Analysis of Species Richness Dynamic of Mesozoic and Cenozoic Radiolarians

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Abstract. In this article was studied dynamic of radiolarians species richness over the last 150 million years with accuracy up to the geological age. The basic regularities of species and taxa of the upper range changing are established for Mesozoic and Cenozoic eras. Changing of the species abundance on the borders of large geological periods and, also significant fluctuations of the species richness connect to a combination of the numerous factors. Most important of these are the geological processes leading to extensive transgressions and regressions, climate variations, general directed evolution of the Earth biota, and competition for important chemical components for radiolarians’ vital processes. The appearance of considerable areas of tropical forests on the land with their enormous productivity and biochemical weathering is connected to the late Cretaceous era. That led to increasing of the dissolved material flow to the sedimentation pool, that recorded by an appearance of classic bauxite. Because aluminum oxide and silicon oxide are geochemically bound, we can state also about increasing of dissolved silica in-flow caused by diatoms development, which became a competitors for radiolarians in the struggle for silica. The last ones are lost in that competition, what led to its species reduction. Mass extinction at the border between the Cretaceous and Paleocene was not a catastrophic event with instant extinction, but a lengthy process.

1. Introduction
The first attempts to apply computer technology to study radiolarians and analyze the species richness variability were undertaken by W. Riedel. He led the BIBLIOTIX program development project. The program included all the materials from English publications on radiolarians. The first databases or information retrieval systems were developed in the USSR by D.M. Chedia in the late 1970s. In the 1990s, an updated computer version was suggested by M.G. Petrushevskaya and V.V. Menshutkin. Later, E.O. Amon improved the program and applied it for the system of radiolarians of the Ural Mountains. In the late 1980s, a group of French experts headed by De Wever introduced three programs: BIOSTRAT (for accounting the ocean radiolarian distribution), GENETAB (for accounting the species distribution by the geochronological scale), and GESPAL (for quantitative taxonomic systematization of Triassic – Jurassic radiolarians). Extensive materials obtained by deep drilling of the ocean bottom required new databases capable of handling lager volumes of information published in various sources, including the World Ocean Cenozoic deposit programs composed by W. Riedel’s group [1].
In recent years, universal databases about extinct radiolarians have been created, including the radiolarian database integrated with PALAEOMDS on micro-paleontological organisms.

The European group of experts in radiolarians (P. Baumgartner, J.P. Caulet, C. Nigrini, and others) developed a database of Thetis Jurassic and Cretaceous radiolarians, which included approximately 450 species, and the RADWORLD database of Cenozoic radiolarian worldwide (up to 6000 species).

For a long time, the authors have been developing an active-synonymous information system, which includes nearly 15,000 species of Phanerozoic radiolarians worldwide, and more than 22,000 species with account of synonyms and species described in open references [2]. Thus, the global radiolarian databases include only half of known radiolarians and cannot be used to analyze biodiversity and identify development crises. Moreover, all of them use strict synonym binding and, accordingly, date species strictly. Due to the fast changing radiolarian system, it causes data corruption. The database is the basis of all calculations on bio-evolution and the primary material for the analysis of phylogenetic connections and for plotting distribution and migration maps [3].

Presently, radiolarians are of significant importance for the decomposition and correlation of sedimentary, volcanogenic-sedimentary, and weakly metamorphosed strata, creation and development of local, regional, and inter-regional stratigraphic scales, and reconstruction of paleo-geographic environments in the geological past. Radiolarians are found in rocks of different ages: from early Cambrian to contemporary sediments. Therefore, they are an efficient tool for bio-stratigraphy of the entire Phanerozoic, with no gaps and breaks.

The relevance of this development is determined by the construction of evolution models of siliceous organisms with powerful information systems to solve fundamental biodiversity problems and identify the centers of species origin and their migration paths [4, 5].

2. Radiolarians’ evolution phases and stages

The origin, general evolution mechanisms and major biotic crises during the organic world development have always been closely interconnected with the Earth’s geological history. The entire history of our planet is a series of often irreversible changes in the atmosphere and hydrosphere structures, an incremental increase in the contrast between the terrain and water areas: from shallow marine reservoirs, epicontinental seas, epicontinental marginal seas and oceans. The first attempts to conduct quantify radiolarians at the species level was undertaken by Y.V. Agarkov for the Mesozoic period and in the joint study by M.S. Afanasyeva, E.O. Anon and D.S. Boltovskoy for the Phanerozoic as a whole and by eras [6, 7]. In the Phanerozoic history of the radiolarian development, we identified nine stages and four phases of evolution [8]:

- Phase I. Early Paleozoic: stage 1 (Cambrian – Silurian).
- Phase II. Late Paleozoic: stage 2 (Devonian – early Carboniferous); stage 3 (middle Carboniferous – Permian).
- Phase III. Mesozoic: stage 4 (Triassic); stage 5 (Jurassic); stage 6 (the Cretaceous period),
- Phase IV. Cenozoic: stage 7 (Paleocene – Eocene); stage 8 (Oligocene – Pliocene); stage 9 (Quaternary).

No quantitative studies of species emergence and disappearance dynamics at the geological age level have been conducted previously.

Our research showed that evolution of the Polycystina subtype of radiolarians did not include periodic cyclic changes, when the formation of new taxa is succeeded by their flourishing, and then extinction. In the general dynamic model of the radiolarian development in the Phanerozoic, the individual simple stage were unidirectional, united in the components forming stages of higher order, which were not always simultaneous and characterize the stages of higher order phases. Stages of various orders were determined by other causes and complicated by the genetic evolution [9].

At each stage of evolution, there were significant variations in the composition and abundance of radiolarians and changes of the leading groups. At the same time, various taxa evolved simultaneously to a certain extent: from the general structure development to the improvement of individual structures.
of the skeleton. The most constructive combination of the morphological attributes determined, at a certain stage, the establishment of new higher taxa and their certain evolutionary advantages.

3. Factors determining the variations of the radiolarian species richness
An analysis of the dynamics of the late Cretaceous and Paleocene radiolarian species richness was based on the data in the Information System (IS) developed by the authors. In total, their main dictionary includes 20,653 terms related to 15,291 valid species. According to the data selected from the IS, 1364 species of radiolarians existed in various ages of the late Cretaceous era [10].

3.1. Geological causes
The changes in the species abundance in absolute and relative values for the Mesozoic and Cenozoic eras are shown in the diagram (Figure 1). An analysis showed that for the last 150 million years of the Earth's history there have been several ages, which are characterized by a significant increase in the species richness. The greatest number of species existed in the Tithonian, Alban, Campanian, Ypresian – Priabonian, and Miocene. The spread of values between the maximum and minimum numbers is fifteen times. These data can illustrate the morphological species diversity at a certain period, but are not suitable for the identification of species formation due to the different duration of the geological ages. Recalculations with account of the age duration indicated that some ages kept their leading position; however, an opposite situation was observed for the Alban and Santonian. If we take into account the age duration factor, we can see that the difference between the highest and lowest values reduces to three times instead of fifteen [11].

![Figure 1. The radiolarians abundance variation during last 150 million years: 1 - total number of species; 2 - number of species/age length in million years.](image)

In the Phanerozoic, the Cretaceous stage is characterized by the highest total number of families and sub-families: 82, with 25 of which appearing for the first time.

The radiolarian species diversity was represented by 1811 species in the early Cretaceous and by 1364 species in the late Cretaceous. The rate of species formation changed from 5.19 to 26.73 species per million years in the early era and from 7.21 to 56.16 species per million years in the late one. At
the same time, the average rate of species formation decreased to 31 species per million years, almost by half, compared to the Jurassic stage. In total, there were 515 genera of radiolarians in the Cretaceous. This value is comparable with the Triassic and Jurassic data. The highest diversity was observed in the late Cretaceous (338 genera).

In the late Cretaceous, 493 (80.56%) species and 482 (93.1%) genera of radiolarians became extinct. In total, 32 families and subfamilies (39%), 2749 (96.56%) species and 328 (63.69%) genera of radiolarians ceased to exist during the Cretaceous.

Thus, the Cenozoic history of the radiolarian development started with 84 ancestors of the Mesozoic species. Despite the obvious continuity at the interface of the Cretaceous and Paleocene, there was a drastic change in the radiolarian faunas. 80% of previously existing species became extinct during that period (Figure 2). The process of active extinction began in the Santonian, 20 million years before the crisis line [12–14].

![Figure 2. Changing radiolarians species abundance (in %) during the last 150 million years. 1 - Extinct; 2 - originated.](image)

3.2. Internal causes
Apart from the geological reasons of changes in the species richness and their extinction, the internal events related to the genetic morphological evolution of species, genera, and families should be taken into account. Although, natural processes play an important role due to the harmful nature of environmental changes for the biota, the absence of new species generation is more critical from our point of view [15].

An example is shown in Figure 3. The observed *Crucella* genus survived the crisis in the late Cretaceous and the early Paleocene; however, only one of its representatives remained in the Cenozoic. We can assume that the rest disappeared during the mass extinction. The figure shows that only two of 80 species survived to the Maastrichtian. Significantly more species became extinct in the
late Maastrichtian and early Campanian, and in general, the substantial extinction of species occurred at various stages.

![Diagram](image.png)

**Figure 3.** Changing abundance of the species of genera of *Hagiastridae* family.

4. **Origin of short- and long-living species**

The diagrams show that the changes in the species population within a genus vary significantly. Large genera have two-tree periods of mass species formation outbursts, and the first outburst takes place in five to six ages (approximately, 30 million years) after some adaptation, which includes an increase in the population and, what is more important, increase in the area and, accordingly, diversity of ecological niches. During such periods, short-living species distributed locally were generated on a massive scale. Thereafter, the species number stabilized and the long-living species mainly dominated [15, 16]. When the environmental conditions change, mass outbursts for individual large genera took place, but as the outbursts were not conditioned genetically, all the new species were short-living endemics that did not cause any evolutionary changes. Then, the next period of extinction occurred.

After the second outburst, new ecological niches opened again and new minor species appeared. Thereafter, extinction of large taxa occurred (sub-family, family, genera) with small genera becoming extinct first.

Such model of evolution was observed for several families and is generally similar for all taxa of this level (Figure 4) [17, 18].
5. Conclusion
We have developed a model of changes in the abundance of radiolarian species in the Mesozoic and Cenozoic. In this publication, we determined the rate of their species formation, appearance, and extinction [19].

An analysis of the species abundance variation indicated the absence of a leading factor influencing the radiolarian evolution. The most important factors are geological processes leading to major transgression and regression, climate variations, the general directed evolution of the Earth’s biota, as well as the competition for chemical components critical for radiolarians’ vital processes, as well as internal genetic factors.

Further research should focus on detailing the factors of evolution and attempting to receive an interference picture of their combination; as well as establishing the centers of the species divergence, which produce most morphological types of radiolarians of endemic nature; identifying the migration paths of bipolar species in the tropical zone. Based on more substantial material on the species abundance change within families, it is necessary to clarify the revealed regularities, try to identify their possible synchrony at different stages of the Earth’s biota development, and evaluate possible influencing factors and their scale.

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