

# Lunulite bryozoan biogeography— a convergent global success with a distinct Western Australian twist

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## Abstract

Lunulites are a polyphyletic group of marine bryozoans that have been a conspicuous element of marine shelf faunas from the Late Cretaceous to the present. They are easily recognisable by their domed colony form and free-living mode of life on sea floor sediments. Here we explore the waxing and waning of the major lunulitiform groups and their unique morphology and mode of life from the Cretaceous to the present day. Because relatively few and simple modifications are needed to transition from an encrusting form into this highly specialised lifestyle, shared colonial features are rampant and we find examples of both convergent and iterative evolution across several unrelated clades, although detailed phylogenetic relationships remain largely unresolved. The early chapter of the 'lunulite story' is focused on the Late Cretaceous European Chalk Sea, which appears to have been a crucible for the evolution of 'lunulites'. At least six, and likely more, cheilostome groups independently evolved a free-living mode of life in this tropical shelf region. To what extent any of these free-living clades gave rise to post-Cretaceous groups remains unclear. The Cenozoic chapter is more complex, comprising at least three independently evolved major clades, two of which are extant: (1) the Lunulitidae *s. str.*, a North American/European cluster, encompassing the classic *Lunulites*, which became extinct in the late Neogene; (2) the Cupuladriidae, which reached circum-global tropical and sub-tropical distribution in the Miocene; and (3) the 'Austral lunulite' cluster, which is almost certainly polyphyletic and through most of its history confined to Australia and New Zealand, bar a comparatively brief colonisation of the southern part of South America, with the earliest representatives from northwestern Western Australia.

**Key words:** free-living bryozoans, biogeography, phylogeography, Cupuladriidae, Lunulariidae, Lunulitidae, Otionellidae, Selenariidae

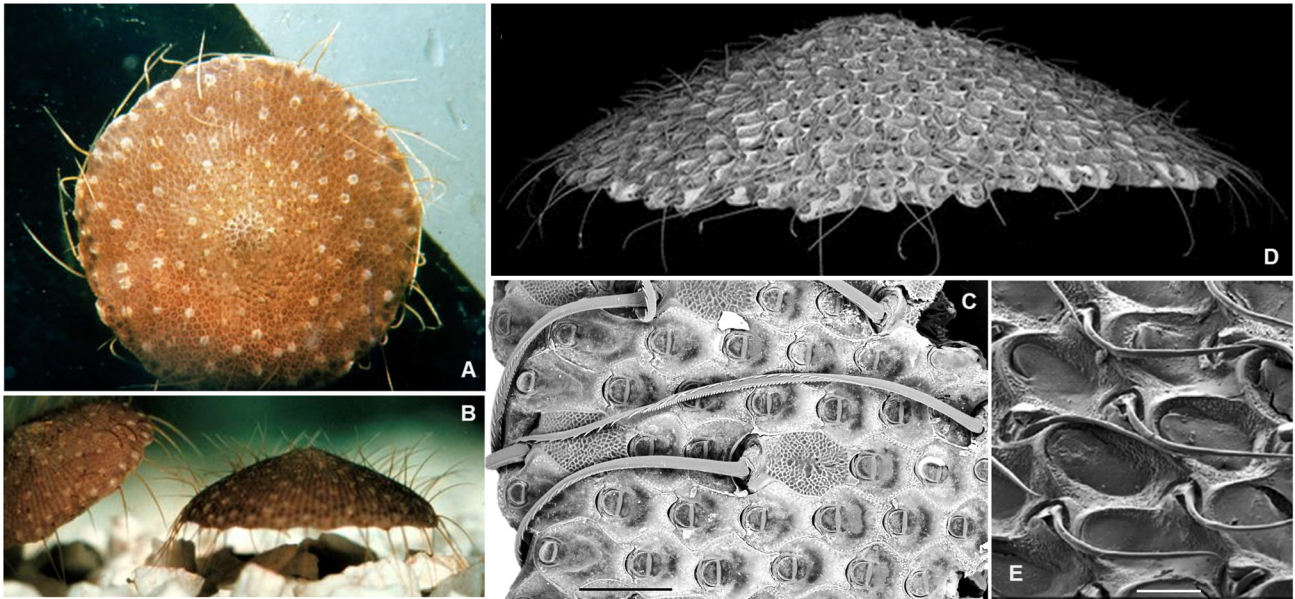
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## INTRODUCTION

The Bryozoa is a diverse, highly successful phylum of suspension-feeding, predominantly benthic marine invertebrates with an excellent fossil record dating back to the Early Ordovician, and with a sporadic, albeit disputed, record commencing at the beginning of the Cambrian (Zhang *et al.* 2021; Yang *et al.* 2023). All members of the phylum (with one possibly derived exception) form colonies by repetitive asexual budding of individual zooids, allowing polymorphic diversification in both the shape and function of zooids. Sexual reproduction involves a freely moving larval stage lasting from a few hours to several months (e.g., Driscoll *et al.* 1971; Cook & Chimonides 1983; Taylor 1988; Winston 1988). The overwhelming majority of bryozoans require a substrate for their larva to successfully settle and metamorphose into an ancestrula or ancestrular complex, thus initiating the new colony. Most bryozoans select

stable positions that provide sufficient space to enable the proper development of the colony (Winston 1988; Håkansson & Thomsen 2001). In the case of the free-living bryozoans, however, the lecithotrophic larvae mostly settle on sand grains, typically less than 2 mm; far too small to provide stability or space for the adult colony. By outgrowing or integrating the small substrate and adopting heteromorphic zooids called vibracula that possess long, bristle-like setae (Fig. 1), the bryozoan colony becomes free-living. The adoption of this mode of life allowed several groups of cheilostome bryozoans to colonise the vast expanses of fine-grained shelf sediments across the globe with tremendous success. In some instances, lunulite bryozoans are the most abundant epifaunal element of benthic soft-sediment communities (Fig. 2) with 2,000 to 3,000 colonies/m<sup>2</sup> reported by Marcus & Marcus (1962) and an exceptional number of more than 15,000 live colonies/m<sup>2</sup> reported by Cadée (1975).

The free-living—or lunulitiform—bryozoans are characterised by small (usually less than 2 cm in

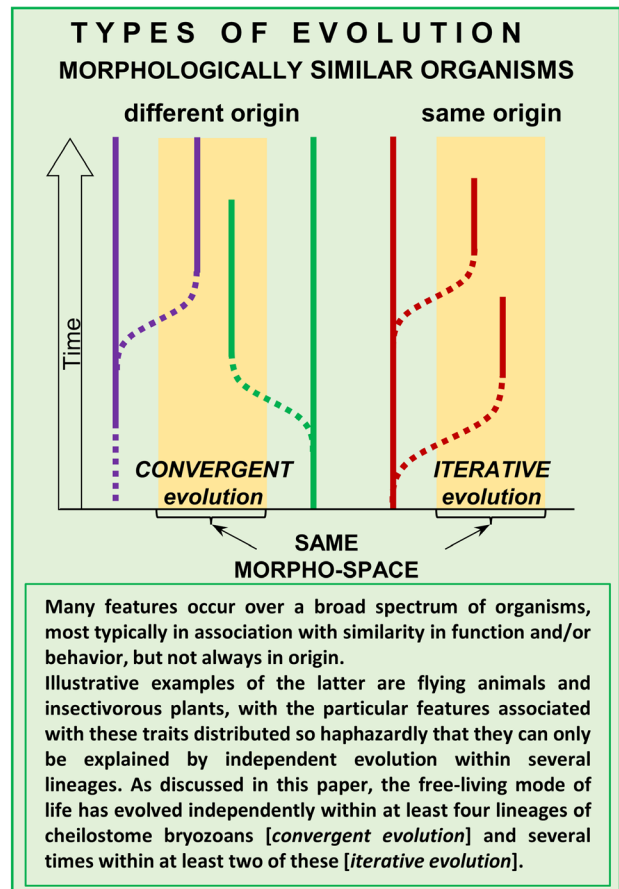


**Figure 1.** Live free-living lunulite bryozoans ‘walking’; note the long, flexible bristle-like setae characterising these species. **A–C**, *Selenaria maculata* (Busk 1852a), Great Barrier Reef (**A–B** colonies are just over 1 cm in diameter; courtesy P. L. Cook); **C**, note the low proportion of vibracula, with extremely long, serrated setae (scale bar 500  $\mu$ m). **D**, *Cupuladria biporosa* (Canu & Bassler 1923), Panama, with comparatively long setae (the colony is about 12 mm in diameter). **E**, *Cupuladria guineensis* (Busk 1854), with short setae (courtesy P. Bock, Melbourne); note the 1:1 proportion between autozooids and vibracula with smooth setae (scale bar 200  $\mu$ m).

diameter) discoid, flat to domed colonies, typically with all zooids confined to the frontal side. Their most conspicuous element is the presence of regularly distributed vibracula with individually movable long setae (Fig. 1) some of which extend beyond the colony margin, raising it slightly above the seafloor. Representatives of two families, Cupuladriidae and Selenariidae, both illustrated in Figure 1, have been observed to move across the seafloor, as well as digging into or out of the seafloor sediment through coordinated movement of their setae (Cook & Chimonides 1978; Håkansson & Winston 1985; O’Dea 2009)—a most unusual capability amongst bryozoans and colonial organisms.



**Figure 2.** Hundreds of living colonies of *Cupuladria biporosa* collected in a van Veen grab sample in Golfo de los Mosquitos, Caribbean Panama (35 m; 8.8750, -80.9992).



**Figure 3.** Convergent and iterative evolution. The yellow zone represents the free-living morpho-space, and the line colors represent separate clades.

Because of the morphological constraints imposed by their mode of life, free-living, lunulitiform bryozoans are generally easily distinguishable and, as such, a few genera were formally recognised early in the study of the bryozoans. Thus, pairs of generic names *Lunulites* Lamarck 1816 vs. *Lunularia* Busk 1884 and *Cupuladria* Canu & Bassler 1919 vs. *Cupularia* de Blainville 1830 [now abandoned], have been confused and sometimes interchanged ever since. Because of their superficial morphological similarities, higher level classification of the groups has been persistently ‘dynamic’ with several family-level taxa proposed, combining the lunulitiform genera in virtually all combinations possible. Although the genus *Lunularia* has been formally restricted to a small group of exclusively Austral (i.e., from Australia and New Zealand) species referred to the monotypic family Lunulariidae (Levensen 1909), the name *Lunulites* remains in broad use.

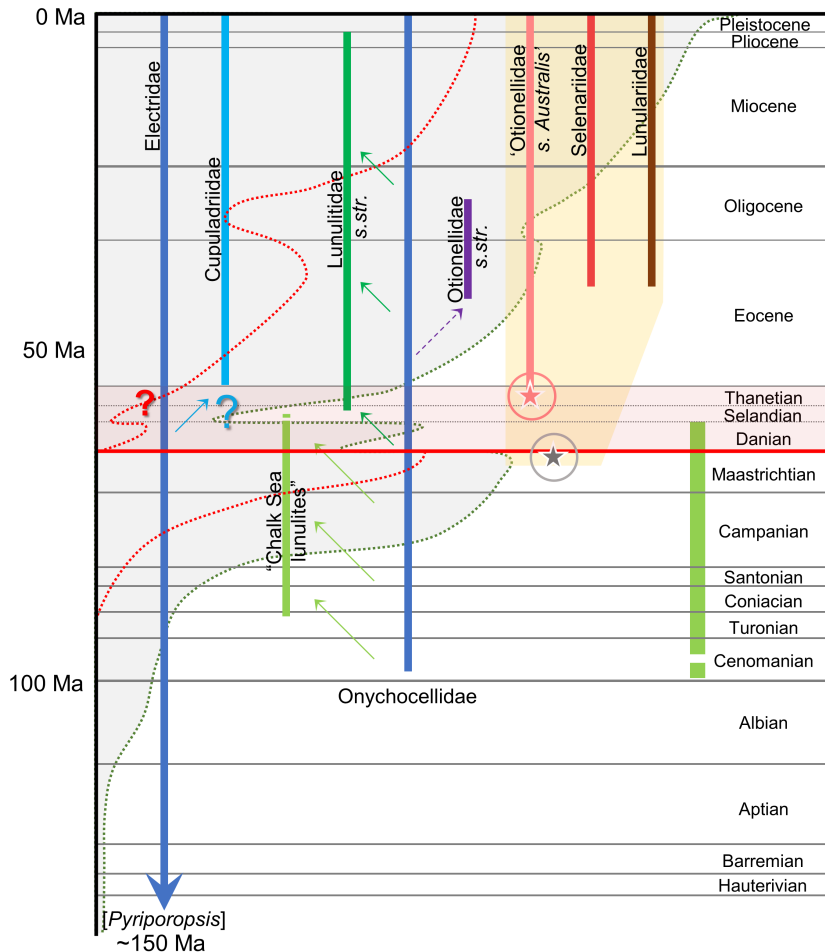
Researchers have attempted to clarify the resulting systematic quagmire. A series of papers by P. L. Cook in collaboration with P. Chimonides (1978–1994) and P. Bock

(1998–1999), among others, led to a growing realisation that convergent and iterative evolution (Fig. 3) were likely widespread among the free-living bryozoans, a notion we support and are exploring further in a parallel investigation.

Currently, all formally described lunulitiform taxa considered here are referred to either the family Cupuladriidae or the superfamily Lunulitoidea (most recently by Bock 2022), albeit commonly with some reservation. Although the Cupuladriidae as a monophyletic family is well-supported, we do not support the unification of all other major lunulite groups into one superfamily.

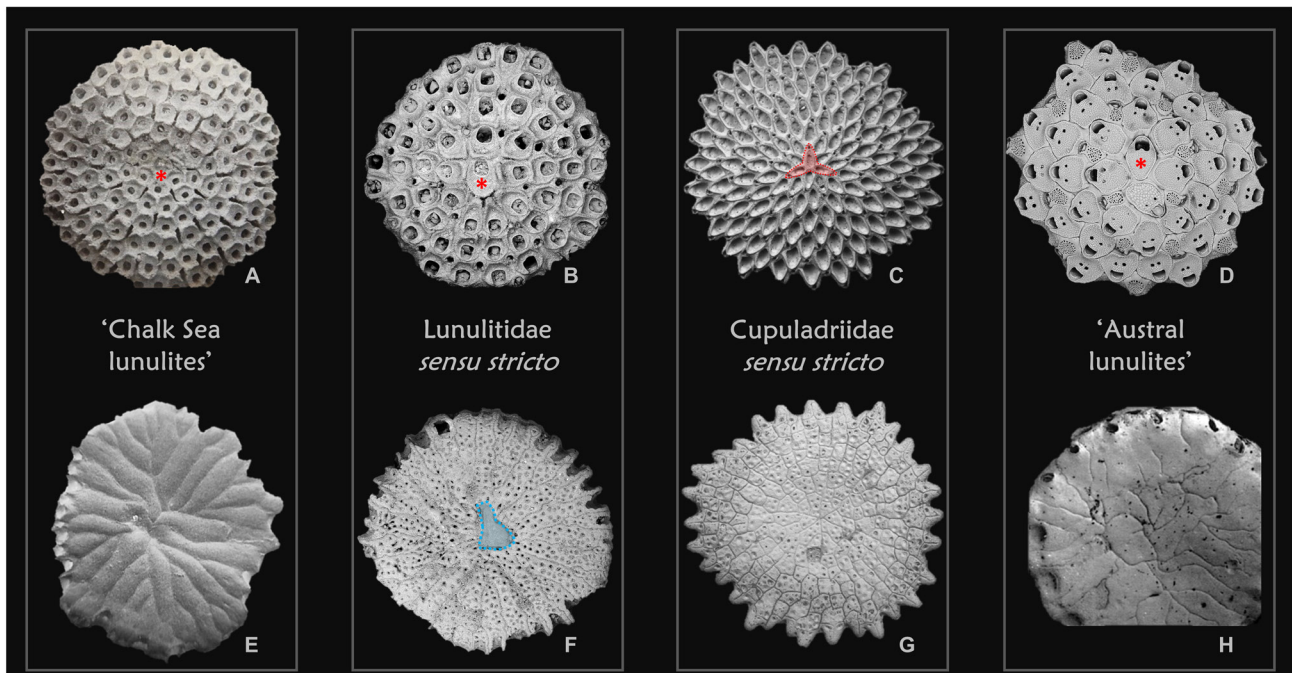
### BIOGEOGRAPHY OF THE FREE-LIVING BRYOZOANS

The general pattern of free-living bryozoan biogeography is rapid occupation (and domination) of soft shelf sediments in warm waters following their emergence



**Figure 4.** Stratigraphic distribution of the main lunulite clades referred to in the text. Two non-free-living families (dark blue lines) are included as the likely ancestors to most or all free-living clades (indicated by thin arrows). Electridae, the longest ranging cheilostome family, includes the probable ancestor to the Cupuladriidae (as well as the oldest known cheilostome genus, *Pyriporopsis* Pohowsky 1973), whereas the Family Onychocellidae is considered the likely ancestor of several ‘lunulite’ clades. Relative temporal diversity estimates in green stippled curves are for the Order Cheilostomata; the red stippled line is for free-living cheilostomes (not to scale). The Paleocene ‘dead zone’ is shaded red; the ‘Austral Realm’, yellow; the temporal extent of the Northern European Chalk Sea is the broad green line; the two asterisks show the stratigraphic position of the two oldest known Austral lunulite records (discussed in the text).





**Figure 5.** The four main clusters of lunulite bryozoans, showing both frontal (top) and basal aspects. Ancestrula and ancestrular complex indicated in red (asterisk and shaded, respectively); substrate visible only in G (shaded blue). **A**, *Lunulites goldfussi* von Hagenow 1839 (Maastrichtian, Denmark). **B**, **F**, *Lunulites androsaces* Michelotti 1838 (Late Pliocene, Altavilla, Italy). **C**, **G**, *Cupuladria biporosa* (Canu & Bassler 1923); (recent, Florida; ancestrular triplet shaded red). **D**, *Selenaria punctata* Tonnison Woods 1880 (recent, New South Wales). **E**, *Lunulites beisseli* Marsson 1887 (Maastrichtian, Denmark). **H**, *Otionellina ampla* Bock & Cook 1999 (Miocene, Victoria).

(Fig. 4). The main trends in their biogeography are explained herein using the dominant four clusters of lunulitiform free-living bryozoans, which we believe are all phylogenetically distinct, although no formal phylogenetic analyses have been made. The following summaries are based on published records and personal observations.

#### 'Chalk Sea lunulites'

This cluster of lunulites (Fig. 5 A, E) originated in the Late Cretaceous northeast Atlantic shelf seas, particularly the Northern European Chalk Sea, where the diversity of free-living bryozoans, from a fledgling beginning in the Late Turonian (Koromyslova & Pervushov, 2022), formed an evolutionary hotspot reaching approximately 100 species in the Maastrichtian. The group appears to have been geographically and ecologically constrained by the unique depositional environments of the Chalk Sea province with an assumed total range of Late Cenomanian to Danian (Håkansson *et al.* 1974; Surlyk 1997). The group is unequivocally polyphyletic (e.g., Håkansson & Voigt 1995), with calcitic skeletons and non-porous basal walls dominating. The group is very rare in the ultimate phase (Danian) of the Chalk Sea as well as within later Paleocene deposits in the region and has uncertain relations to isolated Late Cretaceous species in central Gondwanan fragments (cf. Taylor 2019) and North America (undescribed). There is no indication that any member of this cluster has migrated into the Austral Realm.

#### Lunulitidae

A separate group of lunulites, the family Lunulitidae *s. str.* (Fig. 5 B, F) originated in and dominated, both in abundance and diversity, the North Atlantic shelf seas, with an assumed range of Selandian to Pliocene (e.g., Cipolla 1921; Lagaij 1952; pers. obs.). Within the family, two hotspots developed: one in the northwest Atlantic during the mid-Paleogene, and a minor one in European seas during the Neogene. The group is probably polyphyletic, typically with a bimineralic or, less frequently, an entirely aragonitic skeleton (Taylor *et al.* 2009) with basal-wall pores. There appears to have been little migration outside the North Atlantic Realm, and there is no indication that any member related to this cluster migrated into the Austral Realm.

#### Cupuladriidae

The family Cupuladriidae (Fig. 5 C, G) probably originated in the tropical eastern Atlantic (Gorodiski & Balavoine 1961). It has a known range of Thanetian or Ypresian to Recent, is apparently monophyletic (Dick *et al.* 2003) with a dominantly aragonitic skeleton (e.g., Taylor *et al.* 2009), and commonly exhibits basal-wall pores. Although highly localised and rare through the Paleogene, the family underwent a large-scale expansion into near-circumtropical seas at the onset of the Miocene (e.g., Laagaj 1963), forming a hotspot around the central Atlantic region. The Cupuladriidae have been present, and often prolifically so, in the mid-Atlantic and Caribbean, tropical west Pacific and Indo-Pacific



archipelago since the Miocene, although their diversity and abundance in the latter two realms remains poorly documented. A few taxa are recorded from the Miocene in southern South America (Philippi 1887; Canu 1904, 1908), and a single cupuladriid species migrated into the Austral Realm in the Miocene (Cook *et al.* 2018b).

### ‘Austral lunulites’

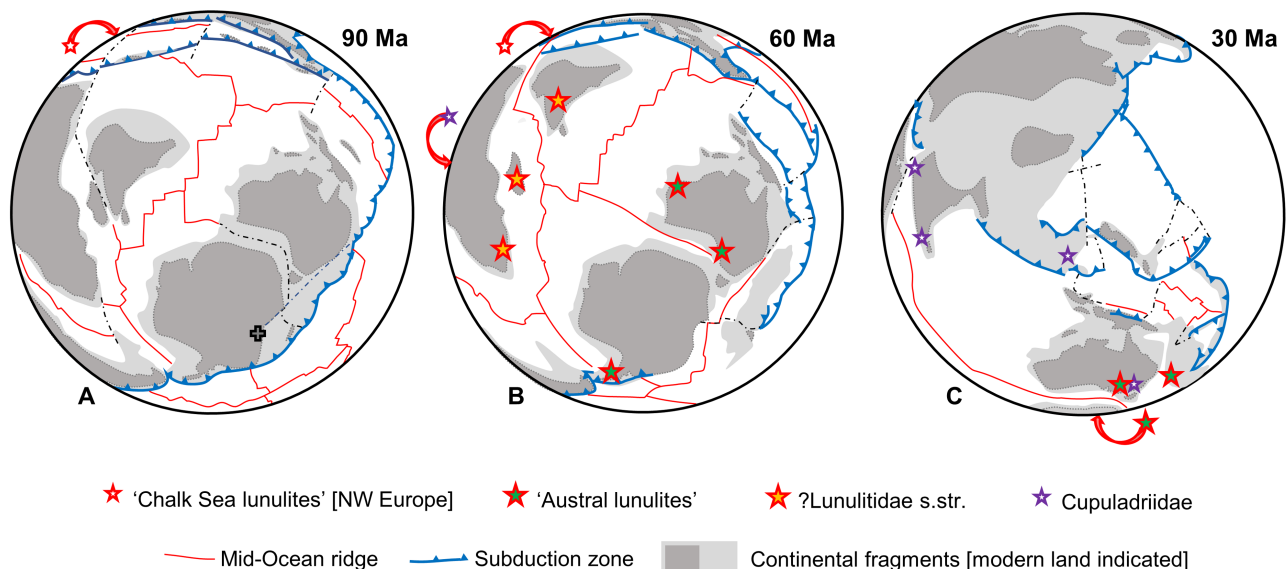
A distinct group of free-living lunulite bryozoans (including Lunulariidae, Selenariidae, ‘Otionellidae *sensu australis*’; Fig. 5 D, H) developed in the Austral Realm. Limited evidence indicates this cluster most likely originated along the northwestern margin of Australia, with a total range of Maastrichtian or Thanetian to Recent (Bock & Cook 1998, 1999; pers. obs.). The group is polyphyletic, comprising at least four families, with dominantly aragonitic skeletons (Taylor *et al.* 2009). Although geographically isolated through most of their history (see ‘The Austral lunulites’ below), they had spread around all of Australia and New Zealand by the Oligocene (Bock & Cook 1999) to form a prominent, ongoing hotspot with temporary migration into southern South America in the Late Oligocene, possibly via Antarctica. No austral ‘lunulites’ are known to have crossed the Wallace Line into Eurasia.

Among the four groups outlined above, the Lunulitidae *s. str.*, together with its nominal genus *Lunulites*, remains particularly loosely constrained. Both names have been assigned extensively to taxa in both clusters of lunulites distinguished above, separated by not only the end-Cretaceous mass extinction, but also the subsequent Paleocene ‘dead zone’ (Fig. 4), which obscures any possible relationship between these two cohorts of ‘*Lunulites*’. It is noteworthy that the scarcity

of free-living bryozoans otherwise characterising the Paleocene does not apply to the Austral Realm, which was the scene of a separate, spectacular evolutionary radiation, seemingly without contribution from any lunulite clade from outside the realm (see below). As demonstrated from the groupings above, we suggest that the two ‘*Lunulites*’ clusters are phylogenetically distinct, with ‘Chalk Sea lunulites’ effectively becoming extinct at the Mesozoic–Cenozoic boundary, bar a few survivors into the Paleocene ‘dead zone’ (Håkansson *et al.* 2019, and ongoing research). Together with a mixed group of unique free-living bryozoans without setae, the ‘Chalk Sea lunulites’ forming an as yet unrivaled diversity hotspot of free-living bryozoans during the later phases of the Late Cretaceous Chalk Sea in northern Europe (e.g., Håkansson & Voigt 1995).

### THE ‘AUSTRAL LUNULITES’

The Austral Realm occupies a prominent position in the study of Cenozoic and modern bryozoans—including the lunulites—with studies of their highly diverse faunas dating back to the early 19<sup>th</sup> century. Initially these studies were based, albeit rather chaotically, on the collections from the French Baudin expedition (1801–1803), but following the British *Rattlesnake* expedition (1846–1850) and subsequent local collecting, more systematic descriptions of the bryozoan faunas commenced (e.g., Busk 1852a, b, 1854; Hincks 1881a,b, 1882; MacGillivray 1881, 1886; and the overview by Cook *et al.* 2018a). The earliest work on fossil bryozoans includes that by Tenison Woods (1865) as well as a monograph by MacGillivray (1895), with early works on fossil lunulite bryozoans by Tenison Woods (1880) and Mapleston (1904). All referred



**Figure 6.** Consecutive plate configurations (simplified from Müller *et al.* 2021) as background for the distribution of lunulite bryozoans from their first appearance in the Late Turonian, in the European Chalk Sea, through to the early Neogene. **A**, The early part of the Chalk Sea; few lunulites and only in northern Europe and Asia. The rough position of the 90 Ma South Pole is indicated (with a cross), with only limited subsequent change in position. **B**, Encompassing the rapid change across the Mesozoic–Cenozoic transition (including data for the period Maastrichtian – Early Eocene). **C**, Encompassing the comparatively short period with invasion of Austral lunulites into southern South America (Late Oligocene – Middle Miocene). Note the continuous isolation of the Australia – Antarctica – New Zealand – southern South America remnants of Gondwana locked in high latitudes traditionally considered unsuited for lunulite bryozoans.

these Austral lunulitids to the family Selenariidae (see below).

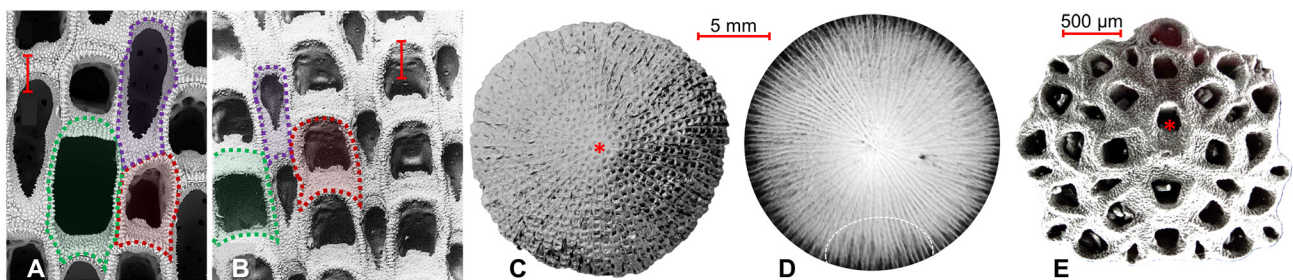
The Austral free-living bryozoans appear to have remained largely isolated from external influences throughout most of their history, a proposition hinted at previously by Cook & Chimonides (1985b) and Bock & Cook (1998), for example. Whereas such propositions were based primarily on ancient and modern distributions of the different groups, they are consistent with Australia's post-Gondwanan history of isolation (Fig. 6). By the time the first free-living cheilostome bryozoans evolved in Eurasia (in the latest Turonian), only Australia and Antarctica, with New Zealand still attached, formed an isolated, southern continent within a major ocean including a cold-water barrier across Antarctica and into South America (see e.g., Müller *et al.* 2019). Late Paleogene separation between these three terranes sent Australia and New Zealand on somewhat different northward trajectories preceding the post-Miocene closure of the Tethyan Ocean north of Australia, with only a few, narrow deep-water straits across the Indonesian archipelago remaining (e.g., Barber *et al.* 2000). In short, these terranes did not reach a position facilitating at least some warm, shallow water connections to the rest of the world until the Middle Eocene (specifically southeast Asia, as shown by the first occurrence of warm-water benthic foraminifera in Australia; Haig *et al.* 1997). Prolonged isolation of the shallow marine margins of the Australian continent, commencing well before the appearance of the first lunulite bryozoan in Europe, supports the notion that the 'Austral lunulites' evolved into free-living organisms independently, with none of the traits particular to this mode of life inherited from other free-living clades. Importantly, this therefore provides an independent parallel to the simultaneous evolution of such traits in the Lunulitidae *s. str.* and the Cupuladriidae (Håkansson *et al.* 2019).

The origin of the distinct Austral group of free-living bryozoans remains somewhat ambiguous due to a

patchy early fossil record. The Late Aptian record of *Lunulites abnormalis* Etheridge 1901 from Queensland was refuted by Håkansson *et al.* (in press) in the absence of the original and only known, but poorly described and illustrated, specimen. The potentially earliest known appearance is a record referred to the uppermost Maastrichtian Miria Formation (following terminology of Hocking *et al.*, 1987) in the Southern Carnarvon Basin of Western Australia, as reported by Cook & Chimonides (1986). Unfortunately, according to their labels, these two specimens were collected loose, leaving the possibility that they may belong to the earliest substantiated free-living fauna, comprising at least 10 species-level taxa from the Thanetian Boongerooda Greensand Member of the Cardabia Calcarene (following terminology of Hocking *et al.*, 1987; EH collections; see 'Origin of the Austral lunulite hotspot' below).

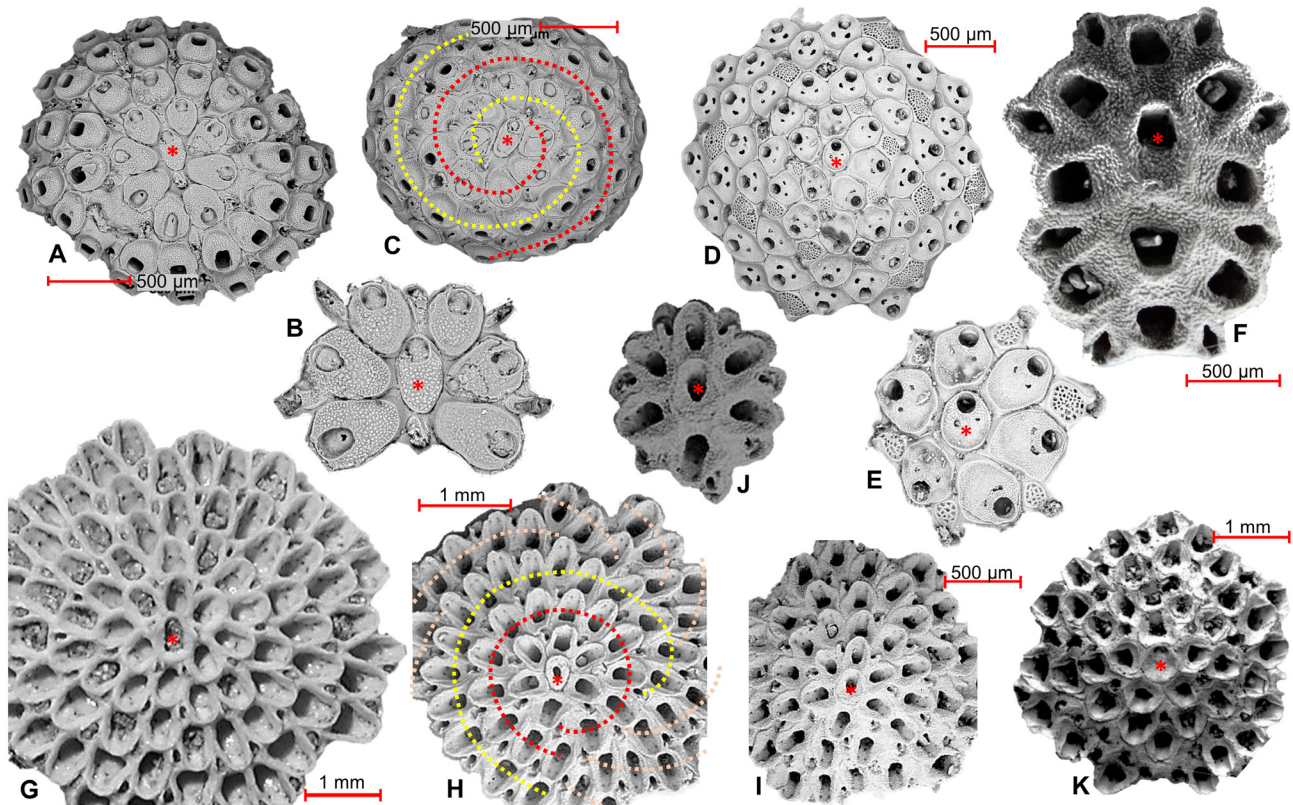
Nevertheless, by the Late Eocene all modern families of lunulite bryozoans in the Austral Realm were already established in the significant expansion of Austral free-living genera, with dominance and diversity peaks shifting to southeastern Australia and, in the Oligocene, to New Zealand, thereby forming an independent Austral lunulite hotspot that reached its diversity maximum in the Miocene (Bock & Cook 1999). Around the same period, the Austral free-living fauna experienced a brief interval of extra-continental expansion into southern South America, possibly facilitated by a more favourable Late Oligocene – Middle Miocene temperature regime (see 'The South American connection' below).

Even though it appears unlikely that any Austral free-living taxon has a free-living ancestral connection outside the region (the apparently Miocene immigrant *Cupuladria guineensis* Busk 1854 being the exception), the group is probably polyphyletic, reinforcing the conclusion that becoming a free-living bryozoan may be relatively easily achieved. We currently consider the following family level clades to have originated in the Austral Realm: Lunulariidae, Selenariidae and 'Otionellidae *sensu australis*' (amended, see below), all of which are



**Figure 7.** Selected species of Lunulariidae. **A**, *Lunularia repanda* Maplestone 1904; Investigator Strait, South Australia, recent. Detail showing zooidal morphology, note the significant size increase in female zooids. **B**, *L. capulus* (Busk 1852a); recent; detail showing zooidal morphology; note that female zooids are externally recognisable only by their slightly enlarged, square opesia. **C**, *L. capulus* (Busk 1852a); recent; frontal side of small, mature colony with perfect radiating symmetry (ancestrula marked with red asterisk), and **D**, X-ray image of the same colony revealing the distribution of the internally enlarged female zooids (diffuse, light grey shades) in incomplete circles near the margin of the colony; one cluster indicated by thin white stipples. Note the complete lack of a substrate. **E**, *L. capulus* (Busk 1852a); (from NHMUK 1984.12.24.71, recent; Juvenile colony). Zooidal colour codes (Figs 7–10): autozooids red, vibracula purple, female zooids (ovicells) green, male zooids blue. Scale bars: **A**, **B** 200 µm. (**A**, **B** courtesy Phil Bock, Melbourne, **E** courtesy P. J. Chimonides, NHM London).





**Figure 8.** Colony architecture and growth pattern in selected free-living Austral species (ancestrula indicated with red asterisk). **A, B**, *Otionellina cupula* (Tennison Woods 1880); Victoria, Miocene. Frontal side of complete colony, with the ancestrular complex magnified (**B**); note closure of the central zooids. **C**, *Helixotionella spiralis* (Chapman 1913); Victoria, Miocene. Frontal side of complete colony, with the two spiral budding rows indicated (red and yellow stipple). **D, E**, *Selenaria punctata* Tennison Woods 1880; New South Wales, recent. Frontal side of complete colony, with the ancestrular complex magnified (**E**). **F**, Ancestrular complex of *Lunularia capulus* (Busk 1852a); from NHMUK 1984.12.24.71, recent; cutout from Figure 6 E. **G**, *Discoradius(?) rutella* (Tennison Woods 1880); Victoria, Miocene. Complete colony with radiating budding; note the four vibracula in association with the ancestrula. **H**, *Kausiaria magna* Bock & Cook 1998; Victoria, Late Eocene. Frontal side of complete colony with the complex spiral growth pattern indicated, with the ancestrular complex magnified (**E**). **I, J, K**, *K. jamesi* Bock & Cook 1998; Victoria, Late Eocene. Complete colony showing the more traditional radial budding pattern. **K**, Complete colony of *Petasosella lata* (Tennison Woods 1880); Victoria, Miocene. (Images courtesy Phil Bock, Melbourne, except **J**, courtesy P. J. Chimonides, NHM, London, and **G**).

well known from Upper Eocene to recent strata (see Bock & Cook 1998, 1999 & references therein). Ongoing work on the undescribed faunas from the Thanetian and Maastrichtian(?) in Western Australia should add at least two new families from the Thanetian (presented informally below) and possibly an additional new family from the Maastrichtian.

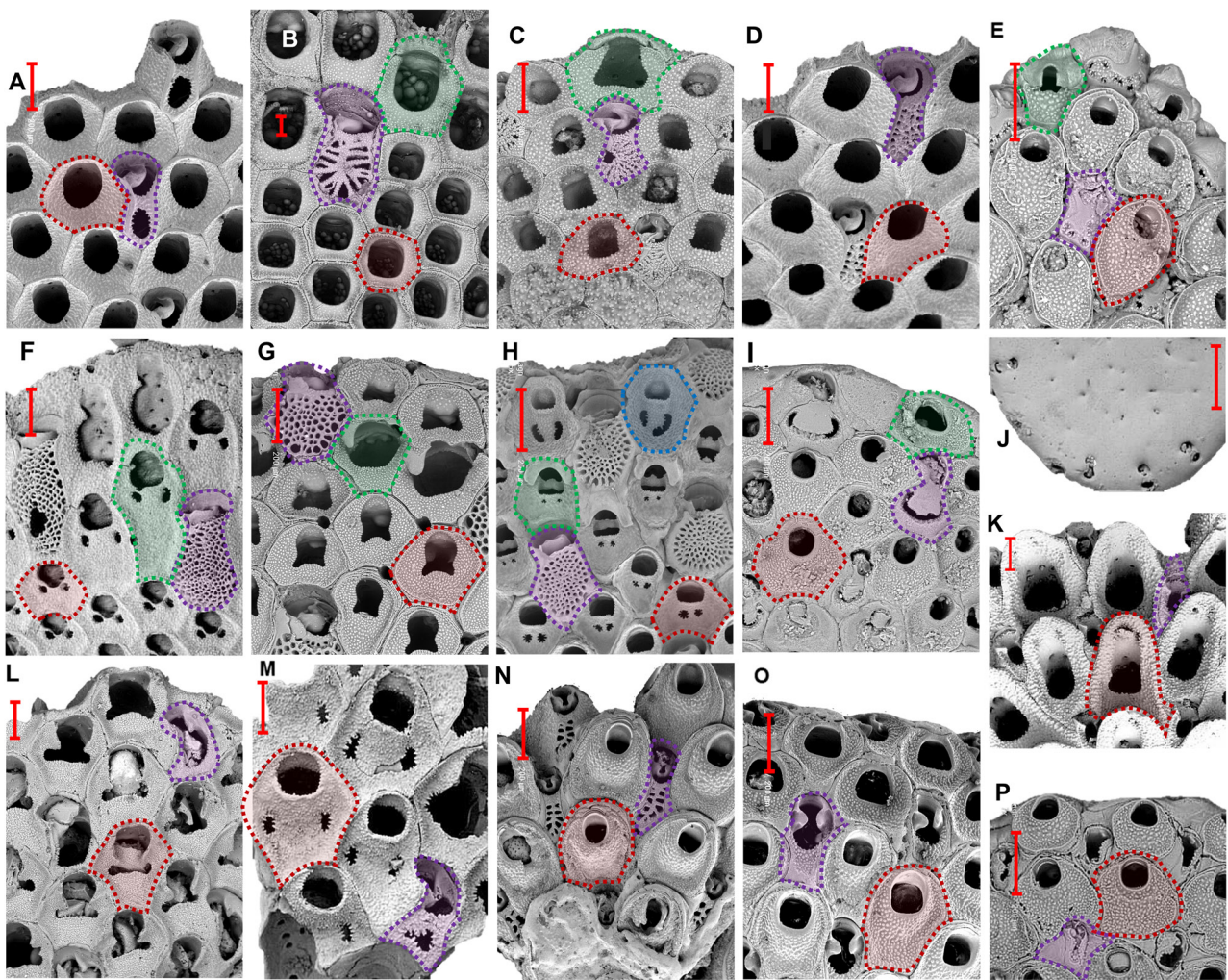
#### Lunulariidae Levinsen 1909

The monogenetic Family Lunulariidae Levinsen 1909 (Figs 7, 8 F) is known from the Late Eocene to modern faunas in Australia and from the Miocene onwards in New Zealand (Bock & Cook 1998). Female zooids (barely distinguishable from the exterior in some species) are interiorly expanded to accommodate the ovicyst for brooding large, presumably nutrient-packed, larva (Cook & Chimonides 1986). This, in turn, allows for a prolonged metamorphosis leading to a large ancestrular complex with up to 12 autozooids (ordinary feeding zooids) before the onset of feeding (EH unpublished data on *Lunularia*

*capulus*, in Cook & Chimonides 1986). Despite several clear statements to the contrary (e.g., Bone & James 1993), the ancestrular complex is consistently found without a substrate (Håkansson 1981; Cook & Chimonides 1986; Cook *et al.* 2018b).

*Lunularia* Busk 1884 is close to the genus *Lunulites*, in many ways, with several morphological features resembling members of both the 'Chalk Sea lunulites' and the Lunulitidae. Conversely, the presence of an interior ovicyst seemingly parallels the reproductive life history strategy of the Cupuladriidae (cf. Ostrovsky *et al.* 2009; Ostrovsky 2013, and references therein). Members of this genus form some of the largest known free-living colonies, reaching diameters over 7 cm, as estimated from the size of fragmented colonies (EH data, from the Geology collections at University of South Australia, Adelaide). The ancestrula is comparable in size to the periancestrular autozooids, and there are no vibracula in direct contact with the ancestrula.





**Figure 9.** Selected Recent and fossil species of Selenariidae (A–H) and ‘Otionellidae sensu australis’ (I–P) illustrating the range of zooidal polymorphism characterising these families: two to four types of zooids in the Selenariidae, and two to three types in the ‘Otionellidae sensu australis’. A, *Selenaria concinna* Tonnison Woods 1880; Victoria, recent. B, *S. hexagonalis* Maplestone 1904, Investigator Strait, South Australia, recent. C, *S. verconis* Parker & Cook 1994; Victoria, Miocene. D, *S. kompsia* Cook & Chimonides 1987; New South Wales, recent. E, *S. initia* (Waters 1883); Victoria, Miocene. F, *S. bimorphocella*, Maplestone 1904; South Australia, recent. G, *S. minor* Maplestone 1911; Victoria, recent. H, *S. punctata* Tonnison Woods 1880; recent. I, J, *Helixotionella scutata* Cook & Chimonides 1984b; Western Australia, recent. K, *Kausaria magna* Bock & Cook 1998; Victoria, Late Eocene. L, *Petasosella alata* Tonnison Woods 1880; Victoria, Miocene. M, *P. magnipunctata* (Maplestone 1904); Victoria, Miocene. N, *Otionellina squamosa* (Tonnison Woods 1880); New Zealand, Pleistocene. O, *O. australis* Cook & Chimonides 1985; Victoria, recent. P, *H. spiralis* (Chapman 1913); Victoria, Miocene. (Scale bars 200  $\mu$ m; zooidal colour codes as in Fig. 6. Images courtesy Phil Bock, Melbourne).

#### Selenariidae Busk 1854

The monogenetic Family Selenariidae Busk 1854 (Figs 8 D, E, 9 A–H) spans the Late Eocene to present, with many Australian species. In addition, a single, recent species was reported from New Zealand (Bock & Cook 1999), and there are at least two taxa from southern Argentina and Chile of Early and Middle Miocene age, respectively (López-Gappa *et al.* 2017; EH collections). The family is characterised by advanced sexual polymorphism with distinct male and female zooids in many taxa (Cook & Chimonides 1985a, 1985b, 1987; Bock & Cook 1999, and references therein).

*Selenaria* Busk 1854 is characterised by the zonal distribution of sexual polymorphs and large, scattered,

commonly highly complex vibracula (significantly fewer than autozooids), with long setae observed to facilitate locomotion in several species (Cook & Chimonides 1978). The frontal walls of both autozooids and vibracula are highly variable. The ancestrula is comparable in size to the periancestrular autozooids and there are typically no vibracula in direct contact with the ancestrula (Fig. 8 E).

#### ‘Otionellidae sensu australis’

At present the family Otionellidae Bock & Cook 1998 (Figs 8 A–C, H–K, 9 I–P) contains five genera: the nominate genus *Otionella* Canu & Bassler 1917; *Otionellina* Bock & Cook 1998; *Helixotionella* Cook & Chimonides 1984b; *Petasosella* Bock & Cook 1998; and *Kausaria* Bock

& Cook 1998. However, the nominal genus of the family Otionellidae only accommodates a few closely related species from the Middle Eocene to Lower Oligocene in North America, whereas all other genera have a distinct Austral distribution. In our opinion, biogeography as well as pronounced morphological differences suggest a separation between a restricted, North American family Otionellidae *s. str.*, and a strictly Austral, – as of yet – unnamed, family, here provisionally referred to as ‘Otionellidae *sensu australis*’. It includes at least four genera, three of which were also briefly present around southern South America (Canu 1904; Bock & Cook 1998; Pérez *et al.* 2015; EH collections). Based on the distribution of the periancestrular autozooids and vibracula, these genera may be further subdivided into two groups: one without vibracula in direct association with the ancestrula (*Petasosella* and *Kausaria*), and the other with a distolateral and proximal vibraculum in direct contact with the ancestrula (*Otionellina* and *Helixotionella*). Based on morphological similarities in the skeletal structure of the vibracula, as well as sexual polymorphism (Fig. 9), it is possible that the latter group of this geographically restricted and currently unnamed family shares a common ancestry with the Selenariidae.

*Petasosella* Bock & Cook 1998 (Figs 8 K, 9 L–M) is characterised by a radiating budding pattern with an ancestrula surrounded only by autozooids. The scattered vibracula are large and significantly less abundant than the autozooids. As no skeletal sexual polymorphism has been noted, brooding was possibly in interior ovisacs. The genus is known from the Upper Eocene to Recent of southeastern Australia and, plausibly, Upper Oligocene to Lower Miocene deposits in southernmost South America (Canu 1904; Bock & Cook 1998; EH collections).

*Kausiaria* Bock & Cook 1998 (Figs 8 H–J, 8 K) is characterised by comparatively large colonies, an ancestrula surrounded exclusively by autozooids, and a variable budding pattern, as radial or composite sinistral spirals (Figs 8 D & I, respectively). The vibracula are small and equivalent in number to autozooids. Colonies consistently lack a substrate. The genus is known from the Upper Eocene to Miocene of southeastern Australia, and from the Upper Oligocene to Lower Miocene of southernmost South America (EH collections).

*Otionellina* Bock & Cook 1998 (Figs 8 A, B, 9 N–O) is characterised by its compact, almost lenticular colonies, with abundant, small vibracula (equal in numbers to autozooids), which are commonly developed also along the colony margin and the basal side of the colony. The ancestrula characteristically has one distal and one proximal vibraculum (Fig. 8 B). The genus—or close relatives—is known from the Thanetian of northwestern Australia (see new informally designated “Family X” below), from the Middle Eocene – Recent in southeastern Australia (Bock & Cook 1998, 1999; Schmidt 2007), from the Oligocene – Recent in New Zealand (Bock & Cook, 1999), and from the Upper Oligocene to Middle Miocene in southern South America (Canu 1904; Pérez *et al.* 2015; EH collections), as well as, possibly, from Lower Eocene deposits in Antarctica (Hara *et al.* 2018, their fig. 7, only).

*Helixotionella* Cook & Chimonides 1984b (Figs 8 C, 9 I–J, P) is characterised by its unusually small, typically lentil-shaped colonies, abundant small vibracula (equal in number to autozooids) and a spiral budding pattern,

with two distinct, dextral budding series. The budding series are initiated from the two vibracula associated with the ancestrula. In late astogeny the budding series may bifurcate, and all or most budding series are associated with a (terminal) vibraculum on the basal side of the colony, strongly suggesting terminate growth of the colonies. The genus is known from the Upper Eocene to recent of southeastern Australia, with a potential relative in the Thanetian of northwestern Australia (see “Family X” below).

#### *Incertae sedis*

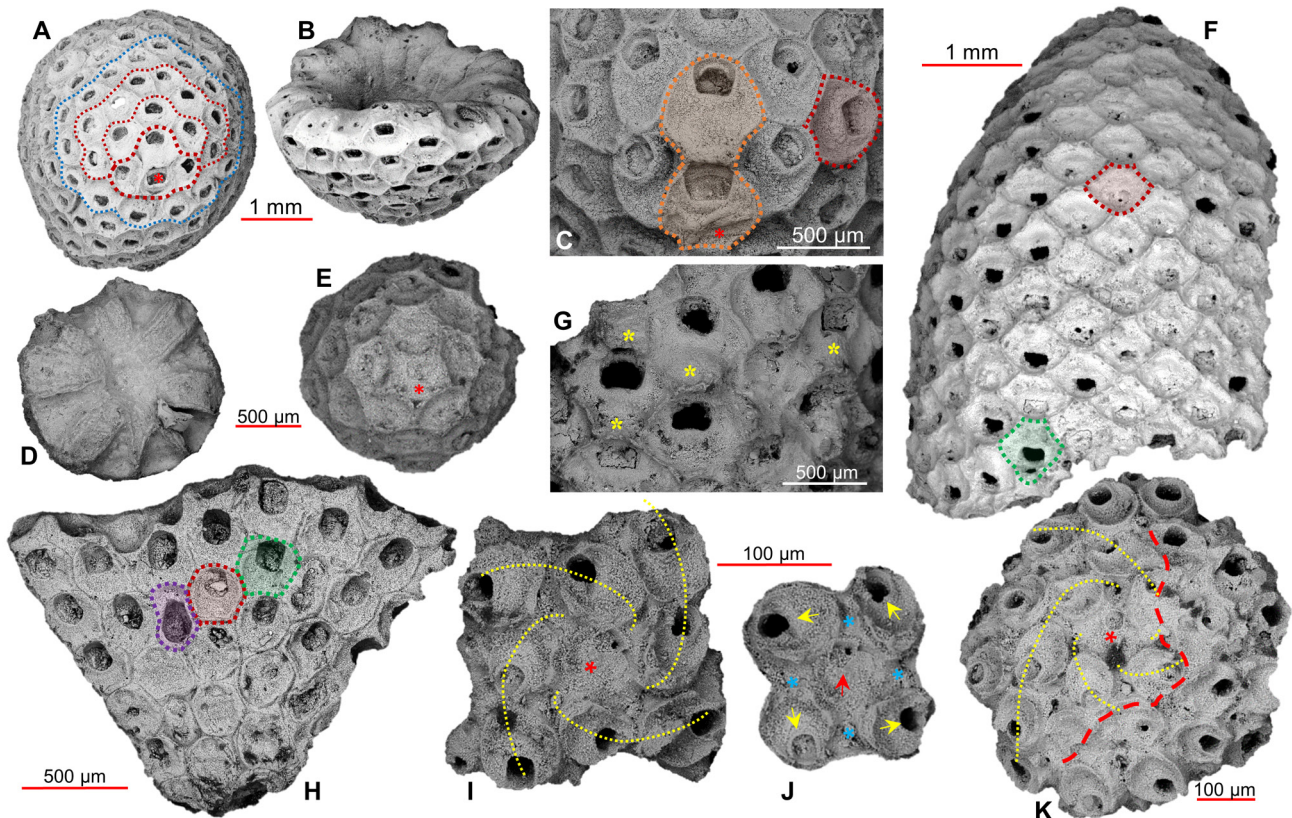
As outlined above, the genus name *Lunulites* has been variously applied also to Austral free-living taxa. Most have subsequently been referred to the endemic Austral genera listed above, but one fossil taxon—quite widespread in the Australian Paleogene and Neogene successions—remains largely unaccounted for in terms of its taxonomic phylogenetic affiliation. Originally described as *Lunulites rutella* Tenison Woods, 1880 (Fig. 8 G), this species has usually been referred to as *Lunulites*, albeit commonly with some reservation (see Bock & Cook 1999, & references therein), but recently it has been transferred to the new genus *Discoradius* Di Martino, Greene & Taylor 2017a, again with some reservation (Di Martino *et al.* 2017b). In our opinion, the zooidal morphology suggests a closer relationship to the austral genus *Kausiaria*. However, the unique early astogeny, with three, or occasionally four, small periancestrular vibracula (a disto-lateral pair of vibracula directed proximally, plus one or two proximal vibracula), suggest yet another independent free-living Austral clade.

#### New “Family X”

This family (in prep.; Fig. 10 A–G) is thus far known only from the Thanetian and possibly Ypresian of the Southern Carnarvon Basin. Taxa referred to the family are interpreted to have been free-living without setal support (free-lying) and without a substrate, a condition otherwise common only in the Late Cretaceous, Northern European Chalk Sea (Håkansson 1975). This new Austral clade has perhaps four different species all sharing essentially identical zooid morphology, but with significant differences in colony architecture—they resemble most free-lying bryozoans from the Chalk Sea in that they lack setal support, and presumably went through metamorphosis without the physical support of a substrate. To what extent the considerable architectural variation within this new family warrants recognition of more than a single genus is still under consideration.

Two members of this new clade are illustrated here. New species *a* (Fig. 10 A–C) is characterised by small (up to ~4 mm diameter) domed to hemispherical colonies with a consistent budding pattern. The early stage is characterized by a gradually expanding fan-shaped growth pattern with the ancestrula in a marginal position which then, after three budding generations, changes into a radial budding pattern gradually bringing the ancestrula into a more central position (cf. Fig. 10 A). When mature, a single ovicell (brood chamber) may develop from the ancestrula through partial skeletal resorption also involving the distal zooid (Fig. 10 C) in a process and position otherwise unknown in the phylum. In contrast, new species *b* (Fig. 10 D–G) has a budding





**Figure 10.** Selected free-living taxa from the Thanetian (Paleocene) of the Southern Carnarvon Basin, Western Australia. A–G, New “Family X”; two unnamed taxa illustrating the morphological range of the family. A–C, New “species a”. A, Mature colony; the early fan-shaped growth stages outlined in red stipples (ancestrulas with red asterisk) and the first, subsequent stage with radial budding outlined in blue stipple. B, Oblique lateral view of the same colony showing the hollow, hemispherical shape. C, Detail of the ancestrular region of the same colony showing the single, ovicell complex (orange shading) developed from the ancestrula (red asterisk) late in astogeny, through partial skeletal resorption in the distal autozoid. D–G, New “species b”. D, Basal view of juvenile, star-shaped colony demonstrating the symmetric budding pattern radiating from the ancestrula. E, frontal view of juvenile colony, maintaining the strict radial budding pattern from the central ancestrula (red asterisk). F, Lateral view of a large fragment of a mature colony demonstrating the highly unusual, tall to near cylindrical colony. G, Detail of the mature part of the same colony with several ovicells/female zooids (yellow asterisks). H–K, Two unnamed taxa referred to the provisionally named ‘*Otionellidae sensu australis*’. H, cf. *Otionellina* n. sp., fragment of discoidal colony with radial budding showing zooidal details. I–K, aff. *Helixotionella* n.sp. I, Complete juvenile colony comprising the first two zooids in each of the four sinistral spiral budding rows (ancestrula indicated with red asterisk, budding rows in yellow stipples). J, Cutaway detail of I showing the distribution and relative orientation of the ancestrula (red arrow), the initial four autozooids (yellow arrows, indicating orientation) and the four primary vibracula (blue asterisks). K, Complete, regenerated colony, with spiral budding (yellow stipples) in the original part of the colony (including the ancestrula, red asterisk) and chaotic budding in the regenerated part (fracture line in red stipples). Additional zooidal colour code as in Figure 6.

pattern with a central ancestrula from the onset (Fig. 10 E) and a subsequent, perfectly radial budding symmetry (Fig. 10 D) that rapidly turns the colony into a tall (>1 cm), hollow column with near parallel sides (Fig. 10 F), maintained through a slow increase in the number of budding series. The ancestrula consistently occupies its original, central position at the apex of the column and, unlike species *a*, this taxon develops multiple ovicells in female zooids in a more ‘normal’ position, several budding generations from the ancestrula (Fig. 10 G).

The remaining, less abundant, free-living taxa from the Boongerooda Greensand consist of several, apparently not closely related taxa, all (potentially) possessing vibracula. The early history of free-living bryozoans

in Western Australia is based entirely on taxa yet to be formally described, although there are morphological features indicating that some of these pioneers may be directly related to well-established entities in the later, more fully known Austral faunas—two such examples are illustrated (Fig. 10 H–K).

The taxon “new genus and species aff. *Otionellina*” (in prep.; Fig. 10 H) has flat, discoidal colonies with zooids confined to one side, radial budding, and resembling *Otionellina* in its zooid morphology and in the absence of a substrate; however, these specimens lack the thick, lenticular shape and basal side vibracula characteristic of that genus. The autozooids have a depressed, granulated cryptocyst with a large, terminal opesium; ovicells are



recognised by their low, hood-like structure distal to the opesium, combined with a more angular, almost quadratic outline of the opesium. The vibracula are large, typically initiating budding rows, and they are mostly slightly asymmetrical with variously developed condyles. Pending information on the early astogeny, this taxon may represent either an early member of the genus *Otionellina* or a new, related genus.

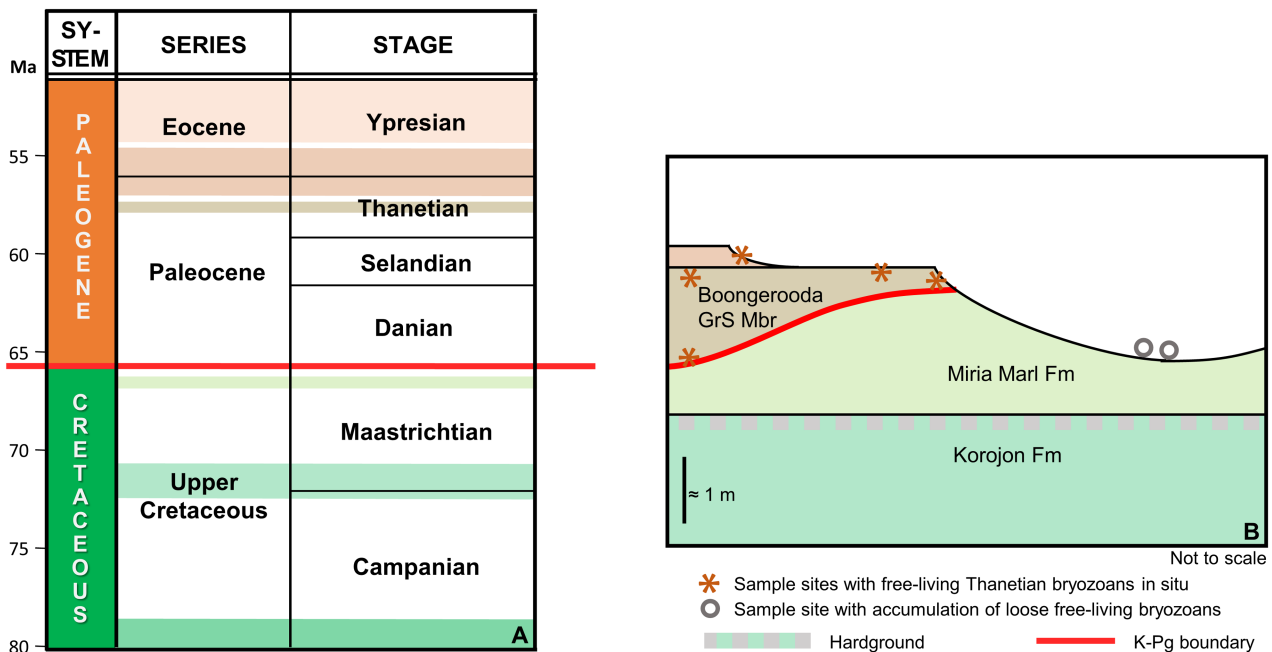
The taxon “new genus and species aff. *Helixotionella*” (in prep.; Fig. 10 I–K) is characterised by its minuscule colonies (mostly <1 mm) with abundant vibracula (equaling autozooids in number) and a spiral budding pattern with four sinistral budding series, each initiated from one of the four vibracula associated with the ancestrula. The taxon is known only from the Thanetian of northwestern Western Australia, and provisionally we consider it to be a relative of, and potential ancestor to, *Helixotionella*.

### ORIGIN OF THE AUSTRAL LUNULITE HOTSPOT

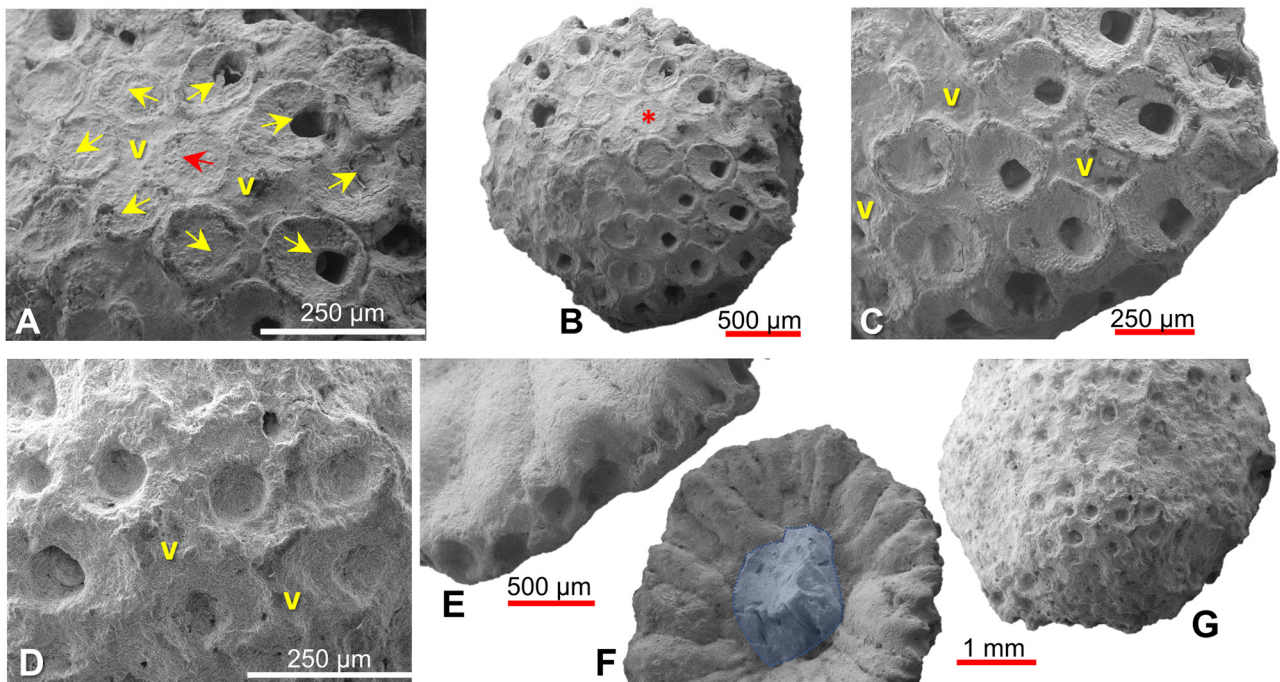
Considering the known distribution of fossil free-living bryozoans within the Austral Realm (see comprehensive summaries in Bock & Cook 1998, 1999, supplemented by EH collections from South America, Australia, and New Zealand), the origin of this evolutionarily isolated lunulite cluster was likely the northwestern margin of the Australian continent, in the proximal part of the broad,

gently sloping shelf bordering the Indian Ocean in a configuration resembling that of the present. Reflecting its proximal position on this platform, the stratigraphic succession containing these faunas is significantly condensed with sediment accumulation restricted to transgression maxima (Fig. 11). Thus, the two main intervals from which free-living bryozoans have been reported—the Upper Maastrichtian Miria Formation (Cook & Chimonides 1986; two loose specimens) and the immediately overlying Thanetian Boongerooda Greensand Member (EH collections), initiating the Thanetian–Ypresian *Cardabia* Calcareenite—are both thin (up to a couple of meters), but separated by a significant lacuna across the Mesozoic–Cenozoic boundary interval (Fig. 11).

The two specimens with a lunulite morphology allegedly originating from the Maastrichtian Miria Formation share a dubious provenance. Notwithstanding that their labels indicate they were collected from loose material, it refers them to the Miria Formation (WAM, 80.648 & 80.649, “Miria Marl, *Cardabia* Station”: Cook & Chimonides 1986; Fig. 12). However, there is no adhering sediment to support this assignment and, as seen from Figure 11 it is equally plausible that they originated from the younger Boongerooda Greensand Member and were simply mislabeled. Both specimens are unequivocally free-living, but are poorly preserved, allowing only a limited certainty as to their taxonomic position. Specimen WAM 80.649 (Fig. 12 A–C) may be an early relative of *Otionellina* (cf. Figs 8, 9), but WAM



**Figure 11.** Stratigraphy of the Upper Cretaceous – Lower Paleogene succession in the onshore part of the Southern Carnarvon Basin on the northwestern margin of the Australian continent. **A**, Chronostratigraphic chart covering the Upper Cretaceous and Paleogene strata in the Giralia Anticline. Note the frequent and extensive breaks in accumulation reflecting the position of this succession in the proximal part of a passive continental margin. **B**, Highly stylised cross section illustrating the field relations of the strata investigated. Asterisks indicate levels yielding free-living in situ bryozoans; grey circles indicate the location of loose specimens, including the two allegedly Late Maastrichtian specimens illustrated in Fig. 12; red line shows the end-Cretaceous mass-extinction event; GrS Mbr = Greensand Member; Fm = Formation.



**Figure 12.** Possibly the oldest lunulite bryozoans from Australia, collected loose and for untold reasons referred to the Upper Maastrichtian Miria Formation (see text). **A–C**, Early, potential representative of ‘*Otionellidae sensu australis*’; WAM 80.649. **A**. The periancestrular region with arrows indicating the interpreted orientation of the ancestrula (red arrow) and the early autozooids; two potential vibracula marked (v). **B**. Overview, centred around the best-preserved part of the frontal surface; ancestrula indicated. **C**. Colony margin with several well-preserved autozooids and scattered, variously preserved vibracula (v). **D–G**, Indeterminate lunulite colony; WAM 80.648. **D**. The ‘best’ preserved part of the frontal side providing enough detail of the autozooidal morphology to exclude the likelihood of conspecificity with WAM 80.649; potential vibracula indicated (v). **E**. Oblique basal view of the well-preserved colony margin. **F**. Basal surface of the colony displaying distinct budding rows with secondarily thickened calcitic walls and widely scattered minute pits, which may represent basal pores; note the sand-sized substrate (shaded blue). **G**. Overview, showing the seriously corroded frontal side of the colony.

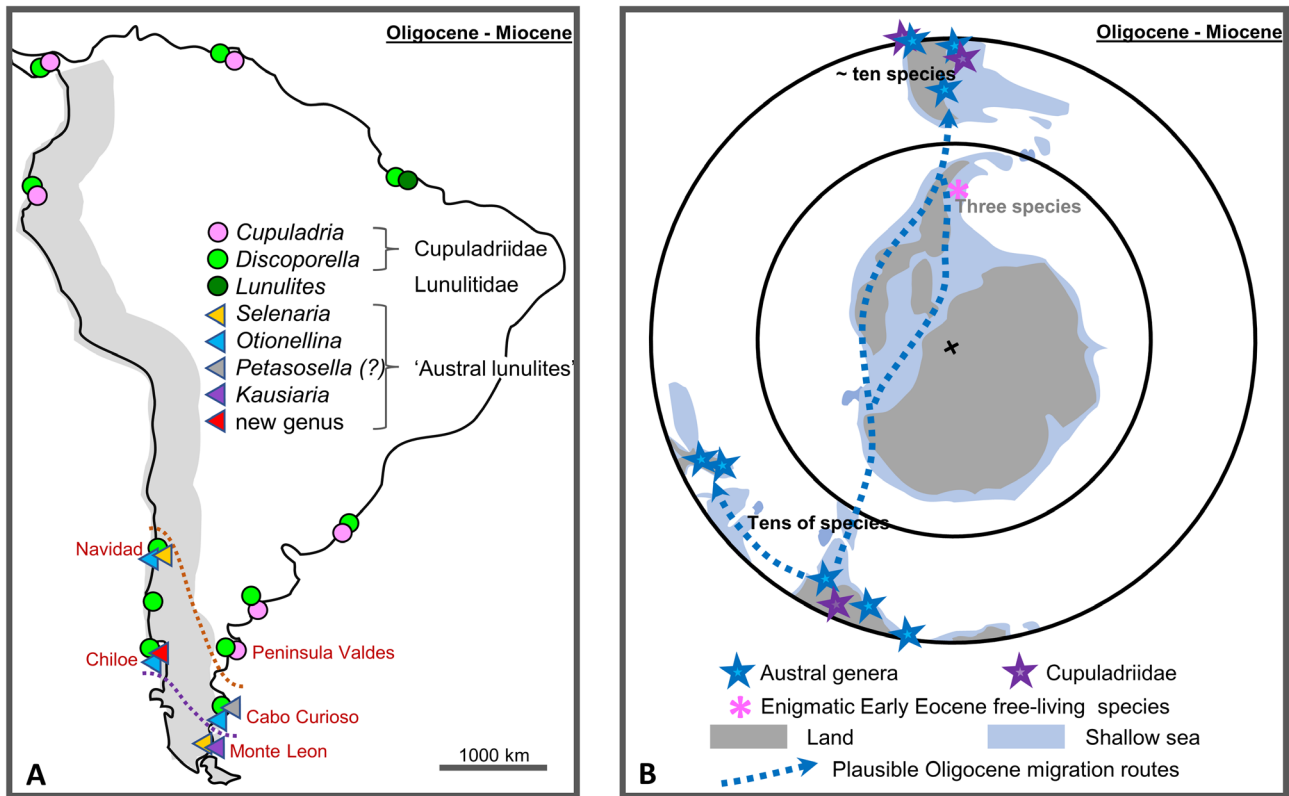
80.648 (Fig. 12 D–G) does not resemble any of the free-living taxa in the overlying Boongerooda Greensand, suggesting it could be Maastrichtian in age. Moreover, the moderately rich free-living fauna from the Thanetian Boongerooda Greensand is reasonably well preserved, and has clear ties with the later, better-known Austral free-living faunas—most obviously, but not exclusively, with the family ‘*Otionellidae sensu australis*’. Here, the taxonomic and stratigraphic status of the two specimens referred to the Miria Formation is left open, pending further investigation.

## THE SOUTH AMERICAN CONNECTION

Prior to the Late Oligocene, the record of free-living lunulite bryozoans is poor in South America with just a single Paleocene species of *Discoradius* from northeastern Brazil (Buge & Muniz 1974; Di Martino *et al.* 2017b). However, during part of the Early to Middle Miocene, a moderately diverse cupuladriid fauna coexisted with the Austral emigrants around the southern part of the continent (Fig. 13 A), commencing at a time where the Cupuladriidae were rare in the rest of the world. However, both groups are today absent from this part of the continent, probably because of considerable late Miocene to Pleistocene cooling.

The Austral lunulite fauna in Upper Oligocene to Middle Miocene strata in southern Argentina and Chile is summarised as follows (Fig. 13 A). Approximately ten taxa with Austral connections have been distinguished: three species referable to *Selenaria*, one referable to *Otionellina*, two taxa closely associated with *Petasosella*, one referable to *Kausiaria*, as well as two taxa that may warrant the creation of new genera, one related to *Selenaria* and one possibly related to *Otionellina* (Canu 1904, 1908; Pérez *et al.* 2015; López-Gappa *et al.* 2017; supplemented by EH data). For all genera listed, these species represent the only record outside their Austral heartland, thus overwhelmingly pointing to a close faunal relation between the Austral and Magallanes biogeographic provinces during this period.

The existence of a significant Late Oligocene to Miocene marine connection between the Austral Realm and the South American Magallanes province has been pointed out previously, particularly based on various Mollusca that were thought to have dispersed in the circum-Antarctic Currents (e.g., Beu *et al.* 1997). Although the time of deep-water opening between Tasmania and Antarctica is reasonably well established at about the Eocene–Oligocene boundary, the Drake Passage between Antarctica and South America is less so, with estimates ranging from Late Eocene to Early Miocene (Scher



**Figure 13.** **A**, Distribution of free-living bryozoan taxa in South America during the Late Oligocene – Middle Miocene as presently known. Note the distribution of cupuladriids across the continent (except the most extreme south) overlapping significantly with the Austral genera in the southern part (Canu 1904, 1908; Pérez *et al.* 2015; López-Gappa *et al.* 2017; own observations). The apparent absence of cupuladriids between the known presence of Miocene cupuladriids in Ecuador and Navidad, Chile is likely to reflect insufficient sampling. However, the influence of cold upwelling along the west coast of South America somewhat comparable to the modern situation cannot be dismissed. **B**, Paleogeographic map showing a plausible migration route connecting the Austral Realm to South America via Antarctica; note that all cupuladriid taxa on either side of Antarctica arrived from the north, with no connections across the polar Antarctic seas. Note also that while there is a significant overlap at the genus level between the Austral Realm and southern South America, the three Early Eocene lunulite taxa from Antarctica (Hara *et al.* 2018) do not appear closely related to either of these regions (see text). The paleogeographic outline in **B** is based on Lawver & Gahagan (2003).

& Martin 2006; Dalziel *et al.* 2013; Hodel *et al.* 2021). Nevertheless, as pointed out by Casadio *et al.* (2010), faunal similarities between the Austral and Magallanes provinces declined after the establishment of the circum-Antarctic Current and, therefore, an alternative, shorter route of dispersal via the archipelago formed in the West Antarctic Rift System seems more likely (Fig. 13 B). Considering the assumed short-lived larval stages of modern lunulite taxa, this alternative seems more likely. Whereas rafting of bryozoans on kelp, debris and ships is widespread, one of the key elements in becoming free-living is precisely the opposite—a preference for minute, typically sand-seized substrates.

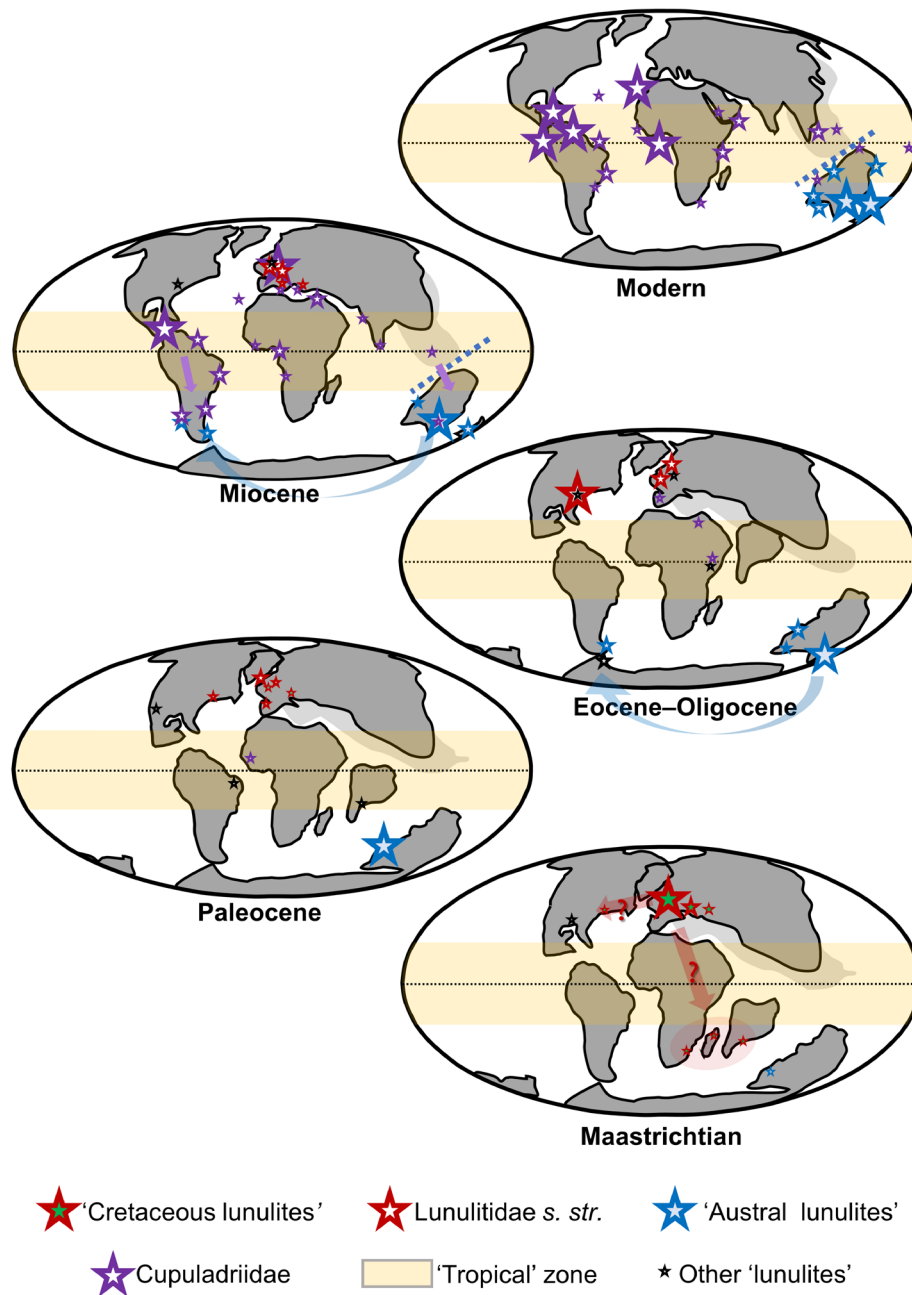
Three lunulite bryozoan species recently described from the mid-Ypresian of the Antarctic Peninsula (Hara *et al.* 2018) offer some support to the existence of an Austral connection across the West Antarctic Rift System, although just a single species—*Otionellina antarctica* Hara, Mörs, Hagström & Reguero 2018—potentially shows any relation to the core Austral province. Nevertheless, the mere presence of a free-living Antarctic bryozoan fauna clearly demonstrates that suitable habitats were present,

providing supporting evidence for a trans-Antarctic route of migration between the Austral Realm and South America along the West Antarctica archipelago (Fig. 13 B; Casadio *et al.* 2010). To further complicate comparisons, it is emphasised that the Antarctic fauna of Early Eocene age is older than both neighbouring faunas and that it shows even less resemblance to the new Late Paleocene – earliest Eocene faunas from northwestern Western Australia.

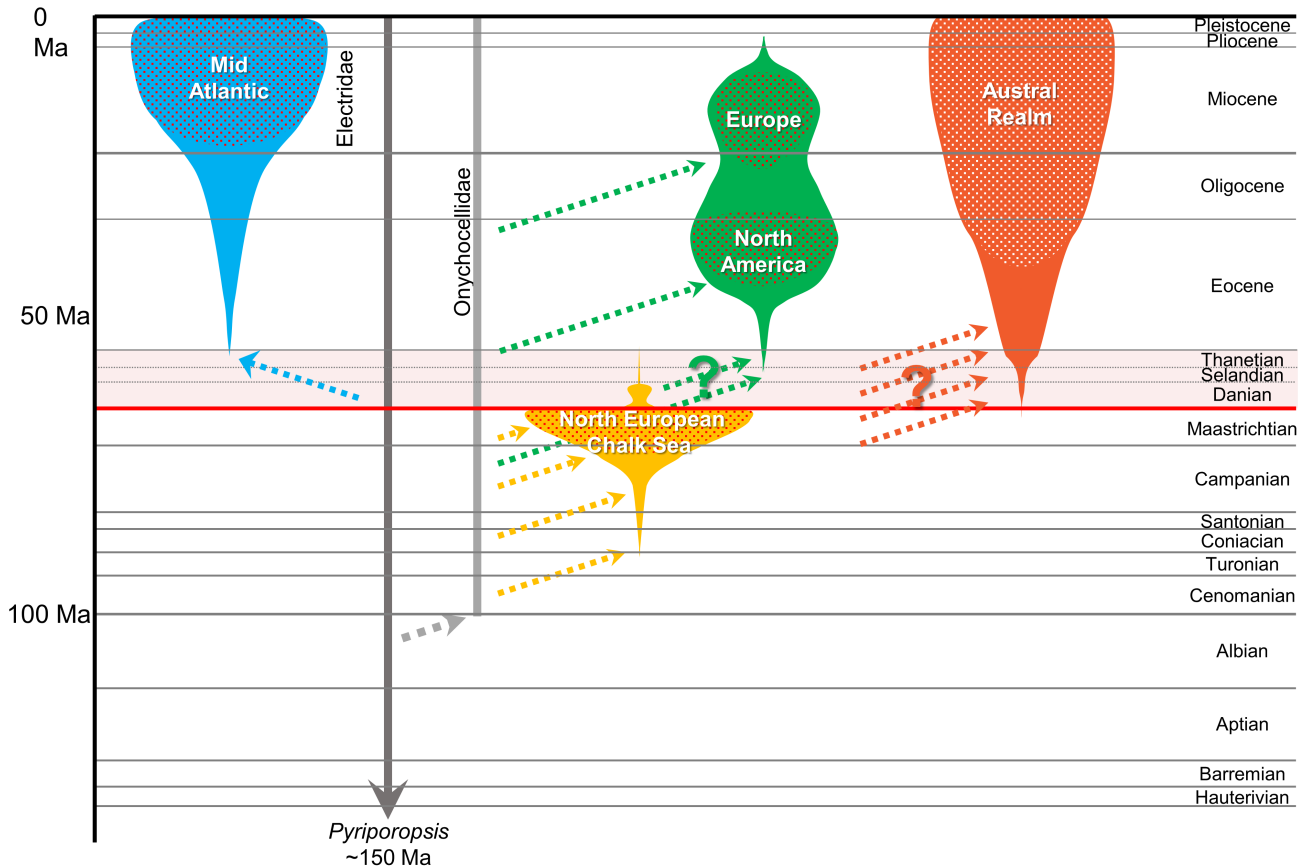
## AN OVERVIEW OF THE GLOBAL BIOGEOGRAPHY OF FREE-LIVING LUNULITE BRYOZOANS

The biogeography of the lunulite bryozoans has been a matter of interest over the years, with a series of distributional maps presented by Cook & Chimonides (1983, figs 3, 4) as the most comprehensive early attempt. Since then, information on the evolution and distribution of these bryozoans has increased considerably. The incorporation of the Austral cluster into the global biogeography of free-living bryozoans





**Figure 14.** The biogeography of the free-living bryozoans in five steps. Maastrichtian: Global dominance of the Chalk Sea fauna in northern Europe, thinning rapidly towards the Chalk Sea extension into Central Asia; questionable connections to taxa in three Gondwana fragments and North America. Note the possible first trace of the Austral free-living group. Paleocene: The Paleocene 'dead zone' marks an all-time low in both density and diversity in the history of the free-living bryozoans, with the Thanetian fauna from northwestern Western Australia as the exception. Note the possible first trace of the Cupuladriidae in western Africa. Eocene–Oligocene: Re-emergence of lunulites in North America and Europe, developing two Lunulitidae hotspot, separate in both time and space (Fig. 15). The Austral hotspot expands to include New Zealand, with early colonisers in southern South America, coexisting with a few cupuladriids, still only sparingly present in the tropics of Africa and the Mediterranean region. Miocene: The diversity patterns shift dramatically, with a hotspot peak in the Austral Realm (now including the southern part of South America), while the Cupuladriidae is rapidly replacing the lunulites in hot- to warm-water areas across most of the globe. Modern: The Austral free-living hotspot maintains its high diversity level, but the clade is no longer present in South America. The Cupuladriidae have completely replaced the lunulites across the globe, with only a single species in Australia. Continent positions from Scotese (2014, PALEOMAP Project).



**Figure 15.** Lunulite hotspots in time and space, main lunulite clusters colour coded, with hotspots dotted. The first, and prominent lunulite hotspot developed in the North European Chalk Sea (yellow): Highly concentrated, ‘within-basin’, high-frequency iterative evolution, mainly—but not exclusively—from onychocellid roots. Peaks in the Maastrichtian, and terminated in the Maastrichtian–Danian faunal revolution, possibly without descendants. The Lunulitidae s.str. (green) has a longer and more complex story, apparently developing two distinct hotspots. Firstly, with a North American Gulf & Coastal Plains emphasis, with high densities combined with moderate diversity; peaks in the Middle to Late Eocene and fade away in the Oligocene. Secondly, a less prominent hotspot develops in Europe in the Miocene, seemingly independent from the North American hotspot. The strictly monophyletic Cupuladriidae (blue) develop a high-diversity, still-thriving, hotspot centred around the Mid Atlantic early in the Miocene. The origin of the polyphyletic Austral Realm lunulites (red) remains enigmatic due to a long history in plate tectonic isolation (Fig. 6); a prominent, still thriving hotspot was established by the Late Eocene with only a single non-Austral lunulite species present from the Miocene. The earliest cheilostome family (dark grey) and the likely family root of many lunulites (light grey) are included. Arrows indicate origin; stipples indicate probable iterative evolution.

is briefly summarised here in five time slots (Fig. 14), highlighting the unique status of this intriguing group as presented briefly herein. The pattern of shifting hotspots for the free-living bryozoan clades outlined below may, of course, be subject to revision following further investigations. Notwithstanding, with prominent hotspots in comparatively high latitudes, it is clearly at odds with the Tethys-centered temporal global hotspot pattern presented by Yasuhara *et al.* (2022).

### Maastrichtian

On a global scale, the Chalk Sea fauna in northern Europe is unmatched in terms of the diversity of free-living bryozoans (Håkansson & Voigt 1995; & EH data). At least 100 free-living taxa may be recognised, including many specialised forms without setal support (Håkansson 1975). From its northern European hotspot (Fig. 15), this

faunal element gradually diminishes to the southeast, towards the Central Asian branch of the Chalk Sea, where only a few lunulite species are found (Voigt 1962, 1967; Favorskaya 1987; Kvachko 1995; Koromyslova & Pervushov 2022). More isolated occurrences of lunulite taxa are known from North America (Ulrich 1901; P. Taylor pers. comm.) and the three separate Gondwana fragments India (*Lunulites annulata* Stoliczka, 1872; Guha & Nathan 1996), Madagascar (*Lunulites pyripora* Canu, 1922; Buge 1951) and South Africa (*Lunulites* sp., Taylor 2019). All three entities had separated from Australia well before the first appearance of any lunulite, with Africa and Madagascar remaining fairly close (Fig. 6). Nevertheless, the three Gondwanan species are quite distinct, and none appears obviously related to taxa from the European Chalk Sea. Note also the possible first appearance of the Austral free-living bryozoans in northwestern Western Australia referred to briefly herein.

As the Chalk Sea clades with some probability suffered near total extinction as a result of the two-step collapse of the long-lived northern European carbonate province and its unique chalk environment (Fig. 4), further exacerbated by the global effects of the K–Pg extinction event (Surlyk 1997; Håkansson & Thomsen 1999; O’Dea *et al.* 2011), the founding role of the few non-European Cretaceous clades is far from obvious due to the Paleocene ‘dead zone’.

Why then was this fauna limited to the European Chalk Sea when there were many coeval flooded continents elsewhere? That most of these other regions received greater siliciclastic input than in the European seas obviously plays a role, but the long-lasting stability of the European Chalk Sea environment (30–35 Ma: Surlyk 1997) strongly suggests that the Chalk Sea fauna was uniquely adapted to this particular habitat (e.g., Surlyk 1972; Håkansson 1975; Håkansson & Thomsen 1999; Heinberg 2007). This is nevertheless surprising given subsequent radiations and dominations of similar siliciclastic shelf habitats by free-living bryozoans in subsequent epochs, and thus requires further exploration.

### Paleocene

The Paleocene ‘dead zone’ marks an overall global low in the history of the free-living bryozoans (cf. Fig. 4) mirroring well-established declines in diversity in all bryozoan groups (e.g., Håkansson & Thomsen 1979, 1999; McKinney & Taylor 2001; Stilwell & Håkansson 2012; Moharrek *et al.* 2022) and other marine groups. In Europe, the last Danian remnants of the Chalk Sea province were home to only a few, rare species (Berthelsen 1962; Kvachko 1995), whereas Selandian and Thanetian free-living bryozoans are even more scarce, with four Thanetian taxa reported from Deep Sea Drilling Project site 117 at Rockall Bank (Cheetham & Håkansson 1972) constituting a post-Danian, Paleocene ‘hotspot’. However, in marked contrast, the Thanetian fauna from northwestern Western Australia, briefly presented above, stands out as the single, remarkable exception in terms of both density and diversity.

Outside the Austral hotspot, there are therefore good reasons to explore the observation that no post-Paleocene free-living species seem to have pre-Paleocene ancestors and, further, to explore whether the groups ‘Chalk Sea lunulites’ and Lunulitidae *s. str.* might have coexisted during this comparatively brief interval of time. However, phylogenetic relationships between faunas have not been formally tested.

Somewhat later, in the late Paleocene–Eocene, the first rare representatives of the family Cupuladriidae appear in West Africa (Gorodiski & Balavoine 1961), heralding the global Neogene takeover by this group.

### Eocene–Oligocene

The Eocene to Oligocene marked the re-emergence of typical lunulite bryozoans in and around the central north Atlantic, which rapidly developed into a hotspot (Fig. 15), at this time mostly formed by the more advanced and more homogenous group Lunulitidae *s. str.* characterised by their porous, aragonitic basal wall. The hotspot was with a distinct North American Gulf & Coastal Plains emphasis, with high densities combined

with moderate diversity, possibly based on iterative evolution from onychocellid roots, peaking in the Middle to Late Eocene and fading away in the Oligocene.

The position of the coeval Austral hotspot changed to the southeastern part of the continent towards the end of the Eocene and expanded to include New Zealand; subsequently, in the latest Oligocene, the first, early Austral colonisers in southern South America appeared. Around Africa and in the Mediterranean, early members of the Cupuladriidae spread sporadically.

### Miocene

During the Miocene diversity and distribution patterns shifted dramatically, with the Cupuladriidae rapidly replacing Lunulitidae *s. str.* (Fig. 15) within shallow tropical and subtropical waters across most of the globe bar the Austral Realm. Notwithstanding, a less prominent, seemingly independent hotspot of Lunulitidae *s. str.* developed across Europe overlapping with the rise of the cupuladriids. Further afield, only a single cupuladriid species, *Cupuladria guineensis* (Busk, 1854; Fig. 1 E) appears to have successfully crossed the Wallace Line into Australia while, somewhat later in the Miocene, several unrelated cupuladriid species reached southern South America. In Australia the Austral free-living bryozoan hotspot peaked in diversity during the Miocene, with a limited number of taxa also reaching the southern part of South America. It should be stressed that the cupuladriid taxa reaching their farthest south in Australia and southern South America, respectively, are not closely related, thus allowing the inference that the temperature tolerance levels were different for the Cupuladriidae and the free-living Austral clades.

### Modern

The Lunulitidae *s. str.* went extinct in the Pliocene, thus terminating the minor Lunulitidae hotspot in Europe, while the two major Miocene hotspots persevered into the modern faunas. In southern South America, however, free-living bryozoans are no longer present. Rapid Late Neogene cooling may have caused their local extinction, but that does not explain why the Austral part of the fauna was not successful in progressing farther north in South America in accordance with their climatic preferences.

## CONCLUDING REMARKS

As we have attempted to illustrate, the free-living lunulite bryozoans had a complex history of rise and demise, with several unrelated groups dispersing and evolving across many continents since the Late Turonian. Their fossils are generally well preserved, their colonial and zooidal characters allow high-level taxonomic differentiation, they are diverse but not excessively so, have modern representatives and are frequently abundant in marine assemblages.

This paper presents new data and a comprehensive review of published information to elucidate the tempo–spatial patterns and morphological evolution of the major free-living groups of bryozoans. Our key findings can be summarised as follows:



1. The fossil record reveals the rise, demise and evolutionary success of several free-living groups over many continents, from the Late Cretaceous (Turonian) to the present, with many of these groups dominating epifaunal loose sediment shelf habitats.
2. The transition to a free-living mode of life in cheilostome bryozoans appears to require only minimal morphological modifications, suggesting a relatively easy shift from a sessile lifestyle to a mobile one.
3. Remarkable morphological convergence among unrelated groups indicates that strong adaptive pressures on habitat, mode of life and growth have shaped the distinctive free-living form.
4. Despite the progress made in understanding the evolutionary history of free-living bryozoans, the relationships between early and subsequent groups remain unclear. Further research using phylogenetic approaches is needed to unravel these evolutionary connections.
5. The absence of free-living groups in high latitudes raises the possibility that the free-living mode of life is metabolically demanding. This observation may provide insights into significant local extinctions within the otherwise highly successful free-living cupuladriid bryozoans during the Cenozoic.
6. The study of free-living bryozoans presents a unique opportunity to explore many evolutionary and ecological questions. However, significant temporal and geographic gaps exist in our knowledge, limiting our ability to confidently understand patterns and processes. We therefore emphasise the importance of focusing on new collections and taxonomic treatments of free-living bryozoans throughout their extensive and intriguing history.

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