The Australasian muricid gastropod *Lepsiella* as Pleistocene visitor to southernmost South America

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Six shells belonging to a muricid gastropod species were recovered from a Pleistocene marine raised beach located on Navarino Island, in southern South America. None of the living species in the Beagle Channel or in the area is close, and none of the fossil species in the vicinity regions shows the diagnostic characters of the Navarino Pleistocene fossils. Our material resembles *Lepsiella baileyana* from southern Australia, although some differences in the suture and in the spire outline are recognized. Haustrinae were previously confined geographically to New Zealand and to the temperate coast of Australia, now extending its range of distribution to southern South America. This finding of *Lepsiella ukika* sp. nov. is best explained on the basis of transoceanic migration from Australasia by means of the Antarctic Circumpolar Current perhaps during a Quaternary glacial period. The presence of this Pleistocene visitor in southern South America is important because it clearly demonstrates that transcontinental traverse of taxa with direct (non-planktonic) development might have happened by rafting on kelp that served as transport platforms.

Key words: Gastropoda, Muricidae, Pleistocene, Beagle Channel, Australasia connection.

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Introduction

Muricids are a diverse group of carnivorous gastropods, very common in shallow marine benthic communities in southern South America (Dell 1971; Adami and Gordillo 1999; Linse 1999; Lomovasky et al. 2005). As fossils they also appear frequently in Quaternary deposits from the same region (Gordillo 1999, 2009). Among them, the genus *Trophon* (sensu lato) has a particular importance because it is a highly diversified taxon in the Southern Ocean and Subantarctic waters (Aldea and Troncoso 2010).

Systematic revisions including living muricids from this region are the reviews on the genera *Xymenopsis* (Pastorino and Harasewych 2000), *Trophon* (Pastorino 2002, 2005), and *Acanthina* (DeVries 2003).

Six muricid shells recently recovered from a Pleistocene marine raised beach located on Navarino Island, on the southern coast of the Beagle Channel look like a cross between an Ocenebridae like *Acanthina*, and a Trophoninae like *Trophon* or *Xymenopsis*. Based on both contour shape and crenulated outer lip, these fossil muricids are closer to *Acanthina* than *Trophon*, but based on the apertural lip shape, with a long siphonal canal, and whorl sculpture of ribs crossed with non imbricate axial lamellae they resemble a *Trophon* shell. Besides, none of the living species in the Beagle Channel or in the greater area is morphologically close, and none of the fossil species in the neighboring regions shows the diagnostic characters of the Navarino Pleistocene fossils.

In turn our shells are very similar to those of haustrine muricids (see Tan 2003 for review), which until now were exclusive to New Zealand and temperate Australia.

Institutional abbreviations.—CEGH-UNC, CIPAL-Centro de Investigaciones Paleobiológicas, CICTERRA, Córdoba, Argentina; NMV, National Museum of Victoria, Victoria, Australia; SGO.PI, Museo Nacional de Historia Natural, Santiago, Chile.

Other abbreviations.—ACC, Antarctic Circumpolar Current; LGM, last glacial maximum; MIS, Marine Isotopic Stage.

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Geological setting

In the Beagle Channel, the Holocene marine transgression is well represented by marine deposits at different altitudes, extending along both northern and southern Beagle Channel coast; therefore, Pleistocene highstands have not been well preserved due to the intense erosive effect of the Last Glaciation (Rabassa et al. 2000). One exception is a marine unit very rich in fossils (Gordillo et al. 2010) located on Navarino Island (Fig. 1), indicating that the Beagle Channel was flooded by sea water at least once before the last glacial (MIS4 to MIS2). During this cold period, the Darwin Mountain icefield in Tierra del Fuego greatly expanded, perhaps at circa 85 kyr BP; reaching the last glacial maximum (LGM) at circa 25 kyr BP, after a relatively warmer period identified as MIS3 (McCulloch et al. 2005; Kaplan et al. 2008; Rabassa 2008). Prior to these events, a marine unit of pre-Holocene age would have been formed during the last interglacial or previous transgressions. Taking into account Pleistocene deposits of similar altitude located on the Atlantic Fuegian coast, it is most likely that the marine layer has formed during MIS5 (Sangamon). The age control of this section is based on a radiocarbon age determined at the NSF Arizona AMS Laboratory, but considering that the obtained age (41,700 ± 1500 BP; AA69648; Rabassa et al. 2008) is close to the accepted reliability boundary of the AMS dating method, the given age was interpreted as older.

Material

The material studied here was recovered together with a large number of species (nearly one hundred, including mollusks, foraminifers, and ostracods) from a muddy marine layer with a thickness of 112 cm. A list of taxonomic composition was given in Gordillo et al. (2010), who recognized in this marine layer a mixture of species inhabiting shallow marine environments characterized by strong currents and belonging to different local communities associated with the spatial heterogeneity of this basin. Other muricid gastropods collected from this paleontological level were *Trophon geversianus* (Pallas, 1769), *Trophon plicatus* (Lightfoot, 1786), *Fuegotrophon pallidus* (Broderip, 1832), *Xymenopsis muriciformis* (King and Broderip, 1832), and *Xymenopsis buccineus* (Lamarck, 1816).

Systematic paleontology

Class Gastropoda Cuvier, 1797

Family Muricidae Rafinesque, 1815

Subfamily Haustrinae Tan, 2003

Genus *Lepsiella* Iredale, 1912

Type species: *Purpura scobina* Quoy and Gaimard, 1833 by original designation; Recent, New Zealand.

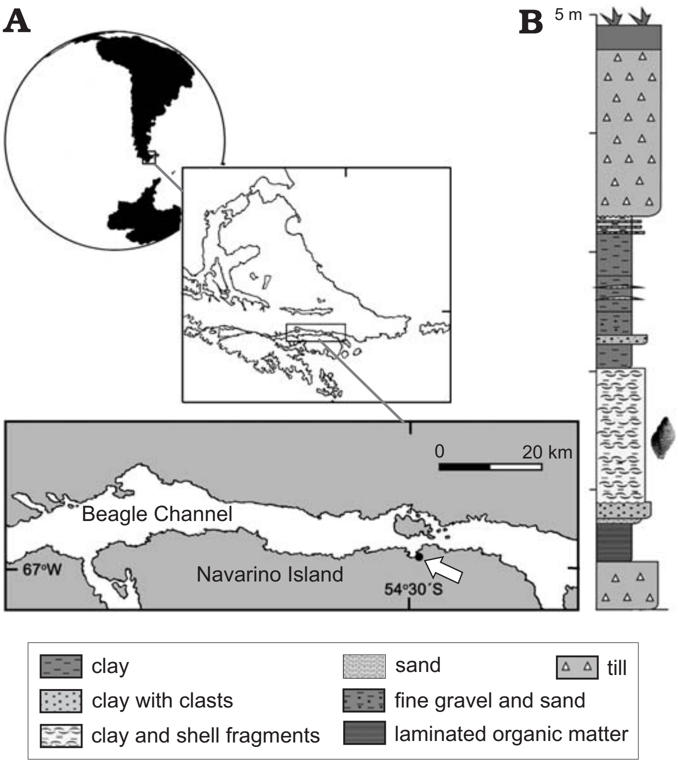

Fig. 1. **A**. Location map. Six specimens of *Lepsiella ukika* sp. nov. were recovered from a Pleistocene marine terrace (arrow) located on Navarino Island (Beagle Channel), in southern South America. **B**. The stratigraphic section containing calcareous shells was described in Gordillo et al. (2010).

Lepsiella ukika sp. nov.

Fig. 2A–C.

Etymology: Ukika is the name of the southernmost village of the world located close to the site, where we recovered the fossil shells. It is considered a historic town, where live the last descendants of the native people (Yagan, Yámana), who inhabited the Beagle Channel and Navarino Island.

Type material: Holotype: one complete specimen (CEGH-UNC 23917; Fig. 2A). Paratypes: two specimens (CEGH-UNC 23896, CEGH-UNC 23897; Fig. 2B, C).

Type locality: Marine terrace located at Caleta Pantalón, 10 km west of Puerto Williams, Navarino Island (Beagle Channel), Chile.

Type horizon: Pleistocene.

Material.—Six specimens including the figured material CEGH-UNC 23917, 23896–97. Two specimens were deposited under SGO.PI.6457–58. Specimens examined range from 13 mm to 20 mm in height.

Diagnosis.—Shell broadly fusiform with convex whorls and straight spire outline. Suture relatively deep. Last whorl axially lamellate, 13 spiral cords without nodes. Outer lip crenulated.

Description.—The protoconch is unknown, teleoconch whorls are convex. The last whorl is sculptured with 13 strong spiral ridges (cords) separated by deep grooves. Ridges are overridden by conspicuous, numerous, often lamellose axials, at regular intervals. There are no axial nodes, only dense growth lines.

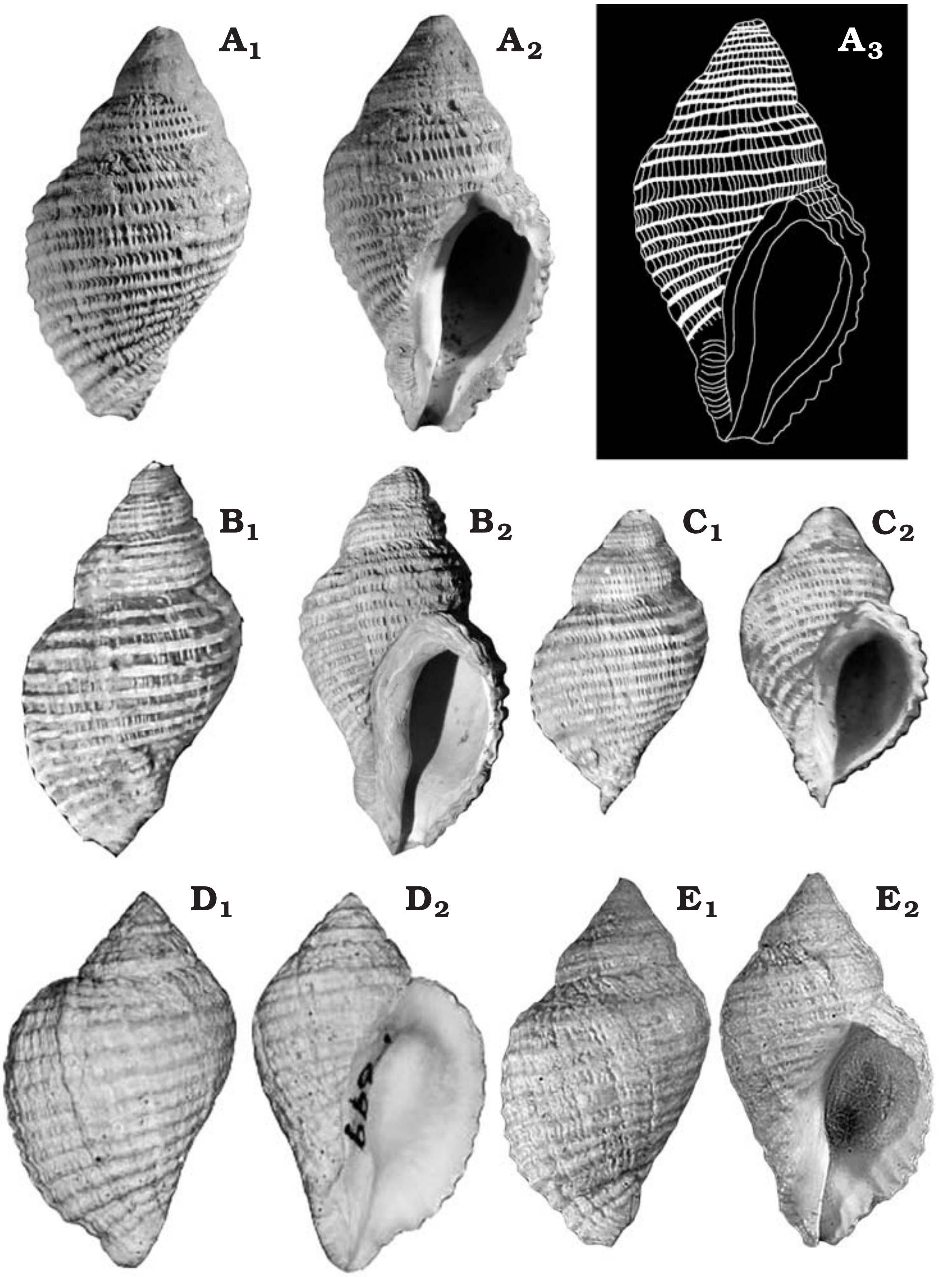

Fig. 2. Muricid gastropod *Lepsiella*. **A**–**C**. *Lepsiella ukika* sp. nov.; three of six recovered Pleistocene specimens, Marine terrace at Caleta Pantalón, Navarino Island, Chile. **A**. CEGH-UNC 23917, holotype, 17.5 mm height. **B**. CEGH-UNC 23896, paratype, 17.7 mm height. **C**. CEGH-UNC 23897, paratype, 19.85 mm height; the outer lip of this specimen is partially broken. **D**, **E**. *Lepsiella baileyana* (Tenison-Woods, 1881); modern specimens from south Australia. **D**. NMV F699, holotype, 29,7 mm height. **E**. Recent, 26 mm height. A_1–E_1 lateral views, A_2–E_2 apertural views, A_3 explanatory drawing.

Sculpture not imbricated. The outer lip is crenulated. The siphonal canal is short and moderately broad.

Remarks.—*Haustrum haustorium* is much more inflated than *Lepsiella ukika* nov. sp. and ribs are flattened with rather narrow grooves between them. The South American *Lepsiella ukika* sp. nov. has 13 spiral cords, while *Lepsithais lacunosa* (Bruguière, 1789) has six to nine very broad ones. *Lepsiella scobina* (Quoy and Gaimard, 1833), *L. vinosa* (Lamarck, 1822) and *L. flindersi* (Adams and Angas, 1863) have node-bearing cords and rather adpressed subsutural ramps, while *Lepsiella ukika* shows no nodes and evenly convex whorls. *Lepsiella baileyana* (Tenison-Woods, 1881) resembles the South American *Lepsiella ukika* sp. nov. because it is axially lamellate and has 10–15 spiral cords. However, it differs through its adpressed suture and its concave spire outline (straight in the South American species). The fossil species *Lepsiella maxima* Powell and Bartrum, 1929 from the New Zealand early to late Miocene and *L. intermedia* Powell and Bartrum, 1929 from the New Zealand early Miocene both have concave subsutural ramps (Powell and Bartrum 1929: figs. 97–102) while the South American *Lepsiella ukika* sp. nov. has evenly convex whorls.

When erecting Haustrinae, Tan (2003) included *Haustrum* Perry, 1811, *Lepsithais* Finlay, 1928, *Lepsiella* Iredale, 1912, and *Bedeva* Iredale, 1924 in this subfamily. Beu (2004) subsequently placed *Lepsiella* and *Lepsithais* in synonymy with *Haustrum*, arguing that the differences between them warrant only specific separation, but, on the other hand, removed *Bedeva* from this group. According to Beu (2004), *Haustrum* in this broader sense includes about ten species from New Zealand and Australia, spanning the time since the late Oligocene instead of being monospecific and appearing suddenly in the Holocene.

Regardless of these differing opinions, the specimens from Navarino Island belong in Haustrinae sensu Tan (2003) and most closely resemble *Lepsiella baileyana*, whether *Lepsiella* is a synonym of *Haustrum* or not. This may probably only be resolved when genetic data for all living species included in *Haustrum* by Beu (2004) as well as *Bedeva* are available for a phylogenetic study and we refrain from supporting one opinion against the other.

Undescribed early Miocene species of *Bedeva* from Chile were listed by Kiel and Nielsen (2010), but no formal treatment was provided. Beu and Maxwell (1990) reported *Bedeva* from the Pliocene of New Zealand without further discussing the genus. If the placement of Chilean species is correct and Beu's (2004) suggestion to remove *Bedeva* from this group is followed, *Bedeva* may have originated in South America or older fossils from New Zealand are not yet identified. However, considering the presence of Haustrinae sensu Tan (2003) at least since the Oligocene (Beu 2004), Miocene species in Chile suggest that this group possibly reached and colonized South America repeatedly, but never established a long-lasting lineage.

Geographic and stratigraphic range.—Only known from type locality on Navarino Island, likely representing MIS5.

Comments on muricid phylogeny

Phylogeny of living and fossil muricids has been investigated by several authors using traditional or alternative methods. Kool (1993) proposed a phylogeny of Rapaninae founded entirely on living members. It is based on a detailed investigation of shell microstructure, the protoconch, opercular characters, and internal anatomy of members of this group, but arguing that shell characters (other than those of microstructure and the protoconch) are too phenotypically plastic and susceptible to functional convergence, Kool (1993) excluded them from his cladistic analysis. In the same way, Tan (2003) performed a phylogenetic analysis of intertidal southern Australian and New Zealand species of muricid gastropods based principally on anatomical characters. More recent studies, incorporating DNA barcoding methods, offer alternative analytically powerful additions to traditional methods of classification of muricids (Barco et al. 2010; Zou et al. 2011).

However, taken alone, these studies on phylogeny of living muricids based mostly on non-preservable parts are difficult to apply to fossil shells. The applicability of shell characters in phylogenetic studies of Muricidae has been evaluated for Rapaninae by Vermeij and Carlson (2000) who concluded that the shell characters evolve faster (high resolution, low consistency) than anatomical features (high consistency, low resolution) and together, these two types of characters can complement each other in reconstructing phylogenetic hypotheses.

Concerning the problem of convergent shell morphology and plasticity discussed by Kool (1993), he refered it to environmental factors (e.g., wave action) strong enough to induce ecophenotypic variation and the existence of different morphs in the same species. Shell characters are, of course, subject to anagenetic influences and evolutionary convergence, but the same is true in principle for all other characters, including molecular ones (Vermeij and Carlson 2000).

Whatever is the source of phylogenetic information it is crucial to obtain unambiguous identification of biological entities prior to arguing on paleoenvironmental reconstructions (De Francesco 2007). Also the other aspects including, marine currents, dispersal strategies, geologic history and ecology of each species (or species group) should be evaluated in order to properly explain the pattern deciphered from fossil record.

Discussion

The fossil record of Haustrinae clearly indicates that this group has its ancestors in Australasia, where their representatives still live today (Fig. 3). This group of muricids is characterized by direct development (Tan 2003). Benthic invertebrates with non-planktonic larval phase have generally been expected to disperse over shorter distances than those with planktonic larval phase, unless the former develop some other efficient strategies for dispersal. Several studies of shallow benthic macrofauna have indicated that drifting by post-settlement juveniles or small adults is an important dispersal mechanism for many marine invertebrates irrespective of their larval development (Martel and Chia 1991; Helmuth et al. 1994; Cummings et al. 1995). Edgar (1987) and Bushing (1994), among other authors, showed that kelp drift with the wind and currents may disperse a large number of individuals from many taxa over relatively long distances. Furthermore, recent works (e.g., Sano et al. 2003, McCormick et al. 2008) showed that complex ecological interactions on floating algae may develop during extended journeys.

With regard to ecological interactions, the Australian *Lepsiella baileyana* is a small predatory gastropod with broad dietary habits including a variety of bivalve mollusks. It also lives in association with the abalone *Haliotis* on which it also feeds (Thomas and Day 1995). In addition, abalones are dependent upon macroalgae as their main source of nutrition and may be transported on drifting kelp (McCormick et al. 2008). Also, in the Beagle Channel muricids were found alive among the rhizoids of *Macrocystis* holdfasts (Adami and Gordillo 1999) where they surely have access to their mollusk prey.

Thus, it is very plausible that muricid gastropods might have migrated by means of rafted kelp transported by surface currents and the incursion of *Lepsiella*/*Haustrum* into South America is best explained on the basis of dispersion by rafting via the Antarctic Circumpolar Current (ACC; Fig. 3). A rafting journey from Australasia to southern South America at 20 to 40 m/s (Hofmann 1985) would take approximately one year.

Beu et al. (1997) showed that migrations of mollusks via the ACC from South America to New Zealand might have occurred during the most extreme Pleistocene glaciations, when this current is displaced northward; and a large burst of dispersed genus-group taxa arrived in South America during the Late Oligocene–Early Miocene time, with virtually no further dispersal from New Zealand to South America. However, one possible exception appears to be the venerid bivalve *Tawera*, which presumably reached South America during the Quaternary (Gordillo 2006). Another example of Pleistocene transoceanic incursions of mollusks, in this case from South America to South Africa, is the muricid *Concholepas concholepas* living only in South America but recorded from Late Pleistocene coastal deposits in southern South West Africa-Namibia (Kensley 1985).

Recent genetic studies show increasing evidence that populations of organisms without planktonic larval stages can also be widely dispersed, and rafting is most frequently involved (Thiel and Gutow 2005a, b; Thiel and Haye 2006; Macaya 2010; Nikula et al. 2010). For example, using the DNA barcoding method Macaya (2010) provides strong evidence that gene flow along the Southern Ocean is occurring over ecological time scales, where rafting of detached reproductive *Macrocystis* kelp seems to be facilitated by the ACC connecting populations in the Southern Hemisphere. This author also provides evidence suggesting that kelp rafts act as an important dispersal mechanism in this species, thus giving important information to understand the factors shaping the evolution of the largest seaweed on earth. Concerning the associated fauna, Nikula et al. (2010) demonstrated that long-distance oceanic rafting explains the broad geographic distribution of two crustaceans across the subantarctic. Fraser et al. (2009), in a recent molecular study pointed out that giant seaweed *Durvillea* has extremely high dispersal potential as it is capable of rafting vast distances, concluding that *Durvillea* in southern Chile originated from source populations in New Zealand.

Moreover, channels and fjords in southern South America appear to act as an extensive retention zone of floating items like rafted kelp, which accumulated in the internal waters, due to different physical features such as local eddies, estuarine fronts or internal waves (Hinojosa et al. 2010, 2011). These authors pointed out that retention zones near the oceanic end of the channels may trap *Durvillea* rafts coming from coastal or distal oceanic sources.

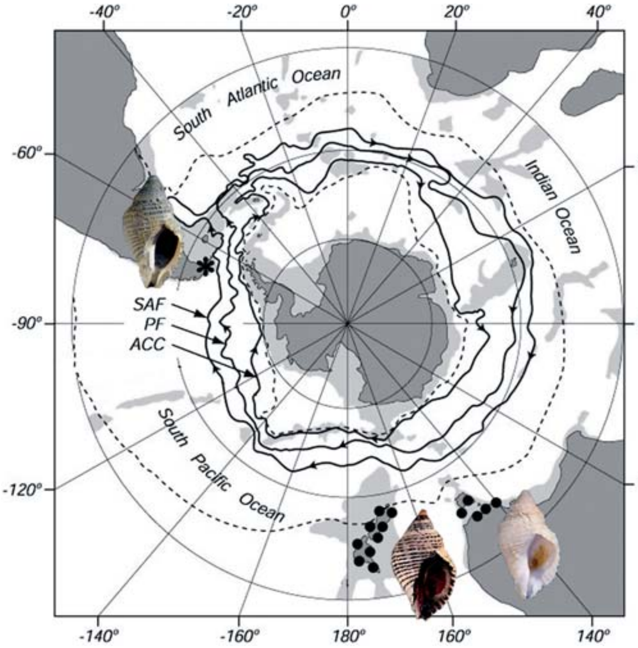

Fig. 3. Polar centric view of the subantarctic region showing the most plausible route of migration of the haustrin muricids from Australasia to southern South America. Previous records indicated by circles, new record is asterisked. Distribution of subantarctic (SAF) and polar fronts (PF) and associated Antarctic Circumpolar Current (ACC) after Orsi et al. (1995) and based on Whitworth (1988). Dashed lines indicate ACC boundary.

Based on these considerations we suggest that kelp rafting constitutes a means of transportation for muricid gastropods having better chance of extending their range or migrating from one region to another. Thus, these gastropods could travel this long distance among kelp holdfasts of *Macrocystis*, *Durvillea*, or other macroalgae.

During the Quaternary period, the southern tip of South America was affected by several glaciations which might have excluded much of the benthic marine fauna inhabiting this region, with the consequent interruption (more than once) of the connection between the Atlantic and the Pacific Oceans (see Gordillo 2009). On the other hand, these glaciations also shaped the receptive southern South American fjord region, which is discussed as a major feature to explain the high biodiversity of the region (Kiel and Nielsen 2010).

In this scenario, the Navarino records of *Lepsiella* probably belong to a derived (or a short lived pioneer) stock from an Australasian population. It is plausible that the arrival of this taxon into southern South America has taken place during a glacial period prior to the MIS4 to MIS2. The polar front might have been shifted northwards during glacial times (Fraser et al. 2009), and the shallower, more northern position of the ACC facilitated the circumpolar traverse of this taxon from Australasia to South America. Later, during the last interglacial (MIS5) at circa 125.000 years ago, this species remained in the Beagle Channel. At that time a rich fauna including foraminifers, ostracods and mollusks developed in this channel (see Gordillo et al. 2010). After that, during the last glaciation, marine taxa living in this interior channel were separated and survived in marine refuges. Therefore, temperate taxa as *Lepsiella* disappeared during this period. When climatic conditions improved, most taxa reoccupied the ecological niches from marine refuges. The extinction of *Lepsiella* in the Beagle Channel could be perhaps related to the fact that this pioneer or derived population of *Lepsiella* was eliminated by competition. This assumption is based on that *Lepsiella* was found with numerous other predatory muricids which implies that these species were contemporaneous and therefore had to compete for food. Another possibility, more difficult to prove, would be a lack of suitable habitat, but it is plausible that as a result of sea-level fluctuations rocky shores at the intertidal level temporarily disappeared.

Based on three different arguments (shell morphology, water masses and oceanic circulation, and ecology) this work highlights the very interesting fact that the Australasian gastropod *Lepsiella* was able to migrate, potentially using kelp as raft, to the southern tip of South America. This alternative dispersal mechanism of non-planktonic taxa is also potentially applicable to other fossils having a disjunct distribution.

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