Shell tubules in Condylocardiinae (Bivalvia: Carditoidea)

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Shell tubules are microscopic canals in the shells of various molluscs. In polyplacophorans and fissurellid gastropods, the canals form by shell growth around multicellular extensions of the mantle epithelium (caeca). Bivalves have unicellular caeca which etch tubules into preformed shell (Reindl & Haszprunar, 1996). These occur in numerous independent bivalve lineages, although more frequently in Pedinomorphia and Carditoida (Taylor, Kennedy & Hall, 1969, 1973). Tubules are a taxonomically constant feature of all postlarval Arcoidea and most likely of all Carditidae, Psidiidae, Sphaeriidae and Corbiculidae (Araujo, Ramos & Bedoya, 1994; Araujo & Korniushin, 1998; Malchus, 2006; Taylor et al., 1973; Waller, 1980; this study). Unionoidae (Palaeheterodonta) seem to be the only taxon with shell tubules in the larval, glochidial shell (Lima et al., 2006; Roe, Simons & Hartfield, 1997; Malchus personal observation). The feature has never been mentioned for the microvolute family Condylocardiidae (e.g. Middelfart 2002a, b and references therein; Coan, 2003), although this group was probably derived from tubulate Carditidae (Taylor et al., 2007). The present study examines the shells of three Condylocardia species (cf. Coan, 2003) from the National History Museum in Los Angeles (LACM) and compares them to Cardita calyculata (Linnaeus, 1738) (Carditidae), Adacnarca limosoides (Thiele, 1912) (Philobryidae) (Swedish Museum of Natural History, SMNH) and Strangula lutea (Linnaeus, 1758) (Noetiidae) (own collection, NMA). Additional photographic support material is available from Morphobank (http://morphobank.org/permalink/?P343; image reference numbers begin with letter M).

A preliminary SEM survey of the depositional surface revealed the presence of numerous, about 2 μm wide pores (Figs M41671–73). In order to examine their distribution, penetration depth, orientation and interrelationships within the shell, three valves of C. digueti (Lamy 1861), two of C. digueti (Lamy, 1917), one of C. geigeri Coan, 2003, and several outgroup specimens were placed in a vacuum chamber and embedded in epoxy resin. Previous experiments with arcoids had shown that the resin penetrates the shell tubules, which can then be exposed by acid etching. Accordingly, the embedded shells were cut, polished and etched with 2% formic acid for 5–15 s, and then prepared for SEM examination.

All three Condylocardia species show a high density of tubules, replaced by epoxy resin strings, within a crossed-lamellar shell matrix (Fig. 1A–G). Overall, tubules are straight, perpendicular to the depositional surface, conspicuously nodular and with diameters between 1 and 0.3 μm. Pillar or brush-like clusters of parallel running strings are common directly below the depositional surface (except for C. geigeri) (Fig. 1B, G; M41612, 39, 40), but true merging or splitting of single strings has not been observed. Tubules may taper and their density decreases drastically towards the shell exterior (Fig. 1D, F; M41642). Shells are typically penetrated down to the pallial myostracum, and both ventral to the umbo and beyond it. Tubules do not normally reach the exterior shell surface (Fig. 1B–E), but strong external tubulation was found in the dorsal shell of C. digueti (M41639, 46); this is thought to be explained by tubulation of originally ventral shell portions before these become overgrown by the advancing pallial line. Endolithic borings into the exterior shell are considerably larger and more vermiculate than true shell tubules (Fig. 1D; M41626, 27, 29).

Tubules in Cardita calyculata are very similar to those of Condylocardia, except for their partially sinusous trajectory and the lack of clustering (Fig. 1H). The tubule types of the Arcoidea (Fig. 1I, J; M41658–65) and other outgroups differ significantly in diameter (2–4 times, even wider in some Sphaeriidae), in non-nodular rather than distinctly nodular outline (but see Adacnarca, Fig. 1J; M41661, 62), in nonsinusous trajectory (cf. Cardita) and in the systematic connection to the periostracum rather than a limited penetration depth (Fig. 1D–F, H vs Fig. 1I; M41661, 63) (cf. Waller, 1980; Araujo et al., 1994; Araujo & Korniushin, 1998; Malchus, 2006).

Three hypotheses are derived from these observations. (1) Shell tubules in Condylocardia reflect mantle cell extensions. This view is supported by their similarity to Cardita as shown here and by independent evidence of 'fine tubules' in identical positions in numerous Carditidae (Taylor et al., 1973). It appears unlikely, therefore, that these features represent post-mortem endolithic borings such as the ichnotaxon Scoleia Radke, 1991 (referred to cyanobacteria). (2) The similarity of shell tubules in Condylocardiidae and Carditidae supports their generally accepted close phylogenetic relationship. According to J.C. Carter (personal communication), shell tubules are also present in astartids indicating a much wider distribution of this feature within the Carditoida than is currently reflected in the literature. (3) The difference between carditoid and arcoid shell tubules indicates different functions and/or origins, and perhaps involvement of different cell types. However, an assessment of this hypothesis requires histological examination of the mantle, which was not available for the present study.

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Figure 1. Shell tubules in *Condylocardia*, *Cardita* (Carditoida), *Adacnarca* and *Striarca* (Arcoida). **A.** *Condylocardia hippopus* (LACM 72-64(3)), transverse overview, umbo to right. Lettered arrows indicate approximate position of following images; H, I and J not in transversal plane. **B.** *Condylocardia digueti* (LACM 86-240(4)). Central, depositional surface uppermost. **C.** *Condylocardia geigeri* (LACM 33.173.3(6)). Central, depositional surface uppermost. **D–G.** *Condylocardia hippopus*. **D.** LACM 72-64(2), umbonal, depositional surface at upper left corner. **E, F.** LACM 72-64(1). **E.** Dorso-central, depositional surface uppermost. Inset showing nodular surface of tubules. **F.** Dorsal, innermost shell layer, depositional surface to left. **G.** LACM 72-64(3). Ventral inner layers. **H.** *Cardita calyculata* (SMNH 72265, SEM stub 183-2). Coronal (anterio-posterior) section, central, depositional surface uppermost. Inset slightly more posterior to right. **I.** *Adacnarca limponsides* (SMNH 169, SEM stub 182-3). Ventral sagittal section, depositional surface uppermost. Inset with spongy epithelial tissue in background. **J.** *Striarca lactea* (NMA 29-1), sagittal, posterodorsal of hinge, depositional surface in upper right corner. Ends of tubules dip into the shell. Inset (NMA 26-1). Scale bars: A = 100 μm, B–H = 10 μm, insets E, H, I, J = 5 μm.
REFERENCES


