Left in the cold? Evolutionary origin of *Laternula elliptica* a keystone bivalve species of Antarctic benthos

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ABSTRACT

The large, burrowing bivalve *Laternula elliptica* is an abundant component of shallow water soft substrate communities around Antarctica but its congeners are temperate and tropical in distribution and their phylogenetic relationships are obscure. A new molecular analysis of Laternulidae species shows that there are two distinct clades; one of *Exolaternula* species, *E. spengleri* and *E. liautaudi* possessing a ligamental lithodesma and a larger clade of species lacking the lithodesma. Of the latter, *Laternula elliptica* is a sister taxon to temperate and tropical species, including the species that live around the coasts of Australia from Tasmania to Darwin. It is suggested that *L. elliptica* was left isolated around Antarctica following the opening of the Tasman Gateway and initiation of the Circum-Antarctic Current as Australia drifted northwards following the final breakup of Gondwana. A further scenario is that as Australia moved closer to Asia species spread into tropical habitats and more widely to the Red Sea and Japan. *Exolaternula* species have a likely Tethyan origin and the present day range is from the Arabian Gulf, around southern Asia and as far north as southern Russia.

ADDITIONAL KEYWORDS: phylogeny – biogeography – Laternulidae - Anomalodesmata

INTRODUCTION

Although the precise origins of the modern Antarctic marine fauna are undoubtedly complex, there has always been a distinct impression that certain elements within it are both of considerable antiquity and endemic to the southern high-latitudes (Lipps & Hickman, 1982; Clarke & Crame, 1989). In all probability these taxa date back to at least the Late Cretaceous – Early Palaeogene, a time when the southern margins of the Gondwana supercontinent were still more or less intact, and polar climates were significantly warmer than those of today. Zinsmeister's (1982) extensive shallow marine Weddellian Province, stretching from southern Patagonia through western Antarctica to New Zealand and eastern Australia, was established on the basis of various endemic molluscan families, one of which, the Struthiolariidae (Littorinimorpha; Stromboidea), still occurs in the region at the present day (Beu, 2009). As our knowledge of both the fossil record and molecular phylogenetics of Antarctic marine taxa has steadily improved it is becoming appropriate to ask how certain specific elements within the fauna may have evolved. Do their roots lie in some form of ancestral Weddellian province, or were they more recent immigrants? This sort of question is particularly apposite for the very common infaunal bivalve, *Laternula elliptica* (Anomalodesmata; Laternulidae), as its congeners can be traced northwards through temperate South Australia into the heart of the tropical Indo-Pacific realm, and then northwards again into the temperate North-West Pacific. Is this a genus that spread either into, or out of, Antarctica, and if so, when?

Laternula elliptica (King, 1832) is a large (>100 mm) infaunal bivalve abundant in shallow water and even intertidal habitats around the Antarctic continent and sub-Antarctic islands (Fig 1 A-C). Its abundance and prominence in benthic communities, and its rank as a keystone species by Harper *et al.* (2012), has attracted considerable research interest with a multitude of publications investigating many aspects of its biology and ecology. A few examples include: physiology (Morley *et al.*, 2009; 2012), biochemistry (González & Puntarulo, 2011), reproduction (Kang *et al.*, 2003), growth rates (Ralph & Maxwell, 1977; Brey *et al.*, 2011), burrowing behaviour (Peck *et al.*, 2004), trace metals (Ahn *et al.*, 1996), shell microstructure and mineralogy (Sato-Okoshi & Okoshi, 2008; Nehrke *et al.*, 2012), ice scour damage (Harper *et al.*, 2012) and proteomics (Clark *et al.*, 2010).

Outside of the Southern Ocean, *Laternula* species range from the southern temperate zone (Tasmania) through subtropical and tropical Australia, southeastern Asia, Philippines, China and Japan as far north as Peter the Great Bay in western Russia; to the west through the northern Indian Ocean, Arabian Gulf, Red Sea and, rarely, to East Africa but are absent from oceanic islands. One species, *L. liautaudi* is exotic to west coast USA (Miller *et al.*, 1999 as *L. marilina*; or *L. gracilis* Fofonoff *et al.*, 2017) and another, *L. anatina*, to the eastern Mediterranean (Gofas & Zenetos, 2003). The genus is particularly speciose around Australia from where 12 nominal species have been described or recorded.

By contrast to the research focus on *L. elliptica* there are relatively few studies devoted to the temperate and tropical species of *Laternula* and most aspects of their biology and systematics remain uninvestigated. Exceptions are the morphological and ecological studies of *Laternula rostrata* by Morton (1973, 1976; Adal & Morton, 1973) and Prezant *et al.* (2008), the physiology of species from Singapore and south Australia (Morley *et al.*, 2009; Lai *et al.*, 2011) and China (Zhuang, 2005), with ecological studies on Korean and Japanese species (Kang *et al.*, 2006; Kanaya *et al.*, 2008).

Laternula species have thin, elongate, nacreous and granular prismatic shells, a posterior gape and the external surface is covered in short spikes (Checa & Harper, 2010). There is a prominent umbonal slit in the shell with an internal shell buttress posterior to the hinge (Savazzi, 1990). The internal ligament is set on a chondrophore and an anterior, transverse lithodesma (a calcified ossicle within the ligament),is present in some species. Siphons are long, fused and periostracum-covered (Fig. 1), with distal tentacles and siphonal eyes (Morton, 1973; Adal & Morton, 1973). The ventral mantle is fused, with a small pedal gape and the foot is small. Arenophilic mantle glands are present on siphons (Sartori *et al.*, 2006) and their sand adherent secretions present on juvenile shells < 10 mm long (Harper unpub. obs). Laternulids live in muddy, intertidal or shallow subtidal habitats, often amongst or near mangroves (Prezant *et al.*, 2008; Lai *et al.*, 2011), in seagrass beds (personal observations) and frequently in habitats of fluctuating or elevated salinities.

Compared with its lower latitude congeners *Laternula elliptica* is larger, thicker shelled (Watson *et al.*, 2012; Prezant *et al.* 2015), and lacks the spikes (spinules) on the shell surface present in all other species. Apart from *L. elliptica,* discrimination of *Laternula* species is extremely confused and misidentifications abound. There is no real agreement on the number of living species; the latest taxonomic account (Huber, 2010) recognised 19 species (followed in WoRMS 2017 with 20 species), previously Lamy (1934) documented 15-20 species and in the best illustrated of the 19th century monographs Reeve (1860-63) illustrated 30 species with 24 of these described as new. The type specimens from the latter work (NHMUK) are a major resource for any taxonomic study of the genus. We agree with Huber (2010) that species depictions and distributional data in many identification guides (e.g. Lamprell & Healy, 1998) and other publications (Morton, 1976) are wrongly assigned and have led to continuing confusion. *Laternula* species have been divided into two subgenera (Habe, 1977) on the basis of the presence (*Exolaternula*) or absence (*Laternula*) of a lithodesma. Nevertheless, the taxonomic or phylogenetic significance of this character has been doubted (Huber, 2010). In a broader context, molecular analyses (Harper *et al.*, 2006: Combosch *et al.*, 2017; Williams *et al.*, 2017) place *Laternula* within the Anomalodesmata in a clade with Lyonsiidae, Clavagellidae and Pandoridae but distinct from *Cochlodesma* (Periplomatidae) that has a similar umbonal slit but which groups with Thraciidae and Myochamidae.

Clearly, *Laternula elliptica* is a prominent and ecologically important element in Antarctic benthic faunas but biogeographically isolated from the warmer water species of the genus. In this study we use a molecular analysis to investigate the phylogenetic relationships of *L. elliptica* to the lower latitude species and evaluate three possible biogeographical scenarios concerning its present isolation in polar seas.

1. Is *Laternula elliptica* a relict species dating from a former, broader, distributional range of the genus and warmer Antarctic conditions (for example during the Early-Middle Eocene) but now isolated by the formation of Circum-Antarctic Current and has subsequently become physiologically adapted to cold conditions? An expectation arising from this scenario might be that *L. elliptica* is most closely related to the temperate southern Australian species.

2. Another possibility is that *Laternula* species originated on Late Gondwanan shallow shores and rafted northwards with Australia into the tropics after the split from Antarctica ca 30 Myr, leaving *L. elliptica* isolated in the Southern Ocean. This may account for the diversity of *Laternula* species around Australia that range from temperate conditions around Victoria/Tasmania to tropical waters to the North. *Laternula* species then spread and diversified into tropical Asian shallow water environments. An expectation would be that *L. elliptica* is sister to all other species or groups with the Australian taxa.

3. A further scenario that matches the ‘out of the tropics’ (OTT) model developed by Jablonski *et al.* (2006, 2013) is that *Laternula* diversified on tropical-subtropical shores and later spread southwards into Antarctica during warmer conditions, with *L. elliptica* as a derived species.

MATERIAL AND METHODS

Molecular methods

The DNA extraction and amplification protocols of Williams *et al.* (2013) were used to amplify portions of four genes from 16 specimens (Table 1). The genes amplified were the nuclear 28S rRNA gene (approximately 1640 bp) and three mitochondrial genes: 12S rRNA gene (approximately 610 bp), 16S rRNA gene (approximately 500 bp) and cytochrome *b* (405bp). *Lyonsia norwegica* (Lyonsiidae) and *Bryopa lata* (Clavagellidae) were used as outgroups having been shown in previous analyses to be sister groups of Laternulidae (Harper *et al.*, 2006; Combosch *et al.*, 2017; Williams *et al.*, 2017). Sequence reactions were performed directly on purified polymerase chain reaction (PCR) products using the BigDye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems) and run on an Applied Biosystems 3730 DNA Analyzer automated capillary sequencer. Sequences for each gene fragment were assembled and edited using Sequencher (v.5.1; Gene Codes Corporation Ann Arbor, Michigan).

Mitochondrial genes of another four taxa, *Lyonsia norwegica*, *Bryopa lata*, *Laternula elliptica* (Antarctica) and *Laternula rostrata* (Singapore, herein *E. spengleri*) were previously published as complete, or nearly complete, mitochondrial genomes (Williams *et al.* 2017) and 12S, 16S and cytB sequence were taken from these sequences (GenBank Acc. KX815957; KX815959; KX815960, KX815963). Sequences for 28S rRNA genes were obtained from the same NGS genomic data set used in Williams *et al.* (2017) to assemble mitochondrial genomes. Briefly, genomic DNA was sequenced on 1/5 of a flowcell on an Illumina MiSeq platform (v.2 chemistry; 2x250 paired-end). Reads were analysed and assembled using Geneious (v.8.1.8; https://www.geneious.com). The data were trimmed allowing no ambiguous base calls and removing bases from the terminal ends of reads with an error probability of 0.05 or higher (i.e. those with a greater than 5% chance of being incorrect). The trimmed reads were first assembled *de novo* and the resulting contigs were interrogated against the NCBI database, using BLAST (Altschul *et al.* 1990), in order to identify ribosomal gene sequences. Gene boundaries were determined by comparison with other molluscan taxa. Coverage data are available in Williams *et al.* (2017).

Phylogenetic datasets analysed included three individual gene datasets and a combined gene dataset including all individuals that had sequences for at least three genes. Alignment of cytB sequences was unambiguous and no stop codons were observed. Sequences of ribosomal genes were aligned in Geneious (Geneious v. 8.1.8; http://www.geneious.com) using ClustalW. Poorly aligned sites in the ribosomal gene alignments were identified using the online Gblock server using all three options for a less stringent selection (v.0.91b; Castresana, 2000, http://molevol.cmima.csic.es/castresana/Gblocks_server.html) and removed from alignments. After removal of ambiguously aligned blocks of data, a total of 2,922 bp of aligned sequence remained to be used in phylogenetic analyses for the combined gene dataset (90% of the original 3,241positions). In individual analyses, alignment lengths after Gblocks were 444 bp of sequence from 16S rRNA (89% of 495 bp in the original alignment), 539 bp of 12S rRNA (90% of 597 bp in the original alignment) and 1575 bp of 28S rRNA (88% of 1785 bp in the original alignment).

The best nucleotide substitution models were determined using jModelTest (v. X; Darriba *et al.* 2012) using the AIC criterion. The best nucleotides substitution models were for cytB HKY+I+G and for all three rRNA genes GTR+I+G. These models were used in Bayesian phylogenies implemented in MrBayes (v. 3.2.6; Huelsenbeck & Ronquist, 2001). The analysis ran for 10,000,000 generations, with a sample frequency of 1,000. The first ten percent were discarded as burn-in after checking that runs had reached stationarity. Stationarity was determined by examining traces in TRACER (v.1.6 http://tree.bio.ed.ac.uk/software/tracer/). Convergence between the two runs was tested by examining traces using TRACER and by checking that the potential scale reduction factors produced by the ‘sump’ command in MrBayes were close to one (Gelman & Rubin, 1992) and that the mean standard deviation of split frequencies approached zero.

Taxonomic rationale

Because the species taxonomy of *Laternula* is so confused care was taken to identify the taxa included in the molecular analyses. Type material of *Laternula* species was examined in NHMUK and MNHN along with images of other relevant specimens from ANSP, NHMD, MHNG and WAM. Using these, plus the taxonomic revisions of Reeve (1860), Lamy (1934) and most recently Huber (2010) and figures in regional faunas (e.g. Lamprell & Healy, 1993; Okutani, 2000; Lutaenko & Noseworthy, 2012) augmented by the results of our molecular analysis herein we have derived an outline taxonomic classification (Appendix) listing what we believe are extant species and their synonyms. Notable taxonomic changes resulting from study of type material (NHMD) are that *Solen spengleri* Gmelin, 1791 (herein *Exolaternula spengleri* Fig. 1 D) is an earlier name for the species variously called *L. anserifera* (Spengler, 1793), *L. truncata* (Lamarck, 1818 auct.) or *L. rostrata* (Sowerby, 1839). Images of newly separated valves of the holotype of *Anatina liautaudi* Mittre, 1844 (MNHN IM- -2000-33234) indicate that it is the earliest name (herein as *Exolaternula liautaudi*) for the variously named northeast Asian margin species. Also genetic data (herein) show that the Australian species variously identified as *Laternula gracilis*, *L. marilina* and *L. recta* are a single species, with *L. gracilis* (Reeve, 1860) having priority. Our present estimate is that there are 15 living species of Laternulidae; further and more comprehensive sampling will likely resolve some problem areas but may also reveal the existence of cryptic species.

Institutional abbreviations: ANSP, Academy of Natural Sciences Philadelphia at Drexel University, USA; BAS, British Antarctic Survey, Cambridge, UK; MAGNT, Museum and Gallery of Northern Territory, Australia; MHNG, Muséum d'histoire naturelle, Geneva, Switzerland; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMD, Natural History Museum of Denmark, Copenhagen; NHMUK, The Natural History Museum, London, UK; WAM, Western Australian Museum, Perth, WA.

RESULTS

All individual gene trees had similar topologies to each other and to the combined gene tree shown in Figure 2. A clear result is that the sequenced Laternulidae species split into two major groups; one comprising *L. spengleri* from Singapore and Philippines and *L. liautaudi* from Japan and southeastern Russia and a second, larger group containing all the other species including *L. elliptica*.

A robust topology in all gene trees is that, in the larger clade, *Laternula elliptica* is sister group, with maximum support ($P = 1.0$), to all the other *Laternula* species from Australia, southeastern Asia and southern Japan. Amongst the temperate and tropical samples there are three well-supported sub-clades. One consists of three *Laternula* collected from near Esperance (southern Western Australia), Papua New Guinea and southern Japan; these are similar to *Laternula anatina* in shell form but are genetically different from each other and we have identified them as *L. creccina*, *L. anatina* and *L. japonica*. The cooler water

Laternula creccina is the sister group to the two warm water species. A second sub-clade includes three samples collected at Darwin, Singapore and eastern Thailand but differ from each other in the molecular tree. The sample from Darwin is closest in shell characters to *L. boschasina.* The specimen from Singapore resembles the syntypes of *L. bullata* and differs from the Kungkraben Bay, Thailand example which we retain as *Laternula* sp. The third sub-clade comprises *Laternula* from southern and eastern Australia (Port Phillip Bay (Victoria), Burrill Lake (New South Wales) and Moreton Bay (Queensland)). *Laternula* from these locations have been variously named in collections as *L. gracilis*, *L. recta* and *L. marilina* but these have only minor genetic differences suggesting that they are conspecific, with *L. gracilis* having taxonomic priority. A species from Shark Bay, Western Australia, that we identify as *L.* cf. *corrugata* is a sister to the eastern Australian *Laternula gracilis*.

Geological record of *Laternula*

Other anomalodesmatans possessing an umbonal slit (Periplomatidae) have been confused with *Laternula* especially in fossils and many records of fossil *Laternula* can be discounted. For example, the so-called *Laternula fuchsi* (Hoernes, 1875) widely reported from the Miocene (Burdigalian) of eastern Europe (Harzhauser *et al.*, 2011) is a periplomatid, as is *Laternula ravni* Schnetler, 2001 from the Paleocene of Denmark. Furthermore, the '*Laternula*' species widely reported from the Cenozoic of far Eastern Russia are now classified as Periplomatidae (Kafanov *et al.*, 2001).

A search of fossil literature for records of bivalves that resemble our concept of *Laternula* indicates that they are rare. This may be a consequence of the poor preservation potential of the thin, fragile, aragonitic shells and also the association with mangrove and organic-rich sediments from estuarine settings. *Anatina burdigalensis* Cossmann & Peyrot, 1909 122-3 pl. LXIII fig 34 from the Miocene (Serravallian 13.82 -11.63 Myr) of Aquitaine Basin, France, resembles the living *Exolaternula spengleri* in shape (Fig. 1 G). Fossils resembling the living *Exolaternula liautaudi* have been recorded as *L. limicola* from the mid Miocene of central Japan (Itiogawa *et al.*, 1981-2). Crame (1984) reported *Laternula* spp. from late Neogene (Pliocene?) deposits from Makran coast, Pakistan and these samples (in NHMUK) have shapes resembling living *L. anatina*. An earlier fossil from the Eocene Rio Turbio Formation of Patagonia (mid Lutetian – mid Priabonian 44.6 – 34 Myr - date from González Estebenet *et al.* (2014) described and figured as *Laternula* sp. by Griffin (1991: fig.10 1-2) is broadly similar to *L. spengleri* in shape (Fig. 1 H,I). A possible Late Cretaceous

(Campanian/Maastrichtian) *Laternula* sp, has been described from Argentina (Parras & Griffin, 2013); this is more equivocal in attribution but has an umbonal slit and buttress. Further back in time some Mesozoic genera have been assigned to the Laternulidae, namely *Anatimya*, *Cercomya*, *Plectomya and Platymyoidea* (Keen & Cox, 1969) but these appear morphologically distant from living *Laternula.*

History of Laternula in Antarctica.

Careful re-examination of both reference collections and the literature indicates that there are no *bona fide* Early Cenozoic representatives of *Laternula* from the extensive Early Cenozoic fossil record of Antarctica. The Oligocene – Miocene interval is much less complete (Beu, 2009; Beu & Taviani, 2014). The earliest unequivocal record of the genus is that known from the Cockburn Island Formation, which forms part of a complex sequence of glacial and interglacial sediments inter-bedded with the late Neogene James Ross Island Volcanic Group (JRIVG), north-eastern Antarctic Peninsula (Smellie *et al*., 2013; Beu & Taviani, 2014). Specimens from the type area of the formation, Cockburn Island (64° 12’S, 56° 50’W), were assigned to *Laternula elliptica* by both Soot-Ryen (1952) and Jonkers (1998a), with the only difference being that their maximum size (150mm+ in length) somewhat exceeded those of the modern form (Fig. 1 F). However, in all other respects they are very close to living *L. elliptica* and we see no need to assign them to a separate taxon. Co-occurring specimens of the large pectinid *Austrochlamys anderssoni* (Hennig) have been reliably dated at 4.7 Myr by ^{87}Sr/^{86}Sr isotopes, and this age agrees well with that of 4.7 – 4.9 Myr for underlying basaltic lavas of the JRIVG (^{40}Ar/^{39}Ar dating) (Smellie *et al*., 2013). The 4.7 Myr age (i.e. earliest Pliocene) for the specimens of *L. elliptica* from Cockburn Island represents the earliest definitive fossil record of the genus from Antarctica. Within the James Ross Island group there are sparse records of *Laternula* from younger glacial/interglacial sediments inter-bedded with the JRIVG (i.e. the Hobbs Glacier Formation and its lateral equivalents). For example, *Laternula* sp. is noted from the southern end of Sykes Cliffs on the western side of Croft Bay (64° 01’S, 57° 49’W) (Jonkers, 1998b), and a poorly constrained ^{40}Ar/^{39}Ar age from overlying lavas was resolved to be 2.38 Myr (Smellie *et al*., 2013). A potentially older Antarctic specimen of *Laternula* has been recovered from the Battye Glacier Formation, Prince Charles Mountains, East Antarctica (70° 48’S, 68° 20’E). Although it clearly possesses a buttressed chondrophore and nacreous inner shell layer, it is very incomplete and can only doubtfully be referred to *Laternula*? sp. (Stilwell *et al.* 2002, figs 2 m-n). The suggested Middle – Late Miocene age range for the Battye Glacier Formation is based on the associated diatom assemblage. Better preserved material is available from the Sørsdal Formation, Marine Plain, Vestfold Hills, East Antarctica (68° 38'S, 78° 8'E), and this has been identified as *L. elliptica* (Quilty *et al*. 2016). The Sørsdal Formation is dated by diatoms as Early Pliocene, 4.2 – 4.1 Myr (Quilty *et al*., 2016). There is an Early Pleistocene record of *L. elliptica* from the Scallop Hill Formation of McMurdo Sound (78° 11'S, 166° 58'E) (Galasian, early Pleistocene, Speden, 1962; Beu & Taviani, 2014), and widespread evidence for a Late Quaternary – Holocene circum-Antarctic distribution of the species (Pickard, 1985).

DISCUSSION

The results show clearly that there are two distinct phylogenetic groups of *Laternula* species; the clade comprising *L. spengleri* and *L. liautaudi* with both species possessing a lithodesma and the larger clade of all the other species where it is lacking in the adult. A lithodesma is present in the majority of anomalodesmatan families including Pandoridae, Lyonsiidae and Clavagellidae, the sister clades to *Laternula* (Harper *et al.*, 2000; 2006). Thus its presence in some species is interpreted as a retained plesiomorphic character and its absence in the larger clade as an apomorphic state. Contrary to Savazzi (1990: 100), only three species of *Laternula* are known to possess a lithodesma in adult shells: *L. spengleri, L. liautaudi* and *L. erythraea* (the latter not molecularly sampled) and the two species form a robust clade that supports their classification in a distinct genus, *Exolaternula,* although other shell characters appear similar to *Laternula* species. Significantly, Sartori (2009) reported and illustrated lithodesmas in juvenile *L. elliptica* with shell lengths less than ca 12 mm but these become resorbed in larger shells. This ontogenetic loss of a lithodesma has also been reported in some Thraciidae species (Sartori & Ball, 2009).

The three known *Exolaternula* species are distributed today along the northern Indian Ocean and Arabian Gulf (*E. erythraea*), through southeast Asia (*E. spengleri*), China, Korea and Japan as far north as Peter the Great Bay, Russia (*E. liautaudi*). The latter also occurs as an exotic on west coast USA (Miller *et al.*, 1999). The distribution of *E. spengleri* touches the very north of Australia, with a single 19th C (NHMUK) record from Port Essington, Northern Territory. The distribution given in Lamprell & Healy (1998) of this species (as *L. rostrata*) around southern Australia and New South Wales and followed in some ecological studies, is erroneous and based on misidentifications.

It seems likely, that *Exolaternula* split from the other *Laternula* in the early Cenozoic with the clade having a different biogeographic history. We suggest that the present day distribution of *Exolaternula*, restricted to the northern Indian Ocean and southern and eastern margins of Asia, reflects a Tethyan origin. The Miocene *Anatina burdigalensis* from southern France resembles *E. spengleri* in shell form and we consider it as a species of *Exolaternula,* the last survivor in western Tethys before the early Miocene closure of the Tethyan Seaway (Harzhauser *et al.,* 2007). Fossils resembling the living *Exolaternula liautaudi* were present in Japan at least by the mid-Miocene (Itiogawa *et al.,* 1981, 1982).

In the *Laternula* clade the sister position of *Laternula elliptica* relative to all other species suggests a separation before the diversification of the temperate and tropical species. This is consistent with the scenario that *L. elliptica* or its precursor was left isolated around Antarctica after the separation and northward movement of Australia with the opening of the Tasman Gateway and onset of the Antarctic Circumpolar Current ca 30 Myr in the early Oligocene (Scher *et al.,* 2015). This final breakup of the Gondwanan-Weddellian Province (Zinsmeister, 1979) would have disrupted larval interchange as Australia progressively moved northwards. Subsequently, as Australia moved into lower latitudes, warmer water species such as *L. anatina* may have spread into southeast Asia and the northern Indian Ocean while Australia retained a diversity of temperate water endemic species such as *L. gracilis*, *L. creccina* and *L. tasmanica* or their precursors. The scenario that *L. elliptica* originated from a southward migration as a more derived taxon (out of the tropics hypothesis (Jablonski *et al.,* 2006, 2013)) during a period of polar amelioration can be rejected.

A single record from Pliocene of New Zealand of a fragmentary fossil, *Laternula synthetica* Marwick, 1948, with an estimated shell length of 120 mm (later renamed *L. laterna* Lamarck, 1818 by Beu, 2004) was interpreted to have arrived during a warm period. However, the long pallial sinus of this fossil precludes identification as *L. laterna* (a tropical species) that has a short sinus, it most closely resembles the southeastern Australian species, *L. gracilis* and *L. tasmanica*.

Although it would be desirable to include more samples in the analysis our results are consistent with an Australian origin for the tropical *Laternula*. For example *Laternula creccina* from temperate southern Australia is a sister species to tropical *L. anatina* from Papua New Guinea and sub-tropical *L. japonica* from Japan. Similarly, *L.* cf. *boschasina* from Darwin, northern Australia, is sister species to two tropical species from Singapore and Thailand. Moreover, the diversity of *Laternula* species around Australia and their wide latitudinal spread compared with other Indo-West Pacific areas is also evidence supporting this idea.

Of the *Laternula* species, *L. anatina* (Fig. 1 E) has the broadest distribution, recorded from Kenya, Red Sea, the northern Indian Ocean, through southeastern Asia, northern Australia to Philippines, China and southern Japan. It is also present as a Lessepsian invader into the eastern Mediterranean (Gofas & Zenetos, 2003). Nonetheless, our preliminary molecular results suggest that cryptic species may exist; for example, the frequently synonymised *L. japonica* is genetically distinct from *L. anatina*. Other species at lower latitudes have narrower ranges, *L. navicula* in the northern Indian Ocean, *L. boschasina* in southeast Asia and *L. laterna* around northern Australia.

Our phylogenetic evidence supports the idea that *Laternula elliptica* or its precursor was isolated around Antarctica following the split and northward movement of the Australian continent with the opening of the Tasman Gateway and initiation of the Circum-Antarctic Current. Following separation and onset of cooling conditions the species became adapted physiologically to lower temperatures (Peck *et al.*, 2009). *Laternula elliptica* differs morphologically from congeners in its much larger size, very wide posterior gape, thicker shell (Watson *et al.*, 2012) and prominent periostracum. It also lacks the exterior shell spikes characteristic of all other *Laternula* species and many other anomalodesmatans (Checa & Harper, 2010). *Laternula elliptica* is abundant in shallow water around Antarctica particularly at depths of 10-30 m and even intertidal (Waller *et al.*, 2017) with population densities reported up to 65/m^2 (Dell, 1990; Zamorano *et al.*, 1986). The general lack of durophagous predators (decapod crustaceans and fish) in Antarctic seas (Clarke *et al.*, 2004) could be a contributory factor in its success. By comparison the lower latitude species of *Laternula* tend to occupy peripheral marine habitats where predation pressure is likely reduced, such as mangrove fringes (Morton, 1973; Prezant *et al.*, 2008), estuaries with fluctuating salinities (Kanaya *et al.*, 2008; Kang *et al.*, 2006), or locations with elevated salinities such as Shark

Bay, Western Australia (Logan & Cebulski, 1970) or the Arabian Gulf (Sheppard *et al.*, 2010).

Corroboration of the biogeographical scenarios with a fossil record would be desirable but as already noted the fossil record of *Laternula* is poor. The only Southern Hemisphere Early Cenozoic occurrence, *Laternula* sp. from the Eocene Rio Turbio Formation, Santa Cruz Province, Argentina, is part of a still imperfectly known molluscan fauna that does show at least some resemblance to that known from the La Meseta Formation of Seymour Island, north-eastern Antarctic Peninsula (Griffin, 1991). Palaeogeographic reconstructions for the Eocene connection between Tierra del Fuego and the northern tip of the Antarctic Peninsula are complex, but some of the most recent ones, based on new marine geophysical data, place the Rio Turbio basin at a significantly higher palaeolatitude than its present day position of 51° 30'S (Maldonado *et al*., 2014, fig. 8). It would certainly have been well within Zinsmeister's (1979, 1982, 1984) Weddellian Province and *Laternula* sp. may represent part of the ancestral lineage of *L. elliptica*. The Rio Turbio Formation does appear to contain a series of distinct sedimentary facies that are missing in the La Meseta Formation, and the two units almost certainly represent slightly different types of shallow marine environment (Griffin, 1991).

As a result of recent taxonomic and stratigraphic studies it has been determined that approximately one-third of the 147 gastropod and bivalve species known from the Middle Eocene section of the La Meseta Formation can now be assigned to modern genera (Beu, 2009; Crame *et al*., 2014). This means that, for at least one key part of the modern Antarctic marine fauna, it was beginning to take shape some 10 – 15 Myr before the onset of significant global cooling at the Eocene – Oligocene boundary (Zachos *et al*., 2008). Molecular phylogenetic evidence suggests that the amphipod genus *Epimeria*, which today forms a species flock in the Southern Ocean, diversified initially in the Middle or Late Eocene (Verheye *et al*., 2017), and the split between the Antarctic/subantarctic limpet *Nacella* and its temperate to tropical sister taxon *Cellana* occurred at 32 Ma (González-Wevar *et al*., 2017). There is even a combination of molecular phylogenetic and biogeographic evidence from the Antarctic terrestrial realm to suggest that a range of taxa had similar Early Cenozoic roots, and have survived to the present day using various types of refugia (Convey *et al*., 2008). All of this evidence suggests that the Antarctic biota is of considerable ancestry and has been able to adapt to progressive global cooling over a period of tens of millions of years. *Laternula* had Eocene or even earlier roots in the Antarctic region and was then able to adapt to both the cooling of Antarctica and the warming of the Australian continent as it moved progressively northwards.

Despite the present day diversity and abundance of *Laternula* species around Australia the fossil record from there is lacking, with no mention of the genus in Darragh's (1985) analysis of the Cenozoic molluscan faunas of southeastern Australia. However, the stratigraphic record is very patchy and suitable facies are not preserved and, coupled with the preferred marginal marine habitats and fragile shells, may account for the lack of *Laternula* fossils. However, Pufahl *et al.* (2004) report *Laternula* sp. from Pliocene estuarine deposits in the Murray Basin, South Australia. The fossils are preserved as casts and molds with aragonitic shells dissolved away and identifications were made in the field (N. James personal communication). If confirmed, these are the only *Laternula* fossils recorded from Australia.

In summary, our molecular results revealed two distinct groups of living Laternulidae; *Exolaternula* species possessing a lithodesma and a distribution largely around the northern Indian Ocean and the southern margin of the Asian continent. The *Exolaternula* clade likely had a Tethyan origin with connections to the western Tethys in the early Miocene but later severed by the closure of the Tethyan Seaway. The more numerous *Laternula* species lack a lithodesma in the adult, with the Antarctic *L. elliptica* as a sister taxon to all other species from Australia and central Indo-West Pacific. The *Laternula* clade likely originated on the Late Gondwanan southern Australia/Antarctica continent, leaving *L. elliptica* isolated around Antarctica after Australia split and drifted northwards opening the Southern Ocean. Temperate and tropical species exist around Australia but we suggest that the tropical species spread and diversified into coastal Asia from the mid-Miocene onwards after the closer approach of Australia.

ACKNOWLEGEMENTS

For generously providing samples we are grateful to Ruytoro Goto (University of Kyoto), Barbara Buge (MNHN), Konstatin Lutaenko (Russian Academy of Sciences, Vladivostok), Koh Siang Tan (National U. of Singapore), Piotr Kuklinski (Institute of Oceanology, Polish Academy of Sciences) and Simon Morley (BAS). Dawn Woods, George Mulvaney and Michael Mulvaney helped collect samples at Burrill Lake, New South Wales.
Grateful thanks are due to Tom Schiotte (NHMD) for images of the *Mya anserifera* holotype, Emmanuel Tardy (MHNG) for images of the lectotype of *Anatina laterna*, Virginie Héros

(MNHN) for arranging opening of valves and images of the holotype of *Laternula liautaudi*, Konstantin Lutaenko and Elena Chaban (Zoological Museum, St Petersburg) for searching for the type of *L. japonica* and Lisa Kirkendale (WAM), Richard Willan (MAGNT) for images of shells in their collections. David Cothran generously allowed reproduction of his images of living *L. elliptica*. Tom Darragh (Museum Victoria) advised on Australian fossil faunas, Pierre Lozouet (MNHN) confirmed dating of fossils and Takuma Haga (NMNS, Tokyo) provided information and literature concerning Japanese living and fossil species. We thank Lisa Smith (NHMUK) for help with molecular analyses and Adrian Glover (NHMUK) who facilitated the process. JAC acknowledges financial support from NERC, including NE/I00582X/1. The work of the late Solene Morris former curator of bivalves at NHMUK is acknowledged for careful curation of the *Laternula* type specimens. We thank Alan Beu and another reviewer for thoughtful comments and suggestions.

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FIGURE LEGENDS

Figure 1. *Laternula elliptica,* type species of *Exolaternula* and *Laternula,* and fossil Laternulidae. **A.** *Laternula elliptica* (King, 1832) James Ross Island, Antarctica (NHMUK), L= 69 mm; **B, C.** *Laternula elliptica,* in life position with fused inhalant an exhalant siphons Images by David Cothran/Lindblad Expeditions, All Rights Reserved. **D.** *Exolaternula spengleri* (Gmelin, 1791) (senior synonym of *A. truncata*, *A. rostrata*) Port Essington, Australia (NHMUK), L = 78.4 mm; **E.** *Laternula anatina* (Linnaeus, 1758), Moluccas (NHMUK), L= 55.2 mm. F**.** *Laternula elliptica,* Early Pliocene, Cockburn Island Formation, Cockburn Island, north-eastern Antarctic Peninsula. (BAS DJ. 351.21), L= 138 mm. **G.** *L. burdigalensis* (Cossmann & Peyrot, 1909) Miocene, Salles, France, L= 80 mm (from Cossmann & Peyrot, 1909). **H. I.** *Laternula.* sp., Eocene, Rio Turbio Formation, Patagonia, Argentina, L = 50 mm, from Griffin (1991) with permission Journal of Paleontology.

Figure 2. Combined gene tree for Laternulidae based on sequences from four genes (28S rRNA, 12S, 16S and cyt b) using Bayesian inference as implemented by MrBayes. Support values are posterior probabilities (PP). Images are of sequenced specimens or proxies – not to scale. Colour code on localities denotes: tropical (red), temperate (green), Antarctic(blue) Locality codes used on tree: BL - Burrill Lake, New South Wales, Australia; DAR – Darwin, Australia; ESP – Esperance, Western Australia; HJ – Higata-Jima Is, Japan; GE – Geelong, Victoria, Australia; KK – Kungkraben Bay, Thailand; KS – Kojima-Shinden, Japan; LP – Luzon, Philippines; MB – Moreton Bay, Queensland, Australia; OB- Olga Bay, eastern Russia; PNG – Papua New Guinea; RO – Rothera, Adelaide Island, Antarctica; SB – Shark Bay, Western Australia; SIN - Singapore; SS – South Shetland Isles.

Figure 3. Distributional ranges of *Exolaternula* and *Laternula* species in the Indo-West Pacific and Southern Oceans. Robinson projection. Red - *Exolaternula*, blue - *Laternula*, green - *Laternula elliptica.*

TABLES

Table 1. Details of species included in molecular analysis

Appendix. Critical assessment of the living species of Laternulidae and their synonyms. Type localities are given where known. Note that number of considered valid species and nomenclature differs from Huber (2010) and WoRMS. The classification will evolve as more samples are included in molecular analyses.

LATERNULIDAE

Genus ***Exolaternula*** Habe, 1977 type species: *Anatina truncata* Lamarck, 1818 = *L. spengleri* (Gmelin, 1791) = *L. rostrata* (Sowerby, 1839). Lithodesma present.

***Exolaternula spengleri* (Gmelin, 1791)**
Solen spengleri Gmelin 1791: 3228.
Synonyms: *Mya anserifera* Spengler, 1793: tab 2 fig 8, holotype NHMD 116367 (Gmelin's name is based on this specimen and figure), Nicobar Islands; *Anatina truncata* auct. non Lamarck 1818; *Anatina rostrata* (G.B. Sowerby II 1839); *Anatina limicola* Reeve, 1863, Japan; *Anatina elegans* Philippi, 1844, China; *Anatina bernicula* Lamy, 1934, Tongatabu.

Remarks: Reeve (1860) used the name *A. anserifera* for a figured specimen from Tasmania now considered to be *Laternula tasmanica* leading to citations of the former in southern Australia (e.g. Morton 1975)

Distribution: Sri Lanka, Southeast Asia, northern Australia, Philippines, China, southern Japan (Ryukyu Ids).

Exolaternula liautaudi (Mittre, 1844)
Anatina liautaudi Mittre, 1844:16, pl. 104, holotype MNHN-IM- 2000-33234. Manila, Philippines. Image: https://science.mnhn.fr/institution/mnhn/collection/im/item/2000-33234
Synonyms: *Laternula limicola* auct. non Reeve 1863; *L. navicula* auct. non Reeve 1863; *L. marilina* auct. non Reeve, 1860; *L. gracilis* auct. non Reeve, 1860; *Anatina kamakurana* Pilsbry, 1895, Kamakura, Japan; *Anatina pechiliensis* Grabau & King, 1928, Peitaiho, NW China; *Laternula nanhaiensis* Zhuang & Cai, 1982, Hepu, Guangxi.

Remarks: There has been much nomenclatural confusion concerning this species; in Japanese, Chinese and Russian literature it is often cited as *L. marilina*, an Australian species lacking a lithodesma and now synonymised with *L. gracilis*. Comparison of type specimens shows that *L. liautaudi*, originally described from the Philippines, is the earliest name.

Distribution: Northern Philippines, China, Taiwan, Korea, Japan and eastern Russia (Peter the Great Bay), exotic to northwest America.

***Exolaternula erythraea* (**Morris & Morris, 1993)
Laternula (Exolaternula) erythraea Morris & Morris, 1993: 8,19, holotype NHMUK 1992175, Fujairah, United Arab Emirates.

Remarks: *L. erythraensis* used in error for *L. erythraea* e.g. Oliver (1995), Fuelner & Hornby (2006).

Distribution: Arabian Gulf, Gulf of Oman.

Genus **Laternula** Röding, 1798, type species: *Solen anatinus* Linnaeus, 1758. Synonym: *Laternulina* Habe 1952, type species *Anatina japonica* Lischke, 1872. Lithodesma absent in adult.

Laternula anatina (Linnaeus, 1758)
Solen anatinus Linnaeus 1758: 673.
Synonyms: *Anatina subrostrata* Lamarck, 1818; *Anatina hispidula* Cuvier, 1829; *Anatina amphora* Reeve, 1863, Island of Burias, Philippines; *Anatina cumingi* Reeve, 1863, Amboina; *Anatina eximia* Reeve, 1863; *Anatina flexuosa* Reeve 1863, Japan; *Anatina labiata* Reeve 1863, Ceylon; *Anatina siphonata* Reeve, 1863, Borneo.

Remarks: no type material for *S. anatinus* exists. Linnaeus based the name on the figure in Rumphius (1705 pl 45 f O and subsequent editions) with locality given as 'O. Asiatici'. The figure is poor but has the upturned posterior 'beak' of shells identified as this species. Also figured in Chemnitz (1782: 62 pl. 6, figs 46-48) and according to Lamy (1934) Lamarck (1818) based his name *A. subrostrata* on these figures.

Distribution: East Africa (rare), Red Sea, SE Asia, NW Australia, Philippines, China, Okinawa, southern Japan. Exotic to eastern Mediterranean

Laternula elliptica (King, 1832)
Anatina elliptica King, 1832: 335, holotype NHMUK 197528, South Shetland Islands.

Synonym: *Anatina prismatica* Sowerby, 1834, South Shetland Islands.

Remarks: usually cited as described by Broderip & King 1832 but see Coan *et al.* (2011) for authorship

Distribution: Circum-Antarctica, Kerguelen, South Georgia, South Shetland Islands.

Laternula boschasina (Reeve, 1860)
Anatina boschasina Reeve, 1860, pl. 2, fig. 13, syntypes NHMUK 197513/1-3, Negros Island, Philippines.

Remarks: Our sequenced species from Darwin is much smaller than the syntypes but has a similar deep sinus, commarginal folds and brown periostracal margin.

Distribution: uncertain but includes southeast Asia, northern Australia.

***Laternula bullata* (Reeve, 1863)**
Anatina bullata Reeve, 1863, pl. 1 fig 3, syntypes NHMUK 197513/1-3, Sibonga, Zebu, Philippines.

Remarks: The species sequenced from Singapore (sometimes called *L. boschasina*) is similar to the type with a rounded anterior, tapering posterior and shallow pallial sinus.

Distribution: Southeast Asia.

***Laternula corrugata* (Reeve 1863)**
Anatina corrugata Reeve, 1863, pl. 4, fig. 25, NHMUK 197523/1-2, Ticao Island, Philippines.

Remarks: The species sequenced from Shark Bay Western Australia is broadly similar to syntypes of this species but maybe distinct.

Distribution: Philippines, ?Western Australia.

Laternula creccina (Reeve, 1860)
Anatina creccina Reeve, 1860 pl. 2 fig. 12, NHMUK 197512/1-2, Adelaide, Australia.

Synonyms: *Anatina vagina* Reeve, 1863, Moreton Bay, Australia; *Anatina attenuata* Reeve, 1863, Sydney, Australia.
Remarks: The Moreton Bay locality for *A. vagina* is likely erroneous.
Distribution: South-eastern, southern and south-western Australia.

Laternula gracilis (Reeve, 1860)
Anatina gracilis Reeve 1860 pl. 2 fig. 9, NHMUK 19759/1-3 Moreton Bay, Queensland.
Synonyms: Anatina marilina Reeve, 1860, Australia; *Anatina recta* Reeve, 1863, Port Phillip, Victoria, Australia; ?*Anatina tasmanica* Reeve, 1863,Tasmania.

Remarks: Molecular analysis indicates that specimens identified as three species above are monospecific with *L. gracilis* taking priority. The status of the larger species *L. tasmanica* is uncertain but shares characters with *L. gracilis*.

Distribution: Eastern Australia from southern Queensland to Victoria and Tasmania.

***Laternula impura* (Pilsbry 1901)**
Anatina impura Pilsbry, 1901: 208, pl. 19 fig. 9, syntypes ANSP 68536, Sagami, Japan.

Remarks: The status of this species is uncertain.

Distribution: Southern Japan

Laternula japonica Lischke, 1872: 107; figd 1874, pl. 9, figs 7-10, types not located, Tokyo, Japan.

Remarks: This species is often synonymised with *L. anatina* but our molecular results indicate it is genetically distinct. An earlier name may be *Anatina blainvillei* Reeve, 1863, pl. 3, fig 17, Island of Burias, Philippines.

Distribution: southern Japan.

Laternula laterna (Lamarck, 1818)
Anatina laterna Lamarck 1818: 463. lectotype MNHG 1082/33 selected Beu (2004: 184, figs 18 C-E).

Synonyms: *Anatina cistella* Reeve 1863, Moluccas; *Anatina constricta*, Reeve, 1863, North Australia; *A. valenciennesii* Reeve, 1863, China.

Remarks: The lectotype is a large specimen with a short posterior beak and differs from the Lamarckian syntype specimens (now paralectotypes) labelled *A. laterna* in MNHN Paris (Lamy, 1934, pl. 1, fig. 7).

Distribution: northern Australia, Indonesia. Beu (2004) wrongly states, citing Lamprell & Healy (1998: 214), that the distribution ranges from southern Western Australia to South Australia, Victoria, Tasmania and New South Wales.

Laternula navicula (Reeve, 1863)
Anatina navicula Reeve, 1863 pl. 4 fig 21, NHMUK 197520/1-3, type locality not cited.
Synonyms: *Anatina barkudaensis* Preston 1915 Lake Chilka, India; *Anatina barkulensis* Preston, 1915, Lake Chilka; *Anatina granulosa* Preston, 1914, Lake Chilka; *Anatina smithi* Preston 1905, Sri Lanka.

Distribution: NW Indian Ocean, Arabian Sea, India, Sri Lanka, Andaman Sea.

***Laternula* sp.**
Remarks: This species collected in Kungkraben Bay, Thailand and called *L. corrugata* by Prezant *et al.* (2008) and then changed to *L. anatina* Prezant *et al.* (2015) is neither of these taxa. It is broadly similar in shape to *L. bullata* Reeve, 1860 but molecularly distinct from Singapore specimens that we identify as that species.

The following species are of uncertain status, all are small shells and probably juveniles.
Anatina faba Reeve, 1863, Pl 4 fig 22, Brisbane, type not located. *Anatina argentea* Reeve 1863 pl. 4 fig 29 NHMUK 197526. *Anatina prolongata* Reeve 1863 pl 4 fig 28. Port Curtis, Queensland, type not located.

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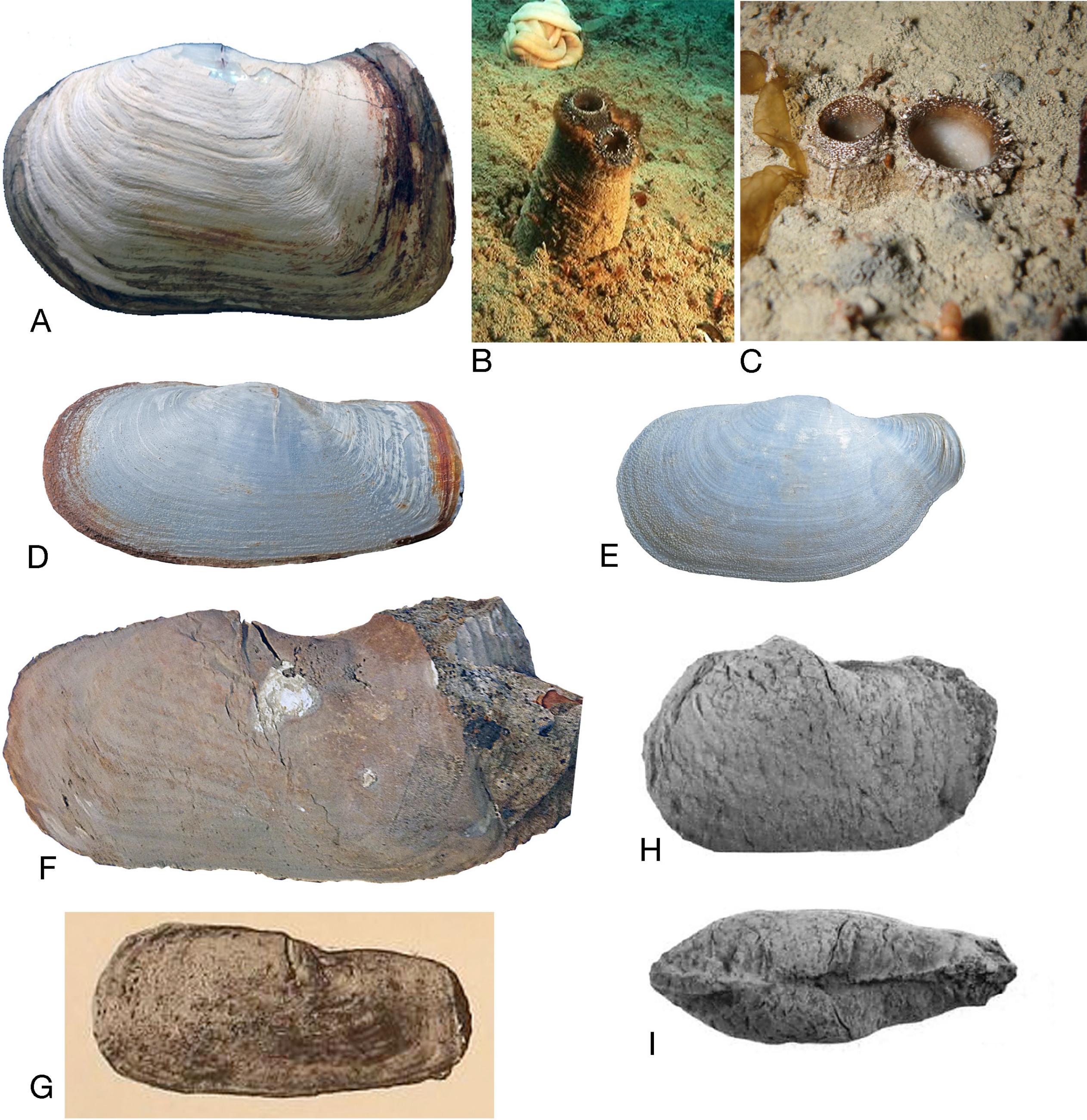
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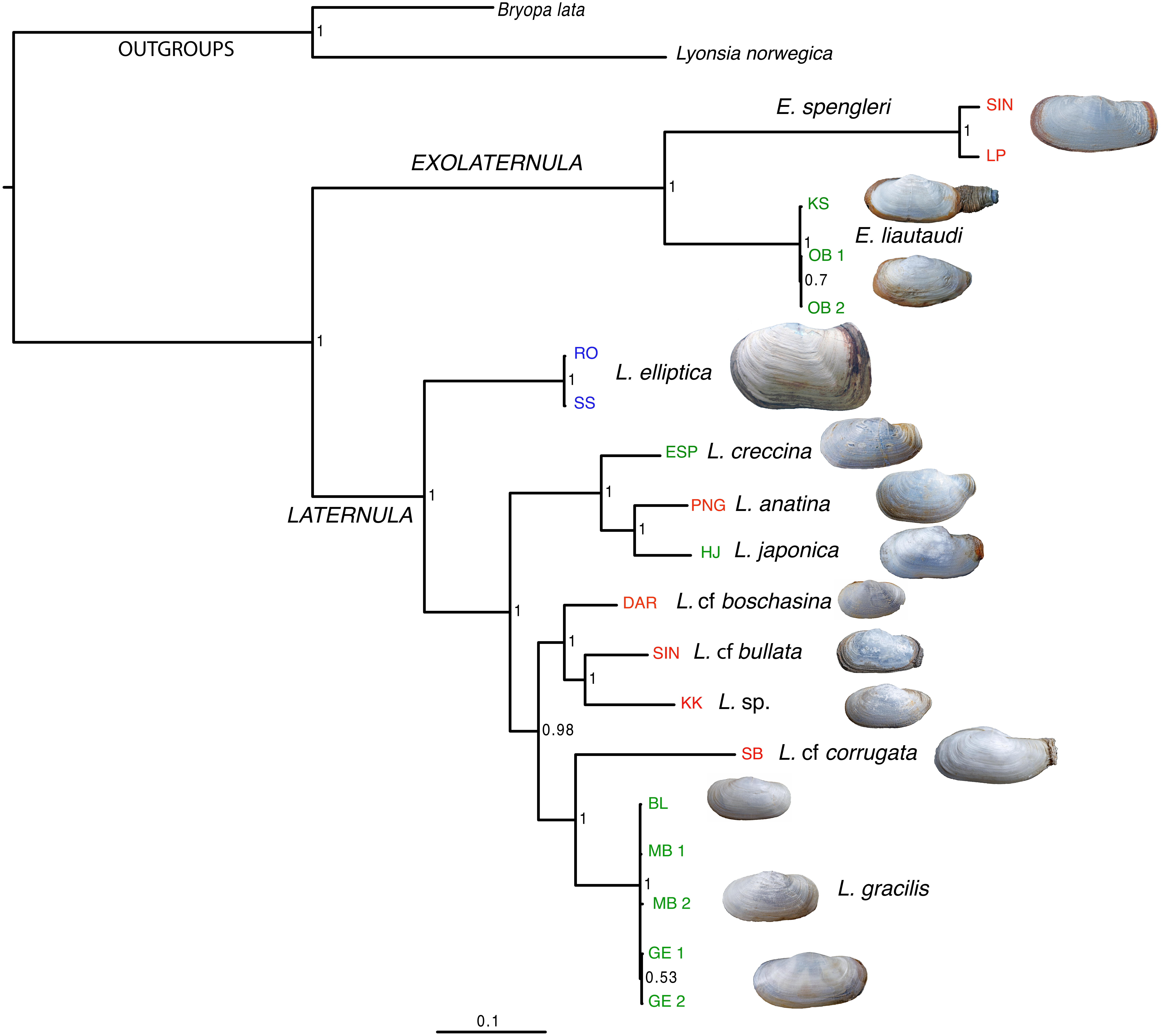
Bryopa lata
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OUTGROUPS
Lyonsia norwegica
E. spengleri
SIN
1
LP
EXOLATERNULA
1
KS
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E. liautaudi
OB 1
0.7
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L. elliptica
SS
ESP
L. creccina
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PNG
L. anatina
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HJ
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L. cf boschasina
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L. cf bullata
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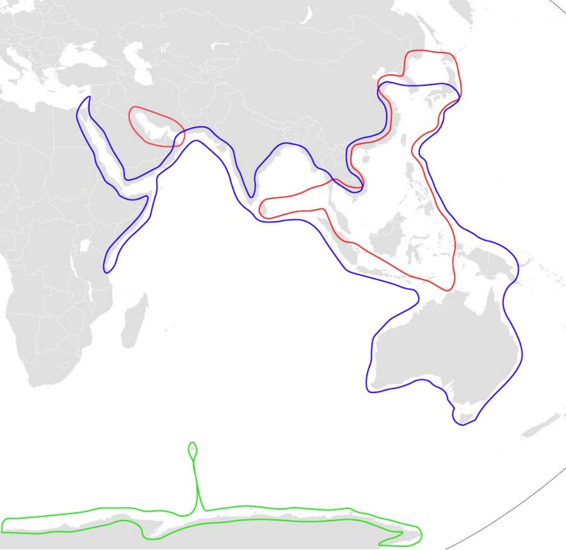

Table 1. Laternulidae species included in the analysis with collection localities, locality codes used in Figure 2, museum registration numbers for vouchers and GenBank accession numbers for the genes sequenced for each taxon. MNHN - Museum national dHistoire Naturelle, Paris; NHMUK - The Natural History Museum, London.

s for vouchers and GenBank accession numbers for t	COLLECTION LOCALITY	Locality code	VOUCHER NUMBER	28S	cyt B	12S	16S
Exolaternula liautaudi (Mittre, 1844)	Olga Bay, Eastern Russia, 43°41'56'' N, 135°15'04''E	OB 1	NHMUK 20170326	LT960470	LT960693	LT960373	LT960384
Exoaternula liautaudi (Mittre, 1844)	Olga Bay, Eastern Russia, 43°41'56'' N, 135°15'04''E	OB 2	NHMUK 20170327	LT960471	LT960694	LT960374	LT960385
Exolaternula liautaudi (Mittre, 1844)	Kojima- Shinden, Kawasaki, Japan, 35°30'52"N, 139°48'29"E	KS	NHMUK 20170328	LT960472	LT960695		LT960386
Exolaternula spengleri (Gmelin, 1791)	Casiguran Bay, Luzon, Philippines, 16°15.95' N, 122°05' E	LP	MNHN IM-2007-41446	LT960473			LT960387
Exolaternula spengleri (Gmelin, 1791)	Sungei Buroh, Singapore, 1°26' 39'' N, 103° 43'39" E	SIN	NHMUK 20160581	LT960474	KX815963	KX815963	KX815967
Laternula elliptica (King, 1831)	Rothera Point, Adelaide Island, Antarctica, 67°34'S, 68°08'W	RO	no voucher	LT960475	KX815959	KX815959	KX815959
Laternula elliptica (King, 1831)	King George Id, South Shetland Islands, 62°09.87'S, 58°33.83'W	SS	NHMUK 20170329	LT960476	LT960696		LT960388
Laternula creccina (Reeve, 1860)	Esperance, Bandy Creek, W. Australia, 33°49'50"S,121°56'10"	ESP	NHMUK 20030177	LT960477	LT960697		LT960389
Laternula anatina (Linnaeus, 1758)	Papua New Guinea, near Rempi, stn PR104, 5°5'6" S,145°48'	PNG	MNHN IM-2013-15152	LT960478	LT960698	LT960375	LT960390
Laternula japonica (Lischke, 1872)	Hakata-jima Island, Ehime pref., Japan, 34°12'N, 133°05'E	HJ	NHMUK 20170330	LT960479		LT960376	LT960391
Laternula cf. *boschasina* (Reeve, 1860)	Ludmilla Creek, Darwin, Australia, 12°24'28'S, 130°50"07"	DAR	NHMUK 20170331	LT960480	LT960699	LT960377	
Laternula cf. *bullata* (Reeve, 1860)	Sungei Buroh, Singapore; 1°26' 39'' N, 103° 43'39" E	SIN	NHMUK 20170332	LT960481	LT960700	LT960378	LT960392
Laternula sp.	Kungkraben Bay, Thailand, 12° 34.42'N, 101° 54.24'E	KK	NHMUK 20170333	LT960482	LT960701	LT960379	LT960393
Laternula cf. *corrugata* (Reeve, 1863)	Denham, Shark Bay, W. Australia, 25°54'11"S, 118°31'16"E	SB	NHMUK 20170334	LT960483	LT960702	LT960380	LT960394
Laternula gracilis (Reeve, 1860)	Geelong, Victoria, Australia, 38°9'07"S, 144°23'44"E	GE 1	NHMUK 20170335		LT960703	LT960381	LT960395
Laternula gracilis (Reeve, 1860)	Geelong, Victoria, Australia, 38°9'07"S, 144°23'44"E	GE 2	NHMUK 20170336	LT960484		LT960382	LT960396
Laternula gracilis (Reeve, 1860)	Burrill Lake, NSW, Australia, 35°22'03"S, 150°26'04"E	BL	NHMUK 20170337	LT960485	LT960704	LT960383	LT960397
Laternula gracilis (as *L. marilina* in Taylor *et al.* 2007)	N. Stradbroke Id, Moreton Bay, Qld, Australia, 27°24'29"S, 153°	MB 1	NHMUK 29970221	AM779661			
Laternula gracilis (Reeve, 1860)	N. Stradbroke Id, Moreton Bay, Queensland, Australia	MB 2	Combosch et al. 2017	KX713395			KX713227
OUTGROUPS							
Bryopa lata (Broderip, 1834)	Singapore, 1°13.9' N, 103° 52'E		NHMUK 20160581	LT960486	KX815957	KX815957	KX815957
Lyonsia norwegica (Gmelin, 1791)	Tjarno, Sweden, 58° 52.42' N, 11° 06.18'E		NHMUK 20160584	LT960487	KX815960	KX815960	KX815960