

# The shell

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## THE SHELL

### Layers

The layer terminology of the pelecypods hitherto employed being very confused and based on a somewhat erroneous view of the general shell morphology, a new terminology has been introduced in the present work.

#### *A. Definition of the layers*

The pelecypod shell is composed of two types of deposits, one evidently secreted by surface of the mantle and here termed palliostracum, and the other secreted in the attachment areas of the muscles and here termed myostracum (fig. 1, C, D).

1. The **palliostracum** is composed of an outer organic layer, the periostracum, and of three major calcareous layers (Pl. I, fig. 14). The following terms are proposed for these three layers<sup>1</sup>:

a) **Ectostracum**. The outer major calcareous layer directly underlying the periostracum, and extending over the entire outer surface of the shell, as well as the marginal parts of the inner surface about the marginal region (fig. 1 C)<sup>2</sup>.

<sup>1</sup> Some critics have claimed that the terms ectostracum, mesostracum and endostracum are confusing, leading one to believe that these layers are secreted by the ectoderm, mesoderm and endoderm. The present author would have no objection, if it indeed proved necessary, to changing these terms to exostracum, mediostracum, entostracum, though these terms would then be «bastard terms», combining latin and greek roots. Moreover, as far as is known to the author, nobody ever believed that endogaous societies were derived from endoderm, or that endoparasites thrived exclusively on that layer.

<sup>2</sup> In some families of pelecypods (Pteriacea, Spondylidae, Limidae) the outer calcareous layer is more extensive than is usually the case for the ectostracum. Whether

- b) **Mesostracum.** The middle of the three major calcareous layers between the ectostracum and the pallial myostracum, or endostracum, where the pallial myostracum is lacking. The mesostracum is exposed on the inner surface of the shell marginally to the pallial line and apically to the marginal region, and includes the hinge (fig. 1 C).
- c) **Endostracum.** The inner major calcareous layer. The endostracum is exposed on the inner surface of the shell within the area surrounded by the pallial line and the adductor and pedal retractor muscle attachments (fig. 1 C). A small isolated area of endostracum may occur in the ligamental area under the prismatic layer of the ligament.

The term **periostracum** is retained for the outermost non-calcareous layer.

2. The **myostracum** is divisible into several components which are all usually very thin. The following types have been differentiated:

- a) **Pallial myostracum.** An extremely thin, sometimes discontinuous, calcareous layer lying between the mesostracum and endostracum when a pallial attachment area of the mantle is present (fig. 1 D). The «pallial line» is the surface exposure of this layer. Actually the pallial line is not a line but a zone inasmuch as it has breadth.
- b) **Adductor myostraca.** Calcareous layers secreted in the adductor muscle attachment areas (fig. 1 D; Pl. III, fig. 2, AdMy). Although usually rather thin, they are yet the thickest of the myostraca.
- c) **Retractor pedis myostraca and other myostraca.** Very thin calcareous layers secreted in the various other muscle attachment areas of the shell.

Layer nomenclature so far has been based essentially on THIELE's work (1893). THIELE originally used the terms **hypostracum** and **ostracum** (in *Arca, Lithodomus*, etc.) to denote what is here referred to as endostracum and mesectostracum respectively; in the last pages of his work, however,

it represents a hypertrophied ectostracum or whether in these pelecypods the outer portion of the mesostracum has taken on a structure entirely similar to that of the ectostracum and totally different from that of the inner portion of the mesostracum could not be determined by the present author; it will certainly require a close examination of the mantle to decide between these two alternatives.

by overemphasis on one factor (i. e., deviation of the growth lines at the layer boundaries) he misapplied his own terminology in the description of *Unio*, where he labels the adductor myostracum as a hypostracum.

This error apparently has led many authors to the belief that by hypostracum THIELE meant the muscle layers (vide JAMESON, 1912; COKER et al., 1919; GUTSELL, 1930; NEWELL, 1937). Other authors have used THIELE's terms in what was evidently their intended meaning (PRASHAD, 1928; MITCHELL, 1935)<sup>3</sup>.

To prevent confusion and because there are two calcareous layers outside the pallial line, and not one as THIELE thought, the present terminology is here preferred.

### B. Thickness and boundaries of the layers

Each of the four palliostracal layers is generally thicker than the one above it. The periostracum is usually a mere film of conchiolin. It tends, however, to be relatively thick in pelecypods which are exposed to acid attack, such as the chemical borers (ex. *Lithophaga*)<sup>4</sup> and fresh water clams. The thickness of the ectostracum appears related in part to the type of marginal region present. Reflected marginal regions (ex. *Codakia tigrina*, Pl. I, fig. 14) are in many cases associated with a relatively thick ectostracum, shelf-like marginal regions (e. g., Pectinidae) with a thin ectostracum. The relative thicknesses of the mesostracum and endostracum depends partly on how far from the marginal region the pallial line occurs.

The boundary between the ectostracum and mesostracum is frequently more or less serrate (Pl. I, fig. 14). This phenomenon is probably the result of repeated withdrawals and expansions of the mantle. From the

<sup>3</sup> Other terms have also been used, such as nacreous, prismatic, and porcellaneous layers, calcitostracum, etc. (HAAS, 1935). In such classifications, however, structure is mixed up with layer arrangement, often inextricably. In HAAS, for example, the term «calcitostracum» is used for various portions of the shell of monomyarians, and denotes not a layer but the foliated portion of the shell; the «prismatic layer» may include the mesostracum, ectostracum, or both, etc.

<sup>4</sup> In such forms as *Lithophaga plumula* and others, not only is the periostracum relatively thick, but additional conchiolin sheets are secreted in the endostracum; these may help resist the corrosive action of the acids, once the periostracum is worn away (fig. 3 N).



character of the serrations, it is evident that the withdrawals were more or less instantaneous, the expansions relatively slow. These serrations may be considered as minor imbrications (see p. 13). The inner boundary of the mesostracum is in most cases relatively even, as the mantle is fused to the shell along the pallial line. However, under certain peculiar circumstances, such as marked expansions of the area of muscle attachments (Pl. IV, fig. 3), this boundary may also be rather irregular.

In shells such as *Hinnites* the adductor myostracum is almost entirely overlain by the endostracum and in *Spondylus* entirely so (fig. 1 Q). In others such as *Chione* (fig. 1 S) it is overlain by the mesostracum, and in still others such as *Anadara* (fig. 1 R) partly by both layers. The cause of these variations is that the pallial line in *Spondylus* is entirely marginal to the muscle scar, in *Hinnites* almost entirely so. In *Chione* the pallial line connects with the lateral side of the muscle scars, in *Anadara* with the marginal side of the scars.

The pallial line in many pelecypods does not extend dorsally to any extent from the adductor muscle attachments, but in others, however, it continues over the hinge and forms a closed ring. In the latter case, the portion of the pallial line apical to the muscle scars may be interrupted as in *Pecten s.s.* or continuous as in *Anadara grandis*. In some genera such as *Meleagrina* the ventral portion of the pallial line is also interrupted. In *Meleagrina*, furthermore, the pallial myostracum is composed of a number of distinct bands, similar to other myostraca.

In *Chama*, the adductor scars often do not have a smooth boundary on the endostracal side, but instead show very complex patterns of projections, embayments and islands (Pl. VI, fig. 5). The pallial line also is irregular and in some specimens locally appears doubled. In this genus, patches of myostracum are found far into the endostracum, and vice versa. This irregular pattern of the adductor scars and pallial line may occur in other shells. In some specimens of *Tridacna gigas*, for example, portions of the pallial line extend, as «peninsulas» and «islands» far into the endostracum.

The endostracum of many shells is pitted with minor muscle scars, each the locus of a minor myostracum. *Mytilus californianus*, *Semele decisa* and *Anodontia alba* show this feature prominently. The resulting pitting of the endostracum should not be confused with pitting arising from the emergence of tubules inside the shell, as in *Noetia ponderosa*.

### C. Combined layers

A seemingly two-layered shell may result from the combination of the outer two layers (mesectostracum) or of the inner two (mesendostracum)<sup>5</sup>. More rarely, all three layers may combine, so that an apparent one-layered shell is produced.

A differentiated combined layer (mesectostracum or mesendostracum) occurs when the two structurally identical component layers can yet to a certain extent be distinguished, either through differing opacity, or through a sudden shifting of the growth laminae at their boundary. The component layers are indistinguishable in an undifferentiated combined layer.

### D. Sublayers

The three major layers are in many cases divided into sublayers. The following three types may occur in pelecypods:

1. **Simple**, or **horizontal** sublayers (fig. 1G). The boundaries of these sublayers are parallel to the general trend or boundaries of the major layers to which they belong. Each such sublayer must have been secreted by a distinct zone of the mantle.
2. **Alternation**, or **transverse** sublayers (fig. 1F). These sublayers are transverse to the trend of the major layers, often do not extend across the whole layer. Such sublayers must be secreted alternately by the same region of the mantle.

Growth sublayers are alternation sublayers wherein the successive sublayers appear clearly to represent alternate phases of fast-growth and slow-growth in this portion of the shell. Growth sublayers thus always appear as alternate fast-growth and slow-growth sublayers. The fast- and slow-growth sublayers often show different structures (true growth sublayers), but sometimes the slow-growth sublayers appear to

<sup>5</sup> In a mesendostracum, however, the mesostracum will usually be separated from the endostracum by the pallial myostracum. The latter, however, is so thin that with the magnifications used here it will scarcely be seen. The mesostracum and endostracum having a similar structure will then appear to form one combined layer, the mesendostracum.

be merely coalescences of slow-growth laminae (lamination growth sublayers), in which case their structure is the same as that of the fast-growth sublayers, differing from the latter only in their lesser opacity.

It might be claimed that all alternation sublayers are growth sublayers; until this be proved, however, it would seem preferable to use the more non-committal term of alternation sublayers, except in cases where fast-growth and slow-growth are most probably involved.

3. **Overlap** sublayers (fig. 1H). These are caused by local overlaps<sup>6</sup> of alternation sublayers, especially slow-growth, of the lamination type and/or by overlaps of individual slow-growth laminae. Thus they usually result from relatively slow secretion. Such sublayers are related to simple sublayers in generally being secreted by a particular region of the mantle. They might even be considered a subtype of simple sublayers. They are, however, also related to alternation sublayers, as they are related to fast- and slow-growth phenomena. They can easily be confused with simple sublayers because of their similar trend and aspect.

Undisputed simple sublayers appear to be of rather unfrequent occurrence among pelecypods. In the ectostracum of *Venus verrucosa*, there is an outer fibrillar and an inner crossed-lamellar sublayer; a somewhat similar situation occurs in *Chione fluctifraga*, but in this shell the mesostracal boundary is uncertain, and hence there is a slight possibility that the fibrillar sublayer may actually represent the whole ectostracum.

In the Pectinidae, a simple sublayer composed of crossed-lamellar structure appears in the upper portion of the endostracum of *Amussium japonicum* and *Aequipecten circularis*, and on the right valve of *Euvola zigzag* and *Pecten vogdesi*.

The most remarkable type of sublayers occur, however, within the foliated portion of the pectinid shell. In this case the upper sublayer is composed of an uppermost unit of rather steeply ( $30^{\circ}$ — $80^{\circ}$ ) reclined folia, and a lower unit where the folia are less steeply reclined. The folia in this sublayer, in the plane of their surfaces appear as narrow rectangles that seem to cross each other in a very complex fashion, giving rise to sharp angulate patterns, crosses, V's, rhombs, triangles, etc. (Pl. III, figs. 3, 5). Actually these folia do not cross each other but differently

<sup>6</sup> These «overlaps» are often more apparent than real, overlap sublayers being mostly secreted at a slow rate while fast-growth laminae are secreted elsewhere.

oriented folia overlap and abut. Often folia occur in sets with a dominant orientation (Pl. III, fig. 5), e. g., folia in one region occurring in two sets: one set sloping inward (as observed in transverse section) from right to left at  $30^\circ$ , with another set sloping inward from left to right at about the same angle.

Below this upper sublayer, the folia spiral inward in a more or less regular corkscrew pattern, which in sections appear as «sublayers» of alternately reclined and inclined folia (Pl. III, figs. 4—7). The whole of this lower unit must however be considered as a single sublayer, as its structure is throughout essentially similar.

In the Spondylidae there is a somewhat similar sublayering. In the major outer portion of the foliated layer, the folia are more or less parallel to the trend of that layer. In the inner portion of that layer, however, there appears what may well be considered a distinct sublayer: this is of highly variable thickness and is composed of strongly inclined folia (Pl. IV, fig. 3). This inner sublayer is derived from the outer by rotation of the folia.

Alternation sublayers have a different aspect depending on whether they occur in the outer layers (mesostracum and ectostracum) or inner layer (endostracum) of the shell.

A typical case of mesostracal alternation sublayering occurs in *Acilacastrensis* (fig. 1 F; Pl. IV, fig. 2). In this case, we have what are evidently fast-growth sublayers composed of a somewhat faded prismatic structure, and slow-growth sublayers with a nacreous structure.

The distribution of the prismatic sublayers is characteristic (fig. 1 F). Near the periphery of adult shells, prisms occur in wedges in the outer mesostracum (Pl. IV, fig. 2). Away from the periphery the wedges penetrate deeper into the mesostracum, while the areas between the outer portions of the wedges tend to become likewise prismatic. Near the beak this prismatic structure includes most of the mesostracum.

Similar sublayers were observed in the mesectostracum of *Clinocardium nuttallii* where the fast-growth sublayers have a fibrillar structure, the slow-growth sublayers being crossed-lamellar; in the ectostracum of *Saxidomus nuttallii* which likewise has fast-growth fibrillar sublayers and slow-growth crossed-lamellar ones; in the ectostracum of *Gnidiella gnidia*, which has a similar structure.

One of the clearest examples of alternation sublayers in the endostracum occurs in *Lithophaga plumula* (fig. 3 M). In this shell, sublayers composed of prisms, nacre and conchiolin are present. The outermost



sublayer in the endostracum is prismatic and usually thicker than the following sublayers. Inside the prismatic sublayer is deposited a conchiolin sheet, and inside this a nacreous sublayer. Then a new cycle begins with a prismatic sublayer (fig. 3 M). The prismatic sublayers extend to the extreme margin of the endostracum, the others not quite that far. Thus near the margin of the endostracum the prismatic alternation sublayers are directly superimposed, forming a true prismatic sublayer. Sometimes the relationship of the conchiolin sheets to the prismatic and nacreous sublayers is not as regular as described above. Occasionally some sheets occur inside instead of outside of the nacreous sublayers, and conchiolin sheets may be lacking in some cycles. The number of cycles varies greatly from individual to individual, but there may be as many as ten cycles with conchiolin sheets or sublayers.

The endostracal structure of *Botula falcata* and *Brachidontes demissus* is similar to that of *Lithophaga plumula*, with, however, fewer conchiolin sheets. In *Septifer bifurcatus*, the conchiolin sublayers appear totally absent. In the family Periplomatidae, *Periploma planiscula* has an endostracum with alternation sublayers of prism and nacre arranged in a pattern very similar to that seen in the above mentioned Mytilidae. Alternation sublayers of crossed-lamellae and conchiolin occur in the endostracum of the Anomiid *Pododesmus macroschismus*, but here the arrangement of the sublayers, especially the conchiolin ones, is much more complex and irregular than in the preceding forms.

The shells of the family Ostreidae show more distinctly than any other pelecypod here examined the phenomenon of alternation sublayers. Here, unlike in other pelecypods, they are present throughout all or almost all of the shell. What are to all appearance slow-growth sublayers are composed of normal densely packed folia, which are gently reclined or inclined and twist strongly in the plane of foliation. The corresponding fast-growth sublayers consist of very narrow, loosely packed folia more or less perpendicular to the growth planes, with the angles varying from  $80^\circ$  inclined to  $80^\circ$  reclined. The orientation of the folia, as observed in a horizontal plane is very irregular. These fast-growth sublayers are the «chalky layers» of oysters and, unlike the slow-growth sublayers, are opaque. The growth sublayers are irregularly distributed in the shell and of quite variable thickness. The fast-growth sublayers appear in the form of irregular lenses, and the slow-growth sublayers surround these lenses, forming a complex braided pattern (fig. 1 B). In the superficial portions of the shell, however, the slow-growth sublayers overlap and

coalesce to form a slow-growth overlap sublayer. This is a result of the shelflike aspect of the marginal region. Other regions of slow-growth similarly devoid of fast-growth structure include the area directly under the hinge and a narrow zone around the muscle scar.

Besides the occurrence just cited, overlap sublayers may be found in other shells with a shelf-like marginal region (e.g., *Laevicardium elatum*) or in the inner mesostracum or mesectostracum of some shells (e.g., *Clinocardium nuttallii*).

### E. Imbrications

Occasionally, imbrications of one layer into another might be confused with growth sublayers. From the configuration of these imbrications, it is evident that they must be caused by withdrawal of the marginal regions of the mantle at more or less periodic intervals. After the mantle has withdrawn it must slowly extend again, secreting the corresponding layers at a lower level. Thus the periostracum and ectostracum might be secreted inside part of the mesostracum. Expansions of the mantle, as in the formation of concentric ridges, may also produce imbrications.

Imbrications are not often developed to the extent shown in the diagram (fig. 1 I); at times they reach down only a minor distance from the surface. They are frequently seen in *Unio*. Moreover if GRAVE (1911) is correct in asserting that in *Pinna* only the mantle margin can produce prisms, then the prismatic «sublayers» observed in the nacreous layer of this genus would also be mere imbrications.

### F. Laminae

Laminae are finer periodical deposits in the shell, reaching often a thickness of about thirty to fifty microns. They occur in both thin translucent and thick opaque varieties. Their position in the shell suggests that they represent respectively intervals of slow-growth and fast-growth. Slow-growth laminae are more resistant to weathering than fast-growth laminae, and in fossil shells are commonly etched in relief.

Laminae are generally continuous across the mesectostracal boundary although often sharply bent. Only rarely, however, can laminae be tra-



ced across the mesendostracal boundary. There may be two reasons for this:

1. Shell secretion may not occur simultaneously within and without the pallial line (heterochronous secretion, fig. 1 O). A number of authors (e. g., MITCHELL, 1935, etc.) seem to believe that in shells of this type deposition takes place continuously within the pallial line and only intermittently without it.
2. Secretion of the myostracum usually appears to be very slow, and it may function as an overlap sublayer. This is suggested by slow-growth laminae and sublayers in the mesostracum reaching the myostracum and following the trend of this layer for some distance before entering the endostracum (fig. 1 N). This occurs in a number of genera, such as *Unio* and *Tivela*, and may be a much more important and common cause for this «break» in the growth laminae along the mesendostracal boundary than has hitherto been assumed. Here secretion is homochronous and occurs at the same time on both sides of the pallial line.

Inasmuch as the lamination in the lower mesostracum and endostracum is often very faint, it is difficult in many cases to determine whether a shell is homochronous or heterochronous. Homochroneity has been proven for several genera, however, by matching laminae on both sides of the myostracum. Heterochroneity, being based on inability to match these laminae is much harder to demonstrate.

The laminae in the endostracum usually diverge somewhat, especially near the pallial line. Upon reaching the myostracum, however, they all bend sharply inwards, and may converge and overlap. This overlap may continue in some genera (e. g., *Clinocardium*) in the inner mesostracum or mesectostracum. Secretion in this region of convergence and overlap is very slow. In the major part of the mesostracum the growth laminae, however, tend to diverge upward and marginally.

In the ectostracum or outermost mesectostracum, the direction of the growth laminae is a direct reflection of the marginal region in which they occur. The following directions of the laminae are most common:

1. They may more or less maintain the trend begun in the major part of the mesostracum, diverging and becoming more steeply inclined as they approach the surface (fig. 1 J). This occurs in steeply inclined to vertical marginal regions.
2. They may become less steeply inclined and even approach a horizontal position (fig. 1 K), with the slow-growth laminae converging and

often forming an overlap sublayer. This occurs in shelf-like marginal regions.

3. They may become reflected, forming a marginally convex curve. This occurs in reflected marginal regions (fig. 1 L).
4. They may show a sigmoid outline (fig. 1 M) where the marginal region is inflected.
5. Various combinations of the preceding patterns may occur, such as sigmoid outline with reflected outer portion, etc.

### Chemical composition

Little has been done here in respect to the chemical composition of the shells. The reader may refer to BOGGILD (1930) and LOPPENS (1920).

The only fact of significance ascertained here is that the adductor myostraca and hence probably all other myostraca seem to be aragonitic in all cases. This is so even in otherwise entirely calcitic shells, such as *Pecten* (BOGGILD, 1930, p. 265) and *Ostrea*. In Miocene species of the latter genus, such as *Ostrea titan*, the adductor myostracum is replaced by coarse-grained calcite and samples of this layer in *O. virginica* analyzed for the author by Dr. R. W. CHAVE were also found to be aragonitic.

### Shell microstructures

The shell microstructures described by BOGGILD (1930) have not been restudied in detail here, as the present observations concern rather the distribution of the various structures within the various shell layers than a close examination of the structures themselves. Only a few remarks need thus be made here on this subject.

Among the subtypes of prismatic structure cited by BOGGILD, the dependent prismatic was not observed here, as polarized light was not used. The composite prismatic subtype of BOGGILD appears to be simply a prismatic structure associated with a peculiar type of peripheral ribbing: the prisms within each «primary» structure are perpendicular to the growth planes. A somewhat similar subtype of perhaps very different origin, here termed flabellate, is observed in many mytilids. In sections,

this subtype shows more or less triangular areas in which prisms radiate from outward-directed apices (Pl. II, fig. 7). The prisms within the triangular areas or fans are not generally perpendicular to the growth planes. In many cases, those on one side of the fan will be inclined, gradually becoming vertical and then finally reclined toward the other side. Actually these fans seen in three dimensions are pyramidal granules with outward-directed apices from which the prisms radiate.

Where the diameters of the prisms are very small (one to several microns) and the length relatively great, the prisms will often appear, under the magnifications here used, as fibers. The structure may in such cases be termed fibrillar. The fibrillar structure is especially common in pelecypods of the complex-lamellar group.

BOGGILD used the term «complex» structure for structure which contains complex crossed-lamellar units associated with «sublayers» of prisms. These prismatic «sublayers» are probably in most cases adductor and other myostraca; when and where this obtains, such «sublayers» are not to be included in the endostracum or its «complex» structure. In the present paper the term complex structure will be used whenever complex crossed-lamellar units predominate and no further analysis of this structure will be attempted.

It must be observed that among BOGGILD's structures the nacreous and foliated are composed of units more or less parallel to the growth planes; the prismatic, crossed-lamellar and complex crossed-lamellar have their primary units more or less perpendicular to the growth planes.

From observations of the «perpendicular» microstructures in the pelecypod shells, e. g., first-order lamellae, it is evident that a single such structure is not secreted always at the same place in the shell. In pelecypods with non-reflected marginal regions, first-order lamellae will often start at the margin on the outside of the ectostracum and end at the inner boundary of the mesostracum (fig. 3 F, A to C); the secreting source in this case must have moved relatively toward the apex, from the margin to the pallial line. In reflected marginal regions, the structures are arranged fan-wise (fig. 3 G), so that those that start just outside the periphery end up at the margin, those starting just inside end up at the inner boundary of the ectostracum or mesectostracum, while new units are constantly appearing about the periphery itself. The relative motion of the secretory sources must therefore have been outwards outside the periphery and inward inside it. The same arrangement of elements is to be noted in peripheral denticles. Where such denticles show a radial arran-

gement of structural elements, sideways motions of the secretory sources must also take place.

Finally, to produce the twisted first-order lamellae of *Schizothaerus nuttallii* (Pl. V, fig. 5), rotary motions of the secretory sources must have obtained. This holds true also for the spiralling folia of the Pectinidae (Pl. III, fig. 6).

### Tubulation

The shells of several pelecypod families are characterized by the presence of tubules. These are very tenuous, the diameter varying from two microns or less in *Septifer* to about twenty microns in the endostracum of *Noetia ponderosa*. Study of this aspect of shell morphology is complicated by burrows of bryozoa, sponges, algae and other organisms which often honeycomb molluscan shells. These burrows in many cases have diameters of the same order of magnitude as the tubules, but the following characters differentiate tubules from burrows:

1. Tubules are relatively straight and regular whereas burrows usually form complex irregular networks.
2. Tubules are systematically arranged with respect to general shell morphology.
3. Tubules usually are systematically present or absent in related genera and species.

In addition to burrows of organisms, fibrils or small prisms might be confused with tubules, especially in the *Mytilidae*, where these two structures are often closely associated. In some sections the conchiolin walls between prisms might also be mistaken for tubules.

The distribution within the shell varies greatly, but is usually quite constant within families or superfamilies. This distribution is as follows:

- Tubules in endostracum only: *Mytilidae*, *Lucinidae*, *Chamidae* (fig. 2 A; Pl. I, figs. 12, 14).
- Tubules in endostracum and mesostracum: *Carditidae*, *Lyonsidae* (fig. 2 B, C; Pl. I, figs. 8, 13).
- Tubules apparently present in all three layers: *Spondylidae* (fig. 2 D, E; Pl. IV, fig. 4).



— Tubules present only in area surrounded by the pallial line, but penetrating all three layers: *Arcacea* (fig. 2F) <sup>7</sup>.

Tubules are also present in at least some *Pectinidae*, *Meleagrindae*, *Pinnidae* and probably in some other families, but their distribution within the shell has not been determined because the structure of these shells or the apparently irregular occurrence of the tubules makes their identification difficult.

The tubules in all the families and superfamilies listed above, except the *Arcacea* and perhaps some *Meleagrindae* were in all probability formed mostly contemporaneously with shell deposition (e. g., in the *Mytilidae*, endostracal tubules developed concurrently with deposition of the endostracum). It is probable that shell substance was deposited around fleshy papillae of the mantle epithelium. IHERING (1874) asserts that the tubules in the glochidia of *Unio* result from more or less rigid protuberances (papillae) on the secreting cells. The papillae themselves do not secrete calcium carbonate, and appear as «blunt, pale processes, 0,007 mm long and 0,0025 mm wide, which at their lower ends are continuous into the main cell body». Whether such short papillae are responsible for the longest tubules remains to be proven.

The outer part at least of the tubules in the *Arcacea* (and perhaps also in some *Meleagrindae*) must result from some type of solution, for:

1. They appear only inside the pallial line (and about the margin of the nacre in some *Meleagrindae*), but they pierce all the outer calcareous layers. Thus they formed after the secretion of these outer layers.
2. They are usually about perpendicular to the growth planes only at the very bottom of the layers or combined layers into which they are intruded, and not to the prolongations of these growth planes further out in these layers. This appears quite clearly in the *Arcacea*.

The character of the individual tubules varies in different families and even in different genera of the same family. For example, in *Lyonsia* they are markedly sinuous (Pl. I, fig. 13), in *Anadara* relatively straight (Pl. II, fig. 1), and in *Chama* they have funnel-like tips (Pl. VI, figs. 6, 7).

Tubules have been observed in association with all the types of shell structures, except granular and homogeneous.

<sup>7</sup> Such tubules were observed not only in the *Arcidae*, including *Glycymeris*, but also in the *Limopsidae* (e. g., in *Limopsis multistriata* Forskal.).

Tubules have a distinct positional relationship to structures whenever they were formed at the same time as these structures (and in the case of *Meleagrina* apparently even after they have been formed). Where a prismatic structure is present, this relationship is especially clear; in some pelecypods tubules occur mostly between prisms, in others within prisms, but they have never been observed to occur at random both within and without these structural elements. For example: in *Meleagrina*, tubules, when found<sup>8</sup>, occur almost exclusively within the prisms, usually with many tubules to a prism (Pl. II, fig. 5). In *Volsella*, the tubules are located largely between the prisms (Pl. II, fig. 6), with more tubules than prisms. In *Spondylus* tubules also occur between the prisms (Pl. II, fig. 3), but here the prisms are more numerous than the tubules. In the last genus, moreover, a similar positional relationship obtains between tubules and the crossed-lamellae of the mesostracum (Pl. IV, fig. 5), the first-order lamellae being in many cases abruptly interrupted and their outline as observed on the inner shell surface greatly modified where tubules appear.

Some sort of positional relationship between tubules and shell structures appears also in the foliated *Hinnites*, where the tubules show many sharp angulations, the angles in many cases corresponding to the boundaries of the various stacks of folia (fig. 2 H).

BOWERBANK (1844) and CARPENTER (1844) first recorded tubules although those recorded by BOWERBANK appear to be of extraneous origin. CARPENTER distinguished between tubules that «form a network which spreads itself out in each layer, parallel to its surface ...» and those which «run a distance from each other obliquely through the shelly layers». Only the latter are here considered as tubules. CARPENTER records such tubules in *Arca*, *Glycymeris* and *Lithodomus*. SOOT-RYEN (1951, p. 14) notes the occurrence of tubules in the Philobryidae. Tubules have also been recorded by TULLBERG (1881), FISCHER (1887) and HAAS (1931).

Strangely, BOGGILD (1930), although constantly referring to CARPENTER's work, never mentions tubules. The nearest approach to describing them is his paragraph (p. 273) on prisms in *Volsella*, «the prisms are very

<sup>8</sup> The occurrence of tubulation in the Meleagriniidae appears to be highly variable. Tubules appeared clearly in some specimens of *Meleagrina margaritifera*, and could not be observed at all in other specimens. Their exact distribution, where they are present, is still rather doubtful.



distinct, but on closer examination we see that there is a system of distinct, black lines running through the middle of the prisms, while their boundaries are not very distinctly marked». These black lines presumably are the tubules so common in that genus.

One of the best examples of well-developed tubulation occurs in the Arcidae (Pl. II, figs. 1, 2). Each tubule in the shell of this family consists of an endostracal portion, evidently appearing with that layer and conate with it, and a portion intruding into the mesectostracum<sup>9</sup>. This intrusion must result from solution or some similar process. The reasons for believing that the mesectostracum has thus been intruded by tubules have been noted above; they are confirmed by the following facts:

1. In longitudinal sections it can be seen that, apically from the pallial line, the tubules do not immediately extend to the external surface of the shell, but that they penetrate with various degrees of gradualness further and further into the mesectostracum, until finally they reach that surface (fig. 2 G). This «lag» between the appearance of the tubules on the inner and outer surfaces of the shell can be checked on many specimens. It can be easily demonstrated whenever the tubules are large enough, by rubbing the surface with ink and thus filling the ends of the tubules. The resulting black dots usually appear further away from the margin on the outer than on the inner surface. The ink-filled tubules may also be readily observed in longitudinal sections. As observed in *Arca truncata*, *Anadara multicostata*, *Noetia ponderosa* and *Glycymeris multicostatus*, the relative rate of penetration of the tubules to the outer shell surface varies considerably. The angle included between the outer end of the tubules as they rise in the mesectostracum and the outer surface of the shell tends to be around 60°, but varies (from about 30° to 120° or more, the latter figure being gotten in some cases where tubules are slightly inclined; Pl. V, fig. 6).
2. Where the tubules in the endostracum are throughout more or less perpendicular to the growth planes, their continuation into the mesectostracum tends to be more or less perpendicular to the growth plane at the very bottom of this combined layer, where the tubules penetrate it. This initial direction is maintained by the tubules throughout the mesectostracum without regard to the attitude of the growth planes in the major portion of this combined layer. Inasmuch as the

<sup>9</sup> Since the tubules penetrate all three layers inside the pallial line, both dentition and myostraca are tubulated.

growth planes often bend inwards at the mesendostracal boundary, the tubules upon passing from the endostracum into the mesectostracum are bent marginally. This characteristic appears especially well in the later stages of shell growth probably due to the increasing lag of endostracum secretion over that of the mesectostracum (Pl. II, fig. 2).

In certain species, such as *Noetia ponderosa*, the endostracal and mesostracal portions of the tubules are especially well differentiated. The endostracal portion is relatively wide and sinuous, the mesectostracal portion narrow and straight (Pl. II, fig. 2).

Another characteristic of the distribution of tubules in most of the Arcaidae is that near the pallial line they usually occur only on radial zones or ridges. Not infrequently they are arranged here in regular rows (Pl. II, fig. 4). Further apically tubules occur also in the spaces between these zones, and their arrangement on the zones becomes less regular. Eventually they occur everywhere in about equal abundance. This linear arrangement of tubules near the pallial line is not evident in the species of *Arca s. s.* studied, and in this genus their occurrence is everywhere irregular.

### Marginal region

The marginal region is the face of the edge of the shell. One must distinguish the «margin» itself, which is a line where the face-edge meets the outer shell surface, and the «periphery», which is a line in the face edge — or «marginal region» — farthest away, in a radial direction, from the apex.

Structures on the marginal region of the shell situated above the periphery will be here termed — supraperipheral, structures situated on the periphery itself — peripheral, and below the periphery — subperipheral.

Marginal regions may vary greatly in their configuration. The following variants are especially noteworthy: The reflected type in which the periphery lies below the margin (fig. 3 G, periphery at extreme left, margin near A'), and the non-reflected type in which the margin and periphery coincide (fig. 3 F, margin and periphery at extreme left). In most reflected margins, the periphery lies within the ectostracum, at its middle or above it. When the periphery occurs at the middle of the ectostracum, the margin is said to be fully reflected, when above it, partially

reflected. These terms, fully and partially reflected are only here used when the periphery lies within the ectostracum. In some pelecypods (e. g., *Anomalocardia*, etc.) the periphery lies about the mesectostracal boundary or even well within the mesostracum.

Non-reflected marginal regions may be shelf-like (Pl. V, fig. 8), in which case the shelf being almost parallel to the direction of shell growth, slow-growth structure will be present.

Inflections may show in both reflected and non-reflected marginal regions, as in many Veneridae (Pl. VI, fig. 4). A particular and partial type of inflection may be seen in the Carditidae (Pl. I, fig. 8). Inflected marginal regions will produce sigmoid growth laminae in longitudinal sections.

Finally, it may be added that, when spines occur on the shell of a pelecypod, the type of marginal region present (or rather the attitude of the mantle margin when secreting such a region) will to a great extent condition the type of spine shown by the shell. A reflected marginal region will be associated with spines opening apically (fig. 1 E). A non-reflected concave, shelf-like marginal region will be associated with spines opening adapically (i. e., in *Spondylus* and many Cardiidae; Pl. V, fig. 3) even if a secondary reflection occurs on the rims of the spine itself (as in the anterior spines of *Trachycardium consors*, Pl. V, fig. 4). The spines of *Trachycardium quadrigenarium* (Pl. V, fig. 1) represent a different phenomenon, as they are first open adapically, but then fill up rapidly with additive deposits of the type mentioned in the chapter on ribbing. The result is that such spines as a whole cannot be said to open either apically or adapically.

## Ribbing

### A. Generalities

The term ribbing or costation is here used in a specialized sense to indicate any continuous radial or semi-radial structure on or in the shell, with the exception of teeth.

Three types of ribbing are defined by their relationship to the surfaces of the shell:

1. Outer ribs.
2. Inner ribs, situated on the inner shell surface. This term applies to purely additive structures, such as the «lyrae» of *Amussium*, but not to ridges and grooves that are, to some extent at least, a reflection of the external ribbing.
3. Internal ribs, rib-like internal structures within the ectostracum and occasionally the outer mesostracum. These are produced by peripheral or subperipheral denticles not positionally related to either outer or inner ribbing.

Ribs are separated from each other by «lows» termed interspaces. Within the interspaces smaller ribs of varying degrees of prominence may be present and may be differentiated as secondaries, tertiaries, and so on. At times major ribs, interspaces and minor ribs are covered by very fine riblets.

On the basis of morphology of the ribbing, three major types of ribs are here recognized:

1. The non-additive type, characterized essentially by some kind of folding of the shell margin. There are two main subtypes:
  - a) The plicate subtype, by far the most easily recognizable, where the folding is approximately perpendicular to the shell surface (Pl. I, fig. 1).
  - b) The lobate subtype, where the folding lies parallel to the shell surface.
2. The additive type, featuring essentially structures that appear added onto the shell surface. Shell secretion on the summits of these structures, where these grow, must be relatively rapid. The additive type is subdivided into the following subtypes:
  - a) The inner additive subtype, including inner ribbing.
  - b) The subperipheral additive subtype, including subperipheral denticles, and hence internal ribbing.
  - c) The peripheral additive subtype, including peripheral denticles and internal ribbing, and also occasionally a vague outer ribbing (Pl. I, fig. 2).
  - d) The supraperipheral additive subtype, with supraperipheral denticles and outer ribbing (Pl. IV, fig. 6).



3. The composite type, including components of both non-additive and additive types, with, in general, a non-additive framework on which are secreted additive structures. The position of the additive structures is directly related to and in most cases apparently determined by that of the non-additive components. In all shells studied the additive structures (subperipheral denticles) lie under the interspaces of the outer ribbing.

It must be pointed out that a strict consideration of the secreting source, i. e., the mantle, might have yielded a slightly modified version of the present classification. It appears likely that additive structures as well as lobate non-additive ribbing are produced by local mantle expansions, while plicate ribbing may derive from simple folds of the mantle edge. Composite ribbing would be the result of a combination of both factors. Whether such mantle expansions actually occur will have to be determined on the living animal itself. In any case the present classification must take into account rather the observed morphology of the shell than the inferred morphology of the mantle.

In plicate ribbing, the ridges and grooves on the inner surface of the shell are subdued replicas of the interspaces and ribs on the outside. Apically, the grooves become shallower and finally disappear. Deposition, then, must be faster in the grooves than on the ridges, and thus even in non-additive ribs secretion does not take place at the same rate at all points. In this case, however, additional secretion serves only to «level out» the ridges and grooves while in composite ribbing the extra-secretion often increases the height of the ridges and denticles, while sharply altering their configuration.

In the case of additive ribbing, it must be noted that for a peripheral denticle to maintain its shape during shell growth requires much slower deposition on its sides than on its summit, and the steeper the side the slower the secretion. Where the sides are vertical no deposition at all would take place (fig. 2L). This applies also to subperipheral and supra-peripheral denticles, shelflike marginal regions, etc. The sides of a denticle are thus generally covered with the translucent shell substance typical of slow-growth secretion. A subperipheral denticle, due to its position in regard to the marginal region of the shell will show such slow-growth deposition mostly or only on its lateral flanks (fig. 2N). In transverse section these slow-growth zones will appear more or less perpendicular to the shell surface. These zones are here called partitions. In composite

ribbing, wherein the denticles underlie the interspaces of the outer ribbing, these partitions will separate out areas under the ribs (rib areas) from areas under the interspaces (interspace areas). It must be noted, however, that partitions are produced by denticles and not by external ribbing and therefore partitions are related to such ribbing only so long as the denticles are so related. The terms rib and interspace areas are here used only for composite ribbing. The term denticle area and indentation area might be employed with additive ribbing.

The denticles of a composite ribbing are generally not flat, but secretion in the marginal portion of the denticle tends to be concentrated at the sides of the denticles to form what are here called lateral flanges<sup>10</sup> (fig. 2M). A secondary pair of flanges may and usually does appear on the lateral flanks of the first, or primary further apically (Pl. V, fig. 2, 2). If the flanges are prominent and the denticle narrow, a deep depression occurs in the middle, or axial portion of the denticle (Pl. I, fig. 4). Such denticles are here termed *excavate*. If the flanges are relatively weak and the denticles wide, more or less flattened denticles here referred to as *planate* denticles are produced (Pl. I, fig. 9). The flanges themselves may be either sharp or rounded<sup>11</sup>.

In reflected marginal regions, a fold or lobe of the mantle margin would evidently produce a denticle, which is an additive deposit. Thus the ribbing in such a case would be both plicate (or lobate) and additive. Because the presence of the additive denticle is the most readily observed factor in this case, such ribbing will here be considered additive.

### B. *Distribution of ribbing types*

#### Cardiidae

The Cardiidae may be divided into three major groups according to their ribbing:

1. Normal composite ribbing, by far the most common, including *Cardium*, *Papyridea*, *Dinocardium*, *Americardium*, *Cerastoderma* and *Clinocardium*.

<sup>10</sup> Flanges may also occasionally appear in simple additive submarginal denticles.

<sup>11</sup> In such flanged denticles the partitions will of course occur on the lateral flanks of the flanges: in rare cases, where the flanges are very sharp, partitions may occur on both sides of a flange.



2. Ribbing almost completely additive, due to obsolescence of the plicate component, including *Laevicardium* and *Nemocardium*.
3. Ribbing obsolete to absent, including *Serripes*.

The secretion pattern in the composite-ribbed Cardiidae, as deduced from the growth lines observed in transverse section would be as follows:

Deposition on the marginal tips of the denticles will often be concentrated at the sides, i. e., on the flanges (Pl. I, figs. 3, 4), with little or no deposition on the axial region, which will tend to remain parallel to the bottom of the interspace just outside it. Such a denticle in transverse section will show at that point three concavities corresponding to the flanges and the concave bottom of the interspace (fig. 2 J, 2<sup>nd</sup> growth line from the top in the interspace area). Further apically, levelling deposition together with the widening of the flanges will eliminate the central concavity and the growth lines in the interspace area will assume a general convex pattern (fig. 2 J, 3<sup>rd</sup> and 4<sup>th</sup> growth lines from the top in the interspace area).

Where the rib area is narrow and the flanges are strongly developed (e. g., *Trachycardium consors*), the convexity of the growth laminae in the rib area becomes tongue-like (fig. 2 J; Pl. IV, fig. 8), with the laminae on both sides of the tongue very closely spaced. Sometimes also, spines on top of the ribs will cause growth laminae to be produced to a point (Pl. VI, fig. 8).

The shell substance in the flanges may be relatively opaque (e. g., *Trachycardium consors*), resulting, as observed in transverse section, in the forming of opaque inverted comas on both sides of the rib area (fig. 2 J; Pl. VI, fig. 1).

In many Cardiidae (e. g., *Trachycardium consors*), a secondary flange appears on each side of the denticle (Pl. V, fig. 2). This appears on the side of the primary or original flange, when this has mostly ceased to grow laterally and is growing vertically. As this flange usually originates in gradual fashion and as its growth is mostly sideways, the secondary partition on its lateral flank generally starts in the primary and then slants strongly towards the axis of the rib area. In most cases the primary flanges will cease to be secreted as they are covered by the secondary flanges. The secondary partition as observed in transverse section will in this case appear as an outturned terminal section of the primary

(fig. 2J; Pl. IV, fig. 8). In some cases, however, the primary flanges may continue to grow vertically: in this case, in transverse section, the secondary partitions will be seen to branch away from the nearly vertical inner region of the primary partition, this primary partition continuing some distance further in the shell (fig. 2I).

A further complication may occur in that near the tip of the denticle, two flanges may be involved almost from the beginning, an axial one growing vertically and a lateral one growing sideways. If the deposits of the lateral flange do not cover all of the lateral slope of the axial flange, two partitions will result, an axial and a lateral.

In some Cardiidae (e. g., *Trachycardium consors*) the primary flanges may show, some distance from the shell margin, a faint axial groove. This shows up in the growth laminae in transverse section as a minor angular upward rise (fig. 2J, under central partition).

Additional very faint additive ribs appear inside the grooves of the inner shell surface of most Cardiidae. These inner ribs start in the apical part of the mesostracum but may involve part of the endostracum as well.

In *Cardium costatum* (Pl. I, fig. 5), the ribbing is unique: the ribs are composed of two distinct parts: a low, rounded base surmounted by a high, narrow, hollow, triangular structure. The hollow portion of the rib must have been produced by a lobe with a non-secretory central region. Levelling deposition is almost totally absent in this species, the denticles persisting almost to the apex of the shell. Cavities may also be found in the levelling deposits filling the excavations of the denticles; moreover the tooth sockets are very deep, extending almost to the apex. From all this it may be seen that great portions of the mantle of this species must secrete little, if any calcareous matter.

### Adacnidae

In the Adacnidae, only *Didacna trigonoides* (Pallas) was studied; the ribbing shows denticles rather similar to that of the composite-ribbed Cardiidae, though the flanges are here poorly developed or absent altogether. In these shells, moreover, there appears to be little, if any trace of a plicate component; the ribbing is thus essentially subperipheral additive.

## Tridacnidae

The ribbing in this family, although usually composite, is in some respects quite different from that of the Cardiidae. In this case, small riblets are superimposed on the main ribs (and interribs, if any). These riblets are, like the underlying ribs, composite. They increase in number through intercalation and bifurcation. Some riblets, on the other hand, reverse the process, that is, unite or peter out. The denticles of both ribs and riblets often persist far away from the marginal region. The denticles of the riblets, especially in *Hippopus maculatus*, are extremely narrow and prolonged far apically.

In some species of *Hippopus* and *Tridacna*, the riblets tend to become obsolete and the denticles of the major ribs tend to disappear (i. e. in *Tridacna squamosa*). This process may lead to the production of simple plicate ribbing in some cases.

## Arcidae

The ribbing in many of the Arcidae is composite, the ribs tending to be rectangular or subrectangular in outline, the denticles relatively broad even at their tips, more or less planate and the flanges, when present, not too prominent. All *Anadaras* studied show such features, and also *Noetia ponderosa*. In *Arcopsis solida*, however, the ribbing is supraperipheral additive, in *Arca* s. s. mostly additive, in *Barbatia reeviana* almost entirely plicate.

In the genus *Glycymeris* a peculiar type of composite ribbing appears (Pl. I, fig. 11). Here the non-additive component of the composite ribbing is usually poorly developed, often with narrow, groove-like interspaces; the denticles start about the margin with a narrow convex segment, the main segment of the denticle appearing only some distance apically. This main segment is marginally raised throughout, becoming excavate further apically. Its appearance is as if the primary flanges on each side of the main denticle segment had a common origin just apically from the small marginal segment of the denticle, then further apically diverged, leaving the space about the denticle axis excavate. It appears likely (though this could not be definitely proven by the author) that to produce this excavation in the denticle, a slight amount of resorption of shell substance might be necessary. Secondary flanges are often to be observed on the sides of this excavate portion of the denticle.

Many variations of this *Glycymeris* pattern are present in different individuals or species of that genus. The subgenera *Axinactis* Mörch and *Tucetona* Iredale show moreover a well developed outer ribbing.

### Carditidae

The ribbing of the Carditidae is composite and quite characteristic: the outer ribbing resulting from the plicate component is generally undulate, though in a number of species the rib slopes may overhang (Pl. I, fig. 7). The denticles show in some cases (Pl. I, fig. 10, especially in denticle to the left) a small marginal segment, narrow, convex and devoid of flanges, similar to that of *Glycymeris*. In other cases, however, this marginal portion is missing. The major segment of the denticles appears near the mesectostral boundary (Pl. I, figs. 9, 10). It is broad and planate, the flanges not too prominent at least in its marginal portion, and with nearly vertical lateral flanks. What is especially noteworthy here is that near the mesectostral boundary rapid secretion takes place also in the indentation: the resulting deposits show a flat inner surface and a vertical marginal slope (Pl. I, fig. 9; Pl. V, fig. 8). The broad planate denticles with more or less vertical sides and the planate indentation deposits together make up a crenate pattern along the mesectostral boundary that is seen but rarely outside this family. The flanges are variously developed, and in many cases, after a slight lateral expansion they build up toward the denticle axis, producing an apically narrowed denticular summit (Pl. I, fig. 10). Secondary flanges appearing further apically on the flanks of the primary flanges grow in the same manner (Pl. V, fig. 7).

The ribbing pattern of the Carditidae, though rather uniform, may show some interesting modifications. For example, in some specimens, a small circular depression may occur on the perpendicular marginal slopes of the deposits in the indentations (Pl. V, fig. 8). This feature in transverse sections causes the growth laminae within the ribs to be arranged in a series of concentric rings (Pl. I, fig. 7).

### Pectinidae

The Pectinidae show great variation in their ribbing. In the Patinopecten type of ribbing (*Patinopecten*, *Chlamys*, *Vertipecten*, *Pseudamussium* and *Aequipecten monotimeris*), the ribbing is non-additive.



In the Amussium type (*Amussium* only), it is additive, with inner ribbing in the form of paired «ledges» or «lyrae».

In the Pecten type (*Pecten*, *Euvola*), the ribbing is composite, in appearance somewhat similar to that of the wide-denticled Cardiidae, the denticles here also showing two pairs of well-developed flanges. The main peculiarity of the present ribbing is that on and about the pair of secondary flanges the deposits are composed of an opaque, somewhat chalky substance quite different from the folia elsewhere in the shell. In transverse sections, these «chalky» deposits appear as irregular inverted commas on each side of the rib area (Pl. III, fig. 5).

In the Lyropecten type of ribbing (*Lyropecten*, most *Aequipecten*), the ribbing is likewise composite and superficially not unlike the preceding. The «chalky» deposits were not, however, clearly visible in any of the specimens observed. On the other hand, the folia within the ribs, which are generally little modified in the Pecten group, have here taken on a very peculiar aspect, easily observable in transverse sections: in each rib area the folia are arranged into two sets, one in each half of the area. The folia in each set are convex outwards and interlock in the center<sup>12</sup> of the rib area (fig. 3, H—K; Pl. II, figs. 9, 11; Pl. III, fig. 1).

To form this interlocking structure the folia of one set, then the other, overlap the mid-point of the rib area in turn; this can be observed on the inner surface of *Aequipecten circularis* where the interlocking structures are represented by very jagged lines, somewhat like those of a seismograph during a severe earthquake. Some of these lines show as many as 150—220 bends or jogs, the jogs not corresponding from one rib to the next (Pl. III, fig. 8).

Some Pectens (e. g., *Pecten maximus*) sometimes show traces of these interlocking structures, but in all cases observed here, these were irregular in occurrence, and the sutures rarely, if ever, appear in the center of the rib areas.

<sup>12</sup> Strictly speaking, the folia of the two sets interlock in the center of rib area only in the central ribs of the shell. In the ribs to the sides, the interlocking suture has likewise shifted sideways within the rib areas, in the same directions as the ribs: for example, in the anterior ribs of the shell, the suture line will be located in the anterior portion of the rib and rib area.

## Spondylidae

The ribbing of *Spondylus* is composite and extremely irregular with ribs sometimes showing several sets of «rib areas» and partitions because of the presence on their flanks of composite riblets. The very fine secondary riblets often observed on these shells are apparently lobate non-additive and thus do not have partitions or rib areas. In transverse sections, the folia appear in general parallel to the growth planes, and the deep, narrow indentations between the denticles of the composite ribbing are reflected inside the shell substance by the deeply arched or looped pattern of the folia in the rib area (fig. 3L), this loop downwards in many cases becoming angulated.

The ribbing of *Plicatula* differs from that of *Spondylus* in that it is usually plicate. Some individuals of *Plicatula gibbosa*, however, show subperipheral denticulations, but these appear positionally unrelated to the plicate ribs, and the ribs thus cannot be considered composite.

## Veneridae

A peculiar type of «decadent» or «dissociating» composite ribbing may be observed in some Veneridae (i. e., *Protothaca grata*, *P. crassicostata*) wherein a normal composite ribbing is present on a portion of the shell (a number of ribs in the posterior-central region of the shell in both of the species mentioned above), while in the remaining portions of the shell there is a loss of positional relationship between outer ribbing and subperipheral denticles<sup>13</sup>.

In many Veneridae (i. e., *Protothaca staminea*, *Antigona puerpera*, «*Venus*» *columbiensis*, *Anomalocardia subrugosa*), there are present positionally unrelated external ribs (often with additive supraperipheral denticles) and subperipheral denticles (Pl. I, fig. 6), these last denticles being generally much more numerous than the ribs. Judging from the preceding «dissociating» ribbing, it appears not unlikely that this present

<sup>13</sup> The reason for such a dissociation of a composite ribbing is not very clear. It is possible that in some cases this dissociation is a result of the progressive reflection of the marginal region. The mantle folds producing the non-additive component of the composite ribbing being elevated at right angles to the general surface of the margin will have no component around the bend of the periphery of a reflected marginal region. The non-additive component above the bend will thus become isolated from the additive subperipheral denticles below the bend.



ribbing may also have originated in ancestral species as a composite ribbing.

Finally, in a number of Veneridae, the ribbing has remained entirely composite (i. e., in *Chione succincta*, *Circe gibba*).

## Tellinacea

In the Tellinacea, the margin is reflected and the ribbing, when present, always additive and composed of more or less peripheral denticles and derived outer ribbing<sup>14</sup>.

In the species of *Donax* studied the denticles are arranged in a single peripheral row. The denticulation of certain Semelidae (i. e., *Semele decisa*) and the resulting outer ribbing are more complex and are described below:

In *Semele decisa*, the denticulation on the marginal region consists of many rows of irregularly distributed denticles. These tend to be coarse and globular near the outer surface, but are finer and elongate transversally to the shell surfaces further in (Pl. IV, fig. 6).

These inner elongate denticles often split inward and occasionally may fuse with each other, forming a rather complex braided pattern.

As the ectostracum which is thus denticulated has a fibrillar structure, the resulting structure in longitudinal section consists of a very complex arrangement of narrow, fan-shaped arrays of fibers (Pl. II, fig. 10). The fans subdivide outwards and inwards from the center of the ectostracum, where the fans originate out of a more or less regular fibrillar structure. The fans then subdivide repeatedly into smaller and smaller units until these fan systems reach the outer and inner surface of the layer. Some of these units, however, are eliminated before they reach the shell surfaces, and in the systems pointing outwards there is occasional fusion of fans.

The fan patterns in longitudinal section indicate that the denticles were originally peripheral, and subsequently migrate outwards and inwards from the periphery. In this process they apparently divide into several units or disappear. This division is not a result of any resorptive pro-

<sup>14</sup> In some Tellinacea, perhaps best illustrated by *Donax punctostriatus*, a complication to the ordinary peripheral additive ribbing may occur in certain regions of the shell. This consists of supplementary grooves, or «secondary interspaces» showing up right above the middle of the additive denticles. In *D. punctostriatus* itself, of course the normal interspaces as well as the secondary ones manifest themselves essentially as a succession of pits on the outer shell surface.

cess, but simply of unequal secretion over the previous surface. These sources of unequal secretion must move relatively outwards and inwards from the periphery, all the time dividing further. Finally, as in *Semele decisa*, the outer edge of the irregularly distributed denticles is elevated above the general level of the outer surface of the shell. The resulting external ornamentation consists of a very peculiar and irregular nodulation with only vague traces of radial arrangement (Pl. IV, fig. 7). The denticles in the inner ectostracum are eventually covered by the mesostracum.

It must be noted that the fibers within each fan radiate as do the fans. It is thus likely that the secreting sources move continually from the center region of the denticles to the denticular margins, even as these denticles themselves move away from the periphery.

### Panopeidae

In *Panope generosa* the ribbing much resembles that of *Semele decisa*. The outer ribbing here is also beaded, but may in addition show a scattering of small ribs, irregular in trend and sometimes even crossing (Pl. II, fig. 8).

### Shell structure groups

On the basis of their structures the shells studied could be fitted into three major groups (see table of microstructures). Two of the present groups seem to have a basic structural plan which shows up in many Recent forms. In the other (the foliated group) no basic structural plan could be detected in Recent forms, but such a plan appears to have existed in Paleozoic ancestors of these Recent forms.

The first group is here termed the nacro-prismatic group and appears to have basically a nacreous mesendostracum and prismatic ectostracum. It is typified by the Unionidae. This structure and its variants occur not only in primitive pelecypods such as *Nucula*, but also in primitive gastropods such as *Pleurotomaria* and *Haliotis*, and with certain modifications in the tebrabranchiate cephalopods such as *Nautilus*. This nacro-prismatic structure appears thus to represent the primitive structure for the mollusks as a whole, or at least an important common structural stage for most mollusk groupings.