THE ANATOMY OF *CALLOCARDIA HUNGERFORDI* (BIVALVIA: VENERIDAE) AND THE ORIGIN OF ITS SHELL CAMOUFLAGE

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ABSTRACT

Callocardia hungerfordi (Veneridae: Pitarinae) lives in subtidal muds (-20 to -40m C.D.) and is covered by a dense mat of mud that, effectively, camouflages the shell.

The periostracum is two layered. The inner layer is thick and pleated, the outer thin and perforated. From the outer surface of the inner layer develop numerous, delicate (0.5 μm in diameter), calcified, periostracal needles. These penetrate the outer periostracum. Mucus produced from sub-epithelial glands in the inner surface of the mantle, slides over the cuticle-covered epithelium of the inner and outer surfaces of the inner fold and the inner surface of the middle mantle fold to coat the outer surface of the periostracum and its calcified needles. Increased production at some times produces solidified strands of mucus which bind mud and detrital material into their fabric to create the shell camouflage.

Calcified periostracal needles have been identified in other venerids, including some members of the Pitarinae, but how they are secreted and how the covering they attract is produced and, thus, how the whole structure functions, has not been explained.

INTRODUCTION

The Veneroidea is a large superfamily of modern bivalves which evolved in the Lower Cretaceous and has radiated widely, typically into soft, usually intertidal, sediments worldwide. The largest family is the Veneridae and there are three other small families: the Petricolidae, Cooperellidae, which Morton (1995a) believes should be subsumed by the Petricolidae, and the Glauconomidae (Keen, 1969), studied by Owen (1959). The Veneridae comprises a number of subfamilies and Ansell (1963) described the functional morphology of the British species although no mention was made, for example, in *Gafrarium* (Ohno, 1996), of a shell covering.

Although many venerids have relatively unornamented shells, a number of species in the majority of subfamilies have specialized shell defences, for example, species of *Irus* (Tapetinae) (Morton, 1985) and *Bassina* ($=Placamen$) (Chioninae) have elevated shell lamellae which deter drilling by naticid predators (Ansell & Morton, 1985). Species of *Hysteroconcha* and *Hecuba* (Pitarinae) have long, sharp, shell spines (Carter, 1967) while other genera and species of the Pitarinae (and other subfamilies) are characterized by thick shells and either strong radial or concentric ribbing. *Callocardia hungerfordi* (Sowerby, 1888) is also a member of the Pitarinae and is, on superficial examination, difficult to identify as a bivalve because the shell is covered almost completely by and enclosed within a mat of fibrous mud, forming a soft ball.

Other bivalves build byssal nests in which they are enclosed and include species of *Musculista* and *Arcuatula* (Mytilidae) (Morton, 1973; 1980). Some bivalves, such as species of the Arcidae and the Mytilidae, e.g. *Trichomusculus* (Morton, 1995b), have a 'hairy' periostracum which obscures the shell margin, particularly posteriorly, and yet others, e.g. the lucinid *Rastafaria* (Taylor & Glover, 1997; Glover & Taylor, 1997), build long periostracal tubes which are responsible for determining the pattern of water flow into and out of the mantle cavity and for supplying ctenidial, chemoautotrophic, sulphur-oxidizing bacteria with free and insoluble sulphides from inside the sediment and interstitial water. The petricolid *Cooperella subdiaphana* entombs itself within a 'castle' of mucus-agglutinated mud (Morton, 1995a). Taylor, Glover & Braithwaite (1999) have recently studied the venerid bivalves *Granicorium* (Tapetinae) and *Samarangia* (Samarangiinae) and shown how they cement sand

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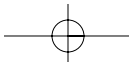
grains to the periostracum of the shell using a pallial secretion to obscure and, thereby, camouflage themselves. Ohno (1996) has shown how six species of *Gafrarium* (Circinae), *Pitar* and *Lioconcha* (Pitarinae) have short, calcified, periostracal needles that help stick sand grains to the shell. Ohno (1996) also reviewed the occurrence of calcified spikes and/or granules embedded within the shell of the Bivalvia and showed that for representatives of the Anomalodesmata, i.e. *Laternula*, *Lyonsia* and *Halicardia*, and *Spengleria* (Myoida), they are within the outer prismatic shell layer and only in *Brachidontes granulatus* (Mytilidae) were aragonitic granules attached to the outer layer of the periostracum.

The shell covering of *Callocardia hungerfordi* superficially resembles mud but this cannot be washed off easily and closer inspection suggests a finely fibrous texture. This study, therefore, had the objectives of investigating the structure of the mat of fibrous mud and, hence, determining how it is produced. That is, assuming it is produced by the bivalve, is it of either byssal or periostracal origin or is it created as a pallial secretion (other than the periostracum) and, if so, from where?

MATERIALS AND METHODS

During April 1998, a trawl survey of the southern and southeastern waters of Hong Kong was conducted using paired beam trawls each of 2.3m width and 25mm cod-end mesh. At each of 48 stations, these were hauled for five minutes bottom time in one fixed direction and in the opposite direction for another five minutes. Single specimens of *Callocardia hungerfordi* were obtained from four of the 48 stations, the positions of which are identified by Leung & Morton (1997, fig. 1).
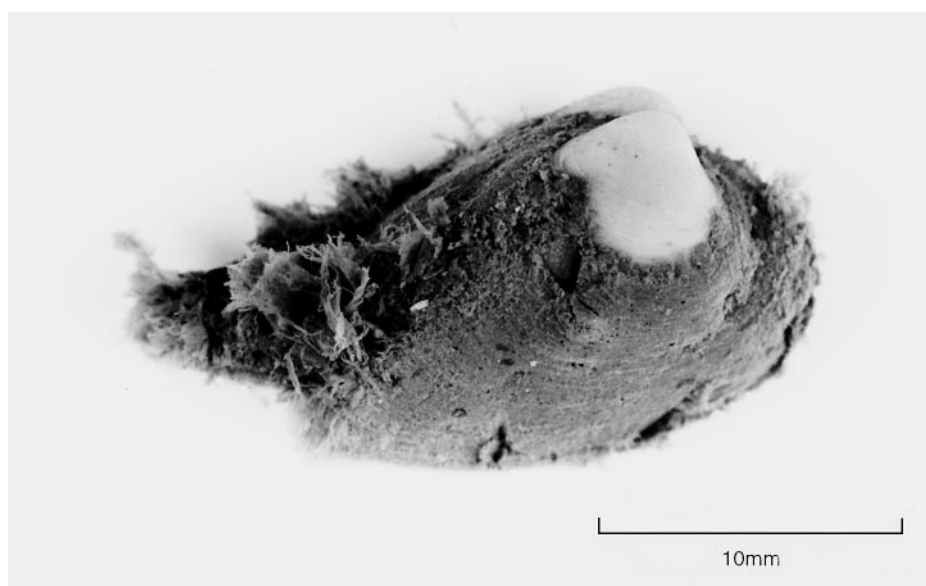
One specimen of *Callocardia hungerfordi* was dissected and details of the anatomy and ciliary currents of the mantle cavity elucidated using carmine suspended in seawater. One individual was fixed in 5% formalin, decalcified and sectioned transversely at 6 μm. One in ten sections was kept and alternate slides stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome.

Two further specimens were sprayed with a fine jet of water to wash off the mud covering their shells. Valves were then removed and fractured into pieces which were oriented on aluminium stubs with double-sided tape. The prepared stubs were air-dried overnight, sputter-coated with gold, and examined in a Leica stereoscan 420 and 440 scanning electron microscope at either 10 or 15 kV accelerating voltage.
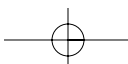
RESULTS

Taxonomy

First described as *Cythera hungerfordi* Sowerby, 1888, the species here under discussion was placed subsequently in the genus *Callocardia* A. Adams, 1864. The type specimen is in the collection of the Natural History Museum,

Figure 1. *Callocardia hungerfordi*. An intact specimen seen from the right side.

London (Reg. No.88.4.2.4), with Hong Kong the type locality. This specimen is illustrated by Vokes (1985) but the shell has no fibrous-mud covering. The oldest, umbonal, component of this shell is a light tan and the younger ventral areas are white, suggesting that it has been cleaned, as often happens in museum collections to bivalves with periostracal spikes and/or coverings of sand grains (Ohno, 1996).

Habe (1977) describes *Callocardia guttata* A. Adams, 1864 from Japanese waters, and places *C. hungerfordi* in junior synonymy with it. Bernard *et al.* (1993) describe the distribution of *C. guttata* as restricted to the South China Sea, Taiwan, Zhejiang, Jiangsu and the Yellow Sea to Honshu, Japan, at depths of between 100–250 m. These authors also suggest that *C. hungerfordi* is a junior synonym of *C. guttata* but Scott (1994) does not accept this. Until the status of the two species is determined, therefore, it seems better to retain the name *C. hungerfordi* for the species described in this study, especially as specimens match most closely the type (and like it, are from Hong Kong) and less so the more truncate type of *C. guttata* (from Japan).

Scott (1994, plate 10A) has illustrated a dried shell of *Callocardia hungerfordi* (Sowerby, 1888) from Hong Kong and a second specimen is shown in Figure 1, here illustrating the posteriorly exaggerated shell covering of fibrous mud and detritus.

Distribution in Hong Kong

Callocardia hungerfordi is restricted locally to the southern waters of Hong Kong (Lueng & Morton, 1997). Trawl surveys of Hong Kong waters in 1992, 1995 and 1998 only record it from Stations 10 (1992, 1995 and 1998), 13 (1992 and 1995), 18 (1992 and 1995), 22 (1992, 1995 and 1998), 28 (1998) and 29 (1992, 1995 and 1998) (Leung & Morton, 1997, fig. 1) at depths of 29m, 40.5m, 31.4m, 34.7m, 19.8m and 23.8m, respectively, and from the sandy (Station 10) but, mostly, muddy sea bed (all other stations).

Anatomy

The shell

The shell of *Callocardia hungerfordi* is white and unornamented. The largest specimen collected was 12 mm in shell length although this is difficult to measure externally in intact specimens, because of the covering of fibrous-
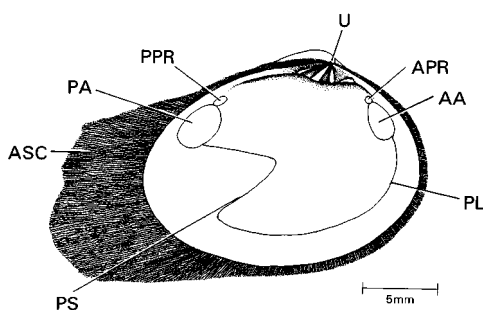
Figure 2. *Callocardia hungerfordi*. An internal view of the left shell valve (For abbreviations see page 30).

mud. The shell is equivalve and, when seen from the inside slightly inequilateral, i.e. posteriorly slightly elongate (Fig. 2). The shell is covered by a dense mat of fine fibres that entraps a mass of mud and detritus, except umbonally, where it is presumably eroded away. This soft, fine, mat conceals the shell margin and is especially long posteriorly (ASC), giving the impression that the shell is more posteriorly inequilatreal than is actually the case.

Internally, the pallial line (Fig. 2, PL) is recessed deeply within the shell margin and the pallial sinus (PS) is long. There are the usual anterior (AA) and posterior adductor (PA) muscle scars and, internal to them, smaller anterior (APR) and posterior pedal retractor (PPR) muscle scars.

The siphons

The siphons of *Callocardia hungerfordi* are long (Fig. 2, IS; ES) and are illustrated in more detail in Figure 3. The siphons are united along their length by fusion of the inner mantle folds only, this being type A (Yonge, 1957; 1982). Both siphons are pigmented slightly brown at their tips. The inhalant siphon has an apical circle of between 20–22 large papillae; that of the exhalant has an apical crown of between 18–20 smaller ones. Only the tips of the siphons project from posterior mat of fibrous mud.

Organs of the mantle cavity

The organs of the mantle cavity and the broad arrangements of their ciliary currents in *Callocardia hungerfordi* are illustrated in Figure 4A. The ctenidia are small, with the outer demibranch (OD) smaller, dorso-ventrally, than the inner (ID) and located in the dorsal region of the mantle cavity. The ctenidia are eulamellibranch, homorhabdic and non-plicate. The
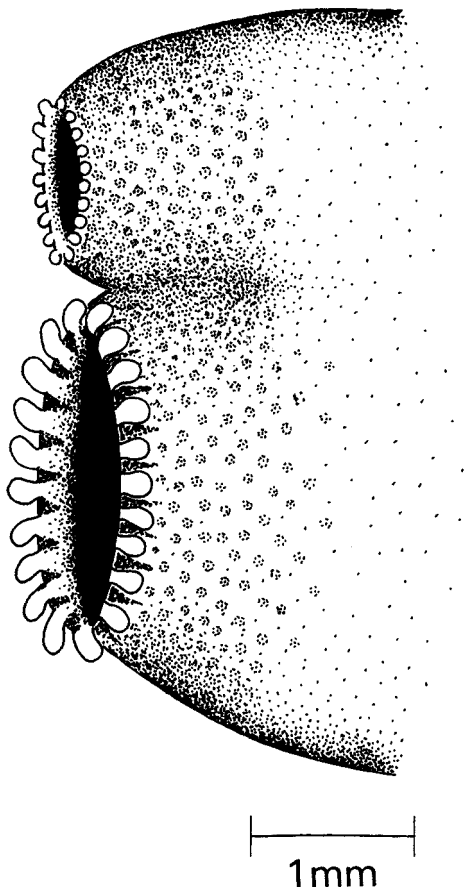
Figure 3. *Callocardia hungerfordi.* The tips of the siphons as seen from the right side. The exhalant siphon is dorsal.

ciliary currents of the ctenidia are illustrated in transverse section in Figure 4B and oral acceptance tracts (●) are located in the ctenidial axes and in the ventral marginal food grooves of the inner demibranchs only. The ciliary arrangement is thus of type C(1) (Atkins, 1937). The ctenidial-labial palp junction is of Category II (Stasek, 1964). The labial palps (IP; OP) are long but, otherwise, the ctenidia and labial palps are of the typical venerid plan (Ansell, 1963; Morton, 1985).

Ciliary rejection tracts on the visceral mass (VM) propel unwanted filtered material downwards towards a major posteriorly-directed rejection tract at the junction of the visceral mass (VM) and large foot (F). Such material arriving at the posterior edge of the visceral mass, falls onto the mantle. The foot is large

and active and does not possess a byssus.

The ciliary currents of the mantle all beat downwards towards the ventral mantle margin where material is accumulated in a rejection tract (RT) on each lobe and passed posteriorly. Accumulated pseudofaeces are rejected from the mantle cavity *via* the inhalant siphon.
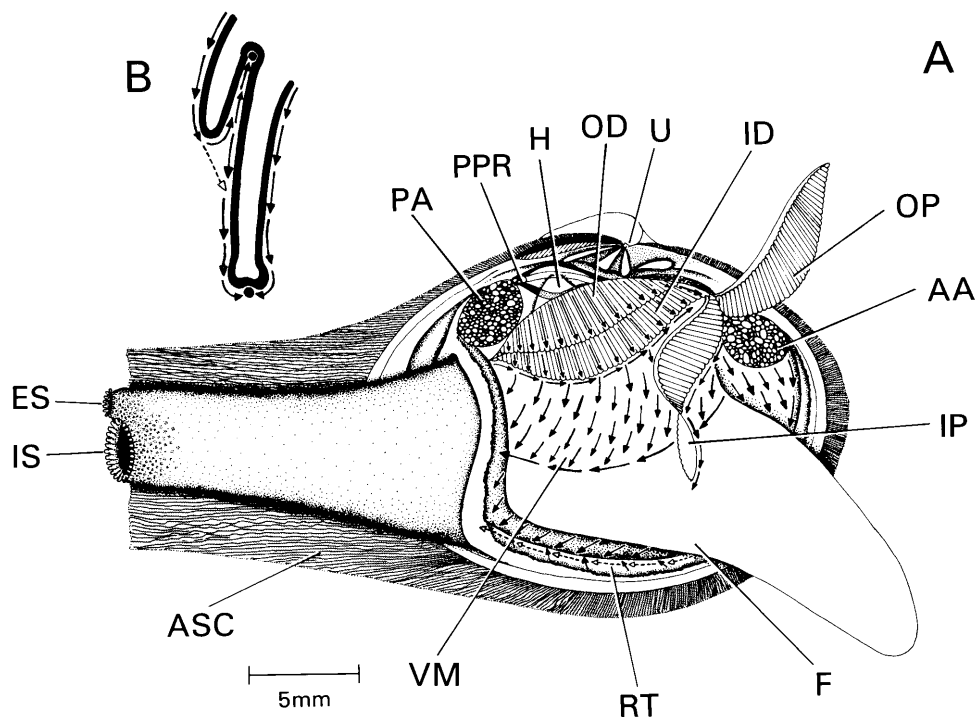
The ciliary currents of the mantle cavity are thus typical of a generalized venerid and are concerned, in the presence of small ctenidia, large labial palps and strong rejection tracts in the mantle cavity, with the processing, acceptance, but mostly rejection, of fine particles of mud that probably enter the mantle cavity, commensurate upon the habit of *Callocardia hungerfordi* living within soft, subtidal, substrata.

The mantle margin

The mantle margins are unfused ventrally, creating a long pedal gape, but fuse posteroventrally to form the long, united, siphons.

The mantle margin is illustrated in Figure 5. It comprises the usual three folds, inner (IMF), middle (MMF) and outer (OMF). There is a long pallial retractor muscle (PRM), reflecting how the pallial line is deeply inset from the shell margin. The general mantle above the inner fold is capacious and contains a large sub-epithelial gland (PG(1)) which stains blue in Ehrlich's haematoxylin and eosin and Masson's trichrome. It thus produces mucus. The inner fold is large and possesses a sub-epithelial gland (PG(2)) that also stains blue in Masson's trichrome but is of a different structure to PG(1), in comprising discrete cells only some 10 μm in diameter. The junction of the inner fold with the general mantle is marked by a strongly-ciliated rejectory tract (RT). The middle fold is long and thin and contains elements of the inner fold gland (PG(2)). This fold is reflected intimately over the small outer fold which also possesses a few small elements of a yet third, blue-staining, gland (PG(3)). Between the two latter folds is a long periostracal groove which secretes a two-layered periostracum. The periostracum is covered by the thick mat of fibrous mud to be described in more detail later (ASC).

The mantle margin is illustrated in greater detail in Figure 6. The outer mantle fold (OMF) is small and thin, as described earlier, and contains sub-epithelial blue-staining glands (PG(3)), some 20 μm in diameter. The middle fold (MMF) is also small and thin, but its inner surface is convoluted and covered along its

Figure 4. *Callocardia hungerfordi*. **A.** An internal view of the organs and ciliary currents of the mantle cavity as seen from the right side after removal of the right shell valve and mantle lobe. **B.** A transverse section through the right ctenidium showing the ciliary currents and oral acceptance tracts (●) (For abbreviations see page 30).

entire length by a cuticle (CL) that is probably produced by the glands contained within the sub-epithelial space of this and the inner mantle folds (PG(2)). These are some 10 μm in diameter. As noted earlier, the middle fold is associated intimately with the outer and between them is the long periostracal groove and contained periostracum (ILP; OLP).

The general surface of the mantle above the pallial line contains a wide haemocoel (Fig. 7A). The outer surface of the mantle (OPE) is a cuboidal epithelium while that of the inner (IPE) is squamous. Both are cross-connected by diagonal muscle fibres (TF) and the haemocoel contains blood cells (BC).

The inner surface of the middle mantle fold is illustrated in greater detail in Figure 7B. The epithelium, as noted above, is covered by a cuticle (CL), some 2–3 μm thick and, presumably, secreted by the sub-epithelial gland cells (PG(2)) beneath it.

The periostracum beyond the shell margin is illustrated in greater detail in Figure 7C. Overlying the outer surface of the mantle (OPE) and the (decalcified) shell is the periostracum. The inner layer (ILP), staining blue in Ehrlich's haematoxylin and eosin, becomes progressively much thicker, has a layered appearance and is folded into radial concentric pleats. It is covered by the red-staining outer periostracum (OLP) which is thin (~ 2 μm) and possesses many holes some 1 μm in diameter. Between the outer surface of the periostracum is an apparent space (PNS) that, as will be described, is usually occupied by the calcified (but here decalcified) periostracal needles. This, in turn, is covered by the mat of fibrous mud (ASC). The mat comprises a basal layer of blue-staining strands from which arise at regular intervals other, long, blue-staining strands. The spaces between these are filled with fine particles of mud and other detrital material (FD), creating the mat of fine fibres (ASC) which covers the shell. At higher magnifications, the blue-staining strands which give the shell mat its fibrous appearance have no structure, i.e. they are not periostracal or byssal in origin, but are strands of solidified mucus.
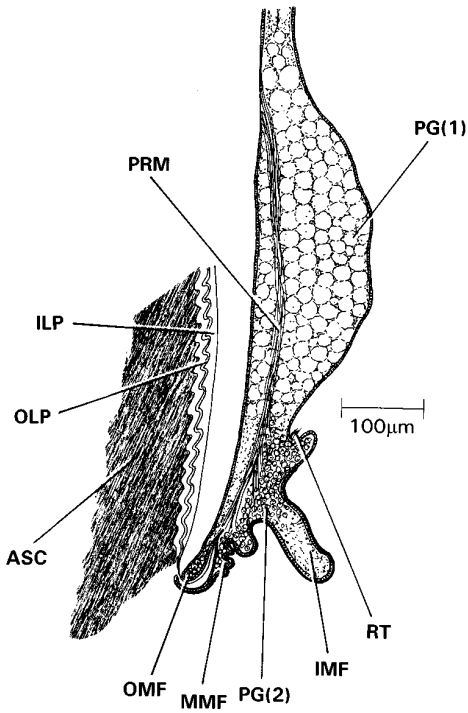
Figure 5. *Callocardia hungerfordi.* A transverse section through the right mantle lobe (For abbreviations see page 30).
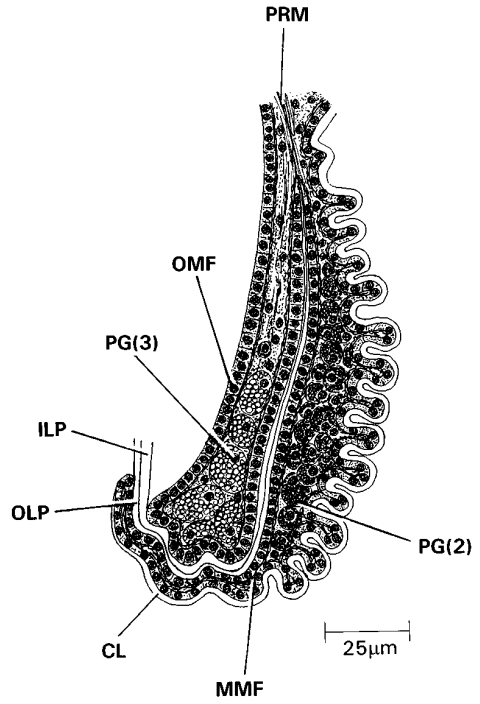
Figure 6. *Callocardia hungerfordi.* A transverse section through the middle and outer mantle folds of the right mantle lobe (For abbreviations see page 30).
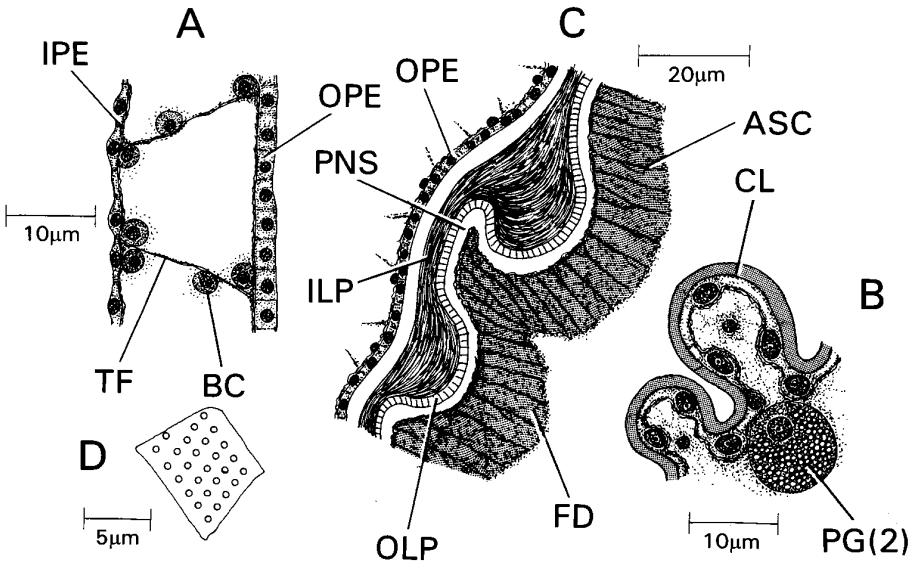
Figure 7. *Callocardia hungerfordi.* **A.** a transverse section through the general mantle; **B.** a section through the inner surface of the middle mantle fold; **C.** a transverse section through the outer surface of the mantle, the periostracum and the covering of mucous threads and mud and **D.** a surface view of the outer layer of the periostracum (For abbreviations see page 30).
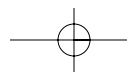
In places, the outer periostracal layer detaches from the inner and can be seen in surface view (Fig. 7D). It contains numerous holes which seem to be arranged in a regular pattern and are some 1 μm in diameter.

The calcified periostracal needles

With decalcification for sectioning, staining and examination at the light microscope level, the periostracal needles of *Callocardia hungerfordi* cannot be seen. They are visible, however, by scanning electron microscopy (Fig. 8).

At low power, the needles are seen as rods ~ 0.5 μm in diameter that have a generally regular arrangement on the periostracum (Fig. 8A). This is not always so, however, and they can occur as dense clusters (Fig. 8B). Because of the spraying with a water jet to remove the mat of fibrous mud and detritus from over them, it is uncertain how long undamaged needles are, but they are at least 20 μm. That the fibrous-mud covering to the shell adheres closely to the apices of the needles is shown in Plate 8C and to comprise the finest particles of detritus and inorganic grains of sandy-mud. The needles are shown in greater detail in Figure 8D and to arise from the inner layer of periostracum and pierce the outer layer. The attachment, or origin, of the needles on the outer surface of the inner layer of periostracum, is at pits (Fig. 8E).
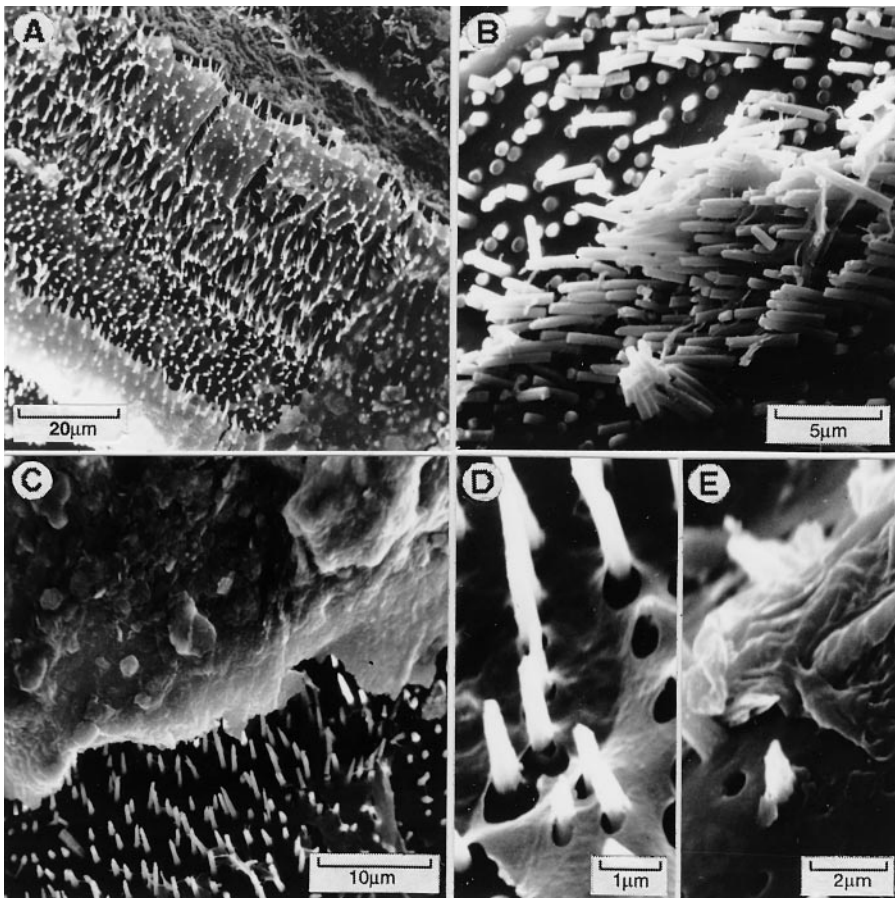
Figure 8. *Callocardia hungerfordi.* **A.** An SEM photograph of the surface of the periostracum with regularly arranged rows of calcified periostracal needles; **B.** A more detailed view of a mass of periostracal needles. **C.** An SEM photograph of the calcified periostracal needles and the mat of overlying mud particles and detritus; **D.** A more detailed picture of the calcified needles piercing the outer layer of periostracum and **E.** Needles arising from the outer surface of the inner layer of periostracum in pits.

DISCUSSION

Callocardia hungerfordi lives in soft subtidal muds in the southern waters of Hong Kong at depths of between −20 to −40 C.D. and is, as this study of the anatomy demonstrates, a typical venerid in terms of structure and the morphology and arrangements of the organs in the mantle cavity except for the mat of mud that covers its shell, effectively camouflaging it. It is superficially similar to the soft, gelatinous, fibrous-mud nest of *Arcuatula elegans* (Mytilidae) (Morton, 1978) except, in the latter case, the fibres are thin byssal threads although the mucus binding the whole structure together is produced, as in *C. hungerfordi*, from large glands in the mantle. The byssal nest of another mytilid, *Musculista senhausia*, is less gelatinous and the pallial glands are proportionately smaller (Morton, 1973). Although such a covering may help to stabilize *A. elegans* and *M. senhausia*, and *C. hungerfordi*, in their muddy habitats, it seems probable that another function is to camouflage them against predators. The effectiveness of such cocoons in this respect has not yet, however, been examined and this study asks first: how is the shell covering of *C. hungerfordi* formed?

The periostracum of *Callocardia hungerfordi* comprises two layers, the outer being perforated. From the outer surface of the inner layer of periostracum, long, calcified, needles are produced that penetrate the outer layer and project from its outer surface. Onto this array of needles is poured, marginally, a coating of mucus. This mucous sheet is produced periodically into long solidified strands that trap particles and mud and detritus and which adhere to them, and thus to the periostracal needles below, to create the shell covering of fibrous mud.

The mucous strands cannot be secreted as periostracum, there being no pallial secretory surface that could achieve this. They are also not byssiferous. There is, however, the large gland (PG(1)) discharging into the mantle cavity above the inner mantle fold. The inner and outer surfaces of the inner folds and the outer surface of the middle folds are, moreover, covered with cuticle, right to the tip of the latter and immediately adjacent to which arises the outer surface of the periostracum. It is believed that the gland PG(1) produces mucus which slides easily over the cuticular covering of the inner and middle folds to, thus, be poured over the surface of the periostracum and attach to the calcified periostracal needles which are also

being formed and starting to grow marginally. Periodically increased production of mucus, creates the strands and to which mud grains and detritus particles adhere. Enlarging progressively with age, the mat continues to attract and has attached to it fine mud and detrital particles so that eventually a soft, posteriorly-elongate, ball is produced around most of the shell. In all bivalves where an enclosing 'nest', e.g. *Arcuatula elegans* (Morton, 1980), or 'castle', e.g. *Cooperella subdiaphana* (Morton, 1995a), is constructed, the binding secretion of mucus is produced by the mantle.

Calcified needles similar to those described above have been studied in other venerids, notably species of *Gafrarium*, *Lioconcha* and *Pitar* by Ohno (1996), and to which are attached material from the habitats occupied, namely sand grains and not the fine particles of mud and detritus here reported upon for *Callocardia hungerfordi*, although the shell and needles of *Lioconcha castrensis* are reported by Ohno (1996, p. 307) to be covered with 'silk yarn luster.'

Ohno (1996) was, however, ambiguous as to how the periostracal needles were produced, describing them as follows: 'needle formation begins and is completed **on** the periostracum stretched between the periostracal groove and the growing valve edge' (p. 309) but, also, 'the base of an aragonitic needle breaking **through** the periostracal sheet'. This study now clarifies the situation; it is the latter.

The heterodont Veneroidea arose in the Lower Cretaceous and has radiated widely into, mostly, soft sediments. The order is diverse and has a virtually world-wide distribution mostly in intertidal and shallow subtidal habitats. Carter & Aller (1975) have studied calcified spicules in the periostracum of a number of molluscan lineages, and suggest that their occurrence is a primitive feature. Given the relatively modern age of the Veneridae, however, the calcified periostracal needles and their attached ball of mucous-bound mud identified here for *Callocardia hungerfordi* would seem to be an adaptation to, principally, avoid predation although this needs to be examined. For the venerids studied by Ohno (1996), however, where the needles are short, it was suggested that they increase the friction of the shell surface and, thereby, increase the stability of the individual in loose, sandy, sediments. This may also be a function of the mat of mucous-bound mud in *C. hungerfordi* living, as it does, in soft subtidal muds.
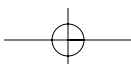
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ABBREVIATION USED IN THE FIGURES

AA	Anterior adductor muscle (or scar)	OLP	Outer layer of periostracum
APR	Anterior pedal retractor muscle	OMF	Outer mantle fold
ASC	Amorphous shell camouflage	OP	Outer labial palp
BC	Blood cell	OPE	Outer pallial epithelium
CL	Cuticle	PA	Posterior adductor muscle (or scar)
ES	Exhalant siphon	PG(1)	Pallial gland (1) in the inner mantle
F	Foot	PG(2)	Pallial gland (2) in the inner and middle mantle folds
FD	Fragments of detritus		
H	Heart	PG(3)	Pallial gland (3) in the outer mantle fold
ID	Inner demibranch		
ILP	Inner layer of periostracum	PL	Pallial line
IMF	Inner mantle fold	PNS	Periostracal needle space
IP	Inner labial palp	PPR	Posterior pedal retractor muscle
IPE	Inner pallial epithelium	PRM	Pallial retractor muscle
IS	Inhalant siphon	PS	Pallial sinus
MMF	Middle mantle fold	RT	Rejection tract
OD	Outer demibranch	TF	Transverse fibres
		U	Umbo
		VM	Visceral mass