

EXTRAORDINARY FLEXIBLE SHELL SCULPTURE: THE STRUCTURE
AND FORMATION OF CALCIFIED PERIOSTRACAL LAMELLAE IN
LUCINA PENNSYLVANICA (BIVALVIA: LUCINIDAE)

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ABSTRACT

The lucinid bivalve *Lucina pensylvanica* possesses an unusual flexible commarginal shell sculpture formed from calcified periostracal lamellae. The lamellae comprise thick, recurved, periostracal extensions with distal calcified scales. The periostracum is also densely embedded with calcareous granules around 2.0–2.5 µm in diameter and a thin (10 µm) layer of prismatic aragonite covers the ventral face of each lamella. Other species of *Lucina* in the western Atlantic possess calcified scales but with different morphologies and the continuous commarginal ridges of the eastern Atlantic *Lucina adansoni* and other African species are similarly constructed and homologous. The periostracal lamellae are a probable apomorphy of the genus *Lucina* and morphology of the calcified structures provides a set of systematic characters of importance in the discrimination of species.

Key words: *Lucina pensylvanica*, periostracum, calcification, shell growth, systematics.

INTRODUCTION

Lucina pensylvanica (Linnaeus, 1758) is one of ten species of chemosymbiotic lucinid bivalves inhabiting intertidal and shallow subtidal habitats in the middle Florida Keys. Remarkably, the shell sculpture consists of closely spaced commarginal lamellae, faced with triangular, calcareous scales that are slightly flexible in live animals. The scales and lamellae become brittle after death and in beach-collected shells the surface is white, relatively smooth with low, thin, commarginal ridges, sometimes with traces of periostracum. Our initial observations suggested that both lamellae and scales were a form of periostracal or extra-periostracal calcification, distinct from the normal shell. Because of the rarity of periostracal calcification in bivalves in general and the probable apomorphy of this character for *Lucina* spp., we decided to investigate the structure and formation of the lamellae in more detail and, if possible, determine the periodicity of their secretion. Additionally, we wanted to compare the form of the periostracal lamellae between *Lucina* species, both to establish

the homology of these as well as investigate their possible use as systematic characters. Detailed understanding of lamellar formation may also suggest hypotheses about their possible function.

Periostracal and extraperiostracal calcification is an unusual feature of bivalves but has been described in different forms from a variety of families. Usually in Lucinidae the periostracum is relatively thin (Harper, 1997), although exceptionally the genus *Rasta* has a dense, shaggy periostracum extended into numerous long pipes (Taylor & Glover, 1997). Prominent, sculpture-forming calcified periostracum appears restricted to the genus *Lucina*, of which *L. pensylvanica* is the type species (ICZN, 1977). The morphology of the calcified scales has been used by Gibson-Smith & Gibson-Smith (1982) as a character to divide "*Lucina pensylvanica*" of the western Atlantic into four separate species. Amongst other bivalve families, Veneridae, such as *Lioconcha* and *Callocardia* possess encrustations formed of fine aragonitic needles projecting through the periostracum (Ohno, 1996; Morton 2000); others such as *Granicornium* and *Samarangia* secrete extra-

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periostracal calcareous cements to form a crust of sediment on the shell (Taylor et al., 1999; Braithwaite et al., 2000). Many Anomalodesmata, such as *Laternula* and *Lyonsia*, possess spines formed within the periostracum as do some Gastrochaenidae, such as *Spengleria rostrata* (Spengler) (Carter & Aller, 1975). Amongst the Mytilidae, intraperiostracal aragonitic granules and projecting spikes have been described in *Trichomya* and *Brachidontes* (Carter & Aller, 1975; Bottjer & Carter, 1980; Carter et al., 1990), while intra- and extraperiostracal calcified structures are a feature of various species of Lithophaginae (Carter et al., 1990).

Little is known of biology of *Lucina pensylvanica*. Stanley (1970) demonstrated using x-rays that animals burrowed with the anterior part of the shell lying uppermost in the sediment, an unusual life orientation for Lucinidae. The general anatomy was described by Allen (1958) and Gros et al. (1996) made a detailed description of the gill ultrastructure and chemosymbiotic bacteria. Additionally, Taylor & Glover (2000) illustrated the large bipectinate mantle gills that lie alongside the pallial blood vessel.

Lucina pensylvanica and its close allies are often referred to in the literature under the generic name *Linga*. However, the name should correctly be *Lucina* as *Lucina pensylvanica* was designated the type species of the genus in 1977 (ICZN, 1977).

MATERIALS AND METHODS

Lucina pensylvanica was live collected from a number of oceanside intertidal and shallow water sites in the Florida Keys during the International Marine Bivalve Workshop (IMBW) in 2002 (Mikkelsen & Bieler, 2004, fig. 1 – map). Live animals were abundant only at Station IMBW-FK-642, mile marker 74.5 (24°51.4'N, 80°43.7'W) on Lower Matecumbe Key. Here they occurred in low intertidal to shallow, subtidal pockets of medium to coarse sand, located on a wide, coral-rock platform. The area was vegetated with patches of *Thalassia* and *Halodule*, as well as growths of *Penicillus* and *Halimeda*. Despite similar collecting effort, *Lucina pensylvanica* was much less common at other sites, such as Anne's Beach, Upper Matecumbe Key (Station IMBW-FK-638) from *Thalassia*-covered sand and Pigeon Key (Station IMBW-FK-657) in a tidal stream with *Thalassia* and *Syringodium*. No

live animals were found at any bayside stations. Animals were collected by extensive digging and hand sieving. Voucher specimens held in BMNH, London.

Live animals were fixed in 75% ethanol, 5% seawater formalin or Bouin's fluid. Tissue samples were also fixed in 2.5% solution of glutaraldehyde in phosphate buffer. Sections of mantle were stained with Mallory's triple. For optical microscopy of the shell, geological thin sections were made from fresh specimens embedded in resin. Pieces of the same embedded shell were also examined by scanning electron microscopy (SEM) after cutting, polishing and etching in EDTA.

Shell sections were also examined by confocal microscopy using a Leica SP NT in reflected light mode. Simultaneous images were collected at several different wavelengths, and a reference image was obtained with the transmitted light detector. We also carried out an initial test for autofluorescence using a wavelength (λ) scan. The section was scanned at a single focal plane with each laser in turn. The detector was programmed to step through 25 pre-determined 10 nm-wide detection windows at wavelengths from 495–750 nm that produced an intensity profile for each emission wavelength. This optimised laser detector position and line. The best results were obtained with the 488 nm Argon laser and this was used for all subsequent imaging. No autofluorescence was detected from within the shell matrix, so the first detector window was set at 486–507 nm. This wavelength gave a direct reflection image of the sample and was false coloured in green. Strong autofluorescence from the periostracum was detected at around 550 nm, so the second detector window was set at 537–568 nm and the images coloured red. A stack of 30 images was collected at ~0.4 μ m intervals. Each frame was scanned three times and run through a frame-averaging filter to reduce background noise. For single images, the z-axis (depth) data from the entire stack was combined and the brightest pixel from each point computed and displayed (maximum projection image).

Growth Periodicity

Twenty valves from live collected animals were used to study growth periodicity. We embedded these in MET20 resin (Struers Ltd), sectioned them transversely from the umbo to the ventral edge. They were then ground, polished and etched for 20 min in 0.01M HCl

and acetate peel replicas prepared following Richardson (2001). Distances between successive periostracal lamellae were measured to the nearest 0.05 mm on 11 shells. Distinctive major lines in the outer and middle shell layers and in the umbonal region (Fig. 22) were correlated with the formation of closely spaced or uncalcified periostracal lamellae. Three separate observers used these major growth marks in both umbo and valve to estimate the age in years of the animal (Richardson, 1993). The major growth increments were treated as annual lines by comparison with a similar study of *Codakia orbicularis* from the Bahamas (Berg & Alatalo, 1984).

RESULTS

Shell Microstructure

The shell consists of three aragonitic layers. The outermost layer is composed of a prismatic layer of irregular acicular crystals, their long axes inclined towards the shell margin (irregular spherulitic structure of Carter & Clark, 1985). This is followed by a middle layer of finely lamellate, crossed-lamellar structure and, within the pallial myostracum comprising irregular prisms, there is an inner layer formed of complex crossed-lamellar structure, intercalated with thin prismatic sheets. This se-

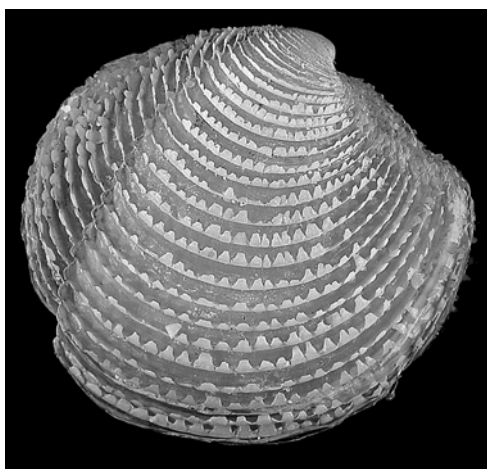


FIG. 1. *Lucina pennsylvanica* exterior of right valve showing commarginal periostracal lamellae with projecting calcareous scales. Shell height = 22.8 mm. Station IMBW-FK-642, Mile Marker 74.5, 24°51.4'N, 80°43.7'W, on Lower Matecumbe Key.

quence of shell layers resembles most other Lucinidae (Taylor et al., 1973).

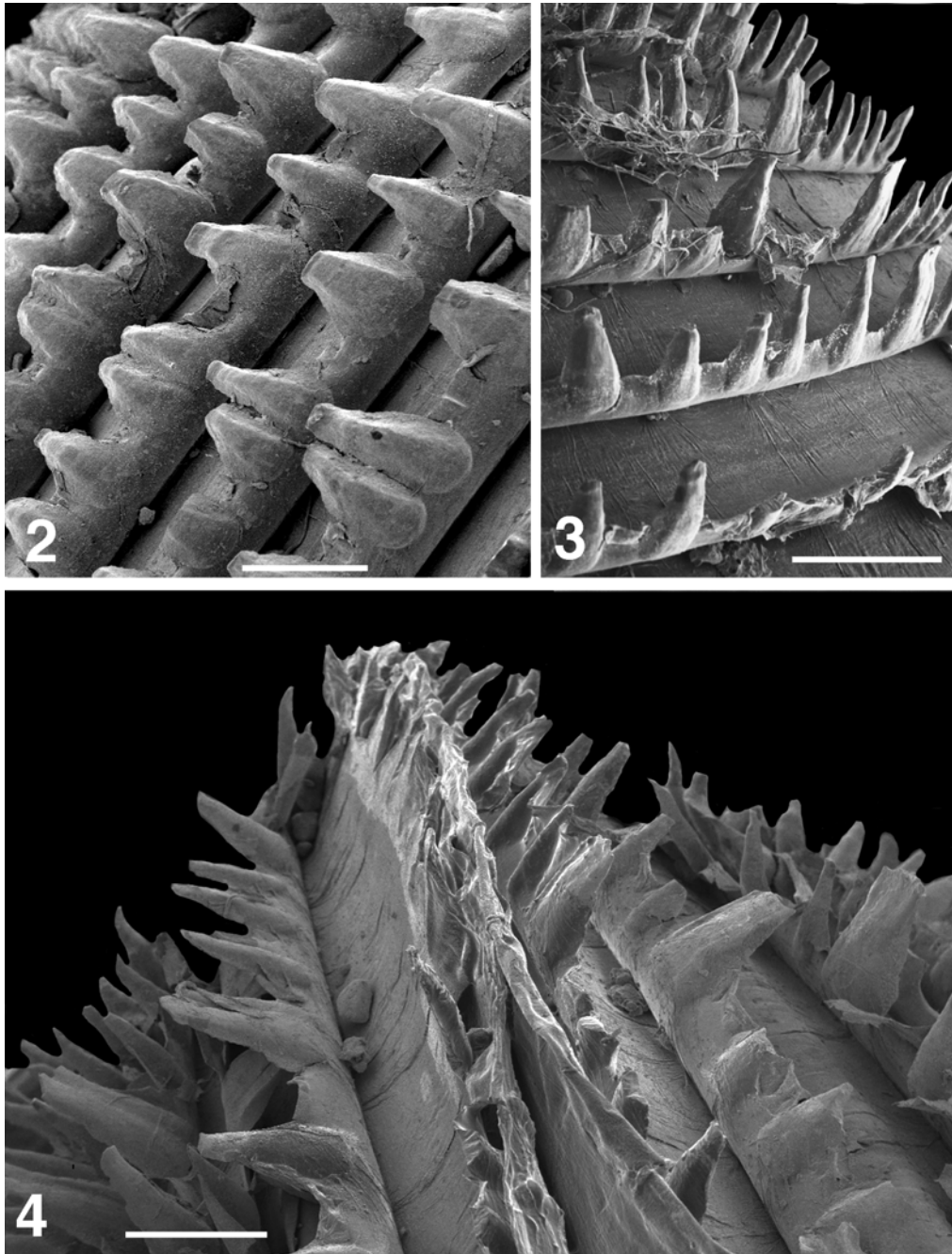
Calcified Periostracal Lamellae

Periostracal lamellae (hereafter referred to as lamellae) consist of an extended periostracum sheet faced with prominent calcified scales (Fig. 1). The lamellae recurve dorsally and are regularly spaced at intervals of 400–1500 μm , extending about 1,000 μm from the shell surface. Interspaces between the lamellae are relatively smooth (Figs. 2, 3) and in live collected specimens are packed with sediment grains (Figs. 8, 9). The discrete, closely-spaced calcareous scales (Fig. 8) are around 600–1,000 μm in height and seemingly embedded into the periostracum. In shape, the scales are triangular to lanceolate, broad at the base (varying between 500–950 μm) and taper distally. When newly formed, they are usually pointed at the tips (Fig. 4) but become truncated with wear. Scale shape varies around the shell; those on the posterior dorsal area are usually broader, more closely spaced and less recurved. Over most of the shell surface, lamellae recurve dorsally but when first formed they extend straight out from the shell margins, with the scales embedded in the sheet of periostracum (Fig. 4). Subsequently, lamellae become progressively recurved away from the commissure (Fig. 4), and the periostracum erodes away from the scales (Figs. 5, 6).

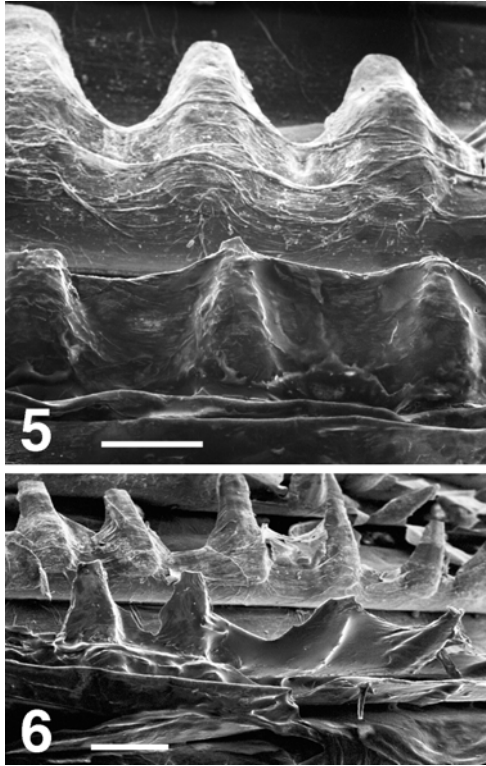
On juvenile shells, the scales are differently shaped (Fig. 7) being lower and quadrate with narrower spaces between, so that they form an almost continuous ridge. The quadrate scales change to a triangular shape at a shell height of around 4.5–5.0 mm.

Sections

Optical, scanning and confocal microscopy shows that each lamella is composed of a periostracal extension in which the calcareous scales occupy the distal ventral face (Figs. 8–11). Each lamella projects from a thin ridge in the true shell (Figs. 8–10). Within a lamella the periostracum is about 55 μm thick and continuous with that of the outer shell surface. Between successive lamellae the periostracum gradually increases in thickness from around 1–2 μm at the termination of one extension to about 50 μm at the base of the succeeding extension (Fig. 12). Higher magnification of the calcareous scales reveals a



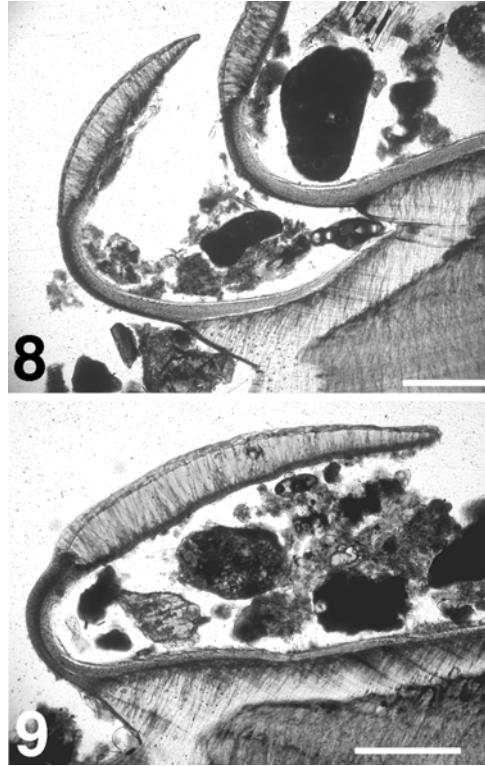
FIGS. 2–4. *Lucina pennsylvanica*. FIG. 2: Surface view of successive commarginal lamellae with scales. Scale bar = 500 μm ; FIG. 3: Periostracal lamellae on posterior of shell with pointed scales with smooth periostracal surface between lamellae. Scale bar = 500 μm ; FIG. 4: Site of formation of periostracal lamellae at valve margins showing lamellae lying parallel with shell margin but becoming recurved dorsally away from the edge. Scale bar = 500 μm .



FIGS. 5, 6. *Lucina pennsylvanica*. FIG. 5: Ventral view of forming lamella at shell margin showing row of scales embedded in periostracum stretched between them, but in the preceding row this has disappeared. Scale bar = 250 μm ; FIG. 6: View of posterior shell margin with pointed scales joined by a membrane of periostracum. Scale bar = 250 μm .



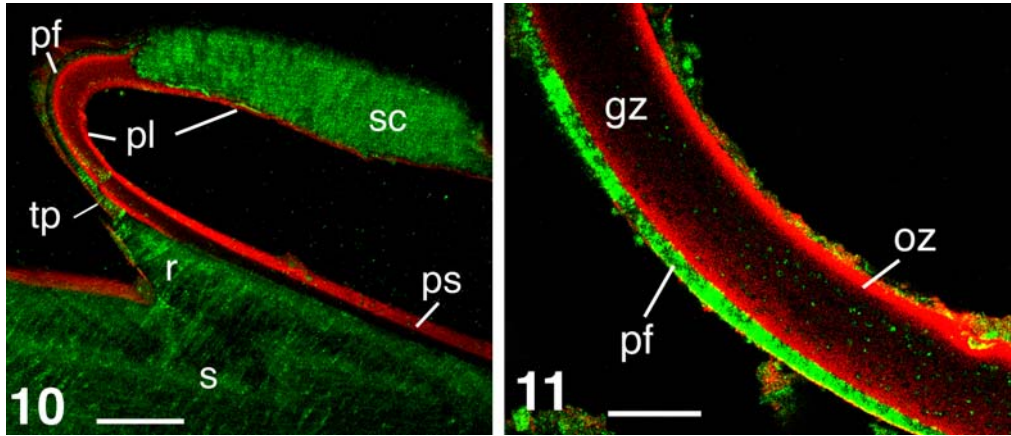
FIG. 7. *Lucina pennsylvanica*, juvenile shell (shell height 3.5 mm) with lamellae formed of closely spaced, quadrate scales. Scale bar = 200 μm .



FIGS. 8, 9. *Lucina pennsylvanica*. FIG. 8: Transverse section of shell showing two lamellae. Note ridges in shell and sediment trapped behind lamellae. Scale bar = 250 μm ; FIG. 9: Transverse section of a single lamella. Scale bar = 250 μm .

thin (1.5–2.0 μm) initial periostracal sheet followed by a layer of aragonitic spherulitic microstructure (Fig. 14). Each scale is about 220 μm thick tapering distally. Within the spherulitic layer of the scale, interpenetrant bundles of long, thin crystals radiate from nucleation sites on the inner periostracal surface. Fine growth lines indicate that the scales are secreted incrementally. Another calcified layer (10–15 μm thick), of short, prismatic aragonite crystals embedded in periostracum, forms the ventral face of each completed lamella (Figs. 11, 13, 18).

Sections of the basal periostracal part of the lamella show that it is densely embedded with tiny calcareous granules about 2–2.5 μm in diameter consisting of aggregations of crystalline aragonite (Figs. 13, 16, 19). Granules are absent in the outermost part of the periostracum but at about 10 μm from the edge of the lamella increase in abundance (Fig. 12).



FIGS. 10, 11. *Lucina pennsylvanica*. FIG. 10: Confocal image of transverse section through a periostracal lamella. Periostracum red; calcified structures green. Scale bar = 100 μ m. Abbreviations: pf, calcified prismatic front of lamella; pl, periostracum of lamella; ps, periostracum above shell; r, ridge in outer shell layer; s, shell; sc, scale; FIG. 11: Confocal image of the proximal region of a periostracal lamella, showing detail of the periostracum and the calcified front of the lamella. Scale bar = 50 μ m. Abbreviations: as for Fig. 10; gz, granule zone; oz, outer granule-free periostracal zone.

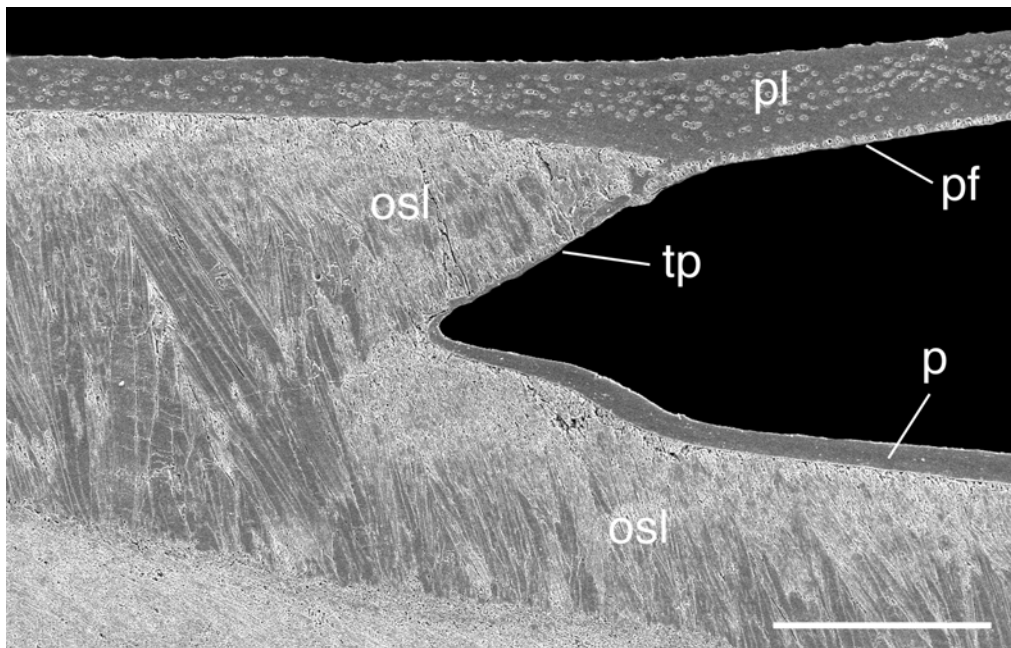
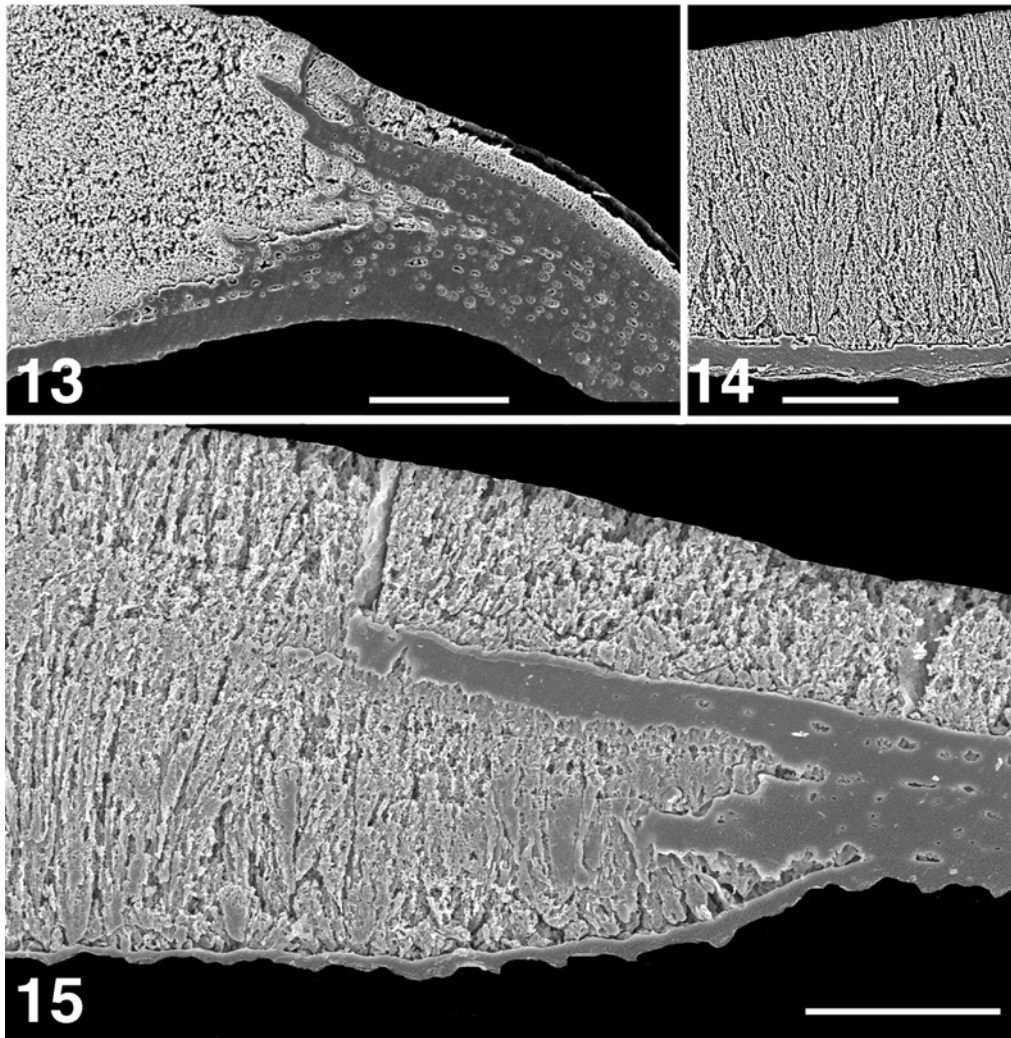


FIG. 12. *Lucina pennsylvanica*, SEM image of transverse section through base of a lamella showing shell ridge and thinned periostracum that thickens towards the succeeding lamella. Scale bar = 100 μ m. Abbreviations: osl, outer shell layer; p, periostracum; pf, prismatic front of lamella; pl, periostracum of lamella; tp, thin periostracum.

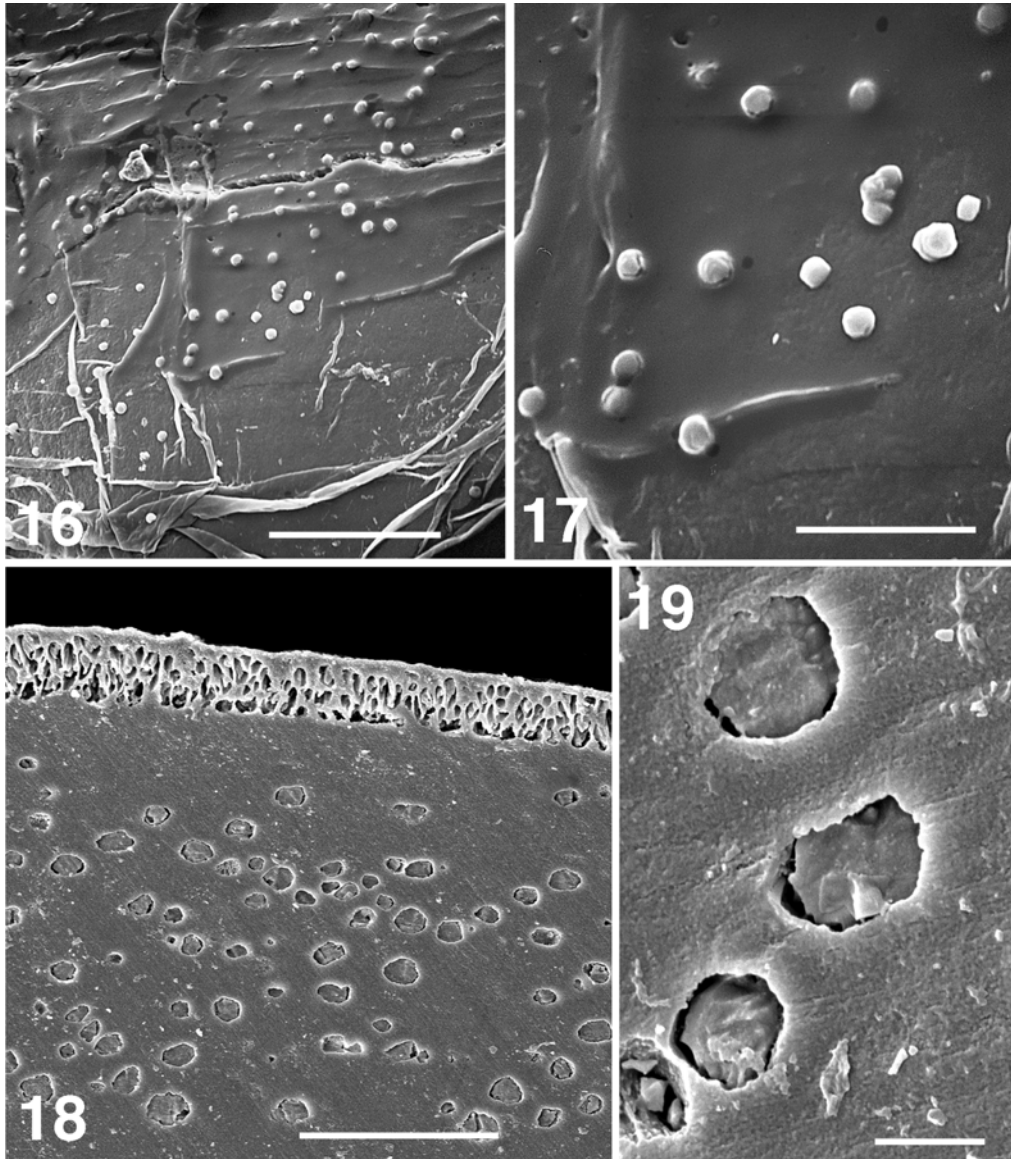
These granules are also present in the normal periostracum secreted above the outer shell layer and gradually increase in frequency between successive lamellae.

Sections of the junction between the calcareous scales and the periostracal lamella show that lines representing growth increments interdigitate from periostracum into the calcified scales and also that the granules increase in

density and fuse at the transitional boundary (Figs. 13, 15). The calcified scales are thus secreted contemporaneously with the periostracal layers of the lamella and not laid down subsequent to it. Images clearly show a covering of periostracum eroding from the scale surfaces. We conclude from these observations that both the granules and scales are forms of periostracal calcification.



FIGS. 13–15. *Lucina pennsylvanica*. FIG. 13: SEM image of a transverse section through junction between calcareous scale and proximal part of the lamella showing interdigitation of calcareous layer with periostracum and granules. Scale bar = 50 μm ; FIG. 14: Section through a calcareous scale showing spherulitic crystal growth arising from thin periostracum layer below. Scale bar = 70 μm ; FIG. 15: Section through junction of calcareous scale and periostracum showing continuity of growth increments from the calcified portion into the periostracum. Scale bar = 50 μm . Abbreviations: gz, granule zone of periostracum; p, periostracum; sp, spherulitic crystal growth.



FIGS. 16–19. *Lucina pensylvanica*. FIG. 16: Surface of a forming periostracal lamella at shell margin showing aragonitic granules embedded in surface. Scale bar = 50 μm ; FIG. 17: Higher magnification image of granules showing crystalline form. Scale bar = 15 μm ; FIG. 18: Section of periostracal lamella showing discrete aragonitic granules in periostracum and the fringe of prismatic aragonite crystals along the front of the lamella. Scale bar = 20 μm ; FIG. 19: Detail of discrete granules embedded in periostracum. Scale bar = 2 μm .

Mantle Edge

The mantle edge of *L. pensylvanica* is thick and divided into several folds (Fig. 20). The large outer fold (of) is thrown into deep corrugations

indicating the potential for considerable extension. Epithelial cells at the margin are tall, with nuclei located towards the midpoint, but decrease in height dorsally to the short, cuboidal cells of the general outer

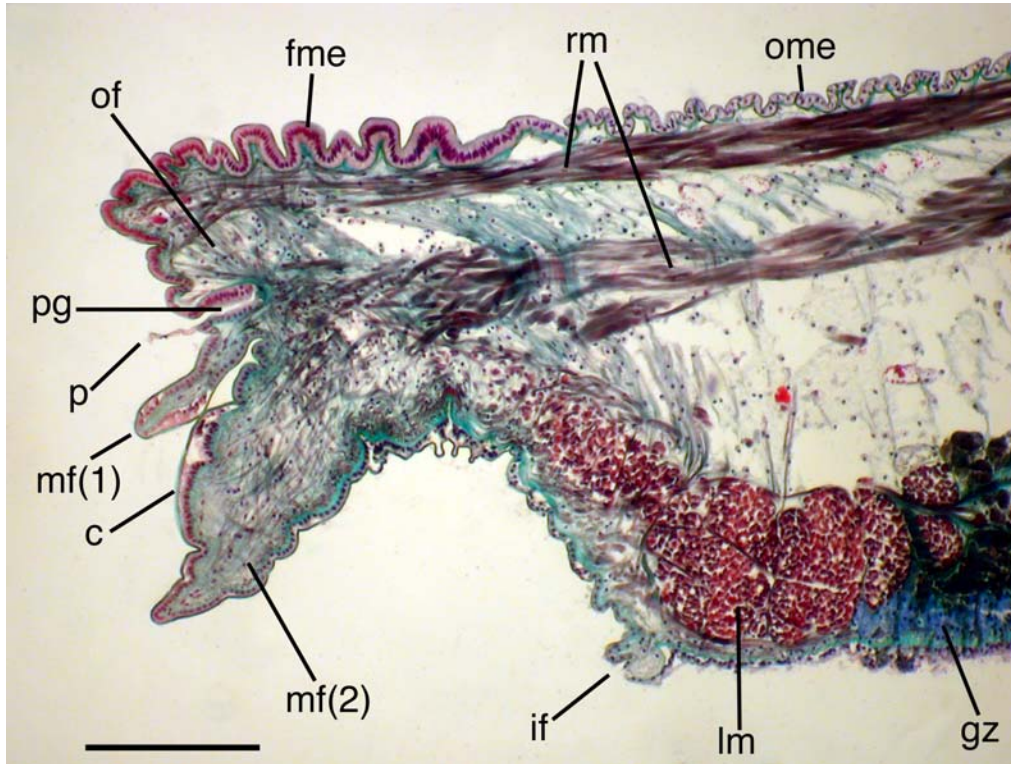


FIG. 20. *Lucina pennsylvanica*. Transverse section of anterior mantle edge. Mallory's triple stain. Scale bar = 250 μ m. Abbreviations: c, cuticle; fme, corrugated mantle epithelium of outer fold; gz, glandular zone; if, inner mantle fold; lm, longitudinal pallial muscles; mf(1) & mf(2), lobes of middle mantle fold; of, outer mantle fold; ome, outer mantle epithelium; p, periostracum; pg, periostracal groove; rm, radial pallial muscles.

mantle surface. The outer fold is separated from the middle fold by a deep periostracal groove, with the forming periostracum lying against the outer surface of the middle fold. The middle fold is divided into two distinct lobes with the outermost of these (mf 1) forming a short, slender lobe whilst the other (mf 2) is broad and longer. The inner fold (if) is a small, low ridge. Cells of the middle lobes are shorter than those of the outer fold and possess basal nuclei. The epithelium of the middle folds is overlain by a thin cuticle (ct) that extends almost to the inner fold. The mantle surface within the inner fold is ciliated.

Two well-defined bundles of radial muscles extend into the outer and middle folds respectively and a thick bundle of longitudinal pallial muscles (lm) is located near the inner fold (seen in transverse section in Fig. 20). The inner part of the mantle within the inner fold is

highly glandular with subepithelial gland cells opening to the inner mantle surface. Two types of gland cell are present; one type, staining blue, is located superficially while the other dark green type lie more deeply.

Periodicity of Lamellae

The lamellae appear regularly spaced but measurements taken from acetate peels of shell sections show that the increments are variable in width and furthermore change with age. Figure 21 demonstrates that for eight live-collected shells widths between successive lamellae increase steadily from around 200–450 μ m to a maximum (up to 1,800 μ m) at around 25–30 mm shell height. Thereafter, interlamellar spacing becomes much narrower but more variable. Observations of the outer surfaces of larger, dead-collected shells show

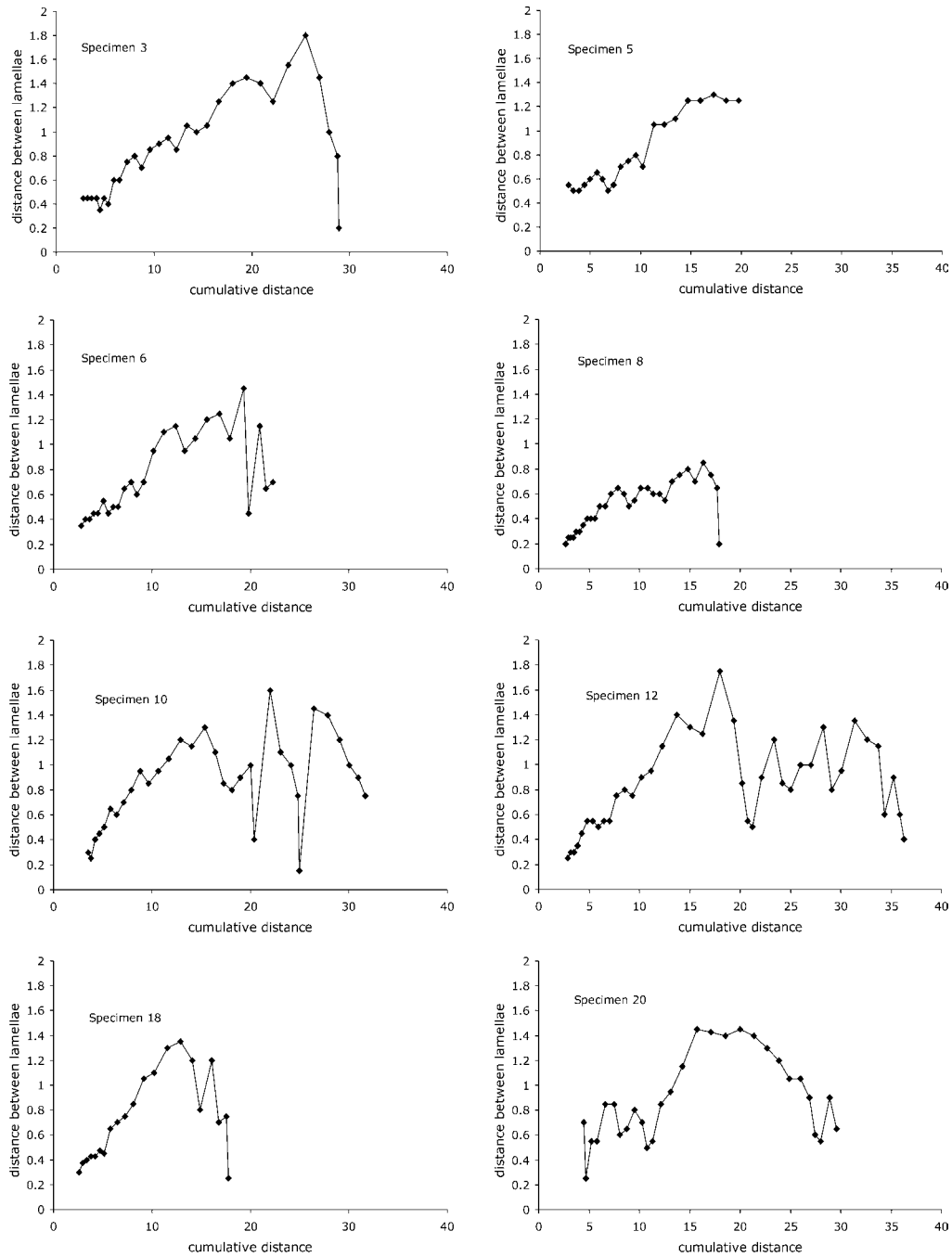


FIG. 21. *Lucina pensylvanica*, interval between successive lamellae plotted against cumulative length around shell circumference for eight individual *Lucina pensylvanica*. Measurements made from acetate peels of transverse sections.

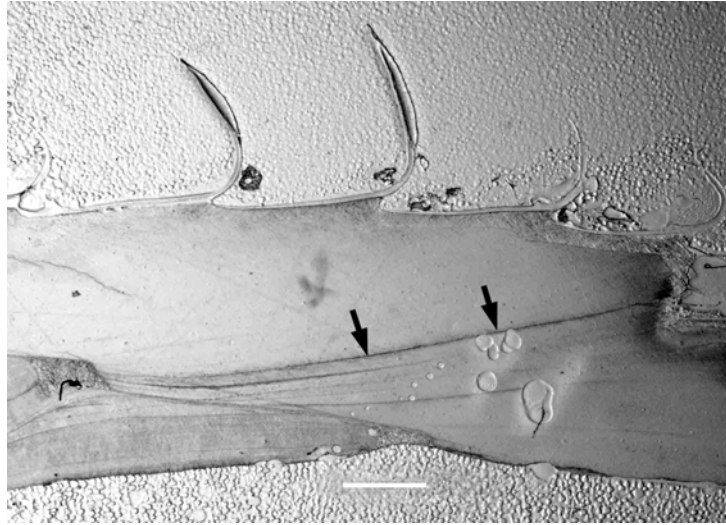


FIG. 22. *Lucina pennsylvanica*, acetate peel of transverse section of shell showing major growth line extending through outer and middle shell layers. Scale bar = 500 μ m.

that this change in the interlamellar interval is visible on all individuals at shell heights of around 22–27 mm. In older individuals the interval between major growth halts is narrower with fewer lamellae (Fig. 21: specimen 12).

Frequently, major growth halts are marked by the secretion of a sequence of several uncalcified periostracal extensions (Figs. 22, 23). Our interpretation of this growth pattern is that shell accretes rapidly and uninterrupted to a

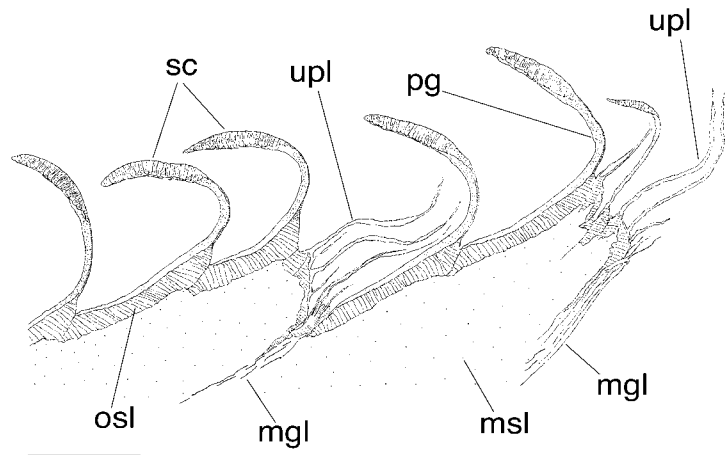


FIG. 23. *Lucina pennsylvanica*, semidiagrammatic summary drawing (based on camera lucida image) of transverse section through shell showing successive lamellae and two growth halts where only uncalcified periostracal sheets were secreted. Scale bar = 1.0 mm. Abbreviations: cf, calcified front of lamella; msl, middle shell layer; osl, outer shell layer; ps, periostracum above shell; pl, periostracum of lamella; r, ridge in outer shell layer; sc, scales; upl, uncalcified periostracal lamellae.

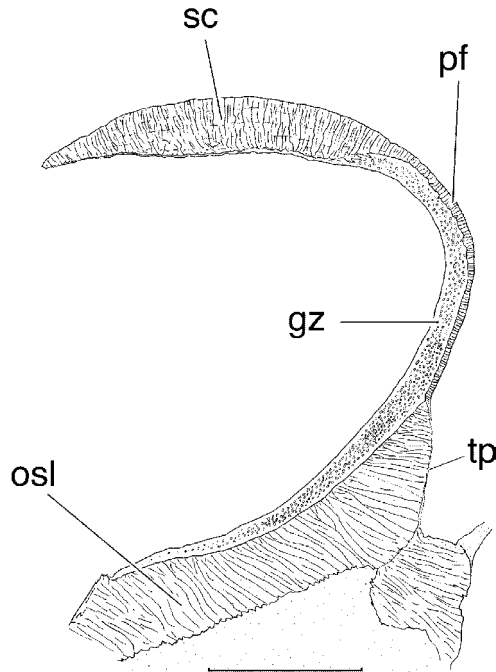


FIG. 24. *Lucina pensylvanica*, semidiagrammatic transverse section through a single periostracal lamella. Scale bar = 500 μ m. Abbreviations: gz, granule zone; osl, outer shell layer; pf, thin prismatic ventral fringe to lamella; tp, thin periostracum.

size of around 25 mm. Thereafter, growth rates decline and become more variable. Study of gonads from our small sample indicates that sexual maturity occurs in these bivalves at shell heights of around 20–25 mm (Bigatti et al., 2004). The major change in shell growth pattern may thus coincide with time of first spawning.

A study of growth in *Codakia orbicularis* (Linnaeus, 1758) from the Bahamas showed that prominent growth rings in the shell were annual (Berg & Alatalo, 1984). Following this, the major growth halt lines seen in shell sections (Figs. 22, 23) in our sample could be tentatively interpreted as annual marks and used to estimate the ages of the animals. Table 1 indicates that 20 sectioned shells show between 0–4 major lines and the interpretation is that the animals vary between one and four years old. Proper age estimation should be done using marked and calibrated shells but this was impossible in the time available for the study.

Sequence of Secretory Events

The structure of the commarginal lamellae is summarized diagrammatically in Figures 23–24. Each commarginal lamella represents an extension of the mantle beyond the normal shell profile. Although the lamellae in *L. pensylvanica* are recurved dorsally, observations at the site of secretion show that the lamellae initially project more or less straight from the valve margin and curve dorsally later (Fig. 4). Thus, the mantle is not extended and reflected dorsally as it would be if secreting commarginal lamellae formed from normal shell layers as seen in other bivalves such as the venerid *Placamen calophyllum* (Philippi, 1836) (Checa, 2002).

Initially, the mantle secretes a thin, periostracal sheet, followed by calcification of the distal portion with spherulitic aragonite crystals. Calcification of the distal edge of the lamella is localised, presumably to groups of cells, so that individual scales are formed. At the same time the proximal part of the lamella is laid down as periostracum, embedded with crystalline granules. Finally, the mantle withdraws from the extended position, leaving a thin layer of prismatic crystals along the ventral face of the lamella. The withdrawal of the mantle is marked by a low, commarginal ridge in the shell profile (Figs. 12, 24). Following termination of a lamella, the periostracum is very thin but gradually thickens and becomes densely embedded with granules prior to the next lamellar extension (Fig. 24). Periodically, there are major growth breaks where only extended uncalcified periostracal sheets are formed (Fig. 23).

Comparison with *Lucina adansoni* and Other Species

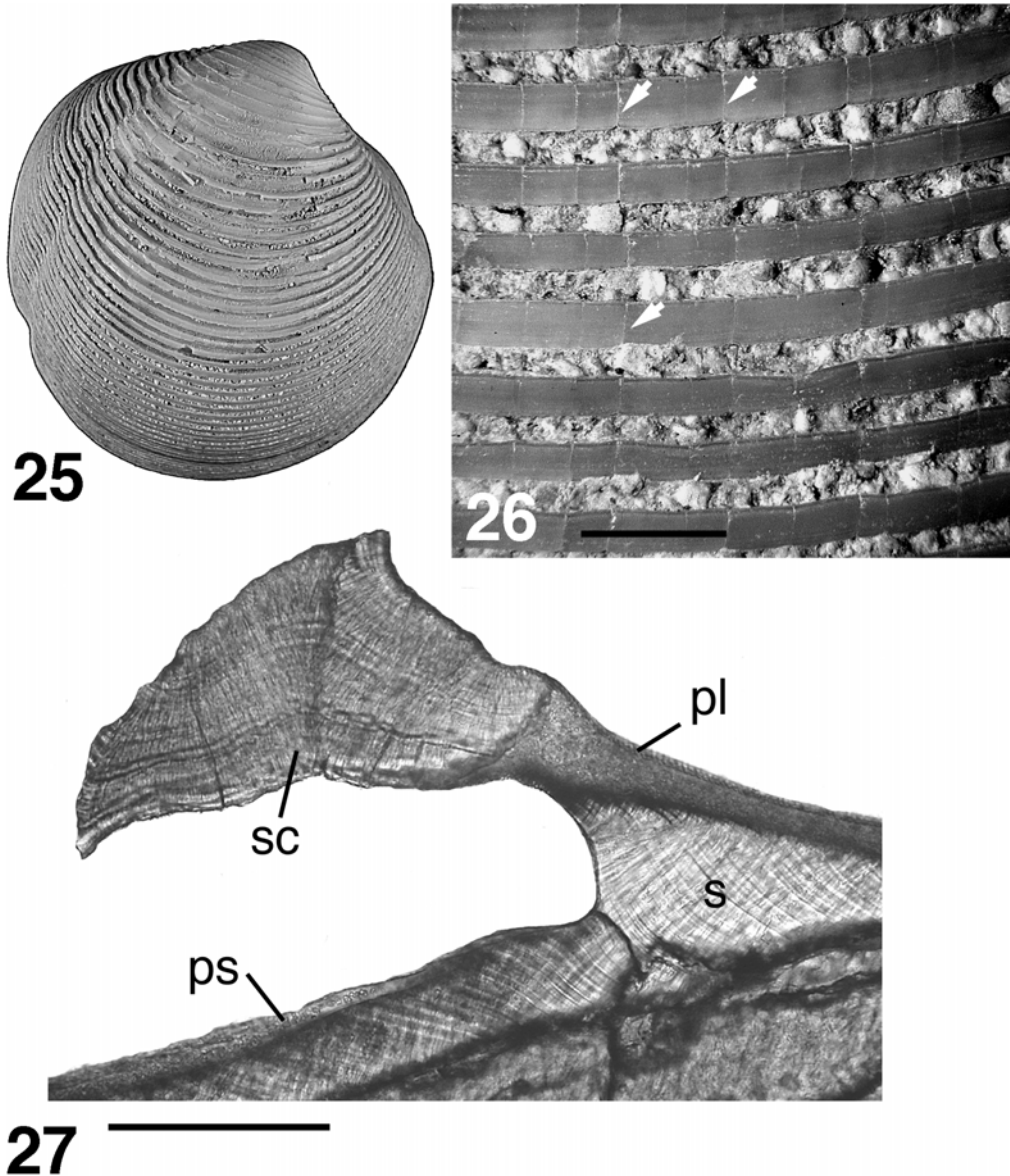
An interesting comparison may be made with another species, *Lucina adansoni* (Orbigny, 1839) from West Africa. This has a thick, subspherical shell, sculptured, with closely spaced, broad commarginal lamellae about 300 μ m in width (Figs. 25, 26). These are often eroded, detached or absent in dead-collected shells or museum specimens. Each lamella is divided into sections (up to 500 μ m long) by narrow sutures aligned between successive lamellae. Interspaces between lamellae are often packed with sediment. Thin sections show that the lamellae are similarly constructed to those of *Lucina pensylvanica* (Figs. 27, 28) but instead of discrete scales, the calcified units are fused laterally to form a continuous ridge

TABLE 1. Shell size, age, sex, reproductive condition, position of growth lines and number of observed lamellae in *Lucina pennsylvanica*.

ID	L	H	W	Sex	Reproductive state	N major growth lines	Age estimate	N observed lamellae (selected specimens)	FK-station	Location
1	27.9	27.5	15.7	F	Spawned	2	3		642	Lower Matecumbe Key
2	17.7	17.5	8.7	F	Maturing	0	1-2		642	Lower Matecumbe Key
3	27	25.7	13.7	F	Mat./spawning	1	2-3	30	642	Lower Matecumbe Key
4	28.2	28.1	17.6	F	Mature	3	3		642	Lower Matecumbe Key
5	17.9	17.6	9.4	F	Spawning	0	1+	21	642	Lower Matecumbe Key
6	20.5	20.6	11.5	F	Spawned	3	2	26	642	Lower Matecumbe Key
7	42.6	42	27	F	Mature full	2	4		642	Lower Matecumbe Key
8	21.6	20.4	10.9	F	Spawned	1	1-2	30	642	Lower Matecumbe Key
9	27.8	27.8	17.2	M	Mature	4	4-5	30	642	Lower Matecumbe Key
10	27.6	26.8	16.8	M	Mature full	3	3-4	33	642	Lower Matecumbe Key
11	35.4	36	21.9	?		3	4	40	647	Pigeon Key
12	32.7	32.4	20.8	F	Spawned	2	3		647	Pigeon Key
13	28.5	29.2	17.7	F	Spawned	2	2-3		647	Pigeon Key
14	31.5	30.7	19.2	F	Spawning	0	2		638	Lower Matecumbe Key
15	15.9	15.4	8.9	M	Mature	2	2	22	642	Lower Matecumbe Key
16	12.8	12.7	7.1	I		0	1+	16	642	Lower Matecumbe Key
17	16.2	15.3	8.5	M	Almost mature	0	1-2		642	Lower Matecumbe Key
18	16.1	15.7	8.8	F	Maturing	1	1+	21	642	Lower Matecumbe Key
19	13.8	13.2	6.8	F	Maturing	1	2		642	Lower Matecumbe Key
20	26.6	25.4	15.9	F	Mature	2	3	29	642	Lower Matecumbe Key

that is triangular in cross section (Fig. 27). The lamellae are tilted towards the ventral shell margin rather than recurved dorsally as in *L. pensylvanica*. Each lamella is composed of a thick periostracal extension that terminates dis-

tally in the calcified unit. This is more heavily calcified than the scales of *L. pensylvanica* but similarly constructed of spherulitic crystal growth. The periostracal extensions are shorter than *L. pensylvanica* but similarly embedded



FIGS. 25–27. *Lucina adansoni*. FIG. 25: Right valve (Leiden RMNH 12179). Cape Verde Islands, SE of Boa Vista 15°59'N, 22°44'W, depth 36 m. Shell height = 32.5 mm; FIG. 26: Detail of commarginal lamellae. Arrows mark suture lines between sections along lamellae. Note sediment grains packed into interspaces between lamellae. Scale bar = 1.0 mm; FIG. 27: Transverse section of a commarginal lamella. Scale bar = 500 μ m. Abbreviations: pl, periostracal lamella; ps, periostracum above shell; s, shell; sc, calcareous scale.

with calcareous granules about 2 μm in diameter (Fig. 28). Also, the periostracum gradually increases in thickness between successive lamellae and then thins dramatically at their termination (Fig. 28). Beneath each lamella the outer shell layer forms a steep-faced lip (Fig. 28) about 200 μm high. In worn shells this is the only shell sculpture remaining after the lamellae have become detached.

Calcified periostracal commarginal lamellae similar to those of *L. adansoni* have been observed (BMNH collections) in the southern African species *Lucina carnosa* Dunker, 1858, and *L. roscoeorum* (Kilburn, 1974). The lamellae in the latter species are described (Kilburn, 1974: 340–341, figs, 4, 5) as being "...apically imbricate, rendering their crests somewhat tabulate (i.e. in cross section each would resemble an inverted "L")..." and "... the crests of the lamellae are regularly but superficially incised transversely..."

DISCUSSION AND CONCLUSIONS

We have demonstrated that the structurally complex commarginal shell sculpture of *Lucina pensylvanica* is a form of periostracal calcification, a rather unusual feature amongst bivalves. The calcareous granules within the periostracum were briefly mentioned by Bottjer & Carter (1980), but no details were given. We are not aware of any similar structures in any other lucinid. Most Lucinidae lack prominent commarginal shell sculpture but two species of *Lamellolucina*, namely *L. dentifera* (Jonas, 1846) from the Red Sea and *L. gemma* (Reeve, 1850) from the Philippines possess thin, elevated lamellae with spinose edges (Taylor & Glover, 2002: fig. 6) reminiscent of the lamellae in *L. pensylvanica*. However, the lamellae and spines of *Lamellolucina* are entirely calcareous and comprise extensions of the outer shell layer rather than periostracal

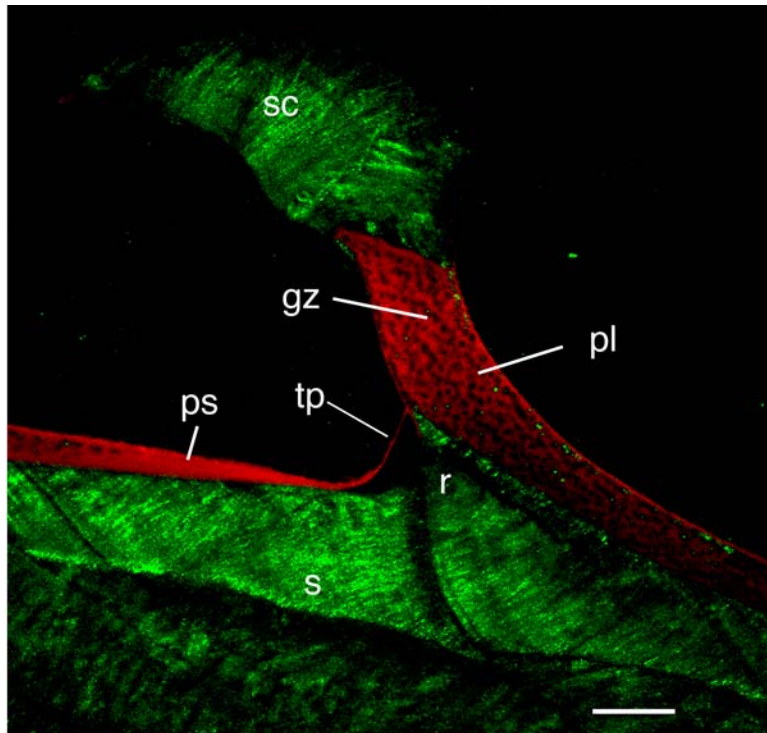


FIG. 28. *Lucina adansoni*, confocal image of transverse section of a commarginal lamella. Periostracum red, calcareous components green. Scale bar = 100 μm . Abbreviations: gz, granule zone of periostracum; pl, periostracal lamella; ps, periostracum above shell; r, ridge in outer shell at base of lamella; s, shell; sc, calcareous scale; tp, thin periostracum.

structures. Similarly, *Lucinisca* species from the western Atlantic and eastern Pacific possess spinose commarginal lamellae, but again these are formed from the outer shell layer rather than periostracum.

A diversity of instances of periostracal calcification has been described from a wide range of different bivalve families (Carter & Aller, 1975; Bottjer & Carter, 1980; Carter et al., 1990; Ohno, 1996; Morton, 2000), but none is comparable with *L. pensylvanica*. Analogous calcareous granules embedded in periostracum have been illustrated for the mytilids *Brachidontes granulatus* (Bottjer & Carter, 1980: fig. 3) and *Trichomya hirsuta* (Carter & Aller, 1975: fig. 1c). Little attention has been paid to this calcification either functionally or as a set of systematic characters and in many cases it is routinely cleaned off specimens.

Function of the Lamellae

Although we have no experimental evidence, we suggest by analogy with sculpture on other bivalves that there might be at least three possible functions of the commarginal lamellae. These include acting as a sculptural aid to burrowing, maintaining stability in the sediment and as a possible deterrent to predators. Unusually amongst bivalves, the commarginal lamellae of *L. pensylvanica* are flexible in life and this property may have added but unknown functional significance.

As demonstrated by Stanley (1970), some lucinids, including *Lucina pensylvanica*, burrow into the sediment vertically with the hinge axis parallel to the sediment surface and rock from side to side to gain purchase into the sand. Unusually for lucinids, *L. pensylvanica* rotates posteriorly after penetrating the sediment to lie with the anterior part of the shell uppermost. The recurved, flexible lamellae and scales might aid this process but we have no experimental evidence similar to that available for the divaricate-ribbed *Divaricella quadrisulcata* (Orbigny, 1846) (Stanley, 1970). However, the external lamellae of *L. pensylvanica* are easily removed to enable a comparison of burrowing performance to be made with and without the structures.

In shallow burrowing bivalves, the ridges and spines on the shell surface have been shown to reduce the effects of scour and may prevent dislodgement from the sediment (Bottjer & Carter, 1980; Stanley, 1981). We have no experimental observations but in *Lucina pensylvanica* and *L. adansoni* the lamellae are

extremely effective in trapping sediment close to the shell surface (Figs. 8, 26) and in most live-collected specimens the interlamellar spaces are full of sediment. Compared to other lucinids of similar size from the Florida Keys, *Lucina pensylvanica* is the most shallowly burrowed, living in medium to coarse, mobile sands rather than the thicker *Thalassia*-bound sediments favoured by *Codakia orbicularis* and *Anodontia alba*.

A further possible function of the lamellae might be to deter predation. Strong commarginal lamellae on the venerid *Placamen calophyllum* have been shown to deter shell drilling predatory gastropods (Ansell & Morton, 1985). Any test of this suggestion would need experimental analysis.

The function of the discrete aragonitic granules embedded in the periostracum and periostracal extensions of *L. pensylvanica* and *L. adansoni* is unclear, but they may provide additional stiffness to the largely proteinaceous part of the lamellae that supports the more heavily calcified distal scales or ridge. Furthermore, the thin calcified layer along the ventral face of the lamellae may also provide stiffness but, additionally, the differential mechanical properties on either face of the lamella may cause the lamellae to curve dorsally.

Systematic Implications of Commarginal Lamellae in *Lucina*

Although *Lucina pensylvanica* is thought to be widely distributed around the Western Atlantic and Caribbean area, from North Carolina to Brazil (Britton, 1970; Abbott, 1974; Bretsky, 1976), it is much more likely that a complex of several species exists. J. Gibson Smith & W. Gibson Smith (1982) used the morphology of the calcareous scales to divide the "*L. pensylvanica*" of the western Atlantic, naming three new species on the basis of differences in the form of the scales. These they distinguished from *L. pensylvanica*, assuming its type locality to be Florida. All the species are similar in general shell morphology but differ in the form of the calcified periostracal lamellae. We have examined the types of the Gibson-Smith species and also the syntypes of *Lucina pensylvanica* (Linnaeus, 1758), but unfortunately the latter material is heavily worn without any trace of lamellae.

Firstly, *Lucina belizana* J Gibson-Smith & W Gibson-Smith, 1982 (Holotype: BMNH 1980103) from Belize is characterised by fine, close lamellae with delicately pointed, lightly

calcified spines. Secondly, *Lucina roquesana* J Gibson-Smith & W Gibson-Smith, 1982 (Holotype and paratype: BMNH 1980105/1–2) from Venezuela has calcified periostracal lamellae, but these bear broad closely spaced, blunt-ended scales that are arranged in a radial rows in successive lamellae. *Lucina podagrina caymanana* J Gibson-Smith & W Gibson-Smith, 1982 (Holotype: BMNH 1980104/1) from the Cayman Islands is similar to *L. roquesana*, but the periostracum is pale brown and the shell less globose (*Lucina podagrina podagrina* Dall, 1903, is a Pliocene fossil species.). J. Gibson Smith & W. Gibson Smith (1982) have undoubtedly highlighted the existence of a species complex within the former "*Lucina pensylvanica*", but in our opinion the taxonomy is even more complicated. For example, another species from the western Atlantic, *Lucina aurantia* Deshayes, 1830, which is usually synonymised with *L. pensylvanica* (Abbott, 1974; Britton, 1971; Bretsky, 1976), has many distinctive shell characters including size and shape, dentition and colour. Some unworn shells have remnants of fine, pointed scales. We are confident that this is yet another unregarded species. Another likely distinct species from the Bahamas has been confused with *L. pensylvanica* but it can readily distinguished by extremely fine pointed scales (specimens from Blue Hole Cay, off Andros Is., collected by P. Mikkelsen and G. Hendler). A thorough systematic revision of the "*Lucina pensylvanica*" complex in the western Atlantic using live-collected animals with morphological and molecular analysis is needed.

On the other side of the Atlantic, *Lucina adansoni*, *L. carnososa*, and *L. rosceorum* seem to form another possibly related clade, linked by the possession of calcified periostracal lamellae that form continuous ridges. As we have demonstrated, these ridges differ in morphology but are similarly constructed and thus homologous with the lamellae of the western Atlantic "*L. pensylvanica*" group. The relationships of the two clades need clarification.

It should be emphasized that in museum specimens the periostracal calcified structures so diagnostic of these *Lucina* species are usually damaged or in the case of beach collected shells, completely worn away. In dried shells, the periostracal lamellae become brittle and are easily damaged without special curatorial care. We recommend wet preservation as the most satisfactory method of preserving these structures.

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