

Radiolarian Skeletons: Formation and Morphology of Skeletal Shells

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Abstract—A new scheme of successive stages in the formation of radiolarian skeletons is proposed. Successive complication of symmetry patterns is considered. The morphology and evolutionary changes of five types of skeletal shells, i.e., latticed, reticulate, spongy, porous, and lamellar, are analyzed.

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INTRODUCTION

Radiolarians are very small. The majority of radiolarians cannot be seen with the naked eye. The size of their living cell ranges from several dozen microns to 1–3 mm, the average being 100–800 μm . The mineral skeleton lies inside the cytoplasm.

The major physiological function of the skeleton is supporting the cytoplasmic body of the radiolarian and, hence, defining its entire shape. Skeletal elements support endo- and ectoplasm and axopodia. At the same time, skeletal constructions facilitate the segmentation of the polyploid nucleus and central capsule, thus, intensifying the cell's metabolism (Anderson, 1983; Petrushevskaya, 1986). Anderson (1983) described the central capsule and mineral skeleton, comparing them to the boards on which physiological processes were performed.

Skeletons of Radiolaria are perfectly beautiful, proportional, well-designed, and elegant. Dogel (1923) marked that all possible constructional designs were embodied in the skeleton structure of radiolarians. Even geometric forms that never occur in other organisms, such as regular icosahedrons, dodecahedrons, and octahedrons, are observed among radiolarian skeletons. In other organisms, Dodecahedrons and octahedrons occur only in pollen grains and antheridia of the Characeae.

However, while being complexly, but geometrically regularly designed, radiolarian skeletons are among the lightest constructions. “Regular shapes in organisms are explained by the economy of material” (Mordukhai-Boltovskoy, 1936, p. 5). Of all regular Plato's bodies (tetrahedron, hexahedron, octahedron, dodecahedron, and icosahedron), the icosahedron with 20 faces has the smallest surface-to-volume ratio. The most economical skeletal shape, which has the smallest surface-

to-volume ratio, is a sphere. Therefore, “if no special places for organs are designed, the shape of the organism should be spherical. However, as soon as this condition is imposed, the organism loses the spherical shape” (Mordukhai-Boltovskoy 1936, p. 14).

Further differentiation is in the distinguishing differences between the oral and aboral parts of the shell. “In this case, one pole should be different from another. If we have descent and ascent, the former caused by gravity, the latter by hydrostatic apparatus, then, although the motion is performed in both directions, it is *different* in each of these directions. During ascent, the resistance of the liquid should be reduced, while it should be increased during descent to slow the fall. This explains the origin of the *unequipolar*, e.g., bell-shaped forms of radiolarian skeletons, which act like parachutes. The spherical shape is a solution of the task of *finding a shape uniform in all its points* (Mordukhai-Boltovskoy 1936, p. 39).

Even greater economy of building material is achieved by the development of pores in the skeleton; “radiolarians have round pores in their skeleton, which are explained by the economy of material” (Mordukhai-Boltovskoy, 1936, p. 33). However, pores on the surface of the skeleton and cells in the spongy, latticed, and reticulate forms are often hexagonal. “Why? Because of a simple calculation. The subdivision into regular polyhedrons, as was noted by Pythagoras in the 6th century BC, is possible only into regular triangles, squares, or hexahedrons” (Mordukhai-Boltovskoy, 1936, p. 5). Mathematical calculations show that at the given surface area (S) triangle will have the largest perimeter ($4.559\sqrt{S}$) followed by a square ($4\sqrt{S}$). A hexahedron will have a smaller perimeter ($3.722\sqrt{S}$);

therefore, the wall in this subdivision (although not perfect geometrically) will use the least material.

Mordukhai-Boltovskoy (1936) showed that different shapes of lattice serve different purposes. The hexagonal lattice is designed to resist uniform pressure (water pressure), whereas the square lattice is stronger and is designed to resist impact. Furthermore, some radiolarians, for instance, from the spumellarian family *Astrosphaeridae*, have various reticulate spheres one inside another: the outer, which resists impact, has square cells, while the inner sphere experiencing uniform water pressure has hexagonal cells (Mordukhai-Boltovskoy, 1936; Khabakov et al., 1959).

When analyzing skeleton constructions pierced by spines, Mordukhai-Boltovskoy (1936) showed that narrow spines change the spherical shape of the skeleton only very little. At the same time, when the spines become thicker, the shape of the skeleton changes in that it becomes elongated along the spine to reach an elliptical, or even fusiform shape. This trend is observed in many taxa of extant and extinct stauraxonic radiolarians.

The mechanical and mathematical calculations and analysis of the knots formed at the places where skeletal elements are joined to make a single construction supports the importance of these bonds for the strength of the entire skeleton. Mechanical formulas show that the bonds of the skeletal construction in radiolarians provide that the strain is the same at each skeletal element, each bar, and each spine (Mordukhai-Boltovskoy, 1936).

According to D'Arcy Thompson (1942), skeletal geometry follows from the same physical laws that work for liquids. The hexagonal radiolarian frame is similar to the frame of the surface tension of artificial materials. The structure of the skeleton of *Callimitra agnesae* Haeckel is similar to the model of a tetrahedron received by the method of the surface tension during the submergence of a wire frame into a soap solution. In addition, in analyzing the geometry of the radiolarian skeleton, D'Arcy Thompson (1942) makes parallels with the spiny skeletons of sponges and coral polyps.

For the second time, the idea of the economy of silica in skeletons was proposed by Moore (1969) after the comparison of the Eocene–Quaternary radiolarians. The skeletons of Recent radiolarians are on average one-quarter of the weight of the oldest taxa analyzed.

Schaaf (1981) used mathematical models to substantiate the hypothesis that in the Cenozoic, the general trend in the evolution of the radiolarian skeletons (e.g., more regular arrangement and shape of pores) was towards the diminishing the amount of silica for the completion of the majority of skeletons.

To date, it is evident that the theoretically conceivable diversity of hollow polyhedrons, the limiting cases of which are the sphere and spheroid, is only partially realized in nature. This is associated with the program

of “thrifty expenditure of substance and energy” after Voitekhovskiy (2002). An important conclusion of Voitekhovskiy (2002, 2004a, 2004b) is the biomineral homology between the polyhedrons of carbon fullerenes,¹ polyhedrons of viruses, radiolarian skeletons, and *Volvox colonies*. This homology is predetermined not only by their material content but mostly by the geometrical optimal shape requiring a minimum of energy and material expenditure. It is of interest that the fullerenes of the C60–C100 range (i.e., most symmetrical, with the least number of contacting faces) are potentially stable. These conditions correspond to the icosahedral and dodecahedral groups of polyhedrons, which are often used by spherical radiolarians (Afanasieva and Amon, 2004).

The exclusive complexity of the skeleton structure and high diversity in shape are determined by the initial type of symmetry and an intricate combination of internal and external skeletal elements.

The internal elements include the internal framework in the shape of a hollow sphere, or a spicule, primary sphere, and spine-framed construction, whereas the outer elements include various skeletal covers and related structures (spines, spinules, apophyses, tunica, apertures, etc.). The outer elements embrace and cover the inner elements. The morphological role and function of the inner elements is in the mechanical protection of the central capsule, which contains the entire endoplasm (nucleus, ribosomes, mitochondria, Golgi body, and endoplasmic reticulum), while the outer skeletal elements work as a mechanical support for the ectoplasm.

At present, because of incomplete knowledge of the primary internal structure and the major patterns of the formation of radiolarian skeletons at different structural levels, possible factors, mechanisms, and the major patterns of the formation of skeletons in the course of radiolarian evolution (questions of the initial differentiation and growth of skeletal elements, basic routes and trends in the development of radiolarian skeletons) remain incompletely certain.

FORMATION OF THE SKELETON

The development of the skeleton in extant radiolarians of the subphyla Polycystina and Phaeodaria may occur in various ways and passes several stages (Haecker, 1908; Enriques, 1932; Petrushevskaya, 1962, 1986; Anderson, 1980, 1981, 1983, 1986; De Wever, 1982; Afanasieva, 1990a, 1990b, 2000a; De Wever et al., 1994, 2001; Afanasieva et al., 2005).

¹ Fullerenes are a new class of hollow mineral polyhedrons, the experimental study of which was awarded the 1996 Nobel Prize for Chemistry. Carbon fullerenes have pentagonal and hexagonal faces, each three faces converging at each vertex. Fullerenes are closed, nontranslating in space, have a noncrystallographic symmetry, and are classified in mineralogy as mineraloids.

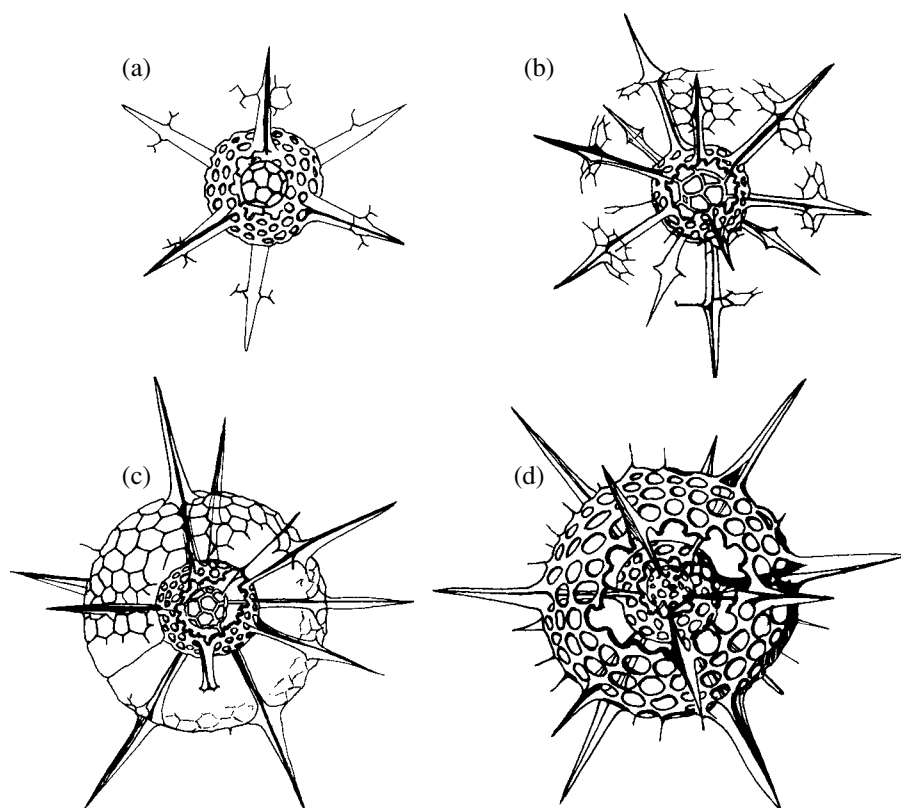


Fig. 1. Growth stages of a radiolarian porous skeleton (after Hollande and Enjumet, 1960): (a) young *Hexacontium* sp.; (b–d) different growth stages of *Actinomma mediterraneensis* Hollande et Enjumet, 1960: (b) formation of the external shell in the shape of spiny branches of the main spines, (c) formation of a slender thin-walled shell with hexagonal pores, and (d) final shape of the porous shell.

Stage 1. Appearance of the Skeleton

In all radiolarians, the beginning of the skeleton development occurs simultaneously on the polysaccharide plates over the entire volume of the organic matrix of the future shell. Here, the primary silica globules first appear to merge later into the larger elements of the skeletal ultrastructure.

Stage 2. Primary Development of the Skeleton

The further development of the skeleton occurs in two ways:

- *Pellicular growth.* Ultrastructural elements of the skeleton form a biomineral basis of the future shell with thin walls and large hexahedral pores in the entire volume of the organic matrix;

- *Bridge growth.* After the formation of primary elements of the skeletal ultrastructure, almost straight bars are formed in the organic matrix of the future skeleton, which elongate and connect with each other by bridges to form a shell with numerous polygonal pores.

Stage 3. Final Stage of the Skeletal Development

The completion of the formation of a skeleton is carried out by two ways:

The development of the skeleton is finalized in two ways:

- *Bridge growth.* Bars and bridges thicken to various extent to form delicate spongy and reticulate or a more coarsely lattice skeletal wall; bridge growth is the basis of the development of various skeletal structures (spicules, spines, apophyses, bars, beams, etc.);

- *Rim growth.* The edges of pores grow inwards, pores gradually narrow to form porous or lamellar shell structure.

All types of the skeletal growth may be observed in the same individual at different ontogenetic stages, or one of the patterns may be dominant (Petrushevskaya, 1962, 1986; Anderson, 1983; De Wever et al., 1994, 2001). For instance, in *Lithomelissa thoracites* Haeckel, the cephalis is formed by the rim growth, while the thorax is developed by the bridge growth (Petrushevskaya, 1962).

The porous skeleton at different stages of *Hexacontium* sp. and *Actinomma mediterraneensis* Hollande et Enjumet is a delicate, very thin-walled shell, with large hexagonal pores, which are formed by the bridge growth (Figs. 1a–1c). The appearance and early growth of the outer shell of the skeleton begin with the main spines (Figs. 1a, 1b). Further, the shell wall thickens by the rim growth, while the pore edges grow inwards, pores narrow, and a delicate skeleton is transformed

into a thick-walled porous shell with rounded pores and a massive three-bladed spine (Fig. 1d) (De Wever, 1982; Anderson, 1986).

In Spumellaria, which have spongy, reticulate, or latticed skeletal tissue formed by the bridge growth, the inner sphere may be porous, formed by the rim growth.

The development of the outer skeleton in the subphylum Phaeodaria by gradual silicification was described in detail by Haecker (1908); it agrees with the scheme proposed by us for the formation of radiolarian skeletons. Haecker (1908) indicated that, at the initial stage of the formation of a skeletal spine in certain Phaeodaria, the spine is in the shape of an extended vacuole with a thin cover filled with gelatinous matter ("Galertvakuole") of the organic matrix; lateral branches deviate at appropriate points at the soft phases of the development of spines. This process corresponds to Stage 1 (appearance of the skeleton) within the entire volume of the organic matrix. Then, the surface layer of the developing spine is silicified; this corresponds to the formation of the ultrastructural elements of the skeleton by the pellicular growth. Subsequently, the spine cavity is filled with granular matter, retaining an open space in the core of the spine. The granular matter, which is probably composed of primary opaline globules *E* (Afanasieva, 1990a, 1990b), is gradually silicified; this also corresponds to the appearance of the skeleton within the entire volume of the organic matrix.

At the initial stage of the formation in phaeodarians of the spiny skeleton of Aulacanthidae, the latticed skeleton of Aulosphaeridae, the porous skeleton of Castanellidae, and the lamellar skeleton of Tuscaroridae and Circoporidae, individual primary spines are formed and enveloped by gelatinous vacuoles. Subsequently, the spiny skeleton of Aulacanthidae and the latticed skeleton of Aulosphaeridae develop by the bridge growth, while the porous skeleton of Castanellidae and the lamellar shell wall of Tuscaroridae and Circoporidae are formed by the rim growth. As gelatinous vacuoles of the organic matrix are rather densely spaced, they undergo gradual centripetal silicification to form a porous or solid skeleton. The network of primary spines is retained in the shell wall of adults in the shape of a system of ribs. Thus, the spiny skeleton of Aulacanthidae, the latticed skeleton of Aulosphaeridae, the porous skeleton of Castanellidae, and the lamellar skeleton of Tuscaroridae and Circoporidae are similar in ontogenetic development.

SYMMETRY OF SKELETONS

The geometry of radiolarian skeletons is very diverse (spheres, often enclosing one another, dumbbells, cylinders, towers, propellers, cones, helmets, crowns, etc.). The use of the basic symmetrical pattern is necessary to classify all these varieties and gain an insight into the possible transformations of skeletons (Fig. 2). The following progressively more complex

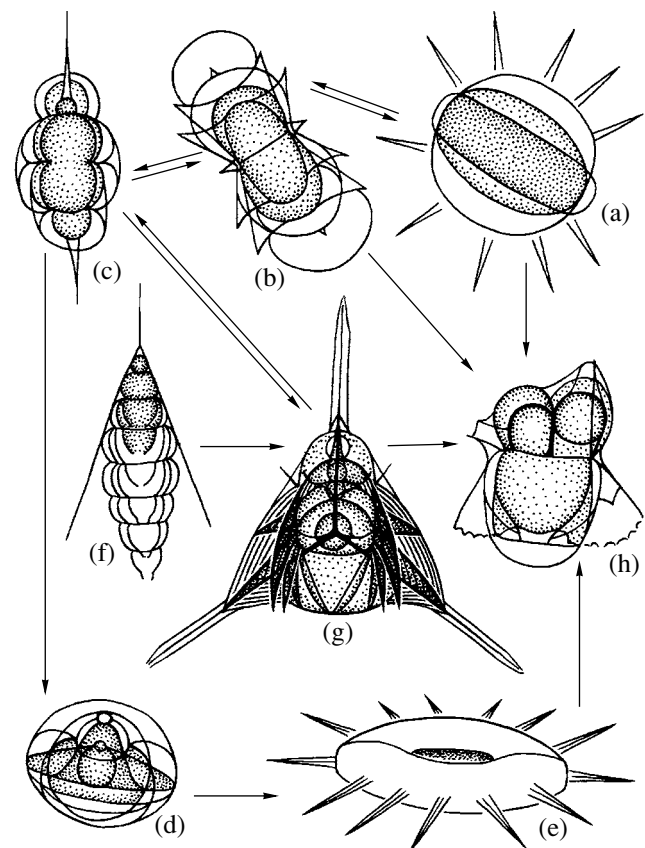


Fig. 2. Symmetry and possible transformations of the skeleton shape in the phylogeny of Polycystina (after Petrushevskaya, 1986, modified): (a) homaxal, subspherical or ellipsoidal; (b–e) monaxal: (b) dumbbell-shaped, (c) spindle-shaped, (d) flattened subspherical, (e) discoidal; (f, g) heteropolar: (f) subconical, (g) tripod; and (h) bilateral, variously shaped.

types of symmetry are recognized (Beklemishev, 1964; Petrushevskaya, 1986):

Homaxal type. Spherical skeletons and their derivatives, with an endless number of similar axes (Fig. 2a). If the number of axes is reduced to 20, 6, or 4, the number of radii of symmetry is also reduced. The radiolarian skeleton is most often similar in shape to a sphere. This is probably the best adaptation to a planktonic mode of life.

Monaxal type. The number of axes is reduced to one. The skeleton is depressed in the direction of this axis, or elongated along it (Figs. 2b–2e).

Heteropolar type. The poles of the only axis are not equal (Figs. 2f, 2g). The number of radii of symmetry is uncertain, it may be two or three. In the latter case, two halves of a skeleton can theoretically be matched by a rotation along the axis. Originally, heteropolar radiolarians (Pylomariata, Mesozoic–Cenozoic Nassellaria and Phaeodaria) have variably elongated skeletons, ranging in shape from a spindle, cylinder, or mushroom to a short cone, or umbrella. The number of

radii of symmetry is 2–4, more rarely, 5–6, the most common number of external apophyses is three (so-called tripod).

Bilateral type. This shape is the completion stage of radiolarian specialization, involving both the interior of the skeleton and the arrangement of chambers and segments, and suggests a plane of symmetry with an axis in it (Fig. 2h). This type of symmetry involves the differentiation of the skeleton in the direction of one morphological axis (conventionally up–down) and towards the anterior–posterior axis. The resulting halves of the skeleton are mirror images, e.g., *Acanthodesmiidae*, *Cannobotryidae*, and *Albaillellata*.

The above succession of the increase in complexity of skeletal symmetry in the phylogeny of radiolarians supports the idea of Haeckel (1887) that the heteropolar *Nassellaria* and *Phaeodaria* evolved from homaxal spherical ancestors. In addition, this succession gives evidence for the hypothetical model for the origin of bilateral pseudoshells of *Lapidopiscidae* from the heteropolar skeletons of *Ceratoikiscidae*, which consist of three spines intersecting to form a triangle (Afanasieva, 2000a, 2000c; Afanasieva and Amon, 2003; Afanasieva et al., 2005).

Symmetry is not only defined by the shape's geometry, but also by the biological properties of organisms. The center, axis, or plane of symmetry are recognized as such only under the condition that they are in a certain way produced by the organismic structure itself, i.e., they can always be found. The uncertainty of axes exists in the case of the indifferent balance, in the absence of active movements, and where the organism is adapted to passive floating. These are diverse spherical forms of the homaxal type of symmetry. The axis appears at the necessity of rotation, for maintaining stability and defining the direction of movement. In the case when the direction of motion is not important, the monaxal type exists. If there is some preference in the direction of motion, the heteropolar, or bilateral type of differentiation appear. This geometrical differentiation is caused by the scheme of biological differentiation (Mordukhai-Boltovskoy, 1936).

SKELETAL SHELLS

In studying polymerization in protists, Dogel (1951) concluded that, among the Foraminifera, multicameral taxa certainly represent the result of the further evolution of the unicameral taxa, similar to the latticed spheres of *Spumellaria*. Such modifications of the skeleton are caused by the periodical growing of cytoplasm of these taxa.

In the Phanerozoic evolution of *Polycystina*, changes in the skeleton show the polymerization of skeletal elements, which was apparently connected with the necessity to create finer subdivisions of the cytoplasm, i.e., an increase in the number of shells, chambers, radial spines, and pores. The trend toward

polymerization began to manifest itself as early as the Paleozoic, but was strongest in Mesozoic radiolarians. Opposite trends are observed in Cenozoic taxa: the number of chambers decreases, their position and size become stable, whereas the skeleton becomes simpler and lighter, i.e., the process of oligomerization is noticeable (Petrushevskaya, 1986; Nazarov, 1988; Nazarov and Petrushevskaya, 1995).

The skeletal shells are to a varying extent characteristic of all classes of *Radiolaria*. Their main function is the support of the entity of the skeleton and of the entire cell. At the same time, the skeleton promotes the subdivision of the external part of the cell and endoplasmic structures (nucleus, axoplast, and central capsule), thereby increasing the intensity of metabolism (Petrushevskaya, 1981, 1986). Compared to other parts of the skeleton, the shells show the highest degrees of the formation of new structures and complication (Nazarov, 1988).

The proportions of the shell sizes in polyspherical taxa is apparently very important for the normal functioning of the *Polycystina* cell. Radiolarians usually have external (cortical) shells and inner (medullar) shells. The cortical shells are usually closely spaced. The medullar shells are usually separated from each other at a distance equal to the half of the radius of the smallest medullar shell (Nazarov, 1988). The diameter of the outer shell in Paleozoic *Radiolaria* ranges from 55 to 360 μm , while the wall thickness ranges from 1 to 8 μm . Based on the ratio of the diameter of the cortical shell and the wall thickness (D/tw), four types of the skeletal wall may be recognized: very thick ($D/tw = 10.0\text{--}20.0$), thick ($D/tw = 20.1\text{--}29.0$), thin ($D/tw = 29.1\text{--}100.0$), and very thin ($D/tw = 100.1\text{--}150.0$).

In the Paleozoic, the number of medullar shells gradually increased (1–2–3– n) in all radiolarian lineages:

- (1) *Inaniguttinae* \rightarrow *Inanibiguttinae*,
- (2) *Oriundoguttinae* \rightarrow *Inanihellinae*,
- (3) *Entactiniinae* \rightarrow *Bientactinosphaerinae* \rightarrow *Thecentactiniinae*,
- (4) *Astroentactiniinae* \rightarrow *Helioentactiniinae* \rightarrow *Multisphaerinae*,
- (5) *Haplentactiniinae* \rightarrow *Pseudorotasphaerinae* \rightarrow *Haplotaeniatainae*,
- (6) *Polyentactiniinae* \rightarrow *Magnisphaerinae*,
- (7) *Retentactiniinae* \rightarrow *Spongentactiniinae* \rightarrow *Pluristratoentactiniinae*,
- (8) *Spongopolyentactiniinae* \rightarrow *Somphoentactiniinae* \rightarrow *Plenoentactiniinae*.

This indicates the high taxonomic importance of the number of shells at the subfamily level.

The Cenozoic *Litheliidae* and some other subspherical spiral taxa have an intermediate position in this respect. The three-dimensional, partly reduced shells, appearing as narrow bands are typical of *Pyloniidae*. The chambers 3–30 μm are usual skeletal elements of

many Polycystina. They are separated by radial and tangential bars and (or) porous plates. The chambers are more often semispherical, similar in shape to the cytoplasmic vacuoles. The chambers may be arranged in one layer or in several layers concentrically (Pseudoaolphacidae), spirally (Litheliidae), or irregularly (Spongiscidae).

The heteropolar skeleton of Nassellaria consists of a cephalis separated from the following chamber (thorax) by a median bar of the multi-rayed spicule. These are followed by the abdomen and other skeletal segments. The last chambers are separated only by the external constrictions of the wall and (or) inner ridges (or septa).

Five types of skeletal shells are recognized. These are combined in two major patterns differing in the way of the skeletal growth: (1) latticed, reticulate, and spongy shells, in which the skeletal tissue is formed by the bridge growth pattern and (2) porous and lamellar shells, the skeletal tissue of which is formed predominantly by the rim growth pattern.

Latticed skeletal shells. Latticed skeletons are formed by a few thick and coarse rods (Pl. 3, figs. 1, 2). Auxiliary rods are arranged quite regularly to form large meshes. These rods outline and define the rounded, square, or isometric meshes of a latticed wall.

Reticulate skeletal shells. The rods forming reticulate spheres are thinner or not wider than the meshes between them and form an integrated net (Fig. 3a; Pl. 3, figs. 3, 4). The net may be single-layered, or multi-layered. The net usually contains thick rods separating large meshes, which in turn contain thinner rods separating smaller meshes. The meshes may be rounded polygonal (Pl. 3, fig. 3) or subtriangular (Pl. 3, fig. 4), with the angles of the meshes always smoothed and rounded to increase the durability of the skeleton.

Spongy skeletal shells. The spongy shells are distinguished by the chaotic twirls of the thinnest skeletal threads that form a muddled fibrous structure (Pl. 3, figs. 5–9). The true spongy tissue is discernible even when radial and tangential rods have different length and thickness and are arranged irregularly to form meshes of various size (3–20 μm) and shape, and lying in different planes.

Spongy tissue is formed by the branching of lateral offshoots of well-developed main radial spines, while the skeleton is a complex tangled of bent fibers. Spongy tissue is known from the Cambrian. Multi-layered loose skeletons are very characteristic of many taxonomic groups of Mesozoic–Cenozoic and Recent Spumellaria. However, in the Cenozoic species, the rods of the spongy tissue are usually thinner than in Paleozoic species, while the meshes are larger (up to 50 μm in diameter), i.e., this skeletal tissue is more open than usual spongy tissue.

The interlacing of straight weblike threads extending between the additional spines in a way similar to telegraph cables is called a weblike tissue. The meshes

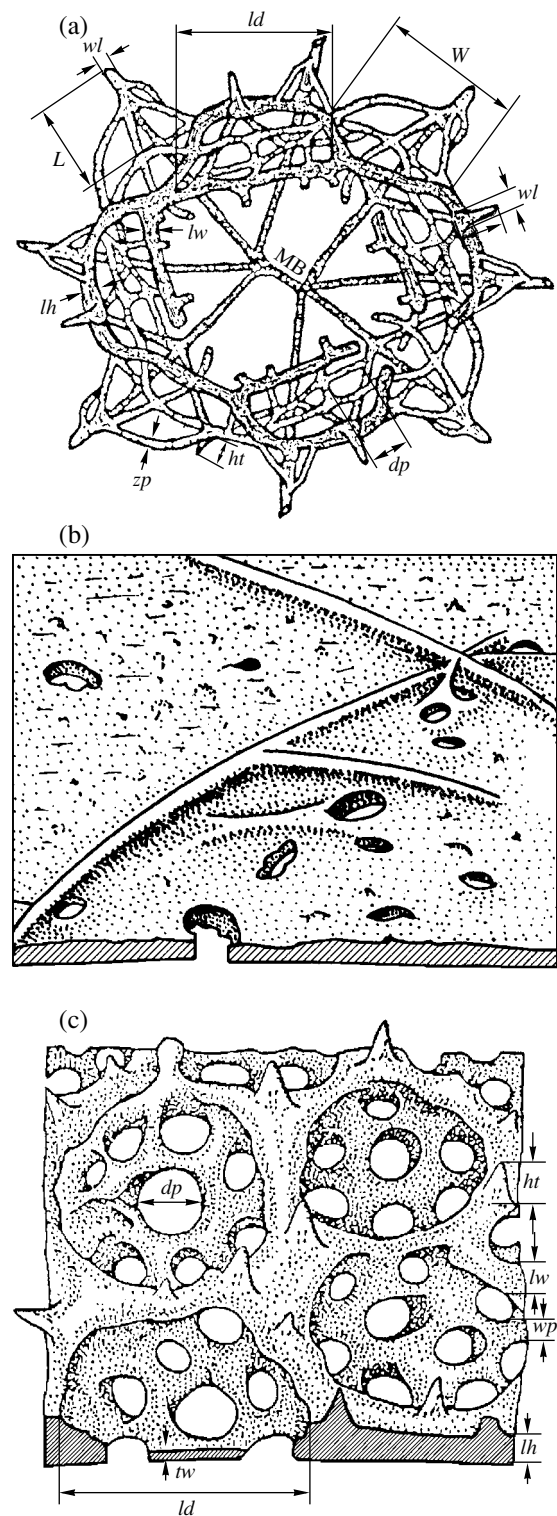


Fig. 3. Structural scheme of (a) latticed, (b) lamellar, and (c) porous skeletons (after Nazarov, 1988; Nazarov and Petrushevskaya, 1995; Afanasieva, 2000a). Designations: (L) length of the main spines, (wL) width of the main spines, (W) distance between the supports of the main spines, (l) length of the by-spines, (wl) width of the by-spines, (lh) height of the ridge, (ld) diameter of the cell surrounded by the ridge, (lw) thickness of the ridge, (ht) height of thorns, (dp) diameter of pores, (zp) thickness of bars, (MB) median bar of the spicule, (wp) width of bars, and (tw) wall thickness.

in the weblike tissue are 1–20 μm in cross section (Nazarov and Petrushevskaya, 1995).

It is noteworthy that, in the polyspheric Polycystina, only the external test is spongy, whereas all inner shells are usually porous.

Two varieties of Paleozoic spherical Polycystina are distinguished based on the way the spongy layer is formed. A spongy layer of varying thickness may rest on a porous base, or the skeleton may consist only of tangled fibers of various shapes (Nazarov, 1988).

In the first case, the dense tangled skeletal fibers and numerous branching apophyses, spiny rims of the meshes and their connections lead to the development of a quite thick outer spongy layer adjoining the porous shell (Pl. 3, fig. 9).

In the second case, the spongy skeletal shell is formed by the intense branching of the apophyses that are connected between each other by numerous bars, pillars, bridges, and short rods, which also branch and are connected to the neighboring structures. This lead to the development of a skeletal shell built from tangled fibers of various thicknesses (Pl. 3, figs. 5–8). In some cases, the bars are arranged more regularly to form regular meshes (Pl. 3, figs. 7, 8). Such a structure is quite similar to the pseudospongy tissue of the Mesozoic–Cenozoic Spongodiscidae. In Cenozoic taxa, the pseudospongy tissue is distinguished in that it is never multi-layered, while the meshes in it are smaller (1–5 μm) than in the spongy tissue.

The shell of Stauraxonaria is mainly spongy. It is formed by the branching of offshoots extending from the proximal and distal zones of the rays of the internal framework (Nazarov, 1988). The shell of the discoidal–triangular and bladed taxa is spongy. Only among the flat subtriangular stauraxonic Polycystina are there taxa with a spongy–lamellar shell (Figs. 4a, 4b).

Lamellar skeletal shells. Nonperforated lamellar skeletal shells are widely known, but they occasionally, although rarely, have polygonal pores (Fig. 3b). The wall thickness ranges from 1 to 8 μm , or, rarely, more or less than this value. The lamellar skeletal tissue is developed in some stauraxonic radiolarians. Flat, subtriangular taxa only have a spongy shell in the Late Carboniferous, but taxa with a lamellar central part and spongy periphery (Figs. 4a, 4b) appear as early as the Early Permian. In this case, the central parts of the skeleton are probably overgrown as a result of “the ageing” of the skeletal tissue.

The pylome opening in Pylomariata is rimmed by a wide nonporous plate appearing as a peristome of various shapes, which often developed on the main spines (Figs. 4c, 4d).

The development of the lamellar skeletal tissue on the spines (columellae) and cavity ribs of the skeletons of Albaillellidae and Follicucullidae leads to the development of a subconical test with an open aperture (pylome) in the basal part (Figs. 4e–4j).

The nonperforated test wall was preserved in evolution over a long time. Only from the Late Carboniferous, radiolarians with a few openings in the basal region appeared (Fig. 4j). In the Late Permian, the shells of such radiolarians became almost entirely porous, except for the apical part (Takemura and Nakaseko, 1981; Ishiga et al., 1982; Nazarov, 1988).

Early bilaterally symmetrical radiolarians with a conical outline had a test undivided into segments. In the Carboniferous–Permian, some taxa developed segmentation, allowing the recognition of the apical, central, and basal parts (Figs. 4e–4i). The segmentation of tests of the bilaterally symmetrical radiolarians was apparently a manifestation of polymerization equivalent to the increase in number of shells in spherical and

Explanation of Plate 3

Latticed, reticular, and spongy structures of the external skeletal sphere of Late Devonian radiolarians: (Figs. 1–6) Middle Frasnian Substage, Domanik Formation of the Timan–Pechora Province; (Figs. 7, 8) Lower Famennian Substage of the Timan–Pechora Province; (Fig. 9) Lower Famennian Substage, Elets'kii Horizon of Belarus, Pripyatskii Depression.

Latticed structure:

Fig. 1. *Haplentactinia labirinthica* (Aitchison, 1993), specimen PIN, no. 004-09315, $\times 270$, borehole Ukhtinskaya-3B, sample 116 (depth 100.6–101 m).

Fig. 2. *Haplentactinia alekseevi* Afanasieva, 2000, specimen PIN, no. 038-04304, $\times 650$, borehole Shuda-Yag-1003, sample 28 (depth 106–107 m).

Fig. 3. *Russirad kazintsovae* Afanasieva, 2000, specimen PIN, no. 026-04524, $\times 455$, borehole Shuda-Yag-1003, sample 29 (depth 105–106 m).

Fig. 4. *Polyentactinia zhamoidai* Afanasieva, 2000, specimen PIN, no. 011-04721, $\times 1000$, borehole Shuda-Yag-1003, sample 68 (depth 73.3–73.5 m).

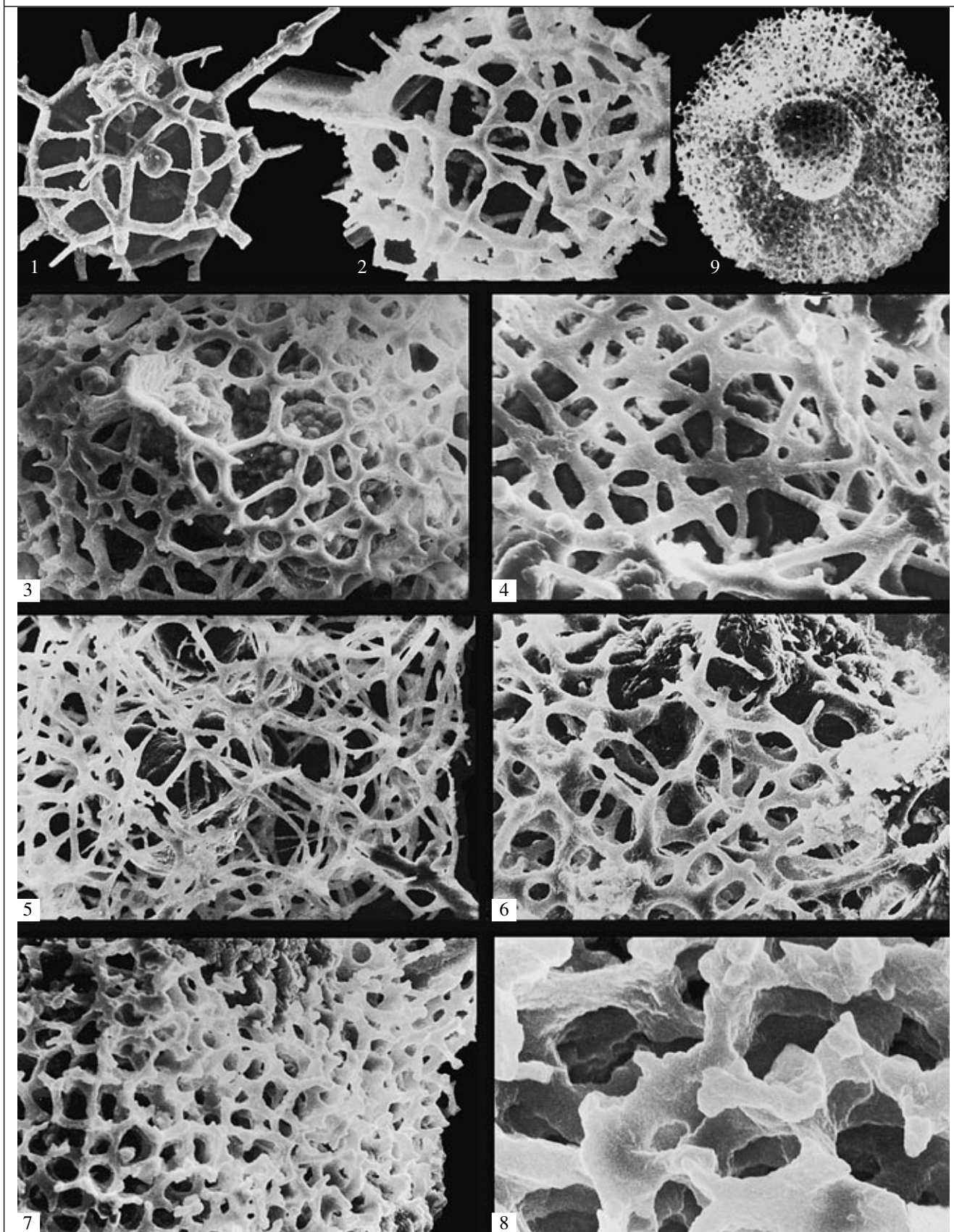
Fig. 5. *Retentactinia kelleri* Afanasieva, 2000, specimen PIN, no. 002-08781, $\times 455$, borehole Shuda-Yag-1003, sample 73 (depth 71.4–71.9 m).

Fig. 6. *Spongentactinella olafi* Afanasieva, 2000, specimen PIN, no. 056-08514, $\times 750$, borehole Shuda-Yag-1003, sample 72 (depth 71.9–72.4 m).

Figs. 7 and 8. *Adamas cathedrarius* Afanasieva, 2000, borehole Zapadnaya Lekkeyaginskaya-65, sample 86g (depth 2460–2467 m): (7) specimen PIN, no. 127-12813, $\times 555$, and (8) specimen PIN, no. 127-12724, $\times 2140$.

Fig. 9. *Somphoentactinia* sp. specimen GIN, no. 4467/90, $\times 175$, borehole Zapadno-Valaevskaya-1-R (depth 3539–35545 m), after Nazarov (1988).

Plate 3



stauraxonic Polycystina (Ormiston and Babcock, 1979; Nazarov, 1988).

Many representatives of the class Aculearia have a tunic, a cover tissue made of lamellar, or lamellar-reticular skeletal tissue that forms a pseudoshell. It is developed on the main spines and cavity ribs of the triangular skeleton of Lapidopiscidae (Fig. 4k) and covers the center of the spine intersection in Palaeoscenidiidae (Figs. 4l–4n).

Porous skeletal shells. A porous shell, i.e., a test wall penetrated by variously shaped openings, is the most common, especially in spherical Polycystina radiolarians (Pl. 4, figs. 1–9). The skeletal tissue of a porous shell is formed by the rim growth, the pore margins expand inside (Pl. 4, fig. 4). Paleozoic radiolarians (Nazarov, 1988; Amon, 1999; Afanasieva, 2000a, 2000b), similar to Recent (Petrushevskaya, 1981, 1984, 1986; Boltovskoy, 1981) and Mesozoic–Cenozoic (Zhamoida, 1972; Lipman, 1974, 1979; Bragin et al., 1999; Amon, 2000a, 2000b; De Wever et al., 2001) Polycystina range widely in pore outline from subcircular (Pl. 4, figs. 1–4), oval (Pl. 4, fig. 5), angularly oval (Pl. 4, figs. 6, 7) to rounded polygonal (Pl. 4, fig. 8).

The pores of the shell wall are usually in the shape of a rather narrow cylindrical canal with a relatively wide opening. However, the external opening of the pore canal is often overgrown by the skeletal tissue; this results in the formation of false cylindrical pore funnels, the central part of which has a small circular opening of the pore canal (Pl. 4, figs. 2, 3). The overgrown external openings give the impression that the skeleton has a very fine-porous wall.

The radiolarian skeleton is usually pierced by identical or variously sized pores. The pores are 1–35 μm in diameter, but sometimes the plates are very thin and have pores of 0.2–1 μm . The distribution of pores may be irregular, if the pores are differently shaped and sized, or regular (mostly in diagonal rows). Sometimes,

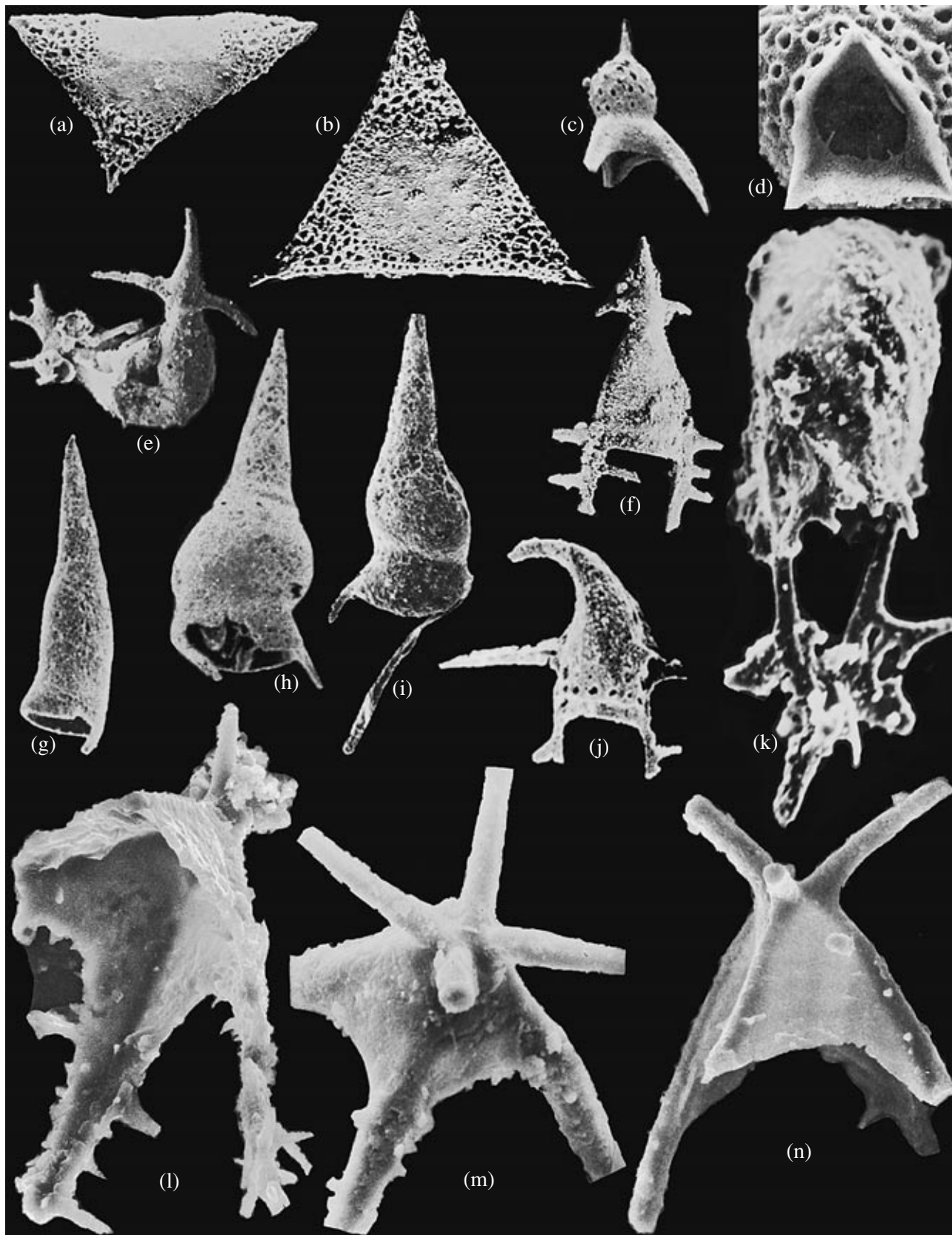
longitudinal or transverse rows of pores are more distinctly outlined because the walls between the rows are wider and (or) thicker than in the pores in the same row. In addition, large pores may be covered by fine open meshwork or porous plates (Nazarov and Petrushevskaya, 1995). The outer shell may be supplemented by a system of relatively high ridges that form a cellular structure of the shell surface, as, for example, in the genus *Ornatoentactinia* (Fig. 3c; Pl. 4, fig. 9).

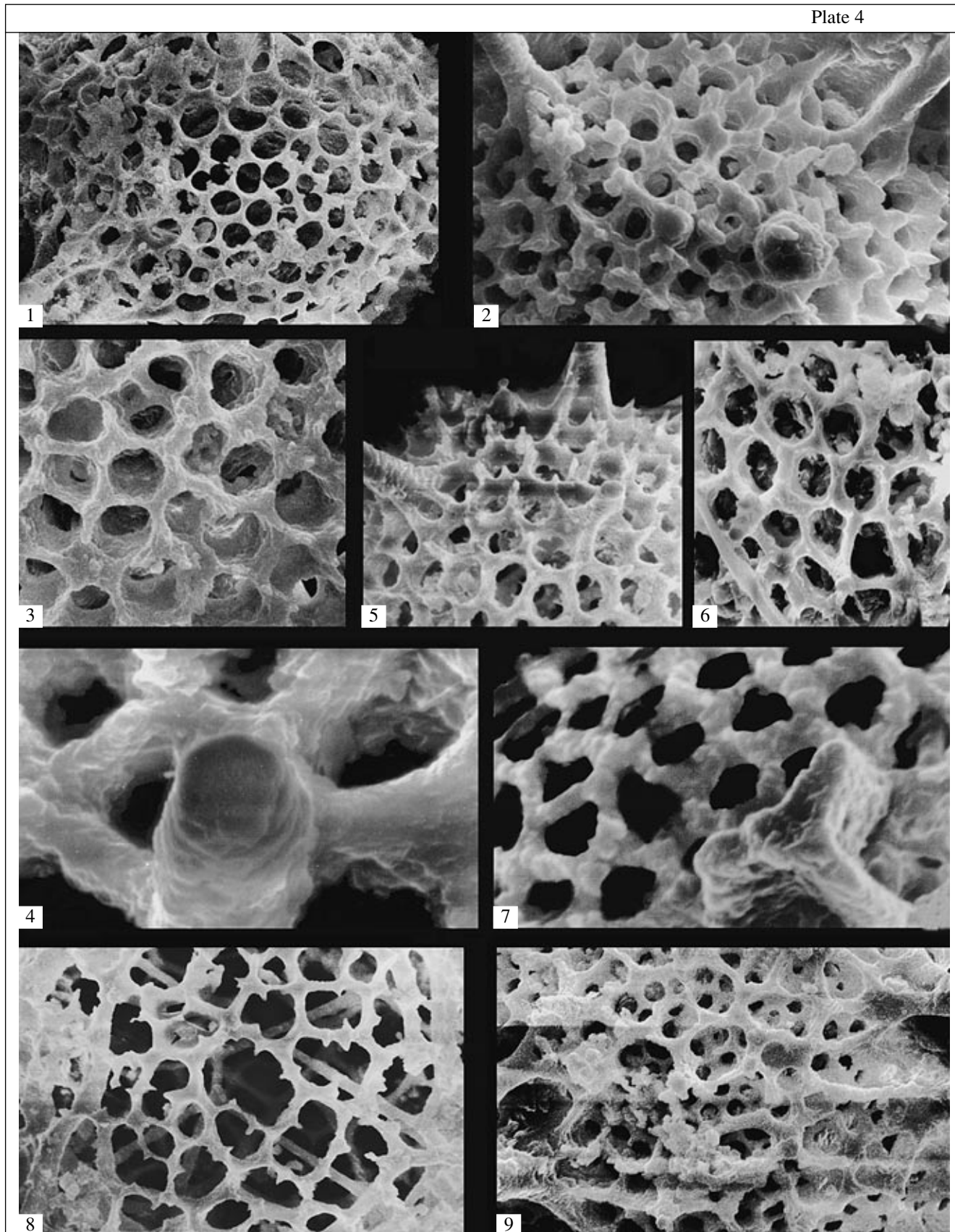
The wall thickness of the external shell ranges from 1 to 8 μm . In some taxa, the wall is thin (1–3 μm), which is comparable in size with the globules of crystalline units of the skeletal ultrastructure (Afanasieva, 2000a). Globules tightly contact each other to form the septa of the skeleton, with an equal height and width (Pl. 4, fig. 7).

Based on the ratio between the pore diameter (dp) and skeleton wall thickness (tw), four types of pores are recognized: (1) very narrow (dp/tw = 0.40–0.85); (2) narrow (dp/tw = 0.86–1.0); (3) wide (dp/tw = 1.01–3.41); and (4) very wide (dp/tw = 3.41–9.5). Based on the ratio of the diameter of the shell (D) and pores penetrating it, the following varieties of pores are recognized: (1) very large pores (D/dp = 4.0–10.0), (2) large pores (D/dp = 10.01–18.5), (3) small pores (D/dp = 18.51–63.0); and (4) very small pores (D/dp = 63.01–105.0).

The interpore bars may be rounded (Pl. 4, figs. 1, 2, 4, 5, 7, 8) or flattened straight (Pl. 4, figs. 3, 6), equipped with interpore denticles (Pl. 4, figs. 5, 6, 8) or supplementary elements, such as thorns and spinules (Pl. 4, figs. 2, 5). The interpore bars are 1–5 μm wide. Based on the ratio between the pore diameter (dp) and the width of the interpore bars (wp), the following varieties are recognized: very narrow bars (dp/wp = 9.50–5.81), narrow bars (dp/wp = 5.80–4.11), wide bars (dp/wp = 4.10–2.01), and very wide bars (dp/wp 2.00–0.50).

Fig. 4. Lamellar structure of the external skeletal sphere in representatives of (a, b) Stauraxonia, (c, d) Pylomariata, and (e–n) Aculearia: (a, b) *Ruzhencevispongus plumatus* Nazarov et Ormiston, 1985, Lower Permian, Sakmarian Stage; southern Ural Mountains, Ural River, village of Donskoe: (a) specimen GIN, no. 4673/74, $\times 100$, and (b) GIN, no. 4472/10, $\times 125$; (c) *Archocyrtium coronaesimile* Won, 1983, specimen no. Pr. 9705-S 1/26, $\times 300$, Lower Carboniferous, Germany, Rheinisches Schiefergebirge; (d) *Cyrtisphaeractenium rurae* Won, 1983, specimen no. Pr. 9705-S 1/18, $\times 400$, Lower Carboniferous, Germany, Rheinisches Schiefergebirge; (e) *Haplodiactanthus circinatus* Nazarov et Ormiston, 1985, specimen GIN, no. 4488/170, $\times 100$, Upper Carboniferous, Gzelian Stage; southern Ural Mountains, Ural River; (f) *Follicucullus scholasticus* Ormiston et Babcock, 1979, specimen no. KUE PR 29-8, $\times 175$, Upper Permian, southwestern Japan, Tamba District, Nabedzeriyama; (g, h) *Follicucullus ventricosus* Ormiston et Babcock, 1979, Upper Permian, Guadalupian Stage, Lamar Limestone, United States, Western Texas, Delaware Basin: (g) specimen no. USNM 250550, $\times 215$, and (h) USNM, no. 250548, $\times 180$; (i) *Albaillella amplificata* Nazarov et Ormiston, 1985, specimen GIN, no. 4488/51a, $\times 100$, Upper Carboniferous, Gzelian Stage; southern Ural Mountains, Ural River; (j) *Neoalbaillella grypis* Ishiga, Kito et Imoto, 1982, specimen no. KUE PR 33-3, $\times 170$, Upper Permian, southwestern Japan, Tamba District, Nabedzeriyama; (k) *Holoeciscus foremanae* Cheng, 1986, specimen PIN, no. 137-01805, $\times 270$, Upper Devonian, Famennian Stage; polar Ural Mountains, Lemvinskaya Zone, sample 101/594k; (l) *Palaeoscenidium robustum* Aitchison, 1993, specimen PIN, no. 081-09929, $\times 715$, Upper Devonian, Middle Frasnian Substage, Domanik Formation, Timan–Pechora Province, Lyajol River, outcrop 1904, sample 6; (m) *Palaeoscenidium scaurum* Afanasieva, 2000, specimen PIN, no. 099-04406, $\times 750$, Upper Devonian, Middle Frasnian Substage, Domanik Formation, Timan–Pechora Province, borehole Shuda-Yag-1003, sample 29 (depth 105–106 m); and (n) *Palaeoscenidium tabernaculum* Aitchison, 1993, specimen PIN, no. 080-13329, $\times 500$, Upper Devonian, Middle Frasnian Substage, Domanik Formation, Timan–Pechora Province, Ukhta River, sampling point no. 4, sample B-22; (a, b, e, i) after Nazarov (1988); (c, d) after Won (1983); (f, j) after Ishida et al. (1982); (g, h) after Ormiston and Babcock (1979); and (k–n) after Afanasieva (2000a, 2000b).





CONCLUSIONS

Presently, it is evident that the classical evolutionary morphology, which is based on what is known as Haeckel's Triad, the concordance between comparative morphological, embryological, and paleontological data proposed by Haeckel, one of the founders of radiolarian analysis, should be modified in accordance with the modern state of knowledge. Each organism and its structural features "may and should be studied from at least four points of view: constructive-morphological, physiological, ecological, and historical. Each of these points of view is permissible, necessary, and unique" (Beklemishev, 1964, p. 78).

Today, the major emphasis in fundamental morphological studies is placed on the revelation of factors and mechanisms of the formation of structures in the course of evolution. From new standpoints, advanced research work brings a new understanding of the relationships of morphology to phylogeny and classification, as the study of macrostructure is supplemented by research at the ultrastructural level.

The study of radiolarian skeletons² at various structural levels in geological time revealed the major patterns of the formation of radiolarian skeletons in the course of evolution, morphological grounds for phylogeny and classification of the phylum Radiolaria, nature and patterns of the appearance–disappearance and expansion in time and space of orders, families, and

genera at the major boundaries within the Phanerozoic (Afanasieva et al., 2005).

A new scheme of the successive stages of the formation of radiolarian skeletons is proposed. The main variants of skeletal shells are combined in two major types according to the growth pattern of skeletal tissue, i.e., (1) latticed, cellular, and spongy shells formed by the bridge growth and (2) porous and lamellar shells formed by the rim growth.

In the phylogeny of the subphylum Polycystina, the following skeletal variants appeared almost simultaneous: (1) the spiny and lamellar skeletons in the class Aculearia, (2) the spherical skeleton in the porous members of the class Sphaerellaria and spongy taxa of the class Spumellaria, (3) the first spongy and porous nassellarians of the order Pylomariata, and (4) the first spongy members of the class Stauraxonaria. In the phylogeny of the subphylum Phaeodaria, the spiny, latticed, porous, and lamellar skeletons also appeared in parallel.

Types of symmetry successively increasing in complexity are considered. It is shown that the heteropolar Nassellaria and Phaeodaria could have evolved from homaxial spherical ancestors, while the bilaterally symmetrical pseudo-shells of Lapidopiscidae evolved from the heteropolar skeletons of Ceratoikiscidae.

All basic skeletal constructions of radiolarians, including spiny, spherical, stauraxonic, and pylomate, emerged almost simultaneously in the Cambrian and gave rise to five classes: Aculearia, Spumellaria, Sphaerellaria, Stauraxonaria, and Nassellaria (order Pylomariata); this suggests a polyphyletic origin of radiolarians.

² The questions of the morphology of spines, internal framework, and primary inner sphere of radiolarian skeletons will be considered in the next paper by M.S. Afanasieva (Paleontol. Zh., 2006, No. 6), devoted to evolutionary morphology of radiolarians.

Explanation of Plate 4

Porous structure of the external shell in Late Devonian radiolarians, Middle Frasnian Substage, Domanik Formation of the Timan-Pechora Province.

Circular pores:

Fig. 1. *Entactinia parva* Won, 1983, specimen PIN, no. 098-13701, ×455, Chut' River, outcrop 8, sample 7d.

Fig. 2. *Moskovistella rozanovi* Afanasieva, 2000, specimen PIN, no. 117-13510, ×1000, borehole Shuda-Yag-1003, sample 8 (depth 120.9–124 m).

Fig. 3. *Entactinia herculea* Foreman, 1963, specimen PIN, no. 035-13323, ×1500, borehole Shuda-Yag-1003, sample 34 (depth 104.1–104.6 m).

Fig. 4. *Radiobisphaera assidera* (Nazarov, 1975), specimen PIN, no. 101-08506, ×3750, borehole Shuda-Yag-1003, sample 72 (depth 71.9–72.4 m).

Oval pores:

Fig. 5. *Astroentactinia crassata* Nazarov, 1975, specimen PIN, no. 050-04124, ×750, borehole Shuda-Yag-1003, sample 29 (depth 105–106 m).

Angular-oval pores:

Fig. 6. *Astroentactinia paronae* (Hinde, 1899), specimen PIN, no. 047-04013, ×750, borehole Shuda-Yag-1003, sample 8 (depth 120.9–124 m).

Fig. 7. *Bientactinosphaera morozovi* Afanasieva, 2000, specimen PIN, no. 116-04033, ×2140, Ukhta River, sampling point no. 4, sample B-29.

Circular-polygonal pores:

Fig. 8. *Borisella pantosompha* (Foreman, 1963), specimen PIN, no. 039-04701, ×880, borehole Shuda-Yag-1003, sample 68 (depth 73.3–73.5 m).

Fig. 9. *Ornatoentactinia solita* Afanasieva, 2000, specimen PIN, no. 043-13126, ×1000, Ukhta River, sampling point no. 4, sample B-29.

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