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Formation of Bivalve Shells and Their Microstructure

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Abstract—The anatomical structure of the bivalve mantle, which is responsible for the formation of the carbonate shell, ontogenetic features of growth, and formation of rhythmical and casual layers are described. Different types of microstructure seen under an optical and electron microscope are illustrated by block-diagrams. Based on the material of different taxonomic groups of Bivalvia, the possibilities of microstructure characters for systematics are discussed.

Keywords: Bivalvia, shell structure, types of microstructure, ontogenetic variations

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INTRODUCTION

Bivalves are an invertebrate group that has been studied with reference to the skeleton structure beginning from the 19th century. The main types of mollusk shell microstructure were established and described as early as the end of the 19th century to the beginning of the 20th century based on the examination with the aid of an optical microscope in thin sections and, later, acetate replicas. The study of members of many taxonomic mollusk groups has shown that almost the entire diversity of their microstructure is reducible to several main types, including the nacreous, foliated, simple prismatic, composite prismatic, crossed lamellar, complex crossed lamellar, and homogeneous structures (Böggild, 1930; Taylor et al., 1969; Popov, 1977; etc.). However, the study of the mineral composition, the use of electron microscopy have shown that finer structure of various microstructural types and relationships of mineral and organic components of the shell sometimes considerably differ within these types. This essentially complicates classification, requires the recognition of varieties and textures (Carter, 1980, 1990; Popov, 1992; Table 1).

Shell Formation

The bivalve shell is usually composed of two forms of calcium carbonate, calcite or aragonite, and covered externally by a thin organic layer. It is formed as a result of secretory activity of the epithelium of the external surface and external fold of the mantle. The formation of the external organic layer covering the shell (periostracum) begins in the groove between the middle and external folds of the mantle and is continued by secretion by the epithelium (Fig. 1, *3*, *10*, *11*). The external calcareous layer of the shell is deposited by the external mantle fold; the middle layer is formed by epithelial cells of the external mantle surface up to the point of insertion of the pallial muscle; finally, the inner layer is secreted by the mantle surface above the point of insertion of the pallial muscle (Fig. 1, *4*, *5*, *6*, *8*).

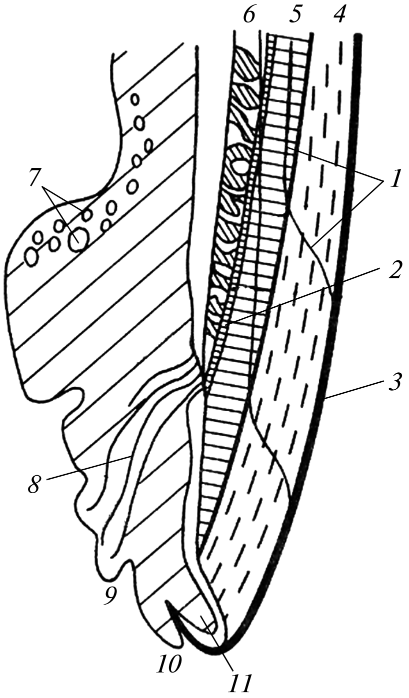

Fig. 1. Schematic radial section of the shell margin and mantle of bivalves (structure of the mantle margin is after Yonge, 1969): (*1*) growth lines, (*2*) pallial myostracum, (*3*) periostracum; (*4*–*6*) main shell layers: (*4*) outer, (*5*) middle, and (*6*) inner layers; (*7*) mucous glands; (*8*) pallial muscles; (*9*) internal fold of the mantle fold; (*10*) middle fold; (*11*) external fold of mantle.

Table 1. Classification of bivalve microstructures

Types, textures, and varieties of structure	Structure and orientation of elements	Occurrence among bivalves
Prismatic	Prisms of first order directed towards external surface	
1. **Simple prismatic**	Calcitic or aragonitic polyhedral prisms of first order, separated by thick interprismatic matrix	Pterioidea, Mytiloidea, Pinnoidea, Ostreoidea, Unionoidea, Trigonioidea, Pandoroidea, Pholadomyoidea, Poromyoidea, and, less frequently, in heterodont mollusks
regular simple prismatic	prisms regular, polygonal	
asymmetric prismatic	prisms flattened, aragonite	
radially elongate simple prismatic	prisms of first order flattened in radial direction	
lathic simple prismatic	prisms irregular wide, elongated, calcitic	
irregular simple prismatic	prisms varying in shape and thickness, calcitic or aragonitic	
blocky prismatic	composed of irregular blocks, aragonite	
pavement prismatic	close to regular simple prismatic, but prisms short, calcitic	
2. **Fibrous prismatic**	Prisms thinner and longer, sometimes inclined towards beak, sometimes grouped in bunches	some Lucinidae and Cardiidae
3. **Acicular prismatic,** Spherulitic prismatic	Composed of small subvertical prisms of second order, considerably longer than wide (by several orders of magnitude)	
with megaprisms	acicular prisms diverging fan-shapedly from center of large megaprisms	some Lucinidae and Mactridae
megaprisms absent	acicular prisms sometimes arranged in bunches	some Psammobiidae
4. **Compound prismatic**	Prisms of first order directed to external surface, composed of prisms of second order diverging from prism center	some *Anadara,* Cardiidae, Veneridae, and Tellinidae
5. **Composite prismatic**	Megaprisms, if present, directed from beak to growing margin; their prisms of second order diverging fan-shapedly	some Lucinidae, Veneridae, and Donacidae
denticular composite prismatic	megaprisms corresponding to marginal serration of shell and composed of small acicular prisms	some Nuculidae
fibrous composite prismatic	megaprisms present, but not forming serration of growing shell margin	some Cardiidae and Tellinidae
fibrous without megaprisms = reclined nondenticular composite prismatic after Carter (1990)	prisms of second order diverging from middle of layer or from upper part of outer layer	some Cardiidae, Tellinidae, Lucinidae, and Donacidae
6. **Compound composite prismatic**	Similar to composite prismatic, but formed of elements of three orders: small prisms of second order united in fan-shapedly diverging prisms of first order usually forming megaprisms or plates	
with megaprisms	megaprisms present, corresponding to weak serration of external margin	some Donacidae
without megaprisms	megaprisms absent, prisms of first order regular, diverging from upper part or middle of layer	
with plates	prisms of first order fused, forming vertical, radially positioned plates	some Veneridae
irregular	prisms of first order irregular, varying in thickness	a few Veneridae and some Tellinidae

Table 1. (Contd.)

Types, textures, and varieties of structure	Structure and orientation of elements	Occurrence among bivalves
7. **Nacreous**	Composed of aragonite plates positioned in parallel to shell surface, embedded in interplate and intercrystal organic matrix	
sheet nacreous	plates arranged in layers parallel to shell surface	inner layer in Nuculoidea, Pinnoidea, Unionoidea, Pholadomyoidea, and Pandoroidea; middle and inner layers in Mytiloidea and Pterioidea
columnar (lenticular) nacreous	plates located one above other, forming vertical columns	middle shell layer in Nuculoidea, Trigonoidea, and Pandoroidea
row stack nacreous	in one section, nacre looking cylindrical, but in another, similar to bricklaying	
8. **Foliated structure**	Individual calcitic leaflets positioned somewhat obliquely, covering plates of preceding layer, looking like shingle	Ostreoidea, Pectinoidea, Limoidea, and Anomioidea
regular foliated	leaflets positioned parallel to internal shell surface, or obliquely inclined to it, forming zigzag structures	
semi-foliated	distinguished by more irregular leaflets	
9. **Crossed lamellar**	Composed of aragonite plates of three orders; in neighboring plates of first order, plate of second order directed oppositely	outer and middle layers in Arcidae, Limopsidae, Glycymeridae, Carditidae, Lucinidae, and Cardiidae and most of Veneridae, Tellinidae, Donacidae, and others
simple crossed lamellar	plates of second order more or less regular	
rod-type crossed lamellar	short oval or rectangular elongated elements representing structures of second order	
crossed foliated	composed of leaflet blocks of calcite, with regularly alternating orientation	
crossed semi-foliated	the same, but with poorly differentiated elements of second order	
10. **Complex crossed lamellar**	Composed of the same plates of second order as preceding variant, but with three or more directions of structural elements	Inner layer of taxa with crossed lamellar structure (Arcidae, Lucinidae, Tellinidae, Cardiidae, etc.)
irregular complex crossed lamellar	blocks of plates alternate with blocks with other or opposite orientation of plates	
cone complex crossed lamellar	plates forming vertical columns of cones enclosed in each other (cone-in-cone structure)	
fine complex crossed lamellar	composed of small blocks, consisting of several plates of second order	
11. **Homogeneous**	Composed of small lenticular aragonite granules, with similar optical orientation	
granular	composed of small granules 0.3–4.0 μm in size	some Veneridae and Tellinidae
crossed acicular	in each section, composed of elongated crystallites oriented in two or more directions	some Veneridae, Tellinidae, and Donacidae
irregular homogeneous	composed of complex irregular elements 0.5–3.0 μm in size	some Veneridae, Tellinidae, Donacidae, and others

The mollusk shell is formed without direct contact with cells of the mantle epithelium; the products of secretion, i.e., calcium carbonate and organic components, pass into extrapallial liquid. An exception is only lime deposited in place of muscle attachment (myostracum) and formation of the periostracum. The periostracum, which forms a continuous film covering the shell, consists of conchiolin resistant to both alkaline and acid media and protects the calcareous shell part from dissolution in water. The structure of the calcareous shell part varies widely in mollusk groups and is determined by the organic matrix, its composition and structure, as was shown in the study of shell regeneration in decalcified sites of the matrix.

During the animal's life, the shell grows irregularly, depending on living rhythms. Therefore, the shell always has growth lines, including both regularly arranged and casual, caused by disease, damage, storms, etc. (Zolotarev, 1989 and others). The most intense growth occurs in the first months and years of life, as a floating larva comes down to the bottom. In high latitudes, during winter months at a low temperature, the growth almost stops; in lower latitudes, it slows down for a shorter time. Each delay is marked by a growth ring caused by an alternative proportions of the organic matrix and carbonate component or changes in the character of microstructure. The rings are either regularly repeated or casual. The largest regular growth layers correspond to seasonal cycles and are frequently manifested in microstructure of the shell, seen on its external surface. Weaker layers correspond to reproductive seasons, tidal effects, and day cycles. The rate of regular growth significantly decreases with the individual age of animals. In particular, after two years of age, *Callista chione* (Linné) displays 353 day growth marks per year, while a 12-year-old mollusk has only 155; at the same time, annual increase in length during the second year of life is on average 13 mm, and during the thirteenth year, only 2.2 mm (Hall et al., 1974). Some mollusk species reach 100 years of age or even more (*Crenomytilus grayanus:* Zolotarev, 1989), but, in this case, pass to the senescent stage, so that the shell continues growing in thickness, while linear growth almost stops.

Ontogenetic changes in structure. At the stage of a smooth, about 0.5-mm-long shell (prodissoconch) is not divided into layers; the structure looks granular. Close to the internal surface, the granules are relatively larger, extended, and their mutually perpendicular orientation is already discernible. At the stage of early dissoconch (about 1 mm of length), the shell is two-layer. The third (outer) layer develops later by the marginal growth, with a different orientation of elements.

In the Cardiidae, members of the genera *Acanthocardia, Parvicardium*, and *Cerastoderma*, the outer layer is initiated in the shells about 1 mm long; in *Serripes groenlandicus* (Clinocardiinae), this occurs in the shell about 5 mm long and, in *Pratulum thetidis* and *Nemocardium edwardsi* (Protocardiinae), about 8 mm long. In radially ribbed forms, it first appears in the intercostal spaces and, later, on the ribs (Popov, 1977, 1983).

In brackish-water conditions, where some Cardiidae dwell, ontogenetic development of the structure is sometimes even slower. In particular, in *Cerastoderma glaucum* from the Sea of Azov, estuaries of the Black and Caspian seas, the outer layer is often initiated only in the shell 8–10 mm long and, in some Caspian specimens, it does not develop at all, so that the shell remains two-layer. In the majority of descendants of ceratoderms (brackish-water cardiids of the subfamily Lymnocardiinae), this incomplete development becomes a stable taxonomic character (Popov, 1977).

Carditids at the stage of smooth prodissoconch lack a certain type of microstructure, it is not yet formed. Elements of crossed lamellar structure emerge at the internal margin of the shell simultaneously with sculptural elements and growth lines (Popov, 1983). At the stage of early dissoconch, shells are approximately 1 mm long, remaining two-layer; the outer layer is crossed lamellar, with vertical plates of the first order reaching the external margin; the inner layer is complex crossed lamellar, blocky prismatic in structure. Later, this becomes the middle layer and the third layer is formed externally; its plates are crossed lamellar and horizontally positioned.

Shell Microstructure

Both early attempts at the classification of microstructures, developed with the use of optical microscopy, and all subsequent studies with the aid of electron microscopy are morphological. It is important to keep in mind that superficially similar structures could have been acquired in unrelated groups, following different evolutionary pathways from different initial structures. On the one hand, this suggests that there were only limited structural transformations in the skeleton, on the other hand, this may follow from a lack of skill for recognition fine microstructural differences, distinguishing elements of different origin. At the same time, many characteristic structures of the same shell may be connected with each other by gradual transitions, which are typical not only for bivalves, but also for gastropods (Bandel, 1990).

Modern classification of microstructures is shown in Table 1. Along with original data obtained mostly during the study of heterodont mollusks (Cardiacea: Popov, 1977; Carditacea: Popov, 1983; Veneracea: Popov, 1986; Lucinacea, Tellinacea: Popov, 1986, 1992) and arcoid groups (Arcacea and Limopsacea: Popov, 1992), published data, primarily a detailed classification developed by Carter (1980, 1990) are taken into account. The last is based on extensive factual material, primarily on pterioid mollusks, including the most ancient representatives. In the case that English terms have been proposed for particular variants and varieties, they are used in Table 1.

Let us consider these types, variants, and varieties of microstructure in more detail.

Prismatic structures of bivalves, like gastropods, usually compose the outer shell layer. They occur in both ancient primitive groups and extant highly specialized taxa. The prisms are usually positioned perpendicular to the external shell surface and have straight subparallel walls or branch.

1. **The simple prismatic structure** is composed of large polyhedral vertical prisms of the first order separated by thick interprismatic matrix. In tangential sections, end faces of prisms are pentahedral, hexahedral, or more irregular (Fig. 2). This structure is usually formed of elongated fan-shapedly diverging elements of the second order. Calcitic prisms are developed in Pterioidea, Mytiloidea, Pinnoidea, and Ostreoidea and aragonite prisms are characteristic of Unionoidea, Trigonioidea, Pandoroidea, Pholadomyoidea, Poromyoidea, and some heterodont mollusks (Taylor et al., 1969).

Carter (1990, p. 610) subdivides it as follows:

Regular simple prismatic, calcitic or aragonitic, composed of more or less regular prisms polygonal in cross section and equal in size (Fig. 2);

Asymmetric prismatic, aragonite, composed of flattened prisms with alternation of the direction of flattening in neighboring prism rows;

Radially elongate simple prismatic, aragonite, composed of prisms of the first order significantly flattened in the radial direction;

Lathic simple prismatic, calcitic, composed of irregular wide and elongated prisms;

Irregular simple prismatic, calcitic or aragonitic, with irregular prisms widely varying in shape and thickness;

Blocky prismatic, aragonite, vertically composed of irregular blocks more or less similar in size;

Pavement prismatic, calcitic, close to regular simple prismatic, but with short prisms.

2. **Fibrous prismatic**, similar to simple prismatic, but prisms are considerably thinner and longer; they are 0.5–1.5 μm in section, frequently inclined towards the beak (Fig. 3), sometimes combined in bunches. A thin prismatic sublayer (mosaicostracum in some lucinids) is sometimes present near the external surface.

3. **Acicular prismatic** (or "spherulitic prismatic" after Carter, 1980; Carter, 1990), comprising several varieties:

With megaprisms: small acicular prisms of the second order are collected in large megaprisms directed towards the external surface (some Lucinidae and Mactridae) (Fig. 4);

Megaprisms absent: acicular prisms are positioned vertically or inclined towards the beak, sometimes united in bunches (some Psammobiidae).

4. **Compound prismatic**. Prisms of the first order are polyhedral, composed of acicular prisms of the second

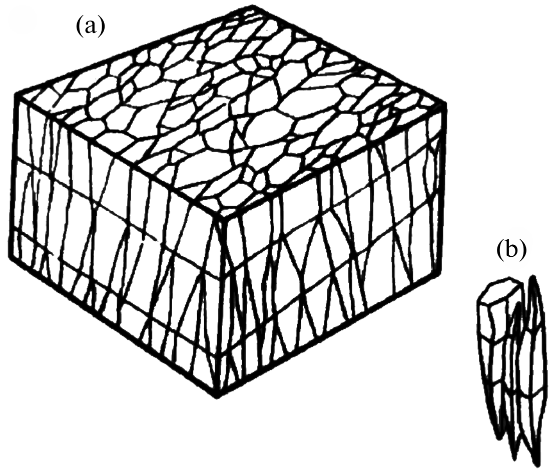

Fig. 2. Simple prismatic structure: (a) block-diagram of a shell site; (b) individual prisms with growth lines.

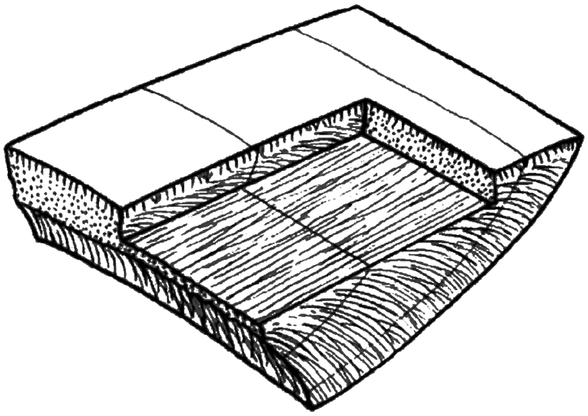

Fig. 3. Block-diagram of fibrous prismatic structure in lucinids.

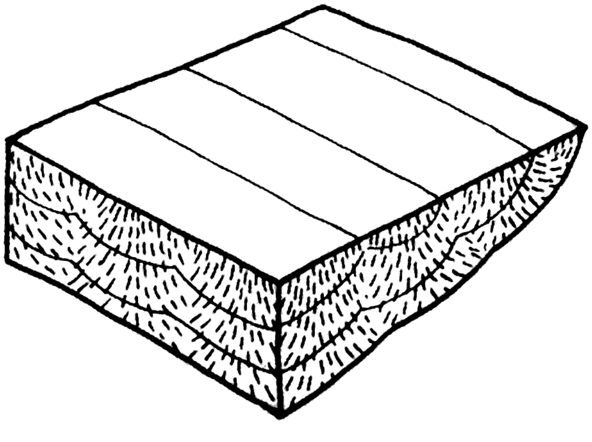

Fig. 4. Block-diagram of acicular prismatic sculpture with megaprisms.

order, fan-shapedly diverging from the prism center, directed to the external surface and inclined towards the beak (Fig. 5). The prisms may be small regular (some Veneridae), larger (10–20 to 50 μm in section), varying in the thickness and shape of cross section, composed of long acicular prisms of the second order (some *Anadara*), or small (1–4 μm), subsquare or more irregular in section, composed of small acicular elements (some Cardiidae and Tellinidae). In the classification of microstructures proposed by Carter (1990), the last type probably corresponds to "vertical nondenticular composite prismatic."

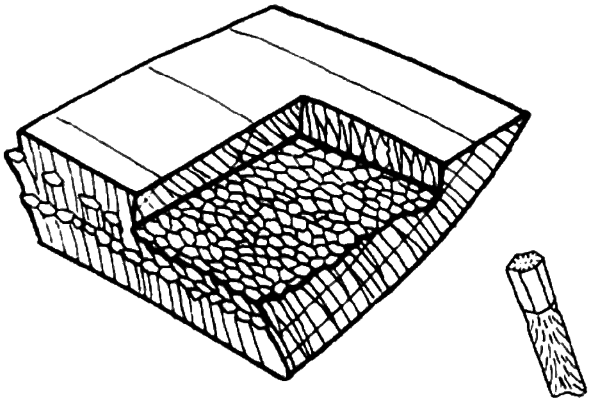

Fig. 5. Block-diagram of compound prismatic structure; the structure of an individual prism is shown on the right.

5. **Composite prismatic** is the microstructural type composed of megaprisms, which are formed of narrow acicular more small prisms of the second order, fan-shapedly diverging from the middle of the layer to its margins (Fig. 6). The structure is present only in the outer shell layer. Megaprisms are usually directed from the beak to margins, where shell grows. Small prisms of the second order are round or polygonal in section, decrease in diameter from the margin to center of megaprisms, 1–5 μm in size, frequently, even smaller. Megaprisms are sometimes absent; in this case, the outer layer is formed of narrow prisms of the second order, with pinnate arrangement (some Lucinidae, Veneridae, and Donacidae: Böggild, 1930; Taylor et al., 1969; Carter, 1980; Popov, 1992):

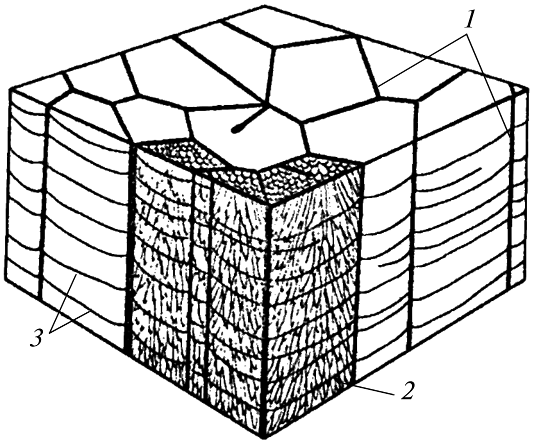

Fig. 6. Block-diagram of the composite prismatic structure of aragonite composition (*Unio pictorum*): (*1*) interprismatic conchiolin walls, (*2*) diverging elements, (*3*) concentric growth lines.

Denticular composite prismatic. Megaprisms correspond to marginal serration of the shell and are formed of small acicular prisms. On the external surface, fine radial undulation corresponds to megaprisms (some Nuculidae).

Fibrous with megaprisms. Megaprisms are composed of narrow fibrous prisms (some Cardiidae and Tellinidae) (Fig. 7).

Fibrous without megaprisms (Fig. 8). Prisms of the second order diverge from the middle of the layer or from the upper part of the outer layer (some Cardiidae, Tellinidae, Lucinidae, and Donacidae). In the classification developed by Carter (1990), this corresponds to "reclined non-denticular composite prismatic."

6. **Compound composite prismatic** type is similar to the composite prismatic type, but differs from it in the small elements of the second order combined in fan-shapedly diverging prisms of the first order, which sometimes in turn united in megaprisms:

With megaprisms, which correspond to undulation on the surface and fine serration of the external margin, composed of complex prisms of the first order, which are in turn composed of small acicular prisms (some Donacidae; Fig. 9);

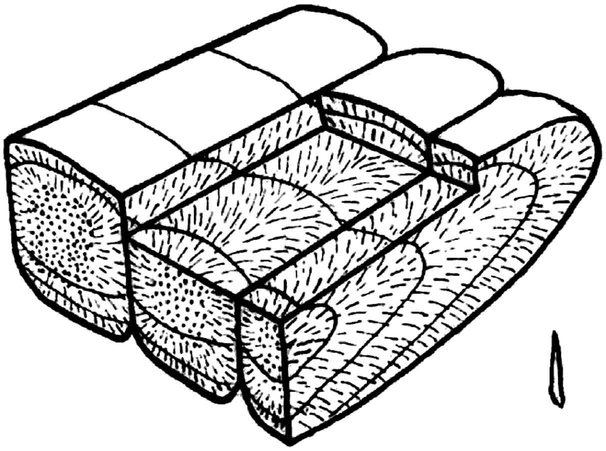

Fig. 7. Block-diagram of fibrous structure with megaprisms.

Megaprisms absent. Regular complex prisms 7–25 μm in section diverge from the upper part or the middle of the layer;

With plates. Prisms of the first order are fused, forming vertical, radially positioned plates, ranging from 10–20 to 50 μm of width (some Veneridae; Fig. 16);

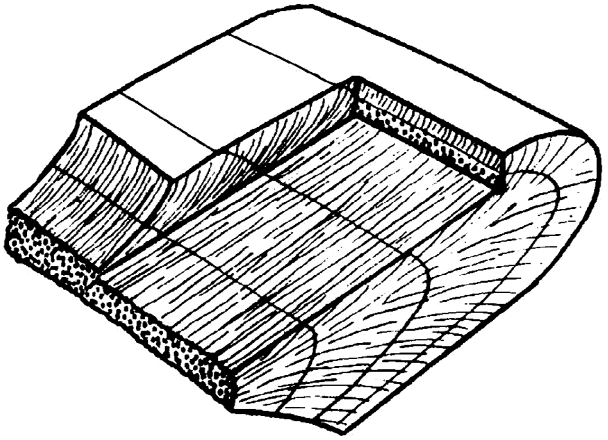

Fig. 8. Block-diagram of fibrous structure without megaprisms.

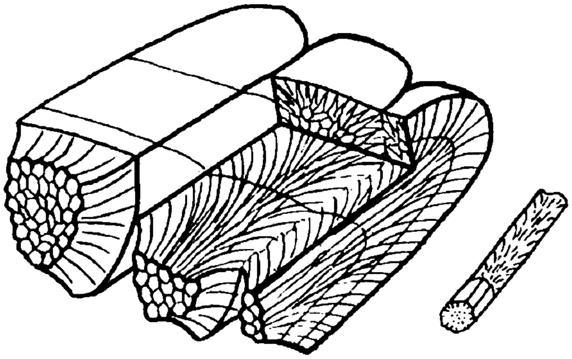

Fig. 9. Block-diagram of compound composite prismatic structure with megaprisms (*Donax trunculus*).

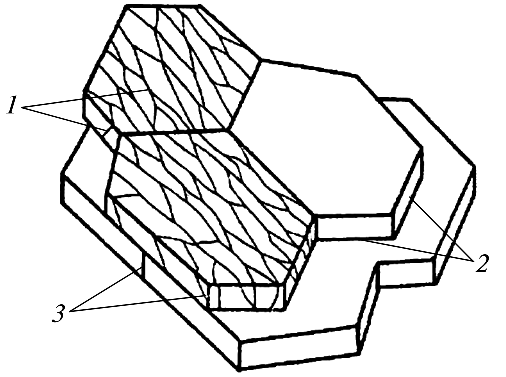

Fig. 10. Block-diagram of nacreous structure for layered nacre: (*1*) intracrystal organic matrix, (*2*) interlamellar matrix, (*3*) intercrystal matrix.

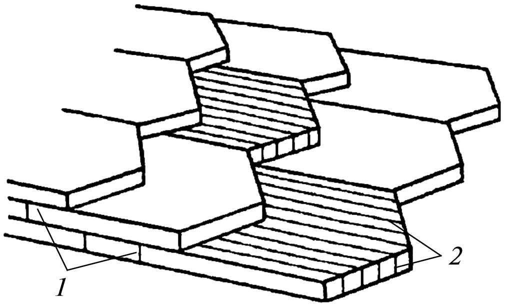

Fig. 11. Block-diagram of regular foliated structure: (a) intercrystal matrix; (b) intracrystal matrix.

Irregular. Prisms of the first order may be irregular, considerably varying in thickness (rare Veneridae and some Tellinidae).

7. **The nacreous structure** is characteristic of mollusks, composed of aragonite leaflets positioned in parallel to the shell surface. These plates are hexahedral in projection, less frequently, square, a rhombic, or irregular in outline. Calcareous plates are enclosed in the organic matrix, which includes interlamellar matrix, which separates one layer of plates from the other, and intercrystal matrix separating plates of one layer.

Sheet nacreous. Plates are arranged in regular layers parallel to the shell surface (Fig. 10). In contrast to gastropods and cephalopods, plates of bivalve mollusks form something like bricklaying in radial section, because individual leaflets are positioned with some displacement rather than one under other. Nacre of this texture is characteristic of the inner layer of many bivalve superfamilies (Nuculoidea, Pinnoidea, Unionoidea, Pholadomyoidea, Pandoroidea) and, in Mytiloidea and Pterioidea, it composes both internal and middle shell layers (Taylor et al., 1969).

Columnar (lenticular) nacreous. All sections display vertical columns of plates located one above other. The height of such a column reaches 20–30 μm. In the middle part, they are approximately identical and, towards the margins, plates usually decreases in size, so that the column shape approaches lenticular. Nacre of this texture is usually observed in the middle shell layer and occurs in Nuculoidea, Trigonoidea, and Pandoroidea (Taylor et al., 1969). Both variants of nacreous structure are frequently observed in one shell; sheet nacre is usually present in the inner layer and lenticular variant is in the middle layer.

Row stack nacreous. Carter (1990) recognized this additional microstructural variant. In this case, in the sections perpendicular to the axes of plate elongation, nacre looks columnar, while in the vertical section parallel to this axis, it is similar to bricklaying.

8. **Foliated structure.** It is close in structure to nacre, but composed of calcitic leaflets. Individual leaflets are hexagonal and positioned somewhat obliquely, covering plates of the preceding layer and looking like shingle rather than parallel to the growth surface (Fig. 11). Within an interlayer of the simultaneously formed plates, their long axes remain parallel

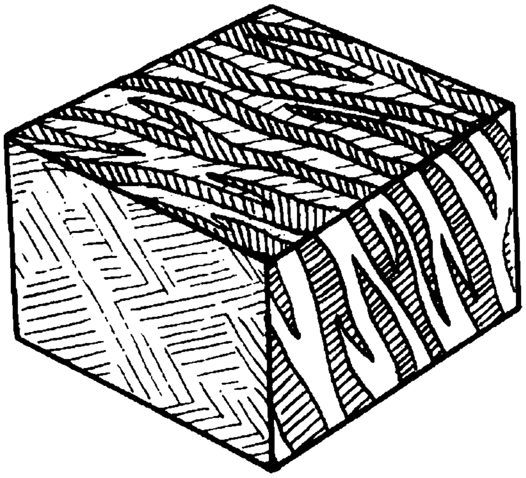

Fig. 12. Block-diagram of simple crossed lamellar structure.

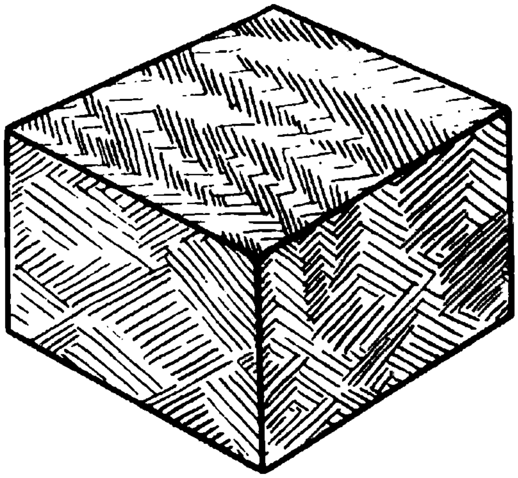

Fig. 13. Block-diagram of complex crossed lamellar structure, with blocky texture.

to each other, but in other sites, it may be different; as a result, the general appearance of the foliated structure in radial section is rather irregular. Leaflets are positioned parallel to the internal shell surface, or obliquely inclined to it and even almost vertical. Alternation of directions is frequently observed within one layer, forming zigzag structures (Ostreoidea and Pectinoidea). A thick interlamellar matrix, which is characteristic of nacre, is absent here and each leaflet is enclosed in a sheath of the intercrystal matrix. Leaflets widely vary in size; they are up to 10–15 μm long, 3–5 μm wide, and 0.2–0.5 μm thick. The foliated structure is characteristic of calcitic shells of Ostreoidea, Pectinoidea, Anomioidea, and Limoidea (Taylor et al., 1969; Carter, 1990).

Carter (1990) have recognized the *regular foliated* and *semi-foliated* structures; the last is distinguished by more irregular leaflets.

9. **Crossed lamellar** structure is most complex and perfect; it is widespread among bivalves and gastropods. It is always composed of aragonite arranged in plates of several orders; in neighboring plates of the first order, the plates of the second order are positioned in opposite directions (Fig. 12). Large plates are usually directed perpendicular to the shell surface and, in projection, extend along the growth lines. However, in the presence of radial ribbing, the plates display a more complex curvature, remaining perpendicular to the growth line at the shell margin. Inside a plate of the first order, orientation of plates of the second order varies, so that, in each section, they remain crossed (the outer and middle layers of Arcidae, Limopsidae, Glycymeridae, Carditidae, Lucinidae, and Cardiidae and the majority of Veneridae, Tellinidae, Donacidae, etc.).

Among crossed lamellar types of structure, Carter (1990) has recognized the following:

Simple crossed lamellar variant, in which the elements of the second order are represented by more or less regular plates;

Rod-type crossed lamellar variant, in which the structures of the second order are short oval or elongated rectangular elements;

Crossed foliated variant, which is composed of calcitic leaflet blocks, with regularly alternating orientation;

Crossed semi-foliated variant, which is the same as the previous case, but with more poorly differentiated elements of second order.

10. **Complex crossed lamellar**. This is composed of the same plates of the second order as the preceding variant, but with three or more directions of the structural elements. It usually forms the inner layer in taxa that are characterized by the crossed lamellar structure (Arcidae, Lucinidae, Tellinidae, Cardiidae, etc.). The following varieties have been recognized:

Irregular (blocky) structures are irregular blocks of plates alternating with blocks of a different or opposite orientation of plates (Fig. 13);

Conical. Plates form vertical columns of cones enclosed in each other, i.e., the cone-in-cone structure (Fig. 14);

Fine complex crossed lamellar. Carter (1990) recognized this variety composed of small blocks consisting of several plates of the second order.

11. **The homogeneous** structure is of small lenticular aragonite granules, with similar optical orientation. Individual granules are elongated, lenticular, or irregular in shape and enclosed in organic sheaths; they widely vary in size. Granules are usually positioned parallel to growth lines; therefore, in the inner layer, they are horizontal and, in the outer layer, they are positioned obliquely or vertically, in parallel to the growth line.

Granular variety is composed of small granules 0.3–4.0 μm in size.

Crossed acicular structure is composed of elongated crystallites, 0.2–0.3 × 5–10 μm; in each section, they are extended in two or more main directions (sometimes shows gradual transition to crossed lamellar structures) (some Veneridae, Tellinidae, and Donacidae).

Irregular homogeneous structure is composed of complex irregular elements 0.5–3.0 μm in size (some Veneridae, Tellinidae, Donacidae, etc.).

Application of Microstructural Features for Taxonomy

Shell substance of both calcitic and aragonitic composition is preserved in the fossil record for a long time due to protective effect of conchiolin sheaths. The primary composition and structure of the shell often remain constant in Cenozoic and Mesozoic forms and nonrecrystallized ones sometimes occur in the Paleozoic beds. However, aragonite is frequently transformed into more stable calcite or replaced by other minerals. In these cases, relicts of the primary structure are frequently retained in some sites of the shell or locules (Carter, 1990).

The microstructural characters which are distinctive for certain taxonomic groups are usually connected with the structure of the outer layer. This is apparently determined by ontogenetic development of the structure; the outer layer, which appears somewhat later in ontogeny, is more readily exposed to phylogenetic changes.

The microstructure of the middle and inner shell layers is usually more stable and distinctions observed in structural details of these layers (transition from the crossed lamellar to homogeneous structures; textural distinctions are of complex crossed lamellar structure) are frequently useless as taxonomic characters, since they co-occur in different specimens of the same species or replace each other within one shell.

Even when the set of structures of different taxa are identical, they can differ essentially in spatial orientation of elements. Let us briefly consider the shell structure in three families:

Arcidae. All members of the superfamily Arcacea are rather uniform in shell structure, which is mostly composed of only two microstructural types, the crossed lamellar structure of the outer and middle layers and complex crossed lamellar structure of the inner layer. This pattern is widespread among different nonrelated bivalve groups. In this case, the orientation of plates of the first order in the outer layer of investigated members of the family varies widely, forming the external sculpture (Fig. 15); and these distinctions are also useful for identification of taxa. In particular, in members of the genera *Arca* and *Barbatia*, plates of the first order of the outer layer in both ribs and intercostal spaces are radially oriented (Fig. 15b). In *Anadara* and *Trisidos*, the same plates are directed radially only in the intercostal spaces, while in the ribs, they are oriented concentrically and inclined towards the beak (Fig. 15c). In members of the genus *Acar*, on the contrary, the orientation in ribs is close to radial and in intercostal spaces, the plate are almost horizontal, positioned in parallel to the shell surface (Fig. 15d).

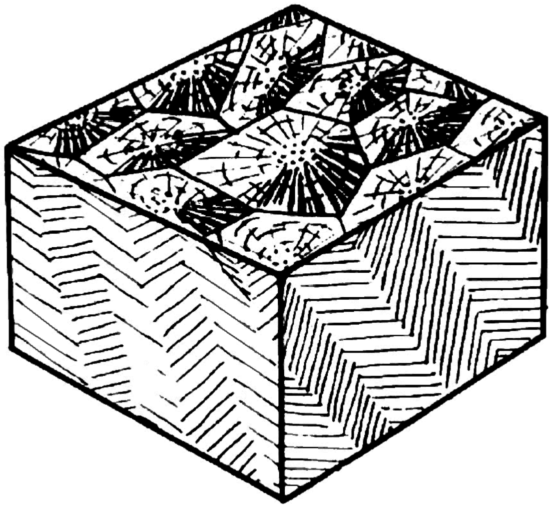

Fig. 14. Block-diagram of complex crossed lamellar structure, with conical texture.

Cardiidae. In the shell structure, primarily in the outer layer, the Cardiidae are distinctly subdivided into four groups (Fig. 16). The most simple structure is characteristic of a large group of warmwater genera (*Cardium*, *Bucardium*, *Europicardium*, *Trachycardium*, *Acrosterigma*, *Mexicardia*, *Phlogocardia*, *Laevicardium*, and *Papyridea*). Secondarily, as a result of reduction of the outer layer, the same structure is acquired by Neogene brackish-water Cardiidae of the Paratethys, which are combined in the subfamily Lymnocardiinae.

In members of the genera *Nemocardium* and *Pratulum,* the shell is composed of the same microstructural types, but the crossed lamellar structure forms both the outer and middle layers, which are distinguished by the orientation of plates. In the middle layer, plate are usually arranged concentrically, whereas in the outer layer, they are almost horizontal in the ribs and form a fan-shaped pattern diverging from the middle of the layer in the intercostal spaces (Fig. 16b).

The third large cardiid group includes members of tropical genera (*Fragum*, *Corculum*, *Trigoniocardia*) and genera of the Tethyan origin (*Acanthocardia, Parvicardium, Plagiocardium*, *Loxocardium, Orthocardium*, and *Cerastoderma*). Their shells are also three-layer, although the outer layer has a composite prismatic structure and is composed of narrow fibrous prisms diverging fan-shapedly from the middle of the layer (Fig. 10c). These fibrous prisms sometimes (in *Acanthocardia*) form elements of the highest order, the megaprisms positioned horizontally. In some *Acanthocardia* and *Cerastoderma,* the external part of this layer

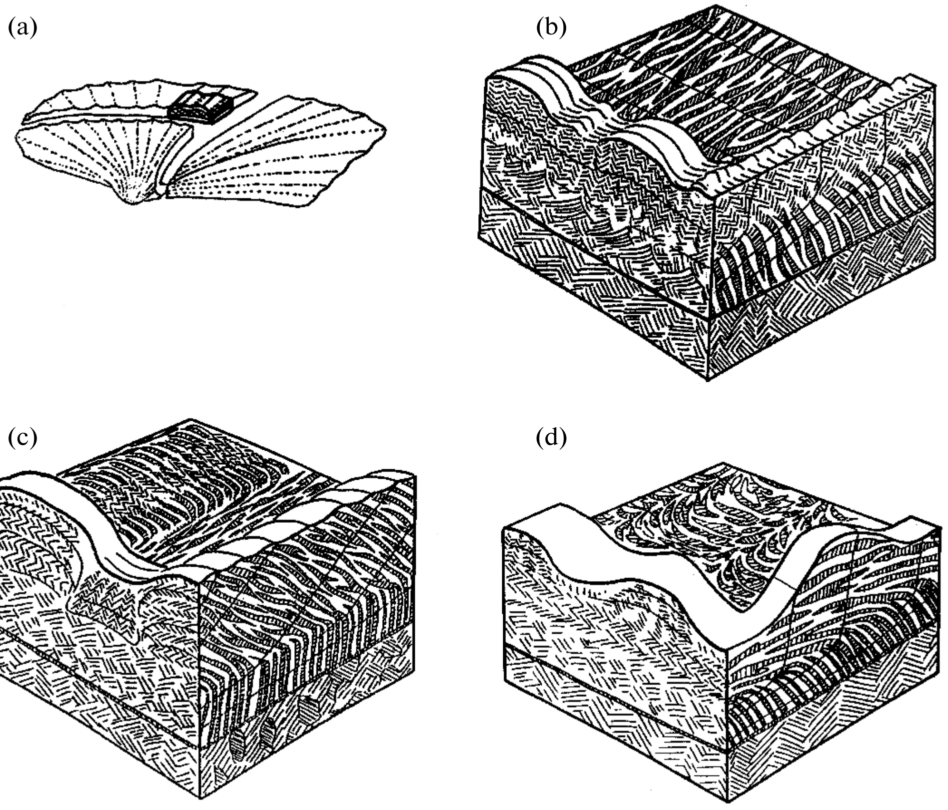

Fig. 15. Shell structure in members of the superfamily Arcidae: (a) scheme of orientation of the main shell sections and positions of the site shown in block-diagrams; (b) block-diagram of shell site of *Arca* and *Barbatia*; (c) block-diagram of shell site of *Anadara* and *Trisidos;* (d) block-diagram of shell site of *Acar.*

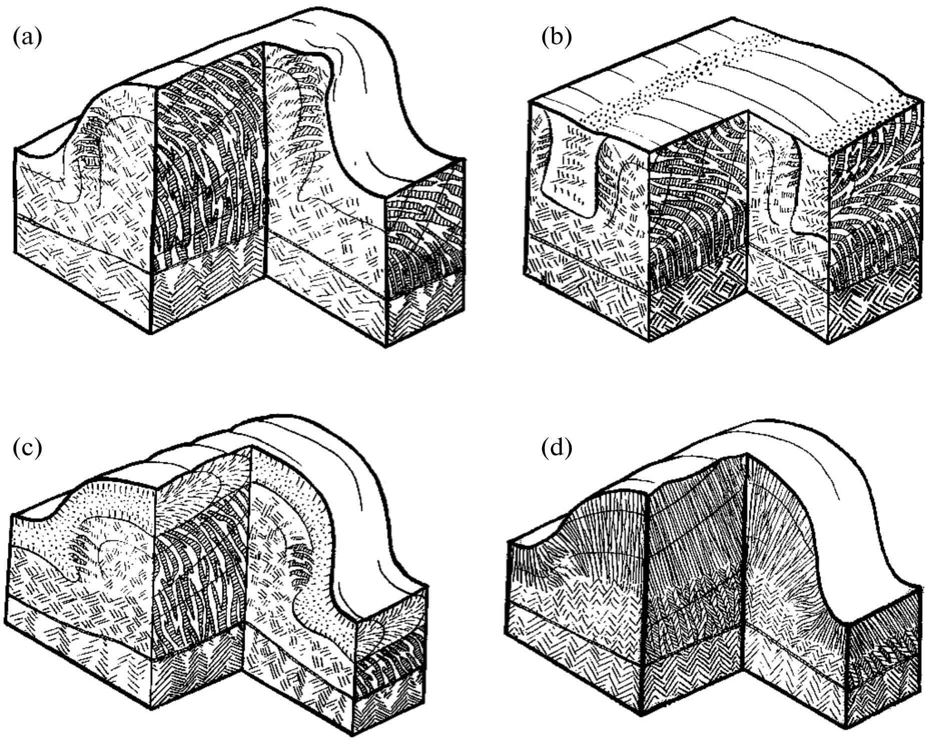

Fig. 16. Shell structure in members of the family Cardiidae: (a) block-diagram of shell site in members of the subfamilies Cardiinae and Lymnocardiinae; (b) block-diagram of shell site of members of the genera *Nemocardium* and *Pratulum*; (c) block-diagram of shell site of Fraginae *(Cerastoderma)*; (d) block-diagram of shell site of the genus *Clinocardium*.

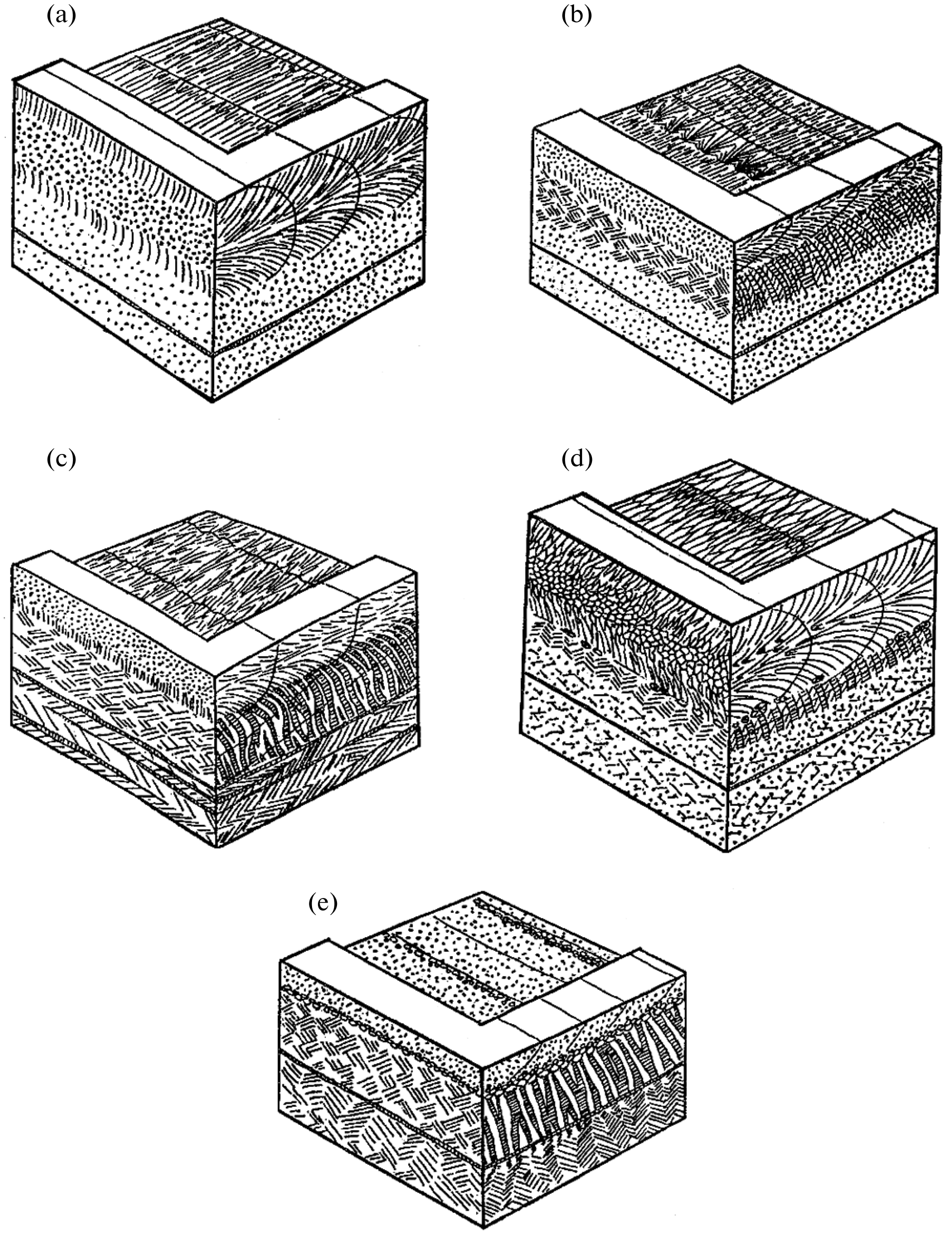

Fig. 17. Shell structure in members of the family Tellinidae: (a) block-diagram of shell site of *Tellina radiata*; (b) block-diagram of shell site of members of the genera *Angulus*, *Moerella*, *Peronidia*, and *Quidnipagus*; (c) block-diagram of shell site of *Angulus nysti*; (d) block-diagram of shell site of *Megaxinus*; (d) block-diagram of shell site of *Macoma*.

has an additional interlayer of the crossed lamellar structure.

Finally, the north Pacific and Arctic cardiid genera *Clinocardium* and *Serripes* are distinguished by the extraordinary structure, with a massive outer layer fibrous prismatic in structure. The prisms are positioned perpendicular to the external surface, slightly inclined towards the beak; the ribs are straight or curved. They are subsquare or more irregular in section and, at high magnification, it is sometimes visible that they are composed of smaller elements directed towards the prism center. In the same shell, the elements forming prisms are sometimes invisible and prisms seem integrated. Plates of the middle layer are frequently poorly differentiated, vague.

A revision of this family has shown that the groups in question are natural and, hence, it is possible to regard them as subfamilies (Cardiinae, Protocardiinae, Fraginae, and Clinocardiinae). This grouping of genera was corroborated by the anatomical study of cardiids (the data provided by Ya.I. Starobogatov).

Tellinidae. The shell of all investigated Tellinidae has three main layers, frequently with additional sublayers (Fig. 17), the structure of which varies even within particular genera. Under an optical microscope, the inner layer usually looks homogeneous, while under an electron microscope, it is irregularly granular or, less frequently, crossed acicular. The inner layer frequently contains interlayers irregular prismatic in structure.

The middle layer of the majority of investigated species has two sublayers; the lower sublayer is homogeneous and the upper one is crossed lamellar; the plates are usually short, irregular, not always distinct.

The outer layer is usually thin and often composed of fibrous prisms inclined towards the beak (Fig. 17b). At high magnitude, it is seen that fibrous prisms are sometimes complex in structure. In *Peronidia planata*, they are composed of short elements converging to the prism center; in other species, they are formed of transverse elements. This structure is typical of the majority of species investigated in Tellinidae from the Mediterranean Region. Among them, some differences are observed in *Angulus tenuis* and *A. nysti*, in which small prisms of the outer layer are combined in megaprisms. In addition, the last species lacks a homogeneous structure; the middle layer is crossed lamellar; the inner layer is complex crossed lamellar, with interlayers of prisms (Fig. 17c). In species of the genus *Arcopagia* and in *Moerella donacina*, the outer layer is more massive and, in the last species, prisms diverge from the middle rather that upper part of the layer.

Microstructural distinctions of Tellinidae from other zoogeographical realms are even more significant. In particular, the central American species *Tellina radiata* is distinguished by the absence of a crossed lamellar structure and massive outer layer of fibrous composite prismatic structure without megaprisms, with narrow fibroid prisms fan-shapedly diverging from the middle of the layer (Fig. 17a). In Far East species assigned into the genus *Megangulus* Afshar, 1969 (*M. venulosa*, *M. lutea*), massive outer layer of complex composite prismatic structure is composed of irregular fan-shapedly arranged prisms of the first order without megaprisms (Fig. 17d).

All known members of the genus *Macoma* (subfamily Macominae) differ from the above described Tellinidae in the absence of homogeneous structure. In this case, the middle layer is crossed lamellar, with well-differentiated radially directed plates; the inner layer is complex crossed lamellar, with a blocky texture, sometimes, with interlayers of prisms. The outer layer, if it differs in structure from the middle layer, is thin and composed of round spherulites, which are very small at the external surface and larger below, at the boundary with the middle layer.

Such a wide diversity of structures in 45 shells of 28 species and 16 genera prevents the use microstructural characters for reliable improvement of the system of Tellinacea.

The structure of these and other mollusk groups has been considered in more detail in special works (Bøggild, 1930; Taylor et al., 1969; Popov, 1977, 1986, 1992; Carter, 1980, 1990; etc.).

It is possible to conclude that, within bivalves, more ancient primitive groups are distinguished by the more stable shell structure. In particular, the majority of palaeotaxodont mollusks, almost all Arcidae, Glycymeridae, and Carditidae are similar in microstructure. The differences are only observed in the relative development of layers and the pattern of internal ribbing in the shell sections. The Lucinidae are the most ancient heterodont mollusks, which are also characterized by relatively weak structural variations (except for several groups, such as *Anodontia*, *Linga*, and *Lucinoma*). The Cardiidae display several distinctive microstructural types, which agree with the general concept of their system. The most diverse structure is characteristic of evolutionarily young, presently flourishing bivalve groups, such as the Veneroidea and Tellinoidea. The shell of these groups is often composed of four or five microstructural types, which sometimes vary even within particular genera and species.

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