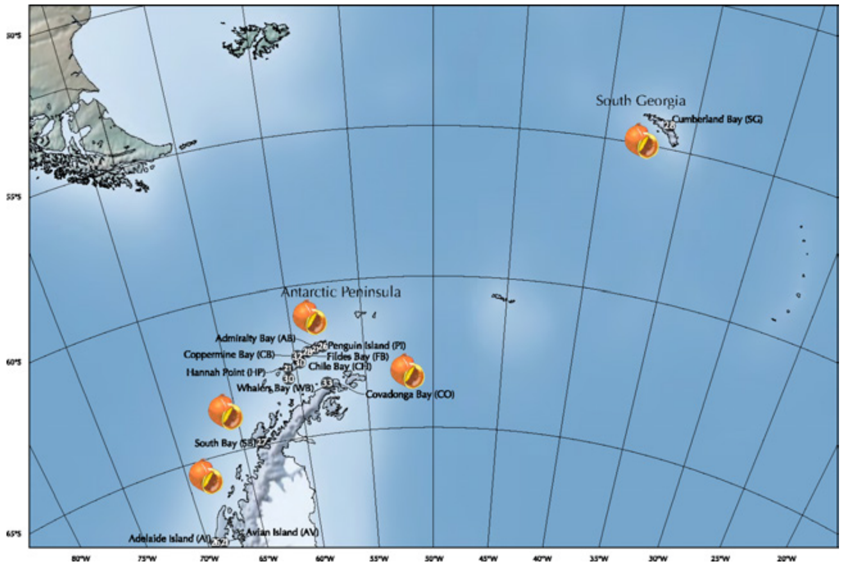


FIGURE 1
Sampling localities of *Laevilacunaria antarctica* populations across its distribution in maritime Antarctica (SSI/AP) and South Georgia (SG).

TABLE 1 Sampled localities of *Laevilacunaria antarctica* across its distribution in maritime Antarctica (MP) and South Georgia.

Locality	Latitude	Longitude	Area	Main Area
Penguin Island (PI)	62°06′00′′S	57°55′41′′W	King George Island	South Shetland Islands
Admiralty Bay (AB)	62°09′41′′S	58°28′10′′W	King George Island	South Shetland Islands
Fildes Bay (FB)	62°12′57″S	58°57′35″W	King George Island	South Shetland Islands
Coppermine Bay (CB)	62°22′17″S	59°42′53″W	Robert Island	South Shetland Islands
Hannah Point (HP)	62°39′19″S	60°36′48″W	Livingston Island	South Shetland Islands
Whalers Bay (WB)	62°59′57′′S	60°40′28′′W	Deception Island	South Shetland Islands
Chile Bay (CH)	62°28′43″S	59°39′48″W	Greenwich Island	South Shetland Islands
Covadonga Bay (CO)	63°19′15″S	57°53′59″W	Covadonga Bay	Antarctic Peninsula
South Bay (SB)	64°52′55′′S	63°35′03′′W	Doumer Island	Antarctic Peninsula
Adelaide Island (AI)	67°46′23′′S	68°55′53′′W	Marguerite Bay	Antarctic Peninsula
Avian Island (AV)	67°46′15′′S	68°53′10′′W	Marguerite Bay	Antarctic Peninsula
Cumberland Bay (SG)	54°14′12′′S	36°28′32′′W	South Georgia	Scotia Arc

mitochondrial codon usage was computed using the Effective Number of Codons (ENC) in DnaSP v5 (Librado and Rozas, 2009). The data presented in the study are deposited in the GenBank repository, accession number COI (ORT701885 - ORT701931) and 28S rRNA (ORT711532 - ORT711533).

Genetic diversity and population structure in *L. antarctica*

We performed a DNA saturation analysis following Xia and Xie (2001) to evaluate how transitions accumulate in relation to nucleotide divergence in the complete *L. antarctica* COI data set. We then estimated levels of population mtDNA polymorphism through standard diversity indices including number of haplotypes (*k*), haplotype diversity (*H*), number of segregating sites (*S*) and the number of private haplotypes (p. hap) per locality. Moreover, we also determined the average number of pairwise differences (*Π*) and the nucleotide diversity (*π*) across the species distribution using DnaSP.

Patterns of population differentiation were estimated following Pons and Petit (1996), using haplotype frequencies (G_{ST}) and mean pairwise differences (N_{ST}) in Arlequin v.3 (Excoffier et al., 2005). The statistical significance of genetic pairwise differences was calculated using permutation tests (20,000 iterations) and the adjustment for multiple testing was done through False Discovery Rate (FDR) correction (Narum, 2006). Moreover, we estimated levels of genetic differentiation using the nearest-neighbor statistic (S_{nn}), which measures how often nearest-neighbor (in sequence space) sequences are from the same locality in geographic space (Hudson, 2000). The statistical significance of S_{nn} was determined using a permutation test (20,000 iterations).

We used two different clustering methods to determine the spatial genetic structure of *L. antarctica*. First, we determined the number and the composition of panmictic groups and the spatial boundaries using a Bayesian model computed in GENELAND v.2.0.0 (Guillot et al., 2005) in the R environment (Ihaka and Gentleman, 1996). This analysis implements a Markov Chain Monte Carlo (MCMC) procedure to estimate the best clustering of samples considering genetic and geographic information. Analyses were run using 50 x 10^6 MCMC iterations sampled every 1,000 steps. Assembled scores were graphed against generations in Tracer v.1.5. (Rambaut et al., 2018) to identify stationarity and the number of generations to be discarded as burn-in. A maximum number of clusters (K = 13) were run to estimate the model parameters and posterior probabilities of group membership. Second, we determined the spatial genetic structure in *L. antarctica* by estimating the number and composition of groups that were most differentiated based on sequence data set using Spatial Analysis of Molecular Variance (SAMOVA) (Dupanloup et al., 2002). This analysis partitions the genetic variance into i) within populations, ii) among populations within groups and iii) among groups.

Demographic analyses in *L. antarctica*

Haplotype genealogical relationships in *L. antarctica* populations were reconstructed using median-joining and maximum-parsimony networks in Network 10 (Forster et al., 2001) and Hapview (Salzburger et al., 2011), respectively. Moreover, we performed neutrality statistical tests (Tajima's D and Fu's FS) using DnaSP for the whole COI data set, for each recognized group, and for each locality to estimate whether sequences deviate from mutation-drift equilibrium. Population demographic histories were estimated comparing the distribution of pairwise differences between haplotypes (mismatch distribution) for each recognized group to the expected distribution under the sudden expansion growth model of Rogers and Harpending (1992). Finally, for comparative purposes, we also constructed genealogical relationships in *L. antarctica* using sequences of the nuclear marker 28S rRNA.

We reconstructed past population dynamics through time in the recognized *L. antarctica*'s genetic clusters using a Bayesian skyline plot method implemented in BEAST v.1.10.4 (Drummond and Rambaut, 2007; Drummond et al., 2012). Three evolutionary models (strict clock, uncorrelated lognormal and uncorrelated relaxed clock) were tested and compared statistically using a Bayes factor test (Suchard et al., 2001) in Tracer and the strict clock model was the best fit for each of the COI data-set clusters. Following this, we performed three independent Bayesian MCMC runs for 250 x 10^6 generations (sampled every 1000 iterations), using the GTR + I + Γ model, previously estimated in MrModeltest v.2.3 (Nylander, 2004). Molecular evolutionary studies have yielded a wide range of rate estimates for different genes and taxa. Several studies based on population-level and intraspecific data have generated remarkably high estimates of mutation rate, which contrast with substitution rates inferred in phylogenetic studies. Consequently, BSP analyses were done using a tenfold evolutionary rate estimated for littorinids (Reid et al., 2012). Such a rate correction was assumed considering the time-dependence of molecular rate proposed by Ho et al (2005; 2007; 2011). The first 10% of the parameter values were discarded as a burn-in and the convergence of runs was confirmed with Tracer, ensuring a minimum of 1000 effective sampling for each statistic (ESSs > 1000).

Results

Genetic diversity in *L. antarctica*

The whole COI data set in *L. antarctica* included 323 specimens (SG = 28; SSI = 188; AP = 107) and comprised 687 nucleotide positions coding for 229 amino acids. No insertion/deletions or stop codons were detected. Moreover, mitochondrial (mtDNA) and nuclear (nucDNA) sequences were not saturated and no evidence of mtDNA codon bias was found (ENC = 46.75). Four amino-acid substitutions (positions 11, 44, 144, and 171) were recorded in *L. antarctica* using the invertebrate mitochondrial table. Low levels of genetic diversity characterized populations of *L. antarctica*, with 48 polymorphic characters (6.9%) and 29 of them (60.4%) were parsimony informative. Sequences were A – T rich (67.2%). The haplotype diversity (*H*) varied between 0.123 (Robert Island, SSI) and 0.675 (Cumberland Bay, SG) (Table 2). The number of polymorphic sites (*S*) varied between 1 (Admiralty Bay, SSI) and 10 (Cumberland Bay, SG). Similarly, the number of haplotypes/private haplotypes varied among the analyzed localities between 2/0 (Admiralty Bay, SSI) and 11/11 (Cumberland Bay, SG) (Table 2). Finally, the average number of nucleotide differences (Π) and the mean nucleotide diversity (π) were very low in most localities across the maritime Antarctica (SSI and AP), whereas the diversity of these indices was higher in SG (Table 2). The mean level of mtDNA genetic divergence between SSI/AP and SG populations of *L.*

TABLE 2 Diversity indices, private alleles, and neutrality tests in *Laevilacunaria antarctica* populations across its distribution in maritime Antarctica and South Georgia.

Locality	n	k	H	S	Π	π	p. hap.	Tajima´s D	Fu´s FS
Penguin Island (SSI)	26	4	0.222	4	0.308	0.0015	1	-1.88*	-2.45
Admiralty Bay (SSI)	21	2	0.095	1	0.095	0.0001	0	-1.16	-0.919
Fildes Bay (SSI)	28	6	0.437	6	0.556	0.0008	2	-1.85*	-3.66*
Hannah Point (SSI)	21	4	0.414	3	0.448	0.0006	1	-1.21	-1.77
Coppermine Bay (SSI)	32	3	0.123	3	0.188	0.0002	1	-1.72	-1.70
Whalers Bay (SSI)	30	7	0.464	6	0.524	0.0007	5	-1.86*	-5.35**
Chile Bay (SSI)	30	7	0.366	7	0.467	0.0006	6	-2.17**	-5.88**
SSI	188	23	0.311	23	0.380	0.0005	n/a	-2.48**	-40.27***
Covadonga Bay (AP)	33	2	0.061	2	0.121	0.0001	1	-1.50	-0.48
South Bay (AP)	27	5	0.396	5	0.507	0.0007	4	-1.70	-2.57
Adelaide Island (AP)	26	9	0.578	7	0.745	0.0010	5	-1.81*	-7.45***
Avian Island (AP)	21	4	0.271	3	0.286	0.0004	2	-1.72	-2.80*
AP	107	17	0.324	14	0.408	0.0005	n/a	-2.29**	-25.57***
MA	295	36	0.405	34	0.405	0.0005	n/a	-2.56***	-75.32***
Cumberland Bay (SG)	28	11	0.675	10	1.167	0.0017	11	-1.91*	-7.86***
Total	**323**	**47**	**0.436**	**48**	**2.296**	**0.0033**		**-2.00***	**-42.19*****

Where AP = Antarctic Peninsula; SSI = South Shetland Islands; MA = Maritime Antarctica (SSI + AP); SG = South Georgia.
n = number of analyzed individuals; *k* = number of haplotypes; *S* = polymorphic sites; *H* = haplotype diversity; Π = average number of pairwise differences; π = nucleotide diversity. *p<0.05, **p<0.01, *** p<0.001; n/a not applicable.

antarctica was 1,74%. Levels of nucDNA diversity were much lower in the species, SSI and AP specimens (n = 123) shared the same allele which was differentiated by two mutation steps from the sequences recorded at South Georgia.

Genetic structure in *L. antarctica*

Mean general values of differentiation estimated were low, especially considering average G_{ST} (0.112) and N_{ST} (0.170). In fact, general levels of differentiation among maritime Antarctic populations were extremely low, considering average G_{ST} (0.043) and N_{ST} (0.034). Pairwise population comparisons did not recognize significant structure among maritime Antarctica populations (Table 3). Nevertheless, some populations showed significant differences after FDR corrections. By contrast, G_{ST} and N_{ST} comparisons recorded significant differences between SG and the rest of the analyzed populations from the maritime Antarctica (Table 3).

The nearest neighbor statistic in *L. antarctica* (S_{nn} = 0.199) showed low but significant levels of phylogeographic signal ($p <$ 0.0001). Nevertheless, when this analysis was carried out considering the main pattern of genetic differentiation recorded in the species (maritime Antarctic vs South Georgia), S_{nn} became extremely high (S_{nn} = 1.00) and significant, showing the high degree of phylogeographic signal found between maritime Antarctica and SG. The pattern of genetic structure was supported by the model based on the Bayesian clustering algorithm, which detected two main clusters (K = 2). Again, the first cluster included all localities from the maritime Antarctica (Figure 2A), while the second one comprised only South Georgia (Figure 2B). Values of cluster membership were very high (P = 1.000) for all the individuals and the mean probability value (P = 0.5) corresponds to the boundary between these clusters and runs across the Scotia Ridge located between South Georgia and the Antarctic Peninsula. Similarly, SAMOVA analyses detected two maximally differentiated genetic groups – maritime Antarctica and South Georgia – accounting for 59.35% of the total variance, in comparison with only 0.83% due to within-group variation among localities (Table 4). Considering the level of mtDNA genetic divergence (1.74%) and the strong phylogeographic signal recorded between SSI/AP and SG we performed divergence time estimations analysis under a phylogenetic framework. For this a relaxed molecular-clock using an uncorrelated-lognormal (ucld) model of molecular evolutionary rate heterogeneity and the GTR + I + G model of substitution was implemented in BEAST v.1.7.5 (Drummond & Rambaut, 2007; Drummond et al., 2012). Four chains were run for 200 x 10^6 generations and trees were sampled every 10,000 generations. For divergence time estimations we include in the analyses several calibration points within the evolution of Littorinidae estimated for the most common ancestors (TRMCA) of the genera *Echinolittorina*, *Littorina*, *Littoraria*, *Austrolittorina*, *Tectarius* and *Afrolittorina*) following Reid et al. (2012), and with special emphasis on higher latitude groups (González-Wevar et al., 2022). According to our divergence-time analyses the separation between SSI/AP and SG genetic clusters occurred around 1.1 Ma (2.0 – 0.55 Ma).

Demographic reconstructions

The parsimony mtDNA network of *L. antarctica* included 47 haplotypes and clearly discriminated two main groups: maritime Antarctica and South Georgia, separated by nine substitutional steps (Figure 3A). Both maritime Antarctica and South Georgia clusters exhibited typical starlike topologies and short genealogies. In maritime Antarctica, the central haplotype (H01) was the most frequent (82%), broadly distributed and surrounded by 35

TABLE 3 Pairwise G_{ST} (below the diagonal) and N_{ST} (above the diagonal) values calculated among the analyzed populations of *Laevilacunaria antarctica*. 20,000 iterations.

Locality	PI	AB	FB	HP	CB	WB	CH	CO	SB	AI	AV	SG
Penguin Island (PI)	-	0.000	0.017	0.038	0.001	0.009	0.000	0.003	0.013	0.017	0.000	**0.938**
Admiralty Bay (AB)	0.000	-	0.014	0.050	0.000	0.004	0.000	0.000	0.010	0.019	0.000	**0.941**
Fildes Bay (FB)	0.021	0.057	-	0.000	0.017	0.022	0.006	0.027	0.024	0.030	0.014	**0.930**
Hannah Point (HP)	0.028	0.071	0.000	-	0.044	0.035	0.029	0.065	0.039	0.039	0.037	**0.930**
Coppermine Bay (CB)	0.000	0.000	0.058	0.076	-	0.013	0.000	0.000	0.019	0.031	0.000	**0.947**
Whalers Bay (WB)	0.021	0.057	0.000	0.003	0.062	-	0.009	0.016	0.019	0.027	0.000	**0.932**
Chile Bay (CH)	0.000	0.022	0.000	0.002	0.024	0.000	-	0.001	0.011	0.017	0.000	**0.934**
Covadonga Bay (CO)	0.013	0.000	**0.097**	**0.120**	0.000	**0.096**	0.053	-	0.015	0.036	0.000	**0.950**
South Bay (SB)	0.009	0.043	0.000	0.005	0.046	0.000	0.000	0.051	-	0.028	0.002	**0.931**
Adelaide Bay (AI)	0.047	0.045	0.004	0.009	0.064	0.000	0.008	**0.144**	0.088	-	0.018	**0.922**
Avian Island (AV)	0.000	0.001	0.005	0.011	0.002	0.000	0.000	0.031	0.000	0.023	-	**0.935**
Cumberland Bay (SG)	**0.546**	**0.588**	**0.444**	**0.446**	**0.613**	**0.432**	**0.482**	**0.649**	**0.463**	**0.372**	**0.510**	-

Statistical significant FDR differences are marked in bold.

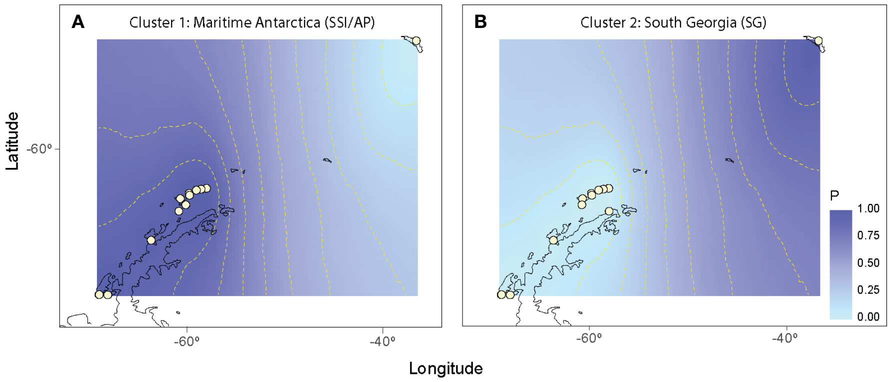


FIGURE 2
Spatial output from Geneland using *Laevilacunaria antarctica* populations. White circles indicate the relative positions of the sampling localities across maritime Antarctica and South Georgia. Darker and lighter shadings are proportional to posterior probabilities of membership to particular genetic cluster (**A** = maritime Antarctica and **B** = South Georgia). Posterior probabilities were plotted against the shapefile of the Antarctic coastline available in GEOdas (NOAA) and filtered using GEOdas Coastline Extractor v.1.1.3.1 (https://www.ngdc.noaa.gov/mgg/geodas/geodas.html).

haplotypes of low frequency (fewer than four individuals). A second dominant haplotype (H02) was found in 57% of the SG individuals and was surrounded by ten closely derived ones (Figure 3A). As expected, for star-like genealogies, global Tajima's D and Fu's neutrality tests were negative and significant for each recognized cluster and for the whole COI data set (Table 2). The distribution of pairwise differences depicted for the maritime Antarctica showed a typical L-shaped distribution. In contrast, the distribution of pairwise differences for South Georgia was bimodal. As stated above, nucDNA parsimony network showed that the maritime Antarctica populations specimens exhibited the same allele (HI) while SG specimens carried another one (HII) separated by two mutational steps (Figure 3B).

Bayesian skyline-plot analyses identified similar trajectories in terms of the time since the most recent common ancestors (trmca) and populations expansions between maritime Antarctica and South Georgia (Figure 4). Population expansion of the maritime Antarctica populations occurred approximately 5,000 years ago while the expansion at South Georgia occurred around 9,000 years ago. The tmrca of SSI/AP occurred around 12,000 years ago while the tmrca for SG occurred 17,000 years ago (Figure 4).

TABLE 4 Spatial Analysis of Molecular Variance (SAMOVA) depicting the percentage of variation explained among groups (maritime Antarctica and South Georgia), among populations within groups and within populations.

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation
Among groups	1	13.232	0.25343 Va	59.35
Among populations within groups	10	2.654	0.00357 Vb	0.83
Within populations	311	52.867	0.16999 Vc	39.81
Total	322	68.752		

F_{SC} = differentiation within populations among groups; F_{CT} = Differentiation among groups (*** p<0.001).
Fixation Indices.
F_{SC}: 0.02054***.
F_{CT}: 0.59354***.

Discussion

Our results show that *Laevilacunaria antarctica* has a remarkably low level of genetic diversity across much of its known range, with the presence of a single dominant COI haplotype in our sampled populations from Penguin Island (62° 06'), the farthest north locality in the South Shetland Islands, to the southernmost point in Avian Island (67°46') in the Antarctic Peninsula. There is marginally more diversity further afield, in South Georgia, although again one haplotype, albeit a very different one, dominates. The only population structure is between South Georgia and the remaining populations, with no shared haplotypes and at least nine substitutional steps between haplotypes from these two parts of the species' range. Effectively, the haplotype map is one of two star-like genealogies linked by a nine-step branch. Nevertheless, such results should be taken with caution, considering that we only included one locality from South Georgia. In this context, future samplings in South Georgia are required to increase our sampling effort across this island and corroborate the diversity pattern here recorded.

Our findings provide only limited support for the predictions of Allcock and Strugnell (2012), and indeed some evidence to the contrary. As *Laevilacunaria* lacks any pelagic dispersal stage, yet the low levels of diversity and the absence of genetic structure showed by star-like networks in the maritime Antarctica across hundreds of kilometers are more congruent with the pattern of genetic diversity these authors envisaged in highly dispersive species. Nevertheless, our analyses detected a marked phylogeographic signal between sub-Antarctic South Georgia and maritime Antarctic localities, fitting more closely with a poor dispersal capacity at large geographical scale. The absence of shared haplotypes, together

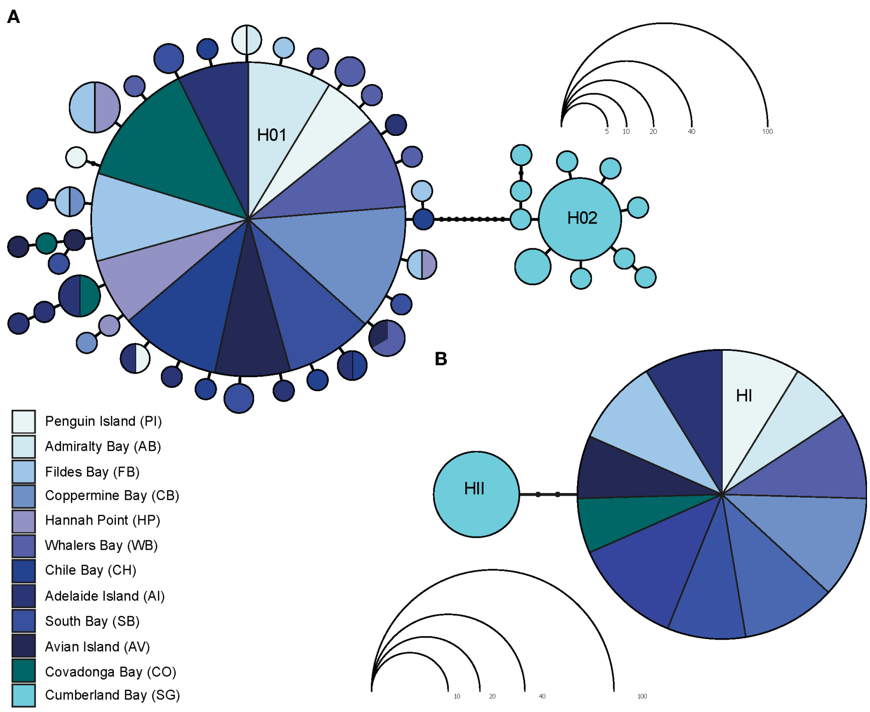


FIGURE 3
Parsimony mtDNA **(A)** and nucDNA **(B)** networks in *Laevilacunaria antarctica* across its distribution in maritime Antarctica and South Georgia. Each haplotype/allele is represented by a colored circle indicating the locality. The size the haplotypes/alleles is proportional to their frequencies.

with the number of fixed mutations (n = 9) between these areas are strong evidence of distinct genetic and evolutionary units in *L. antarctica*. Indeed, divergence-time estimations of these Significant Evolutionary Units (ESUs) suggest that they were separated ~ 1.1 million years ago (Ma), long before the LGM and, ever since, have evolved independently in these areas of the Southern Ocean.

How do we explain these apparently contradictory results? The absence of population structure in the maritime Antarctica matches previous molecular studies of near-shore marine benthic invertebrates such as the Antarctic limpet *Nacella concinna* (Hoffman et al., 2010; González-Wevar et al., 2013), the trochoid gastropod *Margarella antarctica* (González-Wevar et al., 2021), and the sea urchin *Sterechinus neumayeri* (Díaz et al., 2011; Díaz et al., 2018). *Nacella* and *Sterechinus* species possess a pelagic larval stage and such patterns are explained by their respective higher dispersal potentials. By contrast, *Margarella* and *Laevilacunaria* species exhibit benthic protected development, but they live closely associated with macroalgae on which they graze and reproduce. Accordingly, it is possible that *Margarella* and *Laevilacunaria* could maintain connectivity through rafting of adults and/or egg-masses attached to macroalgae. Alternatively, the low levels of genetic diversity and the absence of genetic structure in *L. antarctica* across the maritime Antarctica is probably associated to strong founder effects from bottlenecked refugial population. This same argument would apply to the South Georgian populations of *L. antarctica*. The lower frequency of buoyant macroalgae in the maritime Antarctic represented by *Crystosphaera jacquinotti*, however, presumably limits the extent of this rafting, precluding dispersal of *L. antarctica* (and, indeed, also occur in the trochoid *M. antarctica*) to the more distant areas such as South Georgia. Events of long-distance colonization by rafting have been documented among non-buoyant macroalgae (Fraser et al., 2013; McCay et al., 2016). Evidence of macroalgae fronds enclosed in drift ice have been reported at sea (Guillemin M-L pers. comm.) and these fronds have been recovered far away from the coast (Guillemin et al., 2018). In fact, across the same study are, several non-buoyant red algae also exhibit very low levels of genetic diversity and a complete absence of genetic structure (Guillemin et al., 2018). During Quaternary glaciations, the study area, SSI/AP and SG, have been located south of the Antarctic Polar Front (APF). Hence, the positition of the APF can be excluded as a potential barrier to gene flow between these areas. Drifter-based data have demonstrated that the Antarctic Circumpolar Current flows from the maritime Antarctica to South Georgia with a velocity that would allow to drift between these two areas around two months (Matschiner et al., 2009).

The lack of genetic variation in the maritime Antarctica, with one dominant haplotype in the centre of a star-like genealogy, fits well with the idea that *L. antarctica* survived a bottleneck induced by the LGM in one or (possibly) more shelf refugia. The slightly less star-like pattern, and the smoother historical demographic curve in South Georgia implies, perhaps, a less drastic reduction in population size and/or an earlier population expansion.

We note that the levels of nucleotide diversity recorded in *L. antarctica* are significantly lower than those found in temperate (Doellman et al., 2011; Silva et al., 2013; Sotelo et al., 2020; Blakeslee

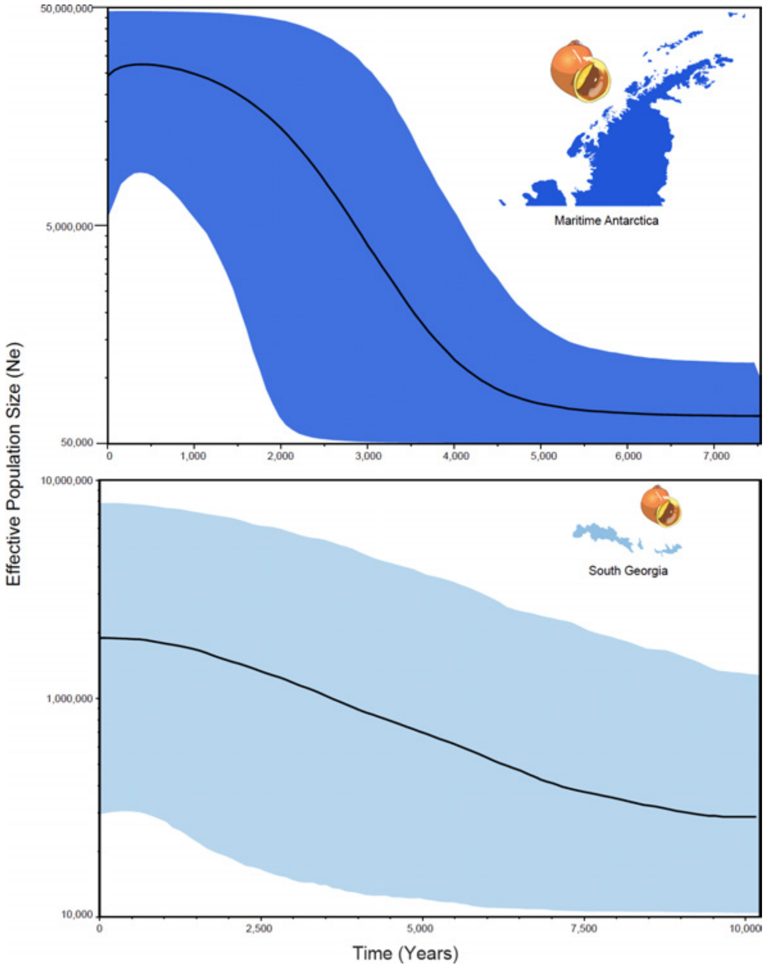


FIGURE 4
Historical demographic trajectories of the effective population sizes (N_e) estimated under a Bayesian skyline-plot approach based on COI sequences of *L. antarctica*. The y-axis represents the effective population size (N_e) while the x-axis shows the time since the present. The median estimates are shown for each genetic cluster recorded in the species (maritime Antarctica and South Georgia).

et al., 2021) and sub-Antarctic littorinids (González-Wevar et al., 2022). In fact, levels of genetic diversity in the species are much lower than those found in most other groups of Antarctic marine molluscs (Wilson et al., 2009; González-Wevar et al., 2013; Fassio et al., 2019; Levicoy et al., 2021) and fishes (Parker et al., 2002; Damerau et al., 2012; Damerau et al., 2014; Hüne et al., 2015). Nevertheless, several species of Antarctic near-shore marine invertebrates are characterized by low genetic diversity including the nemertean *Parborlasia* (Thornhill et al., 2008), the crustacean *Chorismus antarcticus* (Raupach et al., 2010), the echinoid *Sterechinus neumayeri* (Díaz et al., 2011) and the trochoid *Margarella antarctica* (González-Wevar et al., 2021). Drastic reduction of habitats has presumably affected populations of these Antarctic species and left characteristic signatures of drastic bottlenecks and/or founder effects (Aronson et al., 2007; Clarke and Crame, 2010; Allcock and Strugnell, 2012; González-Wevar et al., 2013; Riesgo et al., 2015; Guillemin et al., 2018).

Genetic structure

Our study adds to the diversity of biogeographic patterns seen in different taxa across maritime Antarctica and South Georgia in different taxa. This variation ranges from the absence of genetic differentiation, as in nototheniod fishes like *Gobionotothen gibberifrons* (Matschiner et al., 2009) and *Notothenia rossi* (Young et al., 2015), through marked phylogeographic structure, as in the limpet *Nacella concinna* (Hoffman et al., 2011; González-Wevar et al., 2013) and the notothenioid fish *Champsocephalus gunnari* (Young et al., 2015), to the presence of clearly divergent species-level clades, as in the gastropod *Margarella* (González-Wevar et al., 2021), the nudibranch *Doris* (Wilson et al., 2009), the crinoids of the genus *Promachocrinus* (Wilson et al., 2007), and the notothenioid genus *Lepidonotothen* (Dornburg et al., 2016).

The mtDNA (COI) levels of genetic divergence recorded between maritime Antarctic and South Georgian populations

(1.74%) is lower than those recorded between clearly recognized littorinid species (Williams et al., 2003; Williams and Reid, 2004; Reid et al., 2012) and particularly in higher latitude groups (González-Wevar et al., 2022; Rosenfeld et al., 2023). Under this molecular-based criteria, we would not treat the SSI/AP and SG populations as different species. Appropriate names would be available, however: the type locality of *L. antarctica* is South Georgia, whereas Deception Island, one of the South Shetland Islands, is the type locality for *L. bransfieldensis*, considered a junior synonym by Simone (2018). Nevertheless, our results in *Laevilacunaria* could probably be interpreted as an incipient speciation process, as has been hypothesized for other groups of marine organisms including *Nacella* (González-Wevar et al., 2011; González-Wevar et al., 2017), octocorals (Dueñas et al., 2016), *Doris* (Wilson et al., 2009), *Pareledone* (Allcock et al., 2011), nothothenioid fishes (Near et al., 2012; Dornburg et al., 2016) and even penguins (Vianna et al., 2017; Frugone et al., 2019). To further understand such evolutionary and biogeographic hypotheses in *Laevilacunaria*, future studies through morphological (radular and geometric morphometrics) analyses are needed. Addressing this important question in *Laevilacunaria* will provide new insights concerning biogeographical and diversity patterns in this widespread maritime Antarctica gastropod group. Moreover, integrative systematic studies including phylogenetic, genomic and morphological analyses of the whole genus are also required to evaluate the potential role of vicariance and long-distance dispersal in the biogeography of *Laevilacunaria*. The inclusion of the poorly known Kerguelen species *L. pumilio* and the partially sympatric Antarctic species *L. bennetti* will allow us to determine the origin and diversification of *Laevilacunaria* in different provinces of the Southern Ocean. Finally, through geometric morphometric it will be possible to evaluate the relevance of cryptic speciation in the evolution of the group across the Southern Ocean, a region of the planet that has been relatively neglected in spite of its global relevance.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: GenBank under the following Accession Numbers: COI (ORT701885 - ORT701931) and 28S rRNA (ORT711532 - ORT711533).

Ethics statement

The animal study was approved by Comité de Ética, Facultad de Ciencias, Universidad Austral de Chile. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

CG: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. YP: Formal analysis, Investigation, Methodology, Software, Writing – original draft. NS: Formal analysis, Methodology, Software, Writing – review & editing. SR: Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing. CM: Writing – original draft, Writing – review & editing. VJ: Formal analysis, Methodology, Writing – original draft. AS: Formal analysis, Methodology, Writing – original draft. KG: Writing – original draft. HS: Conceptualization, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. EP: Conceptualization, Formal analysis, Methodology, Supervision, Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This study was funded by Fondecyt Regular Project 1210787, ANID – Millenium Science Intitative program – ICN2021_002, INACH Project RG_18-17 and Program Fondap IDEAL (15150003) to CG-W. We also thank Fondecyt Postdoctoral Project 3210063 to CM and the program ANID/BASAL PR-06-CRN-18 (Universidad de Magallanes) to CM and SR.

Acknowledgments

Many thanks to Angie Díaz, Zambra López, Valentina Bernal, Jaime Ojeda, Cristian Ríos, Javier Naretto, Simon Morley and Paul Brickle for field assistance and samplings in maritime Antarctica and South Georgia. The authors thank the Chilean Antarctic Institute (INACH) and the Chilean Navy Aquiles and Oscar Viel Vessels for ECA53 – ECA55 and the crew of the Betanzos Ship during ECA58 and ECA59. We also would like to thank Commandant Charcot Cruise and the Scientist leader Geoffroy Dekersauson from Ponant Expeditions LEGCC120302023 and SEDNA/PONANT Expedition leg CC171222. We are grateful to the support of the South Atlantic Environmental Research Institute (SAERI) and the Shallow Marine Survey for collection of higher latitude littorinid specimens in South Georgia. At the same time, field access to South Georgia was supported by the British Antarctic Survey (BAS) and the collected specimens were authorized under the permit number 2017/058 to CM. BAS is supported by core funds from UKRI-NERC to the BEA Team. We deeply appreciate the editorial work of the Associate Editor and the useful comments and suggestions of two reviewers.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

References

Aljanabi, S. M., and Martinez, I. (1997). Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Res.* 25, 4692–4693. doi: 10.1093/nar/25.22.4692

Allcock, A. L., Barratt, I., Eléaume, M., Linse, K., Norman, M. D., Smith, P. J., et al. (2011). Cryptic speciation and the circumpolarity debate: A case study on endemic Southern Ocean octopuses using the COI barcode of life. *Deep-Sea Res. Pt II* 58, 242–249. doi: 10.1016/j.dsr2.2010.05.016

Allcock, A. L., and Strugnell, J. M. (2012). Southern Ocean diversity: new paradigms from molecular ecology. *Trends Ecol. Evol.* 27, 520–528. doi: 10.1016/j.tree.2012.05.009

Amsler, C. D., Amsler, M. O., Curtis, M. D., McClintock, J. B., and Baker, B. J. (2019). Impacts of gastropods on epiphytic microalgae on the brown macroalga *Himantothallus grandifolius*. *Ant Sci.* 31, 89–97. doi: 10.1017/S095410219000014

Amsler, C. D., Miller, L. R., Edwards, R. A., Amsler, M. O., Engl, W., McClintock, J. B., et al. (2022). Gastropod assemblages associated with *Himantothallus grandifolius*, *Sarcopeltis Antarctica* and other subtidal macroalgae. *Ant Sci.* 34, 246–255. doi: 10.1017/S0954102022000153

Amsler, M. O., Huang, Y. M., Engl, W., McClintock, J. B., and Amsler, C. D. (2015). Abundance and diversity of gastropods associated with dominant subtidal macroalgae from western Antarctic Peninsula. *Polar Biol.* 38, 1171–1181. doi: 10.1007/s00300-015-1681-4

Arnaud, P. M., and Bandel, K. (1979). Comments on six species of marine Antarctic Littorinacea (Mollusca, Gastropoda). *Tethys* 8, 213–230.

Aronson, R. B., Thatje, S., Clarke, A., Peck, L. S., Blake, D. B., Wilga, C. D., et al. (2007). Climate change and invasibility of the Antarctic benthos. *Ann. Rev. Ecol. Evol. Syst.* 38, 129–154. doi: 10.1146/annurev.ecolsys.38.091206.095525

Baird, H. P., Miller, K. J., and Stark, J. S. (2011). Evidence of hidden biodiversity, ongoing speciation and diverse patterns of genetic structure in giant Antarctic amphipods. *Mol. Ecol.* 20, 3439–3454. doi: 10.1111/j.1365-294X.2011.05173.x

Baird, H. P., Shin, S., Oberprieler, R. G., Hullé, M., Vernon, P., Moon, K. L., et al. (2021). Fifty million years of beetle evolution along the Antarctic Polar Front. *Proc. Natl. Acad. Sci. U.S.A.* 118, e2017383118. doi: 10.1073/pnas.2017384118

Barker, P. F., Diekmann, B., and Escutia, C. (2007). Onset of cenozoic antarctic glaciation. *Deep-Sea Res. Pt II* 54, 2293–2307. doi: 10.1016/j.dsr2.2007.07.027

Barnes, D. K. A., Hodgson, D. A., Convey, P., Allen, C. S., and Clarke, A. (2006). Incursion and excursion of Antarctic biota: past, present and future. *Global Ecol. Biogeogr.* 15, 121–142. doi: 10.1111/j.1466-822x.2006.00216.x

Blakeslee, A. M. H., Whitman Miller, A., Ruiz, G. M., Johannesson, K., André, C., and Panova, M. (2021). Population structure and phylogeography of two North Atlantic *Littorina* species with contrasting larval development. *Mar. Biol.* 168, 117. doi: 10.1007/s00227-021-03918-8

Brey, T., Dahm, C., Gorny, M., Klages, M., Stiller, M., and Arntz, W. E. (1996). Do Antarctic benthic invertebrates show an extended level of eurybathy? *Ant Sci.* 8, 3–6.

Cakil, Z. V., Garlasché, G., Iakovenko, N., Di Cesare, A., Eckert, E. M., Guidetti, R., et al. (2021). Comparative phylogeography reveals consistently shallow genetic diversity in a mitochondrial marker in Antarctic bdelloid rotifers. *J. Biogeogr.* 48, 1797–1809. doi: 10.1111/jbi.14116

Cantera, J. R., and Arnaud, P. M. (1984). Les gastéropodes prosobranches des Iles Kerguelen et Crozet (Sud de L'Océan Indien) comparaison écologique et particularités biologiques. *CNFRA [Comité Natl. Francais Recherches Antarctiques]* 56, 1–170.

Chenuil, A., Saucède, T., Hemery, L. G., Eléaume, M., Féral, J.-P., Améziane, N., et al. (2018). Understanding processes at the origin of species flocks with focus on the marine Antarctic fauna. *Biol. Rev.* 93, 481–504. doi: 10.1111/brv.12354

Clarke, A., and Crame, J. A. (1989). The origin of the Southern Ocean marine fauna. *Geol. Soc London* 47, 253–268. doi: 10.1144/GSL.SP.1989.047.01.19

Clarke, A., and Crame, J. (1992). The Southern-Ocean benthic fauna and climate change – a historical-perspective. *Philos. T R. Soc B* 338, 299–309. doi: 10.1098/rstb.1992.0150

Clarke, A., and Crame, J. (2010). Evolutionary dynamics at high latitudes: speciation and extinction in polar marine faunas. *Phil Trans. R. Soc B* 365, 3655–3666. doi: 10.1098/rstb.2010.0270

Convey, P., Stevens, M. I., Hodgson, D. A., Smellie, J. L., Hillenbrand, C.-D., Barnes, D. K. A., et al. (2009). Exploring biological constraints on the glacial history of Antarctica. *Quat. Sci. Rev.* 28, 3035–3048. doi: 10.1016/j.quascirev.2009.08.015

Crame, J. (2018). Key stages in the evolution of the Antarctic marine fauna. *J. Biogeogr.* 45, 986–994. doi: 10.1111/jbi.13208

Cumming, R. A., Nikula, R., Spencer, H. G., and Waters, J. M. (2014). Transoceanic genetic similarities of kelp-associated sea slug populations: long-distance dispersal via rafting? *J. Biogeogr.* 41, 2357–2370. doi: 10.1111/jbi.12376

Dambach, J., Thatje, S., Rödder, D., Basher, Z., and Raupach, M. J. (2012). Effects of Late-Cenozoic glaciation on habitat availability in Antarctic benthic shrimps (Crustace: Decapoda: Caridae). *PloS One* 7, e46283. doi: 10.1371/journal.pone.0036283

Damerau, M., Marschiner, M., Salzburger, W., and Hanel, R. (2012). Comparative population genetics of seven notothenioid fish species reveals high levels of gene flow along ocean currents in the southern Scotia Arc, Antarctica. *Polar Biol.* 35, 1073–1086. doi: 10.1007/s00300-012-1155-x

Damerau, M., Salzburger, W., and Hanel, R. (2014). Population genetic structure of Lepidonotothen larseni revisited: cyb and microsatellites suggest limited connectivity in the Southern Ocean. *Mar. Ecol. Prog. Ser.* 517, 251–263. doi: 10.3354/meps11061

Díaz, A., Féral, J.-P., David, B., Saucède, T., and Poulin, E. (2011). Evolutionary pathways among shallow and deep-sea echinoids of the genus *Sterechinus* in the Southern Ocean. *Deep Sea Res. Pt II* 58, 205–211. doi: 10.1016/j.dsr2.2010.10.012

Díaz, A., Gérard, K., González-Wevar, C., Maturana, C., Féral, J.-P., David, B., et al. (2018). Genetic structure and demographic inference of the regular sea urchin *Sterechinus neumayeri* (Meissne 1900) in the Southern Ocean: The role of the last glaciation. *PloS One* 13, e0197611. doi: 10.1371/journal.pone.0197611

Doellman, M. M., Trussel, G. C., Grahame, J. W., and Vollmer, S. V. (2011). Phylogeographic analysis reveals a deep lineage split within North Atlantic *Littorina saxatilis*. *Proc. R. Soc B* 278, 3175–3183. doi: 10.1098/rspb.2011.0346

Dornburg, A., Eytan, R. I., Federman, S., Pennington, J. N., Stewart, A. L., Jones, C. D., et al. (2016). Molecular data support the existence of two species of the Antarctic fish genus *Cryodraco* (Channicthyidae). *Polar Biol.* 39, 1369–1379. doi: 10.1007/s00300-015-1859-9

Drummond, A. J., and Rambaut, A. (2007). BEAST: bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* 7, 214. doi: 10.1186/1471-2148-7-214

Drummond, A. J., Suchard, M. A., Xie, D., and Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* 29, 1969–1973. doi: 10.1093/molbev/mss075

Dueñas, L. F., Tracey, D. M., Crawford, A. J., Wilke, T., Alderslade, P., and Sánchez, J. A. (2016). The Antarctic Circumpolar Current as a diversification trigger for deep-sea octocorals. *BMC Evol. Biol.* 16, 2. doi: 10.1186/s12862-015-0574-z

Dupanloup, I., Schneider, S., and Excoffier, L. (2002). A simulated annealing approach to define the genetic structure of populations. *Mol. Ecol.* 11, 2571–2581. doi: 10.1046/j.1365-294x.2002.01650.x

Edgar, R. C. (2004). MUSCLE: A multiple sequence alignment method with reduced time and space complexity. *BMC Bioinf.* 5, 113. doi: 10.1186/1471-2105-5-113

Engl, W. (2012). *Shells of Antarctica* Hackenheim, Conchbooks Publishing, 402pp.

Excoffier, L., Laval, G., and Schneider, S. (2005). Arlequin (version 3.0): An integrated software package for population genetics data analysis. *Evol. Bioinform. Online* 1, 37–50. doi: 10.1177/117693430500100003

Fassio, G., Modica, M. V., Alvaro, M. C., Buge, B., Salvi, D., Oliverio, M., et al. (2019). An Antarctic flock under the Thorson's rule: Diversity and larval development of Antarctic Velutinidae (Mollusca: Gastropoda). *Mol. Phylogenet. Evol.* 132, 1–13. doi: 10.1016/j.ympev.2018.11.017

Folmer, O., Black, M., Hoeh, W., Lutz, R., and Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biotech* 3, 294–299.

Forster, P., Torroni, A., Renfrew, C., and Röhl, A. (2001). Phylogenetic star contraction applied to Asian and Papuan mtDNA evolution. *Mol. Biol. Evol.* 18, 1864–1881. doi: 10.1093/oxfordjournals.molbev.a003728

Fraser, C. I., Nikula, R., Ruzzante, D. E., and Waters, J. M. (2012). Poleward bound: biological impacts of Southern Hemisphere glaciation. *Trends Ecol. Evol.* 27, 462–471. doi: 10.1016/j.tree.2012.04.011

Fraser, C. I., Nikula, R., Spencer, H. G., and Waters, J. M. (2009). Kelp genes reveal effects of subantarctic sea during the Last Glacial Maximum. *Proc. Natl. Acad. Sci. U.S.A.* 106, 3249–3253. doi: 10.1073/pnas.0810635106

Fraser, C. I., Zuccarello, G. C., Spencer, H. G., Salvatore, L. C., Garcia, G. R., Waters, J. M., et al (2013). Genetic affinities between trans-oceanic populations of non-buoyant macroalgae in the high latitudes of the southern hemisphere. *PLoS ONE* 8, e69138. doi:10.1371/journal.pone.0069138

Fraser, C. I., Terauds, A., Smellie, J., Convey, P., and Chown, S. L. (2014). Geothermal activity helps life survive glacial cycles. *Proc. Natl. Acad. Sci. U.S.A.* 111, 5634–5639. doi: 10.1073/pnas.1321437111

Frugone, M. J., López, M. E., Segovia, N. I., Cole, T. L., Lowther, A., Pistorius, P., et al. (2019). More than the eye can see: Genomic insights into the drivers of genetic differentiation in Royal/Macaroni penguins across the Southern Ocean. *Mol. Phylogenet. Evol.* 139, 106563. doi: 10.1016/j.ympev.2019.106563

González-Wevar, C. A., Hüne, M., Cañete, J. I., Mansilla, A., Nakano, T., and Poulin, E. (2012). Towards a model of postglacial biogeography in shallow marine species along the Patagonian province: lessons from the limpet *Nacella magellanica* (Gmelin 1791). *BMC Evol. Biol.* 12, 139. doi: 10.1186/1471-2148-12-139

González-Wevar, C. A., Nakano, T., Cañete, J. I., and Poulin, E. (2011). Concerted genetic, morphological and ecological diversification in *Nacella* limpets in the Magellanic Province. *Mol. Ecol.* 20, 1936–1951. doi: 10.1111/j.1365-294X.2011.05065.x

González-Wevar, C. A., Saucède, T., Morley, T., Chown, S. L., and Poulin, E. (2013). Extinction and recolonization of maritime Antarctica in the limpet *Nacella concinna* (Strebel 1908) during the last glacial cycle: toward a model of Quaternary biogeography in shallow Antarctic invertebrates. *Mol. Ecol.* 22, 5221–5236. doi: 10.1111/mec.12465

González-Wevar, C. A., Hüne, M., Segovia, N. I., Nakano, T., Spencer, H. G., Chown, S. L., et al (2017). Following the Antarctic Circumpolar Current: patterns and processes in the biogeography of the limpet Nacella(Mollusca: Patellogastropoda) across the Southern Ocean. *J. Biogeogr.* 44, 861–874. doi: 10.1111/jbi.12908

González-Wevar, C. A., Segovia, N. I., Rosenfeld, S., Maturana, C. S., Jeldres, V., Pinochet, R., et al. (2022). Seven snail species hidden in one: Biogeographic diversity in an apparently widespread periwinkle in the Southern Ocean. *J. Biogeogr.* 49, 1521–1534. doi: 10.1111/jbi.14453

González-Wevar, C. A., Segovia, N. I., Rosenfeld, S., Noll, D., Maturana, C. S., Hüne, M., et al. (2021). Contrasting biogeographical patterns in *Margarella* (Gastropoda: Calliostomatidae: Margarellinae) across the Antarctic Polar Front. *Mol. Phylogenet. Evol.* 156, 107039. doi: 10.1016/j.ympev.2020.107039

González-Wevar, C. A., Segovia, N. I., Rosenfeld, S., Ojeda, J., Hüne, M., Naretto, J., et al. (2018). Unexpected absence of island endemics: Long-distance dispersal in higher latitude sub-Antarctic *Siphonaria* (Gastropoda: Euthyneura) species. *J. Biogeogr.* 45, 874–884. doi: 10.1111/jbi.13174

Guillemin, M.-L., Dubrasquet, H., Reyes, J., and Valero, M. (2018). Comparative phylogeography of six red algae along the Antarctic Peninsula: extreme genetic depletion linked to historical bottlenecks and recent expansion. *Polar Biol.* 41, 827–837. doi: 10.1007/s00300-017-2244-7

Guillot, G., Mortier, F., and Estoup, A. (2005). GENELAND: a computer package for landscape genetics. *Mol. Ecol. Notes* 5, 712–715. doi: 10.1111/j.1471-8286.2005.01031.x

Halanych, K. M., and Mahon, A. R. (2018). Challenging the dogma concerning biogeographic patterns of Antarctica and the Southern Ocean. *Annu. Rev. Ecol. Evol. Syst.* 49, 355–378. doi: 10.1146/annurev-ecolsys-121415-032139

Ho, S. Y. W., Lanfear, R., Bromham, L., Phillips, M. J., Soubrier, J., Rodrigos, A. G., et al. (2011). Time-dependent rates of molecular evolution. *Mol. Ecol.* 20, 3087–3101. doi: 10.1111/j.1365-294X.2011.05178.x

Ho, S. Y. W., Phillips, M. J., Cooper, A., and Drummond, A. J. (2005). Time dependency of molecular rate estimated and systematic overestimation of recent divergence times. *Mol. Biol. Evol.* 22, 1561–1568. doi: 10.1093/molbev/msi145

Ho, S. Y. W., Shapiro, B., Phyllips, M. J., Cooper, A., and Drummond, A. J. (2007). Evidence for time dependency of molecular rate estimates. *Syst. Biol.* 56, 517–522. doi: 10.1080/10635150701435401

Hoffman, J. I., Peck, L. S., Hillyard, G., Zieritz, A., and Clark, M. S. (2010). No evidence for genetic differentiation between Antarctic limpet *Nacella concinna* morphotypes. *Mar. Biol.* 157, 765–778. doi: 10.1007/s00227-009-1360-5

Hoffman, J. I., Peck, L. S., Linse, K., and Clarke, A. (2011). Strong population genetic structure in a broadcast-spawning Antarctic marine invertebrate. *J. Hered* 102, 55–66. doi: 10.1093/jhered/esq094

Hudson, R. R. (2000). A new statistic for detecting genetic differentiation. *Genetics* 155, 2011–2014. doi: 10.1093/genetics/155.4.2011

Hüne, M., González-Wevar, C., Poulin, E., Mansilla, A., Fernández, D. A., and Barrera-Oro, E. (2015). Low levels of genetic divergence between *Harpagifer* fish species (Perciformes: Notothenioidei) suggests a Quaternary colonization of Patagonia from the Antarctic Peninsula. *Polar Biol.* 38, 607–617. doi: 10.1007/s00300-014-1623-6

Ihaka, R., and Gentleman, R. (1996). R: A language for data analysis and graphics. *J. Comp. Graph Stat.* 5, 299–314. doi: 10.2307/1390807

Iken, K. (1999). Feeding ecology of the Antarctic herbivorous gastropod *Laevilacunaria Antarctica* Martens. *J. Exp. Mar. Biol. Ecol.* 236, 133–148. doi: 10.1016/S0022-0981(98)00199-3

Ingólfson, Ó. (2004). "Quaternary glacial and climate history of Antarctica," in *Quaternary glaciations – extent and chronology, part III: South America, Asia, Australia and Antarctica*. Eds. J. Ehlers and P. L. Gibbard (Development in Quaternary Science. Elsevier ScienceDirect), 3–43.

Krabbe, K., Leese, F., Mayer, C., Tollrian, R., and Held, C. (2010). Cryptic mitochondrial lineages in the widespread pycnogonid *Colossendeis megalonyx* Hoek 1881 from Antarctic and Subantarctic waters. *Polar Biol.* 33, 281–292. doi: 10.1007/s00300-009-0703-5

Lau, S. C. Y., Wilson, N. G., Silva, C. N. S., and Strugnell, J. M. (2020). Detecting glacial refugia in the Southern Ocean. *Ecography* 43, 1–18. doi: 10.1111/ecog.04951

Levicoy, D., Flores, K., Rosenfeld, S., and Cárdenas, L. (2021). Phylogeography and genetic diversity of the microbivalve *Kidderia subquadrata*, reveals new data from West Antarctic Peninsula. *Sci. Rep.* 11, 5705. doi: 10.1038/s41598-021-85042-7

Librado, P., and Rozas, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25, 1451–1452. doi: 10.1093/bioinformatics/btp187

Littlewood, D. T. J., Curini-Galletti, M., and Herniou, E. A. (2000). The interrelationships of Proseriata (Platyhelminthes: Seriata) tested with molecules and morphology. *Mol. Phylogenet. Evol.* 16, 449–466. doi: 10.1006/mpev.2000.0802

Maggs, C. A., Castilho, R., Foltz, D., Henzler, C., Jolly, M. T., Kelly, J., et al. (2008). Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. *Ecology* 89, S108–S122. doi: 10.1890/08-0257.1

Marko, P. B. (2004). 'What's larvae got to do with it?' Disparate patterns of post-glacial population structure in two benthic marine gastropod with identical dispersal potential. *Mol. Ecol.* 13, 597–611. doi: 10.1046/j.1365-294X.2004.02096.x

Marko, P. B., Hoffman, J. M., Emme, S. A., McGovern, T. M., Keever, C. C., and Cox, N. (2010). The 'Expansion–Contraction' model of Pleistocene biogeography: rocky shores suffer a sea change? *Mol. Ecol.* 19, 146–167. doi: 10.1111/j.1365-294X.2009.04417.x

Martens van, E., and Pfeffer, G. (1886). Die Mollusken von Süd–Georgien nach der Ausbeute der Deutschen Station 1882–83. *Jahr Hamb Wiss. Anst* 3, 65–135.

Martin, A., Miloslavich, P., Díaz, Y., Ortega, I., Klein, E., Troncoso, J., et al. (2016). Intertidal benthic communities associated with the macroalgae *Iridaea cordata* and *Adenocystis utricularis* in King George Island, Antarctica. *Polar Biol.* 39, 207–220. doi: 10.1007/s00300-015-1773-1

Matschiner, M., Hanel, R., and Salzburger, W. (2009). Gene flow by larval dispersal in the Antarctic notothenioid fish *Gobionotothen gibberifrons*. *Mol. Ecol.* 18, 2574–2587. doi: 10.1111/j.1365-294X.2009.04220.x

Maturana, C. S., Segovia, N. I., González-Wevar, C. A., Díaz, A., Rosenfeld, S., Poulin, E., et al. (2020). Evidence of strong small-scale population structure in the Antarctic freshwater copepod *Boeckella poppei* in lakes on Signy Island, South Orkney Islands. *Limnol Oceanogr* 65, 2024–2040. doi: 10.1002/lno.11435

McCay, R. M., Barrett, P. J., Levy, R. S., Naish, T. R., Golledge, N. R., and Pyne, A. (2016). Antarctic Cenozoic climate history from sedimentary records: ANDRILL and beyond. *Phil Trans. R. Soc A* 374, 20140301. doi: 10.1098/rsta.2014.0301

McGaughran, A., Stevens, M. I., Hogg, I. D., and Carapelli, A. (2011). Extreme glacial legacies: A synthesis of the Antarctic springtail phylogeographic record. *Insects* 2, 62–82. doi: 10.3390/insects2020062

Moon, K. L., Chown, S. L., and Fraser, C. I. (2017). Reconsidering connectivity in the sub-Antarctic. *Biol. Rev.* 92, 2164–2181. doi: 10.1111/brv.12327

Narum, S. R. (2006). Beyond Bonferroni: Less conservative analyses for conservation genetics. *Cons Genet.* 7, 783–787. doi: 10.1007/s10592-005-9056-y

Near, T. J., Dornburg, A., Kuhn, K. L., Eastman, J. T., Pennington, J. N., Patarnello, T., et al. (2012). Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *Proc. Natl. Acad. Sci. U.S.A.* 109, 3434–3439. doi: 10.1073/pnas.1115169109

Nikula, R., Fraser, C. I., Spencer, H. G., and Waters, J. M. (2010). Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. *Mar. Ecol-Prog Ser.* 405, 221–230. doi: 10.3354/meps08523

Nylander, J. A. A. (2004). *MrModeltest Version 2. Program Distributed by the Author. Evolutionary Biology Centre, Uppsala University, Uppsala.*

Parker, R. W., Paige, K. N., and DeVries, A. L. (2002). Genetic variation among populations of the Antarctic toothfish: evolutionary insights and implications for conservation. *Polar Biol.* 25, 256–261. doi: 10.1007/s00300-001-0333-z

Pearse, J. S., Mooi, R., Lockhart, S. J., and Brandt, A. (2009). "Brooding and species diversity in the Southern Ocean: Selection for brooders or speciation within brooding clades? " in *Smithsonian at the poles: Contributions to International Polar Year science*. Eds. I. Krupnik, M. A. Lang and S. E. Miller Smithsonian Institution Scholarly Press, Washington, DC USA.

Pollard, D., and DeConto, R. M. (2009). Modeling West Antarctic ice sheet growth and collapse through the past five million years. *Nature* 458, 329–332. doi: 10.1038/nature07809

Pons, O., and Petit, R. J. (1996). Measuring and testing genetic differentiation with ordered Versus unordered alleles. *Genetics* 144, 1237–1245. doi: 10.1093/genetics/144.3.1237

Powell, A. W. B. (1951). Antarctic and subantarctic mollusca: pelecypoda and gastropoda. *Discovery Rep.* 26, 47–196. doi: 10.5962/bhl.part.16335

Preston, H. B. (1916). Descriptions of eight new species of marine Mollusca from the South Shetland Islands. *Ann. Mag Nat. Hist* 18, 269–272. doi: 10.1080/00222931608693847

Provan, J., and Bennett, K. D. (2008). Phylogeographic insights into cryptic glacial refugia. *Trends Ecol. Evol.* 23, 564–571. doi: 10.1016/j.tree.2008.06.010

Rambaut, A., Drummond, A. J., Xie, D., Baele, G., and Suchard, M. A. (2018). Posterior summarization in Bayesian phylogenetics using Tracer. *Syst. Biol.* 67, 901–904. doi: 10.1093/sysbio/syy032

Raupach, M. J., Thatje, S., Dambach, J., Rehm, P., Misof, B., and Leese, F. (2010). Genetic homogeneity and circum-Antarctic distribution of two benthic shrimp species of the Southern Ocean, *Chorismus antarcticus* and *Nematocarcinus lanceopes*. *Mar. Biol.* 157, 1783–1797. doi: 10.1007/s00227-010-1451-3

Reid, D. G., Dyal, P., and Williams, S. T. (2012). A global molecular phylogeny of 147 periwinkle species (Gastropoda, Littorininae). *Zool. Scripta* 41, 125–136. doi: 10.1111/j.1463-6409

Riesgo, A., Taboada, S., and Avila, C. (2015). Evolutionary patterns in Antarctic marine invertebrates: An update on molecular studies. *Mar. Genomics* 23, 1–13. doi: 10.1016/j.margen.2015.07.005

Rogers, A. R., and Harpending, H. C. (1992). Population growth makes waves in the distribution of pairwise genetic differences. *Mol. Biol.* 9, 552–569. doi: 10.1093/oxfordjournals.molbev.a04727

Rosenfeld, S., Segovia, N. I., Maturana, C. S., Aldea, C., Saucède, T., Brickle, P., et al. (2023). A revision of the higher latitude periwinkle species *Laevilitorina caliginosa* sensu lato. *Zool. J. Linn. Soc.*. (in press). doi: 10.1093/zoolinnean/zlad171

Salzburger, W., Ewing, G. B., and Von Haessler, A. (2011). The performance of phylogenetic algorithms in estimating haplotype genealogies with migration. *Mol. Ecol.* 20, 1952–1963. doi: 10.1111/j.1365-294X.2011.05066.x

Schmider-Martínez, A., Maturana, C. S., Poveda, Y., López-Farran, Z., Saucède, T., Poulin, E., et al. (2023). Laevilacunaria (Mollusca: Gastropoda) in the Southern Ocean: a comprehensive occurrence dataset. *Biodivers. Data J.* 11, e111982.

Silva, S. E., Silva, I. C., Madeira, C., Sallema, R., Paulo, O. S., and Paula, J. (2013). Genetic and morphological variation in two littorinid gastropods: evidence for recent population expansions along the East African coast. *Biol. J. Linn. Soc* 108, 494–508. doi: 10.1111/j.1095-8312.2012.02041.x

Simone, L. R. (2018). Convergence with naticids: phenotypic phylogenetic study on some Antarctic littorinoideans, with description of the zerotulid new genus *Pseudonatica*, and its presence in Brazil (Mollusca, Caenogastropoda). *J. Mar. Biol. Ass UK* 98, 1365–1381. doi: 10.1017/S002531541700025X

Simpson, R. D., and Harrington, S. A. (1985). Egg masses of three gastropods, *Kerguelenella lateralis* (Siphonariidae), *Laevilitorina caliginosa* and *Macquariella hamiltoni* (Littorinidae), from Macquarie Island (sub-Antarctic). *J. Malacol Soc Aust.* 7, 17–28. doi: 10.1080/00852988.1985.10673973

Smith, E. A. (1879). Mollusca. An account of the petrological, botanical and zoological collection made in Kerguelen´s Island and Rodriguez during the Transit of "Venus" Expedition in the years 1874–75. *Philos. Trans. R. Soc Lond. B* 168, 167–192.

Sotelo, G., Duvetorp, M., Costa, D., Panova, M., Johannesson, K., and Faria, R. (2020). Phylogeographic history of flat periwinkles, *Littorina fabalis* and *L. obtusata*. *BMC Evol. Biol.* 20, 23. doi: 10.1186/s12862-019-1561-6

Suchard, M. A., Weiss, R. E., and Sinsheimer, J. S. (2001). Bayesian selection of continuous-time Markov Chain evolutionary models. *Mol. Biol. Evol.* 18, 1001–1013. doi: 10.1093/oxfordjournals.molbev.a003872

Tamura, K., Stecher, G., and Kumar, S. (2021). MEGA11: molecular evolutionary genetics analysis version 11. *Mol. Biol. Evol.* 38, 3022–3027. doi: 10.1093/molbev/msab120

Thatje, S., Hillenbrand, C.-D., and Larter, R. (2005). On the origin of Antarctic marine benthic community structure. *Trends Ecol. Evol.* 20, 534–540. doi: 10.1016/j.tree.2005.07.010

Thatje, S., Hillenbrand, C.-D., Mackensen, A., and Larter, R. (2008). Life hung by a thread: endurance of Antarctic fauna in glacial periods. *Ecology* 89, 682–689. doi: 10.1890/07-0498.1

Thornhill, D. J., Mahon, A. R., Norenburg, J. L., and Halanych, K. (2008). Open-ocean barriers to dispersal: a test case with the Antarctic Polar Front and the ribbon worm *Parborlasia corrugatus* (Nemertea: Lineidae). *Mol. Ecol.* 17, 5104–5117. doi: 10.1111/j.1365-294X.2008.03970.x

Vianna, J. A., Noll, D., Dantas, G. P. M., Petry, M. V., Barbosa, A., González-Acuña, D., et al. (2017). Marked phylogeographic structure of Gentoo penguin reveals an ongoing diversification process along the Southern Ocean. *Mol. Phylogenet. Evol.* 107, 486–498. doi: 10.1016/j.ympev.2016.12.003

Waters, J. M. (2008). Driven by the West Wind Drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. *J. Biogeogr.* 35, 417–427. doi: 10.1111/j.1365-2699.2007.01724.x

Williams, S. T., and Reid, D. G. (2004). Speciation and diversity on tropical rocky shores: a global phylogeny of snail of the genus *Echinolittorina*. *Evolution* 58, 2227–2251. doi: 10.1111/j.0014-3820.2004.tb01600.x

Williams, S. T., Reid, D. G., and Littlewood, D. T. J. (2003). A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism, and biogeography of the Southern Ocean. *Mol. Phylogenet. Evol.* 28, 60–86. doi: 10.1016/S1055-7903(03)00038-1

Wilson, N. G., Hunter, R. L., Lockhart, S. J., and Halanych, K. M. (2007). Multiple lineage and absence of panmixia in the "circumpolar" crinoid *Promachocrinus kerguelensis* from the Atlantic sector of Antarctica. *Mar. Biol.* 152, 895–904. doi: 10.1007/s00227-007-0742-9

Wilson, N. G., Schrödl, M., and Halanych, K. M. (2009). Ocean barriers and glaciation: evidence for explosive radiation of mitochondrial lineages in the Antarctic sea slug *Doris kerguelenensis* (Mollusca, Nudibranchia). *Mol. Ecol.* 18, 965–984. doi: 10.1111/j.1365-294X.2008.04071.x

Xia, X., and Xie, Z. (2001). DAMBE: Software package for data analysis in Molecular Biology and Evolution. *J. Hered.* 92, 371–373. doi: 10.1093/jhered/92.4.371

Young, E. F., Belchier, M., Hauser, L., Horsburg, G. J., Meredith, M. P., Murphy, E. J., et al. (2015). Oceanography and life history predict contrasting genetic population structure in two Antarctic fish species. *Evol. Appl.* 8, 486–509. doi: 10.1111/eva.12259

Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686–693. doi: 10.1126/science.1059412