# Comparative Shell Microstructure of Two Species of Tropical Laternulid Bivalves from Kungkrabaen Bay, Thailand with After-Thoughts on Laternulid Taxonomy

# Comparative shell microstructure of two species of tropical laternulid bivalves from Kungkrabaen Bay, Thailand with after-thoughts on laternulid taxonomy

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**Abstract:** The anomalodesmatan family Laternulidae represents a group of bivalves with a very few well-known taxa and many more poorly known taxa. *Laternula rostrata* (G. B. Sowerby, 1839) and *L. anatina* (Linnaeus, 1758) occur in close proximity to each other in and along the margins of mangroves of Kungkrabaen Bay, Thailand. *Laternula rostrata* resides in soft to sandy sediments often within the interstices of mangrove roots located in more open portions of the mangrove mud flat. *Laternula anatina* lives deeper in the mangrove in more protected environs. *Laternula anatina* is a smaller bivalve that has a variable shell outline, sometimes a wrinkled shell appearance, thicker periostracum, and frequently extensive umbonal erosion. Both species have high concentrations of external shell spinules anteriorly and closer to the umbos (*i.e.*, in juvenile shell) reflecting functionality in retaining an infaunal position. The larger *L. rostrata* is thinner shelled and more fragile; has more distinct and longer shell spinules composed of flattened lathes; a glossy external appearance; a longer umbonal slit; and a deeper pallial sinus. Additionally, *L. rostrata* has a saddle-shaped lithodesma; a lithodesma is absent in *L. anatina* as is typical of most laternulids. Shell microstructure of both is prismatonacreous, typical of the group, but the prismatic layer is thin and appears truncated into small blocky and/or granular columns in transitional zones. The bulk of the shell is tightly packed sheet nacre. The growth lines in *L. rostrata*, more pronounced but fewer in number than in *L. anatina*, appear as shallow rolling "hills" in both the shell and chondrophore. The differences in shell microstructure in these two species are specific to the taxa but based on different habitats and burrowing depths, albeit within the confines of a tropical mangal, could represent biomineralization events that reflect environmental adaptations. Variations in the thickness of the microstructural shell layers of four species of laternulids is compared and we speculate on possible functional and/or environmental relevance of these differences.

**Key words:** *Laternula*, spinule, biomineralization, lantern shell, Anomalodesmata

Perhaps because of its large size or the deep interest in adaptations to cold Southern Sea habitats and the looming issues of shrinking polar habitats, the anomalodesmatan bivalve *Laternula elliptica* (King and Broderip, 1832) has been examined in extensive detail with a focus on ecology, reproduction and development, physiology, and, to some extent, shell structure (Ralph and Maxwell 1977, Ahn 1994, Barrera *et al.* 1994, Urban and Silva 1995, Ansell and Harvey 1997, Brey and Mackensen 1997, Jonkers 1999, Brockington 2001, Peck *et al.* 2002, Sato-Okoshi and Okoshi 2002, 2008, Ahn *et al.* 2003, Peck *et al.* 2006, 2007, Morely *et al.* 2007, Kang *et al.* 2009, Kim *et al.* 2009, Clark *et al.* 2010, Guy *et al.* 2014). While studies on temperate and tropical laternulids are available (Morton 1973, 1976, Aller 1974, Sartori *et al.* 2006, Prezant *et al.* 2008) they are nowhere near as common as those on this single polar species and those that are available often focus on functional morphology, anatomy, and ecology. Interestingly and probably because of the work of Aller (1974) that suggested a "prefabrication" of laternulid external shell "spikes", others have taken up studies on laternulid shell formation and structure. While the concept of "prefabrication" has since been disproven with documentation by Checa and Harper (2010) who found that the "spikes" are formed within

the periostracum, there remains a deep level of interest in these shell ornaments. In fact, since Aller's 1974 publication there have been several studies on the "spikes" that dot the external surface of many bivalves beyond the laternulids (Checa and Harper 2010, Glover and Taylor 2010, Zieritz *et al.* 2011) that have posed new and interesting questions on shell and associated shell structures formation and functionality.

While genetics is considered the primary regulator in shell development (Dauphin *et al.* 2009, Cuif *et al.* 2011), several studies have offered enticing results that suggest phylogenetic and/or environmental flexibility in laternulid shells. Distinctions have been found between shell microstructures of the Antarctic *Laternula elliptica* (King, 1832), and the temperate *L. marilina* Reeve, 1860 (Sato-Okoshi and Okoshi 2008). In addition, Lai *et al.* (2011) found possible thermal niche separation for two species of tropical laternulids in a Singapore mangrove that could be correlated with burrowing depth (hence thermal variations associated with in-faunal burrowing). Thermal regime, in fact, has long been demonstrated to have at least some control in biomineralization and shell microstructure (for example, see Prezant *et al.* 1988 and more recently Nishida *et al.* 2012). There has also been discussion of the development of laternulid growth lines that

open questions on the rate and cause of their formation. Using isotopic markers, Brey and Makensen (1997) determined that shell growth bands in King George populations of *L. elliptica* are annual although Sato-Okoshi and Okoshi (2008) are less committal in correlating growth bands to a particular time period. With specific habitat in mind, questions might be asked regarding shell microstructure in species of laternulids that demonstrate close proximity but variations in burrowing depth and close but distinct habitats. Furthermore, because of the linkage of thermal changes with shell (growth) line deposition, there are possible correlations to be drawn with the growth demarcations clearly seen in shell valves, chondrophores and, where present, lithodesma of laternulids.

There is considerable confusion in the taxonomy of laternulids of Thailand but it is clear that there are two distinct species that live in very close proximity in the tropical mangrove sand flats of Kungkrabaen Bay. We now consider these as *Laternula rostrata* (G. B. Sowerby, 1839) and *L. anatina* (Linnaeus, 1758). *Laternula rostrata*, a deep but slow burrower, lives in more open areas of the sand flat although usually associated with mangrove tree hammocks. *Laternula anatina* lives close-by but typically deeper into the mangrove forest proper in more protected habitats although in shallower, near surface (and hence warmer) burrows. There are many distinctions between these taxa in both form and habit (Prezant *et al.* 2008) but there is also uncertainty whether the gross differences apparent in the shell forms are a reflection of genetics or environment and no study has previously examined the shells for differences at the microstructural level. The mangrove partitioning of the two species has been discussed in Prezant *et al.* (2008). Here, we examine the comparative shell microstructure and shell spinule differences of these sympatric congeners from Thailand in an effort to denote differentiation through shell structure and better understand shell growth line increments and shell form and function.

**Issues of Laternulid taxonomy**

The placement of species within the laternulid bivalves is well resolved at the level of genus with *Anatina* Lamarck, 1818 and *Exolaternula* T. Habe, 1977 now accepted as the genus *Laternula* Röding, 1798. While we now are suggesting some clarity in the two species of Kungkrabaen Bay as *L. rostrata* and *L. anatina* the resolution was slow and exposed a serious need for future efforts to clarify the taxonomy of the family. Some of the issues of laternulid taxonomy, as relevant to these two species in particular, are offered in Appendix I.

**METHODS**

Live specimens of both *Laternula rostrata* and *L. anatina* were collected in summer 2005 from Kungkrabaen Bay,

Chantaburi Province in southeastern Gulf of Thailand. Specimens of *L. rostrata* were found in large numbers in the expansive intertidal sand flats of the Bay buried to depths of at least 5.0 cm below the surface. Specimens of *L. anatina* were found in lower numbers a short distance off of the sand flat proper and adjacent to Klong Ta-Sook Canal. These smaller bivalves were shallowly burrowed near the sediment surface with siphons exposed. Specimens of both species have been deposited in the invertebrate collection at the Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A. (*L. rostrata* catalog numbers 413583 (dry valves, originally noted as *L. truncata* (Lamarck, 1818)) and A21000 preserved with soft tissues; *L. anatina* preserved with soft tissue catalog number A21001, originally noted as *L.* c.f. *corrugata* (Reeve, 1863) ). Details of other environmental parameters measured at collection sites can be found in Prezant *et al.* (2008).

Right valves from two specimens of *Laternula rostrata* (L = 60.9 mm and L = 62.4 mm) and one specimen of *L. anatina* (L = 16.3 mm) were fractured, sonicated and dehydrated with 100% ethanol for 48 hours and then dried in a 60 °C oven for 24 hours before mounting for scanning electron microscopy. All fragments were mounted on aluminum stubs using carbon adhesive tape and coated with gold in a Denton sputter coater. Samples were examined with a Hitachi S-3400N variable pressure scanning electron microscope at 15 kV. Spinule densities were visually counted using a dissecting microscope over a series of 2x2 mm square grids from several marginal and internal locations, including along the umbonal slit and posteriorly at the spinule onset line.

**RESULTS**

**Shell spinules**

Both *Laternula rostrata* and *L. anatina* have an external coat of short spinules (see "fibrous spike" of Aller, 1974). The spinules of *L. rostrata* average 156 μm in length. In *L. anatina* the spinules are smaller, averaging 67 μm in length (Fig. 1). Non-eroded spinules of *L. rostrata* (Fig. 1A) are acute in contour, abundant, densely distributed and aligned in relatively straight radial lines from umbo to shell margin. The relative distribution of spinules is not homogeneous and they can be distantly located from each other while at other times they abut each other (Fig. 1C). While most point directly away from the shell (*i.e.*, normal to the) surface there are spinules that also have some degree of curvature (Fig. 1D). The more distantly spaced spinules in *L. anatina* are squatter, less acute (1B; Table 1) and less angular in their rise from the shell platform. Periostracum covers spinules of both species (Fig. 2); excessive treatment with sodium hypochlorite erodes the spinules revealing incremental stages of growth (Fig. 2A) and the dissolution of what might be a thinner or already eroded
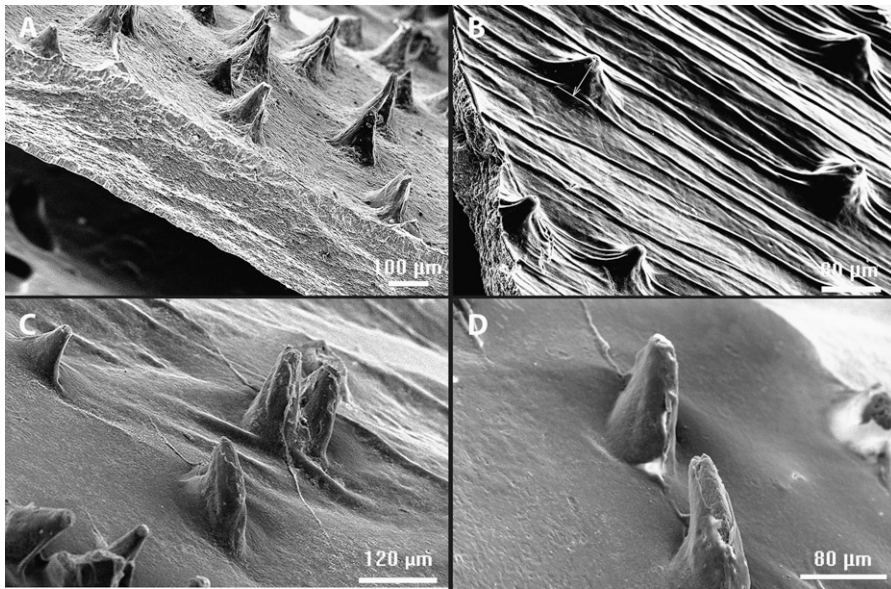
**Figure 1. A,** Spinules of *Laternula rostrata*; **B,** Spinules of *Laternula anatina*; **C, D,** *L. rostrata* spinules often show varying proximities to each other as well as variations in angularity or curvature.

organic cover leaves a base of periostracum surrounding the internal calcified construct (Fig. 2B). External pores seen in the spinules with external periostracum removed (Fig. 2C) reflect irregular spaces found within the substructure of the spinules (Fig. 2D). Spinules in *L. rostrata* are seen to, at least occasionally, have a hollow basal space (Fig. 2E). The internal microstructure of the spinules reflects the modified prismatic (granular/homogeneous) nature of the shell structure. Spinules

in lyonsiid bivalves are often aligned with arenophilic glands of the mantle edge that secrete mucus to secure external sand covers but the wide distribution of spinules in these laternulids and the faculty that these glands are usually only found closer to the siphons, discounts this alignment in these species (Prezant and Smith 1998, Sartori *et al.* 2006). There is a marked decrease in the relative density in number of spinules distant from the umbos in both taxa (Table 1). As many as four times the number of spinules per unit area can be found close to the umbo of a 14 mm long specimen of *L. anatina* when compared to the posterior region of the shell. There are also significantly more spinules in the mid to anterior portions of the shells in both species and the posterior-most portion of the shell is devoid of spinules. Overall, *L. rostrata* has fewer spinules per unit area than *L. anatina* (Table 2).

**Umbonal slit and pallial sinus**

The umbonal slit of *Laternula rostrata* transcends approximately 36% of the shell height while that of the smaller laternulid, *L. anatina*, transcends 30% of the shell height. Reflecting differences in burial depth, the pallial sinus of

**Table 1.** Morphometrical data, measured in microns, comparing shell units and layers in four species of laternulid bivalves. A recalculation of ratios for *Laternula elliptica* in Sato-Okoshi and Okoshi (2008)* is listed here along with their original listing. New data taken from two *L. rostrata* individuals and one *L. anatina*. Ranges shown where wide variation was seen in differing shell locations.

| | *L. rostrata* | *L. anatina* | *L. marilina* (Sato-Okoshi, Okoshi 2008) | *L. elliptica* (Sato-Okoshi, Okoshi 2008) |
|---|---|---|---|---|
| Individual nacre tablet thickness (μm) (posteriodorsal) | 0.50–0.61 | 0.36–0.50 | 0.4–1.0 | 0.295–0.447 |
| Nacreous layer thickness (μm) (posteriodorsal) | ~155 | ~200 | 60–66 | 18.5–26.0 |
| Prismatic or homogeneous layer thickness (μm) (posteriodorsal) | ~18–21 | 15–20 | 25–34 | 70–105 |
| Ratio of outer prismatic or homogenous layer to nacre | 0.12–0.14 | 0.075–0.10 | 0.42–0.52 | 3.78–4.04 (original authors list as 2.69–5.68) |
| Shell growth lines per mm (avg) | 8.53 | 12.5 | | |
| Spinule height (μm) | 156.13 | 67.07 | | |
| Periostracum thickness (μm) (posteriodorsal) | 4.32 | 4 | | |
| Chondrophore growth line thickness (μm) | 22.17 | 16.5 | | |
| Chondrophore growth line per mm | 45.11 | 60.61 | | |

*We believe Sato-Okoshi and Okoshi (2008) made an inversion error in their calculation for prismatic/homogeneous : nacre ratio. Their original range is listed in parenthesis in the table. Our recalculation for *Laternula elliptica* for this ratio is also listed.
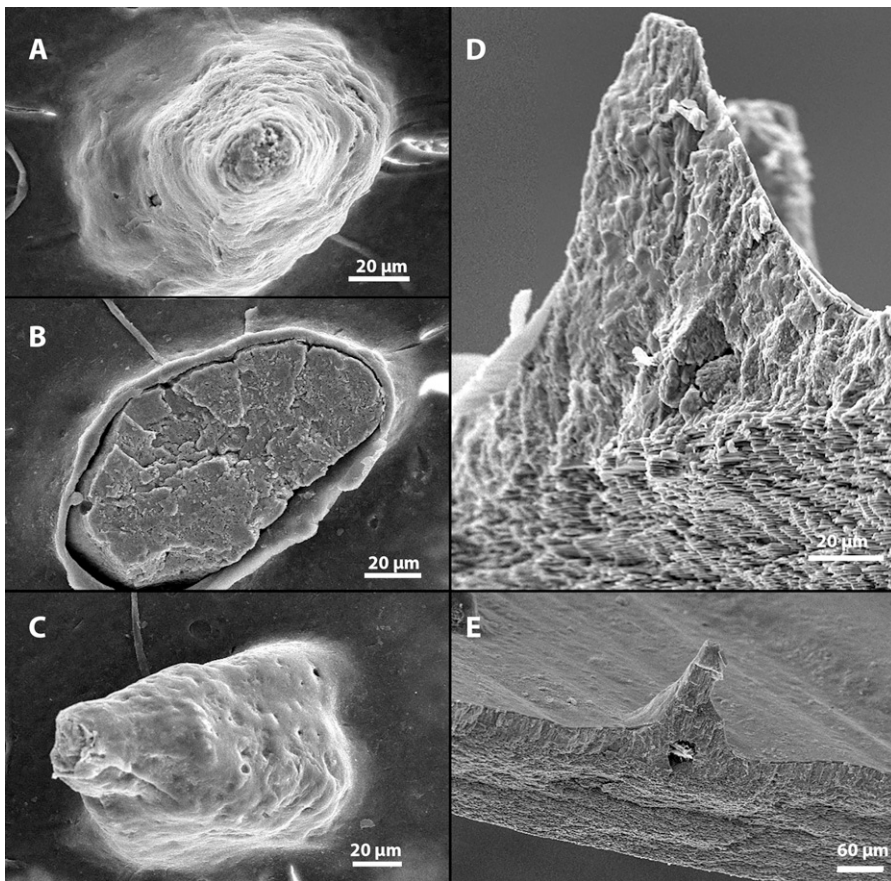
**Figure 2. A,** *Laternula rostrata* spinules after treatment with sodium hypochlorite. Note the basal periostracal gap eroded away from the spinule proper (**B**) and spinule pores (**C**) revealed by the removal of the periostracum. Hollow gaps reside in some spinules in *Laternula rostrata* of approximately 35 µm in diameter (debris trapped within the spinule during preparation) (**D, E**).

*L. rostrata*, a deeper burrower often found 5.0 cm below the mangrove flat surface, approximates at the deepest portion of the curve 38% of the shell length. *Laternula anatina* is usually found very close to the surface and has a pallial sinus that reaches only 29% of total shell length. There appears to be little differentiation of shell microstructure along the umbonal slit; the pallial line contains the usual myostracal band of prismatic shell.

### Shell cross-section

Shells of both taxa in cross section show a well-defined and thick layer of sheet nacre (Fig. 3) with individual tablets of *Laternula anatina* being half as thick as those in *L. rostrata* (Table 2). A blocky/granular prismatic layer appears in irregular patches mixed with a thicker granular homogeneous prismatic layer just beneath the thick periostracum and sometimes is represented by an almost nacre-like set of short, vertically arranged prisms (Fig. 4). The bulk of the shell is composed of sheet nacre that is intermittently infused with submerged pallial myostracum. Adductor myostracum is composed of thinner prisms in *L. rostrata*. In some regions of *L. anatina* a blocky or granular prismatic is evident (Fig. 5) while well-defined prismatic microstructures compose adductor and pallial myostraca in both taxa. There is, however, no well-defined outer prismatic layer. Instead a presumed homogeneous/granular prismatic layer composes the structure just beneath the periostracum (Fig. 4). Periostracum is of equal thickness in both taxa (Table 2). The ratio of outer prismatic/homogeneous layers to inner nacreous layers show *L. rostrata* with a ratio of 0.12–0.14 and *L. anatina* with a ratio of 0.075–0.10.

### Chondrophore and Growth Lines

The chondrophore of *Laternula rostrata* is, as is typical of laternulids, spoon-shaped and dominates the internal hinge region. Densely distributed growth increments line the interior and exterior of the chondrophore (Fig. 6) while the margin has a smooth surface. In a specimen that is 62.4 mm long, there are approximately 50–66 increments per linear millimeter of chondrophore (22.17 µm wide on average) that itself is approximately 3.6 mm long. This approximates about 180 lines along this entire chondrophore length. Growth increments are uniform in width with each between 15–20 µm and composed of prisms composed of spherical granules (Fig 6D). Polygonal prismatic units composed of smaller granules are demonstrated at higher magnifications (Fig. 6). In *Laternula anatina*, in a chondrophore that is 1.15 mm long, growth lines are 16.5 µm in width; this translates into about 60.6 lines/mm, in the same range as *L. rostrata*. The chondrophore microstructure in *L. anatina* approximates the same blocky prismatic units seen in *L. rostrata*.

Growth lines are evident in both the shell and chondrophore of both species of laternulids. In *Laternula rostrata* there is an average of 45.11 lines per millimeter in the chondrophore and 8.53 lines/mm in the shell (Table 1). These averages are 60.6/mm and 12.5/mm respectively in *L. anatina*. The ratio of lines per millimeter in chondrophore vs shell is

**Table 2.** Number of visible spinules in distinct 1 mm² in regions (A–G) shown on accompanying photograph of left valve. (R = right valve; L = left valve). Data averaged from two specimens for each species.
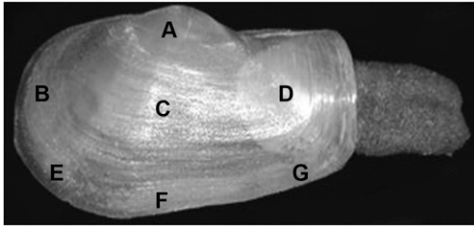


| | L. rostrata | | L. anatina | |
|---|---|---|---|---|
| | R | L | R | L |
| A | 297 | 367 | 436 | 326 |
| B | 176 | 202 | 228 | 215 |
| C | 202 | 237 | 272 | 266 |
| D | 94 | 96 | 97 | 112 |
| E | 125 | 167 | 208 | 204 |
| F | 143 | 182 | 220 | 223 |
| G | 80 | 89 | 97 | 77 |
| **Total** | 1117 | 1340 | 1558 | 1423 |
| $\overline{X}$/mm² | 159.6 | 191.4 | 222.6 | 203.3 |

0.74 in *L. rostrata* and 0.68 in *L. anatina* suggesting that shell and chondrophore grow proportionally at about the same rate and similarly deposit growth lines at comparable rates.

**Lithodesma**

A lithodesma is absent in *Laternula anatina*. In *Laternula rostrata* the lithodesma takes a bilobed form (Fig. 7) as viewed
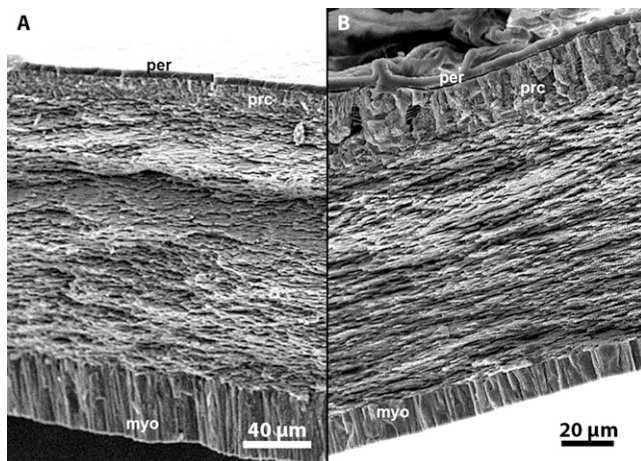


**Figure 3. A,** Cross-section of *Laternula rostrata* shell; **B,** Cross-section of *Laternula anatina* shell showing blocky prismatic layer. Abbreviations: **myo,** myostracum; **per,** periostracum; **prc,** blocky prismatic columns.

from above. Ligament/resilium fits firmly in concave regions of the wings. Growth lines are evident across the lithodesma (Fig. 7B) [not unlike *Mytilimeria nuttalli* Conrad, 1837 (Prezant and Carriker 1983)] of approximately 5.0 μm in width as they are across the chondrophore. Each increment is clearly composed of short granular prisms (Fig. 7C, D). The incremental lines run along the length of the chondrophore "wings" and are tightly packed. Each chrondrophore incremental line measures about 6.0 μm in width with approximately 160 per linear 1.0 mm lithodesma length or about 3.5 times the number seen in the chondrophore and 18.7 times that seen in the shell proper.

## DISCUSSION

The complexities (and questions) of what we know and don't know about molluscan shell formation can fill volumes. A review that seeks to consolidate our knowledge (to date) and contextualize that knowledge as it relates to shell evolution can be found in Furuhashi *et al.* (2009). Intricacies aside, it is clear that the complex biomineralization process in molluscs is ultimately genetically controlled with environmental overtones that can be reflected in both macroscopic and microscopic morphological changes. In addition to changes in microstructural form of crystals or calcified units induced by changes or variations in the environment, (Prezant *et al.* 1988, Tan Tiu and Prezant 1992) there can be changes in relative deposition of individual shell layers. The latter could be associated with induced changes in calcification rates, duration of deposition, or differences in organic matrices. Furuhashi *et al.* (2009) discuss the variations of these matrices even within the same shell. The past decade has also seen new questions that seek to explain some mineralized structures in molluscan shell through a process of "remote biomineralization" (Chinzei and Seilacher 1993). This process, a process that allows for the formation of calcified structures without the direct use of either mantle or organic matrix, has been used as a possible explanation for mostly small structures that occur on, in or inside shells of both bivalves and gastropods (see: Checa 2000, Hickman 2013). The premise of the current study was to seek differences in conspecific laternulid bivalves found in close proximity (thus, gross similarities of environment) but in different microhabitats. Because of previous work by other authors on several molluscan taxa, we specifically sought differences between *Laternula rostrata* and *L. anatina* that might be found in shell surface ornamentation and in relative proportional differences in shell microstructural layers.

Shell spinules and other external ornamentation of infaunal bivalves are considered an adaptation that increases frictional resistance and, thus, help increase stability within loose sediments (Aller 1974, Prezant 1979, Stanley 1981).
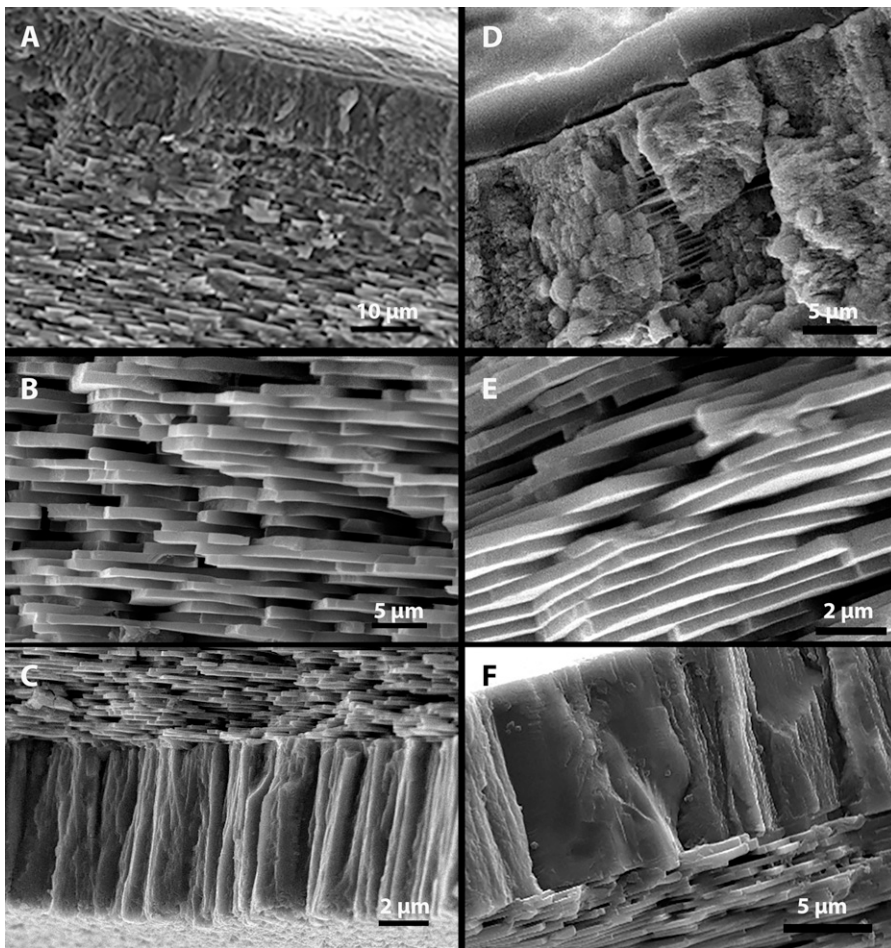
**Figure 4.** Paired scanning electron micrographs of *L. rostrata* (**A–C**) and *L. anatina* (**D–F**) comparing periostracum and associated prismatic layers (A,D), nacreous layers (B,E) and myostracum (C,F). Note changes in scale.

There has been a fair amount of conversation in the literature about the form and function of spinules, granules and spikes that reside on the exterior of various bivalve shells. In the case of species of *Laternula*, the earlier thought that the spinules were preformed has since been disproven (Aller, 1974, Checa and Harper 2010). Spinules in the shells examined here appear continuous with the underlying shell structure (see Fig. 2D) and instead of being formed within the periostracum, as discussed by Checa and Harper (2010) seem to have emerged directly from calcareous shell and are surrounded by periostracum (see Fig. 2B).

Spinules of *Laternula rostrata* are larger than those in *L. anatina* (approx. 156 µm vs 67 µm ) but proportionally they are equivalent (for an average sized *L. rostrata* of 60 mm length and an average adult *L. anatina* of 20 mm length the spinule length of both approximates 0.3% of shell length). The larger spinules in *L. rostrata* are most likely merely a reflection of average total organism size. In both species of laternulids examined here there are considerably more spinules in the portion of the shell that remains fully embedded in the sediments, plus more spinules in portions of the shell closer to the umbos (smallest concentration of spinules is found posteriorly towards the siphonal region of the shell). Both distribution patterns suggest adaptations for enhancing stability within a buried environment. Younger and, thus, typically smaller specimens, located closer to the substratum surface are more prone to dislodgment because of shifting surface sediments and overlying water movement. Thus, higher densities of shell spinules could help stabilize young clams within the substratum. The increased number of spinules from the mid to anterior portion of all valves similarly matches the possible role of using frictional resistance to better remain in place since these portions of the valves are the regions that remain consistently within the sediments. Similarly the expectation that a near surface adult of laternulid such as *L. anatina* would have more spinules is borne out in our samples. Valves of *L. anatina* had over 200 spinules per square millimeter while those of the deeper burrowing (and larger) *L. rostrata* had fewer (approximately 160 and 190 per square millimeter, right and left valve respectively). The difference in left and right valve counts in *L. rostrata* demands additional study. Zieritz *et al.* (2011), while finding variation in taxa, found in the 26 unionid species they examined that there were denser concentrations of small spikes near the umbos in several (reflecting more spikes in younger clams) and also suggest that "spikes" in living infaunal unionids could "increase friction of the shell within the sediment", thus, "stabilizing life position". Callil and Mansur (2005) suggest that external shell microfringes in young *Anodontites* (Etheroidea) could serve to help orient these bivalves in the substratum. We found large remnant populations of deceased but still articulated specimens (albeit without soft tissue) of *Laternula rostrata* in high tidal portions of the Kungkrabaen flat with the valves remaining vertically embedded within the sediment in life position.

Over 35 years ago Bandel (1979) detailed the compositional changes in crossed-lamellar microstructures in gastropods.
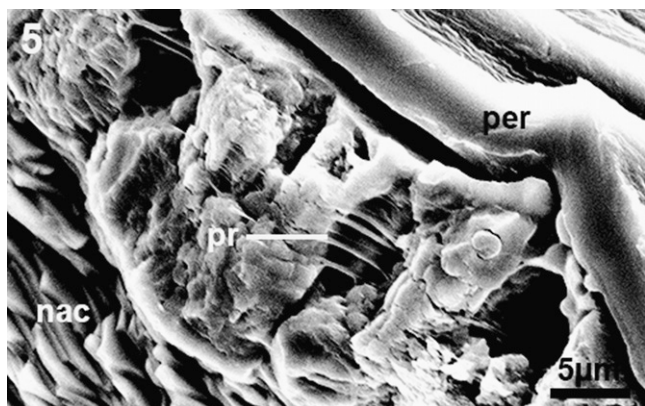
**Figure 5.** Cross-section of *L. anatina* shell near surface showing inconsistently blocky, granular prisms below periostracum. Abbreviations: **myo,** myostracum; **nac,** nacreous layer; **per,** periostracum; **pr,** blocky prismatic.

He suggested that the most complex form of these crossed-lamellar structures transitioned or descended through more simple precursors of spherulitic, spindle-shaped, elongated, small column or acicular crystals. With the growing use of atomic force microscopy and other recent imaging technique (see for example Cuif *et al.* 2012), it has been suggested that, regardless of shell microstructural type, all prisms, laths, tablets etc. are constructed from "small sub-spherical granules with a diameter typically of about 50 nm" (Dauphin *et al.* 2009). Liu *et al.* (2011) have confirmed the fluidity of crystal formation in a study on the "nacre-prism transition layer" in

*Pinctada fucata* (Gould, 1850) demonstrating a "sequential change" in pallial epithelium during production of these two shell microstructures. This complexity in shell microstructural development could account for the diverse and sometimes overlapping language seen in shell microstructure literature describing some shell layers. For laternulid shell we use terms that blend homogeneous – granular – prismatic but this language is a reflection of an instant in development seen in a particular sample. Bandel (1979) noted that at some stage the subunits fuse so deeply in the prism that they lose their distinctness. This may be the case in some individual taxa or shells, or it can also likely reflect the "transition layer" between shell microstructures described by Liu *et al.* (2011) and reviewed by Cuif *et al.* (2011). In particular the latter authors (p. 19) have determined that the "transition between prisms and nacre is not an instantaneous phenomenon" and instead begins as "small granular accumulations". Thus, as we examine shell microstructure in either species of Kungkrabaen Bay laternulid bivalve, we see blocky prisms and granular structures that merge or intermix with a more granular or homogeneous or prismatic layer or some hybrid. In *Laternula anatina* there is no distinct, well defined outer prismatic layer. The nacreous layers are distinct and well organized in both species as are myostracal layers. While the individual nacreous tablets are thinner in *L. anatina*, the total thickness of the nacreous layer is considerably thicker. In both species the external periostracal layers are of similar thicknesses.

The primary shells of most anomalodesmatan bivalves are composed of an aragonitic prismato-nacreous microstructure overlain by a variably thick periostracum and often ornamented with small radially aligned spinules (Morton 1973, Prezant and Smith 1998). Our findings and those of Sato-Okoshi and Okoshi (2008) contradict those of Morton (1976) who suggested that tropical laternulid bivalves have thinner shells but, importantly, ratios of distinct shell layers might reflect broad environmental regimes. Lai *et al.* (2011) found thermal extremes separated two taxa of laternulids living sympatrically in the tropical mangroves of Singapore. The shell microstructure of the tropical laternulids examined here offer sufficient data to distinguish taxa but could also reflect plasticity determined by microhabitat and niche partitions. We know that shell microstructures can show variation as a result of environmental differences, reflecting either seasonal changes or
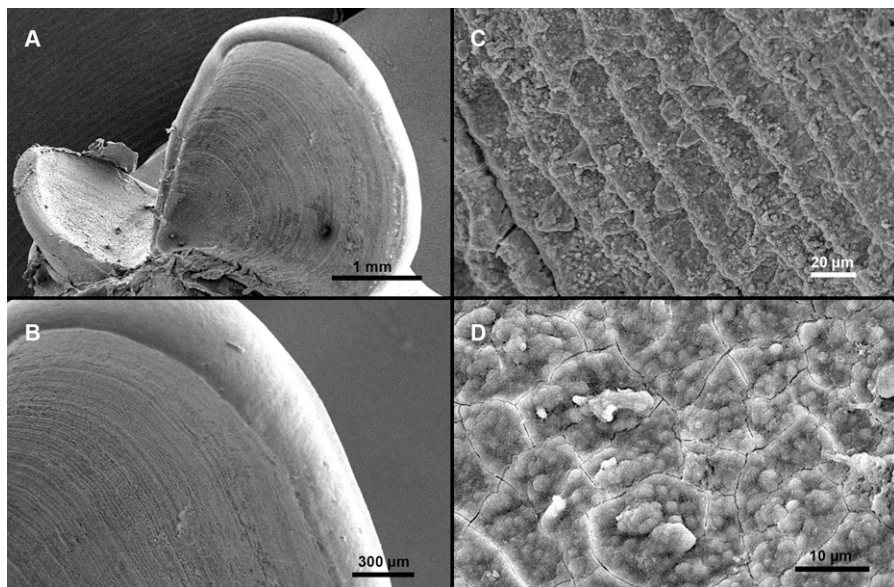


**Figure 6.** Chondrophore from *L. rostrata* shown in increasing magnification. Growth demarcations are particularly clear in the chondrophore and appear as parallel, step-like layers (**C**). Granular substructure emerges as polygonal units at higher magnification (**D**).
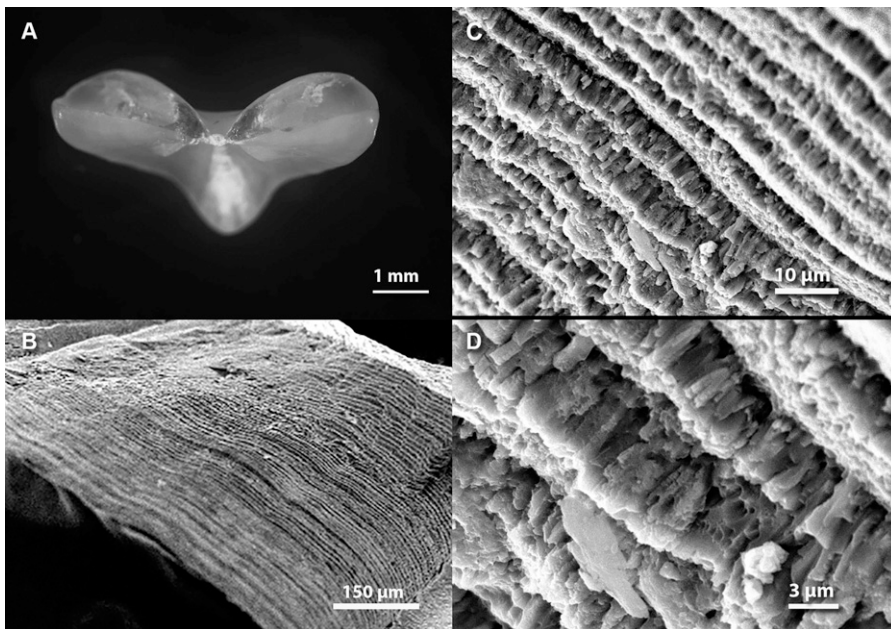
**Figure 7.** Lithodesma from *L. rostrata* shown in increasing magnification. Terraced prismatic growth evident with individual prism-like units densely packed and in strong and organized vertical alignment. The individual units composing these terraces appear pitted with irregular pores.

sudden changes in habitat (see: Prezant *et al.* 1988, Fritz *et al.* 1991, Tan Tiu and Prezant 1989, 1992, Nishida *et al.* 2012). Watson *et al.* (2012) documented mollusc shell thickness varying with latitudinal changes, including species of *Laternula*. In particular the Antarctic *L. elliptica* (from Rothera Point, Adelaide Island) was found to have a shell thickness that was double those species from non-polar habitats (these species included *L. truncata* (tropical) and *L. recta* (Reeve, 1863) (temperate). Here the authors speculate that the thicker shell of *L. elliptica* may be of adaptive value in protecting the animal during ice scour events that can expose the bivalves to serious physical damage. The variation in shell shape and ramification of ice scouring in *L. elliptica* is documented in Harper *et al.* (2012) who demonstrated a correlation between frequency of iceberg scouring and thicker shells.

Sato-Okoshi and Okoshi (2008) examined the shell of the Antarctic laternulid *Laternula elliptica* and the temperate laternulid *L. marilina*, and found distinct differences in microstructure (Table 2). *L. marilina* has a typical prismato-nacreous shell while in *L. elliptica* the prismatic layer is replaced by a homogeneous or granular layer. In addition the overall thickness of the two layers in each species is reversed, with the nacreous layer in *L. marilina* being significantly thicker than the prismatic layer while the nacreous layer in *L. elliptica* is thinner than the homogeneous (Table 2). *Laternula rostrata* and *L. anatina* show similar nacreous tablet thickness to these two former species but have a much deeper

overall nacreous layer thickness. Similarly the prismatic/homogeneous layers in both Thailand species are thinner. The tropical laternulids, however, compared to the temperate *L. marilina* and the polar *L. elliptica,* have a much lower ratio of outer prismatic/homogeneous layer to nacreous layer. It is uncertain if these differences in shell layers are a reflection of environment and associated growth rates or shell creation energetics and genetics. We speculate here that the decrease in ratio of outer to inner shell thickness as we move into warmer waters could reflect an adaptation towards a thicker external shell layer in cooler waters where calcium carbonate is more soluble.

Growth increments are evident across the shells and chondrophores of both laternulids examined here. In polar habitats shell growth lines of *Laternula elliptica* have been shown to form annually (Brey and Mackensen 1997). Sato-Okoshi and Okoshi (2002) used tetracycline to determine growth rate based on lines in the chondrophore of the cold water *L. elliptica*. They determined that the latter bivalve produced growth lines at a rate of 0.71μm/day. In the Kungkrabaen laternulids, growth line increments in the chondrophore are much greater (22.17 and 16.5 μm respectively in *Laternula rostrata* and *L. anatina*) and are clearly not diurnal. While, on average, these increments are shorter in the smaller *L. anatina*, they do fall within the range of those in *L. rostrata*. This close equivalency in growth lines within the chondrophores of these two species presents questions on growth rate and maximum ages. The microstructure of these increments is granular but the grains in turn are arranged in polygonal "packets". Growth lines are spaced more widely in the larger *L. rostrata,* but both are composed of irregular prisms and a granular structure. The very large number of growth lines suggests that these anaerobically induced delineations are deposited more frequently than annually. It is possible that the greater number of lines in *L. anatina* is associated with their shallower habitat that is subject to longer periods of dewatering during low tides, warmer temperatures, and more frequent interactions with predators. In fact, in their ecological study of laternulids on this mangrove mudflat, Prezant *et al.* (2008) found bore holes of the drilling muricid snail *Chicoreus capucinus* (Lamarck, 1822) only in *L. anatina*, never in *L. rostrata*. With increased interactions with surface or near surface infaunal predators, it is likely that the small and more active *L. anatina* also is prone to more

frequent valve closures, possibly inducing a greater number of shell delineations.

The complex nature of the chondrophore has recently been documented by Nehrke *et al.* (2012) who demonstrated that in *Laternula elliptica*, though the shell proper is apparently fully aragonitic, the chondrophore is composed of calcite, aragonite, and vaterite with contiguous growth rings through the latter two calcium carbonate morphs. There is still much to be learned about the chronology, timing and causes of linear increments in the chondrophore. The step-wise progression along the lithodesma of growth lines is similar to that of the chondrophore but the reason for a three-fold increase in these delineations in the lithodesma of *Laternula rostrata* when compared to the number in the chondrophore remains to be discovered.

## ACKNOWLEDGMENTS

## LITERATURE CITED

Ahn, I.-Y. 1994. Ecology of the Antarctic bivalve *Laternula elliptica* (King and Broderip) in Collins Harbour, King George Island: Benthic environment and adaptive strategy. *Memoirs of National Institute of Polar Research* Special Issue **50**: 1–10.

Ahn, I.-Y., J. Surh, Y.-G. Park, H. Dwon, I.-S. Choi, S.-H. Kang, H. J. Choi, K.-W. Kim, and H. Chung. 2003. Growth and seasonal energetics of the Antarctic bivalve *Laternula elliptica* from King George Island, Antarctica. *Marine Ecology Progress Series* **257**: 99–110.

Aller, R. C. 1974. Prefabrication of shell ornamentation in the bivalve *Laternula*. *Lethaia* **7**: 43–56.

Ansell, A. D. and R. Harvey. 1997. Protected larval development in the Antarctic bivalve *Laternula elliptica* (King and Broderip) (Anomalodesmata: Laternulidae). *Journal of Molluscan Studies* **63**: 285–286.

Bandel, K. 1979. Übergänge von einfacheren Strukturtypen zur Kreuzlamellensruktur bei Gastropoden schalen. *Biomineralisation* **10**: 9–37. [In German].

Barrera, E., M. J. S. Tevesz, J. C. Carter, and P. L. McCall. 1994. Oxygen and carbon isotopic composition and shell microstructure of the bivalve *Laternula elliptica* from Antarctica. *Palaios* **9**: 275–287.

bioSearch Biodiversity Database of India. 2009. Bioinformatics Centre, National Institute of Oceanography, Goa, India. Available at: http://biosearch.in/publicOrganismPage.php?id=120568267 27 May 2014.

Brey, T. and A. Mackensen. 1997. Stable isotopes prove shell growth bands in the Antarctic bivalve *Laternula elliptica* to be formed annually. *Polar Biology* **17**: 465–468.

Brockington, S. 2001. The seasonal energetics of the Antarctic bivalve *Laternula elliptica* (King and Broderip) at Rothera Point, Adelaide Island. *Polar Biology* **24**: 523–530.

Callil, C. T. and M. C. D. Mansur. 2005. Ultrastructural analysis of the shells of *Anodontites trapesialis* (Lamarck) and *Anodontites elongatus* (Swaison) (Mollusca, Bivalvia, Etheroidea) from the Mato Gross Pantanal Region, Brazil. *Revista Brasileira de Zoologia* **22**: 724–234.

Checa, A. G. 2000. Remote biomineralization in divaricate ribs of *Strigilla* and *Solecurtus* (Tellinoidea: Bivalvia). *Journal of Molluscan Studies* **66**: 457–466.

Checa, A. G. and E. M. Harper. 2010. Spikey bivalves: Intraperiostracal crystal growth in Anomalodesmatans. *Biological Bulletin* **219**: 231–248.

Chinzei, K. and A. Seilacher. 1993. Remote biomineralization. I: Fill skeletons in vesicular oyster shells. *Neues Jahnbuch für Geologie und Paläontologie Abhandlungen* **190**: 349–361.

Chuang, S. H. 1973. Sea shells. *In*: S. H. Chuang, ed., *Animal Life and Nature in Singapore*. Singapore University Press, Singapore. Pp. 175–201.

Clark, M. S., M. A. S. Thorne, F. A. Viera, J. C. R. Cardoso, D. M. Power, and L. S. Peck. 2010. Insights into shell deposition in the Antarctic bivalve *Laternula elliptica*: Gene discovery in the mantle transcriptome using 454 pyrosequencing. *BMC Genomics* **11**: 362–376.

Cuif, J.-.P., Y. Dauphin, G. Nehrke, J. Nouet, and A. Perez Huerta. 2012. Layered growth and crystallization in calcareous biominerals: Impact of structural and chemical evidence on two major concepts in invertebrate biomineralization studies. *Minerals* **2**: 11–39.

Cuif, J.-.P., Y. Dauphin, and J.E. Sorauf. 2011. *Biominerals and Fossils Through Time*. Cambridge University Press, Cambridge, United Kingdom.

Dauphin, Y., J.-P. Cuif, M. Salomé, and Williams. 2009. Biomineralisation in mollusc shells. *Geophysical Research Abstracts* **11**: 6834.

Feulner, J. R. and R. J. Hornby. 2006. Intertidal molluscs of UAE lagoons. *Tribulus* **16**: 17–23.

Fritz, L. W., L. M. Ragone, and R. A. Lutz. 1991. Seasonal changes in outer shell layer microstructure of *Mytilus edulis* in New Jersey, U.S.A. *The Veliger* **34**: 222–228.

Furuhashi, T., C. Schwarzinger, I. Miksik, M. Smrz, and A. Beran. 2009. Molluscan shell evolution with review of shell calcification hypothesis. *Comparative Biochemistry and Physiology*, Part b **154**: 351–371.

Glover, E. A. and J. D. Taylor. 2010. Needles and pins: Acicular crystalline periostracal calcification in venerid bivalves (Bivalvia: Veneridae). *Journal of Molluscan Studies* **76**: 157–179.

Guy, C. I., V. J. Cummings, A. M. Lohrer, S. Gamito, and S. F. Thrush. 2014. Population trajectories for the Antarctic bivalve *Laternula elliptica*: Identifying demographic bottlenecks in differing environmental futures. *Polar Biology* **37**: 541–553.

Harper, E. M., M. S. Clark, J. I. Hoffman, E. E. R. Philipp, L. S. Peck, and S. A. Morley. 2012. Iceberg scour and shell damage in the Antarctic bivalve *Laternula elliptica*. *PLOS One* **7**(9): e46341. Doi: 10.1371/journal.pone.0046341.

Hickman, C. S. 2013. Interacting constraints and the problem of similarity in gastropod structure and function. *American Malacological Bulletin* **31**: 155–168.

Huber M. 2010. *Compendium of Bivalves. A Full-color Guide to 3,300 of the World's Marine Bivalves: A Status on Bivalvia After 250 Years of Research.* ConchBooks, Hackenheim, Germany. Book + 1 CD-ROM.

Jonkers, H. A. 1999. Aligned growth positions in Pliocene *Laternula elliptica* (King and Broderip) (Bivalvia: Anomalodesmata: Laternulidae). *Antarctic Science* **11**: 463–464.

Kang, D. H., I.-Y. Ahn, and K. S. Choi. 2009. The annual reproductive pattern of the Antarctic clam, *Laternula elliptica* from Marian Cove, King George Island. *Polar Biology* **32**: 517–528.

Kim, M., I.-Y. Ahn, H. Kim, J. Cheon, and H. Park. 2009. Molecular characterization and induction of heat shock protein 90 in the Antarctic bivalve *Laternula elliptica*. *Cell Stress Chaperones* **14**: 363–370.

Lai, C. H., S. A. Morley, K. S. Tan, and L. S. Peck. 2011. Thermal niche separation in two sympatric tropical intertidal *Laternula* (Bivalvia: Anomalodesmata). *Journal of Experimental Marine Biology and Ecology* **405**: 68–72.

Lamprell, K. and J. Healy. 1998. *Bivalves of Australia*: *Volume 2.* Backhuys Publishers, Leiden, Netherlands.

Lamy, É. 1934. Révision des *Anatina* vivants du Muséum National d'Histoire Naturelle de Paris. *Journal de Conchyliologie* **78**: 145-168. [In French].

Liggia, B. 2013. WMSD-Worldwide Mollusc Species Database. Genova, Italy. Available at: http://www.bagniliggia.it/WMSD/HtmSpecies/6270000000.htm 27 May 2014.

Liu, X., C. Liu, J. Sun, Y. Zhou, G. Zheng, G. Zhang, H. Wang, L. Xie, and R. Zhang. 2011 Erosion of the prismatic layer by the organic matrix during the formation of the nacre-prism transition layer in the shell of *Pinctada fucata* (Bivalvia, Mollusca). *Chinese Science Bulletin* **56**: 869–876.

Morley, S. A., L. S. Peck, A. J. Miller, and H. O. Pörtner. 2007. Hypoxia tolerance associated with activity reduction is a key adaptation for *Laternula elliptica* seasonal energetics. *Oecologia* **153**: 29–36.

Morris, S. and N. Morris. 1993. New shells from the UAE's east coast. *Tribulus* **3**: 5–8, 18–19.

Morton, B. 1973. The biology and functional morphology of *Laternula rostrata* (Lamarck, 1818) (Bivalvia: Anomalodesmata: Pandoracea). *Biological Bulletin* **145**: 509–531.

Morton, B. 1976. The structure, mode of operation and variation in form of the shell of the Laternulidae (Bivalvia: Anomalodesmata: Pandoracea). *Journal of Molluscan Studies* **42**: 261–278.

Nehrke, G., H. Poigner, D. Wilhelms-Dick, T. Brey, and D. Abele. 2012. Coexistence of three calcium carbonate polymorphs in the shell of the Antarctic clam *Laternula elliptica*. *Geochemistry Geophysics Geosystems* **13**(5)**.** doi:10.1029/2011GC003996.

Ng, P. K. L., L. K. Wang, and K. K. P. Lim (eds.). 2008. *Private Lives: An Exposé of Singapore's Mangroves.* The Raffles Museum of Biodiversity Research, Singapore. 249 pp.

Nishida, K., T. Ishimura, A. Suzuki, and T. Sasaki. 2012. Seasonal changes in the shell microstructure of the bloody clam, *Scapharca broughtonii* (Mollusca: Bivalvia: Arcidae). *Palaeogeography, Palaeoclimatology, Palaeoecology* **363–364**: 99–108.

Nishijima, W., Y. Nakano, S. Nakai, T. Okuda, and T. Imai. 2014. Macrobenthic succession and characteristics of a man-made intertidal sandflat constructed in the diversion channel of the Ohta River Estuary. *Marine Pollution Bulletin* **82**: 101–108.

Paphavasit, N., C. Sudtongkong, and D. J. Macintosh. 1997. Mangrove macrofauna in different mangrove plantations at Klong Ngao mangrove forests, Ranong Province, Southern Thailand. *Proceedings of the FORTROP'96 Conference:* Tropical Forestry in the 21st Century, 1996. Bangkok, Thailand **2**: 104–117.

Peck, L. S., S. A. Morley, H. O. Pörtner, and M. S. Clark. 2007. Thermal limits of burrowing capacity are linked to oxygen availability and size in the Antarctic clam *Laternula elliptica*. *Oecologia* **154**: 479–484.

Peck, L. S., H. O. Pörtner, and L. Hardewig. 2002. Metabolic demand, oxygen supply and critical temperatures in the Antarctic bivalve *Laternula elliptica*. *Physiological and Biochemical Zoology* **75**: 123–133.

Peck, L. S., D. K. Powell, and R. A. Tyler. 2006. Very slow development in two Antarctic bivalve molluscs, the infaunal clam *Laternula elliptica* and the scallop *Admussium colbecki*. *Marine Biology* **150**: 1191–1197.

Prezant, R. S. 1979. Shell spinules of the bivalve *Lyonsia hyalina* (Bivalvia: Anomalodesmata). *Nautilus* **93**: 93–95.

Prezant, R. S. and M. R. Carriker. 1983. Functional microstructure of the lithodesma of *Mytilimeria nuttalli* (Bivalvia: Anomalodesmata). *The Veliger* **25**: 326–328.

Prezant, R. S. and B. J. Smith. 1998. *Subclass Anomalodesmata. In*: P. L. Beesley, G. J. B. Ross and A. Wells, eds., *Mollusca: The Southern Synthesis. Fauna of Australia,* Vol. **5.** Part A xvi. CSIRO Publishing, Melbourne, Australia. Pp. 397–429.

Prezant, R. S., C. Sutcharit, K. Chalermwat, N. Kakhai, T. Duangdee, and P. Dumrongrojwattana. 2008. Population study of *Laternula rostrata* (Bivalvia: Anomalodesmata: Laternulidae) in the mangrove sand flat of Kunkrabaen Bay, Thailand, with notes

on *Laternula anatina*. *Raffles Bulletin of Zoology* Supplement **18**: 57–73.

Prezant, R. S., A. Tan Tiu, and K. Chalermwat. 1988. Shell microstructure and color changes in stressed *Corbicula fluminea* (Bivalvia: Corbiculidae). *The Veliger* **31**: 236–243.

Ralph, R. and J. G. H. Maxwell. 1977. Growth of two Antarctic lamellibranchs: *Adamussium colbeck* and *Laternula elliptica*. *Marine Biology* **42**: 171–175.

Reeve, L. A. (and G.B. Sowerby II) 1860–63 (in and as cited by Huber, 2010). Monograph of the genus *Anatina*. *Conchological Iconica; or Illustrations of the Shells of Molluscous Animals* **14**: 26 pls.

Sanpanich, K. 1998. An annotated check list of marine bivalves from Chonburi and Rayon provinces, the East coast of Thailand. *Phuket Marine Biological Center Special Publication* **18**: 297–306.

Sartori, A. F., F. D. Passos, and O. Domaneschi. 2006. Arenophilic mantle glands in the Laternulidae (Bivalvia: Anomalodesmata) and their evolutionary significance. *Acta Zoologica* **87**: 265–272.

Sato-Okoshi, W. and K. Okoshi. 2002. Application of fluorescent substance to the analysis of growth performance in Antarctic bivalve, *Laternula elliptica*. *Polar Bioscience* **15**: 66–74.

Sato-Okoshi, W. and K. Okoshi. 2008. Characteristics of shell microstructure and growth analysis of the Antarctic bivalve *Laternula elliptica* from Lutzow-Holm Bay, Antarctica. *Polar Biology* **31**: 131–138.

Satumanatpan, S., S. Thummikkapong, and K. Kanongdate. 2011. Biodiversity of benthic fauna in the seagrass ecosystem of Kung Krabaen Bay, Chantaburi Province, Thailand. *Songklankarin Journal of Science and Technology* **33**: 341–348.

Satyamurti, S. T. 1956. The Mollusca of Krusadai Island in the Gulf of Mannar II. Scaphopoda, Pelecypoda and Cephalopoda. *Bulletin of the Madras Government* **1**(2): 1–202.

Savazzi, E. 1990. Shell biomechanics in the bivalve *Laternula*. *Lethaia* **23**: 93–101.

Stanley, S. M. 1981. Infaunal survival: Alternative functions of shell ornamentation in the Bivalvia (Mollusca). *Paleobiology* **7**: 384–393.

Swennen, C., R. G. Moolenbeck, N. Ruttanadakul, H. Hobbelink, H. Dekker, and S. Hajisamae. 2001. The Molluscs of the Southern Gulf of Thailand. *Thai Studies in Biodiversity* **4**: 1–210.

Tan, K. S. 2008. Mudflat predation on bivalves and gastropods by *Chicoreus capucinus* (Neograstropoda: Muricidae) at Kungkrabaen Bay, Gulf of Thailand. *Raffles Bulletin of Zoology* Supplement No. **18**: 235–245.

Tan, S. K and H. P. M. Woo. 2010. *A Preliminary Checklist of the Molluscs of Singapore*. Raffles Museum of Biodiversity Research, Singapore.

Tan Tiu, A. and R. S. Prezant. 1989. Seasonal variation of microstructure of inner structure of shell in *Corbicula fluminea* (Bivalvia: Heterodonta). *American Malacological Bulletin* **7**: 65–71.

Tan Tiu, A. and R. S. Prezant. 1992. The role of environment in shell growth dynamics of the Asian clam *Corbicula fluminea* (Mollusca: Bivalvia). *Malacological Review* **25**: 109–117.

Urban, H.-J. and P. Silva. 1995. Tolerancia a temperatura maxima de dos molusco antárticos (*Laternula elliptica* y *Nacella concinna*) en Caleta Potter Isla, 25 Mayo (King George). *Antártica VI Congreso Latinoamericano de Mar*, Mar del Plata, Argentina, Libro de Resumenes. Pp. 112. [In Spanish].

Watson, S.-A., L. S. Peck, P. A. Tyler, P. C. Southgate, K. S. Tan, R. W. Day, and S. A. Morley. 2012. Marine invertebrate skeleton size varies with latitude, temperature and carbonate saturation: Implications for global change and ocean acidification. *Global Change Biology* **18**: 3026–3038.

Zieritz, A., A. G. Checa, D. C. Aldridge, and E. M. Harper. 2011. Variability, function and phylogenetic significance of periostracal microprojections in unionid bivalves (Mollusca). *Journal of Zoology and Systematic Evolution Research* **49**: 6–15.

## Appendix 1 - Issues of Laternulid Taxonomy

In their 2008 paper Prezant *et al.*, based on available literature for laternulid bivalves of coastal Thailand, input from other professional malacologists, and yet with hesitation, considered the smaller laternulid found on the outskirts of the mangrove flat at Kungkraeben Bay to be *Laternula* cf. *corrugata*. *Laternula* (*Anatina*) *corrugata* Reeve, 1863 is a synonym of *Laternula liautaudi* (Mittre, 1844) (see Liggia 2013) but the image of valves of this species in various other references (see for example, Huber 2010) bears superficial resemblance to our specimens from the southern Thailand mangrove flat. Instead it is now suggested that the species, with a highly variable shell form, is *Laternula anatina* (Linnaeus, 1758). Our earlier designation of *L.* cf. *corrugata* emerges from Swennen *et al.* (2001) who list only two species of laternulids from the Southern Gulf of Thailand: *L. anatina* and *L.* cf. *corrugata*. Here the authors note that while abundant and burrowing into soft mud sediments, there is some issue with a similar bivalve referred to by "Japanese authors...as *L. navicula*" (Reeve, 1863) and they suggest that "whether they are conspecific needs more study". The Worldwide Mollusc Species Database (Liggia, 2013) also lists *L. anatina* and *L. truncata* (Lamarck, 1818) from Kungkrabaen Bay.

The presence/absence of a lithodesma (ossiculum) is of taxonomic value within the family. Savazzi (1990) inaccurately stated that "...an ossiculum (is) always present in the Laternulidae". *Laternula navicula* (Linnaeus, 1758), among others, lacks a lithodesma and, thus, according to Huber (2010) is within *Laternula* s.s. Species that have been considered within *Exolaternula* possess a lithodesma and this is absent in our smaller specimens. `The shells identified and labeled *L. corrugata* by Satyamurti (1956) from the Gulf of Mannar, India, have descriptions (as repeated in bioSearch Biodiversity Database of India (2009) that better align with our specimens: "shell thick...anterior margin is broad and bluntly rounded; width of the shell gets narrowed down towards the hind margin which is narrow and obliquely truncated; surface of the shell is faintly concentrically striated; anterior part of the shell is inflated...". Nevertheless, the variation of shells as shown by Huber (2010) and confirmed by Huber (2014 personal communication) strongly suggests the species in the 2008 Prezant *et al.* paper and the smaller specimens in the current work are *L. anatina*.

The confusion over laternulid taxonomy is also documented in non-taxonomic works. For example, Tan (2008) in a study on predation by the muricid gastropod *Chicoreus capucinus* (Lamarck, 1822) of molluscs of Kungkrabaen Bay listed *Laternula* cf. *boschasina* (Reeve, 1860) as a potential prey item (with only one specimen seen drilled). Satumanatpan *et al.* (2011) in a study on biodiversity of the seagrass ecosystem of Kungkrabaen Bay listed *Laternula* sp. Paphavasit *et al.* (1997) examined mangrove macrofauna in Southern Thailand and lists *Laternula navicula* as the only laternulid recovered. In a checklist of marine bivalves from Chonburi and Rayong Provinces, Sanpanich (1998) listed 76 species but no members of the Laternulidae. Feulner and Hornby (2006) in a review of molluscs in lagoons of the United Arab Emirates list *L. navicula* and *L. erythraensis* Morris and Morris, 1993 but also note *Laternula* spp. (from Morris and Morris 1993) in mangrove channels of Khor Kalba. In a study of macrobenthic succession in the Ohta River Estuary in Japan, where populations of a laternulid bivalve can reach as high as 12% of the total community, the taxon is listed as *Laternula* sp. (Nishijima *et al.* 2014). Similar taxonomic gaps and confusion has been seen in Singapore. In 2010 Tan and Woo noted *Laternula anatina* in this checklist. This bivalve was previously listed as *Laternula subrostrata* (Lamarck, 1818) by Chuang (1973) and following several others, Ng *et al.* (2008) listed it as *Laternula truncata*. All of these were later "corrected" by Tan and Woo (2010) to *Laternula spengleri* (Gmelin, 1791). According to Huber (2010), *L. spengleri* Gmelin, 1791 is "For the time being...considered a rare, valid, true laternulid, found in the Andaman Sea" but the "identification (by Kilburn) of *Laternula spengleri* ... from Vietnam is enigmatic...".

The most concise and yet comprehensive overview of laternulid taxonomy appears in Huber (2010). Within this work Huber notes that the Laternulidae remain "a confused family in modern literature". He suggests that some of the confusion in the taxonomy resides with misinterpretations by Morton (1976) and Lamprell and Healy (1998). With few other recent works to go on, Huber relies in large part on the work of Lamy (1934) and Reeve (1860–63) in efforts to resolve some of the muddled taxonomy. Huber (2010) recognizes 19 species of *Laternula* with three considered to be within the subgenus *Exolaternula* and, thus, possessing a lithodesma. These include *Laternula limicola* (Reeve, 1863), *Laternula erythraea* (Morris and Morris, 1993) and *Laternula truncata*. Within this comprehensive work, Huber does not include *Laternula corrugata* in the annotated species list nor in his images, but the lack of a lithodesma would place this taxon, if valid, within the larger group of laternulid species that lack this calcareous hinge-related structure. Huber (ibid) however notes that species within the "*Exolaternula*" have a "granulated" shell exterior, the usual umbonal shell slit and the "similar shape (of) *Laternula* s.s.". He also notes similar habitats and anatomical structures and, thus, concludes that "*Exolaternula* is considered a weak subgenus, based on a single criterion of unknown importance". In the current work we seek additional structural shell clues to differences between two species of *Laternula*, one with and one without a lithodesma. Based on the work of Huber (2010) and his personal confirmation, the species in the current work are *Laternula anatina* and *Laternula rostrata*, the latter being the accepted taxon and a synonymy of *L. truncata*.