

# Biotic Crises and Stages of Radiolarian Evolution in the Phanerozoic

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**Abstract**—The questions of ecology and taphonomy of radiolarians are reviewed and reexamined. In Recent oceans and seas, the major part of the “radiolarian rain” (dead individuals) comes from the layer of the water column which is not deeper than 500 m; therefore, the bottom radiolarian thanatocenoses and taphocenoses are formed in all oceanic zones, including the coastal and central oligotrophic regions of oceans. However, radiolarians should not be regarded as indicators of exclusively deepwater oceanic conditions. The crucial moments in the evolution of radiolarians at the major Phanerozoic boundaries are recognized. A dynamic model of cyclic development of radiolarians in the Phanerozoic is proposed and four phases and nine stages in their evolution are recognized. The absence of an outburst of radiolarian biodiversity in the Holocene is shown. Many great extinctions of radiolarians occurred at the boundaries between seasons of galactic years.

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## INTRODUCTION

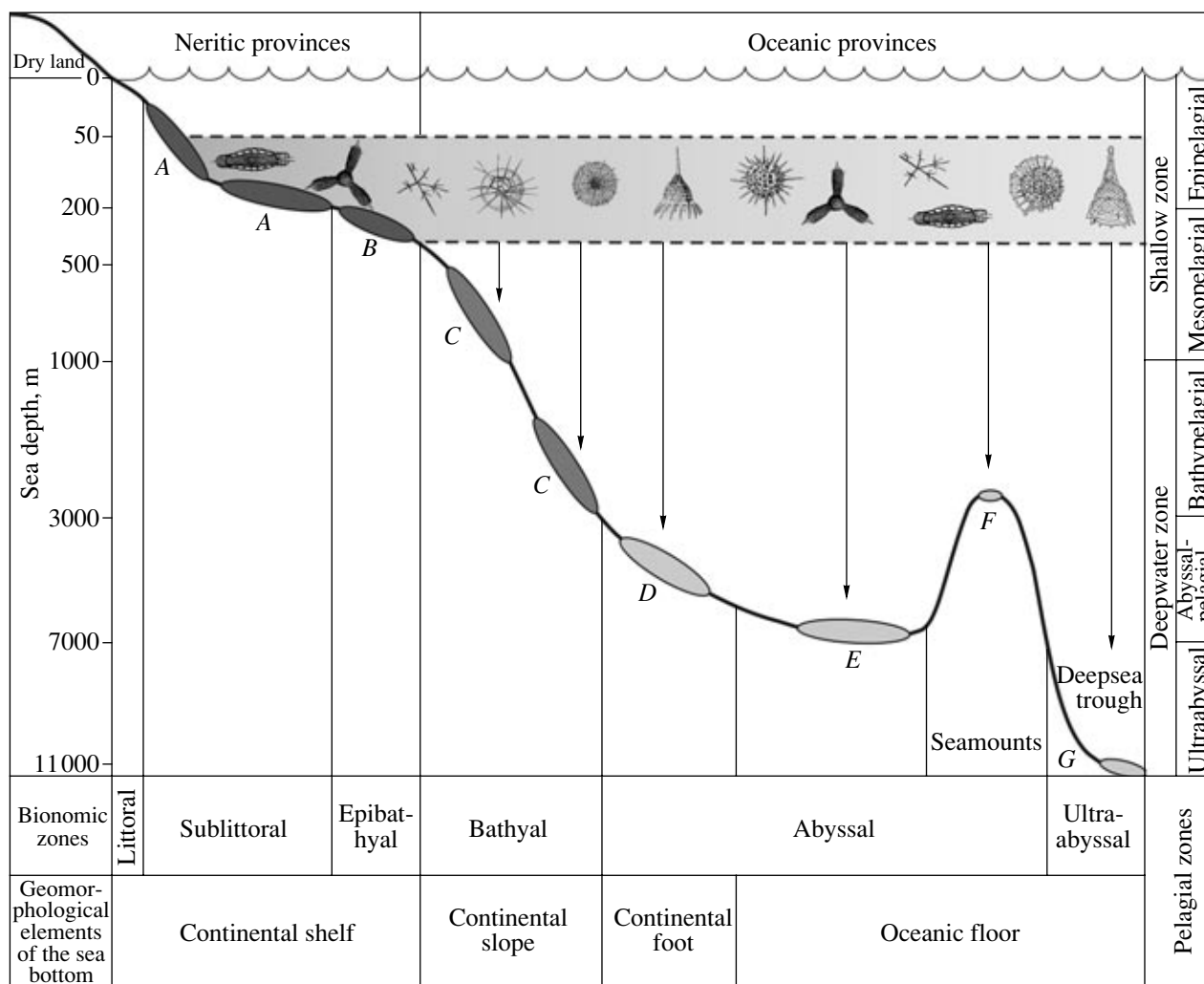
Radiolarians are one of the earliest groups of unicellular microorganisms inhabiting various water areas of the world ocean from the Early Cambrian to the present time. Throughout this long history, the following major biological features of radiolarians remained invariable: (1) existence in basins with predominantly normal oceanic salinity; (2) planktonic mode of life; (3) heterotrophic feeding type; (4) dependence on the concentration of silica in seawater; (5) symbiosis with unicellular algae, which restricts the range of radiolarians basically to the photic zone of the water column; and (6) occurrence mostly in the upper layers of the water column, where the zooplankton feeds on intensely producing phytoplankton and bacteria (Afanasieva et al., 2005b, 2005c).

Radiolarians inhabit basins with a normal oceanic salinity (30–32 to 38–40‰). They are very scarce or absent in conditions of low salinity (below 30–32‰), in coastal waters (Kling, 1978; Anderson, 1983; Caron and Swanberg, 1990; Anderson et al., 2002). Radiolarians have been found neither in land-locked seas (Black and Caspian seas) nor in marginal seas with low salinity, such as the White and Baltic seas (Kruglikova, 1995). At the same time, data on the presence of living radiolarians in brackish waters of estuaries of large rivers are of special interest (Boltovskoy, 1998).

Changes in water temperature have different effects on bioproductivity and species diversity of radiolarians.

Radiolarians originally emerged under tropical conditions; therefore, the bulk of their species are thermophilic (up to 600 species, at the mean productivity more than 100–200 thousand individuals per g) (Kruglikova, 1995, 2003; Boltovskoy, 1998). The cold-water conditions and absence of sufficient illumination at significant depths sharply reduce the number of tropical radiolarians. In conditions of low temperatures, from –2°C to +13°C, the relative diversity of the cold-water radiolarian fauna, with a decrease in mean productivity (to several dozen or, occasionally, ten thousand individuals per g) is recorded. In the Arctic basin, more than 70 species are recorded; in the Norwegian Sea, there are about 70 species; in the Sea of Okhotsk, about 100; in the Antarctic Region, about 100; and in the arctoboreal zone of the Pacific Ocean, about 200 species. Thus, radiolarian associations may have a cold-water, warm-water, and intermediate appearances, which are characteristic of peculiar to arctoboreal, tropical, equatorial, and Antarctic zones of the ocean (Petrushevskaya, 1986; Kruglikova, 1990; Stepanjants et al., 2004).

In the modern oceans, living radiolarians inhabit all bionomic zones. They occur at all levels from the surface to the greatest depths (Petrushevskaya, 1986; Kling and Boltovskoy, 1995; Abelman and Gowing, 1997; Boltovskoy, 1998, 1999; Zasko, 2004). The upper, well-illuminated water layers, 0–75 m of depth, is predominantly inhabited by Acantharia. Representatives of Radiolaria are abundant in the range of depths



**Fig. 1.** Taphocenoses of radiolarians and vertical zonation of oceans and open seas: (A–G) taphocenoses of radiolarians; color designates the interval of the water column with the greatest bioproductivity of radiolarians; out of scale.

from 50 m to the maximum depths. Polycystines are most abundant in the interval of 50–400 m (Fig. 1). Phaeodaria inhabit the interval from 100–200 m to the deepest waters. Many polycystines are probably more shade-tolerant because of the relatively low content of zooxanthellae compared to members of the phylum Acantharea. However, the maximum photosynthesis of planktonic algae in tropics is achieved at the depth of 50–200 m. These conditions are most favorable for Polycystina. Polycystines that dwell below 200 m of depth and phaeodarians that occur from 100 m to the deepest waters lack zooxanthellae.

#### TAPHONOMY OF RADIOLARIANS

The distribution of radiolarians in the sediment depends on a number of factors: (1) various currents (surface, subsurface, bottom); (2) vertical and lateral transport; (3) general and selective dissolution; (4) transportation and redeposition of the skeletons and

their fragments; (5) integration of surface and bottom species in the sediment; (6) different bioproductivity of species; (7) variation in the seasonal dynamics of the population size; (8) predation on radiolarians and total and partial destruction of the shells; and (9) accumulation of organic matter in a form of so-called sea snow. (Afanasieva et al., 2005b, 2005c).

In the modern ocean, less than 4% of the silica contained in opaline skeletons reaches the sea bottom. Most radiolarians dissolve in surface and subsurface waters at depths up to 1000 m, and siliceous microorganisms are exposed to further dissolution, since the bottom waters are also unsaturated with silica (Berger, 1968a, 1968b; Kennett, 1982).

Radiolarians of the subphylum Pheodaria are distinguished by their very fragile skeleton, which is dissolved immediately after the death of the organisms and extremely rarely reaches the sea bottom. Thus, they almost completely absent from the fossil record, and

their geological history is difficult to reconstruct (Petruševskaya, 1986). Isolated finds of Pheodaria are known since the Late Cretaceous (Bragina, 2003).

Radiolarians of the subphylum Polycystina are more resistant to postmortem dissolution and are usually well-preserved in fossils. Hence, the thanatocenoses, taphocenoses, and oryctocenoses of radiolarians are mostly composed of polycystine radiolarians. Moreover, the thanatocenoses and taphocenoses of polycystine radiolarians are mostly formed of populations from the biotopes that are above 500 m of depth (Fig. 1), irrespective of the depth of the basin in this area. Thus, the main *radiolarian rain* comes from a 500-m-deep water column. Therefore, radiolarians cannot be taken as indicators of exclusively deep water facies.

Individual modern territories of accumulation of radiolarian mud are connected with the zones of faults and ozone anomalies. The area of the Eastern Pacific Rift Belt and ozone anomaly above the Eastern Pacific Uplift is very characteristic in this respect (Syvorotkin, 1994). The distribution of radiolarians in subtropical, tropical, and equatorial surface sediments of the eastern Pacific is connected with these areas (Molina-Cruz, 1977); the equatorial association is connected with the influx of subtropical surface currents and the South Equatorial Current; the equatorial deepwater association is connected with a weakening of trade winds and the South Equatorial Current (El Niño); the association of the Peruvian Current is connected with the Peruvian Upwelling; and the association of the Chilean Current is connected with the water temperature in the northern part of the Chilean Current.

The distribution of radiolarians in the deposits of ancient basins demonstrates that, in the geological past, the water areas close to, or at a relatively small distance from, the continents provided the most favorable conditions for radiolarians (in contrast to the pelagic or central zones of oceans). This conclusion is supported by the abundant radiolarian occurrences in the coastal western zone of the epicontinental Late Cretaceous West Siberian Sea; in the coastal basin of the Ural Foredeep in the Late Carboniferous–Early Permian; in conditions of outer shelf of the epicontinental Middle Frasnian Domanik Sea of the Timan–Pechora Basin; in the marginal sea near the South Ural Land in the Late Devonian.

Thus, the richest and most diverse oryctocenoses are composed of radiolarians that dwelt under most favorable conditions: (1) in sublittoral and coastal areas located not far from the continents; (2) in places with a system of currents; (3) under the influence of the upwelling and El Niño; and (4) in regions of increased bioproductivity within the equatorial and tropical zones, above the deep faults and zones of rift systems.

## STAGES OF RADIOLARIAN EVOLUTION

The evolution of radiolarians in the geological past showed a periodic pattern, so that the appearance of new taxa was followed by a peak, and subsequent extinction. The origin, major patterns of evolution, and the great biotic crises in the development of radiolarians in the Phanerozoic were tightly connected with the geological history of the Earth. The general trends in the evolution of the Earth from the Precambrian to the Recent included the increasing contrast of the relief of the planet and development of the basins from shallow-water epicontinental seas to the modern oceans (Timofeev and Kholodov, 1984; Khvorova, 1984). Glaciations and global falls in temperature in the Paleozoic and Cenozoic and also the warm climate of the Mesozoic played important role in the evolution of radiolarians (Chumakov, 2001; Dobretsov, 2003).

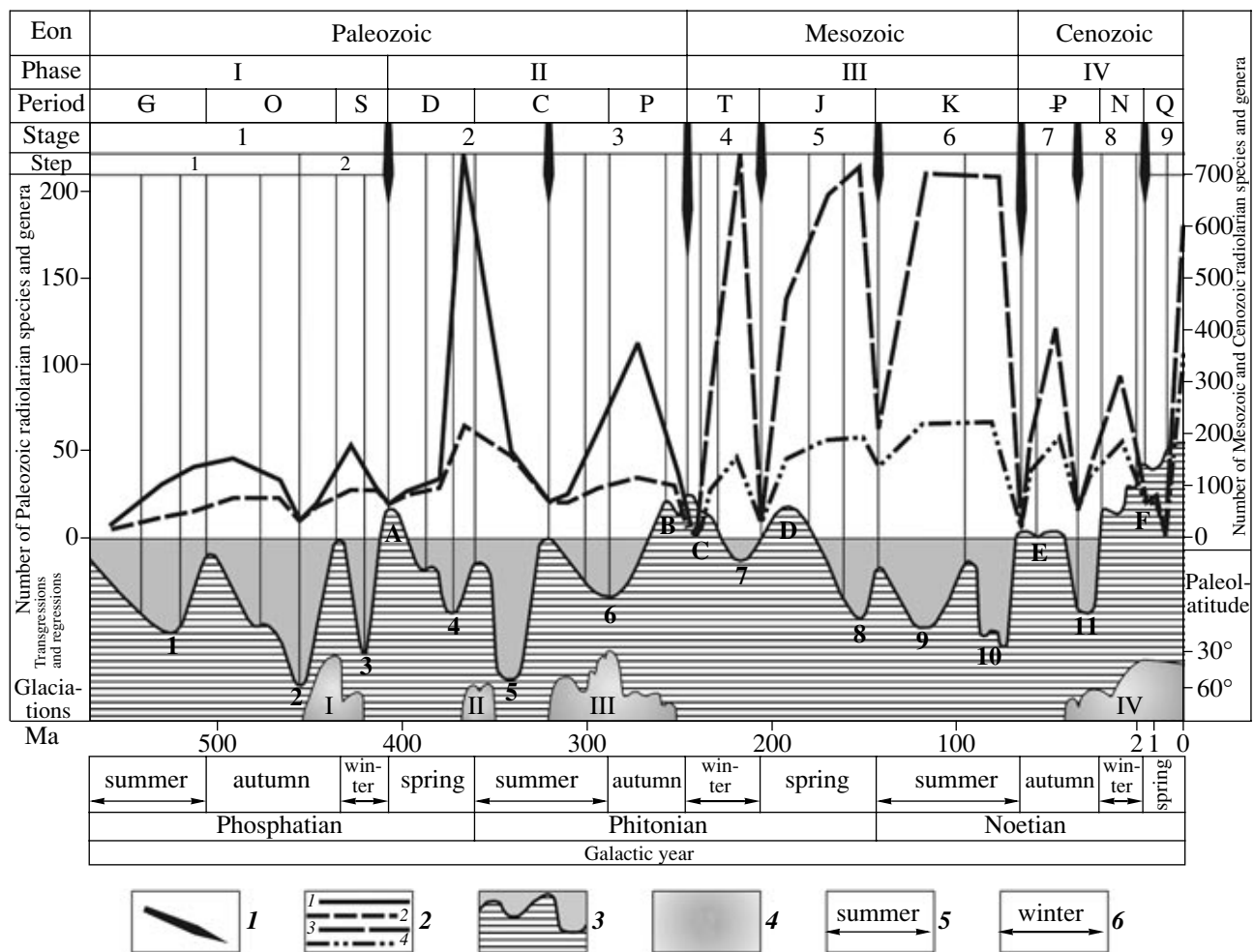
During the last 30 years, comprehensive studies of the temporal dynamics of radiolarian diversity were performed in Russia and other countries. However, the problems of the stepwise nature of the development of radiolarians of the subphylum Polycystina, changes in their biodiversity in time, and various aspects of extinctions were very rarely discussed in the specialist literature (Table 1).

Lipman (1979) was one of the first to recognize four cycles in the evolution of radiolarians: Paleozoic, Mesozoic, Paleogene, and Recent. The cycles are subdivided into stages and substages (Lipman, 1979). Zhamoida (1981) offered a new scheme of for the development of radiolarians throughout the Phanerozoic and recognized nine stages. Based on comprehensive analysis of the evolution of radiolarians, Nazarov (1981; 1988) and Nazarov and Ormiston (1985, 1986, 1993) recognized three stages of the development of radiolarians in the Paleozoic. Bragin et al. (1999) analyzed the evolution and changes in the taxonomic composition of radiolarians in the Mesozoic and established the major crucial boundaries in the development of the Mesozoic radiolarians. De Wever et al. (2001) indicated only the boundaries of the main crises in the development of radiolarians.

The analysis of changes in radiolarian biodiversity in the Phanerozoic and discussion of questions concerning the formation of radiolarian skeletons in different periods of the geological time disclosed the patterns of appearance and disappearance of orders, families, and genera at the basic boundaries of their development. In the general dynamic model of cyclic development of radiolarians in the Phanerozoic, individual simple cycles (steps) are combined into cycles of a higher order (stages), which, in turn, compose the major phases in the evolution of radiolarians in the Phanerozoic. In the Phanerozoic evolution of radiolarians, we recognized nine stages and four major evolutionary phases (Fig. 2; Table 1) (Afanasieva et al., 2005a, 2005b).

**Table 1.** History of the recognition of cycles, phases, stages, and substages in the evolution of radiolarians

Period	Epoch		Lipman, 1979		Zhamoïda, 1981		Nazarov, 1984, 1988; Nazarov and Ormiston, 1985, 1986, 1993		Bragin et al., 1999		Afanasieva, 2000a; Agarkov, 2000; Afanasieva and Amon, 2003		De Wever et al., 2001		Afanasieva et al., 2004, 2005a, 2005b			
	Stage	Substage	Stage	Substage	Stage	Substage	Stage	Substage	Stage	Substage	Stage	Substage	Major boundaries of evolutionary crises	Phase	Stage			
Quaternary	Holocene				IX	Late Miocene – Quaternary								IV Cenozoic	9. Quaternary			
	Pleistocene																	
Neogene	Eopleistocene				VIII	(Middle?) Late Eocene – Early (Late?) Miocene								Oligocene	8. Oligocene – Pliocene			
	Pliocene																	
	Miocene																	
Paleogene	Oligocene				VII	Maastrichtian – Early Eocene								Paleocene	7. Paleocene – Eocene			
	Eocene																	
Paleocene																		
Cretaceous	Late				VI	2. Coniacian – Campanian								Cretaceous	6. Cretaceous			
	Early																	
Jurassic	Late				V	Middle Jurassic – Valanginian								Cretaceous	3. Early Cretaceous (Aptian) – Late Cretaceous			
	Middle																	
	Early																	
Triassic	Late				IV	2. Early Jurassic								Jurassic	5. Jurassic			
	Early																	
Permian	Late				III	Late Permian – Middle Triassic								Triassic	4. Triassic			
	Early																	
Carboniferous	Late				II	2. Late Carboniferous – Early Permian								Permian	3. Middle Carboniferous – Permian			
	Middle																	
	Early																	
Devonian	Late				I	1. Middle Devonian – Middle Carboniferous								Permian	3. Middle Carboniferous – Permian			
	Middle																	
	Early																	
Silurian	Late				I	2. Silurian – Early Devonian								Permian	3. Middle Carboniferous – Permian			
	Early																	
Ordovician	Late				I	1. Cambrian – Ordovician								Permian	3. Middle Carboniferous – Permian			
	Middle																	
	Early																	
Cambrian	Late				I	1. Cambrian – Ordovician								Permian	3. Middle Carboniferous – Permian			
	Early																	



**Fig. 2.** Changes in the taxonomic diversity of radiolarians and the main events in the geological history of Earth in the Phanerozoic: (1) mass extinctions of radiolarians (Polycystina); (2) changes in the taxonomic diversity of radiolarians: (1) Paleozoic species, (2) Paleozoic genera, (3) Mesozoic and Cenozoic species, and (4) Mesozoic and Cenozoic genera; (3) transgressions: (1) Cambrian, (2) Ordovician, (3) Silurian, (4) Middle–Late Devonian, (5) Early Carboniferous, (6) Late Carboniferous–Early Permian, (7) Late Triassic, (8) Middle–Late Jurassic, (9) Early Cretaceous, (10) Late Cretaceous, and (11) Oligocene, geotectonic epochs: (A) Late Silurian–Early Devonian, (B) Permian, (C) Triassic, (D) Early Jurassic, (E) Paleocene–Eocene, and (F) Neogene–Quaternary (after Monin, 1977); and (4) glaciations (after Chumakov, 2001): (I) Late Ordovician–Early Silurian, (II) end of the Late Devonian–beginning of the Early Carboniferous, (III) Middle Carboniferous–beginning of the Late Permian, and (IV) Middle Eocene–Quaternary; (5–6) seasons of galactic year (after Kulikova and Kulikov, 2000).

### Phase I: Early Paleozoic

According to the presently available data, during the Early Paleozoic phase, radiolarians played a minor role in the ecosystem of shallow epicontinental marine basins and sedimentation processes. At the same time, it is possible that, in the Cambrian, there were three regional centers of origin and distribution of radiolarians; they were situated in Altai–Kazakhstan, Australia, and Newfoundland and influenced each other, providing immigrant taxa (Nazarov, 1973, 1974, 1975; White, 1986; Iwata et al., 1997; Won and Below, 1999; Obut and Iwata, 2000; Won and Iams, 2002).

**Stage 1: Cambrian–Silurian.** At the beginning of the Early Paleozoic, all presently known morphotypes of radiolarians emerged and became widespread (Afa-

nasieva and Amon, 2003; Afanasieva et al., 2005b). At the first stage of their evolution, radiolarians as if tested various skeletal alternatives:

- (1) various spiny forms of the class Aculearia appeared;
- (2) spongy layer were formed in the skeletons of radiolarians of the class Spumellaria;
- (3) the first bilaterally symmetrical stauraxonic radiolarians of the class Stauraxonaria appeared;
- (4) distinct morphotypes of radiolarians of the class Sphaerellaria with numerous spines (order Anakrusata) appeared;
- (5) spherical porous Sphaerellaria, with a massive internal framework in the shape of a hollow sphere and

rodlike spines (order Inaniguttata) were widely distributed;

(6) there was a relatively slow evolution of porous Sphaerellaria with internal framework in the shape of a light spicule and three-bladed spines in the order Entactiniata;

(7) radiolarians with a pylome (order Pylomariata, class Nassellaria) became widespread; and

(8) the internal spheres in the skeletons of all spherical, pylomate, and stauraxonic radiolarians began to develop.

At the first stage of the evolution of radiolarians, the overwhelming majority (60) of higher taxa began to develop, including 5 classes, 11 orders (out of 12 orders known in the Paleozoic), 3 superfamilies, 24 families, and 17 subfamilies. In the Cambrian–Silurian, 60 radiolarian genera are known; of these 22 appeared in the Cambrian (Fig. 2). In the Cambrian–Silurian, 223 radiolarian species are recorded. The rate of speciation of radiolarians at the first stage of evolution ranged from 0.3 to 3.0 species/m.y. (on average 1.4 species/m.y.).

The first stage consists of two steps of radiolarian development, i.e., (1) Cambrian–Middle Ordovician, (2) Late Ordovician–Silurian (Fig. 2).

At the first step, the earliest radiolarians emerged. The earliest, Early Cambrian Polycystina are represented by only four genera of two orders of the class Sphaerellaria (Nazarov, 1973; Obut and Iwata, 2000) and the first problematic remains of spiny and pylomate radiolarians (Nazarov, 1973, 1974, 1988). The diversity of radiolarians from the Middle Cambrian increased to 31 species and 12 genera (Nazarov, 1974, 1975, 1988; White, 1986; Won and Below, 1999). They belong to seven orders of four classes: Nassellaria (represented in the Paleozoic by the order Pylomariata), Spumellaria, Sphaerellaria, and Aculearia, existing up to the present. In the Late Cambrian, the diversity of radiolarians increased to 41 species and 16 genera from eight orders (Nazarov, 1974, 1975; Iwata et al., 1997; Won and Iams, 2002; Won et al., 2005). At that time, a new class, Stauraxonaria, descendants of which have survived until now, appeared.

At the first and second developmental steps, the first outbursts of taxonomic diversity of radiolarians were registered: in the Early Ordovician, there were 47 species of 23 genera; in the Early Silurian, 53 species of 30 genera (Fig. 2). The rate of speciation at the first developmental step ranged from 0.3 to 2.8 species/m.y., and at the second step, from 0.4 to 3.0 species/m.y.

The first crucial point in the development of radiolarians was at the Silurian–Devonian boundary (Fig. 2). A marine regression and long geocratic epoch at the end of the Silurian and beginning of the Devonian resulted in the almost complete disappearance of all typically Early Paleozoic taxa: members of the orders Echidninata and Anakrusata and radiolarians with an internal framework in the shape of a hollow sphere from the orders Pylomariata and Inaniguttata became

extinct. At the Silurian–Devonian boundary, a complete renewal of the taxonomic composition of radiolarians took place.

### *Phase II: Late Paleozoic*

The Late Paleozoic Phase was the time of the most favorable conditions for the existence and development of radiolarians in the Paleozoic. A fantastic diversity of skeletons of Paleozoic radiolarians appeared precisely during the Devonian–Permian.

**Stage 2: Devonian–Early Carboniferous.** A large biotic crisis at the beginning of the Devonian was marked by a significant extinction of 66.7% of genera and 91.0% of species of the Early Paleozoic radiolarians, and of 60 genera known from the Cambrian–Silurian, only 20 survived at the beginning of the Early Devonian (Fig. 2).

The second stage of evolution was marked by the maximum taxonomic diversity of radiolarians (67 higher taxa): 5 classes, 10 orders, 3 superfamilies, 23 families, and 26 subfamilies. In the Devonian–Early Carboniferous, there are 19 new higher taxa appeared: the order Radiiformata, superfamily Popofskyelloidea, 5 families (Spongopolyentactiniidae, Popofskyellidae, Corythoecidae, Tormentidae, and Latentifistulidae) and 12 subfamilies.

In the Devonian–Early Carboniferous, 89 genera and 299 species of radiolarians have been recorded. In the Late Devonian, an explosive radiation of radiolarians occurred; the taxonomic composition increased to 67 genera, 37 of which appeared for the first time. The rate of speciation ranged from 0.3 to 15.8 species/m.y., with an average rate of 3.3 species/m.y.

In the Devonian and Early Carboniferous, spherical, spiny, and many bilaterally symmetrical radiolarians intensely transformed their skeletons. Spiny Aculearia were widespread at that time. The orders Fasciculata and Triangulata were very diverse. The bilaterally symmetrical Albaillellata started their evolution.

The evolution of the class Stauraxonaria was relatively slow. Diverse discoidal forms of the family Palaeodiscidae dominated. In the Early Carboniferous, the first radiolarians of the subfamilies Tormentinae and Latentifistulinae appeared. The spongy Spumellaria were characteristic of that time; latticed skeletons belonging to the order Cancelliata and diverse light spongy skeletons of the order Spongiata were widespread. Rapid evolutionary transformations of the spherical porous Sphaerellaria occurred. The Devonian and, especially, the Early Carboniferous were the times of flourishing of Pylentonemoidea

The second stage of the evolution of radiolarians is characterized by one general developmental pattern of the major skeletal elements in the porous Sphaerellaria, spongy Spumellaria, and radiolarians with a pylome of the order Pylomariata: (1) the last radiolarians with an internal framework in the shape of a hollow nonporous

sphere with rays deviating from it (Oriundoguttidae and Cessipylorinae) disappeared; (2) the internal framework became less massive, in the shape of a six- or multi-rayed spicule; (3) the internal shells of the skeleton increased in number; and (4) the shape of the main spines of the skeleton changed, so that the initially cylindrical and conical spines were gradually transformed into three-bladed.

The second crucial point in the evolution of radiolarians was at the boundary between the Early and Middle Carboniferous; by the end of the second stage of the evolution, 66 genera (74.2%) and 276 species (92.3%) of the Devonian–Early Carboniferous radiolarians became extinct (Fig. 2).

By the end of the second stage, four families (Oriundoguttidae, Palaeoscenidiidae, Pylentonemidae, and Lapidopisidae) and 11 subfamilies of the Devonian–Early Carboniferous radiolarians became extinct. At the boundary between the Early and Middle Carboniferous, 53% of genera and 54.9% of species of radiolarians became extinct, and only 23 genera of the Early Carboniferous radiolarians continued to the Middle Carboniferous (Fig. 2).

**Stage 3: Middle Carboniferous–Permian.** A rapid evolution and expansion of the Devonian–Early Carboniferous radiolarians in the world ocean was for a short time interrupted as a result of a global cooling and glaciation in the Middle Carboniferous–Permian, which showed features of a total crisis (Horng-sheng et al., 1999, 2001; Chumakov, 2001; Grossman et al., 2002; Khain, 2003). This fall in temperature resulted in a significant reduction in the total number of radiolarians and a decrease in their taxonomic diversity (Fig. 2).

In the Middle Carboniferous–Permian, 52 radiolarian genera were recorded; the maximum diversity was in the Early Permian, 37 genera (Fig. 2). At the third stage of radiolarian evolution, the species diversity of radiolarians decreased to 202 species, changing from 25 species in the Middle Carboniferous to 112 in the Early Permian (Fig. 2). The rate of speciation of radiolarians in the Middle Carboniferous–Permian gradually decreased from 4.6 to 2.1 species/m.y., with the average rate of 2.4 species/m.y.

At the third stage of the evolution, radiolarians with a pylome of the order Pylomariata completely disappeared. The last ascertained radiolarians with a pylome (the genus *Caspiaza* of the order Pylomariata) were found in the Middle Carboniferous bioclastic limestones on the slope of the reef massif Karachaganak in the northern Caspian Sea Region (Afanasieva, 1987, 2000). The last Popofskyellinae, which were apparently the ancestors of the Meso–Cenozoic Nassellaria, were recorded in the Upper Carboniferous. At the same time, the third stage is distinguished by the accelerated development of stauraxonic radiolarians, which gave rise to two new families (Ruzhencevispongidae, Deflandrellidae) and seven subfamilies. From the Late Carboniferous onward, an intense process of segmenta-

tion of the skeleton in some bilaterally symmetrical radiolarians of the order Albaillellata began. In addition, the skeleton became distinctly segmented into apical, central, and basal parts.

In general, the following evolutionary trends are observed in the Middle Carboniferous–Permian: (1) stabilization in the evolution of the porous Sphaerellaria, (2) somewhat slowed evolution of the spongy Spumellaria, (3) gradual extinction of spiny radiolarians of the orders Fasciculata and Triangulata from the class Aculearia.

The end of the Permian period was marked by the catastrophic extinction of radiolarians. At the end of the Paleozoic, 37 out of 59 higher taxa of radiolarians became extinct, including 4 orders, 2 superfamilies, 14 families, and 17 subfamilies. Of the lower-rank taxa existing at various times during the third stage of the Paleozoic history of radiolarians, 45 genera (86.5%) and 195 species (96.5%) became extinct. In total, during the Paleozoic, 149 genera (95.5%) and 640 species (98.9%) of radiolarians became extinct (Fig. 2).

### *Phase III: Mesozoic*

The cool climate of the Paleozoic was replaced by the warm Mesozoic era (Dobretsov and Chumakov, 2001; Zharkov and Chumakov, 2001; Dobretsov, 2003). “The presence of a warm period that lasted for more than 200 m.y. against the background of the general cooling of the Earth is an evident anomaly” (Dobretsov, 2003, p. 9), which influenced the development of radiolarians in the Mesozoic.

At present, a connection between the Mesozoic–Cenozoic and Paleozoic groups of radiolarians has been established with certainty (Bragin, 2000, 2002). In spite of the fact that, at the Paleozoic–Mesozoic boundary, radiolarians underwent a catastrophic extinction, such that only few Paleozoic taxa survived, they gave rise to a new wave of the evolution of radiolarians in the Mesozoic. The Early Mesozoic was characterized by a rapid development of new taxa, in particular, the appearance of new orders of the class Nassellaria, which perhaps replaced the Paleozoic Pylomariata, and many new morphotypes, which were the intermediate forms between Paleozoic and Mesozoic spherical and stauraxonic radiolarians (Bragin et al., 1999).

**Stage 4: Triassic.** The Mesozoic phase in the evolution of radiolarians began in the Induan from seven genera of Paleozoic ancestors (Bragin, 2000, 2002) (Fig. 2). Only a small part of Paleozoic taxa continued into the Mesozoic and Cenozoic. Some morphotypes disappeared completely. At the same time, certain taxa typical for the Mesozoic and Cenozoic appeared for the first time in the Triassic; therefore, this stage can be regarded as the onset of the evolution of the fauna of Mesozoic radiolarians (Bragin et al., 1999). Triassic radiolarians include 69 families and subfamilies, of which 59 appeared for the first time.

Among the spiny Aculearia, the evolution of the Paleozoic Palacantholithidae and Palaeoscenidiidae continued in the Triassic; and the first Plagiacanthinae appeared. The spongy Spumellaria are represented by 11 families and subfamilies, among which Multiarcusellidae, Austrisaturnalinae, Oertlispongidae, and Pentactinocarpidae are restricted to the Triassic. In the Middle Triassic, the first Eptingiidae and Centrocubidae appeared. The Saturnalidae became widespread. The porous Sphaerellaria, including 11 families and subfamilies, were widespread in the Triassic, including the typical Triassic Capnodocinae and Capnuosphaerinae; the first Pantanelliinae, Xiphostylinae, Kungaliidae, Hexalonchata, and Actinommatia; and the last Entactiniata. The Triassic stauraxonic radiolarians include members of 14 families and subfamilies, of which Hexaporobrachiidae, Patruleiidae, and Relindelidae have only been recorded in the Triassic. The Triassic Nassellaria include members of 28 families and subfamilies. Among radiolarians with a pylome from the order Pylomariata, the last Archocyrtiinae and the first Poulpidae and Tripedurnulidae are present.

In the Triassic, the total number of radiolarian genera rapidly increased to 227 (Bragin, 2002). In the Olenekian Age of the Early Triassic, only 19 genera were recorded; however, in the Middle Triassic, there were 95 genera. A peak of generic diversity (165 genera)<sup>1</sup> occurred in the Late Triassic (Fig. 2).

The total number of radiolarian species sharply increased in the Triassic to 967. The species diversity is changed from 12 species in the Induan (Early Triassic) to 738 species in the Late Triassic (Fig. 2). The rate of speciation in the Triassic grew from 1.4 to 29.0 species/m.y., with the average value 24.1 species/m.y.

The Triassic–Jurassic boundary is characterized by the disappearance of 22 radiolarian families and subfamilies, including the last Paleozoic spiny Palacantholithidae and Follicucullidae, the porous Helioentactiniinae, Entactiniinae, and Bientactinosphaerinae, and seven families and subfamilies Nassellaria. At the end of the Triassic, 709 species (96.1%) and 136 genera (82.4%) disappeared. In total, 938 species (97.0%) and 198 genera (87.2%) of radiolarians became extinct during the Triassic (Fig. 2).

**Stage 5: Jurassic.** The Jurassic radiolarians were represented by 71 families and subfamilies, 25 of which appeared for the first time.

Among spiny Aculearia, Palacantholithidae and Plagiacanthinae continued to exist in the Jurassic. Spongy Spumellaria are represented by nine families and subfamilies. In the Early and Late Jurassic, the first Quinqucapsulariidae and Rhizosphaeridae appeared. Of spumellarians with an internal framework, rare Poly-

tactiniinae continued their existence in the Jurassic. Porous Sphaerellaria, including 11 families and subfamilies, were widespread in the Jurassic. Among these, spherical skeletons with two, three, and four spines; typical Jurassic Heleninae and Leugeoninae; and the first Parvivaccinae and Hexalonchidae were present. At the end of the Jurassic, radiolarians with a tuberculate surface (Acaeniotylinae) appeared. Jurassic stauraxonic radiolarians included members of 13 families and subfamilies, among which Catenopylidae, Emiluviidae, and Pseudoaulophacinae appeared for the first time.

At the Jurassic stage of the evolution of radiolarians, nassellarians flourished. Beginning from the Jurassic and to the present, the taxonomic diversity of nassellarians was greater than that of all other classes of polycystine radiolarians taken together. Nassellaria are represented in the Jurassic by 36 families and subfamilies, among which 16 appeared in the Jurassic, while Hexapylocapsidae and Vallupinae are restricted to the Jurassic.

A total of 286 radiolarian genera were recorded in the Jurassic were, which is similar to the number of genera in the Triassic. The maximum total diversity was in the Late Jurassic (197 genera) (Fig. 2).

The Jurassic stage shows the highest in the Phanerozoic total number of known species of radiolarians (1486). The species diversity of the Jurassic radiolarians changes from 459 species in the Early Jurassic to 711 species in the Late Jurassic (Fig. 2). The rate of speciation in the Jurassic ranged from 16.2 to 28.8 species/m.y., on average 22.7 species/m.y.

The end of the Jurassic was characterized by a significant change in the taxonomic composition of radiolarians; at the end of the Jurassic, 13 (18.3%) families and subfamilies, 57 (28.9%) genera, and 497 (69.9%) species became extinct. In total, Stage 5 of radiolarian evolution was marked by the disappearance of 1272 (85.6%) species and 146 (51.0%) genera of Jurassic radiolarians (Fig. 2).

**Stage 6. Cretaceous.** The Early Cretaceous radiolarians were still very similar to their Jurassic ancestors. They included multi-chambered Cyrtidinata, skeletons of which with an apical spine were ornamented by longitudinal ribbing and transverse girdles, and tuberculate skeletons of Acaeniotylinae. Stauraxonic radiolarians were very numerous and diverse. Most of the Early Cretaceous families of radiolarians continued to the Late Cretaceous. Many of these reached their maximum only in the Late Cretaceous, but generally for the Cretaceous predominance of nassellarians is typical (Lipman, 1979 is marked; Bragin et al., 1999).

The Cretaceous stage showed the highest total number of families and subfamilies in the Phanerozoic (82), of which 25 appeared for the first time.

Among spiny Aculearia, only Plagiacanthinae continued to the Cretaceous (Fig. 2). Spongy Spumellaria are represented by eight families and subfamilies. In the

<sup>1</sup> The database on the diversity of radiolarians in the Mesozoic and Cenozoic, including information on 1722 genera and 25000 species and their synonyms, was compiled by Agarkov based on a multipurpose information system RADBASE (Agarkov, 1998, 1999, 2000, 2004; Afanasieva et al., 2005a, 2005b).

Early Cretaceous, the first Orosphaerinae appeared. Of spumellarians with an internal framework, Polyentactiniinae completed their development in the Cretaceous. Porous Sphaerellaria, including ten families and subfamilies, were relatively widely distributed in the Cretaceous. Of these, Stylosphaerinae appeared for the first time. The Cretaceous stauraxonic radiolarians are very diverse and unite members of 18 families and subfamilies, among which Larnacillinae, Pentapyloniinae, and Spongodiscidae appeared in the Late Cretaceous for the first time. Cavaspongiidae, Miropyliidae, and Phaseliiformidae are restricted to the Cretaceous. Cretaceous Nassellaria are the most diverse and include members of 45 families and subfamilies, of which 17 appeared at this level, while Rotaforminae were restricted to the Cretaceous.

The species diversity of radiolarians decreased from 700 species in the Early Cretaceous to 696 species in the Late Cretaceous. However, the total number of radiolarian species reached 1118 (Fig. 2). The rate of speciation ranged from 10.5 to 16.1 species/m.y. The average rate of speciation decreased to 12.5 species/m.y., i.e., almost halved compared to the Jurassic. The total number of genera the Cretaceous radiolarians were 281, i.e., figure, comparable with those in the Triassic and Jurassic. The maximum generic diversity was in the Late Cretaceous, 226 genera (Fig. 2).

At the end of the Cretaceous, 675 (97.0%) species and 205 (90.7%) genera of the Late Cretaceous radiolarians became extinct. In total, during the Cretaceous, 32 (39%) families and subfamilies, 1097 (98.1%) species, and 260 (92.5%) genera of radiolarians became extinct (Fig. 2).

#### *Phase IV: Cenozoic*

In the Cenozoic, cold climate dominates. From the middle of the Eocene, a systematic cooling began, which was accompanied by sharp fluctuations of the temperature and glaciations (Zharkov and Chumakov, 2001; Dobretsov, 2003) (Fig. 2).

**Stage 7: Paleocene–Eocene.** The Cenozoic evolution of radiolarians began with 21 species of Mesozoic ancestors. Despite the evident continuity of taxa, a sharp shift in the radiolarian faunas took place at the Cretaceous–Tertiary boundary. The multi-chambered nassellarians characteristic of the Jurassic and Cretaceous were replaced by one-, two-, and three-chambered skeletons; moreover, spumellarians gradually became a dominant group in the Paleogene (Bragin et al., 1999).

At Stage 7, radiolarians were represented by 74 families and subfamilies, of which 28 appeared for the first time.

Spiny Aculearia were represented in the Paleocene and Eocene by only Plagiacanthinae. The diversity of spongy Spumellaria decreased to seven families and subfamilies, of which Axoprulinae appeared for the

first time. The diversity of porous Sphaerellaria also decreased to seven families and subfamilies. Among those were typical Paleocene–Eocene Entapiinae and the first Heliodyscidae. The stauraxonic radiolarians underwent a mass extinction of ten families and subfamilies (55.6%) at the end of the Cretaceous. Stauraxonia of the Paleocene–Eocene comprise members of 15 families and subfamilies, of which Suttoniidae, Pyloniidae (Pyloniinae and Pylodyscinae), Larnacillidae (Circodyscinae, Cryptolarnaciinae, and Histriastriinae), and Coccodyscidae appeared for the first time. Members of Palaeotetrapyliinae are known only from the Paleocene. Nassellaria of the Paleocene–Eocene include 41 families and subfamilies, of which 12 appeared at this time.

In the Paleocene and Eocene, the number of radiolarians decreased to 537 species. The species diversity of radiolarians changed from 186 species in the Paleocene to 423 species in the Eocene (Fig. 2). The rate of speciation ranged from 13.6 to 16.2 species/m.y. (on average 15.3 species/m.y.). The total number of radiolarian genera at stage 7 was 213, i.e., figure, comparable with that in the stage of the Mesozoic phase of the evolution. The maximum generic diversity was in the Eocene, 193 genera (Fig. 2).

At the boundary between stages 7 and 8, only four subfamilies became extinct: Neosciadiocapsinae, Zamolxinae, Entapiinae, and Conocaryomminae. However, among genera and species of radiolarians a mass change in the taxonomic composition took place: 370 (87.5%) species and 140 (72.5%) genera became extinct. In total, in the Paleocene and Eocene, 484 (90.1%) species and 160 (75.1%) genera of radiolarians disappeared.

**Stage 8: Oligocene–Pliocene.** This stage is characterized by a new decrease in the total number of radiolarians. Radiolarians of Stage 8 include 71 families and subfamilies, of which only three appeared for the first time.

The spiny radiolarian Plagiacanthinae continued their evolution. The diversity of spongy Spumellaria and porous Sphaerellaria decreased to six families and subfamilies. The stauraxonic radiolarians included members of 14 families and subfamilies, of which Tholoniidae, Coccodyscidae (Artiscinae), and Pyloniidae (Dipylissinae) appeared for the first time. Nassellaria of Stage 8 included 44 families and subfamily, of which Acanthodesmiinae and Paradietynae appeared for the first time, while Androspyridinae, Nephrospyridinae, and Perispyridinae were restricted to the Neogene.

The species diversity of radiolarians included 420 species and ranged from 132 and 130 species in the Oligocene and Pliocene, respectively, to 318 species in the Miocene (Fig. 2). The rate of speciation ranged from 6.1 to 13.7 species/m.y., the average rate of speciation decreased to 10.5 species/m.y. compared to the preceding stages. The total number of radiolarian genera in the Oligocene–Pliocene was 215, i.e., which is com-

parable to that for stages 4 to 7. The maximum generic diversity was in the Miocene, 187 genera (Fig. 2).

The Neogene–Quaternary boundary is marked by the extinction of two families of stauraxonic radiolarians, seven families and subfamilies of nassellarians, 68 species (52.3%) and 65 genera (51.0%) of radiolarians. In total, 358 species (85.2%) and 153 genera (71.2%) of radiolarians became extinct during Stage 8 (Fig. 2). Generally, this stage shows a decrease in the development of radiolarians.

**Stage 9: Quaternary.** The Quaternary is a special stage in the development of radiolarians, embracing a very short period of time (from the geological point of view). The taxonomic diversity of radiolarians of the Quaternary includes 65 families and subfamilies, of which five appeared for the first time.

The spiny radiolarians Plagiacanthinae continued their evolution. Spongy Spumellaria and porous Sphaerellaria are represented by the same families and subfamilies as at the previous stage, in the Oligocene–Pliocene. The diversity of stauraxonic radiolarians decreased to 11 families and subfamilies, of which Myelastridae appeared for the first time. Nassellarians still dominate in the Quaternary, but have become less diverse. They comprise 41 families and subfamily, of which Plectaniinae, Tetrableptinae, Plagoniidae, and Cystidiidae appeared for the first time.

The Quaternary stage consists of two steps in the development of radiolarians, the Pleistocene and Holocene (Fig. 2). At the first step of the Quaternary Stage, the diversity of radiolarians sharply decreased to 79 species in the Eopleistocene and 80 species in the Neopleistocene. The Holocene, as widely believed, showed an explosive biodiversity and reached its maximum of 2114 species of Recent.

However, according to Boltovskoy (1998), the actual number of Cenozoic radiolarian species is much smaller than is usually believed, being limited only to 300–600 species, but certainly not to thousands (!). Kruglikova (Kruglikova, 1995, 2000, 2003) showed that the number of the radiolarian species in the modern bottom sediments varies from 60 species in the Arctic to 200 species in the northern Pacific and is about 400 species in an equatorial zone.

In addition, Petrushevskaya (1986) noticed the pattern in the transition of radiolarians first into sediment and, later, into rock. In the sediment, empty skeletons constitute 10–30% of the total number of living radiolarians; radiolarians. The number of radiolarian skeletons retained in the rock is tens of times less than in the loose sediments. Zasko (2004) studied modern radiolarians and also showed a decrease in the dominant taxa in the sediment by 15–55%.

Hence, it may be assumed that in the distant future only 100 species of Holocene radiolarians will remain in the rocks, i.e., a number comparable with those from the Eopleistocene (79 species) and Neopleistocene (80 species). Thus, we came to a conclusion that no explosive biodiversity of radiolarians occurred in the Holocene.

## MASS EXTINCTIONS

Radical changes in the environment and climate are reflected at the initial stages of the development of new aromorphoses and lead to the irreversible extinctions of the unsuccessful forms (Kanygin, 2001). Periodical pulsation of cooling–warming are what forces the biota to continuously adapt to the changing situation (Dobretsov, 2003).

The transition from the cold climate of the Paleozoic to the warm climate of the Mesozoic was marked, on the one hand, by the extinction of 78.1% of radiolarian genera and 81.1% of species at the Permian–Triassic boundary. The Permian–Triassic extinction changed considerably the evolutionary course of radiolarians. All classes of polycystine radiolarians responded to these catastrophic events in the Mesozoic–Cenozoic by the outburst of taxonomic diversity: Spumellaria (in Pz, 56 genera; in Mz–Cz, 81), Sphaerellaria (in Pz, 24 genera; in Mz–Cz, 107), Stauraxonaria (in Pz, 32 genera; in Mz–Cz, 156), and Collodaria (in Mz–Cz, 15 genera). The exception is the spiny radiolarians Aculearia, represented in the Paleozoic by 46 genera and gradually decreasing in diversity in the Mesozoic and Cenozoic to 20 genera. The class Nassellaria shows the highest taxonomic diversity among the polycystine radiolarians. In the Paleozoic, they are represented by only 20 genera of the order Pylomariata; however, in the Mesozoic and Cenozoic, nassellarians comprise 574 genera and sharply dominate over all other classes of Polycystina, which are represented by 366 genera.

The transition from the warm Mesozoic climate to the cold Cenozoic climate was marked by a similarly significant extinction at the Cretaceous–Tertiary boundary of 90.7% of genera and 97.0% of species of radiolarians. At the onset of the Holocene, a sharp extinction occurred, 98.2% of genera and 99% of species of Cenozoic radiolarians disappeared (Fig. 2).

In total, in the Early Paleozoic (Cambrian–Silurian), 60 genera and 223 species of radiolarians, with the average rate of speciation of 1.4 species/m.y. appeared, while, in the Late Paleozoic (Devonian–Permian), 118 genera and 487 species were recorded (these appeared with an average rate of 2.9 species/m.y.). The Mesozoic shows the greatest number of genera and species (625 and 3328, respectively) and the maximum average rate of speciation of 18.8 species/m.y. In the Cenozoic (excluding extant radiolarians), the total number of radiolarian taxa sharply decreased to 385 genera and 922 species, while the average rate of speciation decreased to 12.8 species/m.y. In the Holocene, 377 genera and about 400–600 species of radiolarians are known (Fig. 2).

The most important changes in the taxonomic diversity and extraordinary extinctions of radiolarians completely coincide with the six Great Extinctions of the biota recognized by Alekseev (1989, 1998) and Alekseev et al. (2001): Frasnian/Famennian, Serpukhovian/Bashkirian, Permian/Triassic, Triassic/Jurassic, Jurassic/Cre-

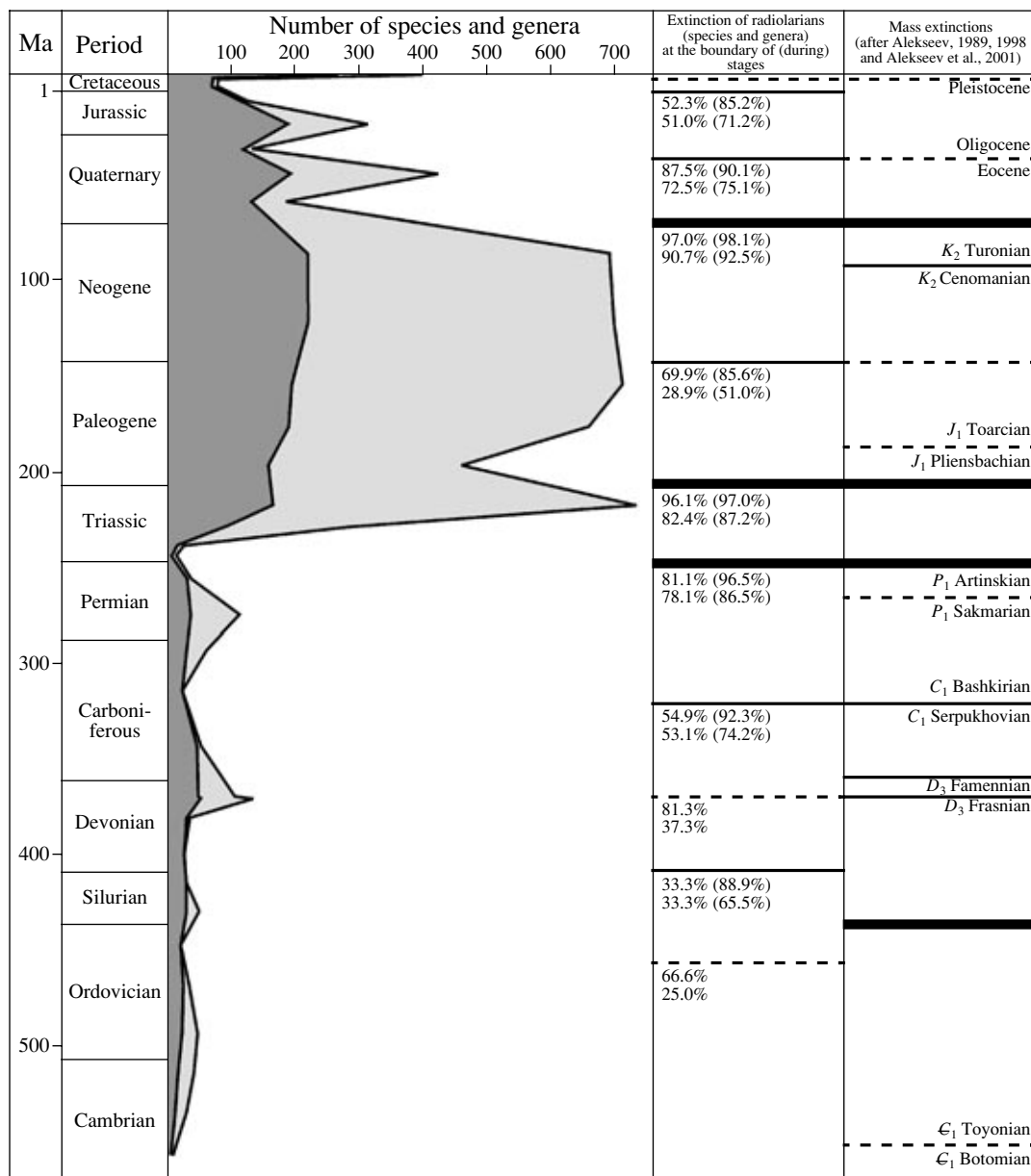


Fig. 3. Mass extinctions in the Phanerozoic.

taceous, Cretaceous/Paleogene, and Pleistocene/Holocene (Fig. 3).

At the Frasnian–Famennian boundary, radiolarians sharply changed the structural pattern of skeletons and the taxonomic composition (Fig. 3): 109 species (81.3%) and 19 genera (37.3%) became extinct. However, this was not accompanied by a sharp increase in the number of radiolarians; 80 new species (76.2%) and 17 new genera (34.7%) appeared in the Famennian.

The Jurassic–Cretaceous boundary is known as a moment of mass extinctions of radiolarians. However, Alekseev (1989, 1998; Alekseev et al., 2001) is in some doubt about this, because no significant changes in marine faunas occurred at this boundary. The level of

extinction of genera of marine organisms does not exceed 30%, and that of families is only 5% (Sepkoski, 1996). At the same time, 13 families and subfamilies (18.3%), 57 genera (28.9%), and 497 species (69.9%) of radiolarians became extinct at the end of the Jurassic (Fig. 3).

At the same time, the Botomian/Toyonian, Ordovician/Silurian, Devonian/Carboniferous, and Cenomanian/Turonian mass extinctions were not marked in the history of radiolarians at the level of the mass extinctions in this group. On the other hand, mass extinctions of radiolarians at the Silurian/Devonian and Neogene/Quaternary boundaries are not recognized on the scale of mass extinctions of the entire biota. At the same

time, on at the Silurian/Devonian boundary, 91.0% of Early Paleozoic radiolarian species and 66.7% of genera disappeared, while at the Neogene/Quaternary boundary, 93.1% of Cenozoic species and 83.5% of genera became extinct (Fig. 3).

#### STAGES OF RADIOLARIAN EVOLUTION AND THE SEASON OF GALACTIC YEAR

The seasonal rhythm of galactic year (or galayear) are marked in both the paleontological record of radiolarians and their evolutionary development. Each galactic year, i.e., a complete rotation of the Sun around the center of the Galaxy (Parenago, 1952), has a special name and is divided into four seasons (the so-called galactic spring, summer, autumn and winter), which in the Phanerozoic approximately correspond to the periods (Kulikova and Kulikov, 2000) (Fig. 2):

20th galayear, Phosphatian (Paleozoic) includes

Cambrian<sup>2</sup> → Ordovician → Silurian →  
Devonian;

21st galactic year, Phitonian (Upper Paleozoic–Mesozoic) comprises

Carboniferous → Permian → Triassic →  
Jurassic;

22nd galactic year, Noetian (Cenozoic) comprises

Cretaceous → Paleogene → Neogene →  
Quaternary.

The boundaries between galactic years almost coincide with the peaks of the number of taxa of the dynamic curve of the biodiversity of radiolarians in the Phanerozoic: the replacement of the Phosphatian galayear by the Phitonian galayear is accompanied by an explosive diversification in the Late Devonian, the replacement of the Phitonian galayear by the Noetian galayear is accompanied by an explosive diversification in the Late Jurassic. The seasons of galactic years are characterized by approximately identical patterns of the dynamics of radiolarian biodiversity. Many great extinctions occurred at the boundaries between seasons (Fig. 2).

**Phosphatian galayear.** The first Early Paleozoic phase and the first stage in the evolution of radiolarians combined two steps in the development of radiolarians and embraced the first three-fourths of the Phosphatian (Fig. 2): Step 1 occurred in the Cambrian–Middle Ordovician (summer and the beginning of autumn), Step 2 corresponds to the Late Ordovician–Silurian (end of autumn and winter). Within the first three seasons of galactic year (summer, autumn, and winter), the pattern of the dynamics of biodiversity was identical: at

first, a slow, gradual increase in the number of taxa, followed by a peak of diversity and, then, a decrease in number.

The second phase of the evolution of radiolarians embraces the final season of the Phosphatian galayear and the first two seasons of the Phitonian galayear. The last season (spring) of Phosphatian shows a different dynamics of radiolarian biodiversity than the preceding seasons; the rate of speciation considerably increased up to the Paleozoic peak, the greatest number of taxa falls on the end of this season. The first crucial point in the development of radiolarians occurred at the Silurian–Devonian boundary. Typical Early Paleozoic taxa disappeared, and the taxonomic composition of radiolarians was renewed at the level of species, genera, and particular families and orders (65.5% of genera and 88.9% of species of Early Paleozoic radiolarians became extinct).

**Phitonian galayear.** The summer of the Phitonian galayear was marked by a drastic shift in the direction of evolutionary development, a large-scale extinction of taxa began and ended at the boundary between the Middle and Late Carboniferous. This second crucial point in the evolution of radiolarians was marked by the loss of 74.2% of genera and 92.3% of species of radiolarians.

The autumn and winter of the Phitonian galayear approximately correspond to Stage 3 of Phase II and Stage 4 of Phase III of the evolution of radiolarians. These seasons are similar in the dynamics of biodiversity to the first seasons of the Phosphatian, but the peaks of the number of taxa were less pronounced.

The third crucial moment in the evolution of radiolarians at the end of the Permian (boundary between the autumn and winter of the Phitonian galayear) was marked by a catastrophic extinction of Paleozoic radiolarians (86.5% of genera and 96.5% of species).

The spring of the Phitonian galayear (Stage 5 of Phase III) has much in common with the spring of the Phosphatian; speed-up of paces of a species origin also is watched, the achievement of a Mesozoic maximum (in a Jurassic was highest in the Phanerozoic a total number of known species of radiolarians), thus the peak of number is sheared by the end of a season.

**Noetian galayear.** The summer of Noetian, corresponding to Stage 6 of Phase III, resembles the summer of the Phitonian; in this case, the direction of evolutionary development also changed towards a decrease in the number of taxa. The next crucial point in the evolution occurred at the end of the Cretaceous and resulted in the loss of 97.0% of species and 90.7% of genera of Cretaceous radiolarians.

The autumn of the Noetian galayear (Stage 7 of Phase IV) is similar in the dynamics of diversity to the autumn of Phosphatian and Phitonian; at the boundary between stages 7 and 8, 87.5% of species and 72.5% of genera of radiolarians became extinct.

<sup>2</sup> One and two lines designate summer and winter seasons, respectively.

However, the winter of the Noetian (Stage 8 of Phase IV) substantially differs from the preceding winters, since Stage 8 is characterized by a new decrease in the total number of radiolarians in the Neogene; 85.2% of species and 71.2% of genera of radiolarians disappeared during Stage 8.

The spring of the Noetian galayear (Stage 9 of Phase IV) is a special epoch in the development of radiolarians, which embraces a very short time interval. The first step of the Quaternary shows a sharp decrease in the diversity of radiolarians to 79 and 80 species in the Eopleistocene and Neopleistocene, respectively. At the second step of the Quaternary, in the Holocene, against the background of the appearance of new, Recent species of radiolarians, an explosive radiation of biodiversity of radiolarians is absent. The Recent Time is merely the most representative stage in the development of the biota, because we can examine living organisms, which has not been changed in the burial. However, the present time is not the most extraordinary stage in the development of radiolarians; the paleontological history of this group was more prominent and more diverse than the Recent.

### CONCLUSIONS

The questions of ecology and taphonomy of radiolarians are reviewed. It is shown that the biomass of polycystine radiolarians reaches the maximum at a depth of 50–400 m. In the modern oceans, the main radiolarian rain comes from a 500-m-deep water column; therefore, on the one hand, the bottom thanatocenoses, taphocenoses, and oryctocenoses of radiolarians can be formed in all zones, including the central regions of oceans and, on the other hand, radiolarian can not be used as an indicator of exclusively deepwater oceanic conditions. In addition, in the geological past, the most favorable habitats were in the coastal zone and areas not far from continents, rather than pelagic or central zones of oceans.

The model of cyclic development of radiolarians in the Phanerozoic is proposed: individual simple cycles (steps) are combined into cycles of a higher order (stages), which, in turn, characterize cycles of the highest order, phases. The analysis of changes in biodiversity of radiolarians in the Phanerozoic revealed four phases and nine stages in the evolution of radiolarians. Each stage was characterized by considerable changes in the taxonomic composition and number of radiolarians and a change in the dominant groups in the classes Aculearia, Spumellaria, Sphaerellaria, Stauraxonaria, and Nassellaria.

The transition from the cold climate of the Paleozoic to the warm climate of the Mesozoic was marked by the extinction of 95.6% of genera and 97.7% of species of Paleozoic radiolarians. The transition from the warm Mesozoic climate to the cold Cenozoic climate was accompanied by the extinction of 96.6% of genera and

99.4% of species of Mesozoic radiolarians. The onset of the Holocene was marked by a sharp extinction of 98.2% of genera and 99.2% of species of Cenozoic radiolarians, which is comparable with the data for the Paleozoic and Mesozoic. No explosive radiation of radiolarians occurred in the Holocene.

The seasons of galactic year correlate with the fossil record of radiolarians. The boundaries between galactic years approximately coincide with the most significant events in the evolution of radiolarians, while the seasons of these years show similar patterns of the dynamics of biodiversity of radiolarians. Many large extinctions occurred at the boundaries between seasons.

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