

A New Classification of the Radiolaria

M. S. Afanasieva* and E. O. Amon**

**Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, Sj 7997 Russia*

e-mail: kem-fotid@mtu-net.ru

***Zavaritskii Institute of Geology and Geochemistry, Ural Division, Russian Academy of Sciences, Pochtovyi per. 7, Yekaterinburg, 620151 Russia*

Received August 20, 2002

Abstract—A new classification of higher radiolarian taxa is proposed. The phylum Radiolaria includes two superclasses, i.e., Pheodaria and Polycystina. The superclass Polycystina is composed of the following five classes: Sphaerellaria Haeckel, 1881; Spumellaria Ehrenberg, 1875; Stauraxonaria Afanasieva, 2000; Aculearia Afanasieva, 1999, status nov.; and Nassellaria Ehrenberg, 1847. The class Aculearia combines three orders, i.e., Fasciculata ordo nov., Triangulata ordo nov., and Albaillellata Deflandre, 1953, emend. Afanasieva, 1999. The class Spumellaria consists of four orders, i.e., Collodariata Haeckel, 1881; Echidninata Kozur, Mostler et Repetski, 1996; Cancelliata ordo nov., and Spongiata ordo nov. A special attention was paid to the systems and evolution of spinaceous and spongy Paleozoic radiolarians.

Key words: New classification, Radiolaria, higher taxa, evolution.

INTRODUCTION

Three major evolutionary stages are distinguished in the Paleozoic history of radiolarians, i.e., Cambrian-Silurian, Devonian-Early Carboniferous, and Middle Carboniferous-Permian. Each stage is characterized by significant changes in the number and composition of the higher taxa and the change of dominant groups. The stages of the radiolarian evolution differ from each other in many ways. The most important of them is the maximum rank of the taxa which underwent changes at crucial points of their development (Fig. 1).

The earliest, Early Cambrian radiolarians are represented by only four spherical genera assigned to two orders of the class Sphaerellaria (Nazarov, 1973; Obut and Iwata, 2000). The earliest well preserved radiolarians are found in the Botoman Stage of the Lower Cambrian of Gornyi Altai (Obut and Iwata, 2000). Finely preserved radiolarians were found in the Middle Cambrian of Australia (Won and Below, 1999) and Canada (Won and Iams, 2002). The taxonomic diversity of the Middle Cambrian radiolarians abruptly increases to 12 genera of 7 orders and 4 classes, i.e., Nassellaria (represented by the order Pylomariata in the Paleozoic), Spumellaria, Sphaerellaria, and Aculearia (Nazarov, 1975, 1988; Won and Below, 1999). In the Late Cambrian, radiolarians are represented by 16 genera of eight orders; a new class, Stauraxonaria, appeared at that time (Nazarov, 1975; Won and Iams, 2002).

During the first stage of the radiolarian evolution, in the Cambrian-Silurian, the major higher taxa appeared (59 taxa), i.e., the entire set of 5 classes, 11 orders, 3 superfamilies, 23 families, and 17 subfamilies. The

Paleozoic evolution of radiolarians underwent the first crucial point at the Silurian-Devonian boundary (Afanasieva, 2002a). At the end of the Silurian, all members of the Early Paleozoic orders Echidninata and Anakrusata, and radiolarians characterized by internal framework shaped into a hollow sphere from the orders Pylomariata and Inaniguttata (two families, Proventocitidae and Aciferopyloridae; and three subfamilies, Inaniguttinae, Inanibiguttinae, and Inanihellinae) became extinct (Fig. 1).

In the Devonian-Early Carboniferous, 19 new taxa appeared, i.e., the order Latentifistulata, superfamily Popofskyelloidae, 5 families (Popofskyellidae, Spongopolyentactiniidae, Corythoecidae, Tormentidae, and Latentifistulidae), and 12 subfamilies (Fig. 1). This evolutionary stage is characterized by the maximum taxonomic diversity, 67 higher taxa (all classes, 10 orders, 3 superfamilies, 23 families, and 26 subfamilies) and 88 genera are present. The peak of the diversity, i.e., 57 higher taxa, falls on the Late Devonian and Early Carboniferous, while the maximum generic diversity, 67 genera, is registered in the Late Devonian.

The second crucial point in the radiolarian evolution corresponds to the boundary between the Early and Middle Carboniferous (Afanasieva, 2002a). By the end of the second evolutionary stage, the following taxa had become extinct: superfamily Pylentonemoidae, five families (Oriundoguttidae, Palaeospiculidae, Palaeosцениdiidae, Pylentonemidae, and Lapidociclicidae), and ten subfamilies (Fig. 1). Only two radiolarian families, i.e., Ruzhencevispongidae and Deflandrellidae, and seven stauraxon subfamilies emerged during the Middle Carboniferous and Permian (Fig. 1).

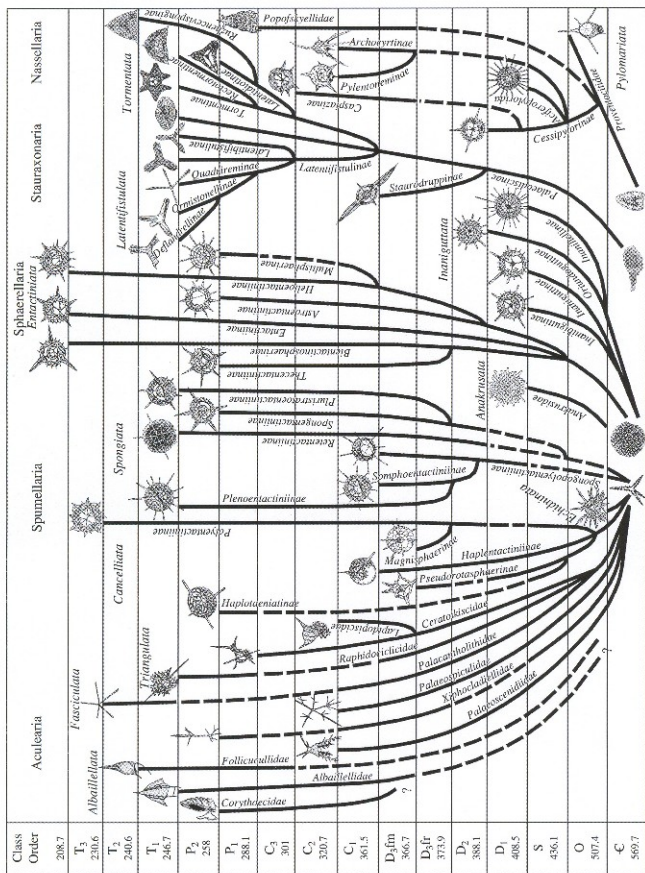


Fig. 1. Phylogenetic tree of the phylum Radiolaria in the Paleozoic.

A catastrophic crisis in the radiolarian evolution happened at the Permian-Triassic boundary. During this time, 37 higher taxa (out of 59 which existed during the third evolutionary stage) disappeared, i.e., 4 orders, 2 superfamilies, 13 families, and 18 subfamilies; and 45 out of 52 genera had become extinct (Fig. 1). A total of 149 radiolarian genera (95.5%) disappeared by the end of the Paleozoic.

One may suppose with certainty that the formation of the higher radiolarian taxa followed the pathway of combination of the high-rank morphological characters, which almost simultaneously appeared in different radiolarian groups during the Early Paleozoic. This is evident from their variety, which is not typical for the later (Mesozoic and Cenozoic) radiolarians and from the fact that the same taxon combines features of spherical and spinaceous forms. For instance, the primary spicule, which is present in the skeleton of almost all Paleozoic members of the Spumellaria, Sphaerellaria, Stauraxonaria, and Pylomariata, is included in the cephalic and postcephalic segments of the Mesozoic and Cenozoic Nassellaria and forms separate skeletal elements of the spinaceous Aculearia. It is not inconceivable that different radiolarian groups evolved, to a certain extent, in parallel ways directed from the development of the general structural plan to the perfection of particular skeletal elements. The most constructive combinations of characteristics determined the emergence and development of new higher taxa, which had evident evolutionary advantages.

Thus, the phylum Radiolaria appeared in the Early Cambrian and was represented by only four genera of spherical forms from the class Sphaerellaria. In the Middle Cambrian, the taxonomic composition of radiolarians increased to seven orders of four classes, i.e., Nassellaria (represented in the Paleozoic by the order Pylomariata), Spumellaria, Sphaerellaria, and Aculearia, which exists up to the Recent. Another class of radiolarians, Stauraxonaria, appeared in the Late Cambrian. Its Mesozoic descendants, i.e., the orders Prunoata, Discoata, and Larcoata, persist till the Recent (Figs. 1, 2).

At the Permian-Triassic boundary, the typical Nassellaria appeared, but the first features of this group were evidently present among the Pylomariata as early as the Late Devonian, or, possibly, even in the Early Ordovician. At the Paleozoic-Mesozoic boundary (in the Early Triassic), the last members of the order Albaillellata (from the class of spinaceous radiolarians, Aculearia) disappeared. The first representatives of the Sphaerellata and Cyrtidinata appeared at the onset of the Mesozoic, while the first members of the Collodariata and Spyridinata appeared in the Paleogene. These taxa represent newly formed young orders of the classes Sphaerellaria, Spumellaria, and Nassellaria.

On the basis of the general structural plan of the skeleton, the high-rank radiolarian taxa first registered in the Early Paleozoic should be regarded as classes, and a number of superfamilies, previously established

by different researchers, especially those that appeared in the Early Paleozoic, should be ranked as orders on the basis of the level of their organization (Afanasieva, 2000a, 2000b, 2002a) (Fig. 2).

Russian protozoologists in 1980 developed a macro-system of protists, which were split into nine phyla (Krylov *et al.*, 1980). The group Actinopoda was not designated in this system, and protists that had previously been assigned to this group were distributed among the phyla Sarcodina and Acantharea. According to this system, radiolarians are referred to the phylum Sarcodina and ranked as subphylum, including two classes, Polycystina and Phaeodaria (Krylov *et al.*, 1980; Amon, 1997, 2000; Afanasieva, 2000a, 2002b). Recently obtained molecular data indicate that Acantharia and Radiolaria are extremely distant phylogenetically. This data is based on the comparison of genes of the ribosomal RNA and make it possible to estimate the phylogenetic relationships between Radiolaria and Acantharia within the general evolutionary tree of protists and give convincing evidence that Radiolaria have branched off from the main protist stem at the dawn of the protist radiation, while the Acantharia are a rather late branch (Zettlerffra *et al.*, 1997; Mikryukov, 2000).

The fundamental monograph (*Protisty: rukovodstvo po zoologii*, 2000) contains a modified system of Corliss (1994) where protists are distributed among five eukariotic kingdoms, i.e., Animalia, Fungi, Plantae, Chromista, and Protozoa. According to this monograph, "Rhizopoda, Myxozoa, Foraminifera, Radiolaria, and other protist phyla are macrotaxa composed of ameboid organisms only" (*Protisty*, 2000, p. 143). According to the opinion of the authors of the monograph, this system does not contradict the modern point of view on the phylogenetic system of eukariotic organisms.

Following the studies of the protist macrosystematics of the last three decades (Margulis, 1974; Levine *et al.*, 1980; Krylov *et al.*, 1980; Corliss, 1984; Cavalier-Smith, 1993; Kusakin and Drozdov, 1994; *Protisty*, 2000), in the present paper, we regard radiolarians as a separate phylum of the subregnum Protozoa. This position is also supported by the fact that each of the five radiolarian classes appeared almost simultaneously in the Cambrian (Fig. 1). The new classification of high-rank radiolarian taxa can be presented as follows (Fig. 2):

- Phylum Radiolaria Müller, 1858
 - Superclass Phaeodaria Haeckel, 1879 Superclass
 - Polycystina Ehrenberg, 1838
 - Class Sphaerellaria Haeckel, 1881
 - Order Inaniguttata Nazarov et Ormiston, 1984
 - Order Anakrusata Nazarov, 1977
 - Order Entactiniata Riedel, 1967
 - Order Sphaerellata Haeckel, 1887
 - Class Spumellaria Ehrenberg, 1875
 - Order Cancelliata ordo nov.
 - Order Spongiata ordo nov.
 - Order Echidninata Kozur, Mostler et Repetski, 1996
 - Order Collodariata Haeckel, 1881

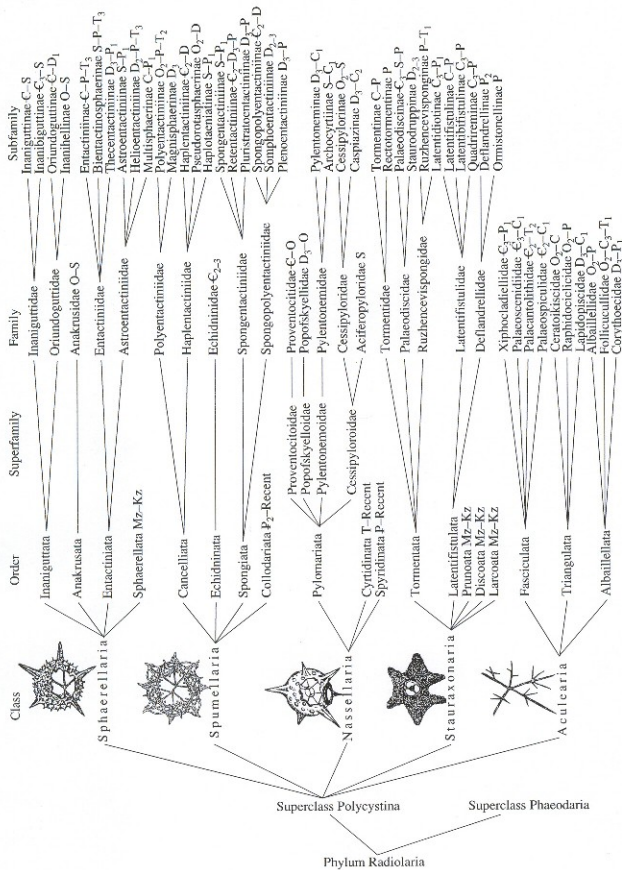


Fig. 2. Classification scheme of radiolarians.

- Class Stauraxonaria Afanasieva, 2000
 Order Tormentata Nazarov et Ormiston, 1983
 Order Latenlifistulata Nazarov et Ormiston, 1983
 Order Prunoata Haeckel, 1883
 Order Discoata Haeckel, 1862
 Order Larcoata Haeckel, 1883 Class Aculearia
 Afanasieva, 1999, status nov.
 Order Fasciculata ordo nov.
 Order Triangulata ordo nov.
 Order Albaillellata Deflandre, 1953, emend.
 Afanasieva, 1999 Class Nassellaria
 Ehrenberg, 1847
 Order Pylomariata Afanasieva, 1999
 Order Cyrtidinata Haeckel, 1862
 Order Spyridinata Ehrenberg, 1847

SPINACEOUS RAD1OLARIANS

Many researchers widely use the loose and freely interpreted term *spinaceous radiolarians*. A more exact definition of spinaceous radiolarians is as follows: this is a group of taxa whose skeleton is formed on the basis of spines or spine bunches crossing each other in one or more points (Fig. 3). These points (or knots) can be regarded as the morphological center of ontogenetic development and growth of the skeleton.

If the spines cross in a single knot, the skeleton takes a crosslike or starlike shape; if three or more knots are present, the skeleton takes a complex spinaceous framelike appearance, which is completely or partly closed (Afanasieva, 2000a, 2000b, 2002b; Amon, 2002a, 2002b). In some cases, two bunches of spines are connected by a bar; this is indirect evidence of fusion between two primary spicules (Fig. 3). In such cases, it is more correct to speak about two centers of the spine crossing. Heteropolar (axial-symmetric) and bilaterally symmetric (dissymmetric) forms prevail among the spinaceous skeletons. The short and massive spines crossing in one center compose a skeleton resembling a primary spicule of spherical Paleozoic radiolarians and Mesozoic-Cenozoic nassellarians.

Spinaceous radiolarians and the primary spicule of spherical radiolarians display superficial similarity to spicules of siliceous sponges. The spicules of poriferans have a wide central canal inside the rays (Pl. 1, figs. 1, 2). Spinaceous radiolarians and primitive spines of spherical radiolarians can also possess a narrow canal for the cytoplasmatic cord or skeletal rod (Petrushevskaya, 1986). Won described such a hollow canal in the earliest spinaceous radiolarians from the Middle and Upper Cambrian of Australia and Newfoundland and considered whether they belonged to poriferans or radiolarians (Won and Below, 1999; Won and Iams, 2002). The question of phylogenetic relationships or convergent similarity of the skeletons of poriferans and spinaceous radiolarians is very interesting and deserves a thorough study. However, it should be kept in mind that the main difference between radiolarians and

poriferans is the spiral growth of the skeleton (Pl. 1, figs. 5, 6), while in poriferans, the spicules grow in a specific concentric manner (Pl. 1, fig. 3).

The internal and external elements of the radiolarian skeleton are commonly recognized. The internal elements include spicule, spiny framelike constructions, and the structures connected with them (spikes, apophyses, lateral spines, tunica, anastomizing threads, etc.). The external elements consist of different envelopes and coatings covering internal elements. The external structures wrap or coat the internal elements. The morphological role and functional significance of the external elements are the mechanical defense of the soft organelles, nucleus, and cytoplasm with its content of radiolarian cells. The internal elements serve as mechanical support for the envelopes and coverings (Amon, 2002a).

Siliceous skeletons are widespread only among the most primitive organisms, i.e., radiolarians, poriferans, diatoms, silicoflagellates, and some foraminifers. In an organism, the silicon is present in different compounds, which mainly participate in the skeleton formation. The radiolarian skeleton is composed of opal ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$), its main structural unit is silicon-oxygen tetrahedron $[\text{SiO}_4]^{4-}$, anion of orthosilicic acid. Oxygen atoms are located at the tops of the tetrahedron, while silicon atom is in the center (Afanasieva and Vishnevskaya, 1992; Afanasieva, 2000a).

A characteristic feature of the biogenic amorphous silica (Francois, 1989) is an ability to form complex structures of short three-dimensional chains of tetrahedrons $[\text{SiO}_3]^{2-}$, which can form combinations of two or more anions by means of common oxygen atom (Fig. 4). The external shape of the skeleton reflects the general pattern of the molecular structure. This ultrastructural element of the primary opal forms the foundation for the formation of the primary four-rayed radiolarian spicule, i.e., the microlevel manifests itself on the macrolevel (Tochilina, 1997). Probably, the four-rayed spicule was a prototype for the primary radiolarian skeleton.

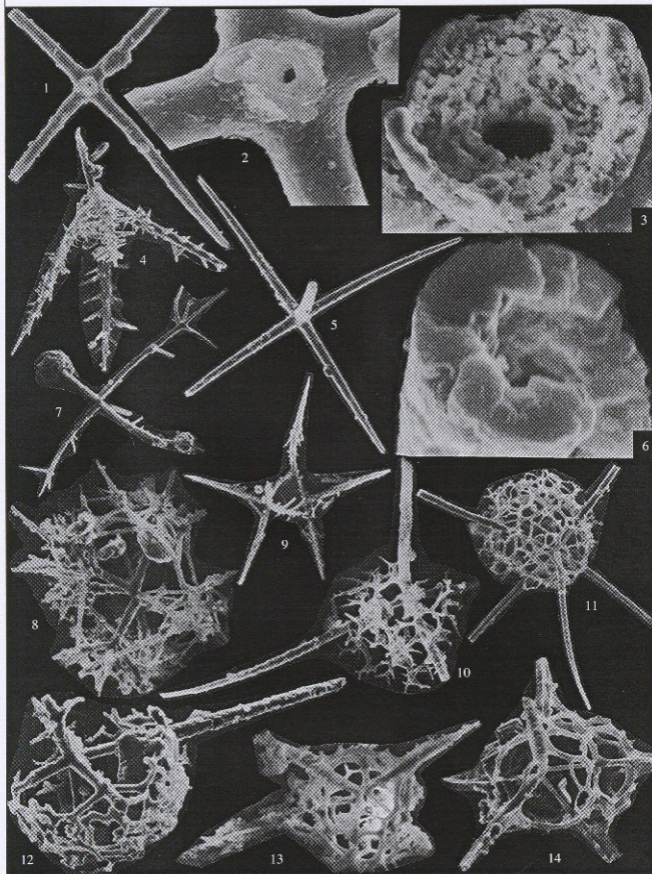
Haeckel (1887) was the first to suggest the hypothesis of a four-rayed tripod as the initial element of the skeleton in Nassellaria. Later, it was developed in detail by Popofsky (1913). He considered the skeleton of *Plagoniscus* (Fig. 5a) to be similar to skeletons characteristic of the family Thalassothamnidae (order Collodaria), and even suggested the origin of nassellarians from these radiolarians. The four-rayed spine of Popofsky's model was not only the initial construction for the formation of all nassellarian skeletons, but also a link between nassellarians and spherical radiolarians. In the course of development of the nassellarian skeleton, the primary tripod changed as follows: (a) the median bar (Figs. 5b, 5c) and apophyses (Fig. 5d) appeared; (b) the spines *Ir*, *II*, and *Vert* (Fig. 5e) was added; and (c) the spines *A* and *Vert* became closed to form the sagittal

Fig. 3. Pattern of skeleton formation in spinaceous radiolarians of the class Aculearia and latticed and spongy skeletons of spherical radiolarians of the class Spumellaria.

ring *R* (Fig. 5e). In addition, Popofsky supposed that different modifications of spinaceous skeleton appeared at the earliest stages of the evolution of Nassellaria, and they repeated in advanced forms.

The four-rayed spicule is the universal primary skeletal element stable in time and space and provides the basis for classification of the Nassellaria proposed by

Tochilina (1997). Thus, the primary four-rayed spicule is the basis of the skeleton of spinaceous radiolarians, and its modification provides the variability of spinaceous radiolarians of the class Aculearia. The main stages in the development of spinaceous radiolarian skeletons (Fig. 3) resemble the general pattern of the formation of the nassellarian skeleton (Fig. 5).



Explanation of Plate 1

The structure of (1-3) poriferan spicules and (4-14) internal radiolarian framework; class Aculearia: orders (4-8) Fasciculata and (9) Triangulata; and class Spumellaria: (10-14) order Cancelliata.

Figs. 1 and 2. *Triaxonida* ? sp. 407: (1) spicule, x375; (2) fragment of spicule, x1000; Upper Devonian, Upper Frasnian; Timan-Pechora Basin, Ukhta River, Locality 1; rock sample no. 7001.

Fig. 3. *Triaxonida* ? sp. 403, fragment, x715; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, Domanik River, quarry 2; rock sample no. 5.

Fig. 4. *Palaeoscenidium cladophorum* Deflandre, skeleton, x225; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, borehole Shuda-Yag-1003; rock sample no. 72 (depth 71.9-72.4 m).

Figs. 5 and 6. *Palacantholithus stellatus* Deflandre: (5) skeleton, x105; (6) fragment of skeleton, x3000; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, Lyaiol' River, outcrop no. 1904; rock sample no. 6.

Fig. 7. *Palaeothalomnus arrhinia* (Foreman), skeleton, x225; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, borehole Shuda-Yag-1003; rock sample no. 68 (depth 73.3-73.5 m).

Fig. 8. *Palaeothalomnus timokhini* Afanasieva, skeleton, x300; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, borehole Shuda-Yag-1003; rock sample no. 73 (depth 71.4-71.9 m).

Fig. 9. *Ceratoikiscum incomptum* Nazarov, skeleton, x180; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, borehole Shuda-Yag-1003; rock sample no. 73 (depth 71.4-71.9 m).

Fig. 10. *Tetragregnon quadrispinosa* (Foreman), skeleton, x180; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, borehole Shuda-Yag-1003; rock sample no. 73 (depth 71.4-71.9 m).

Fig. 11. *Haplentactinia bornazi* Afanasieva, skeleton, x270; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, Lyaiol' River, outcrop no. 1904; rock sample no. 6.

Fig. 12. *Haplentactinia alekseevi* Afanasieva, skeleton, x355; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, Lyaiol' River, outcrop no. 1904; rock sample no. 6.

Figs. 13 and 14. *Haplentactinia barskovi* Afanasieva: (13) skeleton, x405; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, borehole Shuda-Yag-1003; rock sample no. 78 (depth 68.4-69.3 m); (14) skeleton, x405; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, Lyaiol' River, outcrop no. 1904; rock sample no. 6.

(1) The simple primary four-rayed spicule is the basis of the earliest skeletons of the family Palacantholithidae Kozur et Mostler, 1981 (Pl. 1, figs. 5, 6).

(2) The primary four-rayed spicule, which is complicated by apophyses tending to form a pseudospheric clew in the Palaeospiculidae Won in Won et Below, 1999 (Pl. 1, figs. 7, 8) is a link between the latticed and spongy forms.

(3) The primary four-rayed spicule accompanied by lamellar skeletal tissue, which forms a pseudoshell covering the center of the crossing of the spicule rays, is typical for the Palaeoscenidiidae Riedel, 1967, emend. Nazarov, 1981 (Pl. 1, fig. 4).

(4) The fusion of two primary four-rayed spicules is the basis for the development of the main axial spine in the family Xiphocladellidae Nazarov, 1984; it is complicated by the spines crossing in two points, i.e., the apical and basal cross-centers.

(5) The main triangular framework of the order Triangulata ordo nov. is formed by the fusion of two primary four-rayed spicules and development of the spines composing this framework (a-rod, b-rod, and i-intersector) within the same plane (Pl. 1, fig. 9).

(6) A combination of two primary four-rayed spicules provides the basis for the skeleton development in the order Albaillellata. Its spines, i.e., a, b, and i, grow within the same plane, but retain the original H-frame subparallel formation of the spines a and i connected by the spine b at the base of the skeleton. In the apical part of the skeleton, the spines a and i are closed to form the r structure, which displays a convergent similarity to the sagittal ring of the Nassellaria.

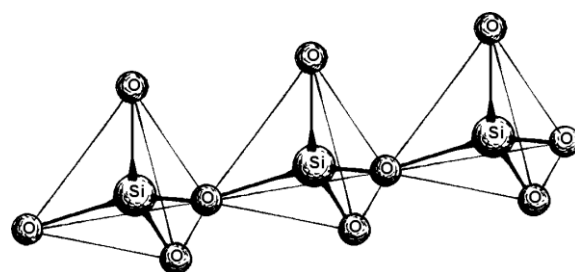


Fig. 4. The tetrahedron chains of $[\text{SiO}_3]^{2-}$, which can be formed by the fusion of two or more anions through the common oxygen atom.

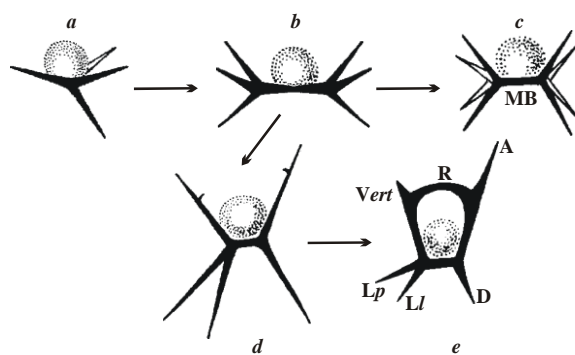


Fig. 5. A simplified model of skeleton formation in some Nassellaria (after Popofsky, 1913, and Petrushevskaya, 1971): (a) *Plagoniscus*; (b) *Plagonium*; (c) *Polyplagia*; (d) *Plagiocarpa*; and (e) *Cortina*.

Morphological features of aculearian skeletons allow recognition of three groups of spinaceous radiolarians (Fig. 3):

(1) The heteropolar skeleton composed of several spines crossing in one or two centers (in other words, composed of one or two bunches of spines connected by the median bar) is characteristic of the order Fasciculata ordo nov.

(2) The bilaterally symmetrical skeleton composed of three crossing main spines, which form an internal triangular framework is characteristic of the order Triangulata ordo nov.

(3) Two long columellae connected below the aperture by the transverse bar to form an H-frame in the basal part of the skeleton and a subsagittal construction *r* in the apical part are characteristic of the order Albaillellata Deflandre, 1953, emend. Afanasieva, 1999.

To date, there is no consensus of opinion among experts in extinct and extant radiolarians regarding the composition, taxonomic rank, and phylogenetic affinities of the heteropolar spinaceous radiolarians. Some experts regard them as an *incertae sedis* group (Riedel, 1967; Nazarov, 1975; Nazarov and Popov, 1980; Nazarov and Rudenko, 1981; Braun, 1990; Won, 1997), others consider them as members of the order Spumellaria (Holdsworth, 1977; Aitchison, 1993; Tochilina, 1997; Won and Iams, 2002). Dumitrica (1978, 1984) assigns Triassic representatives of the families Palaeoscenidiidae and Pentactinocarpidae to the superfamily Hexastyloidea of the order Sphaerellaria.

Petrushevskaya (1969, 1971, 1979, 1984, and 1986) and Deflandre (1973) emphasized the evident similarity in appearance between the spinaceous skeletons of the Palaeoscenidiidae and that of living members of the Thalassothamnidae. On the basis of this similarity, Nazarov and Ormiston placed them in the order Collodaria (Nazarov, 1984, 1988; Nazarov and Ormiston, 1984). Kozur divided palaeoscenidiids into several families and assigned them to the superfamilies Thalassothamnacea and Palaeoscenidiaceae of the suborder Entactinaria, order Collodaria (Kozur and Mostler, 1981).

At the same time, Nazarov and Ormiston (Nazarov, 1974, 1981; Nazarov and Ormiston, 1983, 1985) and Petrushevskaya (1979, 1984, 1986) combined spinaceous radiolarians with the Albaillellaria. In turn, Riedel declared that the Haeckel's classification is unsuitable for systematization of spinaceous-framed radiolarians from the Late Eocene-Middle Pliocene (family Orosphaeridae Haeckel, 1887) and tentatively assigned them to Phaeodaria (Friend and Riedel, 1967). Afanasieva (1999, 2000a, 2000b, 2002b) combined spinaceous and spinaceous-framed forms in the order Aculearia.

However, forms with the elementary skeleton composed of crossing spines are the most simply organized group of early radiolarians (along with primitive spherical forms). Possibly, they were the prototype of more advanced bilaterally symmetrical and spongy spherical

groups, and their crossing spines could be the prototype of the spicule of nassellarians and Paleozoic spherical radiolarians.

The earliest spinaceous skeletons almost lacking spines and spikes were found by Won in the Middle Cambrian of Australia (Won and Below, 1999) and Upper Cambrian of Canada (Won and Iams, 2002). The youngest members of primitive spinaceous radiolarians were described by Yao and Kuwahara (1999, 2000) from the Lower and Middle Triassic of southern China (Guizhou Province).

These facts allow one to combine the most simply organized ancient radiolarians characterized by a skeleton of crossing spines in the new order Fasciculata ordo nov. (Fig. 3; Pl. 1, figs. 4-9). In the majority of publications, framed radiolarians are combined with the forms having conical shells and assigned to the Albaillellaria. At the same time, Tochilina (1997) and Cheng (1986) assigned these radiolarians to the Nassellaria.

According to Foreman (1963) and Holdsworth (1977), albaillellarians are related to the spinaceous Ceratoikiscidae, whose skeleton is shaped into a triangular frame composed of three crossing spines, which are often surrounded by the spongy skeletal tissue, i.e., patagium or pseudopatagium. It was proposed that the conical shell of the Albaillellidae is a result of evolutionary transformation and partial reduction of the spines of the Ceratoikiscidae, i.e., the development of the skeletal tissue on the spines and cavity ribs results in the formation of the bilaterally symmetrical subconical shell with an open aperture in the basal part and two columellae connected below the aperture by a transverse bar. It is assumed that the columellae are the *a* and *i* spines, the transverse bar is the *b* spine, and trabeculae are the cavity ribs. According to this point of view, the skeleton becomes inverted, i.e., "side lying", as compared to the skeleton of the initial forms *Holoeciscus* and *Lapidopiscum*.

Such a change in the skeleton orientation once again proves the suggestion that the bilateral or monaxonic symmetry of many radiolarians is a result of their dwelling at the bottom. The forms with the shell open on one side, like the classical Albaillellidae, "were lying on the bottom, and the direction up-and-down was far from being indifferent for them" (Petrushevskaya, 1984, p. 125).

Beklemishev (1944) studied different types of body symmetry in protists and other invertebrates and proposed that the monaxonic-heteropolar body shape always appears in the case where the opposite sides of the body are subject to different environmental effects and perform different functions. Such a body shape usually develops when one side is attached to the substrate, while the opposite side is free; a similar symmetry type appears in the organisms that dwell in flowing water.

It is not improbable that the conical shape of the shell is an adaptation to dwelling in flowing water. It is

known that the symmetry of quiet waters is a symmetry of regular sphere, $\infty L_{\infty} \infty PC$, while the gravitation in any point results in the symmetry of cone $L_{\infty} \infty P$. The vertical motion in the gravitation field is characterized by one of the subgroups of the cone symmetry, $L_n n P$, while the motion of water current (flow) is also characterized by one of the subgroups of the cone symmetry (Shafranovsky, 1968; Dmitriev and Potapova, 1971). If the radiolarians lived in flowing water (for instance, horizontal oceanic currents, vertical flow of the upwelling zones, horizontal and vertical convectional flows, daily or seasonal, and bottom currents), the moving water put pressure upon the organism. With time, the skeleton acquired the prevailing cone symmetry.

It is not inconceivable that a mere convergent similarity of highly specialized Albaillellata to members of the family Lapidopiscidae (*Holoeciscus* and *Lapidopiscum*) is observed in this case (Petrushevskaya, 1986). In addition, this may be a case of Vavilov's Law of Homologous Series in the hereditary variability. This law states that a family is characterized by a set of variants observed in all of its genera (Nazarov and Petrushevskaya, 1995). The transformation of the primitive skeleton, initially composed of three crossing spines forming a triangle, into the pseudoshell is observed in the series of the family Ceratoikiscidae. In the Albaillellata series, the ancestral forms are unknown, while the other units of the series display the same specialization trend in the process of formation of bilateral skeletons with the most complicated type of symmetry. At the same time, the regularities of integral evolution of higher taxa, which are considered to be system-organized groups (Chemikh, 1986), can also be observed (although to a lesser extent) in the development of the radiolarian taxa.

Possibly, the descendants of the Albaillellidae are present among Recent radiolarians. This may concern modern representatives of the genus *Cornutella*. Therefore, the origin of some Mesozoic-Cenozoic branches of the Nassellaria (Acropyramididae Haeckel, 1881) from the Paleozoic Albaillellidae is quite possible (Petrushevskaya, 1984, 1986; Afanasieva and Vishnevskaya, 1993; Afanasieva, 2000a, 2000b).

Order Fasciculata. The order Fasciculata combines the most simply organized heteropolar radiolarians with the internal elements represented by the spines that cross in one or two centers. This order is naturally divided into four families (Fig. 3).

The family Palacantholithidae Kozur et Mostler, 1981 (Middle Cambrian-Middle Triassic) is characterized by the spines crossed in the sole center. This family is the earliest taxon of spinaceous radiolarians, whose skeleton is derivable from the primary four-rayed spicule (Pl. 1, figs. 5, 6).

The family Palaeosцениidae Riedel, 1967, emend. Nazarov, 1981 (Upper Cambrian-Lower Carboniferous) is characterized by the development of the external

lamellar skeletal tissue forming a pseudoshell on the spines, which cross in the single center (Pl. 1, fig. 4).

The family Xiphocladellidae Nazarov, 1984 (Upper Cambrian, Upper Silurian-Lower Permian) is distinguished by fusion of two primary four-rayed spicules forming a skeleton with two centers where spicules cross each other. As a result, they develop the secondary massive main axial spine, which is complicated by several primary spines of various lengths in the apical and basal parts.

The family Palaeospiculidae Won in Won et Below, 1999 (Middle Cambrian, Upper Devonian-Lower Carboniferous) includes the forms with strongly developed apophyses and anastomizing threads on the spines; this results in the development of a pseudoclew, which is the prototype for the reticulate-latticed skeleton (Pl. 1, figs. 7, 8).

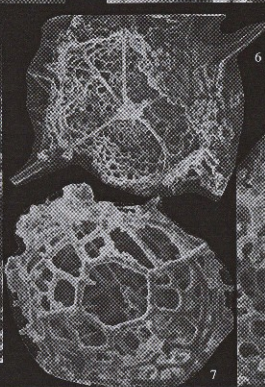
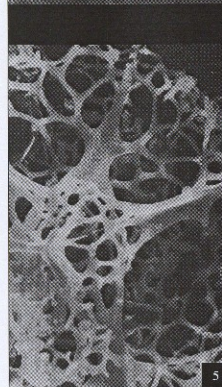
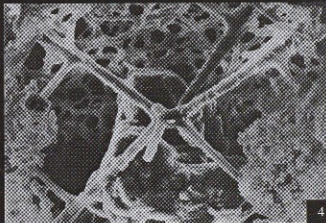
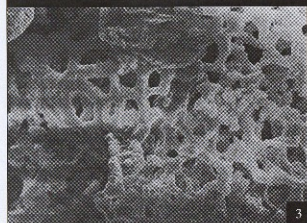
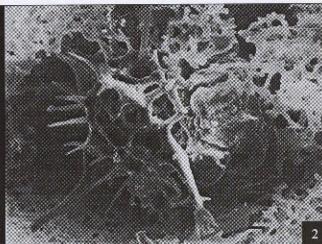
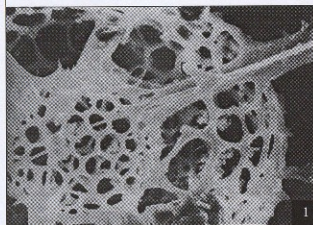
Order Triangulata. The order Triangulata includes radiolarians with the bilaterally symmetrical skeleton composed of three crossing primary spines, which form a triangular internal framework. The main triangular framework is formed by two fused primary four-rayed spicules and the development of its spines *a*, *b*, and *i* in the same plane (Fig. 3).

The family Raphidociclicidae Afanasieva, 1999 (Middle Ordovician-Permian) is the most simply organized and probably the earliest family of the order. It is characterized by the prevailing development of one of three main spines and by the formation of a very small triangular framework.

The family Ceratoikiscidae Holdsworth, 1969 (Middle Ordovician-Carboniferous) is characterized by a skeleton with well-developed almost equilateral triangular framework, often accompanied by spongy or reticulate skeletal tissue (Pl. 1, fig. 9).

The family Lapidopiscidae Deflandre, 1958, emend. Afanasieva, 1999 (Upper Devonian-Lower Carboniferous) is distinguished by the external lamellar skeletal tissue on the spines of the equilateral triangular framework, which forms a pseudoshell.

Order Albaillellata. The order Albaillellata includes three families, i.e., Albaillellidae Deflandre, 1952 (Middle Ordovician, Upper Devonian-Permian), Follicucullidae Ormiston et Babcock, 1979 (Middle Ordovician, Upper Carboniferous-Lower Triassic), and Corythoecidae Nazarov, 1981 (Upper Devonian-Lower Permian). The order is distinguished by a primary skeleton composed of two fused primary four-rayed spicules. The spines *a*, *b*, and *i* develop in the same plane; however, the spines *a* and *i* connected by the spine *b* are shaped into the original H-frame subparallel structure at the base of the skeleton, the *a* and *i* spines are connected to form the subsagittal ring *r* in the apical part of the skeleton (Fig. 3).



Explanation of Plate 2

The structure of the internal framework and internal sphere in representatives of the class Spumellaria: (1, 6, 7) order Cancelliata and (2-5, 8) order Spongiata.

Fig. 1. *Russirad kazintsovae* Afanasieva, skeleton, x750; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, borehole Shuda-Yag-1003; rock sample no. 8 (depth 120.9-124.0 m).

Fig. 2. *Retisphaera exquisita* (Aitchison), skeleton, x455; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, borehole Shuda-Yag-1003; rock sample no. 68 (depth 73.3-73.5 m).

Fig. 3. *Spongectactinia diplostraca* (Foreman), skeleton fragment, x835; Upper Devonian, Famennian; Timan-Pechora Basin, borehole Zapadnaya Lekkeyaginskaya-65; rock sample no. 86g (depth 2460-2467 m).

Fig. 4. *Spongectactinella olafi* Afanasieva, skeleton fragment, x470; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, borehole Shuda-Yag-1003; rock sample no. 72 (depth 71.9-72.4 m).

Fig. 5. *Somphoentactinia gavrilovi* Afanasieva, skeleton, x750; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, borehole Shuda-Yag-1003; rock sample no. 8 (depth 120.9-124.0 m).

Fig. 6. *Polyentactinia zhamoidai* Afanasieva, skeleton, x240; Upper Devonian, Middle Frasnian, Domanik Formation; Timan-Pechora Basin, borehole Ukhinskaya-3B; rock sample no. 158 (depth 69.6-70.4 m).

Fig. 7. *Polyentactinia suave* (Nazarov), skeleton, x195; Upper Devonian, Famennian; Timan-Pechora Basin, borehole Zapadnaya Lekkeyaginskaya-65; rock sample no. 86g (depth 2460-2467 m).

Fig. 8. *Adamas cathedrarius* Afanasieva, skeleton, x650; Upper Devonian, Famennian; Timan-Pechora Basin, borehole Zapadnaya Lekkeyaginskaya-65; rock sample no. 86g (depth 2460-2467 m).

SPONGY RADIOLARIANS

Spongy radiolarians have a complex type of skeleton structure which is composed of three main elements: (1) the primary spicule; (2) the cyst or latticed polyhedron; and (3) one, two, or more spongy, latticed, or reticulate external spherical or spheroid skeletal envelopes. As one can easily note, spongy radiolarians are distinguished from spinaceous forms by the permanent presence of two latter elements.

The spicule is the internal primary structure (Fig. 3) and the morphological center of the skeleton. It has an n -rayed pattern (where n ranges from 4-6 to 24) and is composed of one primary four-rayed spicule (Pl. 1, figs. 6-11) or two fused primary four-rayed spicules (Pl. 2, figs. 4, 6, 7). The primary spicule is usually located in the center of the sphere; however, sometimes it is eccentrically placed. The main skeleton spines are formed on the distal end of the spicule rays. The spicule rays increase in size and branch, and merge by their distal ends to form latticed *polyhedron*, i.e., the primary skeleton envelope (Pl. 2, figs. 1-3, 5). It is still a question, whether the primary skeleton envelope is a secondary formation with reference to the spicule, or if they appeared simultaneously.

The external covering of the skeleton is composed of one, two, or three spherical envelopes, which were initially formed by interlacing apophyses of the main skeleton spines and connected to each other by numerous crossbeams, small bars, and columns. The skeletal rods composing the lattice spheres are thicker and coarser (Pl. 1, figs. 6-11) than the threads of reticulate spheres (Pl. 2, figs. 6, 7), while the spongy radiolarians are distinguished by the disorderly interlacing fine skeletal threads (Pl. 2, figs. 3-5). The surface of the spheres is usually ornamented by additional apophyses and spikes, which can bifurcate at the distal end.

The branching of apophyses on the skeleton spines gave rise to spherical radiolarians with lattice, reticulate,

and spongy skeletons (Fig. 3), assigned by us to the class Spumellaria Ehrenberg, 1875, according to the etymology of the taxon name (from the Latin *spumeus*, covered by foam).

The structure of the primary spicule and external skeleton envelope enable the splitting of the class of spongy radiolarians into four orders, i.e., Collodariata Haeckel, 1881; Echidninata Kozur, Mostler et Repetski, 1996; Cancelliata ordo nov.; and Spongiata ordo nov.

Order Echidninata (Middle-Upper Cambrian). The order comprises the earliest representatives of spongy radiolarians. Their spherical skeleton is composed of numerous randomly interlacing spicules.

Order Cancelliata. The order is distinguished by the lattice structure of the spherical envelope and is divided into two families.

The family Haplentactiniidae Nazarov, 1980 (Middle Cambrian-Lower Permian) is characterized by the simple primary spicule composed of spines crossing in one center (Pl. 1, figs. 6-11; Pl. 2, fig. 1).

The family Polyentactiniidae Nazarov, 1975 (Middle Ordovician-Silurian, Middle Devonian-Middle Triassic) is characterized by fused double primary spicule, which forms the median bar and by the finer reticulate spherical envelope (Pl. 2, figs. 6, 7).

Order Spongiata. The order combines radiolarians with spongy spherical envelopes of the skeleton; it includes two families, Spongectactiniidae Nazarov, 1975 (Middle Cambrian-Permian) and Spongopolyentactiniidae Nazarov, 1975 (Middle Cambrian-Permian) (Pl. 2, figs. 2, 3, 8).

Order Collodariata (Middle Paleogen-Recent). The order includes solitary and colonial radiolarians with multi-rayed spicule and spongy skeleton envelope.

CONCLUSIONS

To date, radiolarians with spongy, reticulate, and lattice skeletons do not have commonly accepted positions in the general radiolarian classification system. Early Paleozoic radiolarians with lattice skeleton envelope (families Secuicollactidae, Rotasphaeridae, Pseudorotasphaeridae, Haplentactiniidae, and Ehidninidae) are often assigned to the order Spumellaria along with spongy and porous forms (Nazarov and Ormiston, 1984, 1993; Nazarov, 1988; Noble, 1994; Kozur *et al.*, 1996). Radiolarians with reticulate skeleton envelope (Polyentactiniidae) were referred to the order Collodaria (Nazarov and Ormiston, 1984, 1993; Nazarov, 1988).

Dumitrica, Caridroit, and De Wever (2000) proposed a new approach to the classification of ancient (Upper Cambrian-Silurian) radiolarians with lattice skeletons. They combined these forms with spinaceous radiolarians within the new order Archaeospiculera.

The presence of homologous elements of the internal framework and its rudiments in the majority of radiolarians suggests the monophyletic origin of this group. As early as 1936, Mordukhai-Boltovskoi came to the conclusion that "the main element of the skeleton is the rods (rays) with quadrangular pyramids overlying their cones. Contacted by the facets, the pyramids form a polyhedron... that we call the "internal polyhedron" (Mordukhai-Boltovskoi, 1936, pp. 39, 40), which in turn transforms into the internal sphere. The rods of some radiolarians have branching apophyses forming the lattice of the external polyhedron, which is transformed into the external sphere. "Thus, we obtain the external polyhedron, which is a lattice enclosing the soft radiolarian body that contains the internal polyhedron" (Mordukhai-Boltovskoi, 1936, p. 40).

It is likely that the primitive skeletons of the spinaceous Aculearia and the primary spicule of the Sphaerellaria, Spumellaria, and Nassellaria are simply the crossing primary rods. Thus, "we have two radiolarian types strikingly different in appearance, but common in origin, and derivable from one and the same simple main type" (Mordukhai-Boltovskoi, 1936, p. 40). Therefore, in regard to spinaceous and spongy Paleozoic radiolarians, the monophyly means origin from the same ancestor. At the same time, the development of spongy radiolarians took some time, probably, the Middle Cambrian-Early Ordovician (Fig. 1).

In the present paper, radiolarians are treated as the phylum including two superclasses, i.e., Phaeodaria and Polycystina (Fig. 2). The superclass Polycystina is composed of the following five classes: Sphaerellaria Haeckel, 1881, Spumellaria Ehrenberg, 1875, Stauraxonaria Afanasieva, 2000, Aculearia Afanasieva, 1999, status nov., and Nassellaria Ehrenberg, 1847. The paper contains a new classification of spinaceous and spongy radiolarians. The classification of other radiolarian groups will be considered in further publications.

SYSTEMATIC PALEONTOLOGY PHYLUM

RADIOLARIA MULLERJ858

SUPERCLASS POLYCYSTINA
EHRENBERG, 1838CLASS ACULEARIA AFANASIEVA 1999,
STATUS NOV.

Diagnosis. Heteropolar and bilaterally symmetrical radiolarians with skeleton composed of several crossing spines: (1) spines crossing in one or two centers; (2) three connected spines composing subtriangular framework; (3) two long columellae connected below aperture by transverse bar, composing H-frame in basal part of skeleton and subsagittal structure *r* in apical part.

Remarks. Spinaceous radiolarians with spiny and spiny-framed skeletons were first described by Afanasieva as the separate order Aculearia (Afanasieva, 1999, 2000a, 2000b, 2002b). However, judging by the morphological peculiarities of the skeleton, spinaceous radiolarians are ranked here as the class Aculearia composed of three orders (Figs. 2, 3).

Composition. Three orders: Fasciculata, Triangulata, and Albaillellata.

Occurrence. Cambrian-Middle Triassic of Europe, Asia, North America, and Australia.

Order Fasciculata Afanasieva et Amon, ordo nov.

Etymology. From the Latin *fasdculus* (bunch).

Diagnosis. Spinaceous radiolarians with heteropolar skeleton composed of several main spines crossing in one or two centers.

Composition. Four families: Palaeoscenidiidae Riedel, 1967, emend. Nazarov, 1981, Palacantholithidae Kozur et Mostler, 1981, Xiphocycladiellidae Nazarov, 1984, and Palaeospiculidae Won in Won et Below, 1999.

Occurrence. Middle Cambrian-Lower Carboniferous of Europe, Asia, Australia, and North America; Upper Silurian-Lower Devonian of Europe and Japan; Upper Devonian-Lower Permian of Europe and North America; Lower-Middle Triassic of China.

Order Triangulata Afanasieva et Amon, ordo nov.

Etymology. From the Latin *triangulum* (triangle).

Diagnosis. Spinaceous radiolarians with bilaterally symmetrical skeletons composed of three crossing spines. Spines forming internal triangular framework. Main triangular skeletal framework composed of two fused primary four-rayed spicules and their spines *a*, *b*, and *i* positioned within same plane.

Composition. Three families: Ceratoikiscidae Holdsworth, 1969, Raphidociclicidae Afanasieva, 1999, and Lapidopiscidae Deflandre, 1958, emend. Afanasieva, 1999.

Occurrence. Middle Ordovician-Permian of Europe, Asia, Australia, and North America.

**Order Albaillellata Deflandre, 1953,
emend. Afanasieva, 1999**

Diagnosis. Bilaterally symmetrical radiolarians characterized by elongated, mainly conical shape of skeleton with pylom. Internal framework composed of two fused primary four-rayed spicules and their spines *a*, *b*, and *i* positioned in the same plane, but with original H-frame subparallel formation of spines *a* and *i* connected by *b* at base of skeleton and formation of subsagittal connection *r* between *a* and *i* spines in apical part of skeleton.

Remarks. The understanding of bilaterally symmetrical radiolarians was initiated by Deflandre (1952, 1953). In 1952, he described the new genus *Albaillella* and the new family Albaillellidae; in 1953 he established a new order, Albaillellidea. Later, a great number of bilaterally symmetrical radiolarian taxa were described from the Upper Devonian-Permian strata; they were assigned to the order Albaillellaria Deflandre, 1953, emend. Holdsworth, 1969, and distributed among the following families: Albaillellidae Deflandre, 1952, Lapidopiscidae Deflandre, 1958, Popofskyellidae Deflandre, 1964, Palaeoscenediidae Riedel, 1967, Ceratoikiscidae Holdsworth, 1969, Follicucullidae Ormiston et Babcock, 1979, and Corythoecidae Nazarov, 1981. In 1984, Nazarov and Ormiston (Nazarov and Ormiston, 1984; Nazarov, 1988) assigned the family Palaeoscenediidae Riedel, 1967, emend. Nazarov, 1981 to the order Collodaria.

Currently, on the basis of morphological characteristics of the skeleton, the order Albaillellata is believed to include three families (Figs. 2, 3) and assigned to the class Aculearia (Afanasieva, 1999, 2000a, 2000b, 2002b).

Composition. Three families: Albaillellidae Deflandre, 1952, Follicucullidae Ormiston et Babcock, 1979, and Corythoecidae Nazarov, 1981.

Occurrence. Middle Ordovician of China; Upper Devonian-Lower Triassic of Europe, Asia, and America.

**CLASS SPUMELLARIA EHRENBERG,
1875**

Diagnosis. Radial symmetrical radiolarians characterized by spherical lattice, reticulate, or spongy skeleton and internal framework represented by spicule.

Composition. Four orders: Cancelliata ordo nov., Spongiata ordo nov., Echidninata Kozur, Mostler et Repetski, 1996, and Collodariata Haeckel, 1881.

Occurrence. Middle Cambrian-Triassic and Cenozoic of Europe, Asia, Australia, and North America.

Order Cancelliata Afanasieva et Amon, ordo nov.

Etymology. From the Latin *cancelli* (lattice).

Diagnosis. Spumellarians with reticulate or lattice external skeleton envelope and internal framework composed of simple or double primary spicule.

Composition. Two families: Haplentactiniidae Nazarov, 1980 and Polyentactiniidae Nazarov, 1974.

Occurrence. Middle-Upper Cambrian of Australia and Canada (Newfoundland); Ordovician-Middle Triassic of Europe, Asia, Australia, and North America.

Order Spongiata Afanasieva et Amon, ordo nov.

Etymology. From the Latin *spongia* (sponge). **Diagnosis.** Spumellarians with spongy wall of external skeletal envelope. Internal framework composed of double primary spicule.

Composition. Two families: Spongentactiniidae Nazarov, 1975 and Spongopolyentactiniidae Nazarov, 1975.

Occurrence. Middle Cambrian-Permian of Europe, Asia, Australia, and North America.

ACKNOWLEDGMENTS

We are grateful to S.V. Rozhnov, who suggested the idea of the present study, to A.S. Alekseev, V.I. Mikhalevich, P.Yu. Parkhaev, and V.S. Vishnevskaya for their valuable comments and criticism, and to Ya.M. Kuz'mina and G.S. Rautian for help in preparation of the paper.

The study was supported by the Russian Foundation for Basic Research, project no. 01-05-64450.

REFERENCES

- Afanasieva, M.S., New Variant of Taxonomy of Paleozoic Radiolarians, *Geologiya i mineral'nye resursy evropeiskogo severo-vostoka Rossii: novye rezul'taty i novye perspektivy. Mater. XIII geol. s"ezda Resp. Komi* (Geology and Mineral Resources of the European Northeast of Russia: New Results and New Prospects. Mat. XIII Geol. Congress of Komi Republic), Syktyvkar: Inst. Geol. Komi Nauch. Tsentr Ural. Otd. Ross. Akad. Nauk, 1999, vol. 2, pp. 253-256.
- Afanasieva, M.S., *Atlas radiolyarii paleozoya Russkoi platformy* (Atlas of Paleozoic Radiolarians from the Russian Platform), Moscow: Nauchnyi Mir, 2000a.
- Afanasieva, M.S., New Radiolarians of the Orders Aculearia and Sphaerellaria from the Upper Devonian of the Timan-Pechora Region of Russia, *Paleontol. Zh.*, 2000b, no. 4, pp. 3-19.
- Afanasieva, M.S., Trend in the Evolution of Paleozoic Radiolarians, *Problemy biokhronologii v paleontologu i geologii. Tez. doki XLVIII sess. Paleontol. 0-va* (Problems of Biochronology in Paleontology and Geology: Abstr. XLVIII Session Paleontol. Soc.), St. Petersburg, 2002a, pp. 13-15.
- Afanasieva, M.S., New Classification of Paleozoic Radiolarians, *Paleontol. Zh.*, 2002b, no. 2, pp. 14-29.

- Afanasieva, M.S. and Vishnevskaya, V.S., Probable Reasons for the Development of Silicon Skeleton in Radiolarians, *Dokl. Ross. Akad. Nauk*, 1992, vol. 325, no. 3, pp. 590-596.
- Afanasieva, M.S. and Vishnevskaya, V.S., Radiolarians: Benthos and Plankton, *Paleontol. Zh.*, 1993, no. 3, pp. 3-13.
- Aitchison, J.C., Devonian (Frasnian) Radiolarians from the Gogo Formation, Canning Basin, Western Australia, *Palaeontographica, Abt. A*, 1993, vol. 228, nos. 4-6, pp. 105-128.
- Amon, E.O., To the Position of Radiolaria in System of Protozoa and Macrosystematics of Fossil Radiolarians, *I Int. Symp. Evolution of Life on the Earth*, Tomsk, 1997, pp. 31-32.
- Amon, E.O., Upper Cretaceous Radiolarians from the Ural Mountains, *Mat. Stratigr. Paleontol. Ural* (Ekaterinburg), 2000, vol. 5, pp. 1-209.
- Amon, E.O., Trait Space in Fossil Spinaceous, Spinaceous-Framc, and Spiculose Radiolarians and Possible Approaches to Their Classification, *Ezhegodnik-200! Inst. Geol. Geokhim. Ural. Old. Ross. Akad. Nauk* (Yearbook-2001 of Inst. Geol. Geochem., Ural. Div., Russ. Acad. Sci.), Ekaterinburg: Ural. Otd. Ross. Akad. Nauk, 2002a, pp. 18-25.
- Amon, E.O., Pulsating Nature of Evolution in Fossil Spinaceous Radiolarians, *Problemy biokhronologii v paleontologii i geologii. Tez. dokl. XLVIII sess. Paleontol. 0-va* (Problems of Biochronology in Paleontology and Geology. Abstr. XLVIII Session Paleontol. Soc.), St. Petersburg, 2002b, pp. 4-5.
- Beklemishev, V.N., *Osnovy sravnitel'noi anatomii bespozvonochnykh* (Fundamentals of Invertebrate Comparative Anatomy), Moscow: Sov. Nauka, 1944.
- Braun, A., Radiolarien aus dem Unter-Karbon Deutschlands, *Cour. Forsch. Inst. Senckenh.*, 1990, vol. 133, pp. 1-143.
- Cavalier-Smith, T., Kingdom Protozoa and Its 18 Phyla, *Microbiol. Rev.*, 1993, vol. 57, pp. 953-994.
- Cheng, Y.-N., Taxonomic Studies on Upper Paleozoic Radiolaria, *Taiwan Nat. Mus. Natur. Sci.*, 1986, spec. pub. no. 1, pp. 1-311.
- Chernykh, V.V., *Problema tselostnosli vysshikh taksmov. Tochka zreniya paleontologa* (Problem of Integrity of Higher Taxa from the Point of View of a Paleontologist), Moscow: Nauka, 1986.
- Corliss, J.O., The Kingdom Protista and 45 Phylla, *Biosystems*, 1984, vol. 17, pp. 87-126.
- Deflandre, G., *Albaillella* nov. gen., Radiolaire fossile du Carbonifere inferieur, type d'une lignee aberrante eteinte, *C. R. Acad. Sci.*, 1952, vol. 234, no. 8, pp. 872-874.
- Deflandre, G., Radiolaires fossiles, *Traite de Zoologie*, Paris: Masson et Gie, 1953, vol. 1, part 2, pp. 389-436.
- Deflandre, G., Sur quelques nouveaux types de Radiolaires *Polycystines viseens*, d'attribution systematique ambigue, certains evoquant a la fois des plectellaires et des spumel-laires, *C. R. Acad. Sci.*, 1973, vol. 276, pp. 289-293.
- Dmitriev, G.A. and Potapova, M.S., Doctrine of Symmetry As the Genera) Approach to the Study of Patterns in the Development of the Earth, in *Puti poznaniya Zemli* (Approaches to the Study of the Earth), Moscow: Nauka, 1971, pp. 153-171.
- Dumitrica, P., Triassic Palaeoscieniidae and Entactiniidae from Vicentinian Alps (Italy) and Eastern Carpathians (Romania), *Dari Seama Medinteler. Inst. Geol. Geofiz.*, 1978, vol. 64, part 3, pp. 39-54.
- Dumitrica, P., Systematics of the Radiolarians Sphaerellaria, in *Morfologiya, ekologiya i evolyutsiya radiolyarii* (Morphology, Ecology, and Evolution of Radiolarians), Leningrad: Nauka, 1984, pp. 91-102.
- Dumitrica, P., Caridroit, M., and De Wever, P., Archaeospicularia, ordre nouveau de radiolaires: une nouvelle etape pour la classification des radiolaires du Paleozoique inferieur, *C. R. Acad. Sci.*, Paris: Sci. Terre et Planetes, 2000, vol. 330, pp. 563-569.
- Foreman, H.P., Upper Devonian Radiolaria from the Huron Member of the Ohio Shale, *Micropaleontology*, 1963, vol. 9, no.3, pp. 267-304.
- Francois, F., Deep Sea Biogenic Silica: New Structural and Analytical Data from Infra-Red Analysis Geological Implications, *Terra Nova*, 1989, vol. 1, no. 3, pp. 267-273.
- Friend, J.K. and Riedel, W.R., Cenozoic Orosphaerid Radiolarians from Tropical Pacific Sediment, *Micropaleontology*, 1967, vol. 13, no. 2, pp. 217-232.
- Haecckel, E., Report on the Radiolaria Collected by H.M.S. "Challenger" during the Years 1873-1876, *Rept. Sci. Results Voy. "Challenger."* *Zool. Edinburgh*, 1887, vol. 18, parts 1-2, pp. 1-1803.
- Holdsworth, B.K., Paleozoic Radiolaria: Stratigraphic Distribution in Atlantic Bordolands, *Stratigraphic Micropaleontology of Atlantic Basin and Bordolands*, Amsterdam: Elsevier, 1977, pp. 167-184.
- Kozur, H. and Mostler, H., Beitrage zur Erforschung der mesozoischen Radiolarien: Teil. 4, *Geol. Palaontol. Mitt. Innsbruck. Sonderbd.*, 1981, vol. 10, pp. 1-208.
- Kozur, H., Mostler, H., and Repelski, J.E., Well-Preserved Tremadocian Primitive Radiolarian from the Wind-Fall Formation of the Antelope Range, Eureka County, Nevada, USA, *Geol. Palaontol. Mitt. Innsbruck. Sonderbd.*, 1996, vol. 21, pp. 245-271.
- Krylov, M.V., Dobrovolskii, A.A., Issi, I.V., et al., New Concept of the System of Unicellular Animals, in *Printsipy postroeniya makrosistemy odnokletochnykh zhivotnykh* (Principles of the Construction of the Macrosystem of Unicellular Animals), Leningrad: Zool. Inst. Akad. Nauk SSSR, 1980, pp. 122-132.
- Kusakin, O.G. and Drozdov, A.A., *Filema organicheskogo mira* (Phylem of the Organic World), St. Petersburg: Nauka, 1994, part 1.
- Levine, N.D., Corliss, J.O., Cox, E.F.G., et al., A Newly Revised Classification of the Protozoa, *J. Protozool.*, 1980, vol. 27, pp. 37-58.
- Margulis, L., The Classification and Evolution of Prokaryotes and Eukaryotes, *Handbook of Genetics*, 1974, vol. 1, no. 4, pp. 1-41.
- Mikryukov, K.A., Modern State of the Sarcodine System, in *Radiolyariologiya na rubezhe tysyacheletii: itogi i perspektivy. Mater. 11 sem. po radiolyariyam* (Radiolarology at the Boundary of Millennium: Results and Prospects- Mat. 11 Workshop on Radiolarians), St. Petersburg-Moscow, 2000, pp. 46-47.
- Mordukhat-Boltovskoi, D.D., Geometry of Radiolarians, *Uch. Zap. Rostov. Univ.*, 1936, no. 8, pp. 1-91.
- Nazarov, B.B., Radiolarians from the Lower Horizons of the Batenevskii Mountain Range, in *Tr. Inst. Geol. Geofiz. Sib. Otd. Akad. Nauk SSSR* (Novosibirsk), 1973, vol. 49 (Problems of Paleontology and Biostratigraphy of the Lower Cambrian of Siberia and Far East), pp. 5-13.

- Nazarov, B.B., Albaillellidae and Palaeoscenediidae from Upper Devonian Deposits of the Southern Ural Mountains, *Tr. Vses. Geol. Inst., Nov. Ser.* (St. Petersburg), 1974, vol. 226 (Systematics and Stratigraphic Significance of Radiolarians), pp. 41-47.
- Nazarov, B.B., Radiolarians from the Lower-Middle Paleozoic of Kazakhstan (Methods, Taxonomy, and Stratigraphic Significance), *Tr. Geol. Inst. Akad. Nauk SSSR* (Moscow), 1975, vol. 275, pp. 1-202.
- Nazarov, B.B., Paleozoic Radiolarians, *Doctoral (Geol.-Mineral.) Dissertation*, Moscow: Geol. Inst. Akad. Nauk SSSR, 1984.
- Nazarov, B.B., *Radiolyarii paleozoya. Prakticheskoe rukovodstvo po mikrofaune SSSR* (Paleozoic Radiolarians: Practical Manual on the Microfauna of the USSR), Leningrad: Nedra, 1988, vol. 2.
- Nazarov, B.B. and Ormiston, A.R., Upper Devonian (Frasnian) Radiolarian Fauna from the Gogo Formation, Western Australia, *Micropaleontology*, 1983, vol. 29, no. 4, pp. 454-466.
- Nazarov, B.B. and Ormiston, A.R., Possible System for Paleozoic Radiolarians, in *Morfologiya, ekologiya i evolyutsiya radiolyarii* (Morphology, Ecology, and Evolution of Radiolarians), Leningrad: Nauka, 1984, pp. 64-87.
- Nazarov, B.B. and Ormiston, A.R., Radiolarian from Late Paleozoic of the Southern Urals, USSR, and West Texas, USA, *Micropaleontology*, 1985, vol. 30, no. 1, pp. 1-54.
- Nazarov, B.B. and Ormiston, A.R., Biostratigraphic Potential of Paleozoic Radiolarians, in *Radiolyarii v biostratigrafii* (Radiolarians in Biostratigraphy), Sverdlovsk: Ural. Otd. Akad. Nauk SSSR, 1990, pp. 3-25.
- Nazarov, B.B. and Ormiston, A.R., New Biostratigraphically Important Paleozoic Radiolaria of Eurasia and North America, *Micropaleontology*, 1993, spec. no. 6 (Radiolaria of Giant and Subgiant Fields in Asia), pp. 22-60.
- Nazarov, B.B. and Petrushevskaya, M.G., Class Radiolaria: Radiolarians, in *Mikropaleontologiya: Uchebnyk* (Micropaleontology: Manual), Moscow: Mosk- Gos- Univ., 1995, pp. 111-158.
- Nazarov, B.B. and Popov, L.E., Stratigraphy and Fauna of Siliceous-Carbonate Deposits from the Ordovician of Kazakhstan (Radiolarians and Hingeless Brachiopods), *Tr. Geol. Inst. Akad. NaukSSSR* (Moscow), 1980, vol. 331, pp. 1-190.
- Nazarov, B.B. and Rudenko, V.S., Some Bilaterally Symmetrical Radiolarians from the Late Paleozoic of the Southern Ural Mountains, *Vopr. Mikropaieontol.*, 1981, no. 24, pp. 129-139.
- Noble, P.J., Silurian Radiolarian Zonation for the Caballos Novaculite, Marathon Uplift, West Texas, *Bull. Am. Paleontol.*, 1994, no. 106, pp. 1-55.
- Obut, O.T. and Iwata, K., Lower Cambrian Radiolaria from the Gorny Altai (Southern West Siberia), *Novosti Paleontol. Stratigr.*, 2000, nos. 2-3, pp. 33-38.
- Petrushevskaya, M.G., Relationships between the Nassellaria and Other Orders of the Subclass Radiolaria, *Zool. Zh.*, 1969, vol. 48, no. 11, pp. 1597-1607.
- Petrushevskaya, M.G., The Radiolarians Nassellaria in the Plankton of the World Ocean, in *Radiolyarii Mirovogo okeana. Issledovaniya fauny morei: 9 (17)* (Radiolarian of the World Ocean: Investigation of the Marine Fauna: 9 (17)), Leningrad: Nauka, 1971, pp. 5-294.
- Petrushevskaya, M.G., New Variant of the Polycystina System, in *Iskopaemye i sovremennyye radiolyarii* (Extinct and Extant Radiolarians), Leningrad: Zool. Inst. Akad. Nauk SSSR, 1979, pp. 101-118.
- Petrushevskaya, M.G., On the Classification of the Radiolarians Polycystina, in *Morfologiya, ekologiya i evolyutsiya radiolyarii* (Morphology, Ecology, and Evolution of Radiolarians), Leningrad: Nauka, 1984, pp. 124-148.
- Petrushevskaya, M.G., *Radiolyariyevyi analiz* (Radiolarian Analysis), Leningrad: Nauka, 1986.
- Popofsky, A., Die Nasselarien des Warmwassergebietes, *Dtsch. Sudpolar-Expedition 1901-1903*, Berlin, 1913, vol.14, pp. 217-416.
- Protisty; Rukovodstvo po zoologii* (Protista: Handbook of Zoology), St. Petersburg: Nauka, 2000, vol. 1.
- Riedel, W.R., Class Actinopoda: Protozoa, *The Fossil Record*, London, 1967, pp. 291-298.
- Shafranovskii, I.I., *Simmetriya v prirode* (Symmetry in Nature), Leningrad: Nedra, 1968.
- Tochilina, S.V., *Problemy sistematiki Nassellaria. Biokhimicheskie osobennosti. Evolyutsiya* (Problems of the Nassellaria Taxonomy: Biochemical Features, Evolution), Vladivostok: DaFnevost. Otd. Ross. Akad. Nauk, 1997.
- Won, M.-Z., Review of Family Entactiniidae (Radiolaria), Taxonomy and Morphology of Entactiniidae in the Late Devonian (Frasnian) Gogo Formation, Australia, *Micropaleontology*, 1997, vol. 43, no. 4, pp. 333-369.
- Won, M.-Z. and Below, R., Cambrian Radiolaria from the Georgina Basin, Queensland, Australia, *Micropaleontology*, 1999, vol. 45, no. 4, pp. 325-363.
- Won, M.-Z. and Iams, W.J., Late Cambrian Radiolarian Faunas and Biostratigraphy of the Cow Head Group, Western Newfoundland, *J. Paleontol.*, 2002, vol. 76, no. 1, pp. 1-33.
- Yao, A. and Kuwahara, K., Permian and Triassic Radiolarian Assemblages from the Yangzi Platform, in *Biotic and Geological Development of the Paleo-Tethys in China*, Peking: Peking Univ. Press, 1999, pp. 1-16.
- Yao, A. and Kuwahara, K., Permian and Triassic Radiolarians from the Southern Guizhou Province, China, *J. Geosci. Osaka City Univ.*, 2000, vol. 43, art. 1, pp. 1-19.
- Zettler, L.A., Sogin, M.L., and Caron, D.A., Phylogenetic Relationships between the Acantharea and the Polycystinea: A Molecular Perspective on Haeckel's Radiolaria, *Proc. Natl. Acad. Sci. USA*, 1997, vol. 94, pp. 11 411-11426.

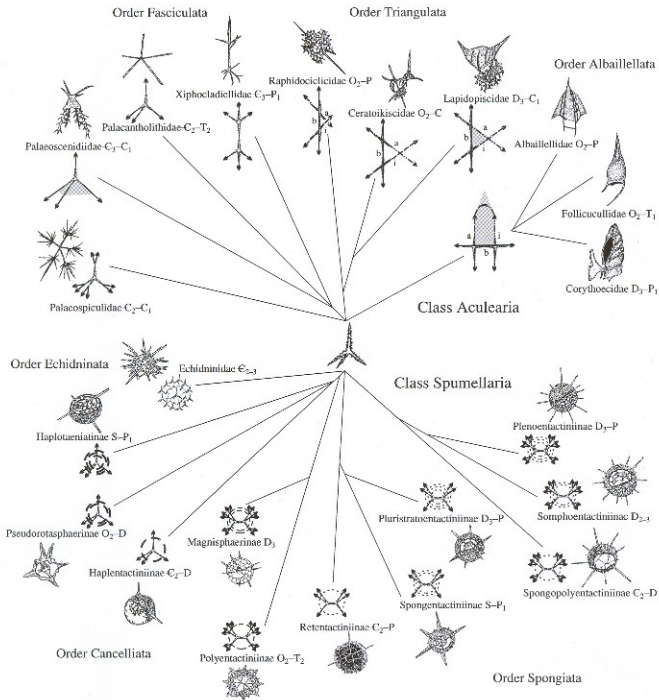


Fig. 3. Pattern of skeleton formation in spinaceous radiolarians of the class Aculearia and latticed and spongy skeletons of spherical radiolarians of the class Spumellaria.