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by S.V. Popov

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Shell microstructure and the classification

of the family Cardiidae

(04 00 09. Paleontology and Stratigraphy)

by

S. V. Popov

Scientific Director: C.A. Nevesskaya, Doctor of Biological Sciences

Introduction

The representatives of the family Cardiidae have been known since
the beginning of the Mesozoic era, but it is only in the Cenozoic era
that they become variegated, and at present they occur in all seas from
the Arctic to the tropics, having adapted to the conditions of inland
seas as well as to freshwater lagoons. The variety and rapid evolution
of the members of Cardiidae determined their stratigraphic importance,
especially for the Cenozoic deposits of Southern Eurasia.

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The present author investigated, along with the usual conchological
characters, the shell microstructure of many members of Cardiidae. The
structure of about 130 species was studied, including that of 24 repre-
sentatives of the 26 known genera of Cenozoic marine Cardiidae and 24

* Numbers in the right-hand margin indicate the page numbers of the original
(Tr.).

genera of Cardiidae of brackish waters which were endemic to the Neogene--Quaternary basins of the Paratethys. In order to determine the effect of environmental conditions on the shell structure, we studied more than 50 specimens of the most euryhaline species--the Cerastoderma glaucum--from seas, estuaries and lagoons with different salinities. We made a total of about 2,000 grindings, 100 polished sections and more than 300 acetate films from etched surfaces. The shell structure of 35 species belonging to 25 genera was studied on a scanning and transmission electron microscope. The work included about 50 spectral semiquantitative analyses of the content of microelements in the shells, and we utilized the results of 25 determinations of isotope composition of the oxygen of the shell carbonate of the Cardiidae. The descriptive part of the dissertation includes diagnoses of 4 subfamilies, 26 genera and 20 subgenera of Cardiidae.

This work would have been impossible without the collections belonging to L.A. Nevesskaya, R.L. Merklin, O.M. Petrov, A.G. Eberzin and N.P. Paramonova, as well as the data received from the following foreign scientists: V. Woodring (USA), A. Denis (France), K. Masuda (Japan) and B. Smith (Australia).

Technical assistance and access to an electron microscope were made possible to the author by M.M. Kalashnikova, V.N. Kumanin (IMEZh), E.G. Popov (of the Moscow Institute of Geological Exploration (MGRI)) and A.Ya. Shevchenko (of the Oceanography Institute). The acetate replicas were prepared according to the method developed by A.M. Popov (of Kharkov State University (KhGU)). The investigation of the isotope composition of the shell was conducted in cooperation with S.D. Nikolaev and S.A.

Gorbarenko (of Moscow State University (MGU)).

The author expresses his special gratitude to his coworkers of the laboratory in which the work was conducted, and to his supervisor L.A. Nevesskaya, Doctor of Biological Sciences, who determined the formulation of this theme.

Chapter 1. Shell Structure of Bivalve Mollusca

The shell of bivalve Mollusca consists of calcium carbonate, has an organic matrix and is covered externally by a thin organic layer--the periostracum. The shell is formed owing to epithelial secretion on the external surface of the animal's mantle. The external layer of the shell is formed by the epithelium at the mantle's edges; the intermediate layer is formed by the external surface of the mantle up to the point where the mantle muscle is attached, and, finally, the inner layer is secreted by the mantle's surface above the mantle muscle (Beedham, 1958).

The mineral composition of the shell layers can be calcite or aragonite. The mineral composition and structure of the carbonate substance is apparently determined by the composition and structure of the organic matrix, which controls the calcification process.

A study of shell sections of Mollusca showed that almost the entire diversity of their structure is made up of a few types of microstructures (Bøggild, 1930; Taylor et al., 1969; 1973):

Mother-of-pearl structure--always aragonite, composed of many-sided or rounded tablets forming layers parallel to the surface of the shell (layered mother-of-pearl), or forming vertical stacks of crystals (lens-shaped mother-of-pearl);

Foliated structure--formed of calcereous leaflets having a polygonal

form and situated horizontally or diagonally relative to the surface, sometimes with alternating orientation;

Simple prismatic structure--always aragonite or calcite, composed of vertical many-sided prisms divided by an organic matrix;

Composite prismatic structure--always aragonite, formed of horizontally situated prisms of the first layer which are made up of smaller prisms radiating in fan-shaped fashion from the center of the large prisms;

Intersecting-lamellar structure--always aragonite, consisting of several layers of lamellae, with the lamellae of the second layer being oriented opposite to the neighboring lamellae of the first layer;

Composite intersecting-lamellar structure--always aragonite, /5
consisting of the same second-layer lamellae as in the previous structure but with a more varied and irregular orientation of blocks of such lamellae;

Homogeneous structure--aragonite, consisting of small carbonate granules with a similar optic orientation inside large sections of the layer.

The layers of the myostracum*, which are deposited beneath the point where the muscles are attached to the shell, are always of an irregular, thinly-prismatic structure.

Chapter 2. Shell Microstructure of Marine Cardiidae and its Significance for Classification and Phylogeny

The shell structure was investigated with an optical microscope in reflected light on polarized radial, transverse and tangential ground sections, and on polished sections and acetate films in transmitted light. The carbonate replicas with slightly etched shell surfaces were

* Translator's note: "myostracum": taken directly from the original Russian "miostrakum", for which no other equivalent English term is available.

studied with the aid of an electron transmission microscope; the radial and transverse shear surfaces of the shell whose natural edges were damaged were studied with the aid of an electron scanning microscope.

The ontogenetic changes in the sculpture and in the ribbed structure were studied on shells of young specimens or in the umbo area of shells of adult forms, provided the material was in a good state of preservation.

The shell of Cardiidae has a two- or three-layered structure (fig.1).

The inner layer of the composite intersecting-lamellar structure is made up of lamellae of the second layer, forming larger, irregular, branching lamellae (tangled lamellar structure), or irregular blocks distinct in their lamellar polarization (block structure), or lamellae that form cones that are enclosed one in the other and oriented with the crown toward the external surface of the shell (cone structure, see fig.2). A certain variation in this structure frequently occurs in members of several related genera of Cardiidae.

The intermediate layer (or the external layer in a two-layered structure) has an intersecting-lamellar structure, which differs from the structure usually described in the literature (Buggild, 1930; Taylor et al., 1969) in that the lamellae of the second layer alter their orientation inside the lamellae of the first layer (fig.3) and remain crossed in a tangential cut as well.

The microstructure of the external layer can be used to identify four large groups of Cardiidae: (1) complete merger with the intermediate layer; then the lamellae of the intersecting-lamellar structure come up to

the external surface of the shell; (2) same intersecting-lamellar structure as the external layer but with horizontally oriented lamellae, diverging from the middle of the layer; (3) consists of thin vertical prisms; (4) has a composite prismatic structure.

A study of the development of the shell microstructure indicated that an identical two-layer structure in the early stages of development is characteristic of all Cardiidae, and that structural distinctions appear later. Thus the outer layer in Cerastoderma glaucum is usually deposited 2--3 mm from the umbo, in Serripes groenlandicus with a shell size of about 5 mm, in Nemocardium edwardsi only 10--12 mm from the umbo, in Pratulium thetidis 7--8 mm. The shell ornamentation in the early stages is also distinct and goes through several stages of formation (fig. 6).

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Ontogenetic and structural shell features in related genera of Cardiidae are very constant and may indicate a genetic relationship of these forms. In this connection, such clearly apparent conservative characters, along with morphological features, may be used to determine the degree of taxonomic relatedness of the Cardiidae.

In contrast to the classification developed by M. Keen as stated in "Treatise on invertebrate Paleontology" (Keen, 1969, Table 1), the obtained data suggest that the marine members of the Cardiidae form only three natural groups of genera which may be regarded as the subfamilies Cardiinae, Fraginae and Protocardiinae.

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The subfamily Cardiinae includes forms with rounded or oval shells without a clearly expressed carinal kink and frequently with unevenly developed cardinal teeth. The shell consists of two or three layers, the outer layer being made up of vertical elements, with the lines of growth

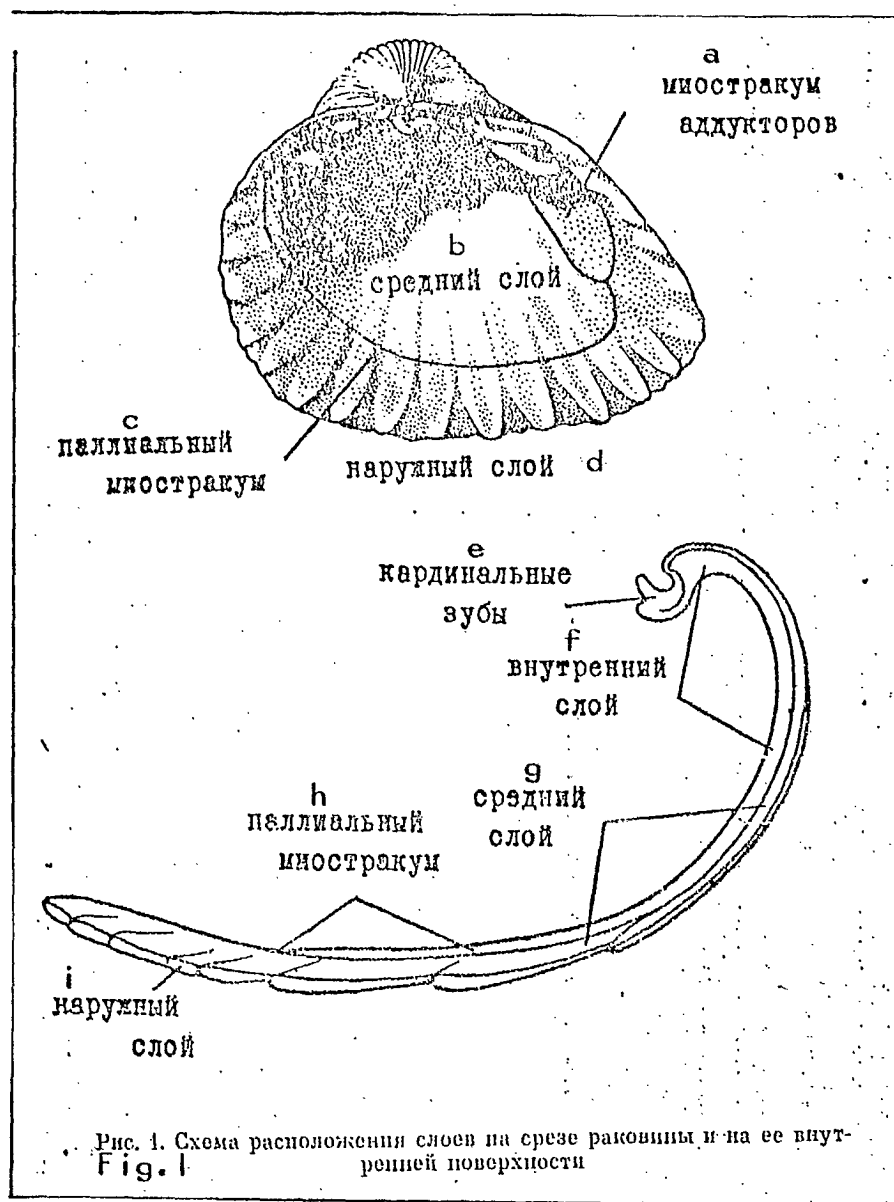


Fig. 1. Arrangement of layers on a shell section and on its inner surface.

a--myostracum of adductors; b- intermediate layer; c-pallial myostracum; d-outer layer; e-cardinal teeth; f-inner layer; g-intermediate layer; h-pallial myostracum; i-outer layer.

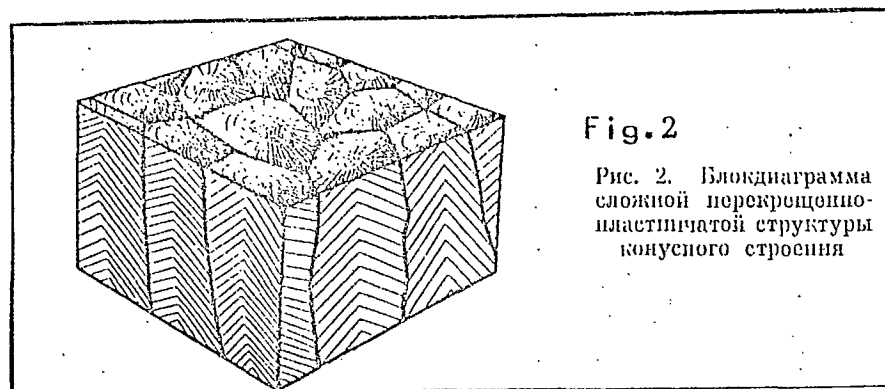


Fig. 2. Block diagram of a composite intersecting-lamellar, cone-shaped structure.

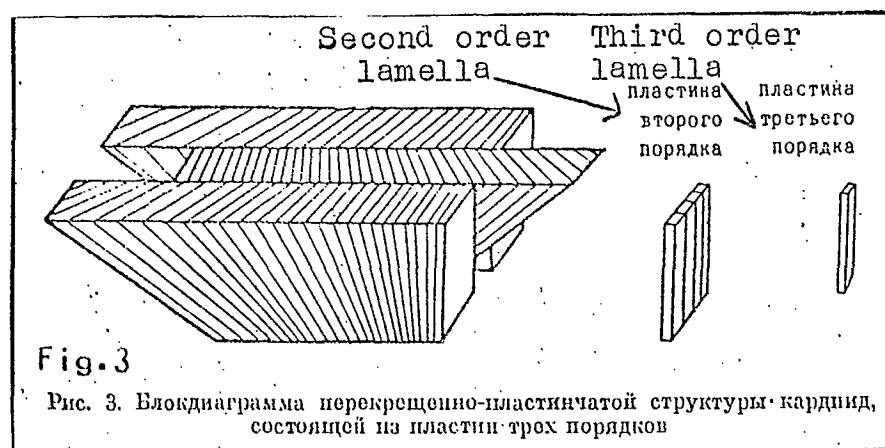


Fig. 3. Block diagram of an intersecting-lamellar structure consisting of three types of lamellae.

remaining straight on the outer surface. Most of the members of this subfamily have a two-layered shell--an outer intersecting-lamellar and an inner composite intersecting-lamellar layer. The lamellae of the outer layer are arranged vertically and penetrate from the intermediate pallial myostracum to the outer surface of the shell. The inner layer usually has a tangled lamellar structure. Such a structure is characteristic of many genera of Cardiidae distributed in tropic and warm seas.

A distinct structure is found only in two genera of Cardiidae of this subfamily--Clinocardium and Serripes, which occur in the northern Pacific and in the Arctic Ocean. These forms are characterized by a peculiar structure of the outer layer which is made up of thin vertical prisms. This subfamily includes the genera identified by R. Stewart (1930) as the subfamily Trachycardiinae, as well as a portion of the genera identified by M. Keen as belonging to the subfamily Laevicardiinae. Morphologically these genera are insufficiently isolated from the members of the subfamily Cardiinae but have an identical microstructure with the latter (except the two above-mentioned genera).

The subfamily Fraginae incorporates genera distinguished by a more angular shell and a sharp carinal kink and usually uniformly developed cardinal teeth. The shell is three-layered, with the outer layer being of a composite prismatic structure and the lines of growth bent, turning toward the umbo at the outer surface. The intermediate layer has an interesting-lamellar structure, and the inner layer has a composite intersecting-lamellar structure which is usually cone-shaped.

This subfamily includes genera of tropical, sharply carinal Cardiidae and a large group of genera distributed in the Mediterranean area (see table 1) which earlier belonged to the subfamily Cardiinae.

The subfamily Protocardiinae includes forms with a peculiar, irregularly developed ornamentation on the shell. The microstructure of the investigated members of this subfamily is distinct from that of other Cardiidae by its thick outer layer of shell; this layer consists of horizontally oriented lamellae with an intersecting-lamellar structure. The lines of growth are flatly bent in the outer layer, and at the surface of the shell they bend toward the umbo. This subfamily consists mainly of fossil forms. A few contemporary members of this subfamily occur in the tropic part of the Pacific. /10

The presence of several transitional structural features and the study of their development make it possible to outline several possible phylogenetic links among Cardiidae. If we accept the shell structure of the Protocardiinae, the oldest subfamily which was widely distributed in the Mesozoic era, as the original structure of all Cardiidae, then the structure of the investigated Eocene representative of the genus Fragum may be considered as a transitional form of the subfamily Fraginae (fig. 4). The two-layered structure which is characteristic of the majority of the members of the subfamily Cardiinae could have formed from any other type of structure as a result of a lag in development, since it corresponds to the structure of all Cardiidae in the early stages of development.

The representatives of the genera Clinocardium, and later of Serripes with a more complex three-layered shell structure, appear at a later geological time, at the end of the Paleogene. The appearance of

that kind of microstructure with a thin outer prismatic layer apparently is a later evolutionary development, although D. Taylor (1973) suggested the existence of this type of structure and considered it to be the most primitive for the Heterodonta.

Along with such divergent development in shell structure there are also cases of a homeomorphous structural development in various phylogenetic lines of Cardiidae. Apparently this parallel development explains the appearance of the composite prismatic structure in the members of the Cardiinae (in an additional rib in Phlogocardia belcheri) and in the Protocardiinae (in the outer layer in Discors lyratum). The stratigraphic distribution of individual genera and subgenera of Cardiidae and their assumed phylogenetic relationships are graphically represented in fig. 5. /12

Thus evolutionary transformations of shell structure occurred by way of a variously altered course of development: by complications in the development (extensions or anabolies during structure formation characteristic of Clinocardium, Serripes, Phlogocardia and some Acanthocardia, see fig. 4), developmental deviations (for example, in the structure of representatives of Fraginae, and structural transformations in Discors lyratum). Sometimes one can observe what are apparently secondary developmental simplifications (shell structure in Cardiinae).

Chapter 3. Descriptive Part

The chapter contains diagnoses of the family [sic] Cardiinae, of three subfamilies, 26 genera and 20 subgenera of Cenozoic marine Cardiidae (table 1), comparisons with other genera, keys for determining subgenera and lists of species. For the Cardiidae from brackish waters, whose classification has received most attention in Soviet literature, we have

Table. 1. System of Cenozoic Cardiidae.

Таблица 1. СИСТЕМА КАНОЗОИЧЕСКИХ КАРДИИД.

KEEN, 1969

Admitted in present paper

1. Семейство CARDIIDAE
2. Подсемейство CARDIINAE
3. Род Cardium
4. Подрод Cardium
- Подрод Bucardium
- Род Vepriocardium
- Подрод Vepriocardium
- Подрод Hedecardium
- Подрод Orthocardium
- Род Acanthocardia
- Подрод Acanthocardia
- Подрод Agnecardia
- Подрод Rudicardium
- Подрод Schedocardia
- Род Loxocardium
- Род Parvicardium
- Род Plagiocardium
- Подрод Plagiocardium
- Подрод Maoricardium
- Подрод Papillicardium
2. Подсемейство TRACHYCARDIINAE
3. Род Trachycardium
- Подрод Trachycardium
- Подрод Dalloccardia
- Подрод Mexicardia
- Подрод Philogocardia
3. Род Acrosterigma
- Подрод Acrosterigma
- Подрод Ovicardium
- Подрод Regozara
- Подрод Vasticardium
3. Род Papyridea
2. Подсемейство LAEVICARDIINAE
- Род Laevicardium
- Подрод Laevicardium
- Подрод Dinocardium
- Подрод Fulvia
- Род Cerastoderma
- Род Clinocardium
- Род Serripes
2. Подсемейство FRAGINAE
- Род Fragum
- Подрод Fragum
- Подрод Lunulicardia
- Род Corculum
- Род Ctenocardia
- Подрод Ctenocardia
- Подрод Afrocardium
- Подрод Microfragum
- Род Trigonocardia
- Подрод Trigonocardia
- Подрод Americardia
- Подрод Apicardia
- 1--family;
- 2--subfamily;
- 3--genus;
- 4--subgenus;
1. Семейство CADRIIDAE Lamarek, 1809
2. Подсемейство CARDIINAE Lamarek, 1809
3. Род Cardium L., 1758
- Род Bucardium Gray, 1853
- Подрод Bucardium s. s.
4. Подрод Vepriocardium Ired., 1929
- Подрод Europicardium subgen. nov.
- Подрод Agnecardia Stew., 1930
- Род Hedecardium Marw., 1944
- Род Trachycardium Mörch, 1853
- Подрод Trachycardium s. s.
- Подрод Dalloccardia Stew., 1930
- Подрод Vasticardium Ired., 1927
- Род Acrosterigma Dall, 1900
- Род Mexicardia Stew., 1930
- Род Philogocardia Stew., 1930
- Род Papyridea Swain., 1840
- Род Laevicardium Swain., 1840
- Род Fulvia Gray, 1853
- Род Dinocardium Dall, 1900
- Род Clinocardium Keen, 1936
- Род Serripes Gould, 1841
2. Подсемейство FRAGINAE Stewart, 1930
3. Род Fragum Röding, 1798
- Подрод Fragum s. s.
- Подрод Ctenocardia H. et A. Adams, 1857
3. Род Corculum Röding, 1789
- Подрод Corculum s. s.
- Подрод Lunulicardia Gray, 1853
3. Род Trigonocardia Dall, 1900
- Подрод Trigonocardia s. s.
- Подрод Americardia Stew., 1930
3. Род Plagiocardium Cossm., 1888
- Подрод Plagiocardium s. s.
- Подрод Maoricardium Marw., 1944
- Род Parvicardium Mont., 1884
- Род Loxocardium Cossm., 1886
- Род Orthocardium Trembl., 1950
- Род Acanthocardia Gray, 1851
- Подрод Acanthocardia s. s.
- ?Подрод Schedocardia Stew., 1930
- Род Cerastoderma Mörch, 1853

2. Подсемейство PROTOCARDIINAE

Род Nemocardium

- Подрод Nemocardium
- Подрод Arctopratulum
- Подрод Discors
- Подрод Dicaricardium
- Подрод Frigidocardium
- Подрод Keenaea
- Подрод Lophocardium
- Подрод Lyrocardium
- Подрод Microcardium
- Подрод Pratulum
- Подрод Trifaricardium
- Подрод Varicardium

1. Семейство LYMNOCARDIIDAE

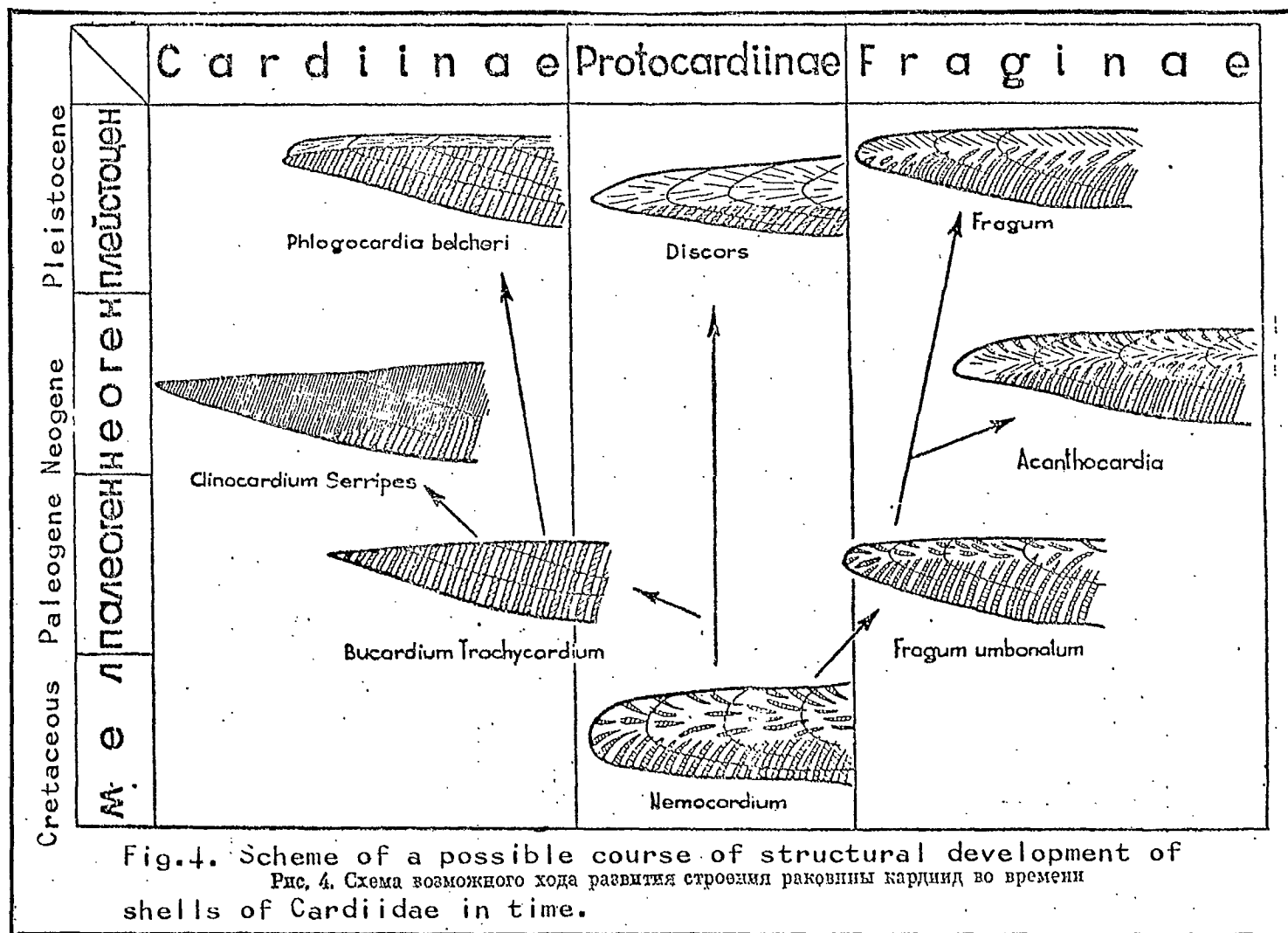
2. Подсемейство PROTOCARDIINAE

Keen, 1951

- Род Nemocardium Meek, 1876
- Подрод Nemocardium s. s.
- Подрод Keenaea Halc, 1951
- Подрод Varicardium Marw., 1944
- Род Pratulum Ired., 1924
- Род Discors Desh., 1858
- Род Lophocardium Fisch., 1887

2. Подсемейство LYMNOCARDIINAE

Stoliczka, 1871



- a-Cretaceous;
b-Paleogene;
b1-Paleocene;
b2-Eocene;
b3-Oligocene;
c-Neogene;
c1-Miocene;
c2-Pliocene;
d-Pleistocene;

Fig. 5. Scheme of stratigraphic distribution and of assumed phylogenetic relationships of genera and subgenera of Cenozoic Cardiidae.

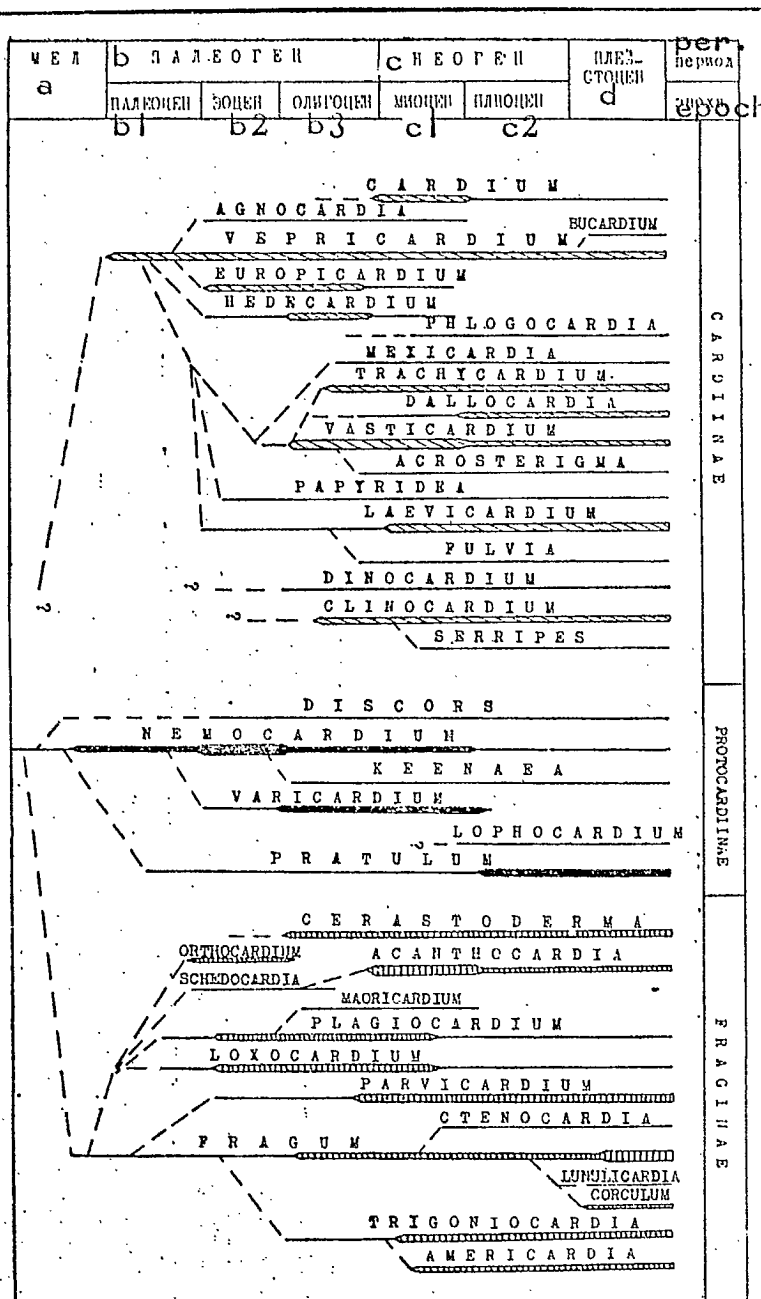


Рис. 5. Схема стратиграфического распространения и предполагаемых филогенетических отношений родов и подродов кайнозойских кардий.

diagnosed only the subfamily Lymnocardiinae and presented a list of its genera and subgenera with indexes of their geological age and distribution.

Chapter 4. Some Patterns of Change in the Microstructure, Chemical and Isotope Composition of the Shell in Landlocked and Semi-Landlocked Water Bodies

The character of the shell microstructure is determined not only by the genetic factor but also by the hydrological conditions of the water body in which the mollusc shell grows. A close relationship exists also between the environment and the composition of the shell. Under stable marine conditions the structure and composition of the shell are rather constant, but these can change substantially in Mollusca from inland water bodies in which the hydrological regime is disturbed. Only 4 species of Cardiidae have been able to penetrate into the present Black Sea, which has a reduced salinity of 17--18‰. The shell structure of three of those species does not differ from that of the same species and genera living in normal marine conditions. The microstructure of the members of the fourth species, the most euryhaline species--Cerastoderma glaucum--which can endure salinity fluctuations from 4--5‰ to 70‰, can change substantially during its life when the hydrological regime is drastically altered.

Modifications in the shell microstructure of Cerastoderma glaucum in brackish water

The most highly developed shell microstructure occurred in members of the species C. glaucum from the Mediterranean and Adriatic seas (data by Denis, 1972). These marine forms have a three-layered shell structure characteristic of the subfamily Fraginae, and some of them are made distinct by the presence of an additional intermediate layer with an intersecting-lamellar structure on the outer shell surface.

In Black Sea and Caspian forms of this species the entire outer layer has a composite prismatic structure, the intermediate layer has an intersecting-lamellar structure and the inner layer has a composite intersecting-lamellar structure, usually conic or block-shaped, and at the umbo a tangled-lamellar structure. The thickness of the lamellae of the intermediate layer, which apparently depends on the rate at which the shell material is deposited, declines with decreasing salinity.

A study of the microstructure with an electron microscope revealed that the internal structure in Caspian forms is sometimes deformed: the lamellae of the intermediate layer may be elongated and of the third order, and second-order lamellae disappear completely; second-order prisms in the outer layer of the composite prismatic structure are arranged at random; the inner layer usually has a more irregular block structure and includes thick intermediate layers of prismatic structure reminiscent of the structure of the myostracum.

Along with the deformations of the inner shell structure, the course of the structural development changes also. Thus the specimens from bays and estuaries with the most unstable hydrological regime are made distinct by a later formation of the outer layer in the development period. If in members of C. glaucum, which inhabit a marine environment, this layer begins to appear when the shell is 1--2 mm in length, in Mollusca from bays and estuaries it frequently appears only 8--10 mm from the umbo and frequently remains very thin on the ribs of a mature shell and in isolated specimens this layer is completely reduced.

Similar modifications in the microstructure also occurred in some fossil members of the genus Cerastoderma from landlocked water bodies with

reduced salinity--C. dombra from the Akchagyl deposits*, and C. obsoletum (Obsoletiforma) from Sarmatian deposits.

Some patterns in the content of elements and isotopes of oxygen in the shell carbonate of bivalve Mollusca

The content of most of the minute amounts of elements in the body and skeleton of the Mollusca is apparently determined by their concentration in the environment: in the sea floor and benthic water layer (Bessonov, 1970). Hence analyses of the element composition of the shell provide important information on the distribution of these elements in the sea, on their places of origin, and on the geochemical features of a given water body. Moreover, the concentration of some elements (Mg, Sr, B) depends on such environmental parameters as salinity and temperature. However, information on the degree of such dependence is frequently controversial. Besides, it should be remembered that in inland water bodies with peculiar hydrological regimes the correlation between the element content and environmental factors can change. Thus it is known that an increase in the temperature usually results in an increase in the shell's magnesium content. Semiquantitative spectral analyses confirmed a weak positive correlation between these values with regard to forms living in normal marine environments. However, the Caspian Mollusca are distinct by their significantly lower magnesium content, which also applies to river forms.

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Waskowiac (1962) established a negative correlation between the content of boron and salinity. For the Mollusca of the Sea of Azov the relation between these values is confirmed but the correlation is positive (Bessonov, 1970).

* Translator's note: "Akchagyl deposits": This term has been taken directly from the original Russian "akchagyl". The two-volume geological dictionary "Geologicheskii slovar'" (Moscow, 1960) refers to these deposits as "the third lowest Pliocene layer of the Black Sea--Caspian Sea basin."

After the death of the mollusc the composition of the shell may be partly altered due to the addition of several elements. Spectral analyses have shown that fossil forms everywhere have increasing contents of aluminum and silicon.

The content of stable isotopes of oxygen (O^{16} and O^{18}) in the shell carbonate varies with the ratio of these isotopes in the water; the constant of such a balance is determined by the temperature.

Parallel tests of the isotope composition of oxygen of the shell carbonate and of the water, conducted at several points in the Caspian and in the Black Sea, have indicated that the relationship between the composition of the water, the shell and temperature, which is established for marine fauna, remains valid for Mollusca of inland water bodies as well.

The distribution of the values of isotopes of oxygen in the shell carbonate of contemporary Mollusca fully reflects the changing pattern of isotope composition in the sea; and the ratio of isotopes in the shell of fossil Mollusca gives an idea about the changing isotope composition of these water bodies in time (Gorbarenko, Nikolaev, Popov, 1973). Such research gives us information on the paleoclimatic conditions and especially on temperature and humidity changes in the atmosphere. A study of the changes in the isotope composition of shells by area from individual horizons of Quaternary deposits of the Caspian Sea has shown that these data can indicate the presence of a freshwater tributary and its source.

Thus on the basis of the trend in the modifications of the micro-structure, of the content of individual elements and of the isotope composition of the shell it is possible in a number of cases to form a picture of the water bodies of the past, particularly with regard to

their salinity and climatic conditions.

Chapter 5. Structural Evolution of the Shell of Cardiidae in Inland Water Bodies

Beginning with the Paleogene, large inland water bodies, landlocked and semi-landlocked, with a peculiar hydrological regime formed on more than one occasion in the south of Eurasia. Such water bodies were inhabited by the most euryhaline representatives of marine fauna among which Cardiidae usually played an important role. Once they appeared in a large water body free from competitors and enemies, the Cardiidae rapidly adapted to their new environment, forming peculiar endemic genera and subgenera in the process. We were able to trace the history of such a development and of the successive changes in the shell microstructure most fully in the fossil remains of the Pliocene-Quaternary deposits of the Caspian basin.

The faunal development of this inland sea begins with the Akchagyl epoch when, along with several other marine Mollusca, representatives of the genus Cerastoderma, which became the progenitors of many endemic species, appeared here.

The shell microstructure of the Akchagyl Cerastoderma corresponded to that of the present members of this genus: the shell is usually three-layered; the cross sections usually reveal a complex pattern of the inner rib structure formed by bent lines of growth. The Akchagyl forms reveal the same structural deviations in the shell that characterize the present Cerastoderma glaucum when their hydrological regime is abruptly altered: the outer layer appeared only 5--7 mm from the umbo, and sometimes it was completely absent from the ribs. The ontogenetic development of the shell ornamentation was also retarded (fig. 6).

Endemic to the Akchagyl epoch was the genus Avicardium, which had become separated from the Cerastoderma and differed substantially from the latter by its morphology, ornamentation, ontogenetic development and shell structure. The outer layer of the Avicardium is usually completely reduced, the shell is two-layered and the inner rib structure is simple: the lines of growth repeated the form of the outer surface. The ontogenetic development of the ornamentation occurred slowly and was incomplete (fig. 6).

The Cardiidae underwent a new formative period at the beginning of the Aptian epoch, when the Akchagyl Cerastoderma originated the typical brackish genera Hyrkania, Monodacna, Adacna, Parapscheronia and Apscheronia.

Fig. 6. Scheme of ontogenetic modification in ornamentation and shell structure of some Cardiidae of the Akchagyl epoch.

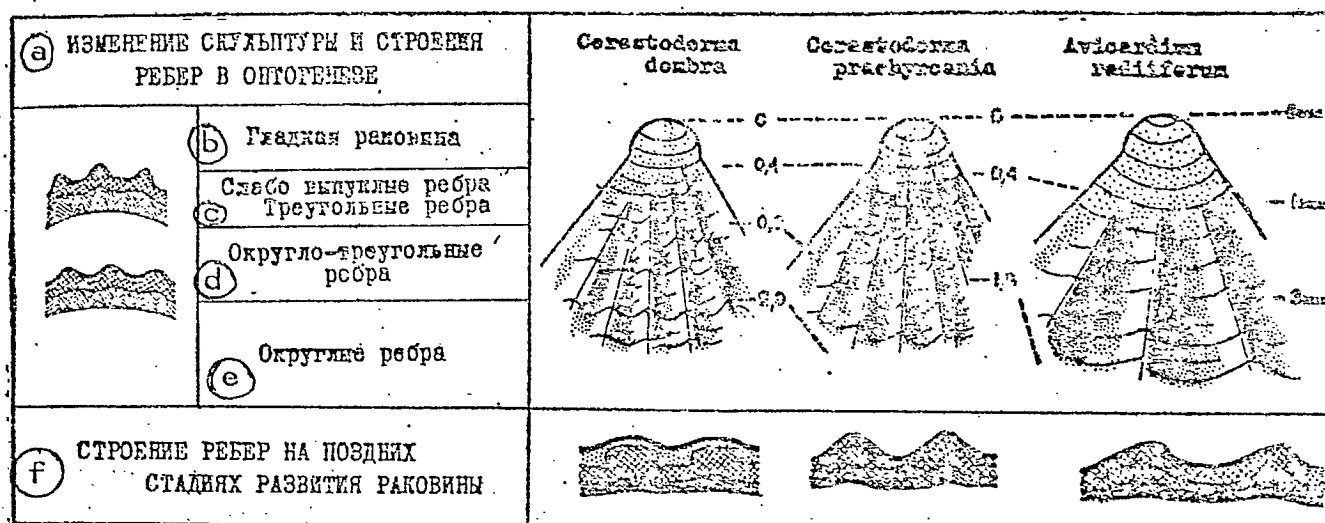


Рис. 6. Схема онтогенетических изменений скульптуры и строения раковины некоторых акчагыльских кардинид.

- a-evolutionary modification in ornamentation and rib structure;
 b-smooth shell;
 c-moderately bulging triangular ribs;
 d-rounded triangular ribs;
 e-rounded ribs;
 f-rib structure during late stages of shell development.

The members of these genera were characterized by a two-layered structure and a slow ontogenetic development in ornamentation; its character frequently continued to change during the later stages of shell development. /17 The shell structure closest to that of Cerastoderma occurred in the members of the genus Hyrcania. The most altered forms are those of the genera Apscheronia and Parapscheronia whose structure and ornamentation character are reminiscent of those of the earliest developmental stages of the Cerastoderma (Fig. 7).

In the Quaternary Caspian there appeared, along with members of genera of the Aptian epoch, species of the genus Didacna, whose origin is controversial. The shell structure of these forms is similar to that of the Aptian Hyrcania (Didacnoides) as well as to that of the Pliocene euxinic Didacna (Pontalmyra).

The largest inland water body of the Neogene epoch was the Late Miocene Sarmatian basin. Of the Cardiidae, only the Cerastoderma could exist in this basin. They became the progenitors of many peculiar forms, which N.P. Paramonova has classified into 4 endemic subgenera (1971). A study of the shell structure indicated that the Sarmatian Cardiidae also differed by their microstructure to a greater or lesser degree from the typical members of the genus Cerastoderma (fig. 7): their outer layer was reduced and only in some species remained extant in the spaces between the ribs; the inner rib structure is usually simple; the ontogenetic development of the ornamentation occurred slowly. A shell structure close to that of typical Cerastoderma was observed only in some Obsoletiforma species; and the members of the subgenera Plicatiforma and Planacardium were most modified both with regard to morphology and shell microstructure.

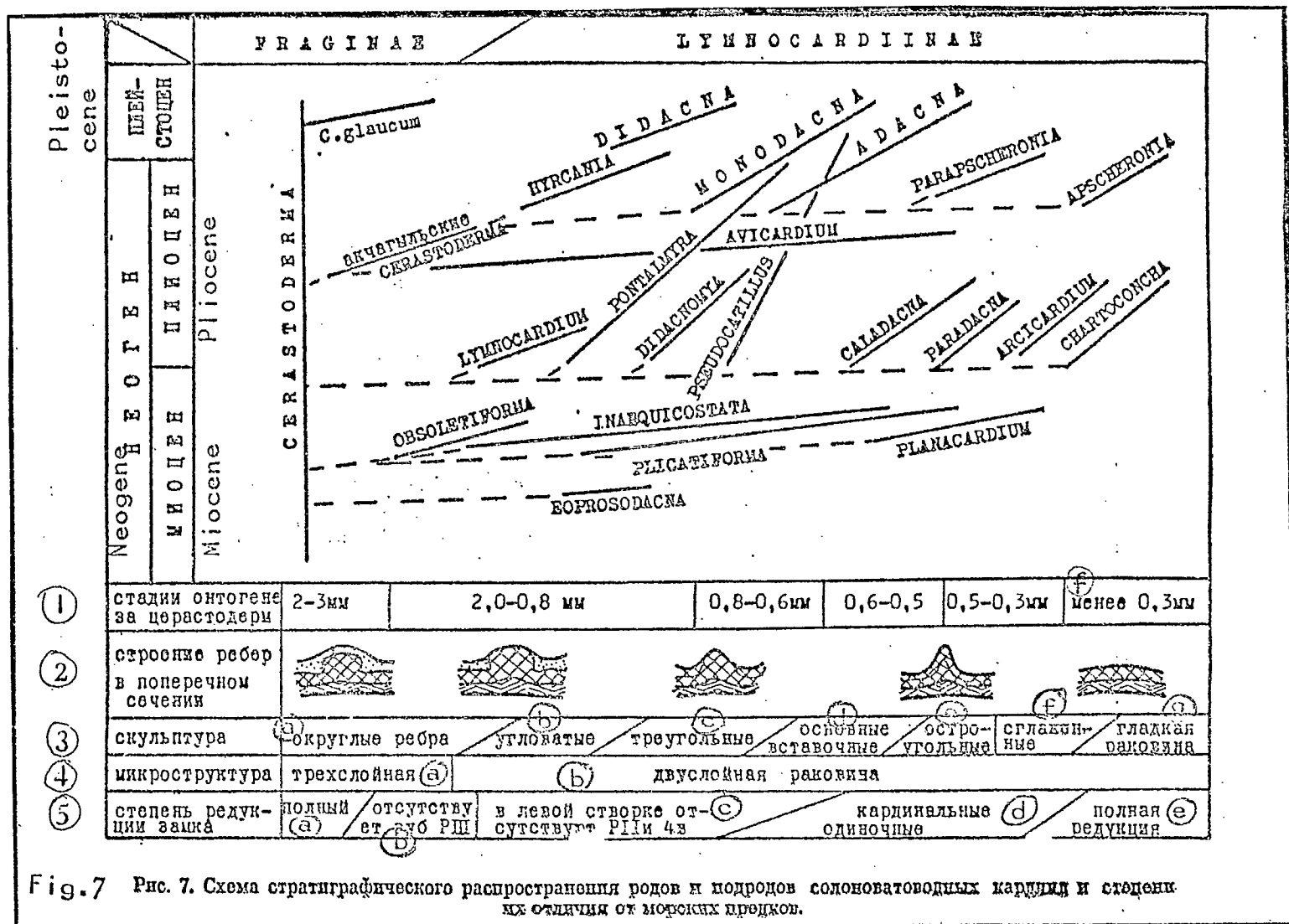


Fig. 7. Scheme of stratigraphic distribution of genera and subgenera of brackish Cardidae and the degree to which they differ from their marine ancestors.

- 1-ontogenetic stages of *Cerastoderma*; 1f-less than;
- 2-cross section of rib structure;
- 3-ornamentation; a-rounded ribs; b-angular ribs; c-triangular ribs; d-main/intercalary; e-sharp-angled; f-flattened; g-smooth shell;
- 4-microstructure; a-three-layered; b-two-layered shell;
- 5-degree of reduction of hinge; a-complete; b-tooth P III absent; c-P II and 4 B absent in the left valve; d-cardinal single; e-completely reduced.

During its ontogeny, the shell of the Sarmatian Cardiidae passed through the same stages of development as the typical Cerastoderma but at a much slower rate. Frequently the microstructure of the shell and the structure of the ribs of adult forms of the Sarmatian Cardiidae corresponded to those of the Cerastoderma inhabiting the sea at the early stages of their development. A more complete structure was observed in Cardiidae from the western--the Pannonian part of the Sarmatian basin, where the environmental conditions apparently closely resembled normal marine conditions.

However, the brackish Cardiidae became most varied in the Pliocene Euxine [Black Sea] basin. The shell structure of the Pliocene euxinic Cardiidae was also varied; they also had a two-layered structure and a slow ontogenetic development. Along with the simplified microstructure characteristic of all brackish Cardiidae, a secondary structural complexity is a characteristic occurrence for these forms: appearance of a peculiar inner ribbed structure in Lymnocardium (Moquicardium) and Prosodacna; formation of folds in the inner layer of the shell in Stenodacna and Didacna (Pontalmyra).

Thus the structural transformation of the shell and ornamentation /18 in Cardiidae in brackish water bodies had a certain trend. These characters, along with the development of the hinge of brackish Cardiidae, became altered in such a way that the structure observable at later developmental stages of their descendants corresponded to the earlier ancestral stages of development (fig. 7). Such slow development of some characters with regard to reproductive organs can be called neotenic in the broad sense of that word (Beer, 1930; Stepanov, 1957; Nevesskaya, 1972). The developmental

trend in different phylogenetic branches of brackish Cardiidae was so similar that some investigators considered it possible to establish a direct link between, for example, the Akchagyl forms and the Sarmatian forms (Andrusov, 1902; Ali-Zade, 1967). The data on the shell structure suggest that the establishment of such a link is impossible, for the microstructure of the Akchagyl forms is similar to that of the typical Cerastoderma, whereas even the earliest Sarmatian Cardiidae had a different, very modified structure.

The morphological and structural similarity of the brackish Cardiidae can most likely be explained by their common origin from a few closely related marine Cerastoderma and by their parallel development in similar conditions of inland water bodies.

The morphological similarity, relatedness and confinement to a certain ecological niche suggest that the Neogene--Quaternary brackish Cardiidae of the Paratethys basins be unified into a single taxonomic group. The rank of such a group is that of family, as determined by some investigators (Keen, 1969). However, it does not seem right to oppose these forms to the entire variety of marine Cardiidae, and hence they might best be classified as a separate subfamily, namely, Lymnocardiinae Stoliczka, 1871, which is part of the family Cardiidae.

The paleontological material on the development of Cardiidae in large inland water bodies during a prolonged geological time was formed as a result of a most interesting experiment which nature has repeated many times. The trend of the modifications and the similarity of forms, which developed independently in isolation from the fauna of the world's oceans, afford a better picture of the possibilities and significance of

parallelisms of evolution.

Many neontologists and paleontologists (for example, Beer, 1958) have proposed that the neotenic character of development may be a way out of the dead end of specialization. Such an hypothesis is confirmed by the history of development of Lymnocardinae. Actually, the marine Cardiidae are characterized by relatively minor morphological variations, which assures them a certain limited ecological niche among the coastal marine fauna. Under the conditions of an inland water body, in order to /19 assimilate varied unoccupied ecological niches, it was necessary to develop morphological characters that were not characteristic of Cardiidae. For example, in many phylogenetic lines of Lymnocardinae there is an appearance of deep-burying forms with long siphons (Eberzin, 1967). Such radical changes could occur only on the basis of the earliest stages of ancestral development, and the neotenic modifications of ornamentation and shell structure apparently made it possible for the brackish Cardiidae to diverge rapidly.

Conclusion

This paper presents a study of the shell structure of the family Cardiidae, whose microstructure was found to be very similar; and certain conclusions were reached on the classification of this group. The main results of this research can be summarized as follows:

1. The shell of Cardiidae consists of two or three calcareous layers. The inner layer always has a composite intersecting-lamellar structure; the intermediate layer (or outer layer in the case of a two-layered structure) has an intersecting-lamellar structure; the outer layer,

given a three-layered shell structure, has a composite or simple prismatic structure, or also an intersecting-lamellar structure but distinct from the intermediate layer by the orientation of its lamellae.

2. On the basis of a morphological study, of data from the literature and of an investigation of the microstructure, the present paper subdivides the family Cardiidae into four subfamilies: Cardiinae, Fraginae, Protocardiinae and Lymnocardiinae (Table 1).

3. The members of the subfamily Cardiinae are characterized by the simplest two-layered structure. Only the shells of the genera Clinocardium and Serripes are distinct by the presence in them of a third outer layer of a fine prismatic structure. The brackish Cardiidae belonging to the subfamily Lymnocardiinae have also acquired a two-layered structure, owing to a reduction of their outer layer.

4. The members of the subfamily Fraginae have a three-layered shell structure whose shell is distinct by the presence of an outer layer of composite prismatic structure.

5. The subfamily Protocardiinae is also characterized by a three-layered shell structure; its thick outer layer has the same intersecting-lamellar structure as the intermediate layer but with horizontally oriented lamellae.

6. The data on the ontogenetic development and the presence of certain transitional features in the structure of the shell suggest certain courses of phylogenetic development for the Cardiidae. The evolution of this group occurred through the development of new processes (extensions or anabolies), deviations, or by simplifying the development through neoteny.

7. In various phylogenetic lines of brackish Cardiidae the transformation of the shell structure, its ornamentation and hinge structure were similar and were characterized by neotenic modifications.

8. The morphological similarity of brackish Cardiidae, their apparently common origin from several closely related species of Cerastoderma, the parallel character of their modifications and their association in a particular ecological niche--all these suggest that it may be expedient to unify them into a single subfamily, Lymnocardiinae.

9. A study of many representatives of the species Cerastoderma glaucum has shown that, along with the genetic factor, the microstructure can be affected by conditions in the habitat. In particular, drastic changes in salinity conditions result in modifications in the inner structure of the layers, in retarded ontogenetic development and in a partial reduction of the outer layer.

10. The patterns in the content of microelements in the shells of Mollusca, which have been established for marine forms, can become altered in brackish water bodies. Conversely, the oxygen content in the shells of Black Sea and Caspian Mollusca conforms to the patterns established for marine organisms.

Papers by the present author on the same subject:

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2. Ways of reconstructing the isotope composition of the oxygen of water of inland and semi-inland water bodies of the Quaternary (together with S.D. Nikolaev). Summaries of reports on the 4th All-Union Symposium on the Geochemistry of Stable Isotopes, p. 55, 1972.

3. Utilization of the isotope-oxygen method for the study of the paleogeography of inland and semi-inland water bodies (thesis abstract prepared together with S.D. Nikolaev). Bulletin of the Moscow Society of Naturalists. Geology Section. Vol. 48, no. 1, p. 158. 1973.

4. Microstructure and shell structure of Caspian Cardiidae and questions regarding their origin (thesis abstract). Bull. of the Moscow Soc. of Nat.. Geol. Section. Vol. 48, no. 1, pp. 158--159. 1973.

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6. A study of the shell structure of Cardiidae with the aid of a scanning microscope (thesis abstract). Bull. Moscow Soc. Nat. Geol. Sec. Vol. 48, no. 6, p. 162. 1973.

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8. The microstructure of present and fossil Cardiidae of the South of the USSR and their classification. In a collection of papers of the 1st Republican Symposium on Malacology (in the press).