

RADIOLARIANS IN THE GEOLOGICAL ANNALS

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Abstract. This study is dedicated to the comprehensive description of radiolarians, the discussion of their morphology, problems of classification, and their important role in the history of the Earth's biosphere. This study contributes to the solution of the fundamental problems of the evolutionary morphology of radiolarians related to the study of the morphogenesis of their skeletons at various structural levels through geological time, aiming at the creation of a morphological basis for the phylogeny and classification of the phylum Radiolaria. The book describes three stages of the history of 200-year old radiolariology. The biology and morphology of radiolarians are discussed. The study deals with the successive stages of the ontogeny of radiolarians and the main patterns of skeletal morphogenesis: appearance and growth of skeletal elements, biomineralization, and secondary transformation of skeletons. A new classification of the phylum Radiolaria, uniting two superclasses Phaeodaria and Polycystina is proposed. The superclass Polycystina is composed of six classes: Aculearia, Sphaerellaria, Spumellaria, Stauraxonaria, Nassellaria, and Collodaria. Patterns in the appearance/disappearance and distribution in time of higher taxa of Polycystina are discussed, and critical levels in the evolution of radiolarians at the major stages of the Phanerozoic are revealed. Four phases and nine stages in the evolution of radiolarians are recognized. The statistical analysis of the biodiversity of radiolarians in the Phanerozoic is conducted based on the informational system "RADBASE" containing the information on 1721 genera of radiolarians and their synonyms. Problems of the biology, ecology, and taphonomy of radiolarians are discussed. It is shown that the biomass of polycystine radiolarians is greatest at depths of 50--400 m. The conclusion is made that radiolarians cannot be regarded as indicators of exclusively oceanic deep-water conditions. In the geological past, the maximum density and diversity of the population of radiolarians was observed in the coastal regions or zones of aulacogenes and active tectonic faults. The study is expected to be of use to a broad range of readers in paleontology, biostratigraphy, paleoecology, and as a textbook for the university courses. It contains 67 figures, 11 tables, 33 plates, and an appendix. The list of references includes 464 names.

Key words: radiolarians, morphology, classification, evolution, habitats, taphonomy, informational technologies

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INTRODUCTION

The 200-year history of radiolarian studies began from the first report of the Russian scientist Tilesius von Tilenau (1806-1809) on extant planktonic unicellular organisms with a siliceous skeleton from the modern oceans. In the history of studies and classification of radiolarians the following basic events are recognized: (1) the rise of the classification base of Radiolaria in the 19th century (1806-1887); (2) establishment of classification schemes of Radiolaria in the middle of 20th century (1953-1979); (3) development of new trends in the classification of Radiolaria at the boundary of the 20th and 21st centuries (1980-Resent).

Radiolarians represent one of the earliest groups of microorganisms, which has been inhabiting various regions of the ocean from the Early Cambrian to the present. Such a long duration and wide distribution are largely explained by the ecological plasticity of this group, which allows radiolarians to inhabit various marine and oceanic bionomic zones. During their evolution radiolarians repeatedly changed the strategy of distribution and colonization of the new zones of the sea, but several main features apparently remained unchanged. These include a planktonic way of life, heterotrophic feeding, and, hence, dependence on the food resource, reliance on the concentration of SiO₂ dissolved in the sea water, mutually beneficial symbiosis with microscopic unicellular algae defining the preferred habitats (mainly the upper layers of the water column, where zooplankton feeds on the intensely producing phytoplankton and bacteria).

In the modern oceans, living radiolarians inhabit all marine and oceanic bionomic zones. They live at all levels, from the surface to maximum depths; however, Polycystina are particularly abundant in the interval 50-400 m of depth, while the Phaeodaria are at more than 100-200 m of depth (Petrushevskaya, 1986; Kling and Boltovskoy, 1995; Abelman and Gowing, 1997; Boltovskoy, 1998, 1999; Zasko, 2004).

In addition, heterotrophic feeding by bacteria, silicoflagellates, diatom algae, etc. provides radiolarians with proteins, fats, and carbohydrates, allowing them to live and reproduce in an environment of competition with other planktonic organisms.

Bottom tanatocenoses and taphocenoses of radiolarians may form in all zones, including the central oligotrophic regions of the oceans. However, the main "radiolarian rain" occurs in the zone which is not deeper than 500 m. It would have been a serious mistake to regard radiolarians as indicators of exclusively oceanic depths comparable with the depths of the modern bathyal and abyssal.

The geological past of radiolarians is much richer than their modern state. This is seen from the example of radiolarians inhabiting the Domanik basins with anoxic conditions in the Late Devonian, or on the example of the distribution of radiolarians of the Carboniferous and Early Permian epochs in the regions of reefs, or on the example of different environments of accumulation of radiolarian mud in the Paleozoic, Mesozoic, Cenozoic, and modern oceans.

The modern science acknowledges that the evolutionary morphology of radiolarians is a wide field for the comprehensive study of the appearance and development of taxa to reveal the morphological patterns of the evolutionary process. Each organism and its structural features "may and should be studied from at least four points of views: constructive-morphological,

physiological, ecological, and historical. Each of these points of view is permissible, necessary, and unique" (Beklemishev, 1964, p. 78).

The present study is directed toward the solution of the fundamental problem of the evolutionary morphology of radiolarians, related to the complex study of the patterns of the radiolarian skeletal morphogenesis in time, at different structural levels with the purpose of creating a morphological basis for the phylogeny and classification of the phylum Radiolaria. The study of radiolarians was conducted from various aspects, considering their morphology and ecology, and with a obligatory reference to all evolutionary transformations in the geological past.

Advanced scientific research brings a new understanding of the relationships between morphology and phylogeny and classification, because the study of macrostructure is supplemented by research at ultrastructural level. Knowledge of the evolution of the internal and external skeletal elements of radiolarians requires a complex approach to the study of this faunal group. Hence, emphasis in this study is placed on the successive stages of individual development of radiolarians. The study revealed major patterns in the morphogenesis of the skeleton of radiolarians: problems of the appearance and growth of skeletal elements. Biomineralization and secondary transformation of the skeletons is considered.

A new radiolarian classification is developed. The phylum Radiolaria consists of two superclasses Phaeodaria and Polycystina. The superclass Polycystina includes six classes: Aculearia, Sphaerellaria, Spumellaria, Stauraxonaria, Nassellaria, and Collodaria. The diagnoses of 285 higher radiolarian taxa are given: 1 phylum, 2 superclasses, 6 classes, 26 orders, 14 superfamilies, 132 families, and 104 subfamilies, comprising 1131 genera of Phanerozoic Radiolaria.

The study of the historical morphogenesis of the skeletons of radiolarians at various structural levels in geological time revealed patterns of the appearance/disappearance of higher taxa of polycystine radiolarians through time which aimed to recognize critical moments (crises, catastrophes) in the evolution of radiolarians in the history of the Earth at major boundaries within the Phanerozoic. Four phases and nine stages of the evolution of radiolarians are recognized. At each of the evolutionary stages of radiolarians, various taxa experienced considerable changes in composition and quantity, with a change in the leading group. The statistical analysis of the change in biodiversity of radiolarians in the Phanerozoic was based on the informational system (IS) RADBASE, containing the information of 1722 genera of radiolarians and their synonyms (Agarkov, 1998, 1999, 2004).

The novelty of the study conducted is that it was based on a uniquely broad material, which has no equivalents worldwide. This, in turn, provided a fundamental study of morphology, ecology, and history of the evolution of radiolarians in the Phanerozoic, and allowed new information on the total biodiversity of radiolarians. The new classification of Phanerozoic radiolarians proposed in this study uses a computer-based system of fixed combinations of morphological characters of the skeletons used for describing radiolarians of different taxonomic ranks.

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The novelty approach to the creation of the uniform classification of radiolarians is a complex study of various groups of radiolarians with different durations and ecology, to reconstruct a general pattern of the biodiversity of radiolarians and more complete characterization of the evolution of the phylum Radiolaria.