

# THE MOLLUSCAN PERIOSTRACUM: AN IMPORTANT CONSTRAINT IN BIVALVE EVOLUTION

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**ABSTRACT.** The temporary, and often inconspicuous, nature of the bivalve periostracum has led to its relative neglect. As the first part of the valve to be secreted, onto which the calcareous shell is then deposited, the periostracum has great potential in governing basic valve form. Herein, periostracal thickness is shown to be an extremely variable character amongst members of the Bivalvia but within specific clades and life habits the range of variation is much narrower. It is suggested that differences in periostracal thickness have played a vital rôle in the evolution of different bivalve clades acting as an important preadaptation and constraint in the formation of various valve morphologies. Fine flexible periostraca allow the manufacture of intricate shell morphology and ornamentation, whilst a thickened sheet protects the calcareous part of the shell against environmental and biotic agents of dissolution.

Despite the poor preservation potential of the molluscan periostracum, its evolution and its primitive state are worthy of consideration. The distribution of periostracal thickness in Recent bivalves and the relative lack of fine ornament in early members of the class suggest that it was of at least moderate thickness. The findings of this survey have potential relevance to other molluscan classes and other phyla which use an analogous method of shell construction.

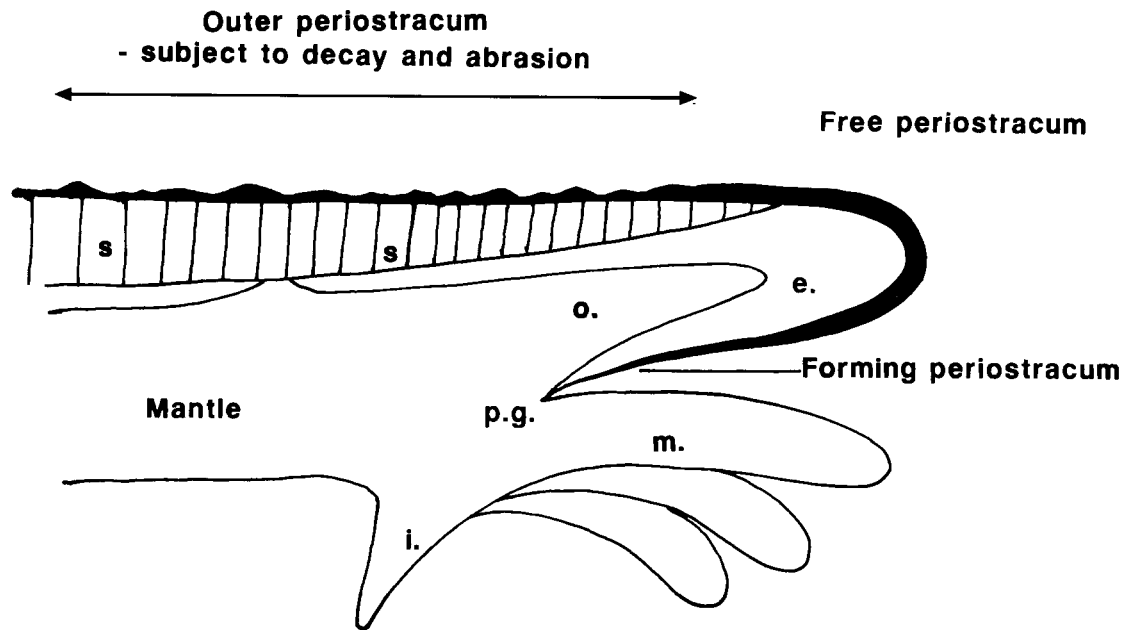
COMPARED with the attention that has been given to the microstructure of the calcareous part of the bivalve shell (e.g. Taylor *et al.* 1969, 1973; Carter 1990), little study has been made of its outer organic layer. The periostracum is the layer of sclerotized protein which covers the exterior of the calcified shell of all shell-bearing molluscs, with the exception of members of the Polyplacophora. It is, however, easily removed by decay processes and hence its presence may often be overlooked. Within the class Bivalvia this organic sheet is of very variable character. It may be very obvious, as in the brilliant green outer covering of *Perna viridis*, or the shaggy outer layer of many arcoids, whilst in other taxa, for example ostreoids and pectinoids, it is scarcely detectable beyond the extreme valve edge. The occurrence of this organic layer as a discrete conchological entity was first recognized by Gray (1825) who named it the periostracum. Although he believed this structure to be wholly organic, more recent studies have shown that the periostraca of certain members of the Mytiloidea, Modiomorpha, Myoidea and Pholadomyoidea also contain calcareous elements embedded within the protein (Carter and Aller 1975; Bottjer and Carter 1980).

This paper considers some of the variation seen in the periostraca of Recent bivalved molluscs in particular in relation to their taxonomic position and their life habits, and considers its importance in the evolution of the class.

## PERIOSTRACUM FORMATION AND FUNCTION

The periostracum is the first part of the shell to be formed. In the embryo, periostracum is secreted by the cells that border the shell gland (Kniprath 1979), whilst later in ontogeny this task is taken over by mantle tissue. With the increasing interest in the mechanisms of biomineralization (Carter 1990), periostracum formation has been studied in various gastropod and bivalve taxa, the findings of which have been reviewed excellently by Saleuddin (1980), Saleuddin and Petit (1983) and Watabe (1984). The process is briefly summarized here.

As with the rest of the shell, the periostracum is secreted by the mantle folds (Text-fig. 1).



TEXT-FIG. 1. Simplified valve and mantle margins of a generalized bivalve illustrating periostracum formation, following Saleuddin and Petit (1983). e. = extrapallial space; i. = inner mantle fold; m. = middle mantle fold; o. = outer mantle fold; p.g. = periostracal groove; s. = calcareous shell.

Saleuddin and Petit (1983) divided the periostracum into three zones; forming, free and outer periostracum. These terms are instructive when considering the development of the sheet and its function, although some of the terminology when referring to the inner and outer faces of the sheet is rather confusing. In the present account the inner face of periostracal sheet refers to the surface which is always closest to the cells of the outer mantle fold. The *forming periostracum* is initiated by cells at the base of the periostracal groove which lies between the outer and middle mantle folds. From here it moves ventrally as a continuous sheet between the two mantle folds, in close association with the middle fold. Epithelial cells of the middle fold along the route are responsible for further secretions thickening the sheet by addition of outer layers, and maturing it. Maturation involves sclerotization by quinone tanning, a process which has been investigated for *Mytilus edulis* by Waite and Anderson (1980) and *Perna viridis* by Barrantheni and Ramalingham (1989). The *free periostracum* spans from the edge of the mantle lobe to the extreme valve edge. Here it is freed from the influence of the mantle cells, being bathed on its inner surface by the extra-pallial fluid and on the outer surface by sea water. From this point no further thickening may occur. Just beyond the edge of the calcified shell the sheet doubles back upon itself, dorsally, so that it now covers the outside of the mantle lobe, becoming the *outer periostracum*. It is on to the inner surface of the reflected sheet that the calcareous shell is now seeded from the extra-pallial fluid. Exposed on the outside of the shell, the *outer periostracum* is subject to thickness diminution by physical and biotic abrasion and to fungal and bacterial decay.

The primary rôle of the periostracum is believed to be in shell secretion (Taylor and Kennedy 1969). Here it has two principal functions: first, as a template on which the calcareous part of the shell is initiated; Taylor and Kennedy (1969) have shown the intimacy between the periostracum and crystal growth by demonstrating the continuity of protein of the periostracum with that of the organic sheaths which surround the aragonite prisms of *Margaritifera margaritifera*; second, by providing a barrier between the extra-pallial space and the external aqueous environment, so allowing crystallization of either calcite or aragonite to occur in a compartment isolated from the

inhibiting presence of magnesium ions from sea water and from contamination by sediment (Clark 1976). In addition to these important rôles in shell secretion, a number of secondary functions have also been identified: protection of shell from the corrosive effects of acidic water (Tevesz and Carter 1980); protection from infestation by epibionts and endoliths (Bottjer 1981), and deterrence of predatory borers (Harper and Skelton 1993a). Araujo *et al.* (1994) showed the presence of extensions between the mantle and the periostracum in *Corbicula fluminea* and pointed out that these may allow the latter to play an active rôle in monitoring the environment also. These projections do not, however, penetrate the periostracal sheet.

Although there is a wealth of fine descriptive papers on the biology and functional morphology of a wide range of bivalves (see Morton 1992), few authors provide details of the periostracum. It is only in those taxa when it is conspicuously 'odd' (for example having a distinctive colour or ornament), and hence a useful character in species identification, that the periostracum is described. In most Recent taxa it seldom lasts intact throughout the life span of the mollusc, let alone surviving taphonomic processes. This poor preservation potential has led palaeontologists to pay even less attention to the periostracum than zoologists. There are very few published accounts of fossilized periostracum (discussed later). However, given the pivotal rôle that the periostracum plays in the construction and maintenance of bivalve (and most other molluscan) shells, particularly in the construction of ornament, it is likely to have also been influential in their evolution. Yet despite this importance there has so far been no attempt to discuss the taxonomic and adaptive significance of this variation.

#### PERIOSTRACAL THICKNESS IN THE BIVALVIA

Even a cursory foray through the literature on Bivalvia reveals that one of the periostracal characters which is most variable is thickness. It is, generally, those taxa with the greatest periostracal thickness that have the more persistent and hence more conspicuous periostraca, and the literature on bivalve periostraca is biased towards the description of these. Detailed accounts of its formation and structure have dwelt on taxa with substantial periostraca, for example *Mytilus edulis* (Dunachie 1963), *Anodonta cygnea* (Bubel 1976), and *Astarte castanea* and *A elliptica* (Saleuddin 1974). Such a bias is, at least partly, explained by the relative ease of manipulation and investigation of these more robust structures compared with the gossamer-thin sheets of other bivalves. In the literature, terms referring to thickness include 'thick', 'thin' and 'excessively thin'. Using such qualitative terms may be misleading for, often, taxa with darker periostraca give an erroneous impression of being thicker than those which are more translucent, and the lack of agreed conventions about these descriptions means that they are very subjective and of little use when comparing taxa. For example, Morton (1974) refers to the periostracum of *Cleidotherus maorianus* as 'thin', yet it is at least an order of magnitude thicker than that of virtually all pteriomorphs and of many of the heteroconchs. Precise measurement, however, may be difficult, and the value obtained will vary depending on where it was taken, lower values being recorded in the forming periostracum where it is yet to attain its full thickness, or the outer periostracum where material has been lost. For comparative purposes it is essential that measurements are made from the free periostracum where thickness is neither increasing or decreasing, or from the outer periostracum in cases where it is judged to be intact. Although the periostracum produced by the very earliest juvenile individuals is less substantial than that of the full-grown adult, no evidence has been published of thickness variation in the dissoconch stage of any taxon.

Is periostracal thickness important? Are various clades characterized by periostracum of a particular range of thicknesses? A number of possible links between periostracal thickness and various life habits and surface ornamentation may be suggested: e.g. Harper (1992) suggested that an ultra-thin periostracal sheet is essential for the cementation process, whilst Taylor and Kennedy (1969) and Kennedy *et al.* (1969) pointed out that bivalves which use chemical secretions to bore into hard substrates are covered in thick, protective periostraca. Are such perceived links important preadaptations in the evolution of certain habits, selected by that particular habit (i.e. adaptive) or merely coincidental? In this context the term preadaptation is used as defined by Skelton (1985,

p. 95) as 'a feature or a complex of features of an organism, whether already serving a functional role or merely a constructional product, which by virtue of its *fortuitous* suitability for novel functional effects becomes *co-opted* as a new adaptation...in descendants of the organism'. There is no implication of consciousness.

Since the periostracum is the first formed part of the shell and subsequent shell layers are deposited onto it, it must form the template for the ornamentation of the outside of the valve. It is not possible to create the calcareous part of the shell in a particular shape unless this has already been described by the periostracum. Thus the intricacy and extravagance of the surface ornamentation must depend, at least in part, on the flexibility of the periostracal sheet. In this context, surface ornamentation is taken to mean the occurrence of ribs, spines, flanges, furrows and ridges and tubercles on the external surface of the calcareous shell. Two models for the production of valve ornament in bivalves (or indeed other molluscs) may be advanced: (1) the periostracum maintains a constant thickness and the ribbed ornament is achieved by folding the sheet; and (2) the periostracum is of variable thickness and the inner surface is sculpted to provide a negative of the ornament. Can studies of periostracal thickness be used to differentiate between these two models? In order further to investigate these questions, the taxonomic and adaptive significance of periostracal thickness within the *Bivalvia* is discussed in detail below.

#### MATERIALS AND METHODS

Collections of living bivalves were made during field work in the United Kingdom, Hong Kong, Panama and the eastern coast of Australia. Entire animals were fixed in either 3 per cent. glutaraldehyde, 70 per cent. ethanol or 5 per cent. neutral formaldehyde, depending upon availability. In order to sample as large a range of taxa as possible, covering a wide geographical area, material was also assembled from the 'wet' collections of The Natural History Museum (London) and the Australian Museum (Sydney), whilst Antarctic species were made available by S. Hain from the Alfred-Wegener Institute (Bremerhaven, Germany). In all cases only fully grown animals were used.

In the majority of cases fixed animals were opened and mantle tissue was excised from the ventral edges of the right mantle lobe. Although it has yet to be demonstrated conclusively that there are any significant differences between various characters of the right and left mantle lobes of any bivalve species, this consistency of approach was used to negate the effect of any such variation. It is not anticipated that the mantle lobes of equivalve taxa are any different, but the possibility cannot be discounted for those which have inequivalve or discordant morphologies. Once so obtained, the mantle tissue was dehydrated through a series of acetones and then critical point dried, using carbon dioxide as the ambient fluid, in the manner described by Martill and Harper (1990).

In taxa which possess a particularly thick periostracum the time-consuming process described above was avoided. In these instances individuals were inspected with a binocular microscope to select areas with no damage to the periostracum on the ventral shell margin (therefore no thickness loss) and these areas removed.

Once so prepared the specimens were mounted on stubs, sputter coated with gold and inspected using scanning electron microscopy (Jeol 820). Periostracum suitable for measurement was identified as it emerged between the mantle folds and the specimens were tilted so that the fractured edge of the periostracum was perpendicular to the electron beam so as to reveal true thickness. The fractured edges were photographed for later measurement; additional information, such as the presence of spicules, vacuoles, obvious layering and hairs, was also noted.

Additional thickness data were also obtained by recording existing measurements mentioned in the literature, or by measuring directly from previously published photographs. Caution was required in this approach because it is uncertain from which part of the periostracum these were taken. Only 7 per cent. of the data-base was acquired in this manner.

The possibility of intraspecific variation of periostracal thickness must be considered, particularly as the time involved in preparation and the scarcity of some of the material meant that it was

often impracticable to make measurements from more than one individual. Without carrying out an extensive survey it is impossible to rule out such a problem; however, earlier work (Harper 1992) on the mantle margins of several hundred individuals of the oysters *Crassostrea gigas* and *Ostrea edulis* revealed no significant variation in periostracal thickness. Comparison of measurements made in this study with figures published by other authors for the same taxa also revealed no significant differences. However, intraspecific variation does occur: periostraca of *Mytilus edulis* from different localities showed a variation of some 20 per cent. in sheet thickness (Harper 1991).

In order to examine the two models of ornament formation, individuals of bivalve taxa with strong radial ornament, such as the mytiloids *Septifer virgatus*, *Geukensia demissa* and *Hormomya mutabilis* and the veneroids *Donax panamensis* and *Prototharca megintyi* (which had intact periostracal cover) were selected. These valves were cut along lines normal to the radial ornament and then studied using SEM. Specimens of *Mya truncata*, an anomalodesmatan bivalve, were also examined. Although largely smooth, they commonly show wrinkling on the posterior part of the shell. The task of examining the relationship between periostracum and more intricate styles of ornamentation, such as spines and flanges, was rather more problematical, as there is no universally accepted measure of valve ornament. Although Stanley (1970) produced an ornamentation index for his study on burrowing efficiency, it is unsuitable for the present work because it deals with overall relief rather than expressing the radius of curvature, ornament depth, spacing or aspect. Instead Nicol's (1965) survey of spinose and non-spinose families was used as a basis of the analysis.

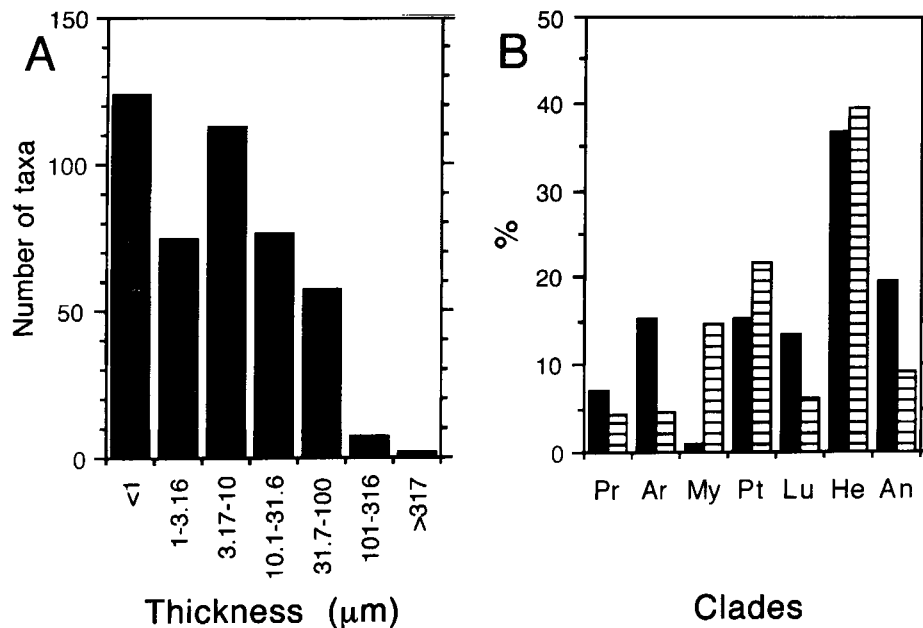
#### RESULTS AND ANALYSES

Periostracal thickness measurements were obtained for more than 450 bivalve species. The data are presented in Appendix 1. For analysis, each taxon was assigned to its family, and hence into one of the seven major groupings used by Skelton *et al.* (1990): protobranchs, arcoids, mytiloids, periomorphs, heteroconchs, lucinoids and anomalodesmatans, which they regarded as monophyletic clades. Each taxon was also assigned to one of five life habits: burrowing within a soft sediment (with some distinction between shallow and deep burrowers), byssate attachment, boring into hard substratum, attachment to a hard substratum by cementation and free-living on the sediment-water interface. Such designations were based on either personal observation at the time of collection, previously published accounts, or on functional morphological criteria (as in Stanley 1970). Stanley (1970) recognized a further two types of life habit: nestling and reclining. Most nestlers are also byssally attached and so these bivalves were placed in the latter category (see also Nicol 1983), and the recliners were grouped with the free-livers.

A very wide range of periostracal thickness was recorded from values of less than 1  $\mu\text{m}$  in a number of taxa to 428  $\mu\text{m}$  in the mussel *Musculus laevigatus*. Within this range nearly 60 per cent. of those taxa studied had periostraca less than 10  $\mu\text{m}$  thick. Such a wide range with its strong negative skew makes linear plots difficult to handle and, therefore, it was decided to utilize a logarithmic scale. This led to the recognition of seven thickness classes (Table 1).

TABLE 1. Periostracal thickness classes and their descriptive terms.

| Thickness ( $\mu\text{m}$ ) | Descriptive term used herein |
|-----------------------------|------------------------------|
| < 1.0                       | Ultrathin                    |
| 1.0-3.16                    | Thin                         |
| 3.17-10.0                   | Moderate                     |
| 10.1-31.6                   | Thick                        |
| 31.7-100                    | Very thick                   |
| 101-316                     | Grossly thickened            |
| > 317                       | Grossly thickened            |



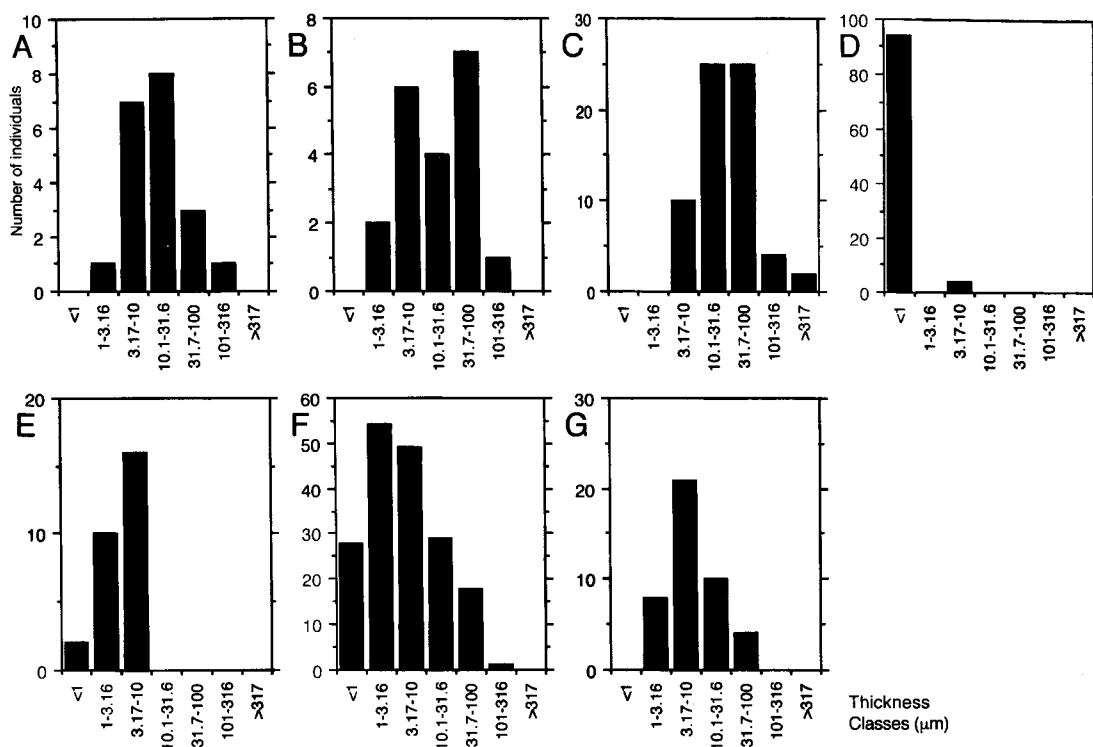
TEXT-FIG. 2. A, distribution of periostracal thickness for the entire data set. B, histogram demonstrating the bias of the data set; dashed bars show the percentage of extant bivalve families which fall into each clade and solid bars the percentage of taxa from this study belonging to each. An = anomalodesmatans; Ar = arcoids; He = heteroconchs; Lu = lucinoids; My = mytiloids; Pr = protobranchs and Pt = pteriomorphs.

#### Taxonomic variation

Text-figure 2A shows the distribution of periostracal thickness observed for the entire data set. Such a plot cannot be considered as representative of the variation in this parameter for the class Bivalvia, as it is undoubtedly biased by the specifics of the set, for example by the over-representation of pteriomorphs and mytiloids and the comparatively low number of anomalodesmatan, lucinoid and arcoid species measured (Text-fig. 2B). Only the lucinoids were seriously under-sampled; of the 13 extant families only seven were investigated. Such incomplete coverage was, in part, due to the small size and fragility of members of the missing families, and their paucity in museum collections. Both of these reasons are in turn the result of their mainly cryptobysate habits (Yonge and Thompson 1976). Histograms showing the range of periostracal thickness recorded in each clade are given in Text-figure 3, and are discussed below, together with statistical analyses of their significance.

*Protobranchs.* Members of the protobranch clade are characterized by a moderate to thick, obvious and persistent periostracum (Text-fig. 3A). The thickness recorded for these taxa ranges between  $3\ \mu\text{m}$  for *Leda minuta* and *Nucula nucleus* to over  $100\ \mu\text{m}$  for species of *Solemya*. Measured *S. borealis* attain a periostracal thickness of  $100\ \mu\text{m}$ , whilst Beedham and Owen (1965) reported that of *S. parkinsoni* as being  $140\ \mu\text{m}$ . In the solemyoids the periostracum extends ventrally some way beyond the edge of the calcareous shell to form a flexible, radially pleated flange, which Beedham and Owen (1965) showed to be in intimate contact with the mantle epithelium, being the site of orbicular muscle insertions. In all protobranchs examined, the periostracum was smooth with no external ornament or indication of internal structures.

*Arcoids.* Arcoids appear to possess a very thick and persistent periostracum (Text-fig. 3B). However, in many genera, e.g. *Limopsis* and *Glycymeris*, the layer is densely covered by conspicuous hairs, the presence of which often makes the precise thickness of the sheet difficult to ascertain. In fact, when

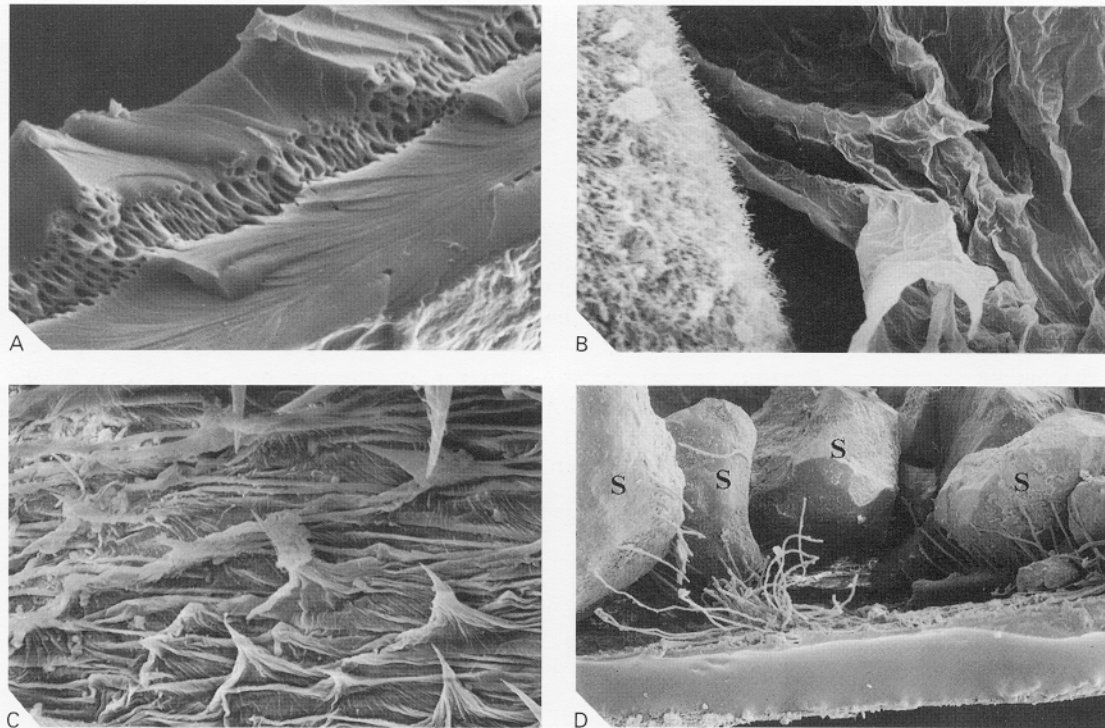


TEXT-FIG. 3. Histograms showing the range of periostracal thickness recorded for each clade. A, protobranchs; B, arcoids; C, mytiloids; D, pteriomorphs; E, lucinoids; F, heteroconchs; G, anomalodesmatans.

one subtracts the thickness of the hairy sub-layer, the basal sheet, to which the hairs are attached, is only moderately thick. For example, *Limopsis marionensis* has a very conspicuous shaggy pile attached to a sheet of a mere  $5\ \mu\text{m}$  thickness. Hair formation in arcoids has been described by Waller (1980) who argued that they are formed during maturation of the periostracal sheet, and not under direct mantle control.

*Mytiloids.* This clade comprises one extant family, the Mytilidae, but contains a great diversity of genera and species. In general the mussels possess a particularly thick and persistent periostracum, and have the thickest periostraca recorded herein (Text-fig. 3C). The recorded range is from  $5\ \mu\text{m}$  for *Ciboticola lunata* (a questionable mytilid; Moore 1969) to  $428\ \mu\text{m}$  for *Musculus laevigatus*. The median value for the data sub-set was  $30\ \mu\text{m}$ , with seven taxa registering values of over  $100\ \mu\text{m}$ .

The mytiloids also display a range of periostracal structures. As noted by Dunachie (1963) the periostracum of *Mytilus edulis* is tri-layered (Text-fig. 4A), the central layer often being vacuolated. This layer is not continuous over the entire periostracal area, and its adaptive significance is not clear. Such vacuolation has not been observed in the periostracum of other mussels studied. Hairs were encountered in a number of taxa, e.g. *Modiolus modiolus*, *Modiolus capax* and *Trichomya hirsutus*. They are not simple projections but display a variety of flattened, serrated and palmated morphologies as illustrated by Ockelmann (1983). The functional morphology of these structures was discussed by Bottjer and Carter (1980) who suggested a variety of functions, for example supplementation of shell ornamentation for stabilization, extension of mantle sensors and deterrence of settling by fouling epibionts. These authors considered that the hairs are produced by the outer middle mantle fold, but Ockelmann (1983) observed their formation in *Modiolus* and juvenile *Mytilus* on areas of the shell away from the valve edges (and hence away from mantle



TEXT-FIG. 4. A, *Mytilus edulis* (mytiloid); SM X.27504; Oban, UK; note the vacuous middle layer;  $\times 1500$ . B, *Pinna saccata* (pteriomorph); SM X.27505; New Caledonia; note the fine, wrinkled periostracal sheet emerging from beside the ciliated surface of the middle mantle fold;  $\times 500$ . C, *Cardita affinis* (heteroconch); SM X.27506; awn-like processes arising on the outer surface of the fine periostracal sheet;  $\times 500$ . D, *Lyonsia norwegica* (anomalodesmatan); SM X.27507; Northumberland, UK; note adherent sand grains (S) on outer surface of periostracum;  $\times 1500$ .

influence). He concluded that they are, like the byssus, produced by the foot and further noted that taxa with the greatest development of these hairs are also those with large anterior byssal gland complexes.

*Pteriomorphs.* Extremely thin ( $< 1 \mu\text{m}$ ) periostracal sheets characterize virtually all of the pteriomorph taxa measured (Text-figs 3D, 4B). Fourteen of the 15 extant families of this clade possess such a gossamer-thin sheet that is not easily perceived on the external surface of the shell, and indeed seldom persists past the valve margins. Only in the Anomiidae were thicker periostraca recorded, for example *Anomia ephippium* ( $10 \mu\text{m}$ ), *A. archaeus* ( $8 \mu\text{m}$ ) and *Monia squamosa* ( $10 \mu\text{m}$ ).

*Lucinoids.* Members of this clade possess a moderately thick periostracum (Text-fig. 3E), the highest values recorded being  $10 \mu\text{m}$  for *Diplodonta diplodonta* and *Myrtea botanica*. The periostracum is often conspicuous as a straw-yellow, varnish-like coating to the shell, and is reasonably persistent.

*Heteroconchs.* The heteroconch clade is the largest considered here, with 36 extant families, and displays the greatest variation in periostracal thickness (Text-fig. 3F). Values as thin as  $1 \mu\text{m}$  (or less) have been recorded in 15 taxa, whilst the thickest periostracum measured was that of *Trapezium sublaevigatum* at  $110 \mu\text{m}$ . Despite the large range for the clade, that within constituent superfamilies is much narrower, for example Arcticoidea  $70\text{--}110 \mu\text{m}$ , Chamoidea  $1\text{--}2 \mu\text{m}$ , most Cardioidea



1–2  $\mu\text{m}$  and Solenoidea 10–50  $\mu\text{m}$ . There is also great variation in periostracal structures and ornaments within this clade. Many taxa bear smooth, apparently featureless, periostracal sheets whilst others show a range of ornaments and structures. The external surface of the periostracum of members of *Astarte* shows a reticulate ornament (see Saleuddin 1974, figs 16–17), whilst several of the carditids (e.g. *Cardita affinis*, see Text-fig. 4c) have hairy periostraca.

*Anomalodesmatans*. These possess a moderate to thick, persistent periostracum (Text-fig. 3G). The finest measured was 2  $\mu\text{m}$  for *Jounettia cumingi*, whilst the thickest recorded belonged to *Lyonsia norwegica* at 80  $\mu\text{m}$ . Members of the clade also display a number of interesting periostracal features, for example the development of calcareous elements within the organic periostracum (Carter and Aller 1975). Aller (1974) described how calcareous spicules, manufactured by the outer mantle fold of *Laternula flexuosa*, are incorporated into the periostracal sheet where they may provide stabilization. Carter (1978) described similar spicules in the periostracum of the boring gastrochaenid *Spengleria rostrata*, which he considered may aid the boring process. Other anomalodesmatans, including many of the Pandoroidea, appear to be characterized by having a 'sticky', semi-fluid outer layer to the periostracum. In the lyonsiids, sand grains and other debris adhere to this mucoid layer (Text-fig. 4D), which Prezant (1981) believed may camouflage and protect the shell, or assist with stabilization within a shifting substratum. He described the presence of arenophilic glands within the outer mantle fold which, in *Lyonsia*, he suggested secreted the mucoid into the periostracal groove on to which the rest of the periostracum is then secreted, whilst in *Entodesma* he suggested that the glands are positioned more distally and secretions pass through the periostracum, perhaps by localized dissolution of the sheet. However, Morton (1987a) has shown that such glands in members of the Thracioidea, Pholadomyioidea and Clavagelloidea are located in the middle mantle folds where they empty on to the (eventual) outside of the newly formed periostracum.

*Analysis*. The Mann–Whitney test was used to test for significant differences in location between pairs of clades to ascertain whether apparent differences were valid. The results of these tests are

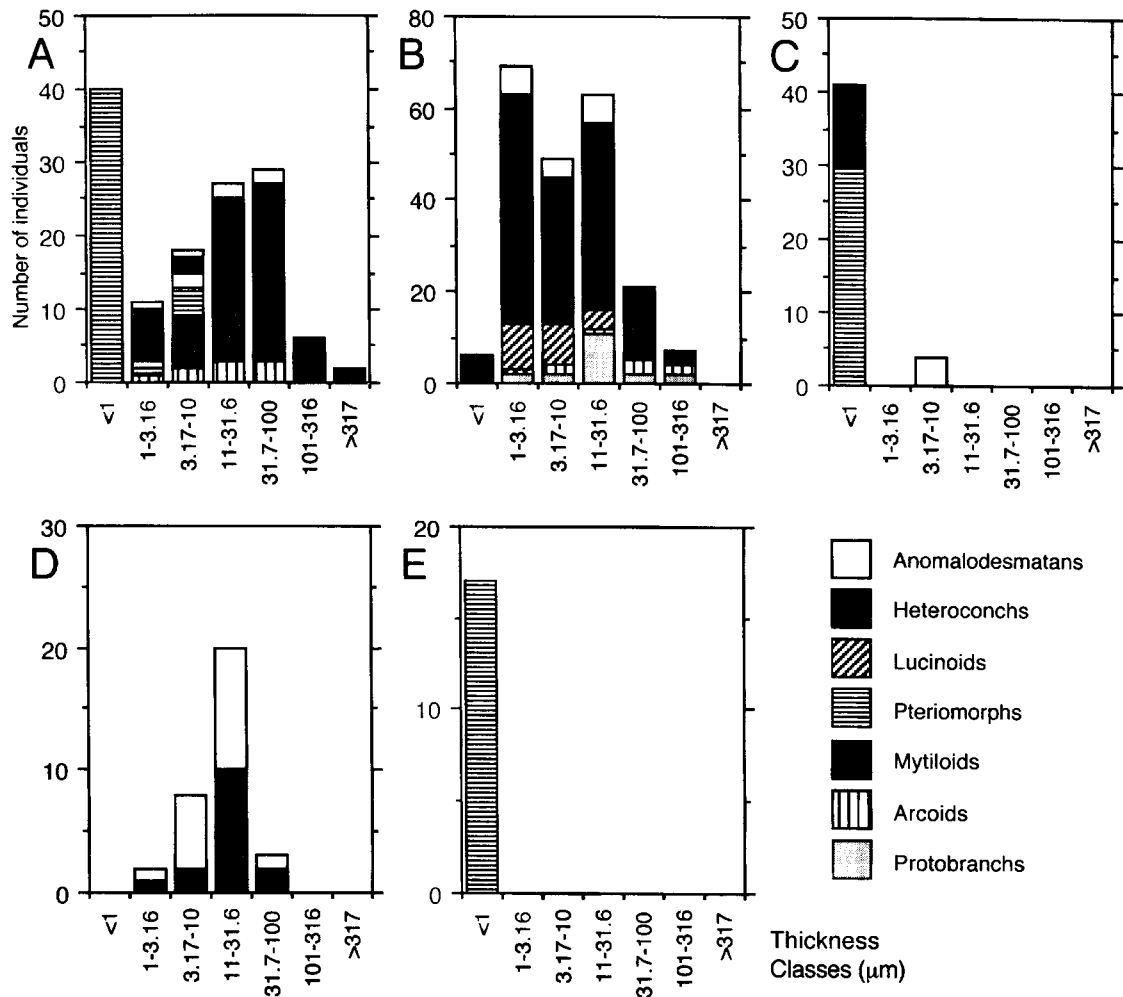
TABLE 2. Results of the Mann–Whitney test for the significance in location between pairs of clades. In the upper right hand portion of the table significant differences at the 5 per cent. level are marked +, whilst non-significant differences are marked  $\times$ . The calculated percentage significances are given in the lower left part of the table.

|      | An    | Ar    | Het   | Luc      | Myt      | Pr       | Pter |
|------|-------|-------|-------|----------|----------|----------|------|
| An   | —     | +     | +     | +        | +        | +        | +    |
| Ar   | 5%    | —     | +     | +        | $\times$ | $\times$ | +    |
| Het  | 0.25% | 0.05% | —     | $\times$ | +        | +        | +    |
| Luc  | 0.08% | 0.01% | 97.5% | —        | +        | +        | +    |
| Myt  | 0%    | 9.0%  | 0%    | 0%       | —        | $\times$ | +    |
| Pr   | 1.4%  | 89.9% | 0.01% | 0%       | 7.9%     | —        | +    |
| Pter | 0%    | 0%    | 0%    | 0%       | 0%       | 0%       | —    |

shown in Table 2. At the 5 per cent. level most were significant except the following pairs: heteroconch and lucinoid, arcoid and protobranch, arcoid and mytiloids and protobranch and mytiloids. Using a Wilcoxon test, 95 per cent. confidence intervals were established for the median of each clade (Table 3). These show clearly that the anomalodesmatan, heteroconch, pteriomorph and lucinoid clades display relatively small ranges of periostracal thickness, whilst in the others the range is far greater. It is also clear that although there is a great deal of similarity in the thicknesses shown by members of the arcoid, mytiloid and protobranch clades, the others are more distinct, albeit with some overlap.

TABLE 3. Results of the Wilcoxon test to establish the 95 per cent. confidence interval for the median value of each clade.

| Clade            | 95 per cent. confidence intervals ( $\mu\text{m}$ ) |
|------------------|---|
| Anomalodesmatans | 7.5–12.5  |
| Arcoids          | 10.0–52.5   |
| Heteroconchs     | 2.2–8.5   |
| Lucinoids        | 3.5–6.0   |
| Mytiloids        | 26.5–45.0   |
| Protobranchs     | 11.5–54.0   |
| Pteriomorphs     | 0.5–0.5   |



TEXT-FIG. 5. Histograms showing the periostacial thickness recorded for different life habits, A, byssally attached; B, burrowers; C, cementers; D, borers; E, free living (including nestlers and recliners).

*Life habits*

Text-figure 5 shows the distribution of periostracal thickness in the exponents of various life habits. The byssate and burrowing habits are exploited by a number of bivalves, not limited to those with a specific periostracal value. It is, however, worth noting that those taxa which have acquired convergently the ability to burrow to great depths, such as *Tagelus* (Tellinoidea), *Solemya* (Solemyoidea), and *Solen*, *Pharella* and *Ensis* (Solenoidea) are characterized by thick periostraca. A thick periostracum is shared by those which are active deep burrowers and those which live entombed at depth. Of the more specialized habits, cementers and free-living bivalves appear to be dominated largely by taxa possessing an ultra-thin periostracum, whilst the borers belong to clades with at least moderate development of the periostracal sheet. Possible adaptive significance of these findings are discussed below.

*Analysis.* As above, the Mann-Whitney test was used to test for the significance of differences in location between each pair of life habit groupings. These results are shown in Table 4. At the 5 per

TABLE 4. Results of the Mann-Whitney test for the significance in location between pairs of life habit groups. In the upper right hand portion of the table significant differences at the 5 per cent. level are marked +, whilst non-significant differences are marked ×. The calculated percentage significances are given in the lower left part of the table.

|          | Borer | Byssate | Cementer | Burrower |
|----------|-------|---------|----------|----------|
| Borer    | —     | ×       | +        | +        |
| Byssate  | 16%   | —       | +        | ×        |
| Cementer | 0%    | 0%      | —        | +        |
| Burrower | 0.06% | 21%     | 0%       | —        |

cent. level there were significant differences for all pairs except two: borers and byssate, and byssate and burrowers. Table 5 shows the 95 per cent. confidence interval ranges of periostracal thickness for each life habit calculated by the Wilcoxon test. The wide range of values displayed by byssate taxa overlaps with those of the borers and burrowers, although the latter two can be distinguished. The narrow ranges shown by cementers and free-living taxa are well separated from the other life habit groups, but are not distinguishable from one another.

*Relationship to ornament*

Bivalve taxa with pronounced radial ornament, and the 'wrinkled' shells of *Mya truncata* show no evidence to support the second model of ornament formation. In all cases examined, the periostracal sheet maintained even thickness over the ridges and troughs. There are some instances where bivalves have a very fine scale of surface ornamentation which does appear to support Model 2, for example micro-tubercles (a few micrometres in diameter) on the surface of neotrigoniids (Taylor *et al.* 1969) and *Myochama* (pers. obs.) fit into corresponding depressions on the inner surface of their periostraca. However, as shown by Taylor *et al.* (1969), these depressions are actually caused by the growth of prismatic crystals and post-date the formation of the periostracal sheet.

Nicol (1965) noted that the families which make up the clades here considered as protobranches, arcoids, mytiloids, anomalodesmatans and most of the lucinoids never bear spines. As noted above these are clades with at least moderately thick periostraca. By contrast, the pteriomorphs, with their mostly ultra-thin periostraca, contain some of the most extravagantly ornamented families (e.g. Spondylidae, Ostreidae and Pectinidae). The heteroconch clade contains both virtually unorna-

| Life habits | 95 per cent.<br>confidence<br>intervals |
|-------------|---|
| Borers      | 11.5–19.5                               |
| Byssate     | 10–25                                   |
| Cementer    | 0.5–0.5                                 |
| Burrower    | 6.5–10                                  |
| Free living | 0.5–0.5                                 |

TABLE 5. Results of the Wilcoxon test to establish the 95 per cent. confidence interval for the median value of each life habit group.

mented (e.g. solenoids, most venerids and mactrids) and very spiny families (chamids, cardiids and some venerids (e.g. *Pitar* and *Chione*)).

#### INTERPRETATIONS

In this survey it has been shown that although there is a great variation of periostracal thickness within the Bivalvia, specific clades, life habit groups and styles of ornamentation are characterized by much narrower ranges. Is there any evolutionary significance to these observations?

In his review of Ordovician bivalves Pojeta (1978) considered them to be predominantly either shallow non-siphonate burrowers or forms that were byssally attached either within (endobysate) or on (epibysate) the sediment. Both of these life habits may be considered as primitive within the Bivalvia, from which all the other life habits were ultimately derived. Several authors have suggested that many of the specialized life habits have a defensive value and appear to have evolved chiefly after, and in direct response to, the increase in predation pressure at the beginning of the Mesozoic (Vermeij 1987; Harper and Skelton 1993b). They observed that one of the most interesting aspects of the adaptive radiations of the bivalves is identifying the constraints and preadaptations which have determined the pathways taken by various clades. Is it possible that the form, in particular the thickness, of the periostracum may have had an important influence?

Shallow burrowing and byssate bivalves show a wide range of periostracal thickness and it is difficult to argue that there is any particular primary advantage to any of these, although there are secondary advantages, as discussed above. Patterns only develop when considering the more specialized life habits, and where the acquisition of new habits has been polyphyletic it may be possible to test whether certain habits are associated with particular periostracal characters.

Particularly thin periostracal sheets appear to correlate with the cementing and free-living modes of life. The cementing bivalves examined include members of each of the nine clades of extant marine forms of these (Harper 1991). All but two of these clades are characterized by the possession of an ultra-thin periostracum. Harper (1992) considered that the ability of these cementers to construct their shells in extremely close proximity to the micro-topography of the substratum is vital to their attachment. This by necessity means that they have a very thin periostracum, and Harper (1991, p. 45) noted that 'no periostracum can follow substratal irregularities whose radii of curvature are less than twice the periostracal thickness'. Even within the freshwater cementers, Gregoire (1974) noted that although the periostracum of the unionid *Etheria* is thick over the non-cementing part of the shell, over the attachment scar it is considerably thinned. The two clades of cementing bivalves which do have more substantial periostraca, *Cleidotherus* and *Myochama* are anomalodesmatans. Morton (1974) suggested that *Cleidotherus* cements by means of a 'sticky' outer periostracal layer, presumably analogous to the secretions of the arenophilic glands of other pandoroids (Prezant 1981; Morton 1987). If this is correct, the problem of creating close proximity between the bivalve and the substratum is solved by the fluid nature of this outer layer.

The possession of an ultra-thin periostracum by free-living bivalves is considered to be less significant for two reasons. First, in contrast with the other life habits recognized here, all free-living bivalves belong to a single major clade, the pteriomorphs. Although undoubtedly polyphyletic within that clade, virtually all pteriomorphs measured had ultra-thin periostraca and hence constancy in this autecological category can be assumed to result primarily from their phylogenetic legacy. Any putative advantages of possessing such a thin periostracum, for example as suggested by Moore and Trueman (1971) in the reduction of drag in swimming scallops, are likely to be fortuitous secondary benefits shared with non-swimming members of the same family. Second, this life habit represents a 'mixed bag' of occasional swimmers (e.g. some pectinids and limids), recliners (e.g. most pectinids, gryphaeid oysters and placunids) and even free crawlers, in the case of the anomiid *Enigmonia engimatica* (Yonge 1977). There is no immediately obvious reason why a pleurothetic mussel (with its attendant thick periostracum), if it were to exist, should not succeed in a 'free-living' life habit.

Particularly thick periostraca appear to be associated with those bivalves which bore chemically into hard substrates and those which burrow deeply within the sediment. Taylor and Kennedy (1969) first noted that borers generally possess thick periostraca and suggested that it protected them from their own boring secretions. It is now confirmed that each of the seven clades of extant boring bivalves recognized by Vermeij (1987) does indeed possess a thickened periostracum (although I was unable to obtain suitable material of the boring arcoid *Litharca* for the quantitative survey, rather worn valves of *L. saxicava*, from the collections of The Natural History Museum (London), confirmed the presence of a persistent periostracum). It has been demonstrated that members of each of these clades, with the exception of the pholads, use acidic secretions, produced from glands in either the middle or inner mantle fold, to assist, at least partly, with the boring process (Morton 1990). It seems likely, therefore, that the possession of a thick periostracum is preadaptive for the life habit. Suggestions for the adaptive significance of the thick periostracum in deep burrowing clades are rather more problematical. It may offer the shells of those taxa which burrow actively some protection from sediment scour, or, since the interstitial water in many sediments is undersaturated with respect to calcium carbonate (see Davies *et al.* 1989), protection against shell dissolution.

Therefore, it seems likely that the possession of specific types of periostraca has been preadaptive in the evolution of many specialized life habits and that exponents of these habits have evolved from either shallow-burrowing or byssate taxa. The form of the periostracum in these primitive stocks influenced the pathways used by specific clades during the radiation. Clearly, periostracal traits are not the sole factors involved in the acquisition of these specialized habits; cementation requires also the assumption of a pleurothetic habit and the production of a suitable cement (Harper 1992), while boring requires the evolution of acid-secreting glands (Morton 1990) and deep burrowing the development of a powerful foot and extensive mantle fusion to allow siphon formation (Stanley 1968).

The results of this survey also appear to show that surface ornamentation is produced by folding a periostracal sheet of constant thickness, and that the finer the sheet the finer the ornament attainable. There is a simple analogy of attempting origami with cardboard instead of thin paper. Interestingly, Checa (1995) recently published a survey of micro-ornament in ammonoids in which he attributed their formation to folding of the periostracum.

The inability of a periostracal sheet of a given thickness to describe an ornament more intricate than a certain scale can be considered in the light of three limiting models: (1) a space-limited periostracum which is highly flexible and limited only by the need to fit physically into the space between the elements of ornament; (2) an energy-limited periostracum where, if too much energy is stored by bending of the sheet, it will pull free of the shell surface; and (3) a strain-limited periostracum where if the sheet is bent too sharply, it will crack.

It is tempting to attempt to derive a standard equation whereby it is possible to predict the minimum scale of ornamentation that a periostracum of a given thickness could produce (and which conversely could be used perhaps to calculate the periostracal thickness for fossil taxa). Such an

equation would, however, depend upon the constant elasticity of the periostracal sheet, and it seems likely that periostraca composed of heterogenous layers, for example the vacuous central layer of the periostracum of *Mytilus edulis*, or those which appear to possess more fibrous layers, would have a different flexibility from those with a more homogenous structure. Again the periostracum may not be held solely responsible for the evolution of shell ornament. Certainly, the very small scale tubercles on the external surfaces of trioniids are, as noted previously, the result of individual crystals standing proud. Waller (1972) described how, amongst the pectiniform bivalves (all of which have ultra-thin periostraca), those with outer calcareous shell layers of foliated calcite (e.g. Pectinidae) are able to form shells with sharper radial corrugations and projecting spines and squamae than the generally smoother propeamussids with their outer prismatic shell layers. He attributed this to the smaller size of the microstructural elements which make up foliae rather than prisms, thus enabling the former to take up finer surface ornamentation. This idea is persuasive but is not perhaps the whole story, as many of the pinnids bear intricate hyote spines despite having an outermost prismatic shell layer. That the microstructural unit does not necessarily define the minimum scale of the ornament of bivalves with an outer prismatic shell layer was shown by Carriker *et al.* (1980), who illustrated the external surfaces of prisms in modern oysters which show distinct keels and furrows. This observation has been repeated for the outer surfaces of Jurassic gryphaeid oysters (Todd and Harper, unpublished data). In these cases the delicate keels and intervening furrows must be produced by minute deflections of the ultra-thin periostracal sheet on to which the prism was seeded.

There is a number of advantages that accrue to bivalves able to produce intricate shell ornamentation. Logan (1974) considered a number of functions for the spiny outgrowths of spondylids, which might easily be applied to similar structures in other epifaunal taxa. These include defence (either directly or by promoting camouflaging epibionts), assistance with attachment and stability and protection from fouling. Similarly infaunal bivalves may be shown to gain defensively (Carter 1967) or from stabilization within the sediment (Savazzi 1985). It seems likely, therefore, that the possession of a thick, inflexible periostracum may have been an important constraint in preventing certain bivalve groups from exploiting these morphological benefits. Thomas (1978) regarded the arcoids as having been limited in their evolutionary potential by the relative inflexibility of key elements of their body plan such as shell microstructure, a weak ligamenture and dentition. To this list may be added their thick periostraca and it seems likely that the mussels too have been constrained from great morphological diversity by this trait. No doubt both epifaunal mytiloids and arcoids would benefit in their exposed life habits from the ability to form spines and flanges but they have been unable to produce any more elaborate shell ornament than the coarsest of ribbing (e.g. *Geukensia* and *Septifer*). Such disadvantages may be mitigated, at least in part, by the evolution of periostracal hairs, which may be shown to have some defensive and stabilizing value (Bottjer and Carter 1980; Wright and Francis 1984). Similarly the inability to form intricate micro-ornament may be solved, again partially, by the evolution of prefabricated calcareous bodies which can then be incorporated into the periostracum, as described by Aller (1974) for the anomalodesmatan *Laternula*.

#### THE FOSSIL RECORD AND THE EVOLUTION OF THE PERIOSTRACUM

If the form of the bivalve periostracum has played a vital rôle in their evolution, it would be interesting to know how it has altered over geological time. It might then be possible to answer questions such as whether certain traits are preadaptive or adaptive to certain habits or morphologies.

If we accept that the bivalves are a monophyletic group then we must presumably accept that the great variety of periostraca observed in modern representatives is a result of evolution, influenced by different selection pressures away from a primitive periostracum. Presumably thickening and thinning may be achieved either by addition or subtraction of periostracal layers or by varying the thickness of individual layers. But what was the nature of the primitive

periostracum? Clark (1976) considered that this was a question that we could never answer but suggested that the ultra-thin periostraca of oysters and scallops are just as derived as the very thickened sheets of mytiloids. Given the apparent distribution of periostracal thickness within the class (Text-fig. 2A), and the characteristics of those bivalves, such as the protobranchs, which are considered to show a number of primitive characteristics (Morton 1996), it seems likely that the primitive periostracum was moderately thick. Direct evidence, however, is difficult to muster because, as noted above, the preservation potential of periostracum is very low. Nevertheless, there is a small number of instances where periostracal preservation has been reported (see Table 6) and

TABLE 6. Instances where periostracum preservation has been recorded. § = Crampton (1990); † = Hudson (1968); \* = Kříž (1972).

| Taxon                                | Clade           | Thickness ( $\mu\text{m}$ ) | Age             |
|--------------------------------------|-----------------|-----------------------------|-----------------|
| <i>Pholadidea wiffenae</i> §         | anomalodesmatan | > 5                         | late Cretaceous |
| <i>Praemytilus strathairdensis</i> † | mytiloid        | 5–15                        | mid Jurassic    |
| <i>Cardiola alata</i> *              | arcoïd          | 30–60                       | late Silurian   |
| <i>Cardiola tix</i> *                | arcoïd          | 30–60                       | late Silurian   |

Dr T. J. Palmer has pointed out to me that Pojeta (1978, pl. 15, fig. 6) figured a specimen of the mytiloid *Modiolopsis* cf. *modiolaris* which has a substantial outer layer which could be interpreted as periostracum. It is not surprising that the rare cases where bivalves have been preserved with their periostracum are those that belong to clades whose modern representatives have particularly thick periostraca. Comparison of the figures given in Table 6 with the Recent data set show that each falls within the modern range of their respective clades. As noted by Harper and Skelton (1993a), the value for the Jurassic mytiloid is lower than that recorded for most extant mussels, but we cannot tell if these periostraca were preserved intact. Further cases are required before it would be possible to test whether there has been a post-Jurassic selective thickening of the mussel periostracum (perhaps in response to the radiation of boring gastropod predators; Harper and Skelton 1993b).

Undoubtedly the preservation of fossil periostraca is biased towards those taxa with thicker periostracal sheets, and in any case is an exceptional event. A possible avenue for the study of periostracum evolution may be afforded by the examination of ornamentation. Very few Palaeozoic bivalves bear intricate ornamentation and Vermeij (1987) suggested that the first spiny bivalves appeared in the Carboniferous. Although it might be argued that this early lack of ornamentation may be due to the lack of an appropriate extrinsic cue, most obviously intense predation pressure, which would favour its evolution (see Vermeij 1987; Harper and Skelton 1993b), it might equally be plausible to suggest that it was an intrinsic constraint, i.e. possession of an at least moderately thick periostracum, that prevented it.

#### CONCLUSIONS AND IMPLICATIONS FOR OTHER GROUPS

Periostracal thickness has been shown to be an extremely variable character amongst members of the Bivalvia but within specific clades the range of variation is much narrower. It is suggested that difference in periostracal thickness has played a vital rôle in the evolution of the various bivalve clades, by determining the pathways open to them. Periostracal thickness has been important in the evolution of specific specialized life habits and of different styles of ornamentation.

A similar study may also prove enlightening in investigating the evolution of other invertebrate groups. As noted in the introduction, the basic shell secretion mechanism used by the Bivalvia is used by all Recent members of shell-bearing molluscan classes, with the exception of the Polyplacophora. The possession of a periostracum and this mechanism can be regarded as primitive

for the phylum, and it seems intuitively obvious that all ancient members of these groups would have had periostraca. In particular, a study of the variation of periostraca in Recent gastropods (which do seem to have a great range of thickness) and any link that this might have with styles of ornamentation and life habit might be particularly rewarding. Additionally, there is scope for consideration of the brachiopods. Members of this phylum also secrete their shells on to an outer organic sheet, also termed the periostracum (see Williams and Mackay 1979). The structure is analogous but not homologous to the molluscan periostracum, and there are key differences in the manner in which the mineralized shell material is applied to the periostracum, most notably that it is secreted directly by the cells in the outer mantle lobe rather than by an extrapallial fluid. However, many aspects, such as the flexibility of the periostracal sheet and its implications for micro-ornament, must be similar to those found in molluscs and, therefore, the effects of variation of the periostracum are worthy of investigation.

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#### REFERENCES

- ALLER, R. C. 1974. Prefabrication of shell ornamentation in the bivalve *Laternula. Lethaia*, **7**, 43–56.
- ARAUJO, R., RAMOS, M. A. and BEDOYA, J. 1994. Microtubules in the shell of the invasive bivalve *Corbula fluminea* (Müller, 1774) (Bivalvia: Heterodonta). *Journal of Molluscan Studies*, **60**, 405–413.
- BARANTHI, M. S. and RAMALINGHAM, K. 1989. Sclerotization of the periostracum of the marine bivalve *Perna viridis* (Linnaeus). *Proceedings of the Indian Academy of Science*, **98**, 243–248.
- BEEDEHAM, G. E. and OWEN, G. 1965. The mantle and shell of *Solemya parkinsonia* (Protobranchia: Bivalvia). *Proceedings of the Zoological Society of London*, **145**, 405–430.
- BEVELANDER, G. and NAKAHARA, H. 1967. An electron microscopic study of the formation of the periostracum of *Macrocallista maculata*. *Calcified Tissue Research*, **1**, 55–67.
- BOTTJER, D. J. 1981. Periostracum of the gastropod *Fusitriton oregonensis*: natural inhibitor of boring and encrusting organisms. *Bulletin of Marine Sciences*, **31**, 916–921.
- and CARTER, J. G. 1980. Functional and phylogenetic significance of projecting periostracal structures in the Bivalvia (Mollusca). *Journal of Paleontology*, **54**, 200–216.
- BUBEL, A. 1976. An electron microscope study of the formation of periostracum in the freshwater bivalve *Anodonta cygnea*. *Journal of Zoology, London*, **180**, 211–232.
- CARRIKER, M. R., PALMER, R. E. and PREZANT, R. S. 1980. Functional ultramorphology of the dissoconch valves of the oyster *Crassostrea virginica*. *Proceedings of the National Shellfisheries' Association*, **70**, 139–183.
- CARTER, J. G. 1978. Ecology and evolution of the Gastrochaenacea (Mollusca, Bivalvia) with notes on the evolution of the endolithic habitat. *Bulletin of the Peabody Museum of Natural History*, **41**, 1–92.
- 1990. *Skeletal biomineralization: patterns, processes and evolutionary trends*. Van Nostrand and Reinhold, New York, 832 pp.
- and ALLER, R. C. 1975. Calcification of the bivalve periostracum. *Lethaia*, **8**, 315–320.
- CARTER, R. M. 1967. The shell ornament of *Hysteroconcha* and *Hecuba* (Bivalvia): a test case for inferential functional morphology. *The Veliger*, **10**, 59–71.
- CHECA, A. 1995. A model for the morphogenesis of ribs in ammonites inferred from associated microsculptures. *Palaeontology*, **37**, 863–888.
- CLARK, G. R. 1976. Shell growth in the marine environment: approaches to the problem of marginal calcification. *American Zoologist*, **16**, 617–626.
- CRAMPTON, J. S. 1990. A new species of Late Cretaceous wood boring bivalve from New Zealand. *Palaeontology*, **33**, 981–992.



- DAVIES, D. J., POWELL, E. N. and STANTON, R. J. 1989. Relative rates of shell dissolution and net sediment accumulation – a commentary: can shell beds form by gradual accumulation of biogenic debris on the sea floor? *Lethaia*, **22**, 207–212.
- DUNACHIE, J. F. 1963. The periostracum of *Mytilus edulis*. *Transactions of the Royal Society, Edinburgh*, **65**, 383–411.
- GRAY, J. E. 1825. Conchological observations, being an attempt to fix the study of conchology on a firm basis. *Zoological Journal (London)*, **1**, 204–223.
- GREGOIRE, L. 1974. On the organic and mineral components of the shells of the Aetheriidae. *Revue de Zoologie Africaine*, **88**, 847–896.
- HARPER, E. M. 1991. The evolution of the cemented habit in the bivalved molluscs. Unpublished Ph.D. Thesis, The Open University.
- 1992. Post-larval cementation in the Ostreidae and its implications for other cementing Bivalvia. *Journal of Molluscan Studies*, **58**, 37–48.
- and SKELTON, P. W. 1993a. The Mesozoic Marine Revolution and epifaunal bivalves. *Scripta Geologica, Special Issue*, **2**, 127–153.
- 1993b. A defensive value of the thickened periostracum in the Mytiloidea. *The Veliger*, **36**, 36–42.
- HOOKE, J. E. and GOLUBIC, S. 1988. Mussel periostracum from deep-sea redox communities as a microbial habitat: the scalloping periostracum borer. *Marine Ecology*, **9**, 347–364.
- HUDSON, J. D. 1968. The microstructure of a Jurassic mytilid (Bivalvia). *Palaeontology*, **11**, 163–182.
- KAWAGUTI, S. and IKEMOTOTO, N. 1962. Electron microscopy of the mantle of a bivalve, *Fabula nitidula*. *Biological Journal of Okayama University*, **8**, 21–30.
- KENNEDY, W. J., TAYLOR, J. D. and HALL, A. D. 1969. Environmental and biological controls on bivalve shell mineralogy. *Biological Reviews*, **44**, 499–530.
- KNIPRATH, E. 1979. The functional morphology of the embryonic shell-gland in the conchiferous molluscs. *Malacologia*, **18**, 549–552.
- KŘÍŽ, J. 1972. Periostracum in Palaeozoic Bivalvia? *Nature Physical Science*, **237**, 28–30.
- LOGAN, A. 1974. Morphology and life habits of the Recent cementing bivalve *Spondylus americanus* Hermann from the Bermudan Platform. *Bulletin of Marine Science*, **24**, 568–594.
- LUTZ, R. A., KENNISH, M. J. and TAN, A. S. 1994. Shell microstructure of the vesicomid clam, *Calyptogena magnifica*. *Malacological Review*, **27**, 75–85.
- MARTILL, D. and HARPER, L. 1990. An application of critical point drying to the comparison of modern and fossilized soft tissues of fishes. *Palaeontology*, **33**, 423–428.
- MOORE, J. D. and TRUEMAN, R. E. 1971. Swimming of the scallop *Chlamys opercularis*. *Journal of Experimental Marine Biology and Ecology*, **6**, 179–185.
- MOORE, R. C. 1969. (ed.). *Treatise on invertebrate palaeontology. Part N. Mollusca 6. Bivalvia*. The Geological Society of America and the University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 952 pp.
- MORTON, B. 1974. Some aspects of the biology and functional morphology of *Cleidothaerus maorianus* Finlay (Bivalvia: Anomalodesmata: Pandoracea). *Proceedings of the Malacological Society of London*, **41**, 201–222.
- 1979a. The biology, functional morphology and taxonomic status of *Gaimardia* (*Neogaimardia*) *finlayi* (Bivalvia: Gaimardiidae). *Journal of Zoology, London*, **188**, 123–142.
- 1979b. Some aspects of the biology and functional morphology of *Trapezium* (*Neotrapezium*) *sublaevigatum* (Lamarck) (Bivalvia: Arcticacea). *Pacific Science*, **33**, 177–194.
- 1980a. Some aspects of the biology and functional morphology (including the presence of a ligamental lithodesma) of *Montacutona compacta* and *M. olivacea* (Bivalvia: Leptonacea) associated with coelenterates in Hong Kong. *Journal of Zoology*, **192**, 431–455.
- 1980b. Some aspects of the biology and functional morphology of *Coralliophaga* (*Coralliophaga*) *coralliophaga* (Gmelin 1791) (Bivalvia: Arcticacea): a coral associated nestler in Hong Kong. 311–330. In MORTON, B. (ed.). *Proceedings of the First International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong*. Hong Kong University Press, Hong Kong, 345 pp.
- 1987a. The mantle margin and radial mantle glands of *Entodesma saxicola* and *E. inflata* (Bivalvia: Anomalodesmata: Lyonsiidae). *Journal of Molluscan Studies*, **53**, 139–151.
- 1987b. The functional morphology of *Neotrigonia margaritacea* (Bivalvia: Trigonicea) with a discussion of phylogenetic affinities. *Records of the Australian Museum*, **39**, 339–354.
- 1990. Corals and their bivalve borers – the evolution of a symbiosis. 1–46. In MORTON, B. (ed.). *The Bivalvia – Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986*. Hong Kong University Press, 355 pp.
- 1992. The Bivalvia: future directions for research. *American Malacological Bulletin*, **92**, 107–116.

- 1996. The evolutionary history of the Bivalvia. 337–356. In TAYLOR, J. D. (ed.). *Origin and evolutionary radiation of the Mollusca*. Oxford University Press, Oxford, xiv + 392 pp.
- NICOL, D. 1965. Ecological implications of living pelecypods with calcareous spines. *Nautilus*, **78**, 109–116.
- 1983. Nestling pelecypods. *Florida Scientist*, **46**, 57–59.
- OCKELMANN, K. W. 1983. Descriptions of mytilid species and definition on the Dacrydiinae (n. subfam.) (Mytilacea: Bivalvia). *Ophelia*, **22**, 81–123.
- POJETA, J. 1978. Review of Ordovician pelecypods. *Professional Paper of the United States Geological Survey*, **695**, 1–46.
- PREZANT, R. S. 1981. The arenophilic radial mantle glands of the Lyonsiidae (Bivalvia: Anomalodesmata) with notes on lyonsiid evolution. *Malacologia*, **20**, 267–289.
- SALEUDDIN, A. S. M. 1974. An electron microscope study of the formation and structure of the periostracum in *Astarte* (Bivalvia). *Canadian Journal of Zoology*, **52**, 1463–1470.
- 1980. Shell formation in molluscs with special reference to periostracum formation and shell regeneration. 47–81. In SPOEL, S. van der, BRUGGEN, A. van and LEVER, J. (eds). *Pathways in malacology*. Scheltema and Holkema, Utrecht, 294 pp.
- and PETIT, H. P. 1983. The mode of formation and the structure of the periostracum. 199–234. In SALEUDDIN, A. S. M. and WILBUR, K. M. *The Mollusca. Volume 4: Physiology, Part 1*. Academic Press, New York, 523 pp.
- SAVAZZI, E. 1985. Adaptive themes in cardiid bivalves. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **170**, 291–321.
- SKELTON, P. W. 1985. Preadaptations and evolutionary innovations in rudist bivalves. *Special Papers in Palaeontology*, **33**, 159–173.
- CRAME, J. A., MORRIS, N. J. and HARPER, E. M. 1990. Adaptive divergence and taxonomic radiation in post-Palaeozoic bivalves. 91–117. In TAYLOR, P. D. and LARWOOD, G. P. (eds). *Major evolutionary radiations*. The Systematics Association Special Volume 42. Clarendon Press, Oxford, 437 pp.
- STANLEY, S. M. 1968. Post-Palaeozoic adaptive radiation of infaunal bivalve molluscs – a consequence of mantle fusion and siphon formation. *Journal of Paleontology*, **42**, 214–229.
- 1970. Relation of shell form to life habits of the Bivalvia. *Memoirs of the Geological Society of America*, **125**, 1–296.
- TAYLOR, J. D. and KENNEDY, W. J. 1969. The influence of the periostracum on the shell structure of bivalve molluscs. *Calcified Tissue Research*, **3**, 274–283.
- and HALL, A. D. 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea–Trigoniacea. *Bulletin of the British Museum (Natural History), Zoology Series, Supplement*, **3**, 1–125.
- — 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea–Clavagellacea, Conclusions. *Bulletin of the British Museum (Natural History), Zoology Series*, **22**, 225–294.
- TEVESZ, M. J. and CARTER, J. G. 1980. Environmental relationships of shell form and structure of unionacean bivalves. 295–322. In RHOADS, D. C. and LUTZ, R. A. (eds). *Skeletal growth of aquatic organisms*. Plenum Press, New York and London, 750 pp.
- THOMAS, R. D. K. 1978. Limits to opportunism in the evolution of the Arcoidea (Bivalvia). *Philosophical Transactions of the Royal Society of London, Series B*, **284**, 335–344.
- VERMEIJ, G. J. 1987. *Evolution and escalation. An ecological history of life*. Princeton University Press, Princeton, New Jersey, 537 pp.
- WAITE, J. H. and ANDERSON, S. O. 1980. 3,4-dihydroxyphenylalanine (DOPA) and sclerotization of periostracum in *Mytilus edulis* L. *Biological Bulletin*, **158**, 164–173.
- WALLER, T. R. 1972. The functional significance of some shell microstructures in the Pectinacea (Mollusca: Bivalvia). *Proceedings of the International Geological Congress, 24th Session, Montreal, Canada, Section 7, Palaeontology*, 48–56.
- 1980. Scanning electron microscopy of shell and mantle in the order Arcoidea (Mollusca: Bivalvia). *Smithsonian Contributions to Zoology*, **313**, 1–58.
- WATABE, N. 1984. Shell. 448–485. In BEREITER-HAHN, J., MTOLTSY, A. G. and RICHARDS, K. S. (eds). *Biology of the integument. 1, invertebrates*. Springer-Verlag, New York, 825 pp.
- WILLIAMS, A. and MACKAY, S. 1979. Differentiation of the brachiopod periostracum. *Palaeontology*, **22**, 721–736.
- WRIGHT, M. W. and FRANCIS, L. 1984. Predator deterrence by flexible extensions of the horse mussel *Modiolus modiolus*. *The Veliger*, **27**, 140–142.
- YONGE, C. M. 1977. Form and evolution in the Anomiacea (Mollusca: Bivalvia) – *Pododesmus*, *Anomia*,

*Enigmonia* (Anomiidae) and *Placunomia*, *Placuna* (Placunidae). *Philosophical Transactions of the Royal Society of London*, 276, 453–523.

— and THOMPSON, T. E. 1976. *Living marine molluscs*. Collins, London, 288 pp.

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#### APPENDIX

Average periostracal thicknesses and locality data for each species investigated herein. Where the data have been extracted from the literature, either as values given by other authors or determined from published micrographs, the reference is given.

| Taxon                         | Average<br>periostracal<br>thickness ( $\mu\text{m}$ ) | Locality                        |
|-------------------------------|--|---------------------------------|
| <b>Protobranchs</b>           |  |                                 |
| <i>Acila divaricata</i>       | 42   | Arabian Coast                   |
| <i>Ennucula obliquaa</i>      | 15   | Malabar, N.S.W., Australia      |
| <i>Leda minuta</i>            | 3  | Loch Goil                       |
| <i>Malletia obtusa</i>        | 8  | Norway                          |
| <i>Nucula nitida</i>          | 10   | Millport, Scotland              |
| <i>Nucula nucleus</i>         | 3  | Millport, Scotland              |
| <i>Nucula sulcata</i>         | 25   | Millport, Scotland              |
| <i>Nucula turgida</i>         | 10   | Unknown                         |
| <i>Saturnia sulcata</i>       | 10   | Argentina                       |
| <i>Solemya australia</i>      | 100  | Taylor <i>et al.</i> (1969)     |
| <i>Solemya borealis</i>       | 100  | Maine, USA                      |
| <i>Solemya occidentalis</i>   | 29   | Kenya                           |
| <i>Solemya parkinsoni</i>     | 140  | Beedham and Owen (1965)         |
| <i>Solemya velum</i>          | 10   | Rhode Island, USA               |
| <i>Yoldia eightsei</i>        | 31   | Signy Island, Antarctica        |
| <i>Yoldia hyperbola</i>       | 23   | Greenland                       |
| <i>Yoldia thracinae</i>       | 13   | North-west Atlantic             |
| <i>Yoldiella sabrina</i>      | 5  | Weddell Sea, Antarctica         |
| <b>Arcoids</b>                |  |                                 |
| <i>Anadara erthraensis</i>    | 57   | Unknown                         |
| <i>Anadara ferrugianea</i>    | 10   | Gulf of Papua                   |
| <i>Anadara grandis</i>        | 8  | Panama                          |
| <i>Anadara trapeziana</i>     | 100  | Port Jackson, N.S.W., Australia |
| <i>Arca tortuosa</i>          | 17   | Unknown                         |
| <i>Arcopsis solida</i>        | 10   | Naos, Panama                    |
| <i>Barbatia rostrae</i>       | 35   | Naos, Panama                    |
| <i>Barbatia helbergi</i>      | 8  | Kenya                           |
| <i>Barbatia obliqua</i>       | 200  | Unknown                         |
| <i>Barbatia</i> sp.           | 10   | Panama                          |
| <i>Glycymeris flamma</i>      | 2  | Two Fold Bay, N.S.W., Australia |
| <i>Glycymeris glycymeris</i>  | 11   | North Sea                       |
| <i>Glycymeris holosericus</i> | 45   | Jervis Bay, N.S.W., Australia   |
| <i>Glycymeris maculata</i>    | 24   | Bottjer and Carter (1980)       |
| <i>Limatula hodgsoni</i>      | 1  | Weddell Sea, Antarctica         |
| <i>Limopsis enderbyensis</i>  | 9  | Weddell Sea, Antarctica         |

| Taxon                             | Average<br>periostracal<br>thickness ( $\mu\text{m}$ ) | Locality                              |
|-----------------------------------|--|---------------------------------------|
| <i>Limopsis marioensis</i>        | 5  | Weddell Sea, Antarctica               |
| <i>Modiolarca tulipa</i>          | 14   | Millport, Scotland                    |
| <i>Scapharca globosus</i>         | 100  | Unknown                               |
| <i>Scapharca inaequalvis</i>      | 54   | Unknown                               |
| <b>Mytiloids</b>                  |  |                                       |
| <i>Adipicola pelagica</i>         | 15   | Shetland                              |
| <i>Adula californianus</i>        | 47   | Washington (Carter 1990)              |
| <i>Adula falcata</i>              | 19   | New Zealand                           |
| <i>Amygdalum beddomei</i>         | 32   | Cape Banks, Sydney, N.S.W., Australia |
| <i>Aulacomya ater</i>             | 81   | Peru (Carter 1990)                    |
| <i>Austromytilus rostratus</i>    | 75   | Two Fold Bay, N.S.W., Australia       |
| <i>Bathymodiolus</i> sp.          | 110  | Hook and Golubic (1988)               |
| <i>Bathymodiolus thermophilus</i> | 15   | East Pacific (Carter 1990)            |
| <i>Botula cinnamonea</i>          | 24   | Kenya                                 |
| <i>Botula siliqua</i>             | 50   | Marlborough Sound, New Zealand        |
| <i>Brachidontes granulatus</i>    | 15   | Bottjer and Carter (1980)             |
| <i>Brachidontes niger</i>         | 6  | Lagos, Nigeria                        |
| <i>Brachidontes rostratus</i>     | 35   | Victoria, Australia                   |
| <i>Brachidontes variabilis</i>    | 15   | Tai Tam, Hong Kong                    |
| <i>Choromytilus chorus</i>        | 400  | Chile                                 |
| <i>Cibiticola lunata</i>          | 5  | Cape Ginger                           |
| <i>Crenella decussata</i>         | 5  | Carter (1990)                         |
| <i>Crenella discors</i>           | 10   | Unknown                               |
| <i>Crenella glandula</i>          | 11   | Massachusetts, USA                    |
| <i>Fluviolamatus amarus</i>       | 14   | Woolgoolga, N.S.W., Australia         |
| <i>Geukensia demissa</i>          | 92   | North America                         |
| <i>Hormomya mutabilis</i>         | 15   | Cape d'Aguilar, Hong Kong             |
| <i>Ischadium recurvum</i>         | 15   | West Florida (Carter 1990)            |
| <i>Limnoperna sinensis</i>        | 28   | China                                 |
| <i>Lioberus castaneus</i>         | 22   | Bottjer and Carter (1980)             |
| <i>Lioberus salvadoricus</i>      | 8  | Panama                                |
| <i>Lithophaga</i> sp.             | 45   | Telegraph Bay, Hong Kong              |
| <i>Lithophaga aristata</i>        | 8  | Naos, Panama                          |
| <i>Lithophaga cumingiana</i>      | 29   | Masirah Island, Oman                  |
| <i>Lithophaga erthraensis</i>     | 27   | Red Sea                               |
| <i>Lithophaga kuehneti</i>        | 11   | Oman                                  |
| <i>Lithophaga kuentienti</i>      | 5  | Oman                                  |
| <i>Lithophaga lima</i>            | 14   | Oman                                  |
| <i>Lithophaga nasuata</i>         | 25   | Aldabara                              |
| <i>Lithophaga nigra</i>           | 21   | Carter (1990)                         |
| <i>Lithophaga teres</i>           | 16   | Addu Aldabra                          |
| <i>Modiolus</i> indet.            | 10   | Galeta, Panama                        |
| <i>Modiola striatula</i>          | 53   | Siput Fedo, Malaysia                  |
| <i>Modiolus americanus</i>        | 7  | West Atlantic (Carter 1990)           |
| <i>Modiolus areolatus</i>         | 13   | Two Fold Bay, N.S.W., Australia       |
| <i>Modiolus barbatus</i>          | 25   | Unknown                               |
| <i>Modiolus capax</i>             | 80   | Naos, Panama                          |
| <i>Modiolus elongatus</i>         | 60   | Moreton Bay, Queensland, Australia    |
| <i>Modiolus metcalfei</i>         | 30   | Wu Kwai Sha, Hong Kong                |
| <i>Modiolus modiolus</i>          | 50   | Firth of Lorn, Scotland               |
| <i>Modiolus pseudotulipus</i>     | 35   | Coco del Mar, Panama                  |
| <i>Musculista senhausia</i>       | 34   | Tai Tam Bay, Hong Kong                |

| Taxon                            | Average<br>periostracal<br>thickness ( $\mu\text{m}$ ) | Locality                              |
|----------------------------------|--|---------------------------------------|
| <i>Musculus cumigianus</i>       | 20   | Narrabeen Beach, N.S.W., Australia    |
| <i>Musculus laevigatus</i>       | 428  | Hokkaido, Japan                       |
| <i>Musculus marmatus</i>         | 10   | Unknown                               |
| <i>Musculus nanus</i>            | 50   | Two Fold Bay, N.S.W., Australia       |
| <i>Mytella guayensis</i>         | 15   | Panama (Carter 1990)                  |
| <i>Mytilospsis domingensis</i>   | 4  | Grand Cayman                          |
| <i>Mytilus californianus</i>     | 294  | La Jolla, California                  |
| <i>Mytilus edulis</i>            | 35   | Two Fold Bay, N.S.W., Australia       |
| <i>Parapholas californica</i>    | 20   | Carter (1990)                         |
| <i>Perna canaliculus</i>         | 152  | New Zealand                           |
| <i>Perna palliopunctatus</i>     | 75   | Botljer and Carter (1980)             |
| <i>Perna perna</i>               | 160  | Zululand, S. Africa                   |
| <i>Perna pictus</i>              | 43   | Algiers                               |
| <i>Perna viridis</i>             | 45   | Wu Kwai Sha, Hong Kong                |
| <i>Septifer bilocularis</i>      | 36   | Wu Kwai Sha, Hong Kong                |
| <i>Septifer virgatus</i>         | 60   | Cape d'Aguilar, Hong Kong             |
| <i>Stavelia horrida</i>          | 90   | Keppel Bay, Queensland, Australia     |
| <i>Stavelia tortia</i>           | 75   | Unknown                               |
| <i>Trichomya hirsutus</i>        | 100  | Unknown                               |
| <i>Trisodos semitorta</i>        | 5  | Unknown                               |
| Unknown modiolid                 | 37   | San Felipe Market, Panama             |
| <i>Xenostrobus securus</i>       | 61   | Port Stephen                          |
| <b>Pteriomorphs</b>              |  |                                       |
| <i>Adamussium colbeci</i>        | < 1  | Weddell Sea, Antarctica               |
| <i>Aequipecten gibbosus</i>      | < 1  | Unknown                               |
| <i>Alectryonella crenulifera</i> | < 1  | Hong Kong                             |
| <i>Alectryonella haliotoidea</i> | < 1  | Hoi Sing Wan, Hong Kong               |
| <i>Amussium ballotti</i>         | < 1  | Broken Bay, N.S.W., Australia         |
| <i>Amussium caudacum</i>         | < 1  | Zanzibar                              |
| <i>Amussium papiraceum</i>       | < 1  | Caribbean, Panama                     |
| <i>Amussium pleuronectes</i>     | < 1  | Unknown                               |
| <i>Anomia archaeus</i>           | 8  | Seychelles                            |
| <i>Anomia descripta</i>          | < 1  | Two Fold Bay, N.S.W., Australia       |
| <i>Anomia ephippium</i>          | 10   | Galway, Eire                          |
| <i>Atrina inflata</i>            | < 1  | Sai Kung Market, Hong Kong            |
| <i>Atrina maura</i>              | < 1  | Panama                                |
| <i>Atrina pectinata</i>          | < 1  | Cape d'Aguilar, Hong Kong             |
| <i>Atrina vexillum</i>           | < 1  | Zanzibar                              |
| <i>Chlamys asperrimus</i>        | < 1  | Victoria, Australia                   |
| <i>Chlamys opercularis</i>       | < 1  | Dunstaffnage Bay, Scotland            |
| <i>Chlamys pusio</i>             | < 1  | Galway Bay, Eire                      |
| <i>Chlamys senatoria</i>         | < 1  | Seychelles                            |
| <i>Chlamys varia</i>             | < 1  | Galway Bay, Eire                      |
| <i>Crassostrea angulata</i>      | < 1  | Courseilles, France                   |
| <i>Crassostrea gigas</i>         | < 1  | Ministry of Agriculture and Fisheries |
| <i>Crassostrea virginica</i>     | < 1  | Carriker <i>et al.</i> (1980)         |
| <i>Decatopecten plica</i> L.     | < 1  | Unknown                               |
| <i>Dimya corrugata</i>           | < 1  | Australia                             |
| <i>Electroma alacorvi</i>        | < 1  | Paula Salu, Singapore                 |
| <i>Enigmonia aenigmatica</i>     | < 1  | Singapore                             |
| <i>Equichlamys bifrons</i>       | < 1  | Coffin Bay, South Australia           |
| <i>Foramulina exempla</i>        | < 1  | Sydney, N.S.W., Australia             |

| Taxon                              | Average<br>periostracal<br>thickness ( $\mu\text{m}$ ) | Locality                              |
|------------------------------------|--|---------------------------------------|
| <i>Hinnites giganteus</i>          | < 1  | Canadian Shellfisheries               |
| <i>Hyotissa hyotissa</i>           | < 1  | Addu Atoll, Maldives                  |
| <i>Hyotissa latissimus</i>         | < 1  | Maldives                              |
| <i>Hyotissa numissima</i>          | < 1  | Oman                                  |
| <i>Hyotissa sinensis</i>           | < 1  | Hong Kong                             |
| <i>Isognomon bicolor</i>           | < 1  | Unknown                               |
| <i>Isognomon dentifer</i>          | < 1  | Oman                                  |
| <i>Isognomon ephippium</i>         | < 1  | Tai Tam Harbour, Hong Kong            |
| <i>Isognomon janus</i>             | < 1  | Naos, Panama                          |
| <i>Isognomon legumen</i>           | < 1  | Cape d'Aguilar, Hong Kong             |
| <i>Isognomon perna</i>             | < 1  | Aldabara, Maldives                    |
| <i>Isognomon recognitus</i>        | < 1  | Naos, Panama                          |
| <i>Lima colrata</i>                | < 1  | New Zealand                           |
| <i>Lima excavata</i>               | < 1  | Norway                                |
| <i>Lima fragilis</i>               | < 1  | Hervey Bay, Queensland, Australia     |
| <i>Lima hians</i>                  | < 1  | Millport, Scotland                    |
| <i>Lima lima</i>                   | < 1  | Grand Cayman                          |
| <i>Lima scabra</i>                 | < 1  | Belize                                |
| <i>Lyropecten antillarum</i>       | < 1  | Grand Cayman                          |
| <i>Malleus regula</i>              | < 1  | Oman                                  |
| <i>Melina samoensis</i>            | < 1  | Ellice Island, Pacific                |
| <i>Mimachlamys gloriosa</i>        | < 1  | Moreton Bay, Queensland, Australia    |
| <i>Monia squama</i>                | 10   | Galway, Eire                          |
| <i>Neopycnodonte cochlear</i>      | < 1  | Atlantic Ocean                        |
| <i>Neopycnodonte hyotissa</i>      | < 1  | Fairfax Island, Queensland, Australia |
| <i>Ostrea angasi</i>               | < 1  | Two Fold Bay, N.S.W., Australia       |
| <i>Ostrea conchophila</i>          | < 1  | Naos, Panama                          |
| <i>Ostrea edulis</i>               | < 1  | Galway Bay, Eire                      |
| <i>Ostrea iridescens</i>           | < 1  | Naos, Panama                          |
| <i>Ostrea virescens</i>            | < 1  | Manly, N.S.W., Australia              |
| <i>Pecten diegensis</i>            | < 1  | Clark (1974)                          |
| <i>Pecten fumatus</i>              | < 1  | Long Beach, Sydney, N.S.W., Australia |
| <i>Pecten jacobeus</i>             | < 1  | Atlantic Ocean                        |
| <i>Pecten maximum</i>              | < 1  | Millport, Scotland                    |
| <i>Pedum spondyloideum</i>         | < 1  | Shimoni, Kenya                        |
| <i>Pinctada margaritacea</i>       | < 1  | Aldabra Atoll                         |
| <i>Pinctada martensii</i>          | < 1  | Cape d'Aguilar, Hong Kong             |
| <i>Pinctada radiata</i>            | < 1  | Addu Atoll, Maldives                  |
| <i>Pinna bicolor</i>               | < 1  | Zanzibar                              |
| <i>Pinna carnea</i>                | < 1  | Grand Cayman                          |
| <i>Pinna deltoides</i>             | < 1  | Townsville, Queensland, Australia     |
| <i>Pinna menkei</i>                | < 1  | Vauchuse Bay                          |
| <i>Pinna rudis</i>                 | < 1  | Unknown                               |
| <i>Pinna saccata</i>               | < 1  | New Caledonia                         |
| <i>Placunomia foliata</i>          | 10   | Mediterranean Sea                     |
| <i>Plicatula plicata</i>           | < 1  | Tolo Channel, Hong Kong               |
| <i>Plicatula imbricata</i>         | < 1  | Phuket, Thailand                      |
| <i>Pseudamussium septemradiata</i> | < 1  | Millport, Scotland                    |
| <i>Pteria brevialeta</i>           | < 1  | Hong Kong                             |
| <i>Pteria atlantica</i>            | < 1  | Ghana                                 |
| <i>Pteria chinensis</i>            | < 1  | Maldives                              |
| <i>Pteria penguin</i>              | < 1  | Hoi Sing Wan, Hong Kong               |
| <i>Saccostrea</i> sp.              | < 1  | Galetos, Panama                       |

| Taxon                          | Average periostracal thickness ( $\mu\text{m}$ ) | Locality                               |
|--------------------------------|--|--|
| <i>Saccostrea commercialis</i> | < 1  | Lizard Island, Queensland, Australia   |
| <i>Saccostrea cucullata</i>    | < 1  | Tai Tam Bay, Hong Kong                 |
| <i>Scaechlamys livida</i>      | < 1  | Unknown                                |
| <i>Semipallium tigris</i>      | < 1  | Mombasa                                |
| <i>Spondylus americanus</i>    | < 1  | Tropical Shellfish Suppliers           |
| <i>Spondylus ducalis</i>       | < 1  | Tolo Channel, Hong Kong                |
| <i>Spondylus marisrubri</i>    | < 1  | Oman                                   |
| <i>Spondylus</i> sp.           | < 1  | Hong Kong                              |
| <i>Stabilima strangei</i>      | < 1  | Port Jackson, N.S.W., Australia        |
| <i>Streptopinna saccata</i>    | < 1  | Addu Atoll, Maldives                   |
| <i>Striostrea margaritacea</i> | < 1  | Sri Lanka                              |
| <i>Vulsella vulsella</i>       | < 1  | Cook Island, N.S.W., Australia         |
| <b>Lucinoids</b>               |  |  |
| <i>Ambuscintilla praemium</i>  | 2  | Two Fold Bay, N.S.W., Australia        |
| <i>Anodontia edentula</i>      | 10   | Kenya                                  |
| <i>Codakia tigerina</i>        | 3  | Kenya                                  |
| <i>Corbis fimbriata</i>        | 5  | New Caledonia                          |
| <i>Ctena divergens</i>         | 5  | Kenya                                  |
| <i>Diplodonta codakia</i>      | 8  | Mirs Bay, Hong Kong                    |
| <i>Diplodonta diplodonta</i>   | 10   | Ghana                                  |
| <i>Diplodonta globulosa</i>    | 5  | North Heads, Sydney, N.S.W., Australia |
| <i>Diplodonta lateralis</i>    | 5  | Kenya                                  |
| <i>Diplodonta tellinoides</i>  | 6  | Naos, Panama                           |
| <i>Galeomma</i> sp.            | 1  | Unknown                                |
| <i>Kellia adamsi</i>           | 5  | Unknown                                |
| <i>Lasaea australis</i>        | 3  | Two Fold Bay, N.S.W., Australia        |
| <i>Loripes clausus</i>         | 2  | Watanua, Kenya                         |
| <i>Loripes lucinalis</i>       | 3  | Isle of Wight, England                 |
| <i>Lucina pennsylvanica</i>    | 5  | Grand Cayman                           |
| <i>Lucina rugifera</i>         | 2  | Shell Harbour, N.S.W., Australia       |
| <i>Montacutona compacta</i>    | 5  | Morton (1980a)                         |
| <i>Montacutona olivacea</i>    | 5  | Morton (1980a)                         |
| <i>Myrtea botanica</i>         | 10   | Malabar, N.S.W., Australia             |
| <i>Myrtea spinifera</i>        | 1  | Unknown                                |
| <i>Parathysira resupina</i>    | 8  | Cronulla, N.S.W., Australia            |
| <i>Parvilucina fieldingi</i>   | 3  | Oman                                   |
| <i>Phacoides borealis</i>      | 5  | Outer Hebrides, Scotland               |
| Unknown erycinid               | 6  | Unknown                                |
| <b>Heteroconchs</b>            |  |  |
| <i>Abra alba</i>               | 30   | Millport, Scotland                     |
| <i>Abra milaschewichi</i>      | 2  | Black Sea, Rumania                     |
| <i>Acanthocardia echinata</i>  | 1  | Millport, Scotland                     |
| <i>Americardia media</i>       | 2  | Unknown                                |
| <i>Angulus tenuis</i>          | 1  | Oban, Scotland                         |
| <i>Angulus tenuis</i>          | 2  | Millport, Scotland                     |
| <i>Anomalocardia squamosa</i>  | 1  | Hoi Sing Wan, Hong Kong                |
| <i>Arctica islandica</i>       | 70   | Millport, Scotland                     |
| <i>Asaphis deflorata</i>       | 5  | Addu Atoll, Maldives                   |
| <i>Astarte borealis</i>        | 83   | Komandor Island, N. Pacific            |
| <i>Astarte compressa</i>       | 5  | Arctic                                 |

| Taxon                           | Average<br>periostracal<br>thickness ( $\mu\text{m}$ ) | Locality                           |
|---------------------------------|--|------------------------------------|
| <i>Astarte elliptica</i>        | 26   | Dunstaffnage Bay, Scotland         |
| <i>Astarte sulcata</i>          | 29   | Millport, Scotland                 |
| <i>Astarte willeti</i>          | 10   | Gulf of Alaska                     |
| <i>Atactodea glabrata</i>       | 1  | Addu Atoll, Maldives               |
| <i>Atactodea striata</i>        | 1  | Addu, Maldives                     |
| <i>Bassina multilamellata</i>   | 1  | Hoi Sing Wan, Hong Kong            |
| <i>Calyptogena magnifica</i>    | 60   | Lutz <i>et al.</i> (1994)          |
| <i>Cardita affinis</i>          | 1  | San Felipe Market, Panama          |
| <i>Cardita astartoides</i>      | 10   | Kengelan Islands                   |
| <i>Cardita laticosta</i>        | 2  | Naos, Panama                       |
| <i>Cardita variegata</i>        | 2  | Tolo Channel, Hong Kong            |
| <i>Cerastoderma edule</i>       | 2  | Dunstaffnage Bay, Scotland         |
| <i>Cerastoderma glaucum</i>     | 1  | Sussex, England                    |
| <i>Cerastoderma lamarkii</i>    | 1  | Wells, Norfolk, England            |
| <i>Chama aspersa</i>            | 1  | Aldabra Atoll                      |
| <i>Chama buddiana</i>           | 1  | Naos, Panama                       |
| <i>Chama fibula</i>             | 1  | Moreton Bay, Queensland, Australia |
| <i>Chama imbricata</i>          | 1  | Aldabara Atoll                     |
| <i>Chama jukesii</i>            | 1  | Great Barrier Reef, Australia      |
| <i>Chama lazarus</i>            | 1  | Philippines                        |
| <i>Chama reflexa</i>            | 1  | Cape d'Aguiar, Hong Kong           |
| <i>Chama solida</i>             | 1  | Naos, Panama                       |
| <i>Chamalea gallica</i>         | 20   | Millport                           |
| <i>Chione mariae</i>            | 1  | Panama                             |
| <i>Chione subrugosa</i>         | 1  | Panama                             |
| <i>Circumphalus cassina</i>     | 3  | Millport, Scotland                 |
| <i>Claudioconcha japonica</i>   | 1  | Tai Tam Bay, Hong Kong             |
| <i>Clausinella fasciata</i>     | 3  | Millport, Scotland                 |
| <i>Clementia crassiplica</i>    | 1  | Broome, Western Australia          |
| <i>Clinocardium nutalli</i>     | 2  | Unknown                            |
| <i>Caecella chinensis</i>       | 4  | Hong Kong                          |
| <i>Coelomactra antiqua</i>      | 14   | Sai Kung Market, Hong Kong         |
| <i>Congerina cochleata</i>      | 7  | North Sea                          |
| <i>Corbula crassa</i>           | 89   | Tolo Channel, Hong Kong            |
| <i>Corbula gibba</i>            | 100  | Millport, Scotland                 |
| <i>Corbula smithiana</i>        | 100  | Two Fold Bay, N.S.W., Australia    |
| <i>Corbula sp.</i>              | 50   | Panama, Naos                       |
| <i>Crassatella florida</i>      | 2  | Florida Keys                       |
| <i>Cutellus lacteus</i>         | 20   | Thailand                           |
| <i>Cutellus hanleyi</i>         | 16   | Unknown                            |
| <i>Cyclocardia australoidea</i> | 2  | Weddell Sea, Antarctica            |
| <i>Cyclocardia borealis</i>     | 2  | Bottjer and Carter (1980)          |
| <i>Donacilla carnea</i>         | 17   | Turkey                             |
| <i>Donax cueatus</i>            | 8  | Thailand                           |
| <i>Donax faba</i>               | 10   | Wu Kwai Sha, Hong Kong             |
| <i>Donax obesus</i>             | 2  | Panama                             |
| <i>Donax panamensis</i>         | 2  | Naos, Panama                       |
| <i>Donax scalpellum</i>         | 10   | Oman                               |
| <i>Donax variabilis</i>         | 3  | Florida                            |
| <i>Donax vittatus</i>           | 25   | Oban                               |
| <i>Dosinia dunkeri</i>          | 10   | San Felipe Market, Panama          |
| <i>Dosinia exoleta</i>          | 10   | Millport, Scotland                 |



| Taxon                           | Average periostracal thickness ( $\mu\text{m}$ ) | Locality                              |
|---------------------------------|--|---------------------------------------|
| <i>Ensis directus</i>           | 60   | Narangasett Bay, USA                  |
| <i>Ensis ensis</i>              | 30   | Dunstaffnage Bay, Scotland            |
| <i>Ensis siliqua</i>            | 50   | Millport, Scotland                    |
| <i>Etheria elliptica</i>        | 14   | West Africa                           |
| <i>Eucrassaella kingicola</i>   | 40   | South West Australia                  |
| <i>Eucrassatella cummingii</i>  | 23   | Hervey Bay, Queensland, Australia     |
| <i>Eucrassatella cummingii</i>  | 30   | N.S.W., Australia                     |
| <i>Fabula nitida</i>            | 4  | Kawaguti and Ikemoto (1962)           |
| <i>Florimetis cognatus</i>      | 2  | San Felipe Market, Panama             |
| <i>Gafrarium divaricatum</i>    | 28   | Cape d'Aguilar, Hong Kong             |
| <i>Gafrarium tumidum</i>        | 5  | Hoi Sing Wan, Hong Kong               |
| <i>Gaimardia finlayi</i>        | 5  | Morton (1979a)                        |
| <i>Gaimardia trapeziana</i>     | 2  | Discovery Expedition                  |
| <i>Gari fervensis</i>           | 5  | Millport, Scotland                    |
| <i>Glauconometta plankta</i>    | 8  | Two Fold Bay, N.S.W., Australia       |
| <i>Glossus humanus</i>          | 100  | Lyn of Lorn, Scotland                 |
| <i>Glossus vulgaris</i>         | 15   | Unknown                               |
| <i>Iphigena brasilliana</i>     | 30   | Florida, USA                          |
| <i>Kellia suborbicularis</i>    | 10   | Friday Harbour, Washington, USA       |
| <i>Laevicardium crassum</i>     | 70   | Plymouth, England                     |
| <i>Lutraria angustior</i>       | 8  | Northern Atlantic Ocean               |
| <i>Macoma balthica</i>          | 5  | Wexford, Eire                         |
| <i>Macoma grandis</i>           | 2  | Panama                                |
| <i>Macoma tenta</i>             | 5  | Trinidad                              |
| <i>Macrocallista maculata</i>   | 20   | Bevelander and Nakahara (1967)        |
| <i>Mactra corallina</i>         | 3  | Scotland                              |
| <i>Mactra fonescana</i>         | 10   | San Felipe Market, Panama             |
| <i>Mactra laevicardia</i>       | 8  | Cockle Cove, Patagonia                |
| <i>Mactra mera</i>              | 1  | Tolo Channel, Hong Kong               |
| <i>Meretrix costa</i>           | 6  | Unknown                               |
| <i>Meropesta nicobarica</i>     | 10   | Oman                                  |
| <i>Mulinia pallida</i>          | 1  | Bicque, Panama                        |
| <i>Nemocardia bechei</i>        | 10   | Seychelles                            |
| <i>Neotrigonia bednalli</i>     | 4  | St Francis Island, Southern Australia |
| <i>Neotrigonia gemma</i>        | 3  | Malabar, Sydney, N.S.W., Australia    |
| <i>Neotrigonia margaritacea</i> | 8  | Morton (1987b)                        |
| <i>Neotrigonia sp.</i>          | 12   | Taylor <i>et al.</i> (1969)           |
| <i>Notocallista diemensis</i>   | 3  | Long Bay, N.S.W., Australia           |
| <i>Notospisula parva</i>        | 1  | Gosford, N.S.W., Australia            |
| <i>Nutallia ezonis</i>          | 10   | Hokkaido, Japan                       |
| <i>Orbiculana orbiculata</i>    | 33   | Penang, Malaysia                      |
| <i>Periglypta multicosata</i>   | 2  | Panama                                |
| <i>Periglypta retisulcata</i>   | 1  | Yeppoon, Queensland, Australia        |
| <i>Petricola lucasana</i>       | 2  | Naos, Panama                          |
| <i>Pharaonella perna</i>        | 20   | Funzi, Kenya                          |
| <i>Pharella javanica</i>        | 15   | Unknown                               |
| <i>Pharella acutidens</i>       | 4  | Tsu Sha Tsui Market, Hong Kong        |
| <i>Pharella japonica</i>        | 18   | Sungei, Malaysia                      |
| <i>Pharella jovanettia</i>      | 10   | Sungei, Malaysia                      |
| <i>Phaxas cutellus</i>          | 5  | Kenya                                 |
| <i>Pitar tortuosa</i>           | 1  | Panama                                |
| <i>Placamen molimen</i>         | 2  | Long Bay, N.S.W., Australia           |
| <i>Plagiocardia setosa</i>      | 1  | Hervey Beach, Queensland, Australia   |

| Taxon                            | Average<br>periostracal<br>thickness ( $\mu\text{m}$ ) | Locality                             |
|----------------------------------|--|--------------------------------------|
| <i>Plebidonax deltoidea</i>      | 5  | Woolgoolga, N.S.W., Australia        |
| <i>Polymesoda inflata</i>        | 23   | San Francisco, Panama                |
| <i>Prototharca grata</i>         | 1  | Panama                               |
| <i>Prototharca megintyi</i>      | 1  | Panama                               |
| <i>Psammotellina semmelinki</i>  | 15   | Thailand                             |
| Psamorbid sp.                    | 12   | Clyde River, N.S.W., Australia       |
| <i>Pseudopythina subsinuata</i>  | 14   | Hong Kong                            |
| <i>Quadrans gargadia</i>         | 10   | Aldabra                              |
| <i>Quidnipagus palatau</i>       | 3  | Kenya                                |
| <i>Quidnipagus palatum</i>       | 2  | Maldives                             |
| <i>Raeta plicatella</i>          | 2  | Sanibal Island                       |
| <i>Sanguinolatia donacioides</i> | 8  | Lake Irrawarra, N.S.W., Australia    |
| <i>Schizothaerus</i> sp.         | 70   | British Columbia                     |
| <i>Scintilla</i> sp.             | 2  | Tolo Channel, Hong Kong              |
| <i>Scintilla striata</i>         | 1  | Oman                                 |
| <i>Scrobicularia plana</i>       | 2  | Millport, Scotland                   |
| <i>Sinovacula</i> sp.            | 6  | China                                |
| <i>Solecurtus chamasolen</i>     | 5  | Unknown                              |
| <i>Solecurtus divaricatus</i>    | 10   | Carter (1990)                        |
| <i>Solen cylindraceus</i>        | 8  | Port Elizabeth                       |
| <i>Solen marginatus</i>          | 10   | Unknown                              |
| <i>Solen regularis</i>           | 100  | Thailand                             |
| <i>Solen sicarius</i>            | 62   | Tofino, British Columbia             |
| <i>Solen</i> sp.                 | 10   | Tai Tam, Hong Kong                   |
| <i>Solen vitreus</i>             | 4  | Unknown                              |
| <i>Soletellina vitatacea</i>     | 4  | Kokan, India                         |
| <i>Sphenia binghami</i>          | 5  | Oban, Scotland                       |
| <i>Spisula calcar</i>            | 5  | Unknown                              |
| <i>Spisula elliptica</i>         | 30   | Millport, Scotland                   |
| <i>Spisula solida</i>            | 10   | Millport, Scotland                   |
| <i>Spisula subtruncata</i>       | 2  | Millport, Scotland                   |
| <i>Strigilla eutronia</i>        | 5  | Ingham, Queensland, Australia        |
| <i>Tagelus dombei</i>            | 63   | Panama                               |
| <i>Tagelus politus</i>           | 16   | San Felipe Market, Panama            |
| <i>Tagelus</i> sp.               | 50   | San Felipe Market, Panama            |
| <i>Tapes philippinarum</i>       | 5  | Hoi Sing Wan, Hong Kong              |
| <i>Tellina deltoidalis</i>       | 5  | Two Fold Bay, N.S.W., Australia      |
| <i>Tellina donacina</i>          | 1  | Unknown                              |
| <i>Tellina donacina</i>          | 2  | Atlantic Ocean                       |
| <i>Tellina fabula</i>            | 2  | Atlantic Ocean                       |
| <i>Tellina tenuis</i>            | 4  | Scotland                             |
| <i>Theora fragilis</i>           | 10   | Queensland, Australia                |
| <i>Tivela compressa</i>          | 10   | Kenya                                |
| <i>Trachycardium maculosum</i>   | 1  | Northern Oman                        |
| <i>Trachycardium</i> sp.         | 1  | Addu Atoll, Maldives                 |
| <i>Transenella puella</i>        | 2  | Naos, Panama                         |
| <i>Trapezium sublaevigatum</i>   | 110  | Morton (1979b)                       |
| <i>Tridacna crocea</i>           | 2  | Lizard Island, Queensland, Australia |
| <i>Tridacna maxima</i>           | 1  | Cook Islands                         |
| <i>Venericardia amabilis</i>     | 2  | Long Bay, N.S.W., Australia          |
| <i>Venerupis pullastra</i>       | 5  | Loch Torridon, Scotland              |
| <i>Venerupis senegalensis</i>    | 25   | Millport, Scotland                   |
| <i>Venus ovata</i>               | 1  | Addu Atoll, Maldives                 |

| Taxon                              | Average<br>periostracal<br>thickness ( $\mu\text{m}$ ) | Locality                              |
|------------------------------------|--|---------------------------------------|
| <i>Vepricardium asiaticum</i>      | 1  | Unknown                               |
| <i>Vepricardium sinensis</i>       | 1  | Unknown                               |
| <b>Anomalodesmatans</b>            |  |                                       |
| <i>Aspidopholas objecta</i>        | 23   | Lau Fau Shan, Hong Kong               |
| <i>Cleidothaerus albidus</i>       | 7  | N.S.W., Australia                     |
| <i>Cleidothaerus maorianus</i>     | 10   | Morton (1974)                         |
| <i>Cochlodesma praetenua</i>       | 3  | Northumberland, England               |
| <i>Coralliophaga coralliophaga</i> | 15   | Morton (1980b)                        |
| <i>Corbula porcina</i>             | 3  | Montevideo, Uruguay                   |
| <i>Cuspidaria latesulcata</i>      | 10   | Cape Banks, Sydney, N.S.W., Australia |
| <i>Cuspidaria rostratus</i>        | 10   | Norway                                |
| <i>Cuspidaria tenella</i>          | 5  | South Orkney                          |
| <i>Cyrtodaria siliqua</i>          | 33   | N. Europe                             |
| <i>Ectorisma granulata</i>         | 2  | Malabar, Sydney, N.S.W., Australia    |
| <i>Fulvia mutica</i>               | 1  | Tai Tam Bay, Hong Kong                |
| <i>Gastrochaena cuneiformis</i>    | 8  | Kenya                                 |
| <i>Gastrochaena dubia</i>          | 18   | Eire                                  |
| <i>Gastrochaena hians</i>          | 10   | Carter (1978)                         |
| <i>Gastrochaena mytiloidea</i>     | 10   | Kenya                                 |
| <i>Gastrochaena ovata</i>          | 8  | Carter (1978)                         |
| <i>Hiatella arctica</i>            | 40   | Millport, Scotland                    |
| <i>Hiatella australis</i>          | 2  | Two Fold Bay, N.S.W., Australia       |
| <i>Hiatella orientalis</i>         | 11   | Hoi Sing Wan, Hong Kong               |
| <i>Hiatella striata</i>            | 8  | Fowey, Cornwall, England              |
| <i>Jouannetia cumingi</i>          | 2  | Phuket, Thailand                      |
| <i>Laternula elliptica</i>         | 10   | Unknown                               |
| <i>Laternula flexuosa</i>          | 3  | Aller (1974)                          |
| <i>Laternula gracilis</i>          | 5  | Western Point, Victoria, Australia    |
| <i>Laternula moratina</i>          | 2  | Lake Macquarie, N.S.W., Australia     |
| <i>Lyonsia norwegica</i>           | 80   | Northumberland, England               |
| <i>Lyonsia californica</i>         | 5  | San Juan Island                       |
| <i>Lyonsia hyalina</i>             | 3  | Naragansett Bay, USA                  |
| <i>Martesia striata</i>            | 10   | Cape d'Aguilar, Hong Kong             |
| <i>Mya japonica</i>                | 15   | China                                 |
| <i>Mya truncata</i>                | 20   | Dunstaffnage Bay, Scotland            |
| <i>Myadora complexa</i>            | 15   | Sydney, N.S.W., Australia             |
| <i>Myochama anomioides</i>         | 14   | N.S.W., Australia                     |
| <i>Myochama strangei</i>           | 60   | Port Jackson, N.S.W., Australia       |
| <i>Offadesma angasi</i>            | 3  | New Zealand                           |
| <i>Parapholas quadrizanatta</i>    | 8  | Oman                                  |
| <i>Pholas</i> sp.                  | 10   | Naos, Panama                          |
| <i>Pholas dactylus</i>             | 5  | Margate, Kent, England                |
| <i>Pholas parva</i>                | 10   | Devon, England                        |
| <i>Saxicava rugosa</i>             | 20   | Brighton, England                     |
| <i>Spengleria rostrata</i>         | 15   | Carter (1978)                         |
| <i>Sphenia fragilis</i>            | 10   | Naos, Panama                          |
| <i>Thracia beningi</i>             | 5  | Cook Inlet, Alaska                    |
| <i>Xylophaga dorsalia</i>          | 10   | Unknown                               |